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Series Editor: Jeff Atherton, Professor of Tropical Horticulture, University of the West Indies, Barbados

This series examines economically important horticultural crops selected from the major production systems in temperate, subtropical and tropical climatic areas. Systems represented range from open field and plantation sites to protected plastic and glass houses, growing rooms and laboratories. Emphasis is placed on the scientific principles underlying crop production practices rather than on providing empirical recipes for uncritical acceptance. Scientific understanding provides the key to both reasoned choice of practice and the solution of future problems.

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BLUEBERRIES

Jorge B. Retamales
University de Talca, Chile
and
James F. Hancock
Michigan State University, USA
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INTRODUCTION

Blueberry production and commerce have expanded greatly in the last 20 years. From a crop that was mainly consumed and cultivated in North America, we have come to an era of worldwide blueberry cultivation. This expansion has encompassed plantings in a greater diversity of environments and the use of innovative cultural practices and conditions. This situation has challenged researchers to increase both the scope and depth of their activities. The number of articles and meetings on blueberries has grown at a steady pace. However, the information for people involved in blueberry research, culture or marketing is dispersed and usually difficult to access or interpret. It has been more than 20 years since Paul Eck published his Blueberry Science which comprehensively reviewed the available information on blueberries. Even though there have been some books on blueberries published recently, we felt there was a need to prepare a volume that would update readers with the current status of knowledge on blueberry science and management.

The book is structured in nine chapters. In Chapter 1 the industry is described with information on the history of cultivation, the most important locations, the species and the cultural practices employed in the different production regions. Chapter 2 deals with the taxonomy of blueberry species, the history of improvement and current breeding efforts, tools and goals, and describes the most important blueberry cultivars grown worldwide. In Chapter 3 the anatomy and morphology of the highbush and rabbiteye blueberry are discussed, along with vegetative and reproductive growth and development. Chapter 4 deals with the generation and distribution of carbohydrates, and the factors involved in dry matter production and partitioning among the various plant organs. Chapter 5 concentrates on the mineral nutrition of blueberries, the factors that affect the availability of nutrients and the methods to establish and supply the nutrients to satisfy crop demands. Chapter 6 covers various management practices that are important in blueberry cultivation, including mulching, irrigation, pruning, pollination and harvest. Chapter 7 examines plant growth regulators in regard to their application and the factors that affect their performance. Current and potential uses of these substances are presented. The most relevant pest, diseases and weeds that attack blueberries
are covered in Chapter 8. The information on diseases (virus, bacteria and fungi) is presented based on the organs affected and the symptoms associated with diseases and pests are described. Chapter 9 discusses the pre- and postharvest management of fruit quality. The attributes and factors affecting fruit quality are defined, as well as the factors that influence the postharvest life of the fruit and the approaches used to extend fruit quality.

This book is meant to be an overview of the various aspects of blueberry science and culture. It is targeted towards blueberry researchers and students in horticulture, but it should also be useful for growers and people in the industry who want to update their knowledge on this crop. Our approach has been to explain in an understandable manner the basic science behind the growth and development of blueberries, their botanical characteristics, as well as the implications and effects of various management practices and environmental conditions.

The authors are indebted for the encouragement and assistance of many people who made the work possible. The University of Talca financed a sabbatical leave for the senior author to start the writing of this book. Our wives, Beatriz and Ann, along with JBR’s children (Beatriz, Jorge and Gabriela), were tremendously supportive throughout the two years of preparation of this book. Several people have provided help in various tasks, as follows:

- Randy Beaudry, Michigan State University, reviewed Chapter 9;
- Pilar Bañados, Universidad de Católica, reviewed sections of Chapters 3 and 6;
- Ridley Bell, Mountain View Orchards, reviewed sections of Chapter 1;
- Peter Caligari, Universidad de Talca, reviewed the book proofs;
- Reinaldo Campos, Universidad Andrés Bello, reviewed Chapter 9;
- Bill Cline, University of Georgia, reviewed sections of Chapter 8;
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- Rebecca Darnell, University of Florida, reviewed Chapter 6;
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- José Manuel López-Aranda, Junta de Andalucía (Spain), provided soil data;
- Scott NeSmith, University of Georgia, reviewed sections of Chapter 2;
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• Narandra Patel, Gourmet Group of Companies, reviewed sections of Chapter 1;
• Alejandro del Pozo, Universidad de Talca, reviewed Chapter 4;
• Julio Retamales, Universidad de Chile, reviewed Chapter 7;
• Sebastián Romero, Universidad de Talca, prepared drawings and tables;
• Takato Tamada, Japan Blueberry Association, reviewed sections of Chapter 1;
• Claudio Valdes, SQM-Chile, reviewed Chapter 5;
• Ed Wheeler, MBG Marketing, reviewed sections of Chapter 2;
• Garry Wright, BerryExchange, reviewed sections of Chapter 1;
• Wei Yang, Oregon State University, provided soil data.
INTRODUCTION

The predominant cultivated blueberry species are *Vaccinium corymbosum* L. (highbush blueberry), *Vaccinium ashei* Reade (rabbiteye blueberry; syn. *Vaccinium virgatum* Ait.), and native stands of *Vaccinium angustifolium* Ait. (lowbush blueberry). Highbush cultivars are further separated into northern, southern or intermediate types depending on their chilling requirements and winter hardiness. Half-high types are also grown that are hybrids of highbush and lowbush species.

Where the different types of blueberry are grown is to a large extent determined by their chilling requirement and winter cold hardiness. All blueberries require a well-drained, acid soil with ample moisture. The lowbush types require at least 1000 chilling hours for normal floral development and can tolerate temperatures as low as −30°C. Rabbiteye cultivars require about 600 h of chilling and their floral buds cannot tolerate temperatures much below freezing. Northern highbush varieties are adapted to quite cold mid-winter temperatures below −20°C, and grow well anywhere there are 800–1000 h of chilling. Southern highbush varieties do not tolerate winter temperatures much below freezing and require chilling hours under about 550 h. Intermediate highbush varieties have a wide range in chilling requirements from 400 to 800 h. They generally fail in the colder climates because they bloom too early and are too slow to harden in the autumn, resulting in freeze damage to the flower buds.

Most of the commercial production of blueberry now comes from highbush and lowbush types, although rabbiteyes are important in south-east North America and hybrids of highbush×lowbush (half-highs) have made a minor impact in the upper mid-west USA. Some rabbiteye cultivars are grown in the US Pacific Northwest and Chile for their very late ripening fruit and wider soil adaptability. Northern highbush are grown primarily in Australia, France, Germany, Italy, New Zealand, the USA (Pacific Northwest, Michigan,
New Jersey, Poland and Chile. Southern highbush are grown predominantly in Australia, Argentina, the USA (California, Florida), Chile and southern Spain. The intermediate highbush types are grown mostly in Chile and the USA (North Carolina, Arkansas and Pacific Northwest).

Highbush and rabbiteye blueberries have become a major international crop, with about 40,500 ha planted in North America, 16,200 ha in South America, 7300 ha in Europe, 2000 ha in China and Japan, and 1200 ha in Australia and New Zealand (Brazelton, 2009). Overall, world production of highbush and rabbiteye now exceeds 300 t. Of that total, about 75% is northern highbush, 10% southern highbush and 15% rabbiteye. Lowbush blueberries are also harvested from over 60,700 ha of natural stands in eastern North America, with annual production over 110 t.

**EARLY HISTORY OF Highbush Blueberry CULTIVATION**

Many of the wild, edible *Vaccinium* species have been harvested for thousands of years by indigenous peoples (Moerman, 1998). Native Americans in western and eastern North America intentionally burned native stands of blueberries and huckleberries to renew their vigour and eliminate competition. Highbush and rabbiteye blueberries were domesticated at the end of the 19th century. Plants were initially dug from the wild and transplanted into New England and Florida fields.

The northern highbush blueberry, *V. corymbosum*, was first domesticated in about 1908 by Frederick Coville of the US Department of Agriculture (USDA). He was the first to establish the fundamental requirements of the blueberry, determining that blueberries need acid, well-drained soils, have no root hairs, and require a low-temperature rest period (Coville, 1916). He also learned how to propagate blueberries by stem cuttings, and established that bumble bees were the best pollinators. In addition, Coville learned that some genotypes are self-unfruitful and that the highbush blueberry is a tetraploid (Coville, 1927).

Coville began breeding highbush blueberries in 1908, with the help of a private grower in New Jersey, Elizabeth White (Ehlenfeldt, 2009). White grew out Coville’s hybrid populations and was particularly helpful in identifying elite wild clones by offering a reward to individuals sending her samples of blueberries that were unusually large. The best clones identified by Coville and White were named after their discoverers including ‘Adams’, ‘Brooks’, ‘Dunfee’, ‘Grover’, ‘Harding’, ‘Sam’, ‘Sooy’, ‘Rubel’ and ‘Russell’. ‘Rubel’ is still grown today, being favoured as a processed berry.

In an address to the Philadelphia Society for the Promotion of Agriculture in 1934, White stated:
The best of the hundred bushes located was that found by Rube Leek. In my notes on the variety, I at first used his full name, but Dr. Coville said Leek savored of onions and used in his notes the name Rube. Rube! What a name for such an aristocratic a plant! Finally on Dr. Coville's suggestion, a happy solution was found in the name 'Rubel'; the finder's first name plus the initial of his surname.

(White, 1934)

Coville bred blueberries from 1908 to 1937, and left 30,000 seedlings for his replacement George Darrow to sort through (Mainland, 1998). His first releases came in 1920, 'Pioneer' and 'Katherine' ('Brooks'×'Sooy'). Coville remains the most successful breeder, as over half of the current blueberry hectarage is still composed of his hybrids including 'Rubel' (1911), 'Jersey' (1928), 'Weymouth' (1936), 'Bluecrop' (1952), 'Croatan' (1954) and 'Blueray' (1955).

GROWTH OF THE BLUEBERRY INDUSTRY IN NORTH AMERICA

In the period from 1910 to 1940, the culture of northern highbush blueberry gradually spread across the USA, with the most significant industries emerging in New Jersey (1910), North Carolina (1920), Michigan (1930) and Washington (1940) (Eck and Childers, 1966). However, hectarage remained small and it was not until the late 1940s that the planting of blueberries began to grow substantially. The area covered by highbush blueberries grew from less than 100 ha in 1940, to about 1000 ha in 1955, to over 5500 ha in 1965. By the early 1970s, the greatest concentrations of highbush blueberries were located in New Jersey (3000 ha) and Michigan (3100 ha), followed by North Carolina (1640 ha) and then Washington (370 ha). There were also about 1400 ha of rabbiteye blueberries cultivated in the southern USA in 1965, primarily in Georgia and Florida.

Through the 1970s and early 1980s the northern highbush area continued to expand in Michigan, and large new plantings began to appear in British Columbia and Oregon (Table 1.1). The area covered by highbush blueberries increased from about 370 to 1540 ha (+316%) in the Pacific Northwest and from 3100 to 4900 ha (+58%) in Michigan. Rabbiteye hectarage also grew by about 40% in the 1970s and early 1980s, primarily in Florida and Georgia. Only limited planting was done in North Carolina and New Jersey.

In the 1980s, steady growth continued in the northern production regions of Oregon (+168%), Washington (+53%), British Columbia (+100%), and Michigan (+41%), and major new plantings of northern highbush also began to appear in New York and Indiana. Significantly less planting was done in New Jersey (+11%) and North Carolina (0%) (Table 1.1). In the south, the
## Table 1.1. Growth patterns of major centres of highbush and rabbiteye blueberry production in North America. (Adapted from Moore, 1994; Strik and Yarborough, 2005; Brazelton, 2009.)

<table>
<thead>
<tr>
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<td>6,980</td>
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<tr>
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<td></td>
<td>New York</td>
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<td>4,330</td>
<td>+1</td>
<td>-6</td>
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<td>1,820</td>
<td>4,510</td>
<td>7,500</td>
<td>+100</td>
<td>+148</td>
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</tr>
<tr>
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<td></td>
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<td>+16</td>
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<tr>
<td>Southwest</td>
<td>California</td>
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<td>–</td>
<td>50</td>
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<td>0</td>
<td>325</td>
<td>790</td>
<td>–</td>
<td>–</td>
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<tr>
<td></td>
<td>All</td>
<td>0</td>
<td>0</td>
<td>375</td>
<td>2,925</td>
<td>–</td>
<td>–</td>
<td>+680</td>
</tr>
<tr>
<td>North America</td>
<td>All</td>
<td>15,532</td>
<td>20,914</td>
<td>26,390</td>
<td>38,871</td>
<td>+35</td>
<td>+26</td>
<td>+47</td>
</tr>
</tbody>
</table>

*Mostly highbush.

*All highbush.

*Largely highbush and rabbiteye.

*Mostly rabbiteye.
The Blueberry Industry

The surface area of blueberries increased by 112% in Florida and 39% in Georgia, and Mississippi and Texas emerged as significant blueberry-producing states. The first plantings of southern highbush were made during this period in Florida and Georgia, and by 1992 southern blueberry hectarage was about 7% southern highbush and 93% rabbiteye.

Growth in the blueberry industry generally slowed during the 1990s in the primary northern growing states of Michigan, New Jersey, Oregon and Washington; however, substantial gains were observed in British Columbia (148%) and the newer producing states of New York (+105%) and Indiana (+132%). Growth across the southern states was relatively stagnant, except in the newer Gulf States of Mississippi (+82%) and Texas (+41%), where rabbiteye hectarage began to expand.

In the early 2000s, there was another boom in planting across the cultivated blueberry industry, and California emerged for the first time as a major blueberry-growing state, along with Mexico. The greatest growth in hectarage was in California (+4100%), Washington (+371%), Oregon (+275%) and Georgia (+173%). Growth was also strong in British Columbia (+66%), Mississippi (+66%), Florida (+64%) and North Carolina (+59%). By the early 2000s, southern highbush was more widely planted in the south than rabbiteye; the percentage of the area planted to southern highbush rose to 34% in 2003.

Today, the total hectarage in North America is at about 40,500 ha, an increase of nearly 50% over the last 5 years. The western region now accounts for the majority of the area at 37%, while the southern region represents 27%, the Midwest is 25% and the Northeast is 11% (Table 1.2). This distribution pattern is quite a contrast from 25 years ago, when the western region represented less than 5% of the total hectarage in North America. British Columbia is now only about 1100 ha behind Michigan, the industry leader for the last 50 years.

### Table 1.2. Proportion of total highbush and rabbiteye hectarage found in different regions of North America; see Table 1.1 for the states included in each region.

<table>
<thead>
<tr>
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<td>17</td>
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<td>Midwest</td>
<td>35</td>
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<td>30</td>
<td>25</td>
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<tr>
<td>South</td>
<td>26</td>
<td>28</td>
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<td>27</td>
</tr>
<tr>
<td>West</td>
<td>10</td>
<td>14</td>
<td>28</td>
<td>37</td>
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</table>

(Adapted from Moore, 1994; Strik and Yarborough, 2005; Brazelton, 2009.)
GROWTH OF THE BLUEBERRY INDUSTRY OUTSIDE NORTH AMERICA

The first planting of highbush blueberry outside of North America was made in 1923 by a Mr Borgesius in Assen, the Netherlands. Dr Piort Hoser, the founder of the Faculty of Horticulture of Warsaw Agricultural University, also imported some blueberries from the USA in 1924, but they were killed by winter cold in 1929. The northern highbush blueberry was introduced into Germany in the 1930s by Dr Walter Heermann, who also started breeding blueberries and introduced commercial production techniques. His fields encompassed 50 ha by 1951. Other early plantings were made by David Trehane in the UK in 1959 and Wilhelm Dierking in Germany in 1962. The first commercial plantings in Poland, the Netherlands and Italy were made in the 1970s. Planting of blueberries began in France in the 1980s and Spain in the 1990s.

Blueberry hectarage remained small across Europe until 1990, with the most planting being done in Italy, France, Germany and the Netherlands. In the 1990s, hectarage rose from about 1000 to 4000 ha across Europe, with the greatest growth occurring in Poland (1520 ha) and Germany (1370 ha) (Table 1.3). Since 2003, the European hectarage has continued to expand dramatically to about 7400 ha, an increase of 86%. The greatest growth in the last 5 years has been in Spain/Portugal (+363%), Poland (+86%), Italy (+53%) and Germany (+51%). The blueberry hectarage in Germany, Poland and the Netherlands is fairly well spread across them, while it is concentrated in the south-eastern corners of France and Spain. Northern highbush are grown at all locations in Europe, except in Spain/Portugal, where southern highbush predominate.

The first blueberries were planted in Australia and New Zealand in the 1960s and 1970s, primarily as a crop for export markets (Table 1.3). The industry in New Zealand had its greatest growth period during the late 1980s to 1990s; however, there was a period of consolidation from the late 1990s as export markets became oversupplied. The industry in Australia has undergone relatively steady growth since the 1980s. The industry in New Zealand and Australia is dominated by a few larger grower-marketers, some of which have close ties with northern hemisphere producers and marketers, as they pursue a year-round supply model for the Asia Pacific and European regions. From 2003 to 2008, hectarage in Australia rose from 520 to 600 ha (+15%), and in New Zealand from 405 to 530 ha (+31%). The hectarage in Australia is found in New South Wales, Victoria, Tasmania, South Australia and the southern areas of West Australia (Bell, 2006). The biggest blueberry region is around Coffs Harbour. In New Zealand most of the hectarage is in the northern Waikato region, with some new plantings being made in the east coast of the North Island (Furniss, 2006). Northern highbush predominate in northern New Zealand and southern Australia. Southern highbush predominate in northern New South Wales and southern New Zealand.
The Blueberry Industry

Table 1.3. Growth patterns of major centres of blueberry production across the world. (Adapted from Eck and Childers, 1966; Brazelton, 2009.)

<table>
<thead>
<tr>
<th>Region</th>
<th>Country</th>
<th>First plantings</th>
<th>Major growth period</th>
<th>Area (ha)</th>
<th>2003</th>
<th>2008</th>
<th>% Change</th>
</tr>
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<tr>
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<td>South Africa</td>
<td>1970s</td>
<td>1990s</td>
<td></td>
<td>355</td>
<td>200</td>
<td>-44</td>
</tr>
<tr>
<td>Asia</td>
<td>China</td>
<td>1980s</td>
<td>2000s</td>
<td></td>
<td>51</td>
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<td>+2,230</td>
</tr>
<tr>
<td>Asia</td>
<td>Japan</td>
<td>1950s</td>
<td>2000s</td>
<td></td>
<td>355</td>
<td>860</td>
<td>+142</td>
</tr>
<tr>
<td>Asia</td>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>406</td>
<td>2,090</td>
<td>+415</td>
</tr>
<tr>
<td>Europe</td>
<td>Poland</td>
<td>1970s</td>
<td>Mid 1990s to now</td>
<td></td>
<td>1,520</td>
<td>2,830</td>
<td>+86</td>
</tr>
<tr>
<td>Europe</td>
<td>Germany</td>
<td>1960s</td>
<td>Late 1990s to now</td>
<td></td>
<td>1,370</td>
<td>2,075</td>
<td>+51</td>
</tr>
<tr>
<td>Europe</td>
<td>France</td>
<td>1980s</td>
<td>Late 1980s</td>
<td></td>
<td>415</td>
<td>345</td>
<td>-17</td>
</tr>
<tr>
<td>Europe</td>
<td>Netherlands</td>
<td>1970s</td>
<td>Late 1980s</td>
<td></td>
<td>300</td>
<td>245</td>
<td>-18</td>
</tr>
<tr>
<td>Europe</td>
<td>Spain/Portugal</td>
<td>1990s</td>
<td>2000s</td>
<td></td>
<td>215</td>
<td>995</td>
<td>+363</td>
</tr>
<tr>
<td>Europe</td>
<td>Italy</td>
<td>1970s</td>
<td>Early 1980s</td>
<td></td>
<td>160</td>
<td>245</td>
<td>+53</td>
</tr>
<tr>
<td>Europe</td>
<td>UK</td>
<td>1950s</td>
<td>2000s</td>
<td></td>
<td>0</td>
<td>220</td>
<td>-</td>
</tr>
<tr>
<td>Europe</td>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>3,985</td>
<td>7,395</td>
<td>+86</td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>Australia</td>
<td>1960s</td>
<td>1990s</td>
<td></td>
<td>520</td>
<td>600</td>
<td>+15</td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>New Zealand</td>
<td>1970s</td>
<td>Late 1980s</td>
<td></td>
<td>405</td>
<td>530</td>
<td>+31</td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>925</td>
<td>1,130</td>
<td>+23</td>
</tr>
<tr>
<td>South America</td>
<td>Chile</td>
<td>1980s</td>
<td>2000s</td>
<td></td>
<td>2,135</td>
<td>11,300</td>
<td>+429</td>
</tr>
<tr>
<td>South America</td>
<td>Argentina</td>
<td>1990s</td>
<td>2000s</td>
<td></td>
<td>710</td>
<td>4,470</td>
<td>+529</td>
</tr>
<tr>
<td>South America</td>
<td>Uruguay</td>
<td>2000s</td>
<td>2000s</td>
<td></td>
<td>0</td>
<td>665</td>
<td>-</td>
</tr>
<tr>
<td>South America</td>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>2,845</td>
<td>16,278</td>
<td>+478</td>
</tr>
<tr>
<td>World</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8,511</td>
<td>27,250</td>
<td>+220</td>
</tr>
</tbody>
</table>

The first blueberries were planted in Asia in the 1950s (Table 1.3). A significant industry emerged in Japan in late 1980s (180 ha), but only a few blueberries were planted in China until recently. From 2003 to 2008 the surface area of blueberries increased from 51 to 1190 ha (+2,230%) in China and from 355 to 860 ha (+142%) in Japan. Production in China predominates in Jilian Province, with significant hectarage also being found in Shandong, Liaoning, Yunnan and Zhejiang (Li et al., 2006; Yu et al., 2011). Northern highbush and half-highs predominate across China, although southern highbush and rabbiteye are found in Shandong, Yunnan and Zhejiang. Japanese production is scattered in small hectarages across the country (Tamada, 2006). Northern highbush and half-highs are grown in the north of Japan; northern, southern and rabbiteye in central Japan; and southern highbush and rabbiteye in southern Japan.
The blueberry was first brought to South Africa in the 1970s, but was not widespread until the 1990s (Table 1.3). A peak hectarage of about 350 ha was reached in the early 2000s, which has declined to about 200 ha (~44%). South African blueberry production is scattered across the country, with concentrations along the Cape, Eastern Free State and Lydenburg/Nelspruit (Greef and Greef, 2006). Southern highbush predominate in the southern coastal areas, while northern highbush are grown in the more inland areas with higher chilling hours.

The first blueberry plantings were made in Chile in the 1980s and Argentina in the 1990s (Table 1.3). By 2003, there were 2135 ha of blueberries in Chile and 710 ha in Argentina. Strong growth continued from 2003 to 2008, with Chile then having 11,300 ha (+429%) and Argentina having 4470 ha (+529%). Significant hectarages have also emerged recently in Uruguay (665 ha). The largest area of blueberries in the world now resides in Chile, exceeding Michigan and British Columbia by 23 and 33%, respectively.

There are three major production regions in Argentina that all grow predominantly southern highbush – Tucumán, Entre-Ríos, and Buenos Aires and San Luis (Taquinini, 2006). In Chile, blueberries are grown from Region IV to XIV, with concentrations in VII and VIII (over 49% of the hectarage) (www.censoagropecuario.cl/index2.html). In the north-central Regions of IV and V only southern highbush are grown, while in the south central Regions IX and X northern highbush predominate. In the middle regions of VII and VIII there is a transitional zone, where both southern and highbush types are grown.

**CLIMATES OF MAJOR PRODUCTION REGIONS**

Highbush blueberries are grown across a broad range of climatic types: (i) mild, moist summers and very cold winters; (ii) mild, moist summers and moderate winters; (iii) hot, wet summers and mild winters; and (iv) hot, dry summers and mild winters.

Jillian Province in China, Italy, Germany, Michigan, New Jersey, the Netherlands and Poland fall into the first climatic class with mild, wet summers and very cold winters (Tables 1.4 and 1.5). At these locations, winter temperatures commonly fall below 0°C and summer temperatures are generally below 30°C. Chilling hours exceed 1000 h and the number of frost-free days ranges from 130 to 180. Most of the soils in this climatic type are rich organic sands or loams that do not require acidification for blueberries. Northern highbush varieties are commonly grown, with ‘Bluecrop’, ‘Duke’, ‘Elliott’ and ‘Jersey’ predominating and ‘Liberty’, ‘Aurora’ and ‘Draper’ being widely planted. In the coldest zones of China, half-highs are also grown (Table 1.7).
Table 1.4. Climates of major North American highbush and rabbiteye blueberry production regions. (Adapted from Lyrene, 2008; The National Climate Data Center, http://www5.ncdc.noaa.gov.)

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>City</th>
<th>Rainfall (mm)</th>
<th>Temperature (°C)</th>
<th>Chilling hours (&lt;7°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Annual</td>
<td>Summer</td>
<td>Mid-summer high</td>
</tr>
<tr>
<td>Atlantic</td>
<td>North Carolina</td>
<td>Wilmington</td>
<td>1378</td>
<td>478</td>
<td>33.0</td>
</tr>
<tr>
<td>Northeast</td>
<td>New Jersey</td>
<td>Hammonton</td>
<td>1097</td>
<td>284</td>
<td>30.0</td>
</tr>
<tr>
<td>Midwest</td>
<td>Michigan</td>
<td>Holland</td>
<td>1021</td>
<td>294</td>
<td>27.0</td>
</tr>
<tr>
<td>Southeast</td>
<td>Florida, north</td>
<td>Gainesville</td>
<td>1234</td>
<td>495</td>
<td>33.5</td>
</tr>
<tr>
<td></td>
<td>Florida, central</td>
<td>Orlando</td>
<td>1228</td>
<td>528</td>
<td>33.0</td>
</tr>
<tr>
<td></td>
<td>Georgia</td>
<td>Alma</td>
<td>1248</td>
<td>432</td>
<td>33.5</td>
</tr>
<tr>
<td></td>
<td>Mississippi</td>
<td>Poplarville</td>
<td>1606</td>
<td>414</td>
<td>33.5</td>
</tr>
<tr>
<td>Northwest</td>
<td>British Columbia</td>
<td>Vancouver</td>
<td>1201</td>
<td>134</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>Oregon</td>
<td>Corvallis</td>
<td>1168</td>
<td>92</td>
<td>28.0</td>
</tr>
<tr>
<td></td>
<td>Washington</td>
<td>Vancouver</td>
<td>1267</td>
<td>71</td>
<td>25.0</td>
</tr>
<tr>
<td>Southwest</td>
<td>California</td>
<td>Bakersfield</td>
<td>163</td>
<td>5</td>
<td>36.0</td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>Guadalajara</td>
<td>927</td>
<td>676</td>
<td>32.4</td>
</tr>
</tbody>
</table>
Table 1.5. Climates of major global highbush and rabbiteye blueberry production regions. (Adapted from Novoa et al., 1989; Lyrene, 2008; World Meteorological Organization, http://www.wmo.int/index-en.html.)

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>City</th>
<th>Rainfall (mm)</th>
<th>Temperature (°C)</th>
<th>Chilling hours (&lt;7°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Annual</td>
<td>Summer</td>
<td>Mid-summer high</td>
</tr>
<tr>
<td>Africa</td>
<td>South Africa</td>
<td>Cape Town</td>
<td>515</td>
<td>52</td>
<td>26.1</td>
</tr>
<tr>
<td>Asia</td>
<td>China</td>
<td>Dalian</td>
<td>632</td>
<td>405</td>
<td>26.1</td>
</tr>
<tr>
<td></td>
<td>Japan</td>
<td>Tokyo</td>
<td>1465</td>
<td>481</td>
<td>30.8</td>
</tr>
<tr>
<td>Europe</td>
<td>Poland</td>
<td>Warsaw</td>
<td>520</td>
<td>203</td>
<td>23.6</td>
</tr>
<tr>
<td></td>
<td>Germany</td>
<td>Hamburg</td>
<td>773</td>
<td>224</td>
<td>22.1</td>
</tr>
<tr>
<td></td>
<td>France</td>
<td>Bordeaux</td>
<td>986</td>
<td>179</td>
<td>22.6</td>
</tr>
<tr>
<td></td>
<td>Spain</td>
<td>Huelva</td>
<td>490</td>
<td>16</td>
<td>29.6</td>
</tr>
<tr>
<td></td>
<td>Netherlands</td>
<td>Amsterdam</td>
<td>778</td>
<td>194</td>
<td>21.8</td>
</tr>
<tr>
<td></td>
<td>Italy</td>
<td>Venice</td>
<td>810</td>
<td>154</td>
<td>27.5</td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>Australia</td>
<td>Coffs Harbour</td>
<td>1704</td>
<td>570</td>
<td>27.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Melbourne</td>
<td>665</td>
<td>154</td>
<td>24.8</td>
</tr>
<tr>
<td></td>
<td>New Zealand</td>
<td>Auckland</td>
<td>1135</td>
<td>246</td>
<td>25.0</td>
</tr>
<tr>
<td>South America</td>
<td>Chile, north-central</td>
<td>Santiago</td>
<td>311</td>
<td>3</td>
<td>29.7</td>
</tr>
<tr>
<td></td>
<td>Chile, south-central</td>
<td>Osorno</td>
<td>1383</td>
<td>160</td>
<td>23.8</td>
</tr>
<tr>
<td></td>
<td>Argentina</td>
<td>Buenos Aires</td>
<td>1215</td>
<td>348</td>
<td>30.4</td>
</tr>
</tbody>
</table>
### Table 1.6. Main cultivars grown in major North American highbush and rabbiteye blueberry regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>Principal cultivars&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic</td>
<td>North Carolina</td>
<td>NH: 'Croatan', ‘Reveille’</td>
</tr>
<tr>
<td></td>
<td>Mississippi</td>
<td>SH: ‘O’Neal’, ‘Star’</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SH: ‘O’Neal’, ‘Bluecrisp’</td>
</tr>
</tbody>
</table>

<sup>a</sup>NH, northern highbush; RE, rabbiteye; SH, southern highbush.

France, Japan, northern New Zealand, south-central Chile, the Pacific Northwest and southern Australia have climates that fall into climate type 2 with mild, moist summers and moderate winters (Tables 1.4 and 1.5). At these locations, chilling hours generally exceed 600 h, average winter low temperatures are above freezing and the number of frost-free days ranges from 170 to 200 (or more). The soils range from sands and loams with high organic content and low pH to mineral soils requiring acidification. Northern highbush predominate with ‘Bluecrop’, ‘Duke’, ‘Elliott’, ‘Reka’, ‘Brigitta’ and ‘Legacy’ being common (Tables 1.6 and 1.7). In New Zealand and Japan, a wide array of southern highbush and rabbiteye cultivars are grown alongside these northern cultivars.

Argentina, Mexico, northern New South Wales, north-central Chile, south-eastern USA and Uruguay represent climatic type 3 with hot, wet summers and mild winters (Tables 1.4 and 1.5). At these locations, available chilling hours (<7°C) are low ranging, from 0 (Mexico) to 500–800 h in North Carolina. Low winter temperatures generally remain above freezing, summer temperatures average above 28–30°C and the number of frost-free growing days exceeds 250. Mexico has the most unique climate of the group, being
### Table 1.7. Main cultivars grown in major global highbush blueberry regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>Principal cultivars&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Japan</td>
<td></td>
<td>SH: 'Misty' 'O'Neal', 'Star', 'Sapphire'&lt;br&gt; RE: 'Climax', 'Woodard', 'Brightwell', 'Tifblue'</td>
</tr>
<tr>
<td>Europe</td>
<td>Spain/Portugal</td>
<td>SH: 'O'Neal', 'Misty', 'Star', Atlantic Blue varieties&lt;br&gt; NH: 'Duke', 'Bluecrop', 'Elliott', 'Brigitta', 'Draper', 'Liberty'</td>
</tr>
<tr>
<td></td>
<td>France,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Netherlands,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Germany,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Italy, UK</td>
<td></td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>Australia</td>
<td>NH: 'Brigitta', 'Bluecrop', 'Legacy', 'Elliott', private breeding programmes&lt;br&gt; SH: 'Sharplblue', 'Misty', 'Biloxi'&lt;br&gt; RE: 'Britewell', 'Powderblue'</td>
</tr>
<tr>
<td>New Zealand</td>
<td></td>
<td>SH: 'Misty', 'O'Neal'&lt;br&gt; RE: 'Rahi', 'Maru', 'Tifblue', 'Powderblue', 'Delite'</td>
</tr>
<tr>
<td>Argentina</td>
<td></td>
<td>SH: 'O'Neal', 'Misty', 'Star', 'Jewel', 'Bluecrisp', 'Emerald', 'Millennia', 'Santa Fe'</td>
</tr>
</tbody>
</table>

<sup>a</sup>SH, southern highbush; NH, northern highbush; RE, rabbiteye; HH, half-high.

The only one with no chilling hours and mostly dry winters. Most of these regions have mineral soils with high clay content that require acidification to grow blueberries. Southern highbush and rabbiteye varieties predominate in these zones, with 'Emerald', 'Star', 'Jewel' and 'O'Neal' being the most widely planted highbush and 'Brightwell', 'Tifblue', 'Climax', 'Premier' and 'Powderblue' being the most widespread rabbiteye (Tables 1.6 and 1.7). The northern highbush cultivar 'Croatan' is also common in North Carolina.
North-central Chile, southern South Africa and Spain represent zone 4 with hot, dry summers and mild winters (Table 1.5). Chilling hours generally fall between 250 and 450, mean winter low temperatures rarely fall below freezing, summer temperatures average above 30°C, and growing seasons exceed 250 days. Most of these regions have mineral soils with high clay content that require acidification to grow blueberries. Mostly southern highbush are grown in this climate type with ‘Emerald’, ‘Star’ and ‘Jewel’ predominating (Table 1.7), although new private cultivars from Atlantic Blue in Spain are making inroads.

**CULTURAL CONDITIONS OF MAJOR PRODUCTION REGIONS**

There is considerable variation across the blueberry-growing regions in production systems. In eastern and mid-western USA, south-central Chile, Japan and the cold climates of Europe, plants are typically planted in the spring at in-row spacings of 1.0 to 1.2 m with 3 m between rows (‘pick-your-own’ in Japan is at 2 m spacing). Most plantings are on natural acidic soils with high organic matter (>3%). Pine chips or sawdust is sometimes used for mulching, most commonly in Chile. Overhead irrigation is more common than trickle irrigation, although some plantings are not irrigated at all. Dormant pruning is done annually or biannually by removing the least productive canes; only limited fine pruning in the canopy is employed except in Chile. Fertilizer is generally broadcast on the soil in the eastern USA and Europe, while fertigation is most common in Chile.

In the Pacific Northwest, southern USA, north-central Chile, Argentina and Spain, higher-density plantings are generally employed (0.7–0.9 m within rows and 3 m between rows), on raised beds, with considerable attention often paid to pH management. Plants are commonly set in the autumn or early winter. Plastic mulches are common, along with sawdust and pine bark. Trickle irrigation is more prevalent than overhead irrigation, although some plantings in north-west Oregon and British Columbia are not irrigated. Fertigation is commonly employed.

Growth regulators (Dormex) are commonly used in the southern USA to enhance leaf development in the spring and advance ripening in southern highbush blueberries. Gibberellic acid has been used to increase fruit set and to ‘rescue’ frost-damaged rabbiteye in Georgia. Rabbiteye and highbush are commonly hedged to control plant size, encourage branching and enhance fruit set.

While most of the highbush hectarage across the world is grown in open fields, protected culture is used locally at many locations. Tunnels are used extensively in Spain to hasten fruit development. Some tunnels are also used
in California to speed up harvest and in Japan to protect against rain damage. Hail-proof netting is used in Argentina and Mexico for season extension and hail protection. Netting is also used in Australia to protect against hail and birds. Shading nets are being tested in Chile and the USA as a means to delay harvest and prevent sunburn of leaves and fruit.

WORLDWIDE PRODUCTION PATTERNS

Blueberry fruit is now available all year round across the world (Tables 1.8 and 1.9). In North America, the season starts in Florida in March, followed soon by California, then Georgia and the Gulf Coast in mid-April. North Carolina begins harvest in mid-May followed by New Jersey, Oregon, Washington in mid-June and finally Michigan in July. The last fruit comes out of Michigan in late September and Washington and British Columbia in mid-October. Fruit is exported to North America from Chile and Argentina in the North American winter, starting with Argentina in mid-September and finishing with southern Chile in mid-March. Fruit is harvested in Mexico from October to February.

Most of the fruit coming out of Florida, Mexico, California, New Jersey and North Carolina is sold fresh (Table 1.8). About half of the fruit harvested in Georgia, Mississippi, British Columbia and Oregon goes to the fresh market, while 25–40% of the fruit produced in Michigan and Washington is sold fresh. Almost all of the fruit going to the fresh market is harvested by hand.

Table 1.8. Production and marketing patterns in major North American highbush blueberry production regions. (Adapted from Brazelton, 2009.)

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>Season</th>
<th>Utilization (%)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Processed</td>
<td>Fresh</td>
<td></td>
</tr>
<tr>
<td>Atlantic</td>
<td>North Carolina</td>
<td>Mid-May to August</td>
<td>25</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>Midwest</td>
<td>Michigan</td>
<td>July to late September</td>
<td>60</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Northeast</td>
<td>New Jersey</td>
<td>Mid-June to early August</td>
<td>15</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td>Northwest</td>
<td>British Columbia</td>
<td>Mid-July to mid-October</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Oregon</td>
<td>Mid-June to mid-September</td>
<td>55</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Washington</td>
<td>Mid-June to mid-October</td>
<td>75</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Southeast</td>
<td>Florida</td>
<td>March to mid-June</td>
<td>0</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Georgia</td>
<td>Mid-April to mid-August</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mississippi</td>
<td>Mid-April to mid-August</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>Southwest</td>
<td>California</td>
<td>March to mid-July</td>
<td>10</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>October to February</td>
<td>0</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>
The Blueberry Industry

Table 1.9. Production and marketing patterns in major global highbush blueberry regions. (Adapted from Brazelton, 2009.)

<table>
<thead>
<tr>
<th>Region</th>
<th>State</th>
<th>Season</th>
<th>Utilization (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Processed</td>
</tr>
<tr>
<td>Africa</td>
<td>South Africa</td>
<td>August to January</td>
<td>73</td>
</tr>
<tr>
<td>Asia</td>
<td>China</td>
<td>April to mid-October</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>Japan</td>
<td>May to mid-August</td>
<td>1</td>
</tr>
<tr>
<td>Europe</td>
<td>Poland</td>
<td>August and September</td>
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</tr>
<tr>
<td></td>
<td>Germany</td>
<td>Mid-July to September</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>France</td>
<td>July and August</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Netherlands</td>
<td>July to September</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Spain/Portugal</td>
<td>March to June</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Italy</td>
<td>June to September</td>
<td>3</td>
</tr>
<tr>
<td>Pacific Rim</td>
<td>Australia</td>
<td>August to February</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>New Zealand</td>
<td>November to March</td>
<td>43</td>
</tr>
<tr>
<td>South America</td>
<td>Chile</td>
<td>November to mid-March</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Argentina</td>
<td>Mid-September to January</td>
<td>4</td>
</tr>
</tbody>
</table>

although success with machines is growing. Almost all of the processed fruit is harvested by machine, except in British Columbia and Washington.

In Europe, the season starts in March in Spain and Portugal, followed by Italy beginning in June, France and the Netherlands in July, Germany in mid-July and Poland in August. The last fruit in Europe is picked in late September. Australia begins shipping fruit to Europe and Asia in August and continues until February. New Zealand begins harvesting in November and its season ends in March. The season begins in China in April, but most fruit is produced in the autumn. Japan produces blueberry fruit from May to mid-August. Almost all of the European, Asian and Pacific Rim fruit is hand-harvested and goes to the fresh market (Table 1.9). In China and New Zealand, hand-harvested fruit is split between the fresh and processed markets. Almost all Argentinean and Chilean fruit is sold fresh and hand-harvested (Table 1.9).

CONCLUSIONS

While highbush and rabbiteye blueberries are native to the USA, they have now become an international crop, being widely planted in North America, South America, Europe, China and the Pacific Rim. Most of this growth
has come in the last 10 to 20 years. Traditionally the greatest amount of
hectareage has been in Michigan of the USA, but the amount of land planted
to blueberries is now larger in Chile than Michigan and the Pacific Northwest
is not far behind. Highbush blueberries are grown across a very broad range of
environmental conditions ranging from hot, dry climates with limited chilling
hours (<7°C) to cold, wet climates with considerable chilling hours. Southern
highbush types are grown where chilling hours are less than about 550, while
northern highbush are grown in regions with more chilling hours. Highbush
blueberries are typically grown at in-row spacings of 1.0 to 1.2 m with 3 m
between rows. Overhead irrigation is more common than trickle, and annual
dormant pruning is typical. Southern highbush is generally grown at closer
spacings, with trickle irrigation being most common and bushes are typically
heded after harvest for size control. Most of the highbush hectarage across
the world is in open fields, although protected systems are common in Spain,
Argentina and Mexico. Blueberry fruit is now available almost all year round.
In the northern hemisphere harvest begins in Florida and Spain in March and
ends in the Pacific Northwest and Poland in late September. In the southern
hemisphere harvest starts in August in Australia and ends in Chile in March.

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BLUEBERRY TAXONOMY AND BREEDING

TAXONOMY OF BLUEBERRIES

The genus of blueberries, *Vaccinium*, is widespread, with species being found in the Himalayas, New Guinea and the Andean region of South America. The origin of the genus is thought to be South American and estimates of species numbers range from 150 to 450. Crop species are found in the sections *Cyanococcus* (blueberries), *Oxycoccus* (cranberries), *Vitis-Idaea* (lingonberry) and *Myrtillus* (bilberry, whortleberry). Many of the species in the genus are polyploid and carry multiple sets of chromosomes. Chromosome numbers range from diploid (2N=2X=14) to tetraploid (2N=4X=28) to hexaploid (2N=6X=42).

Most blueberry production comes from cultivars derived from *Vaccinium corymbosum* L. (highbush blueberry), *Vaccinium ashei* Reade (rabbiteye blueberry; syn. *Vaccinium virgatum* Ait.), and native stands of *Vaccinium angustifolium* Ait. (lowbush blueberry). Highbush cultivars are further separated into northern or southern types depending on their chilling requirements and winter hardiness.

The identification of species in the blueberry subgenus *Cyanococcus* has been problematic due to polyploidy, overlapping morphologies, extensive hybridization and a general lack of chromosome differentiation. In the first detailed taxonomy of the group, Camp (1945) described nine diploid, 12 tetraploid and three hexaploid species, but Vander Kloet (1980, 1988) reduced this list to six diploid, five tetraploid and one hexaploid taxa. He included all the crown-forming species into *V. corymbosum* with three chromosome levels. Most horticulturists and blueberry breeders feel that the variation patterns in *V. corymbosum* are distinct enough to retain Camp’s diploid *Vaccinium elliottii* Chapm. and *Vaccinium fuscatum* Ait., tetraploid *Vaccinium simulatum* Small and hexaploid *V. ashei* Reade and *Vaccinium constablaei* A. Gray (Table 2.1).

All of the polyploid *Cyanococcus* are likely of multiple origins and active hybridization between many species is ongoing. The tetraploid highbush blueberry *V. corymbosum* is genetically an autopolyploid, with two sets of
Table 2.1. Important native species of Vaccinium. (Adapted from Hancock et al., 2008.)

<table>
<thead>
<tr>
<th>Section</th>
<th>Species</th>
<th>Ploidy</th>
<th>Location</th>
</tr>
</thead>
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<tr>
<td>Batodendron</td>
<td>V. arboreum Marsh</td>
<td>2X</td>
<td>South-east North America</td>
</tr>
<tr>
<td>Cyanococcus</td>
<td>V. angustifolium Ait.</td>
<td>4X</td>
<td>North-east North America</td>
</tr>
<tr>
<td></td>
<td>V. ashei Reade</td>
<td>6X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. boreale Hall &amp; Aald.</td>
<td>2X</td>
<td>North-east North America</td>
</tr>
<tr>
<td></td>
<td>V. constablaei Gray</td>
<td>6X</td>
<td>Mountains of south-east North America</td>
</tr>
<tr>
<td></td>
<td>V. corymbosum L.</td>
<td>2X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. corymbosum L.</td>
<td>4X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. darrowii Camp</td>
<td>2X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. fuscatum Ait.</td>
<td>2X</td>
<td>Florida</td>
</tr>
<tr>
<td></td>
<td>V. myrtilloides Michx.</td>
<td>2X</td>
<td>Central North America</td>
</tr>
<tr>
<td></td>
<td>V. pallidum Ait.</td>
<td>2X, 4X</td>
<td>Mid-Atlantic North America</td>
</tr>
<tr>
<td></td>
<td>V. tenellum Ait.</td>
<td>4X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. elliottii Chapm.</td>
<td>2X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. hirsutum Buckley</td>
<td>4X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. myrsinites Lam</td>
<td>4X</td>
<td>South-east North America</td>
</tr>
<tr>
<td></td>
<td>V. simulatum Small</td>
<td>4X</td>
<td>South-east North America</td>
</tr>
<tr>
<td>Oxyccocus</td>
<td>V. macrocarpon Ait.</td>
<td>2X</td>
<td>North America</td>
</tr>
<tr>
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<td>V. oxyccocos L.</td>
<td>2X, 4X</td>
<td>Circumboreal</td>
</tr>
<tr>
<td>Vitis-Idae</td>
<td>V. vitis-idea I.</td>
<td>2X</td>
<td>Circumboreal</td>
</tr>
<tr>
<td>Myrtillus</td>
<td>V. cespitosum Michx.</td>
<td>2X</td>
<td>North America</td>
</tr>
<tr>
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<td>V. chamissonis Bong.</td>
<td>2X</td>
<td>Circumboreal</td>
</tr>
<tr>
<td></td>
<td>V. deliciosum Piper</td>
<td>4X</td>
<td>North-west North America</td>
</tr>
<tr>
<td></td>
<td>V. membranaceum</td>
<td>4X</td>
<td>West North America</td>
</tr>
<tr>
<td></td>
<td>Dougl. ex Hook</td>
<td></td>
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<tr>
<td></td>
<td>V. myrtillus L.</td>
<td>2X</td>
<td>Circumboreal</td>
</tr>
<tr>
<td></td>
<td>V. ovalifolium Sm.</td>
<td>4X</td>
<td>North-west North America</td>
</tr>
<tr>
<td></td>
<td>V. parvifolium Sm.</td>
<td>2X</td>
<td>North-west North America</td>
</tr>
<tr>
<td></td>
<td>V. scoparium Leibeg ex Cowile</td>
<td>2X</td>
<td>North-west North America</td>
</tr>
<tr>
<td>Polycodium</td>
<td>V. stamineum L.</td>
<td>2X</td>
<td>Central and E. North America</td>
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<td>Pyxothanmus</td>
<td>V. consanguineum Klotzch</td>
<td>2X</td>
<td>South Mexico and Central America</td>
</tr>
<tr>
<td></td>
<td>V. ovatum Pursh</td>
<td>2X</td>
<td>North-west North America</td>
</tr>
<tr>
<td></td>
<td>V. bracteatum Thunb.</td>
<td>2X</td>
<td>East Asia, China and Japan</td>
</tr>
<tr>
<td>Vaccinium</td>
<td>V. uliginosum L.</td>
<td>2X, 4X</td>
<td>Circumboreal</td>
</tr>
</tbody>
</table>
similar chromosomes. The primary mode of speciation in *Vaccinium* has been through unreduced gametes (Qu and Hancock, 1995; Vorsa and Rowland, 1997; Qu and Vorsa, 1999).

**HISTORY OF IMPROVEMENT**

Blueberry breeding is a very recent development (Lyrene, 1998; Hancock, 2006a, b). Highbush breeding began in the early 1900s in New Jersey, with the first hybrid being released in 1908 by Frederick Coville of the USDA. He conducted the fundamental life history studies of the blueberry that served as the basis of cultivation such as soil pH requirements, cold and day-length control of development, pruning strategies and modes of propagation. Working with Elizabeth White and others, he collected several outstanding wild clones of *V. corymbosum* and *V. angustifolium*, which he subsequently used in breeding improved types. Over 75% of the current blueberry hectarage is still composed of his hybrids, most notably 'Bluecrop', 'Jersey', 'Weymouth', 'Croatan', 'Blueray', 'Rubel' and 'Berkeley' (Mainland, 1998, 2011).

George Darrow assumed the USDA programme after Coville died in 1937 and made important contributions on the interfertility and phylogeny of the native *Vaccinium* species in cooperation with the taxonomist W.H. Camp (Hancock, 2006a). He formed a large collaborative testing network that encompassed private growers and Agricultural Experiment Station (AES) scientists in Connecticut, Florida, Georgia, Maine, Massachusetts, Michigan, New Jersey and North Carolina. From 1945 to 1961, he sent out almost 200,000 seedlings to his cooperators for evaluation.

Arlen Draper followed Darrow and focused on incorporating the genes of most wild *Vaccinium* species into the cultivated highbush background (Draper, 1995; Hancock, 2006b). He maintained and strengthened Darrow’s collaborative network and released a prodigious number of southern and northern highbush cultivars with improved fruit colour and firmness, smaller pedicel scars and higher productivity (Hancock and Galletta, 1995). His 'Duke' and 'Elliott' have been major successes, along with the newer releases 'Nelson' and 'Legacy'. Mark Ehlenfeldt assumed the USDA–Agricultural Research Service (ARS) programme in 1998.

Ralph Sharp began working in the 1950s in Florida on the development of southern highbush types in collaboration with Darrow (Sharp and Darrow, 1959; Lyrene, 1998). He was the first collector of *Vaccinium darrowii* for breeding and, until very recently, all southern highbush cultivars contained genes from his wild clones. Sharp, and his colleague Wayne Sherman, developed several successful cultivars, including 'Sharpblue', which was grown commercially until very recently. Paul Lyrene took over the breeding work in Florida in 1977.
Chapter 2

Stanley Johnston at Michigan State University spent a considerable amount of time in the 1950s and 1960s improving the cold tolerance of highbush by crossing it with *V. angustifolium*. Out of this work came the half-high cultivar ‘Northland’ and the mostly pure highbush type ‘Bluejay’, which was released by his successor Jim Moulton. The programme was abandoned in 1978, but was renewed in 1990 by Jim Hancock.


Outside the USA, blueberry breeding work was conducted in Australia, Germany and New Zealand. Johnston sent open pollinated seed to D. Jones and Ridley Bell in Australia in the 1960s that generated the important cultivar ‘Brigitta Blue’ along with several others. Narandra Patel at HortResearch Inc. in New Zealand released the cultivars ‘Nui’, ‘Puru’ and ‘Reka’ from breeding material initially provided by the University of Arkansas and the USDA at Beltsville in the 1960s and 1970s. Walter Heermann in Germany working with seed provided by Frederick Coville released several varieties in the 1940s and 1950s including ‘Blauweiss-Goldtraube’, ‘Blauweiss-Zuckertraube’, ‘Heerma’, ‘Rekord’, ‘Ama’ and ‘Gretha’.

Rabbiteye breeding was initiated in 1939 by George Darrow in collaboration with Otis J. Woodard at the Georgia Coastal Plain Experiment Station (Tifton, Georgia) and Emmett B. Morrow at the North Carolina Experiment Station, although a collection of wild selections from Florida and Georgia had been planted at Tifton in the 1920s (Austin, 1994). This work was continued by Max Austin and then Scott NeSmith in Georgia, Gene Galletta followed by Jim Ballington in North Carolina, and Ralph Sharp, Wayne Sherman and then Paul Lyrene in Florida. These breeding programmes have resulted in significant improvements in fruit colour, size, texture and appearance over the original wild selections. The most important cultivars have been ‘Tifblue’ (1955) and ‘Brightwell’ (1971) from Georgia, ‘Bluegem’ (1970) and ‘Bonita’ (1985) from Florida, and ‘Powderblue’ and ‘Premier’ (1978) from North Carolina. Rabbiteye cultivars were also bred in the New Zealand HortResearch Inc. programme of Narandra Patel. Several releases came from this programme in the 1990s including ‘Maru’ and ‘Rahi’.

Lowbush blueberries have been hybridized with *V. corymbosum* to produce half-high cultivars. The major releases of this type were ‘Northland’ developed by Stanley Johnston in Michigan and ‘Northblue’, ‘Northsky’, ‘Northcountry’, ‘St. Cloud’, ‘Polaris’ and ‘Chippewa’ released by Jim Luby in Minnesota. The half-higos have much higher yields and larger fruit than lowbush, but have low enough stature to be protected by snow in areas with extreme winter cold.
CURRENT BREEDING EFFORTS

The current goals of southern highbush breeders are to obtain early-ripening cultivars with high plant vigour, improved disease resistance and a later flowering (particularly in the south-east USA, where late freezes are a problem). Higher yields, better flavour and characteristics favourable for mechanical harvest are also being sought. Cultivars and advanced breeding lines are being used to breed southern highbush, along with hybrids derived from native, low-chill highbush selections from Florida and Georgia (V. ashei, V. elliottii and V. darrowii). Because of their low chilling requirement and the influence of genes from the evergreen species V. darrowii, many southern highbush cultivars can be grown as evergreens that avoid dormancy in areas with mild winters, with a harvest season that extends for several months through the winter and early spring (Darnell and Williamson, 1997; Lyrene, 2008). Rabbiteye breeders hope to expand harvest dates, improve berry size and fruit quality, reduce susceptibility to rain cracking and extend storage life.

Southern highbush cultivars are being developed at several locations, including Arkansas, Australia, California, Florida, Georgia, Mississippi, Chile and Spain. Paul Lyrene and now Jim Olmstead at the University of Florida have the most active programme dealing with very-low-chill genotypes and many high-impact cultivars have been released from this effort including ‘Emerald’, ‘Jewel’, ‘Misty’ and ‘Star’. Jim Ballington in North Carolina has the most significant programme operating at the interface between northern and southern highbush types, and has generated a number of important cultivars including ‘Lenore’, ‘New Hanover’, ‘O’Neal’, ‘Reveille’ and ‘Sampson’. Jim Moore and now John Clark at the University of Arkansas have focused on mixing southern wild species with northern types and recently released ‘Ozarkblue’, a very-high-quality late type. Scott NeSmith at the University of Georgia has generated several new early varieties including ‘Rebel’, ‘Camellia’ and ‘Palmetto’. He also has an active rabbiteye breeding programme and his late-season cultivar ‘Ochlocknee’ has generated considerable interest. Steve Stringer, Arlen Draper and Jim Spiers at the USDA-ARS in Mississippi have developed a number of southern highbush types including ‘Biloxi’, ‘Gupton’ and ‘Magnolia’. Several private breeding programmes have also emerged that are developing southern highbush types including Atlantic Blue in Spain (Ulf Hayler), Berry Blue in Michigan and Chile (Ed Wheeler), Driscoll Associates in California (Bruce Mowrey), Mountain Blue Orchard in Australia (Ridley Bell) and Vital Berry in Chile (Enrique Acevedo). Berry Blue is also devoting some effort to rabbiteye types.

Northern highbush breeders are concentrating on flavour, longer-storing fruit, expanded harvest dates, disease and pest resistance, and machine harvestability. Established breeding lines are being used in these efforts, along with complex hybrids made up of V. darrowii, V. angustifolium, V. constablaei and most of the other wild species. Even though it has limited winter hardiness,
V. darrowii has proved to be an interesting parent in colder climates because it passes on a powder blue colour, firmness, high flavour, heat tolerance and potential upland adaptation (Hancock, 1998).

Northern highbush blueberries are currently being bred in New Jersey, Michigan, Oregon and Chile. Jim Hancock at Michigan State University is focusing on late-maturing, long-storing genotypes and has released three new northern highbush cultivars that show high promise, 'Aurora', 'Draper' and 'Liberty'. Mark Ehlenfeldt of the USDA programme in New Jersey is focusing on identifying genotypes with high disease resistance and tolerance to winter cold, and has released several cultivars including 'Chanticleer' and 'Hannah's Choice'. Nicholi Vorsa at the Cranberry and Blueberry Research Station of Rutgers University has begun a programme in New Jersey to develop locally adapted highbush cultivars with machine harvestability and high fruit quality. Chad Finn of the USDA in Oregon is active in identifying genotypes that are well suited to the Pacific Northwest. Narandra Patel developed the HoriResearch Inc. programme in New Zealand into a major programme and Jessica Scalzo is currently leading that effort. Other worldwide northern highbush breeding projects include Berry Blue in Michigan and Chile (Ed Wheeler), Fall Creek Farm and Nursery in Oregon (Peter Boches), Driscoll Associates in California and Washington (Bruce Mowrey), the University of Talca (Gustavo Lobos, Jorge Retamales and Peter Caligari) and Vital Berry in Chile (Enrique Acevedo).

BLUEBERRY BREEDING GOALS

Fruit and flowering characteristics

Among the most important characteristics being sought after by blueberry breeders are flavour, large size, light blue colour (a heavy coating of wax), a small scar where the pedicel detaches, easy fruit detachment for hand or machine harvest, firmness and a long storage life (Hancock et al., 2008). Most people prefer a sweet, crunchy fruit with a trace of acidity; however, high-acid fruit tend to store longer than low-acid ones. The best compromise is to develop varieties with high sugar and moderate amounts of acid. Other important fruit characteristics are uniform shape, size and colour, high aroma and the ability to retain texture in storage. Much genetic improvement has been made in all of these traits through conventional breeding. V. darrowii has been a particularly important source of powder blue colour, intense flavour and fruit that remain in good condition in hot weather.

Interest is growing in the antioxidant capacity of blueberry fruit, although little breeding has been undertaken for this trait (Hancock et al., 2008). Blueberries are among the most antioxidant-rich fruit crops. Genetic improvement could be rapid, as considerable amounts of variability have been observed in this trait.
Plant architecture

The most sought-after bush habit is one that is upright, open and vase-shaped, with a bush height of 1.5 to 2.0 m and a modest number of renewal canes. This is the ideal bush shape for both hand and mechanical harvest. Many cultivars have been developed that meet this ideotype. In general, plant height appears to be quantitatively inherited, although the short stature of *V. angustifolium* and *V. darrowii* can be dominant to highbush in many interspecific crosses. High percentages of dwarf plants are found in many southern highbush breeding populations.

Another common breeding goal is to identify genotypes that can be easily picked, with open fruiting clusters and fruit that are well separated. Long pedicels and peduncles are the major components of this feature. There is considerable genetic variability for this characteristic in the current highbush breeding populations, but Paul Lyrene in Florida has also found the wild species *Vaccinium arboretum* to also be a valuable donor of this characteristic.

Physiological adaptations

Expanding the range of adaptation of the northern highbush blueberry by reducing its chilling requirement has been an important breeding goal for over 50 years (Hancock et al., 2008). This has been successfully accomplished by incorporating genes from the southern diploid species *V. darrowii* into *V. corymbosum* via unreduced gametes, although hybridizations with native southern *V. corymbosum* and *V. ashei* have also played a role. Cultivars are now available with an almost continuous range of chilling requirements, from 0 to 1000 h. The genetics of the chilling requirement has not been formally determined; however, segregation patterns suggest that it is largely quantitatively inherited with the low chilling requirement showing some dominance.

Most blueberry breeding programmes are working on expanding the harvest season. Earliness is at a particular premium in the southern parts of the USA, Spain, Argentina and north-central Chile, while lateness is extremely important in Michigan and the Pacific Northwest. Increases in earliness have been successfully achieved by selecting for earlier bloom dates and shorter ripening periods, while lateness has been increased primarily by selecting individuals with very slow rates of fruit development. Bloom date is strongly correlated with ripening date, but early-ripening cultivars have been developed that have later-than-average flowering dates such as ‘Duke’ and ‘Spartan’.

Winter cold often causes severe damage to blueberry flower buds and young shoots in the colder production regions. In general, northern highbush types survive much colder mid-winter temperatures than southern highbush cultivars, although considerable variability within groups exists that has been exploited by breeders.
Spring frosts commonly damage flower buds in most production regions. The stage of floral development when a frost occurs appears to be much more important than relative bud hardiness. Those cultivars with late bloom dates tend to suffer less frost damage than those flowering earlier because frosts are less common later in the season. As previously mentioned, breeders have produced a number of early-ripening cultivars with later bloom dates that can avoid frosts.

A major focus of many blueberry breeders has been adaptation to heat. Most blueberry species are negatively impacted by high temperature and drought; however, southern highbush are generally superior to northern highbush. Breeders have had some success in producing more heat-tolerant cultivars, although the hottest temperatures of summer still have a major impact on the storage life of harvested fruit in all areas of blueberry production.

Among the other abiotic factors limiting blueberries, high pH and tolerance to mineral soils are very important. The Vaccinium are ‘acid-loving’ and as such generally require soils below pH 5.8 for high vigour. Most blueberry breeders have not focused on this characteristic, even though a number of interspecific hybrids have been generated by Arlen Draper and Jim Ballington that have considerable upland adaptations.

**Pest resistance**

The most important problems in highbush and rabbiteye blueberry are mummy berry (*Monilinia vaccinii-corymbosi* (Reade)), blueberry stunt phytoplasma, *Blueberry shoestring virus*, *Blueberry shoot virus (BlShV)*, *Tomato ringspot virus (TmRSV)*, *Blueberry scorch virus (BlScV)*, stem blight (*Botryosphaeria dothidea* (Moug.: Fr.) Ces and de Not.), stem or cane canker (*Botryosphaeria corticis* Demaree and Wilcox), *phytophthora root rot* (*Phytophthora cinnamomi* Rands), *phytophthora canker* (*Phomopsis vaccinii* Shear), and botrytis (*Botrytis cinerea* Pers.: Fr.) and anthracnose fruit rots (*Colletotrichum gloeosporioides* (Penz.) Penz. and Sacc.). Resistant or tolerant cultivars have been produced for most of the fungal diseases in highbush blueberries; however, only limited sources of resistance have been found to most virus diseases. See Chapter 8 for more detailed descriptions of cultivar resistances.

The most important insect and arthropod pests of highbush and rabbiteye blueberries include the blueberry maggot (*Rhagoletis pomonella* Walsh), blueberry gall midge (*Dasineura oxyacocca* Johnson), blueberry bud mite (*Acaditus vaccinii* Kefler), flower thrips (*Frankliniella* ssp.), Japanese beetle (*Popillia japonica* Newman), sharp-nosed leaf hopper (stunt vector) (*Staphytopius magdalenis* Prov.), blueberry aphid (*shoestring and blueberry scorch virus vector*) (*Illinoia pepperi* Mac. G.), cranberry fruit worm (*Acrobasis vaccinii* Riley), cherry fruit worm (*Grapholita packardi* Zell) and the plum
Little variation in resistance has been reported to most of these pests in Vaccinium, except for sharp-nosed leaf hopper, blueberry aphid, bud mite and gall midge. See Chapter 8 for more detailed descriptions of cultivar resistances to these pests.

USE OF NATIVE GERMPLASM RESOURCES IN BLUEBERRY BREEDING

Interspecific hybridization within Vaccinium section Cyanococcus has played a major role in the development of highbush blueberries. Most species with similar chromosome numbers freely hybridize and crosses between species with different chromosome numbers are frequently successful, through unreduced gametes. Even pentaploid hybrids of diploid × hexaploid crosses have been shown to cross relatively easy to tetraploids.

Numerous interspecies crosses have been made by breeders within section Cyanococcus including (Lyrene and Ballington, 1986; Hancock et al., 2008): (i) tetraploid V. corymbosum × tetraploid V. angustifolium; (ii) tetraploid Vaccinium myrsinites Lam. × tetraploid V. angustifolium and V. corymbosum; (iii) colchicine-doubled diploid hybrids of Vaccinium myrtillusoides Michx. × tetraploid V. corymbosum; (iv) diploid V. darrowii × hexaploid V. ashei, hexaploid V. constablaei × tetraploid V. corymbosum and hexaploid V. ashei; and (v) diploid V. elliottii × tetraploid highbush cultivars. Probably the most widely employed interspecific hybrid has been ‘US 75’, a tetraploid derived from the cross of diploid V. darrowii selection ‘Fla 4B’ × tetraploid highbush cultivar ‘Bluecrop’ (Fig. 2.1). In spite of its being a hybrid of an evergreen, diploid species crossed with a deciduous, tetraploid highbush, ‘US 75’ is completely fertile and is the source of the low chilling requirement of many southern highbush cultivars.

A number of important characteristics have been associated with the various native species (Ballington, 1990, 2001; Luby et al., 1991; Galletta and Ballington, 1996; Lyrene, 2008). V. angustifolium is known for its winter hardiness, early ripening, blossom frost tolerance, adaptation to high pH, stem blight and phytophthora root rot resistance, light blue fruit colour, small scar, high soluble solids and low acidity. V. ashei possesses drought tolerance, low chilling requirement, upright plant habit, late ripening, long flowering to ripening period, fruit firmness, small scar, loose fruit cluster, cane canker, stem blight and phytophthora root rot resistance and resistance to sharp-nosed leaf hopper. V. constablaei has strong winter hardiness, high chilling requirement and a light blue fruit colour. V. darrowii has a low chilling requirement, heat tolerance, resistance to mummy berry, adaptation to high pH, tolerance to mineral soils, late flowering, late ripening, long flowering to ripening period, fruit firmness, excellent complex flavour, small scar, light blue fruit colour, fruit that hold well in heat, high soluble solids and low acidity, and a loose fruit that cluster. V. elliottii has drought tolerance, adaptation to high pH, tolerance
to mineral soils, low chilling requirement, upright plant habit, late flowering, early ripening, upright habit, small fruit scar, excellent flavour, cane canker, stem blight and phytophthora root rot resistance and resistance to sharp-nosed leaf hopper. *V. myrsinites* has low chilling requirement, small scar, low acidity and firm fruit. *Vaccinium myrtilloides* has strong winter hardiness, early ripening, blossom frost tolerance, resistance to mummy berry, small scar, high soluble solids and low acidity.

Many of the highbush types now being released are complex hybrids. Some of the most dramatic examples are ‘O’Neal’ which contains genes from four species (*V. corymbosum*, *V. darrowii*, *V. ashei* and *V. angustifolium*) and ‘Sierra’ which possesses the genes of five species (*V. corymbosum*, *V. darrowii*, *V. ashei*, *V. constablaei* and *V. angustifolium*). ‘Biloxi’ contains the genes from five taxa (*V. corymbosum* (diploid and tetraploid), *V. darrowii*, *V. ashei* and *V. angustifolium*), and has fewer *V. corymbosum* genes than non-*V. corymbosum* genes in its genome.

Intersectional crosses have generally proved difficult, although partially fertile hybrids have been derived from *Vaccinium tenellum* Ait. and *V. darrowii* × *Vaccinium stamineum* L., *V. darrowii* and *V. tenellum* × *Vaccinium vitis-idaea*, *V. darrowii* × *Vaccinium ovatum* Pursh, *Vaccinium arboreum* Marshall and *V. stamineum*, tetraploid *Vaccinium uliginosum* × highbush cultivars, (*V. darrowii* × *V. arboreum*) × highbush cultivars, and colchicine-doubled *V. arboreum* × highbush cultivars (Hancock et al., 2008). Of all these wide species crosses, those containing *V. arboreum* are probably the most interesting as this species is known for its drought tolerance, adaptation to basic, mineral soils, open

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**Fig. 2.1.** Morphological differences in hybrids of *Vaccinium darrowii* and *Vaccinium corymbosum*: (a) *V. corymbosum*; (b) backcross hybrid; (c) F₁ hybrid (‘US 75’); (d) *V. darrowii*. 
flower clusters, upright bush habit, stem blight resistance and resistance to sharp-nosed leaf hopper. Lyrene has produced numerous fertile F₁ hybrids of *V. arboretum* × *V. corymbosum*.

**BREEDING TECHNIQUES**

Blueberries are asexually propagated through cuttings and tissue culture, so elite genotypes can be directly utilized without the need to develop pure lines. Self-pollinations are rarely used in *Vaccinium* breeding due to reduced seed set and germination, and because seedlings from selfing tend to be weak. Most breeding programmes have relied primarily on pedigree breeding where elite parents are selected each generation for intercrossing. The Florida southern highbush and rabbiteye breeding programmes have relied on recurrent selection.

In most northern highbush breeding programmes, evaluation begins two years after planting and selections are made over the next two years. Traditionally, the selected seedling plants were dug and moved to further spacing distances and evaluated for another year or two, before the most elite types were propagated and tested in rows of 25 to 50 plants for several years. The most promising selections from this row trial were then again propagated and tested in small numbers (five to ten plants) in replicate designs across multiple sites. The whole process took from 15 to 20 years for release of a new cultivar from the original cross. One problematic issue in the selection process of highbush cultivars for large commercial plantings of one genotype is the self-fruitness of a selection. Inherently, breeders' trials are heterogeneous in the composition of genotypes, selections and standards being tested, which usually facilitates the opportunity for cross-pollination resulting in a quite different environment than that of commercial plantings.

An accelerated programme is now being conducted by Michigan State University where the selected plants in the original planting are propagated and tested directly in replicated plantings at multiple sites. It is expected that about 1% of the progeny plants will go into this trial. After 3–5 years, the elite types will be released as cultivars. It is hoped that this approach will speed the release time to 8 to 10 years, even though it will result in the final testing of a larger number of ultimately rejected genotypes.

Most breeding programmes set the plants at spacings of about 60 cm apart in the row, although many use a higher density, with the extreme being the Florida breeding programme which does its primary selections in a ‘fruiting nursery’ at much closer spacings of 10,000 to 15,000 seedlings in a 0.2 ha field nursery. In the close-spaced southern highbush programme, the first selections are made within 12 months of planting (Stage I). Ninety per cent of the seedlings are removed and the remaining plants are left in place for three more years (Stage II). Each year they are evaluated for possible
advancement to Stage III, with about 300 selections being advanced each year into 15-plant plots. These plantings are observed for 10 years, with about 15 clones being selected each year and propagated for planting at multiple locations in larger plots (Stage IV). Cultivars are ultimately selected from these blocks at a rate of about one genotype from each Stage IV test (Lyrene, 2008). The fastest moving varieties can go through this system in 10 to 12 years, although many are evaluated for much longer.

**BIOTECHNOLOGICAL APPROACHES TO BLUEBERRY GENETIC IMPROVEMENT**

**Micropropagation**

Blueberries are now routinely micropropagated for commercial sale using tissue culture techniques (Hancock et al., 2008). Axillary meristems are used as explants. The basic micropropagation steps include surface sterilization, proliferation and rooting. Lloyd and McCown’s (1980) woody plant medium (WPM) or modified WPM is the most important basal medium used for all *Vaccinium* species. The cytokinins, 6-(γ-γ-dimethylallylamino)-purine (2iP) and zeatin, are generally used for shoot proliferation. Most *Vaccinium* cultures are maintained at 20–25°C under a 16-h photoperiod of 10–75 μmol/m²/s. Rooting is generally done under mist in the greenhouse or in covered flats.

**Genetic linkage maps**

The first genetic maps of blueberries are beginning to emerge that will set the groundwork for marker-assisted breeding. Rowland’s group at the USDA-ARS in Beltsville, Maryland, developed the first blueberry map using a diploid population segregating for chilling requirement (Rowland and Levi, 1994). Their population was a cross between an F₁ interspecific hybrid (*V. darrowii* × *V. elliottii*) and another clone of *V. darrowii*. They have continued to periodically add markers and, at last report, the map had 72 randomly amplified polymorphic DNA (RAPD) markers mapped to 12 linkage groups, which is in agreement with the basic chromosome number of blueberry. Later, her group constructed RAPD-based maps of diploid *V. corymbosum* (*Vaccinium caesariense* Mack.) × *V. darrowii* hybrids crossed with other *V. darrowii* and *V. corymbosum* selections. The goal was to develop populations that were segregating for chilling requirement and cold tolerance. First RAPD and more recently simple sequence repeat (SSR) (Rowland *et al.*, 2003a; Boches *et al.*, 2005, 2006) and expressed sequence tag (EST) PCR markers were added to this map. A qualitative trait locus (QTL) was identified that explained about 20% of the genotypic variance associated with cold hardiness (Rowland *et al.*, 2003b).
Hancock's group at Michigan State University constructed an RAPD-based genetic map of a tetraploid population resulting from the cross of 'US 75' × tetraploid V. corymbosum, 'Bluecrop' (Qu and Hancock, 1997). One hundred and forty markers were mapped to 29 linkage groups. The map was essentially that of V. darrowii, as 'US 75' was produced from an unreduced gamete of V. darrowii and only unique markers for 'Fla 4B' were used. 'Fla 4B' was one of the V. darrowii clones used by Rowland's group.

Most recently, a major research initiative has been spearheaded by Lisa J. Rowland, Nahla Bassil, Julie Graham and Jim Hancock to develop a linkage map of the tetraploid cross 'Jewel' (southern highbush) × 'Draper' (northern highbush), as part of a grant 'Generating Genomic Tools for Blueberry Improvement' funded through the Specialty Crop Research Initiative (SCRI) of the USDA (Brevis et al., 2007; Rowland et al., 2011).

Genomic resources

The first few thousand ESTs have been generated and made publicly available for the Ericaceae family, about 5000 from blueberry and about 1200 from rhododendron (Rowland et al., 2008, 2011). These ESTs from blueberry and rhododendron were generated as parts of projects focused on cold acclimatization research, and the ESTs are from non-acclimatized and cold-acclimatized flower bud libraries in the case of blueberry (Dhanaraj et al., 2004, 2007) and from non-acclimatized and cold-acclimatized leaf libraries in the case of rhododendron (Wei et al., 2005). Another ~16,000 ESTs have been generated from blueberry fruit by the New Zealand Institute for Plant & Food Research Ltd (formerly HortResearch Inc.), but they are not publicly available.

As part of the SCRI project mentioned above, there is an ongoing effort to: (i) generate more ESTs from different blueberry organs, such as fruit, flower buds, leaves and stems; (ii) develop EST-PCR and SSR markers based on these ESTs; and (iii) use these markers to map QTLs for chilling requirement, cold hardiness and fruit quality in diploid and tetraploid mapping populations (the tetraploid population is an actual breeding population) (Rowland et al., 2011). The project will also conduct genetic diversity studies on wild populations of the commercial lowbush blueberry, and examine the evolutionary relationships of the Vaccinium species within section Cyanococcus.

Recombinant DNA techniques

Two groups have reported on the transformation of blueberry using Agrobacterium (Graham et al., 1996; Song and Sink, 2004). The screenable reporter gusA driven by either the cauliflower mosaic virus (CaMV) 35S or a
chimeric super promoter \((Aocs)_3AmasPmas\), and each terminated by T-nos, has been transformed into blueberry cultivars using nptII as a selectable marker (Ni et al., 1995; Graham et al., 1996; Song and Sink, 2004). After selection with the herbicide GS, three chimeric bar genes with the promoter nopaline synthase (nos), CaMV 35S or CaMV 34S yielded transgenic plants; whereas the synthetic \((Aocs)_3AmasPmas\) super promoter did not lead to successful regeneration of transgenic plants. The herbicide Rely (Bayer CropScience) was applied at five levels using a track sprayer (GS in mg/l: 0, 750, 1500, 3000 and 6000) on 3-month-old plants in the laboratory, representing three separate transgenic events each for the 35S and nos promoters. Evaluations of leaf damage 2 weeks after spraying indicated that all transgenic plants exhibited much higher herbicide resistance than non-transgenic plants. After application of eight times the standard level of GS (6000 mg/l) in the field, over 90% of the leaves on transgenic plants with the 35S-bar showed no symptoms of herbicide damage, whereas 95% of the leaves on non-transgenic plants were abscised. Transgenic plants with 35S-bar showed higher herbicide resistance than those with nos-bar, in which 19.5 to 51.5% of the leaves had no damage (Song et al., 2007, 2008).

Most recently, a CBF/DREB transcription factor gene identified from \(V. corymbosum\) and posted in GenBank (FJ222601) has been transformed into the relatively cold-sensitive highbush blueberry ‘Legacy’. Over 60 independent transgenic events have been produced (G.-Q. Song, unpublished results). The preliminary indications are that over-expression of CBF will improve the cold tolerance of leaves and perhaps flower buds in this cold-sensitive, southern blueberry cultivar.

**PATENTING AND LICENSING**

Currently, all new blueberry cultivars are being patented and licensed. What is called the 'plant patent' is being used in the USA and applies to plants that can be asexually reproduced (and cannot be reproduced by seed). In the Townsend-Purnell Plant Patent Act of 1930 it is stated that:

Whoever invents or discovers and asexually reproduces any distinct and new variety of plant, including cultivated sports, mutants, hybrids, and newly found seedlings, other than a tuber propagated plant or a plant found in an uncultivated state, may obtain a patent therefore, subject to the conditions and requirements of this title.

An amendment was made to the Plant Patent Act in 1998 that adds:

In the case of a plant patent, the grant shall include the right to exclude others from asexually reproducing the plant, and from using, offering for sale, or selling the plant so reproduced, or any parts thereof, into the US.
It has been suggested that such 'plant parts' includes gametes, and as a result, patented cultivars cannot be used in breeding by anyone except the inventor. However, this issue has not been challenged legally and thus is unresolved. This revision also restricts the importation of plant parts from patented cultivars into the USA.

The international protection offered for blueberries is termed 'plant breeders' rights'. The International Union for the Protection of New Varieties of Plants was established by the UPOV (Union internationale pour la protection des obtentions végétales) Convention in 1961 (with additional Conventions following in 1978 and 1991 providing additional provisions), and the UPOV system provides for cultivar protection using plant breeders' rights in 65 member countries. Plant breeders' rights have no restriction on breeding activity using a protected cultivar.

Both general and restricted licences have been awarded to nurseries for the propagation and sale of patented cultivars. General licences are generally made available to a group of companies without territorial limitations, while restricted licences are awarded to only one or a few companies by territory. In a few instances, partnerships have been developed prior to licensing that include trialling of advanced selections before cultivar release. In these trialling arrangements, a number of nurseries spanning the range of likely cultivar adaptation have been awarded testing rights and are required to provide production and quality data.

Both plant royalties and production royalties have been paid for blueberry varieties. In the plant royalties, a set fee is paid per plant that is generally passed on to the grower by the propagator. This is the standard practice so far with blueberries, and ranges from US$0.20 to 0.30 per plant. In the production royalties, the grower or fruit production company pays a royalty based on fruit produced or more often on the sales price of the fruit. This has been done in a few instances. Plant rental fees and plant production area fees have been discussed but have not been implemented yet.

**CHARACTERISTICS OF THE MOST IMPORTANT BLUEBERRY CULTIVARS GROWN WORLDWIDE**

**Most popular southern highbush cultivars**

‘Emerald’ (1991 – Florida) is early with a chilling requirement of ~250 h. Bush is spreading, vigorous and highly productive, although leaf bud break can be poor in spring. ‘Emerald’ has a very early bloom date which can be subject to frost. Berries are very large, firm, medium blue with a medium scar and excellent flavour. Resistant to cane canker and stem blight. Popular in south Florida, Georgia and California.
‘Jewel’ (1998 – Florida) is early mid-season with a chilling requirement of ~200 h. Bush is slightly spreading and very vigorous. ‘Jewel’ can be slow to leaf in spring and is highly subject to foliar diseases. Berries are large, moderately firm and light blue, with a small scar and slightly tart flavour. Resistant to cane canker and stem blight, although it flowers heavily and can overbear. Popular in south Florida, Chile and California.

‘Legacy’ (1988 – USDA) is late mid-season with a chilling requirement of ~400–600 h. Bush is upright and very vigorous with only modest winter hardiness. ‘Legacy’ has medium to large sized fruit that are powder blue in colour with good flavour, firmness and scar. Machine harvests well. Widely planted in areas with mild and moderate winter climates.

‘Misty’ (1989 – Florida) is mid-season with a chilling requirement of 150 h. Bush is slightly spreading and very vigorous. Leaf bud break in spring can be poor, but responds well to Dormex. Picking season is long and bush needs to be heavily pruned to avoid over-bearing. Berries are medium sized and very firm, with a small scar and mild flavour. Widely planted in California and locally important in Chile.

‘O’Neal’ (1987 – North Carolina) is early with a chilling requirement of ~400 h. Bush is erect, but slightly spreading. Berries are large sized, firm, sweet and medium blue in colour. Early blooming and subject to frost. Resistant to stem canker. Locally important in North Carolina, California, Georgia, Chile and Argentina, but its popularity is waning.

‘Ozarkblue’ (1996 – Arkansas) is a late season cultivar with a chilling requirement of 600–800 h. Bush is vigorous and upright. Berries are medium to large, light coloured, small scar, firm and sweet. Widely planted in areas with mild and moderate climates, although diminishing in popularity.

‘Star’ (1981 – Florida) is early with a chilling requirement of ~400 h. Bush is upright and slightly spreading with moderate vigour. Leaves well in spring. Blooms later than ‘O’Neal’ but is harvested at about the same time. Berries are large and medium blue with good firmness, a small scar and good flavour. Excellent postharvest fruit quality. Fruit can crack after heavy rains. Widely planted in Florida, Georgia and California and Chile.

Other locally important southern highbush cultivars

‘Biloxi’ (1998 – Mississippi) is early with a chilling requirement below 500 h. It may be adapted to evergreen culture with very little chilling. Plant habit is bushy with high vigour and productivity. Berries are small to medium sized, with only a medium scar, light blue, very firm and well flavoured. Popular in Mexico for evergreen culture.

‘Millennia’ (1986 – Florida) is early with a chilling requirement of ~300 h. Bush is spreading, vigorous and very productive. Slow to leaf in spring. Berries are large and firm with a tiny scar, medium blue colour and a mild flavour. Locally important in Florida and Georgia.
'Sapphire' (1980 – Florida) is early with a chilling requirement of ~200 h. Bush is semi-spreading and its vigour is medium. Leaf bud break in spring is good. Berries are medium sized, light blue, very firm with a small scar and excellent flavour. Not widely planted.

'Sharpblue' (1976 – Florida) is early with a chilling requirement below 150 h. It has been successfully grown in evergreen culture. Bush is slightly spreading and extremely vigorous. Berries are very large with only medium scar, colour and firmness; flavour is excellent. Fruit quality is sensitive to hot temperatures. Once popular in Florida, but no longer planted.

'Windsor' (2000 – Florida) is early mid-season with a chilling requirement of 300–500 h. Bush is spreading and vigorous. Leaf bud break in spring is very good. Berries are large, firm and good flavoured, but scar is wet and tears. Not widely planted.

Newly released southern highbush cultivars

'Abundance' (2006 – Florida) is early mid-season with a chilling requirement of ~300 h. Bush is upright, very vigorous and leafs out well in spring. Very high yield potential. Berries are large, medium blue, crisp textured and excellent tasting with a small, dry scar.

'Alba' (2009 – Spain) is mid-season with a very low chilling requirement. Fruit are attractive, firm, light blue with a mild acid flavour. Plant is evergreen, requires cross-pollination and displays a generally upright growth habit.

'Arlen' (2000 – North Carolina) is late with a chilling requirement of ~700 h and only modest winter hardiness. Bush is upright and vigorous with good self-fertility. Fruit are large, light blue and firm with good flavour and scar. Sister to 'Ozarkblue'.

'Beauford' (2005 – North Carolina) is late mid-season with a chilling requirement of 600–700 h. Bush is very vigorous and may be adapted to machine harvest for the fresh market. Only modest winter hardiness. Needs a pollinizer. Fruit are medium sized with good colour, scar, firmness and flavour. Sibling of 'Craven', 'Lenoir' and 'Pamlico'.

'Bluecrisp' (1997 – Florida) is mid-season with a chilling requirement of 500–600 h. Bush is slightly spreading, moderately vigorous and leafs out well in spring. Production is average with some autumn blooming. Little winter hardiness. Berries are medium sized, extremely firm with a medium blue colour and small scar. Flavour is excellent, having a crisp texture.

'Camellia' (2005 – Georgia) is early mid-season with a chilling requirement of 450–500 h. Bush is upright with moderate to high vigour and only modest winter hardiness. Berries are large, sky blue, firm with an excellent flavour and small picking scar.

'Cartaret' (2005 – North Carolina) is late mid-season with a chilling requirement of 600–800 h. Upright bush that may be adapted to mechanical
harvest for the fresh market. Has only modest winter hardiness. Fruit are small, firm, well flavoured with good colour and an excellent scar.

‘Celeste’ (2010 – Spain) is mid-season, evergreen with a very low chilling requirement. Bush is upright and vase-shaped with high vigour. Berries are light blue with excellent flavour and long postharvest fruit quality. Cross-pollination is not needed. It performs well in a wide range of soil types.

‘Corona’ (2009 – Spain) is mid-season with a very low chilling requirement. Fruit are extremely large, attractive, medium–dark blue and have a medium scar and good flavour. Plant is evergreen, vase-shaped, very vigorous, and grows well in a wide array of soil types. It requires cross-pollination.

‘Craven’ (2003 – North Carolina) is early mid-season with a chilling requirement of 600–700 h. May be machine harvestable for the fresh market. Bush is upright and vigorous. Leaves show some variegation. Self-fruitful. Only modest winter hardiness. Fruit are small to medium sized, moderately firm, powder blue, have a good flavour with a small picking scar.

‘Dolores’ (2009 – Spain) is mid-season with a very low chilling requirement. It has a very large berry that is dark blue with medium firmness, medium scar and mild flavour. Its corollas tend to stay attached to the fruit.

‘Dixiblue’ (2005 – USDA/Mississippi) is mid-season with a chilling requirement of ~500 h. Bush is vigorous, moderately spreading with limited cold hardiness. Berries are medium to large with good colour, picking scar, flavour and firmness.

‘Farthing’ (2008 – Florida) is early with a chilling requirement of ~300 hours. Bush is slightly spreading, vigorous and high yielding. It leafs well in spring and is late blooming. Fruit are medium to large sized with good colour, slightly tart flavour and small scar.

‘Flicker’ (2010 – Florida) has a chilling requirement of ~200 h. It is adaptable to early-season, deciduous or evergreen production. It has had problems with leafing in some years. Fruit are large, light blue, sweet and very firm, and have a small, dry picking scar and a long storage life. The fruit clusters are very loose. It has above-average resistance to root rot (P. cinnamomi), average resistance to stem blight (Botryosphaeria spp.) and has shown no signs of cane canker (B. corticis).

‘Lupton’ (2005 – Mississippi) is mid-season with a chilling requirement of ~500 h. Bush is vigorous and upright. Fruit are medium to large with good colour, firmness, flavour and picking scar.

‘Kestrel’ (2010 – Florida) ripens very early and has high evergreen fruiting potential. The fruit are large, firm, aromatic and sweet, even at early stages of ripening. The berry clusters are medium loose and the fruit are easily detached.

‘Lenoir’ (2003 – North Carolina) is mid-season with a chilling requirement of 600–700 h. Semi-upright with only moderate winter hardiness, it may be adapted to machine harvest for the fresh market. Berries are small to medium sized with good colour, firmness and flavour (tart) and a small picking scar. Sibling of ‘Beauford’, ‘Craven’ and ‘Pamlico’.

‘Lucero’ (2009 – Spain) is mid-season with a very low chilling require-
ment. The fruit are attractive, light blue, round and well flavoured, in compact clusters. Berries are well adapted to mechanical harvest. The plant is self-fertile and evergreen with an upright growth habit.

‘Lucia’ (2009 – Spain) is late-season with a very low chilling requirement. Its fruit are attractive, firm and light blue, with an excellent sweet flavour. The plant has a vase-shaped growth habit and defoliates during the winter. Cross-pollination is required. It is best grown in well-drained soils outside tunnels.

‘Meadowlark’ (2010 – Florida) is extremely early-ripening, upright, with a very low chilling requirement. Produces very open clusters of berries that detach with medium force. It may have potential for mechanical harvesting. Fruit have a mild flavour with a good balance of sugar and acid, and the mature berries maintain quality for a long time when hanging on the plant.

‘New Hanover’ (2005 – North Carolina) is early mid-season with a chilling requirement of 600–800 h. Good self-fruitfulness. Upright, but can be floppy with heavy crop. Berries are medium to large, firm with excellent colour. Flavour is a little tart and the scar is small but can tear.

‘Palmetto’ (2003 – Georgia/USDA) is early with a chilling requirement of 300–450 h. Bush is open and spreading with medium vigour. Blooms very early so it may need frost protection and it has only modest winter hardiness. Berries are medium sized and medium blue with good firmness, good flavour and a medium scar.

‘Pamlico’ (2003 – North Carolina) is early mid-season with a chilling requirement of ~600 h. An upright bush that may be adapted to machine harvest for the fresh market, it has only modest winter hardiness. Fruit are small to medium sized with a small scar, excellent colour, medium firmness and good flavour. Sibling of ‘Beauford’, ‘Craven’ and ‘Lenoir’. Resistant to stem blight.

‘Primadonna’ (2007 – Florida) is very early with a chilling requirement of ~200 h. Bush is upright and round with medium vigour. It may leaf out poorly in the spring. Berries are large, firm and medium blue with excellent flavour. Fruit size can be irregular.

‘Rebel’ (2006 – Georgia) is very early with a chilling requirement of 400–450 h. Bush is spreading and vigorous. Leaks well following mild winters. Berries are very large, medium light blue and very firm with a bland flavour.

‘Rocio’ (2009 – Spain) is very early with a very low chilling requirement. Its fruit are attractive, medium sized, medium blue in colour, extremely firm and exhibit a pleasant balance of acid and sweetness. The plant is evergreen, self-fertile and has an upright growth habit.

‘Sampson’ (1998 – North Carolina) is mid-season with a chilling requirement of 600–800 h. Bush is vigorous, very productive and semi-upright. Fruit are large and medium blue with modest firmness, mild flavour and a small scar. Tendency to overcrop.

‘San Joaquin’ (2008 – Florida) is early ripening with a chilling requirement of 400–500 h. Bush is very vigorous and upright. Fruit are large, sweet and firm with good colour and an excellent picking scar. It is more upright than ‘Star’ with a higher yield potential.
‘Santa Fe’ (1999 – Florida) is early with a chilling requirement of ~600 h. Little winter hardiness. Bush is upright and vigorous. Leaf bud break in spring is good. Berries are large, light blue and medium firm with a small scar and sweet flavour. Late blooming and may be adapted to machine harvest.

‘Scintilla’ (2008 – Florida) is very early with a chilling requirement of ~200 h. Bush is upright, vigorous with modest yields and an early blooming date. Fruit are large, light blue and firm, with a small scar and good flavour.

‘Sebring’ (2003 – Florida) is very early with a chilling requirement of 200–300 h. Bush is upright with moderate vigour. Leaves well after mild winters and has long flower to ripening interval. Berry is medium to large and dark blue with good scar, firmness and flavour. Resistant to stem blight.

‘Sevilla’ (2009 – Spain) is late-season with a very low chilling requirement. It has an open-round, somewhat sprawling growth habit and defoliates during the winter. Plant requires cross-pollination. Fruit are large, light blue and have an aromatic sweet flavour. It is recommended for dry climates outside tunnels.

‘Snowchaser’ (2007 – Florida) is very early with a chilling requirement at 200 h or less. Bush is upright and round with medium vigour. It tends to flower in autumn and blooms very early in the spring when frost is likely. Berries are medium sized, firm, medium blue with good flavour and a tiny scar. It is highly susceptible to stem blight.

‘Southern Belle’ (2002 – Florida) is early with a chilling requirement of 400–600 h. Leaf bud break in spring is fair, but improved with Dormex. Bush is spreading and vigorous when healthy, but is very susceptible to phytophthora fruit rot. Berries are large, very firm and medium blue in colour with a small scar and good flavour.

‘Southmoon’ (1996 – Florida) is mid-season with a chilling requirement of ~500 h. Bush is upright with medium vigour. Leaf buds break well in spring. In Florida, mortality has been a problem, but in California it has done well and appears to be highly productive. Berries are very large, sky blue and firm, with a small scar and excellent flavour.

‘Springhigh’ (2005 – Florida) is very early with a chilling requirement of ~200 h. Strong upright growth and leafs well in spring. Berries are large, dark blue, medium firm with a small scar and good flavour. Berries can get soft in hot weather.

‘Springwide’ (2006 – Florida) is early with a chilling requirement of ~200 h. Bush is somewhat spreading, vigorous and may overcrop. Leaf buds break well in spring. Berries are large, firm and well flavoured, with medium colour and a good scar.

‘Summit’ (1998 – North Carolina, Arkansas) is late mid-season with a chilling requirement of ~700 h. Bush is moderately vigorous and semi-upright. Fruit are large, light blue, firm and flavourful with an excellent scar. Sibling of ‘Ozarkblue’.

‘Suziblue’ (2009 – Georgia) is early with a chilling requirement of 400–450 h. Bush is spreading and vigorous. Leaf well after warm winters,
although it holds some leaves through winter. Berries are large, firm and have

good flavour, along with light blue colour and a small scar.

‘Sweetcrisp’ (2007 – Florida) is early with a chilling requirement of ~200 h. Bush is upright, fast growing and leafs out early in spring. May be well adapted to machine harvest. Berries are medium sized with excellent firmness, flavour and scar. Texture is crisp.

**Most popular northern highbush cultivars**

‘Aurora’ (2003 – Michigan) is very late with a chilling requirement >800 h. Vigorous and bushy with high productivity and excellent winter hardiness. Berries are large, light blue, firm with a tiny scar and slightly tart flavour. New variety that is being widely planted in cold winter climates for its late season.

‘Bluets’ (1952 – New Jersey) is mid-season with a chilling requirement >800 h. Bush is upright but flops when carrying a heavy crop. High yielding with good winter hardiness. Berries are medium sized and firm, with a small scar. Most widely planted variety, although its popularity is diminishing.

‘Croatan’ (1954 – North Carolina) is early with a chilling requirement >800 h. Very productive, erect bush with only medium fruit quality and modest winter hardiness. Fruit are soft with a mild flavour and ripen very quickly in hot weather. Resistant to stem canker. Important in North Carolina.

‘Draper’ (2003 – Michigan) is early mid-season with a chilling requirement >800 h. Upright, moderately vigorous bush with excellent winter hardiness. Fruit are large, light blue, very firm with excellent flavour, a tiny scar and superior shelf-life. Possible it can be mechanically harvested for the fresh market. New variety that is being widely planted in cold winter climates.

‘Duke’ (1986 – New Jersey/USDA) is very early with a chilling requirement >800 h. Bush is upright, open with good winter hardiness. Machine harvests well. Vigour declines over time without expert culture. Fruit are medium sized, firm, medium coloured with a small scar and weak flavour. Resistant to mummy berry. The most widely planted early cultivar in production regions with cold winters.

‘Elliot’ (1973 – Michigan/USDA) is late with a chilling requirement >800 h. Bush is upright, bushy with good winter hardiness. Fruit are medium sized, firm, medium blue with a tart flavour. Machine harvests well. Resistant to mummy berry, phomopsis canker and anthracnose fruit rot. It has been very widely planted because of its late season, but interest is diminishing.

‘Jersey’ (1928 – New Jersey) is late mid-season with a chilling requirement >800 h. Bush is tall, upright and very winter hardy. Berries are medium sized, dark and somewhat soft, with a moderate scar and a good flavour. Machine harvests well. Very broad soil adaptations. Locally important in Michigan, but little planted any more.
‘Liberty’ (2003 – Michigan) is very late with a chilling requirement >800 h. Upright, vigorous bush with excellent winter hardiness. Fruit are large, light blue and firm, with excellent flavour and a tiny scar. Probably machine harvestable. New variety being widely planted in all cold and moderate winter climates.

Other locally important northern highbush cultivars

‘Bluegold’ (USDA – 1988) is late mid-season with a chilling requirement >800 h. Bush is low growing with many branches and good winter hardiness. Berries are medium in size with small dry scars, good flavour and firmness. Machine harvests well. Not widely planted, but interest is growing.

‘Bluejay’ (1978 – Michigan) is early mid-season with a chilling requirement >800 h. Upright, open, rapidly growing bush that produces moderate yields of medium sized, firm fruit. Has small stem scar and mild, slightly tart fruit. Field resistance to shoestring virus. Locally important as a machine picked, processed berry.

‘Blueray’ (1959 – New Jersey) is early mid-season with a chilling requirement >800 h. Upright, spreading habit and is very winter hardy. Berries are large, dark blue, firm and of excellent flavour. May overproduce if not regularly pruned. Locally important, but not widely planted any more.

‘Bluetta’ (1968 – New Jersey/USDA) is very early with a chilling requirement >800 h. Bush is small, low growing and spreading. Produces moderate yields of medium sized, dark fruit. Flavour and firmness only fair and stem scar is broad. Resistant to phomopsis canker, but very susceptible to Botryosphaeria canker. Once widespread, but is not widely planted any more.

‘Brigitta’ (1980 – Australia) is late mid-season with a chilling requirement >800 h. Bush is upright with moderate winter hardiness. Berries are large, dark blue, firm and sweet with a small scar and long storage life. Machine harvests well. Locally important across the world in areas with mild winters.

‘Chandler’ (1994 – USDA) is late mid-season with a chilling requirement >800 h. Bush is spreading with good winter hardiness. Berries are large, dark blue with excellent flavour and a long ripening season. Locally important in the Pacific Northwest of North America for ‘pick-your-own’ and direct sales.

‘Coville’ (1949 – New Jersey) is late mid-season with a chilling requirement >800 h. Bush is moderately upright with limited winter hardiness. Has very large, dark fruit with a medium scar and a good, tart flavour. Little planted any more.

‘Darrow’ (1965 – USDA) is mid-season with a chilling requirement >800 h. Bush is low and bushy with only limited winter hardiness. Fruit are very large, light blue, firm and flavourful when fully mature. Locally important in the Pacific Northwest of North America for pick-your-own and farm sales.
‘Earliblue’ (1952 – New Jersey) is very early with a chilling requirement >800 h. Bush is vigorous, upright and moderately winter hardy. Fruit are medium sized with medium colour, firmness and flavour. Scar is medium and tends to hold fruit pedicel. Resistant to powdery mildew. Locally important in the Pacific Northwest of North America where earliness is at a premium.

‘Hardyblue’ or ‘1613A’ (early 1900s – New Jersey) is mid-season with a chilling requirement >800 h. Bush is upright and vigorous. Berries are medium sized, light blue and very sweet. Locally planted in the Pacific Northwest of North America as a machine-harvested, processed berry with an open fruit cluster and concentrated ripening.

‘Nelson’ (USDA – 1988) is mid-season with a chilling requirement >800 h. Bush is very productive, upright and very winter hardy. Berries are large, firm and good flavoured with a small picking scar. Machine harvests well. Not widely planted, but interest is growing in it as a pollinator of ‘Aurora’ and ‘Liberty’.

‘Nui’ (1989 – New Zealand) is very early with a chilling requirement >800 h. Bush is spreading with moderate vigour and medium yields. Good winter hardiness. Berries are very large and light blue with good firmness and excellent flavour. Locally important in the Pacific Northwest of North America.

‘Olympia’ (Washington – 1933) is mid-season with a high chilling requirement >800 h. Bush is vigorous and spreading. Fruit are medium size, dark blue and soft, with a medium large scar and excellent flavour. Locally important in the Pacific Northwest of North America.

‘Patriot’ (1976 – Maine/USDA) is early mid-season with a chilling requirement >800 h. Bush is small to medium in height and slightly spreading. Very good winter hardiness, but blooms very early and is subject to frost. Fruit are large and firm with a small scar and excellent flavour. Locally important for pick-your-own or farm sales, but not widely planted.

‘Reka’ (1986 – New Zealand) is early with a chilling requirement >800 h. Bush is upright and vigorous with modest winter hardiness. Reaches adult productivity very quickly. Broad soil adaptations. Berries are medium to large and dark blue with an excellent flavour. Has found a niche in the Pacific Northwest of North America as a machine-harvested, processed berry.

‘Reveille’ (1990 – North Carolina) is very early with a chilling requirement >800 h. Bush is upright and suitable for mechanical harvest. Fruit are small, firm, light blue and have an excellent flavour. Early bloom is subject to frost, fruit cracking during rain can be a problem and some berries are slow to turn blue at the stem end. Resistant to stem canker. Locally important in North Carolina and Georgia.

‘Rubel’ (1911 – New Jersey) is late mid-season with a chilling requirement >800 h. Bush is tall and upright with excellent winter hardiness. Harvests well by machine and is used primarily in processed market. Fruit are small and firm with fair flavour, a medium scar and high levels of antioxidants. Locally important in Michigan, but interest is growing elsewhere.
Chapter 2

’Spartan’ (1978 – USDA) is early with a chilling requirement >800 h. Bush is upright and open. Blooms unusually late for an early variety. Fruit are firm, very large, medium scar and highly flavoured. Has narrow soil adaptive range, but has become locally important in the Pacific Northwest of North America.

‘Toro’ (USDA – 1987) is mid-season with a chilling requirement >800 h. Bush is upright, open and has good winter hardiness. Fruit are medium in size, powder blue and firm with good flavour and a small scar. Has not been widely planted, but interest is growing due to its high, consistent production.

‘Weymouth’ (1936 – New Jersey) is very early with a chilling requirement >800 h. Bush is low growing with good winter hardiness. Fruit are soft, dark blue and weakly flavoured. Locally grown in New Jersey and Washington, but rarely planted today.

Newly released northern highbush cultivars

‘Beauford’ (2005 – North Carolina) is late mid-season with a chilling requirement >800 h. Extremely vigorous and tolerant to a wide range of soils. May be machine harvestable for the fresh market. Low tolerance to winter cold. Berries are medium sized, firm, light blue and flavourful, with a good scar.

‘Chanticleer’ (1997 – USDA/New Jersey) is very early with a chilling requirement >800 h. Upright and moderately tall bush. Good winter hardiness with modest yields. Fruit are medium sized with good colour, firmness and flavour (mild). Has not been widely planted.

‘Echota’ (1998 – North Carolina) ripens in late mid-season with a chilling requirement >800 h. Bush is semi-upright and vigorous with limited winter hardness. Good self-fertility. Fruit are medium sized and very light blue with good firmness and high acid flavour. Excellent shelf-life. Resistant to stem canker.

‘Hannah’s Choice’ (2005 – USDA) is early with a chilling requirement >800 h. Upright and vigorous with good winter hardiness. Yields are modest. Fruit are medium to large, medium blue in colour and very sweet, with a good scar and excellent firmness.

‘Huron’ (2009 – Michigan) is early with a chilling requirement >800 h. It is upright and vigorous with excellent winter hardness. Yields are excellent. Fruit are large, light medium coloured and very sweet with excellent scar and firmness.

‘Tender’ (1997 – North Carolina) is mid-season with a chilling requirement >800 h. Bush is semi-upright and has good self-fertility. Only modest winter hardiness. Fruit are small, light blue, tiny scared with good firmness and flavour.
Half-high cultivars

‘Chippewa’ (1997 – Minnesota) is mid-season with a chilling requirement >800 h. Medium-stature bush with excellent winter hardiness. Berries are medium sized, very light blue, medium firm with a medium scar and good flavour. Locally important in areas with extreme cold.

‘Northblue’ (1986 – Minnesota) is early mid-season with a chilling requirement >800 h. Medium-stature bush with superior cold hardiness. Medium to large sized, dark blue fruit with medium scar, firmness and flavour (a little acid). Resistant to mummy berry. Locally important for ‘pick-your-own’ and farm sales where winters are extremely cold.

‘Northcountry’ (1986 – Minnesota) is early mid-season with a chilling requirement >800 h. Medium-stature bush with superior cold hardiness. Berries are small, light blue and soft with a medium scar and good, sweet flavour. Locally important for pick-your-own and farm sales where winters are extremely cold.

‘Northsky’ (1986 – Minnesota) is mid-season with a chilling requirement >800 h. Bush of very low stature with superior cold hardiness. Berries are very small, light blue and soft with a medium scar and good sweet flavour. Resistant to mummy berry. Locally important for pick-your-own and farm sales where winters are extremely cold.

‘Polaris’ (1996 – Minnesota) is early with a chilling requirement >800 h. Low-stature plant with superior cold hardiness. Medium sized, light blue fruit with good firmness and flavour. Locally important for pick-your-own and farm sales where winters are extremely cold.

‘St. Cloud’ (1991 – Minnesota) is early with a chilling requirement >800 h. Medium-stature bush with excellent winter hardiness. Berries are firm, flavourful and medium sized. Scar is small. Locally important for ‘pick-your-own’ and farm sales where winters are extremely cold.

Superior’ (2008 – Minnesota) is late with a chilling requirement >800 h. Medium-stature bush with a spreading habit and mature height of 3.3–3.5 m. Very productive and has extreme cold tolerance. Fruit are small to medium sized and light to medium blue coloured with good colour, scar and flavour. Recommended for trial in areas with extremely cold winters.

Most popular rabbiteye cultivars

‘Alapaha’ (2001 – Georgia) is an early-ripening variety with a chilling requirement of 450–500 h. It is a vigorous, productive, upright bush that leafs very well in spring. Flowers after ‘Climax’ but ripens at the same time. Medium sized berry with excellent colour, firmness, flavour and a small, dry scar. Has a considerable degree of self-fruitfulness. Resists fruit cracking. New variety being widely trialled in Georgia.
'Austin' (1996 - Georgia) is early, productive and upright with a chilling requirement of 450–500 h. It is widely adapted. Flowers and ripens a few days after 'Climax'. Fruit are large and light blue with good scar, firmness and flavour. Needs a pollinator. Modest hectarage has been planted in Georgia.

'Brightwell' (1981 – Georgia) is early mid-season variety with a chilling requirement of 400–450 h. Bush is vigorous, productive and upright. Widely adapted and machine harvestable. It is at least partially self-fertile, and has a medium sized berry that is medium blue in colour with a good scar, firmness and flavour. Variety is susceptible to fruit cracking under rainy conditions. Most widely planted rabbiteye blueberry in the last 15 years.

'Briteblue' (1969 – Georgia) is late harvesting with a chilling requirement of ~600 h. Bush is moderately vigorous and upright. Berries are light blue, large, very firm with good flavour. Was once popular for pick-your-own operations, but not marketed much any more.

'Centurion' (1978 – North Carolina) is late with a chilling requirement of 600–700 h. It ripens one or two weeks after 'Tifblue'. Bush is vigorous, productive and upright. Fruit are dark blue with a good scar and medium firmness; can crack after heavy rains. Now planted primarily to extend the harvest season as a pick-your-own variety.

'Climax' (1974 – Georgia) is early with a chilling requirement of 400 h. Bush has medium vigour and is slightly spreading. Fruit is medium sized and coloured, with excellent firmness, a good scar and nice flavour. It has concentrated ripening and may be suitable for machine harvest for the fresh market. Once was the most popular early variety in the south-east USA, but is now less popular due to its high susceptibility to spring freezes, the gall midge and flower thrips.

'Delite' (1969 – Georgia) is mid-season with a chilling requirement of 500 h. It ripens with 'Tifblue'. Bush is moderately vigorous and upright. Fruit are medium to large in size, medium coloured with a good scar and firmness, sweet flavour and high aromatics. Highly susceptible to blueberry rust and is no longer recommended for planting.

'Ira' (1997 – North Carolina) is late with a chilling requirement of 700–800 h. Bush is upright with medium to high vigour. It has a late bloom that avoids freeze damage in the spring, and good self-fertility. Fruit are medium in size and medium in colour with good scar, firmness and flavour. Fruit are aromatic and store well. Recommended as a pick-your-own variety in the Piedmont and mountain regions of North Carolina.

'Maru' (1992 – New Zealand) is very late with a chilling requirement of 600–750 h. Bush is slightly spreading with high vigour and productivity. Fruit are large, firm, medium blue and mild flavoured. Locally important in New Zealand and being trialled in the Pacific Northwest.

'Ochlockonee' (2002 – Georgia) is very late with a chilling requirement of 600–700 h. Bush is moderately upright, vigorous, with narrow crowns
and very high productivity. Flowers late enough to miss most frosts in south Georgia. Fruit are large, medium blue, medium firm with a small scar and sweet flavour. Requires cross-pollination. Being widely trialled in the south-east USA and Pacific Northwest. Has shown good resistance to fruit cracking in rainy conditions.

'Towerblue' (1978 – North Carolina) is late mid-season variety with a chilling requirement of 550–600 h. Bush is upright, vigorous and productive. It is not very self-fertile. Fruit are medium to large, light blue, with good firmness, scar and flavour. Fruit are resistant to cracking. Has been a popular variety in recent years.

'Premier' (1978 – North Carolina) is early with a chilling requirement of 550 h. It is vigorous and productive, but has poor self-fertility. Fruit are large with good scar, medium firmness, good flavour and dark blue colour. Very susceptible to blueberry gall midge. Still widely planted, but needs frequent harvests to retain adequate firmness. Late-season flowers often malformed with partial or no corolla.

'Rahl' (1992 – New Zealand) is late with a chilling requirement of 600–750 h. Spreading and vigorous with medium yields. Fruit are medium sized, very firm and light blue with excellent flavour. Locally important in New Zealand and being trialled in the Pacific Northwest of North America.

'Tifblue' (1955 – Georgia) is a late mid-season variety with a chilling requirement of 600–700 h. Bush is vigorous, upright and productive. It has poor self-fertility. Fruit are medium sized, light blue with good scar, firmness and flavour. It is susceptible to rain cracking. Well adapted to machine harvest. Up until the early 1990s was the most planted rabbiteye, but now little planted.

'Woodard' (1960 – Georgia) is early mid-season with a chilling requirement of 350–400 h. Bush is vigorous, spreading and productive. Fruit are large and dark blue, with soft to medium firmness, excellent flavour and medium scar. Poor shipper and freezer; often damaged by spring frosts. Once widely grown, but now popular only for pick-your-own and farm markets.

Newly released rabbiteye cultivars

'Centra Blue' (2008 – New Zealand) is a very late variety with a chilling requirement of 600–750 h. Bush is semi-erect and of medium vigour. Fruit are large, light blue, with a small scar, good firmness and flavour. The fruit have minimal grittiness.

'Ventra Blue' (2008 – New Zealand) is a very late variety with a chilling requirement of 600–750 h. Bush is upright, vigorous and productive. It is not very self-fertile. Fruit are medium to large, light blue, with a small scar, good firmness and flavour. The fruit have minimal grittiness.

'Columbus' (2003 – North Carolina) is early mid-season to mid-season with a chilling requirement of >600 h. Ripens a little before ‘Tifblue’. Bush is semi-upright, with medium vigour and good productivity. Fruit are large and powder blue, with an average scar, high aroma and good flavour. It has good storage life and is resistant to cracking, but is not self-fruitful.
'Desoto' (2007 - Mississippi) fruits in the late mid-season with a chilling requirement of 600 h or more. The bush is vigorous, semi-dwarf and somewhat spreading. It will not grow taller than 2 m at maturity, removing the need for top-pruning. Fruit are medium to large, light blue, firm and flavourful, with a small picking scar.

'Ocean Blue' (2010 - New Zealand) is a mid-season variety with a chilling requirement of 600-750 h. The bush is medium vigorous and upright. It has medium sized fruit that are medium blue with little grittiness, a small scar, good firmness and a sweet flavour. It is recommended for trial as a fresh market, mid-season variety.

'Onslow' (2001 - North Carolina) is a late mid-season variety with a chilling requirement of 600 h or more. Bush is upright, vigorous and self fruitful. Fruit are large, medium blue and firm with a good scar and pleasant, aromatic flavour.

'Robeson' (2007 - North Carolina) is early ripening with a chilling requirement of 400-600 h. It is vigorous and upright, and is unusually adapted to soils with higher pH. Fruit are medium sized with good colour and scar, although they are a little soft. This is a pentaploid.

'Savory' (2004 - Florida) is early with a chilling requirement of 300 h. Bush habit is between upright and spreading; tends to overbear. Fruit are large, light blue, with a good scar, firmness and flavour. It is very susceptible to flower thrips and gall midge. Early flowering in the spring often results in freeze damage.

'Vernon' (2004 - Georgia) is early with a chilling requirement of 450-500 h. Bush is vigorous and open. Fruit are large, light blue and firm with a sweet flavour. It needs a pollinator. Has become popular in last few years due to good fruit quality for harvesting, handling and shipping.

**CONCLUSIONS**

Most blueberry production comes from cultivars derived from *V. corymbosum* L. (highbush blueberry), *V. ashei* Reade (rabbiteye blueberry; syn. *V. virgatum* Ait.), and native stands of *V. angustifolium* Ait. (lowbush blueberry). Highbush cultivars are further separated into northern or southern types depending on their chilling requirements and winter hardiness. The identification of wild species in the subgenus *Cyanococcus* has been problematic due to polyploidy, overlapping morphologies, extensive hybridization and a general lack of chromosome differentiation.

Among the most important characteristics being sought by blueberry breeders are flavour, large fruit size, light blue colour (a heavy coating of wax), a small scar where the pedicel detaches, easy fruit detachment for hand or machine harvest, firmness and a long storage life. Expanding the range of adaptation of the highbush blueberry by reducing its chilling requirement has
been an important breeding goal, along with season extension and winter cold
tolerance. The chilling requirement has been reduced by incorporating genes
from the southern diploid species *V. darrowii* into *V. corymbosum* via unreduced
gametes, although hybridizations with native southern *V. corymbosum* and
*V. ashei* have also played a role. Cultivars are now available with an almost
continuous range of chilling requirements from 0 to 1000 h.

Most breeding programmes have relied primarily on pedigree breeding
where elite parents are selected each generation for intercrossing. The
Florida southern highbush and rabbiteye breeding programmes have also
relied on recurrent selection. There are now a number of blueberry breeding
programmes found across the world that are releasing a steady stream of new
cultivars. All new blueberry cultivars are being patented and licensed.

Blueberries are now routinely micropropagated for commercial sale using
tissue culture techniques. Other biotechnological techniques have not been
widely utilized with blueberries, although the first genetic maps of blueberries
are beginning to emerge that will set the groundwork for marker-assisted
breeding.

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INTRODUCTION

In this chapter, the anatomy and morphology of the highbush and rabbit-eye blueberry are discussed, followed by a discussion of vegetative and reproductive growth and development. Environmental effects on growth and development are also presented.

ANATOMY AND MORPHOLOGY

Plant habit

All species of *Vaccinium* are woody perennials and stature is one of the most striking differences among the various cultivated blueberries. Lowbush blueberries range from 0.1 to 0.15 m in height, while highbush plants can reach 1.8 to 4.0 m and rabbiteyes may grow to 6 m tall.

The blueberry shrub is composed of shoots that emerge from newly formed buds or previously formed dormant buds located in the crown. The shoots emerging from the base of plants are called canes and they become woody in the second season of growth.

A dormant 1-year-old blueberry shoot typically has inflorescence buds at the top, with vegetative buds below (Fig. 3.1). Flower buds are large and round, while vegetative buds are smaller, narrow and pointed. The dormant vegetative bud is about 4 mm long, with a single apex (Gough and Shutak, 1978).

The number of flowers found in the inflorescence buds is negatively correlated with distance from the tip. In ‘Bluecrop’, the primary buds at the tip of the shoots average nine or ten flowers, while the 3’ ones have eight, and the 4’ ones have seven (Gough, 1994). There is usually only one flower bud at a node, although some of the upper nodes have a secondary bud, with only one to five flowers. The number of flower buds on a shoot is related to shoot thickness, cultivar and light penetration. There are large differences among
cultivars in flowers per bud, buds per cane, laterals per cane and canes per bush (Table 3.1).

**Leaves**

Blueberry leaves are simple, entire to serrated and alternately arranged along the stem. Most highbush and rabbiteye species are deciduous, although some of the lower chilling varieties can be evergreen if temperatures remain above freezing. Leaf shape ranges widely from elliptic, spatulate, oblanceolate to ovate. Highbush and rabbiteye varieties have varying amounts of pubescence and glands on the underside of the leaves.

**Roots**

Highbush and rabbiteye blueberries have two major types of root: thick storage roots (up to 11 mm) and fine, thread-like roots (as small as 1 mm). The former anchor the plants and perform a storage function, while the latter are

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Flowers/bud</th>
<th>Buds/cane</th>
<th>Laterals/cane</th>
<th>Canes/bush</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Elliott'</td>
<td>10.8</td>
<td>4.8</td>
<td>9.6</td>
<td>24.9</td>
</tr>
<tr>
<td>'Spartan'</td>
<td>7.7</td>
<td>4.2</td>
<td>7.4</td>
<td>20.6</td>
</tr>
<tr>
<td>'Jersey'</td>
<td>7.8</td>
<td>6.1</td>
<td>8.2</td>
<td>26.3</td>
</tr>
<tr>
<td>'Bluejay'</td>
<td>7.1</td>
<td>4.7</td>
<td>8.2</td>
<td>23.9</td>
</tr>
<tr>
<td>'Bluecrop'</td>
<td>7.8</td>
<td>4.0</td>
<td>7.2</td>
<td>23.9</td>
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<tr>
<td>Standard error</td>
<td>1.3</td>
<td>1.2</td>
<td>0.9</td>
<td>4.7</td>
</tr>
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</table>

Table 3.1. Mean yield components of six highbush blueberry cultivars at Grand Junction, Michigan, over two years. (Adapted from Hancock, 1989.)
primarily responsible for water and nutrient absorption. Blueberries do not have root hairs and are inhabited by an endotrophic mycorrhiza (Coville, 1910; Jacobs et al., 1982). In general, about 50% of the roots are located within 30 cm of the crown and 80–85% are within 60 cm (Table 3.2). Over 80% of the root dry mass is found in the top 36 cm. Mulching tends to concentrate roots near the surface. Abbott and Gough (1987) found that highbush plants with mulch had 83% of their roots in the upper 15 cm of soil compared with 40% in plants not mulched. They also found that high rates of irrigation tended to increase root depth.

Abbott and Gough (1987) studied the size distribution of highbush roots and placed roots in seven categories of size from 40 µm (first order) to ~1 mm (seventh order). They found that blueberry roots are 1/5 to 1/10 of the diameter of those of other temperate fruit crops. Length decreased steadily as root width decreased, with first- and second-order roots representing nearly 75% of total root length. The root fresh weight followed the opposite trend, with third, fourth and fifth order representing approximately 25, 29 and 29% of the total root fresh weight. They also determined that first- and second-order roots were the ones primarily involved in nutrient absorption. Fifth- and higher-order roots were primarily used for conduction and anchorage. Third- and fourth-order roots were transitional.

Flowers and inflorescences

The inflorescence of the blueberry is a raceme. The corolla of the blueberry is united, with four or five lobes; and is coloured solid white to pink fringed. The corolla is inverted and shaped like a globe or urn (Fig. 3.1). The pistil can be slightly longer to slightly shorter than the corolla. The ovary is inferior and has four to five cells (locules), with several to many ovules in each locule.

Table 3.2. Percentage of 'Coville' roots (dry weight) at various depths and distances from the crown of 13-year-old plants in Bridgehampton fine sandy loam soil with sawdust mulch. (Adapted from Gough, 1980.)

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>31</th>
<th>61^a</th>
<th>94</th>
<th>122</th>
<th>153</th>
<th>183</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>26</td>
<td>15</td>
<td>5</td>
<td>3</td>
<td>T^b</td>
<td>T</td>
<td>49</td>
</tr>
<tr>
<td>36</td>
<td>11</td>
<td>11</td>
<td>5</td>
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<td>30</td>
</tr>
<tr>
<td>58</td>
<td>11</td>
<td>5</td>
<td>1</td>
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<td>0</td>
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<td>18</td>
</tr>
<tr>
<td>81</td>
<td>2</td>
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<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>50</td>
<td>34</td>
<td>11</td>
<td>7</td>
<td>T</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

^a Drip line.
^b Trace amounts.
There are eight to ten stamens per flower that insert at the base of the
corolla and circle the style. The stamens are composed of an anther and
filament; the anther has two awns, which have pores at their end through
which pollen emerges. The blueberry pollen grain is a tetrad, although it rarely
produces multiple germ tubes (Brewer and Dobson, 1969).

The fruit is a true berry with many seeds, and it ripens two to three
months after pollination, depending on cultivar and environmental conditions.
High temperatures tend to advance fruit ripening. Blueberry fruit range in
colour from light blue to black and they have a waxy, cuticle layer that is about
5 μm thick. Pigments are found in the epidermal and hypodermal layers,
which are separated from the rest of the cortex by a ring of vascular bundles.
The majority of the blueberry flesh is white. At the centre of the fruit is a
carpel with five, lignified placentas with numerous seeds attached. Stone cells
are found sporadically throughout the mesocarp, but are most prevalent just
below the epidermis.

GROWTH AND DEVELOPMENT

Vegetative and floral growth

In most climates, differentiation of flower buds starts on 1-year-old wood in
mid- to late summer (Gough et al., 1978). Initiation along the cane proceeds
basipetally, and florets within the individual racemes are initiated acropetally
(Gough et al., 1978; Lyrene, 1984; Huang et al., 1997).

Floral initiation in northern highbush begins in late July in New Jersey
and by October all floral parts are developed (Gough et al., 1978). In southern
highbush, floral bud initiation begins in early September in Louisiana and by
December, all floral parts are developed. However, unlike northern highbush
in the north-east USA, floral differentiation continues throughout the winter
in southern highbush. Pollen development is arrested in northern highbush
after the formation of microspore mother cells in November, while in southern
highbush the development of pollen grains and ovules continues throughout
the winter (Huang et al., 1997). As photoperiods become short in the autumn
and temperatures diminish, blueberries become dormant and subsequently
require a certain number of chilling hours to begin normal floral and leaf
growth in the spring.

When plants begin to grow in the spring, flower buds start to crack
and then open over a period of 3 to 4 weeks, depending on cultivar and
temperature. Several stages of bloom development are generally recognized
including bud swell and crack, tight cluster, early pink, late pink, early bloom,
full bloom, petal drop and fruit expanding (for examples see http://www.
Blueberries.msu.edu).
Vegetative buds begin to swell in the early spring as the leaves begin to develop within the buds. Vegetative bud break tends to occur more slowly than floral bud break depending on cultivar, chilling duration and temperatures in the spring. As the vegetative buds open, the leaves are closely clustered around the stem, but over time the internodes expand and the leaves become separated. Up to six leaf primordia are present in vegetative buds, and as the shoots grow, additional leaves are initiated by the shoot apex every 5 days (Gough and Shutak, 1978).

Growth of the shoots is sympodial and episodic. Individual shoots initially grow rapidly and then stop due to apical abortion, which is called 'black tip'. Shoots can have one, two or multiple growth flushes depending on cultivar and environmental conditions (Shutak et al., 1980). Growth is renewed when an axillary bud is released from dormancy and the black tip is sloughed off. Generally, only one axillary bud is released from dormancy, leaving the shoot unbranched; however it is not uncommon to have two or three buds break. Typically, there are two or three growth flushes in northern highbush. There is a tendency for earlier-ripening cultivars to have more growth flushes than later ones, but this is not always the case. For example, 'Lateblue' tends to have as many flushes as a mid-season cultivar (Gough, 1994).

When a new shoot breaks from the base of the plant, it generally remains unbranched in the first year and all growth flushes arise from a single vegetative bud. After fruiting in the second year, two or more vegetative buds below the inflorescence break dormancy and begin to grow, resulting in the first branching. In subsequent years, multiple vegetative buds break each year after fruiting, resulting in increased branching and 'twiginess' of the shoot over time. Fruit size and yield per cane diminish as the fruiting canes become twiggier.

**Root growth**

Studies done in young containerized highbush plants growing in sawdust showed that root growth has two peaks during the season (Abbott and Gough, 1987). The first and weaker peak occurs in spring, starting near the time of fruit set and extending to the immature green stage of fruit development. The second peak occurs after fruit harvest has started and ends before plants go into dormancy.

Abbott and Gough (1987) found that the lifespan of blueberry roots ranges from 115 to 120 days for first- and second-order roots, while third-order roots have a lifespan of 136–155 days. Mycorrhizal colonization was highest in youngest roots (first- and second-order roots), decreased steadily in third and fourth order, and was not detectable in higher-order roots.
Pollination/fruit set

The receptivity of stigmas to pollen varies from 5–8 days in highbush (Moore, 1964) to 5–6 days in rabbiteye (Young and Sherman, 1978). However, percentage fruit set drops dramatically in highbush and lowbush blueberry if pollination is delayed by 3 days (Merrill, 1936; Wood, 1962). In contrast, Young and Sherman (1978) found high levels of fruit set in rabbiteye plants pollinated 6 days after anthesis, and Breviš et al. (2005, 2006) documented that stigmatic receptivity in the rabbiteye cultivars 'Brightwell' and 'Tifblue' actually increased from 0 to 6 days before levelling off. Cultivars can also vary in their periods of stigma receptivity; Moore (1964) showed that pistils of 'Blueray' are receptive longer than are pistils of 'Coville'. Growth of pollen tubes is favoured by warm temperatures (Knight and Scott, 1964).

Seed number has a significant influence on final fruit size in northern highbush (White and Clark, 1939; Darrow, 1958; Moore et al., 1972; Krebs and Hancock, 1988), southern highbush (Lang and Danka, 1991) and rabbiteye blueberries (Moore et al., 1972; Kushima and Austin, 1979). Cultivars can vary greatly in their response to increased seed numbers (Eaton, 1967). While seed numbers are important in determining final fruit size, more than 50% of the variation in fruit size is accounted for by other factors including amount of pollinator activity, air temperature, crop load and water availability (Brewer and Dobson, 1969; Eck, 1988).

Typically, only a fraction of the ovules develop into seeds. Highbush and rabbiteye blueberries have in excess of 110 ovules per fruit (Darrow, 1941; Parric, 1990), but developed seed numbers rarely exceed half that number. Darrow (1958) found highbush cultivars had from 16 to 74 seeds per fruit, while rabbiteye cultivars had from 38 to 82 seeds per fruit. Normally developed seeds are plump and brown, while those that have aborted are small and collapsed. Most seeds abort during late Stage I and early Stage II of fruit development (Edwards et al., 1972), depending on the level of self-fertility. Huang et al. (1997) found that most ovule abortion occurred from 5 to 10 days after pollination in the southern highbush 'Sharpblue'. Vander Kloet (1991) observed the first deterioration in highbush embryos about 20 days after pollination.

Many of the seeds that abort in highbush and rabbiteye blueberries do so because of early-acting inbreeding depression. Seeds abort as deleterious alleles are expressed during seed development (Krebs and Hancock, 1988, 1990, 1991). Krebs and Hancock developed several lines of evidence that support this in highbush blueberry including: (i) a range in self-fertility between different cultivars; (ii) a significant correlation between self- and outcross fertility; and (iii) a significant correlation between percentage of aborted ovules and the inbreeding coefficient. In similar work, Vander Kloet and Lyrene (1987) and Vander Kloet (1991) also found an association between level of relatedness and seed set in diploid, tetraploid and hexaploid races of Vaccinium corymbosum.
Fewer outcrossed pollen tetrads are needed for stigmatic saturation of blueberries than selfed ones. Parrie and Lang (1992) discovered that cross-pollination resulted in a cessation of stigmatic fluid production at lower tetrad densities than self-pollination. The number of pollen tetrads necessary for stigmatic saturation ranged from 295 (selfed 'Gulfcoast') to 201 (outcrossed 'O'Neal') in southern highbush, from 256 (selfed 'Meader') to 195 (outcrossed 'Bluechip') in northern highbush and from 218 (selfed 'Northland') to 186 (outcrossed 'Northland') in half-higos.

Once germinated, selfed pollen tubes grow in the style at the same rate as outcrossed ones. When Krebs and Hancock (1988) compared rates of pollen tube growth in selfed 'Spartan' versus 'Spartan' x 'Bluejay' using fluorescence microscopy, they found that both selfed and crossed pollen reached the base of the style at day 2 after pollination, and at day 6 after pollination, both types of pollen were entering the ovules. El-Agamy et al. (1981) found that the percentage of pollen that travelled the full length of the style was higher after 48 h in outcrossed versus selfed pollen of southern highbush and rabbiteye, but by 72 h both classes had travelled the full length. Vander Kloet and Lyrene (1987) also found that self-pollen could eventually fertilize ovules.

Fruit drop in blueberries occurs about 3 to 4 weeks after flowering, and is less common in highbush than rabbiteye. The fruit that drop usually do not expand during the initial phase of fruit growth and have an abnormal red coloration. There is considerable variability among highbush cultivars in fruit set, ranging from about 50% to nearly 100%. Lyrene and Goldy (1983) observed a range in fruit set among open-pollinated rabbiteye cultivars from 36% in 'Tifblue' to 75% in 'Southland'. Davies (1986) also found that 'Tifblue' set only 21–27% of its flowers compared with 46–60% in 'Woodard' and 55% for 'Bluegem'. The position of flowering shoots in a bush had no consistent influence on fruit set.

**Fruit development**

All blueberry fruit exhibit a double sigmoid growth curve (Fig. 3.2). Stage I is characterized by rapid cell division and dry weight gain (Birkhold et al., 1992; Cano-Medrano and Darnell, 1997) and lasts from 25 to 35 days depending on cultivar and environmental conditions. Little fruit growth is observed in Stage II, but it is an active period of seed development (Edwards et al., 1972). This period lasts from 30 to 40 days depending on cultivar and environment, and also on the number of viable seeds (Darnell, 2006). Highbush cultivars tend to have shorter Stage II than rabbiteyes, but there is considerable overlap (Edwards et al., 1972). Stage III is characterized by very rapid fruit growth through cell enlargement (Eck, 1986; Birkhold et al., 1992; Cano-Medrano and Darnell, 1997). Stage III lasts for 30 to 60 days, again depending on species, cultivar and environment. During Stage III, sugars accumulate and
the berry turns from green to blue as anthocyanins accumulate. The total length of the fruit development period ranges from 42 to 90 days in northern highbush, from 55 to 60 days in southern highbush and from 60 to 135 days for rabbiteye (Darnell, 2006).

There is some question as to whether blueberry fruit are climacteric. Bergman (1929), Ismail and Kender (1967, 1969) and Windus et al. (1976) measured a rise in carbon dioxide evolution during fruit development in lowbush and highbush blueberries that peaked during Stage III. Lipe (1978) also observed an increase in ethylene production at the red berry stage in rabbiteye blueberry. However, Hall and Forsyth (1966) and Frenkel (1972) could not find any surge in respiration or ethylene production during ripening in their studies of lowbush and highbush blueberry. Janes et al. (1978) also could not induce respiration surges in highbush blueberries through treatments with acetaldehyde or ethylene.

A number of studies have been conducted to follow changes in organic composition in blueberry fruit as it matures. Perhaps the most complete analysis was done by Woodruff et al. (1960) on field-grown ‘Jersey’ fruit in Michigan (Table 3.3). The intensity of colour increased over the first six days after the fruit began to colour and then stabilized. Percentages of lipids and waxes decreased in the early stages of ripening and then remained constant. Starch and other complex carbohydrates were relatively stable throughout maturation. Soluble pectin decreased throughout development as pectin methyl-esterase activity increased. They found that the percentage of total sugars increased for 9 days after colour change and then levelled off. The level of non-reducing sugars increased during the latter stages of development, but the concentration of reducing sugars decreased, keeping overall sugar levels constant. Titratable acidity decreased continually during berry ripening.
Table 3.3. Composition of 'Jersey' fruit at different days after coloration (percentage of dry weight). (Adapted from Woodruff et al., 1960.)

<table>
<thead>
<tr>
<th>Constituent</th>
<th>0</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>16</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reducing sugars</td>
<td>54.9</td>
<td>58.5</td>
<td>62.2</td>
<td>63.8</td>
<td>64.0</td>
<td>64.0</td>
<td>63.1</td>
</tr>
<tr>
<td>Non-reducing sugars</td>
<td>4.6</td>
<td>6.7</td>
<td>4.8</td>
<td>6.9</td>
<td>6.9</td>
<td>7.8</td>
<td>7.2</td>
</tr>
<tr>
<td>Total sugars</td>
<td>59.5</td>
<td>65.2</td>
<td>67.0</td>
<td>70.7</td>
<td>70.9</td>
<td>71.8</td>
<td>70.4</td>
</tr>
<tr>
<td>Titratable acid (as citric)</td>
<td>9.0</td>
<td>4.4</td>
<td>2.6</td>
<td>2.0</td>
<td>1.6</td>
<td>1.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Sugar/acid ratio</td>
<td>5.4</td>
<td>3.8</td>
<td>3.6</td>
<td>3.5</td>
<td>3.7</td>
<td>3.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Acid-hydrolysable polysaccharides</td>
<td>4.1</td>
<td>3.5</td>
<td>3.4</td>
<td>3.0</td>
<td>4.3</td>
<td>4.2</td>
<td>4.6</td>
</tr>
<tr>
<td>Starch</td>
<td>6.6</td>
<td>6.8</td>
<td>6.2</td>
<td>6.9</td>
<td>6.8</td>
<td>6.8</td>
<td>7.1</td>
</tr>
<tr>
<td>Cellulose</td>
<td>4.5</td>
<td>3.8</td>
<td>4.1</td>
<td>3.4</td>
<td>3.7</td>
<td>3.5</td>
<td>3.5</td>
</tr>
<tr>
<td>Lignin</td>
<td>6.8</td>
<td>5.4</td>
<td>4.6</td>
<td>4.2</td>
<td>4.3</td>
<td>5.4</td>
<td>4.9</td>
</tr>
<tr>
<td>Soluble pectin</td>
<td>1.1</td>
<td>1.0</td>
<td>1.0</td>
<td>0.9</td>
<td>0.9</td>
<td>0.6</td>
<td>0.7</td>
</tr>
</tbody>
</table>

resulting in a steady increase in the ratio of sugar to acid during ripening; others have noted similar patterns (Woodruff et al., 1960). Sugar accumulation has been found to stop when berries are detached (Shutak et al., 1957).

Ballinger et al. (1963) and Kushman and Ballinger (1963) measured the effect of a number of management practices on the sugar and acid composition of highbush blueberry. They found that increases in crop load decreased sugar levels in the fruit but had no effect on acidity levels or fruit storage quality. Higher nitrogen decreased acidity but had little effect on sugar levels or postharvest quality. Expanding the number of days between harvests increased sugar content and reduced titratable acidity, as well as shelf-life. Fruit from the third harvest had higher sugar levels and lower acidity than those from the first two harvests and reduced shelf-life.

As fruit ripen, there are changes in the specific types of sugars and acids. Kushman and Ballinger (1968) and Ballinger (1966) found that as 'Wolcott' fruit ripen, there are increases in glucose and fructose and decreases in citric acid. Malic and quinic acids also decrease slightly during ripening. Markakis et al. (1963) found that ripening 'Rubel' and 'Jersey' berries also declined in citric acid over time, and that 'Rubel' had higher overall levels of citric acid than 'Jersey'.

Blueberries become softer during ripening through the enzymatic digestion of the cell wall components, pectin, cellulose and hemicelluloses (Eskin, 1979; Proctor and Miesle, 1991). This process accelerates as the fruit become overripe, with concomitant increases in sugar content and decreases in acidity. Thus, fruit get sweeter with the advancement of ripening, but also softer. Blueberry cultivars vary greatly in their ability to maintain firmness after ripening (Ehlenfeldt and Martin, 2002; Hancock et al., 2008).
FINAL FRUIT COMPOSITION

An average blueberry fruit is composed of approximately 83% water, 0.7% protein, 0.5% fat, 1.5% fibre and 15.3% carbohydrate (Hancock et al., 2003). Blueberries have 3.5% cellulose and 0.7% soluble pectin, while cranberries contain 1.2% pectin. The total sugars of blueberries amount to more than 10% of the fresh weight, and the predominant reducing sugars are glucose and fructose, which represent 2.4%.

The overall acid content of Vaccinium fruit is relatively high, with blueberries falling in the range of 1–2%. The primary organic acid in blueberries is citric acid (1.2%). They also contain significant amounts of ellagic acid, a compound thought to reduce the risk of cancer (Maas et al., 1991). Compared with other fruits and vegetables, blueberries have intermediate to low levels of vitamins, amino acids and minerals (Hancock et al., 2003). Blueberries contain 22.1 mg of vitamin C per 100 g of fresh weight; blueberries are unusual in that arginine is their most prominent amino acid. The major volatiles contributing to the characteristic aroma of blueberry fruit are trans-2-hexanol, trans-2-hexanal and linalool (Parliment and Dolor, 1975).

In general, blueberries are one of the richest sources of antioxidant phytonutrients among the fresh fruits, with total antioxidant capacity ranging from 13.9 to 45.9 μmol Trolox equivalents/g fresh berry (Ehlenfeldt and Prior, 2001; Connor et al. 2002a,b). Berries from the various Vaccinium species contain relatively high levels of polyphenolic compounds, with chlorogenic acid predominating. Total anthocyanins in blueberry fruit range from 85 to 270 mg per 100 g, and species in the subgenus Cyanococcus carry the same predominant anthocyanins, aglycones and aglycone-sugars, although the relative proportions vary (Ballington et al., 1988). The predominant anthocyanins were delphinidin-monogalactoside, cyanidin-monogalactoside, petunidin-monogalactoside, malvidin-monogalactoside and malvidin-monoorarinobioside.

ENVIRONMENTAL EFFECTS ON GROWTH AND DEVELOPMENT

Temperature and photoperiod

A number of studies have shown that flower bud initiation in highbush and rabbiteye blueberries is induced by short-day photoperiods. In northern highbush, 8 weeks of 8-, 10- or 12-h photoperiods at constant 21°C in the greenhouse resulted in much greater flower bud initiation than 14- or 16-h photoperiods (Table 3.4; Hall et al., 1963). Darnell (1991) found that 6 weeks of 8-h photoperiods initiated more flower buds than day lengths of 11–12 h
in rabbiteye ('Climax' and 'Beckyblue') in Gainesville, Florida. In southern highbush ('Sharpblue' and 'Misty') and *Vaccinium darrowii*, Spann et al. (2003) found that many more flower buds were induced under 21 than 28°C constant temperatures for 8 weeks (Spann et al., 2004), although plant dry weight and cane height were not affected by these temperatures.

The number of flower buds initiated in highbush blueberries generally increases with time of exposure to short days (Darnell, 1991; Hall and Ludwig, 1961; Hall et al., 1963). The full induction of flowering requires 5 to 6 weeks of shortening day lengths; however, Bañados and Strik (2006) found some flower buds were initiated in 'Duke' and 'Bluecrop' after only 2 weeks of 8-h photoperiods.

In some climates with long growing seasons, floral initiation in southern highbush occurs in both early and late summer on new growth. In the Corinidk Plateau of New South Wales (Wright, 1993), central Mexico and northeastern Buenos Aires Province, Argentina, floral initiation occurs on 1-year-old shoots after the first harvest (spring shoots) and then again on new growth later in the summer (summer shoots). These two periods of floral induction result in multiple crops in Mexico and New South Wales, but not in Argentina where the first flush of floral initiation remains dormant until the following year. Late summer temperatures in Argentina may inhibit floral development.

Temperature also has a dramatic effect on root, shoot and fruit growth in highbush and rabbiteye blueberries. Abbott and Gough (1987) found that peaks in the root growth of mature highbush blueberries grown in sawdust mulch occurred when temperatures were between 14 and 18°C. Spiers (1995) reported that root, shoot and total dry weight in containerized southern highbush and rabbiteye cultivars was negatively correlated with root temperatures from 16 to 38°C.

Bloom date, ripening interval and harvest dates vary greatly in highbush and rabbiteye blueberries (Lyrene, 1985; Hancock et al., 1991; Finn et al.,

### Table 3.4. Average number of flowers per plant on three varieties of highbush blueberry during 8 weeks of photoperiod treatment at 18°C night and 21°C day temperatures. (Adapted from Hall et al., 1963.)

<table>
<thead>
<tr>
<th>Photoperiod (h)</th>
<th>'Coville'</th>
<th>'Earliblue'</th>
<th>'Jersey'</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>14&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>64&lt;sup&gt;b&lt;/sup&gt;</td>
<td>103&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>10</td>
<td>41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>96&lt;sup&gt;b&lt;/sup&gt;</td>
<td>133&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>12</td>
<td>13&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>61&lt;sup&gt;b&lt;/sup&gt;</td>
<td>104&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>14</td>
<td>12&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>26&lt;sup&gt;c&lt;/sup&gt;</td>
<td>15&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>16</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a,b</sup> Mean values within a column with unlike superscript letters were significantly different at P=0.05 level.
2003), and there is a strong interaction with temperature (Carlson and Hancock, 1991). High spring temperatures generally accelerate bloom date and hasten petal drop. Bloom date is strongly correlated with ripening date, but early-ripening cultivars have been developed that have later-than-average flowering dates such as the northern highbush ‘Duke’, ‘Huron’ and ‘Spartan’, and the southern highbush ‘Santa Fe’ and ‘Star’. There is a positive relationship between ripening interval and crop load in half-high cultivars, although genotypes with high yield potential and uniform ripening can be found (Finn and Luby, 1986; Luby and Finn, 1987). Fruit set, size and harvest period in highbush blueberries were greater in a cool greenhouse (8–24°C) than in a warm one (16–27°C) (Knight and Scott, 1964). Fruit set, size and harvest period were lower in rabbiteye blueberries grown under warm night conditions (21°C) compared with cool ones (10°C) (Williamson et al., 1995).

**Chilling requirement**

Blueberries will flower if maintained under long days for extended periods, even if they receive no chilling hours. In highbush blueberries held under 16-h photoperiods, floral bud break occurred eventually after floral initiation, although it was not as uniform as in plants held under a normal dormancy cycle (Hall et al., 1963). Rabbiteye blueberries have been shown to flower and fruit normally under long days without dormancy, if the plants are not defoliated and are vigorous (Sharpe and Sherman, 1970).

Once blueberries enter dormancy, they require a period of low temperatures for normal growth and development to occur (Table 3.5). Highbush cultivars with a range of chilling requirements are now available; with southern highbush ranging from 150 to 800 h, northern highbush ranging from 800 to 1200 h (Norvell and Moore, 1982; Darnell and Davies, 1990), and rabbiteye cultivars requiring 300 to 700 h (Williamson et al., 2002). Too little chilling results in delayed, irregular bud break (Norvell and Moore, 1982; Darnell and Davies, 1990). Spiers (1976) found in the rabbiteye ‘Tifblue’ that floral bud break was more influenced by insufficient chilling hours than was vegetative bud development.

There is some controversy as to what temperatures are most effective in satisfying the chilling requirement of highbush and rabbiteye blueberries. The optimal chilling temperatures for buds of rabbiteye blueberries and southern highbush are thought to be higher than those for northern highbush (Mainland, 1985; Darnell, 2006), although comparative data are limited. Mainland et al. (1977) determined that a constant 0.5°C satisfied the chilling requirement of floral and vegetative buds of the highbush cultivars ‘Croatan’ and ‘Wolcott’, but 6°C was more effective in the rabbiteyes ‘Woodard’ and ‘Tifblue’. They also found that intermittent temperatures above 10.5°C had a negative effect on the number of accumulated chilling hours. Norvell
Table 3.5. Chilling requirement of selected southern highbush and rabbiteye cultivars.

<table>
<thead>
<tr>
<th>Chilling requirement</th>
<th>Cultivar*</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;300</td>
<td>SH: 'Emerald', 'Jewel', 'Misty', 'Prima donna', 'Scintilla', 'Sebring', 'Sharblue', 'Snowchaser', 'Spring high', 'Spring wide', 'Sweetchrisp'</td>
</tr>
<tr>
<td>300-400</td>
<td>SH: 'Abundance', 'Farthing', 'Palmetto'</td>
</tr>
<tr>
<td></td>
<td>RE: 'Savory', 'Woodard'</td>
</tr>
<tr>
<td>400-500</td>
<td>SH: 'Biloxi', 'Camelia', 'Dixieblue', 'O Neal', 'Rebel', 'Southern Belle', 'Southmoon', 'Star'</td>
</tr>
<tr>
<td></td>
<td>RE: 'Alapaha', 'Austin', 'Brightwell', 'Climax', 'Delight', 'Vernon'</td>
</tr>
<tr>
<td>500-600</td>
<td>SH: 'Bluecrisp', 'Gupton', 'Legacy', 'Santa Fe'</td>
</tr>
<tr>
<td></td>
<td>RE: 'Columbus', 'Powderblue', 'Premier'</td>
</tr>
<tr>
<td>600-700</td>
<td>SH: 'Beauford', 'Briteblue', 'Cartaret', 'Centurian', 'Craven', 'Lenoir', 'Ozarkblue', 'Pamlico'</td>
</tr>
<tr>
<td></td>
<td>RE: 'Desoto', 'Ochlockonee', 'Onslow', 'Tifblue'</td>
</tr>
<tr>
<td>700-800</td>
<td>SH: 'New Hanover', 'Sampson', 'Summit'</td>
</tr>
<tr>
<td></td>
<td>RE: 'Ira'</td>
</tr>
<tr>
<td>800-900</td>
<td>SH: 'Arlen', 'Bladen', 'Reville'</td>
</tr>
</tbody>
</table>

*SH, southern highbush; RE, rabbiteye.

and Moore (1982) found that temperatures ranging from 1 to 12°C satisfied the requirements of highbush blueberry for vegetative bud break in 'Coville', but that 6°C was most effective. Alternating 6 to 1°C and 6 to 12°C at weekly intervals had little impact on leaf bud break, compared with constant 6°C.

Gilreath and Buchanan (1981) found that the rate of floral bud break was similar at 0.6, 3.3, 7.0 and 10°C for 'Woodard', 'Bluegem' and 'Tifblue'. At 15°C, the rate of bud break in 'Bluegem' was similar to that at the other temperatures, but the higher temperature slowed the rate of development in the other two cultivars. Diurnal fluctuations of 0/7°C and 7/15°C for 14/10 h had little impact on days to terminal flower bud break compared with constant temperatures. A period of 14 days at 30°C in the middle of the chilling period did not affect the final level of floral and vegetative bud break in plants of 'Woodard', but floral bud break did occur faster in the high-temperature interruption treatment. Spiers (1976) found that an alteration of 10 h at 18°C with 14 h at 7°C delayed floral and vegetative bud break in 'Tifblue', but did not completely nullify the effect of low temperature.

Mainland et al. (1977) and Spiers (1976) recommended that the chilling requirement of blueberries be estimated using a modification of the Utah Chill Unit Model for peach (Table 3.6). This was proposed to take into consideration that the chilling requirement of highbush and rabbiteye blueberries is at least partially satisfied by temperatures below 1.4 and up to 12.4°C. More fine-tuning is likely necessary for individual cultivars, as responses to higher temperatures may vary. Gilreath and Buchanan (1981) found that
Table 3.6. Conversion of selected temperatures to chill units for peach, highbush blueberry and rabbiteye blueberry. (Adapted from Spiers, 1976; Norvell and Moore, 1982.)

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Chill units</th>
<th>Temperature (°C)</th>
<th>Chill units</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Peach</td>
<td>Highbush</td>
<td>Rabbitsye</td>
</tr>
<tr>
<td>&lt;1.4</td>
<td>0.0</td>
<td>0.5</td>
<td>&lt;2</td>
</tr>
<tr>
<td>1.5–2.4</td>
<td>0.5</td>
<td>0.5</td>
<td>3–5</td>
</tr>
<tr>
<td>2.5–9.1</td>
<td>1.0</td>
<td>1.0</td>
<td>6–15</td>
</tr>
<tr>
<td>9.2–12.4</td>
<td>0.5</td>
<td>0.5</td>
<td>15–18</td>
</tr>
<tr>
<td>12.5–15.9</td>
<td>0.0</td>
<td>0.0</td>
<td>19–24</td>
</tr>
<tr>
<td>16–18</td>
<td>-0.5</td>
<td>-0.5</td>
<td>22–24</td>
</tr>
<tr>
<td>&gt;18</td>
<td>-1.0</td>
<td>-1.0</td>
<td>&gt;25</td>
</tr>
</tbody>
</table>

fewer chilling hours were required for lateral floral bud break in 'Tifblue' at 3.3°C (450–650 h) than at 7.0 or 10°C (650–850 h), while there was little difference in chilling requirement across the same temperatures in 'Bluegem'. Shine and Buchanan (1982) also found that the chilling temperature optimum and effective range of 'Aliceblue' (7.2°C optimum, -2.5 to 15.9°C range) and 'Woodard' (11.0°C, -2.5 to 13.8°C) were higher and broader than those of 'Tifblue' (6.7°C, -1.2 to 12.9°C). Southern highbush cultivars with complex ancestry may be particularly variable in their temperature thresholds, although this has not been documented.

Damage from cold

Winter cold often causes severe damage to blueberry flower buds and young shoots in the colder production regions. The key to survival in very cold temperatures is the ability to limit ice crystal formation to bud scales, floret scales and bud bracts (Flinn and Ashworth, 1994). In general, northern highbush types survive much colder mid-winter temperatures than rabbiteye and southern highbush cultivars, although considerable variability exists (Hancock et al., 1987; Ehlenfeldt et al., 2003, 2006; Hanson et al., 2007). In full dormancy, northern highbush genotypes have been found to range in tolerance from -20 to -30°C, while rabbiteye genotypes range from -14 to -22°C. Few southern highbush have been evaluated, although 'Legacy' has been found to tolerate temperatures down to -17°C and 'Ozarkblue' to -26°C. 'Sierra', which is composed of 50% southern germplasm, has tolerated temperatures below -32°C (J.F. Hancock, personal observation). The wood of half-high cultivars, such as 'Northblue', can survive to -40°C and their flower buds can tolerate -36°C (C.E. Finn, personal communication).

Spring frosts commonly damage flower buds of all blueberry species. Overall, southern highbush flower buds and developing flowers appear to be
more cold-tolerant than rabbiteye flower buds (Lyrene, 2008) and northern highbush flower buds tend to be more tolerant than southern highbush types. Those cultivars with late bloom dates tend to suffer less frost damage than those flowering earlier because frosts are less common and the stage of floral development is correlated with relative bud hardiness (Hancock et al., 1987; Lin and Pliszka, 2003). Terminal flower buds also tend to be less hardy than median or basal buds (Biermann et al., 1979; Cappiello and Dunham, 1994), and styles are more sensitive to cold than corollas. In controlled experiments, NeSmith et al. (1999) showed that ovaries in opened flowers of the rabbiteye ‘Brightwell’ could withstand −4.4°C, while styles survived −3.4°C and corollas −3.8°C.

Considerable variation in the frost tolerance of highbush cultivars has been noted. After a −6°C evening, Bailey (1949) found a wide range of damage (10–74%) among nine highbush cultivars in Massachusetts when blossoms were distinctly separated but corollas were still closed. Johnston (1939) observed damage ranging from 10 to 58% in seven cultivars after a similar freeze in Michigan. Reiman (1977) found ‘Blueray’ and ‘Darrow’ to have more buds killed (7–10%) than ‘Bluecrop’, ‘Lateblue’ and ‘Jersey’ (0–1%) after an evening of −8.5°C in Poland. Lin and Pliszka (2003) found that ‘Lateblue’ had significantly less damage (11%) than seven other cultivars that bloomed much earlier (52–84%) after a night of −6°C in Poland. When Hancock et al. (1987) assessed flower bud injury in 17 highbush blueberry cultivars after two spring frosts in Michigan, they found significant differences in the proportion of brown ovaries among cultivars, ranging from 25 to 94% (Table 3.7). Most of the variation was associated with stage of bud development.

Spiers (1978) found that the temperature required to damage floral buds in rabbiteye blueberries was also inversely related to their development, similar to highbush blueberries. Swollen buds with individual florets still enclosed withstood temperatures of −6°C, those with individual flowers exposed after the bud scales abscised were killed at −4°C, those with well-separated flowers before corolla expansion survived to −2°C and fully opened flowers were killed at 0°C. A comparison of percentage of buds killed in rabbiteye blueberries after a night of −9°C in Mississippi found that ‘Delite’ (98%) and ‘Woodard’ (85%) showed the greatest damage, ‘Climax’ (53%), ‘Briteblue’ (56%), ‘Southland’ (63%) and ‘Tifblue’ (63%) had the least (Spiers, 1981). These plants were in a later stage of floral development where the individual flowers could be discerned but were not distinctly separated. Gupton (1983) found that fully opened flowers of ‘Southland’ were much harder at −2°C than those of ‘Delite’, ‘Woodard’, ‘Climax’ and ‘Tifblue’.

Rate of deacclimatization likely plays a role in early spring flower bud tolerance. Ehlenfeldt et al. (2003) found that the northern highbush ‘Duke’ deacclimatized fastest in a mixed group of 12 cultivars, while the southern highbush ‘Magnolia’, the northern highbush x rabbiteye pentaploid hybrid ‘Pearl River’, the rabbiteye x Vaccinium constablaei cultivar ‘Little Giant’ and the
Table 3.7. Developmental stage and proportion of brown ovaries in terminal flower buds of 17 highbush cultivars in Michigan after spring freezes in 1983 and 1986. (Adapted from Hancock et al., 1987.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Developmental stage</th>
<th>Proportion of brown ovaries</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1983</td>
<td>1986</td>
</tr>
<tr>
<td>'Elliott'</td>
<td>2.0</td>
<td>3.7</td>
</tr>
<tr>
<td>'Lateblue'</td>
<td>2.0</td>
<td>3.2</td>
</tr>
<tr>
<td>'Rubel'</td>
<td>2.0</td>
<td>4.6</td>
</tr>
<tr>
<td>'Coville'</td>
<td>2.2</td>
<td>4.2</td>
</tr>
<tr>
<td>'Bluejay'</td>
<td>2.7</td>
<td>4.8</td>
</tr>
<tr>
<td>'Berkeley'</td>
<td>2.5</td>
<td>4.3</td>
</tr>
<tr>
<td>'Jersey'</td>
<td>2.0</td>
<td>4.5</td>
</tr>
<tr>
<td>'Spartan'</td>
<td>2.5</td>
<td>4.8</td>
</tr>
<tr>
<td>'Bluecrop'</td>
<td>2.2</td>
<td>5.0</td>
</tr>
<tr>
<td>'Collins'</td>
<td>2.0</td>
<td>6.0</td>
</tr>
<tr>
<td>'Bluejay'</td>
<td>2.7</td>
<td>4.8</td>
</tr>
<tr>
<td>'Darrow'</td>
<td>2.5</td>
<td>4.5</td>
</tr>
<tr>
<td>'Earliblue'</td>
<td>2.7</td>
<td>5.4</td>
</tr>
<tr>
<td>'Meader'</td>
<td>2.0</td>
<td>4.0</td>
</tr>
<tr>
<td>'Bluetta'</td>
<td>2.5</td>
<td>5.6</td>
</tr>
<tr>
<td>'Patriot'</td>
<td>2.5</td>
<td>5.6</td>
</tr>
<tr>
<td>'Bluehaven'</td>
<td>3.0</td>
<td>4.9</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.5</td>
<td>0.8</td>
</tr>
</tbody>
</table>

*1 = first swell, 2 = scales separated, 3 = terminal florets exposed, 4 = all florets exposed, 5 = florets separated, 6 = corollas expanding.

Half-highs 'Northcountry' and 'Northsky' were the slowest. Northern highbush 'Bluecrop' and 'Weymouth', southern highbush 'Legacy' and 'Ozarkblue', and rabbiteye 'Tifblue' were intermediate.

Flower buds can also be damaged by rapid freezes in the autumn. The flower buds of rabbiteye and southern highbush cultivars are generally considered to acclimatize more slowly in the autumn than those of northern highbush cultivars and as a result are more subject to late autumn freezes (Rowland et al., 2005; Hanson et al., 2007). Hanson et al. (2007) found that leaf retention in autumn was not a good predictor of rate of deacclimatization, as 'Ozarkblue' and US 245 retain their leaves until the very late autumn, but they are just as hardy as the mid-season standard 'Bluecrop'. Bittenbender and Howell (1975) also found no correlation between flower bud hardiness and autumn leaf retention.

Blueberry fruit set is also very sensitive to cold damage, although data are limited in highbush blueberry. Hall et al. (1971) found decreases in fruit set in lowbush blueberry ranging from 42 to 77% by holding plants for 4 h at -2°C or 2 h at -3°C. Results were similar whether the cold was presented right after
pollination or 6 days later. NeSmith et al. (1999) showed that plants exposed to -1°C for 1 h after flowering had significantly reduced fruit set without any visible damage.

CONCLUSIONS

All species of *Vaccinium* are woody perennials, ranging in height from 0.1 to 0.15 m in lowbush, 1.8 to 4.0 m in highbush, and up to 6 m in rabbiteye. Blueberry shoots emerge from buds located in the crown. One-year-old blueberry shoots typically form flower buds at the top, with the vegetative buds located below. Winter cold often causes severe damage to blueberry flower buds and young shoots in the colder production regions. In full dormancy, northern highbush genotypes range in cold tolerance from -20 to -30°C, while rabbiteye and southern highbush genotypes range from -14 to -26°C. Spring frosts commonly damage flower buds of all blueberry species. Root and shoot growth occurs in cycles; root growth is greatest in the early spring and autumn, while shoot growth occurs in two or three flushes during the growing season. Individual shoots initially grow rapidly and then stop due to apical abortion, which is called 'black tip'. Over 80% of the root dry mass is found in the top 36 cm. Most floral initiation occurs under short days and the chilling requirement of cultivars varies greatly. Cultivars are now available with an almost continuous range of chilling requirements: from 150-800 h in southern highbush, to 800-1200 h in northern highbush, and 300-600 h in rabbiteye cultivars. There is some controversy on what temperatures are most effective in satisfying the chilling requirement of highbush and rabbiteye blueberries, but most researchers use a modification of the Utah Chill Unit Model for peach. A pollinator is necessary in blueberries and a wide range of self-fertility is found among blueberry cultivars due to early-acting inbreeding depression. Rabbiteye blueberries are less self-fruitful than highbush types. The fruit is a true berry with many seeds, and it ripens two to three months after pollination. Seed number has a significant influence on final fruit size. All blueberry fruit exhibit a double sigmoid growth curve with a fruit development period ranging from 42 to 92 days in northern highbush, from 55 to 60 days in southern highbush, and from 60 to 135 days in rabbiteye. After fruit colour change, the percentage of total sugars increases while titratable acidity decreases, resulting in a steady increase in the sugar/acid ratio during ripening.

REFERENCES

Chapter 3


Growth and Development


INTRODUCTION

In this chapter a global vision of the physiology (functioning) of a blueberry plant is described with regard to the generation and distribution of carbohydrates. We look at the factors that are involved in dry matter production and partitioning among the various plant organs, as well as the effect of several environmental variables and management practices on dry matter partitioning to vegetative and reproductive organs.

The plant is a set of organs (roots, shoots, leaves and fruits) that grow and develop harmonically. Most of the dry matter (what is left after removal of water from tissues) is carbohydrates, which is the main product of the photosynthetic process. During photosynthesis, solar energy is converted into chemical energy, which is then transformed into different compounds and stored in various organs within the plant, among which are the fruits (Fig. 4.1). In order for a crop, such as blueberry, to be productive in the long term, there is a need to provide the conditions to maintain high rates of photosynthesis and also establish equilibrium in the partitioning of carbohydrates to the various organs that are growing in the plant.

FACTORS THAT AFFECT YIELD

For any crop (including blueberries), yield ($Y$) can be expressed as the product of the amount of photosynthetically active radiation (PAR) that reaches the crop in a given period ($I_o$), the fraction of PAR intercepted by the crop ($F_{PAR}$), the efficiency with which the canopy converts that radiation into new biomass (radiation-use efficiency, $E$) and the proportion of the carbohydrates that are apportioned to harvestable organs (harvest index, $H$):

$$Y = I_o \cdot F_{PAR} \cdot E \cdot H \quad (4.1)$$

In order to reach high and sustained yields, the cultural practices must be focused on maximizing the level of each individual factor.
The quantity of PAR that arrives to a blueberry field defines the amount of energy available for the growth and development of the crop. Such quantity of radiation is a function of the season of the year and the geographical zone in which the orchard is located; also, in the short run, this radiation will vary according to cloudiness and competition with other plants in that environment (Table 4.1).

The great majority of blueberry varieties (both rabbiteye and highbush) are hybrids of different blueberry species (see Chapter 2). The materials used for generating varieties originate from temperate latitudes and such species

**Table 4.1.** Summer and winter months' averages of daily solar radiation (photosynthetically active radiation, PAR, in W/m²) for various zones where blueberries are cultivated.

<table>
<thead>
<tr>
<th>Location</th>
<th>Latitude</th>
<th>Summer</th>
<th>Winter</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Fernando, Chile</td>
<td>34°35'S</td>
<td>244.0</td>
<td>99.1</td>
<td>Sarmiento (1995)</td>
</tr>
<tr>
<td>Collipulli, Chile</td>
<td>37°55'S</td>
<td>224.9</td>
<td>85.7</td>
<td></td>
</tr>
<tr>
<td>Karlsruhe, Germany</td>
<td>49°03'N</td>
<td>385.1</td>
<td>137.2</td>
<td>Hader et al. (2007)</td>
</tr>
<tr>
<td>Pisa, Italy</td>
<td>43°43'N</td>
<td>390.3</td>
<td>180.4</td>
<td></td>
</tr>
<tr>
<td>Malaga, Spain</td>
<td>36°43'N</td>
<td>414.2</td>
<td>219.4</td>
<td></td>
</tr>
<tr>
<td>Athens, Greece</td>
<td>37°58'N</td>
<td>393.8</td>
<td>214.1</td>
<td></td>
</tr>
<tr>
<td>Forest Grove, Oregon, USA</td>
<td>45°33'N</td>
<td>226.8</td>
<td>108.0</td>
<td>Bryla et al. (2008)</td>
</tr>
</tbody>
</table>

*a* Seasonal average.

*b* Clear skies.
often live naturally as understorey plants (below deciduous forests), which
means that in their natural environment they grow under intermediate light
intensity and diffuse light (Eck et al., 1990). However, several Vaccinium species
come from open areas in the tropics.

The amount of radiation that a blueberry plant receives not only determines
the potential production of carbohydrates through photosynthesis, but also defines
the fruit quality (colour), plant morphology (shoot length, leaf size, stomatal
density, etc.) and number of flower buds for the next season. This is the reason
why shaded zones within the canopy of plants not only generate a lower amount
of carbohydrates, but also fewer fruits (because of a lower potential to induce
flower buds) that are slower in developing fruit colour (because anthocyanin
formation would be enhanced by light exposure, the pigments which are responsible
for the blue colour of blueberry fruit).

**Light intensity and floral induction**

For fruit crops in general, the formation of flower buds requires at least 30% of
full sun. The light levels needed to induce flower buds in highbush blueberries
have not been published; however, in rabbiteye blueberries minimum light
levels around 25% of full sun have been shown to be required for flower
induction (Table 4.2). Light levels decrease sharply within the canopy; thus,
60 cm from the periphery, light levels are less than 40% of full sun, except
near the end of the season (24 weeks after full bloom, WAFB) when the weight
of fruit opens the canopy (Table 4.2). In the field, it is common to observe
low numbers of fruit in the centre of the canopy, especially in adult plants of
varieties with dense canopies that have not received adequate pruning.

**Table 4.2.** Light availability (percentage of full sun) at different levels within 15-year-
old 'Choice' rabbiteye blueberry plants during the season (in terms of weeks after
full bloom, WAFB) and the number of flower buds at each level the following
winter. Data are for Cato, Chillán, Chile (36°21'S, 71°50'W). (Adapted from Yañez et
al., 2009.)

<table>
<thead>
<tr>
<th>Canopy level</th>
<th>Height (cm)</th>
<th>Percentage of full sun</th>
<th>Flower buds/cane (winter)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8 WAFB</td>
<td>13 WAFB</td>
<td>24 WAFB</td>
</tr>
<tr>
<td>1</td>
<td>180-200</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>2</td>
<td>160-179</td>
<td>75</td>
<td>69</td>
</tr>
<tr>
<td>3</td>
<td>140-159</td>
<td>38</td>
<td>39</td>
</tr>
<tr>
<td>4</td>
<td>120-139</td>
<td>21</td>
<td>25</td>
</tr>
<tr>
<td>5</td>
<td>100-119</td>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td>6</td>
<td>80-99</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>7</td>
<td>60-79</td>
<td>4</td>
<td>13</td>
</tr>
</tbody>
</table>
Another important factor influencing fruit load is that sufficient light must be present during specific periods for floral induction to occur. Gough (1994) speculated that increased canopy density might reduce flower bud initiation. Information from morphological studies of buds, and also on the use of the growth regulator gibberellic acid to alter the magnitude of flower induction (Retamales et al., 2000), framed flower induction in highbush blueberries to occur around 12–17 WAFB. To test this, an experiment was conducted in south-central Chile on 14-year-old rabbiteye blueberries cv. ‘Choice’, in which canopies were opened for 4 weeks at different times during the season (Yañez et al., 2009). It was found that the timing of canopy opening does indeed have a major impact on flower bud induction. However, flower induction would occur earlier in rabbiteye as compared with highbush blueberry, since opening the canopy in December (which corresponds to 8–12 WAFB) almost doubled the total number of flower buds per cane in this rabbiteye blueberry variety, especially in the 100–179 cm range. It was also observed that most flower buds were induced at the top 60 cm of the canopy in all treatments (Table 4.3).

**Shading and blueberry performance**

As mentioned above, many native blueberries grow in the shade; thus the commercial cultivation of these plants in the open field likely would subject them to light and temperature stress. For this reason, the use of shading nets

<table>
<thead>
<tr>
<th>Height (cm)</th>
<th>8–12 WAFB</th>
<th>13–17 WAFB</th>
<th>18–23 WAFB</th>
<th>24–28 WAFB</th>
<th>29–33 WAFB</th>
</tr>
</thead>
<tbody>
<tr>
<td>180–200</td>
<td>7.1</td>
<td>11.4</td>
<td>15.6</td>
<td>10.4</td>
<td>5.8</td>
</tr>
<tr>
<td>160–179</td>
<td>14.9</td>
<td>32.2</td>
<td>20.1</td>
<td>23.4</td>
<td>29.0</td>
</tr>
<tr>
<td>140–159</td>
<td>13.2</td>
<td>26.6</td>
<td>11.6</td>
<td>17.7</td>
<td>26.4</td>
</tr>
<tr>
<td>120–139</td>
<td>10.8</td>
<td>16.1</td>
<td>5.8</td>
<td>8.0</td>
<td>11.1</td>
</tr>
<tr>
<td>100–119</td>
<td>2.6</td>
<td>7.3</td>
<td>2.3</td>
<td>2.4</td>
<td>5.8</td>
</tr>
<tr>
<td>80–99</td>
<td>3.4</td>
<td>3.3</td>
<td>0.8</td>
<td>1.3</td>
<td>0.9</td>
</tr>
<tr>
<td>60–79</td>
<td>1.3</td>
<td>0.6</td>
<td>0.9</td>
<td>0.4</td>
<td>0.3</td>
</tr>
<tr>
<td>40–59</td>
<td>0.8</td>
<td>0.1</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>20–39</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>0–19</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Total</td>
<td>55.3</td>
<td>100.1</td>
<td>56.9</td>
<td>63.6</td>
<td>79.2</td>
</tr>
</tbody>
</table>
Yield in Blueberries

(Also known as photoselective films) in areas of high solar irradiance might reduce stress and allow for better growth and higher yields (Lobos et al., 2009). Such increases in yield were obtained in experiments done in central Chile (latitudes 35–37°S) (Table 4.4), as well as in Michigan, USA (latitude 42°N) (Fig. 4.2).

Shading can alter various characteristics of blueberries, among which are: (i) radiation availability and quality; (ii) physiological traits such as leaf photosynthesis, stomatal conductance and chlorophyll fluorescence ($F_v/F_m$); (iii) leaf characteristics such as angle, weight, temperature, and chlorophyll and nitrogen contents; (iv) fruit yields; and (v) fruit quality (soluble solids, size, colour, weight loss).

Radiation availability and quality

It has been found that the percentage shading provided by suppliers of nets does not always correspond to the light availability for the plant, thus results may vary depending on actual shade provided. Net colour can affect plant responses. Results showed that red nets had the highest alteration of light quality, especially in the 430–590 nm range (Lobos et al., 2011).

| Table 4.4. Effect of the use of shading nets (for two seasons on the same plants) on photosynthetically active radiation (PAR) levels and the yield of 'Berkeley' highbush blueberries (planted in 1994). Data are for Miraflores, Linares, Chile (35°S). (Adapted from Retamales et al., 2008.) |
|-------------------------------------------------|-----------------|-----------------|-----------------|
| Treatment                                       | Net colour      | % shading       | Total (W/m²)    | 2003–2004        | 2004–2005        | Effect on yield (% of control) |
| Control                                         | –               | 910             | 12.5”c           | 22.1”c’d         | –               |
| Black                                           | 50              | 495             | 12.1”c           | 16.0”e           | -18.8           |
| Black                                           | 35              | 500             | 17.2”hbc         | 20.4”hle         | +8.7            |
| White                                           | 35              | 710             | 13.9”hbc         | 26.6”hbc         | +17.1           |
| Red                                             | 35              | 695             | 16.5”hbc         | 24.6”hbc’d       | +18.8           |
| Grey                                            | 50              | 640             | 18.0”hbc         | 27.6”hbc         | +31.8           |
| Grey                                            | 35              | 685             | 20.0”hbc         | 27.8”hbc         | +38.2           |
| Red                                             | 50              | 625             | 23.0”hbc         | 29.4”hbc         | +51.4           |
| White                                           | 50              | 706             | 23.9”hbc         | 32.2”hbc         | +62.1           |

PAR was measured in February–March 2004; yield was estimated based on 3300 plants/ha; effect on yield is the 2-year average.

Average values within a column with unlike superscript letters were significantly different at $P<0.05$ level (Duncan test).
Fig. 4.2. (a) Total chlorophyll content, (b) chlorophyll a/chlorophyll b ratio, (c) total chlorophyll/leaf nitrogen ratio and (d) chlorophyll fluorescence (maximum PSII photochemical activity, \(F_{v}/F_{m}\)) in relation to light level (percentage of photosynthetically active radiation, %PAR). Data were obtained 7 days before harvest from ‘Elliott’ plants growing under nets of different colours: black (○, ■), red (□, ■) and white (△, ■), and control at full sun (☆, ★), in two locations: Chillán, Chile (open symbols) and Gobles, Michigan, USA (closed symbols). Bars show standard error. (Adapted from Lobos et al., 2011.)

**Physiological traits**

Studies done in the USA (Lobos et al., 2009) showed that leaf photosynthesis decreased linearly as shading intensity increased. The red and black nets at 70% shading had the lowest rates. Stomatal conductance was not significantly altered by shading treatments. Chlorophyll fluorescence (measured as \(F_{v}/F_{m}\)) also increased linearly with the percentage of shading (Fig. 4.2(d)), being significantly lower in plants without shading (control) than in bushes under 70% shading (white, black or red). Nevertheless, no treatment was below 0.8, which is considered a normal level for non-stressed plants.

**Leaf characteristics**

Experiments done on cv. ‘Brigitta’ in Chile during the 2008/09 season showed that as shading increased, the leaf angle increased. Thus, while leaves in the control treatment had a 25° angle, leaf angles under white nets
with 25 and 70% shading were 45° and 63°, respectively (Cobo, 2010). In trials done in Michigan with cv. ‘Elliott’ (Lobos et al., 2009), leaf dry weight under the various nets was negatively correlated with percentage of shading (R=0.85). Leaf temperature decreased as shading increased (R=0.92), with ranges between 29.9°C (control) and 26.4°C (black 75%). No matter what net colour was used for shading, leaves under shade increased their chlorophyll (the light-collecting pigment within leaves) content as shading intensity increased (R=0.91 and 0.93 in USA and Chile, respectively) (Fig. 4.2(a)), presumably to compensate for lower light intensity. The same tendency was observed in the total chlorophyll/leaf nitrogen ratio (Fig. 4.2(c)), with it being significantly (P<0.01) lower in plants without shading (control) compared with plants under 75% shading (white, black or red). Chlorophyll a/chlorophyll b ratio showed a positive correlation with %PAR (Fig. 4.2(b)). The increase in both total chlorophyll content and total chlorophyll/leaf nitrogen ratio, as well as the decrease of chlorophyll a/b, as the level of shade increased clearly indicate an acclimatization response of highbush blueberry to the light environment.

**Fruit yields**

Studies done in Chile with highbush blueberry ‘Berkeley’ showed that when 50% shading was used, only black shading decreased yields while the other colours of netting (grey, white or red) markedly increased fruit yields (Retamales et al., 2008). The highest increases in yields were obtained with 50% shading of either red or white nets (Table 4.4). In Michigan (Fig. 4.3), it was observed that nets began to have a negative impact on yields when shading levels were greater than 50%. In the case of black nets, they had a positive effect on yield (20.1% greater than control) only for 25% shading, while with 75% shading they had the strongest negative impact (47.3% lower than control) among all treatments. Red nets had either no impact on yield (at 25 and 50% shading) or a negative impact with 75% shading (28.2% lower than control). White nets produced similar increases in yields at either 25% (16.4% increase) or 50% shading (14.9% increase), while they had the lowest negative impact on yields (−19.4%) among the treatments with 75% shading (Lobos et al., 2009).

**Fruit quality (soluble solids, size, colour, weight loss)**

No effects of shading on fruit quality (fruit size, soluble solids) were detected when 35 or 50% shading (white, black, red or grey nets) was used in Chile (Retamales et al., 2008). In Michigan, the various shading treatments increased fruit weight of cv. ‘Elliott’ but decreased fruit soluble solids, with black nets at 50 and 70% shading having the greatest impact. Colour development was delayed by many of the shading treatments, particularly by
the most severe shading treatments. Black 50 and 70% nets also significantly reduced soluble solid levels (Lobos et al., 2009). There were no significant differences due to the colour or degree of shading of nets on fruit weight loss after storing cv. ‘Berkeley’ fruit for 30 days at 4°C.

These differences between the two sites could in part be explained by higher radiation and ambient temperatures (and higher water stress) in Chile as compared with Michigan. The date when the nets were placed over the fields may also have influenced the yield differences between Michigan and Chile, as the nets were installed immediately after petal fall in Chile while in Michigan they were placed one month after petal fall.

When the different effects are analysed in conjunction, it is clear that blueberries are able to adjust their physiological processes and morphology to varying light levels. Since fruit quality under shading nets is either not affected or increased, the sustained increases in fruit yields and the delays in fruit maturity obtained with the use of shading nets could prove advantageous and profitable in many blueberry-growing regions. Even though the selection of the appropriate net colour and degree of shading would depend on latitude, the results obtained so far indicate that 50% shading using white (grey) or red nets would provide the most benefits. However, since appreciation of fruit colour is greatly impaired under red nets, the use white or grey nets would be the best alternative in most cases.
In agricultural crops, most of the radiation is intercepted by the organs which are specialized for that function, the leaves. However, green fruit can intercept radiation and possess anatomical characteristics that allow them to photosynthesize. In rabbiteye blueberries, fruit photosynthesis provided 85 and 50% of the carbohydrates required by this organ at 5 and 10 days after full bloom, respectively. In a whole season, 15% of the carbohydrates required by the rabbiteye blueberry fruit were generated by this organ (Birkhold et al., 1992; Darnell and Birkhold, 1996).

Since an important function of the leaves is to intercept and utilize solar radiation, it should not come as a surprise that for any crop there is a high association between total foliar area (number of leaves \times average leaf size) and the amount of intercepted radiation; the association is somewhat weaker between foliar area and total production of dry matter. In rabbiteye blueberries, a high association or correlation ($r=0.77$) has been established between canopy volume and yield. A sensitivity analysis in apples revealed that light interception was influenced most by changes in leaf area and leaf optical properties (Green et al., 2003).

The quantity of radiation intercepted by a crop at a given time will depend, among other factors, on: (i) plant density (number of plants per hectare); (ii) early cropping; (iii) rate of leaf development; (iv) leaf area duration (period from leaf unfolding until leaf drop); (v) rate of leaf area removal (the speed at which leaves are detached or removed from the plant); and (vi) distribution of leaves within the plant (plant architecture).

**Plant density**

In all fruit crops, denser plantings have higher early yields per hectare than less dense plantings. This could be a function of the surface area of leaves, but the effect tends to level off as the plantings fill up the allotted space and the block of plants reaches maximum light interception. Strik and Buller (2002) found that cumulative yield of the mid-season highbush variety ‘Bluecrop’ from years 3 to 7 was 104% higher at an in-row spacing of 0.45 m compared with 1.2 m, but to our knowledge, no other research has been done examining the long-term effect of planting density in blueberries. If the crop canopy becomes too dense, several negative side-effects can occur: (i) fruit bud induction and colour development could be impaired; (ii) spray coverage becomes more difficult; (iii) pruning would need to be more intense; and (v) drying of above-ground organs after rain or overhead sprinkler would be slower.
Early cropping

Since leaves have to compete for carbohydrates with other organs, another factor that affects canopy development is the fruit load in the first years of the orchard. In an experiment to establish the effect of early cropping on the performance of highbush cultivars 'Duke' (early), 'Bluecrop' (mid-season) and 'Elliott' (late), it was found that plant growth at the start of year 3 was adversely impacted by early cropping in years 1 and 2. Evaluations done in year 3 showed that early cropping reduced the dry weight of the root system, crown and 1- to 3-year-old wood in all cultivars. Early-cropped plants had a lower percentage of fruit buds than control plants. In addition, early cropping reduced yield by 44, 24 and 19% in year 3, compared with control plants, in 'Elliott', 'Duke' and 'Bluecrop', respectively (Strik and Buller, 2005). In their trials, Strik and Buller found that early cropping did not improve cumulative yield (years 1 to 4) of 'Bluecrop' and 'Duke', and significantly reduced cumulative yield in 'Elliott'. This supports the hypothesis that early cropping is more stressful on late-season cultivars, since the fruit is competing with vegetative growth for a longer period. Thus, there is a long-term risk associated with early cropping.

Rate of development of leaf area

In perennial crops, such as blueberries, the rate of leaf area development is greater than in annual crops. This is because perennial fruit crops already have an existing structure (roots, canes of different sizes, laterals, buds), and only require the opening of leaf buds to expose the foliage that will allow them to capture sunlight. Most temperate-zone plants, including blueberry, enter a dormant period during late autumn and winter which is characterized by no growth and greatly reduced metabolic activity of above-ground parts. This dormant condition is a defence mechanism which enables plants to survive cold. The development of dormancy and cold hardiness is a gradual process which begins in late autumn or early winter in response to shorter days and lower temperatures during the autumn (see Chapter 3).

Once fully dormant, a blueberry plant must be exposed to a period of cool temperatures before it will break dormancy and grow normally the following spring. It is known that the chilling requirement varies according to the species and cultivar. Temperatures between 0 and 7°C appear to be most effective at satisfying the chilling requirement of blueberries; while temperatures between 7 and 13°C contribute little to chilling and temperatures above 21°C in late autumn and winter probably negate some chilling (Lyrene and Williamson, 2004). Darnell and Davies (1990) found in rabbiteye blueberries that the percentage of vegetative bud break (calculated as the amount of bud break at a given chilling time relative to the maximum amount of bud break which
Yield in Blueberries

increased with increasing chilling duration (100 to 1000 h at 7°C) in all cultivars (‘Tifblue’, ‘Climax’ and ‘Woodard’). Another factor that affects the accumulation of chilling is the presence of leaves; thus, in regions with mild climates, leaves remain attached to the plants and the bushes will not accumulate chilling as quickly as defoliated plants (Lyrene and Williamson, 2004). In highbush and rabbiteye blueberry, the emergence of leaves might occur simultaneously with bloom (as in ‘Bonita’ rabbiteye), before bloom (as in ‘Climax’ rabbiteye) or after bloom (as in most blueberry cultivars in mild climates such as Florida) (Lyrene and Williamson, 2004). When the emergence of flower buds occurs before leaf emergence, the development of flowers will depend for several days exclusively on carbohydrate reserves from the previous season.

Leaves of most crops are photosynthetically self-sufficient when they reach a third to half their final size. Before that, they depend on stored reserves or surplus carbohydrate from mature leaves. Leaves of rabbiteye blueberry approach maximum photosynthetic potential at full expansion (Andersen et al., 1979). However, the rate at which leaf gas exchange declines after full expansion is extremely species dependent; ageing is associated with the reduction of leaf osmotic potential, lower responsiveness of stomata to climatic variations, lower nitrogen and chlorophyll contents, and reduced maximum rates of leaf gas exchange (Andersen et al., 1979; Andersen, 1989).

Under conditions of high competition for carbohydrates between vegetative and reproductive growth, carbohydrate availability can restrict or delay leaf area expansion. This condition is due to: (i) an unusually high number of fruit produced the previous season (this effect is especially deleterious in late varieties because fruit growth will consume for a longer period the carbohydrates that could otherwise go to storage); (ii) environmental conditions that reduce the photosynthetic rate (cold temperatures, low light intensities); or (iii) an excessively high fruit load at the time of leaf expansion in the spring, especially in those varieties where leaves and flowers develop simultaneously.

Leaf area duration

If winter temperatures are mild, rabbiteye and southern highbush blueberries will retain an important proportion of their leaves during winter, while highbush blueberries lose their foliage in autumn as day length gets shorter and minimum temperatures approach freezing. The retention of some leaves by certain blueberry species and varieties will reduce their accumulation of chilling in the autumn and winter, which will delay bud break and canopy development (Lyrene and Williamson, 2004). Trials in rabbiteye blueberry showed that the reduction in final fruit load caused by defoliation was restricted only to the flower buds in the vicinity of the defoliation and that
a late defoliation (when natural leaf fall was starting) did not alter plant performance (Lyrene, 1992).

At the time buds open in the spring, up to six leaf primordia exist in each vegetative blueberry bud. As the shoot grows after bud opening, a new leaf bud will be formed about every 5 days in the shoot apex. Growth of individual shoots of the blueberry is simpsoidal (zigzag or irregular form) and episodic, being accompanied by a varying number of apical abortions ('black tip stage'). Each abortion terminates a 'flush' of growth (Eck et al., 1990). The aborted shoot apex usually remains visible on individual shoots for a short period, after which it falls off and usually the next bud down resumes growth (next flush). The length of individual shoots and the number of flushes that occur on a single shoot vary and may affect the potential number of flower buds. Recent research (Bañados, 2006) has found that the late-season cultivar 'Elliott' had more flushes of shoot growth (four or five) than early-season or mid-season cultivars like 'Duke' and 'Bluecrop'.

Nutrition and soil mulching can markedly influence shoot growth. In mature 'Bluecrop', high rates of nitrogen (200 kg N/ha versus 0 or 100 kg N/ha) increased the number of vigorous shoots per bush and the number of flushes of growth (three flushes instead of two; Bañados, 2006). Mulching or amending the soil with sawdust in 2- to 4-year-old 'Bluecrop' plants produced more and longer shoots than when bark was used (Kozinski, 2006). During fruit maturation in mid-summer, fruits provide a highly competitive sink for nutrients and carbohydrates, considerably reducing the availability of resources to other parts of the plant (Gough, 1994). Consequently, leaf expansion will be reduced near fruit harvest, and another flush of vegetative growth will occur after fruit harvest (if temperatures are adequate). The effect of competition between leaf and fruit tissues is local, as leaves of the current season (without fruit) have greater vigour and are larger than those of the previous season (when the fruit are swelling).

The expansion and development of each leaf is controlled by several meristems (tissues with the capacity to undergo cell division). The form and final size of a leaf depend on the plant's genetic makeup and environmental/cultural factors. For example, only black (35 or 50% shading) or grey nets (50% shading) significantly increased both leaf length and width compared with control (open field) in 'Berkeley' highbush plants, although the leaf length/width ratio was not altered (Retamales et al., 2008).

**Rate of removal of leaf area**

Besides the more or less predictable effects of environment (photoperiod and temperature) on leaf area duration (leaf emergence and leaf fall), there are unpredictable biotic and abiotic stresses that are faced by the crop during a given season and cause the removal of a proportion of the leaf area. In this
context, various abiotic stresses (temperature, soil moisture, salinity) reduce both the photosynthetic rate and the length of time that the leaf remains active. Water stress (both flooding and scarcity of water) will reduce leaf size and accelerate leaf senescence and leaf drop. Both in rabbiteye and highbush blueberry, the photosynthetic rate is reduced significantly after one or two days of flooding (Davies and Flore, 1986a,b); after 10 to 14 days of flooding, the use of carbohydrates by respiration exceeds the formation of these compounds by photosynthesis (i.e. the plant is living on its food reserves). It has been shown that new spring vegetative flushes can be killed by the same temperatures (−2.2°C) that kill open flowers and fruit (Lyrene and Williamson, 2004). Young blueberry plants are sometimes damaged in field nurseries during late autumn and winter if they have not been properly hardened.

Pest damage can also induce early leaf fall and reduce leaf photosynthetic potential. Experiments in 'Premier' rabbiteye and 'Bluecrisp' southern highbush showed that 15–20% of necrotic leaf area caused by the fungus Septoria (S. albopunctata) reduced the photosynthetic rate by 50% (Roloff and Scherm, 2004). Leaves with higher disease severity abscised significantly earlier than healthy leaves. Lyrene (1992) demonstrated that defoliation of rabbiteye blueberries in early autumn resulted in a significantly lower percentage of nodes that produced flower buds the following spring. This evidences the need for early control of pests and diseases that damage the foliage.

Plant architecture

Plant architecture refers to the natural (genetic) or artificial (training, pruning, growth regulators) arrangement of the aerial plant parts. Within each species architectural differences are found in branching intensity, branch extension and leaf display. Such differences in plant architecture have been interpreted in terms of their potential adaptive value in different light environments (Kawamura and Takeda, 2002). As a rule, the higher the density of leaves on the outside of the canopy, the less light is available in the more internal layers. Hence, any training methods that alter plant architecture must focus on maximizing light interception and reducing internal shading. For these goals to be reached, new leaves growing within the canopy should be properly distributed spatially to expand light interception and avoid shading within the plant.

Pruning can have a marked effect in changing plant architecture. Base pruning (elimination of older, poorly illuminated and less productive canes at the centre of plants) is used in many northern climates to reduce the number of canes per plant in mature bushes. This practice can result in yield gains by increasing light penetration into the bush and enhancing flower bud formation (Strik et al., 2006). Fine pruning and chemical thinning of reproductive
organ (through the application of gibberellic acid at flower induction time) can have a positive impact on fruit weight in over-bearing plants, by reducing competition among fruits for limited resources (see section on pruning in Chapter 6).

Plant organs have plastic reactions in response to the environment they face. Depending on the amount of available radiation, plants will alter: (i) shoot elongation (internode length); (ii) foliar angle; (iii) leaf size; and (iv) rate of branching. Leaves fully exposed to the sun are quite different from those that grow under shade; among other variables, shade leaves have greater leaf area, greater leaf angles, reduced thickness and stomatal density, and lower rates of photosynthesis and respiration. Experiments on the effect of shading in cv. 'Berkeley' done in Chile (latitude 35°S) showed that shading had no effect on shoot number; however, internode and shoot length were significantly increased with black nets at both 35 and 50% shading (Retamales et al., 2008).

The ability a plant has to capture solar radiation can be expressed in a number of different ways, but the most commonly used are the leaf area index (LAI) and the leaf/fruit ratio (LF), expressed as numbers of each organ. LAI is defined as the relationship between foliar area (measured only on one side of the leaf) and the area of soil that a plant occupies (related to planting density); the evolution of the LAI is very important not only for photosynthesis, but also with respect to pesticide application, estimation of nutrient status of the plant, and modelling leaf shading in different sectors of the plant (and with it the capacity of the various sectors to induce flowers and grow fruit).

LF relationships have been studied in blueberries. In adult highbush cv. 'Jersey', reductions in fruit weight and the accumulation of soluble solids were observed when LF was below 0.5. Studies done on potted 'Northland' half-high and 'Bluecrop' northern highbush showed that berries on shoots with five leaves per fruit (LF ratio 5:1) matured 3 days earlier, were heavier (22% in 'Bluecrop' and 35% in 'Northland'), had similar soluble solids content and lower titratable acidity (0.58 versus 1.29 in 'Bluecrop' and 0.92 versus 1.00 in 'Northland') than fruits on control shoots with a 1:1 ratio. As compared with the 1:1 ratio, the 5:1 ratio also increased the number of vegetative buds and shoot length in both varieties, while the number of flower buds was not altered in 'Bluecrop' and was reduced in 'Northland' (Suzuki et al., 1998). Blueberry fruit weight has been correlated with shoot vigour (Eck et al., 1990; Suzuki et al., 1998). In young commercial blueberry orchards in Chile, LF relationships of 0.25 to 0.50 have been measured, but the impact of such relationship on current-season fruit quality as well as flower induction for the coming season has not been studied.

Studies done on various wine grape varieties across years and with a variety of training systems discovered that about 0.8 to 1.2 m² leaf area/kg fruit was needed for optimum fruit maturity in vines trained to single-canopy trellis systems and 0.5 to 0.8 m²/kg for vines trained to divided-canopy
trellis systems (Kliever and Dokoozlian, 2005). We have not been able to find similar studies in blueberries; however, maintaining a balance between vegetative and reproductive growth must be needed to optimize blueberry yield and quality. Our subjective observations are that LF between 2:1 and 3:1 should provide an adequate balance. The means to regulate vegetative/reproductive balance are various. Chemical fruit thinning may be a viable method for regulating blueberry crop load (Matta et al., 2005). Fruit size of rabbiteye blueberries has been increased by selective cane removal, while mature highbush blueberries should be pruned annually to reduce overbearing (Eck et al., 1990).

PHOTOSYNTHETIC EFFICIENCY IN TRANSFORMING SOLAR INTO CHEMICAL ENERGY, E

Nearly 90% of the dry matter in plants is derived from the action of photosynthesis (DaMatta, 2007). In this process, carbon dioxide (CO₂) enters through the pores (stomata) located on the surface of leaves as well as fruits. The energy from the light is stored as sugars formed from CO₂ and water (obtained from the soil) in leaf cells that contain substances capable of trapping the light (pigments, such as chlorophyll and carotenes). However, through the same stomata where CO₂ gets into the plant, water is lost to the environment through transpiration (needed to regulate plant temperature and to move nutrients from the soil). A low resistance for CO₂ capture coincides with high permeability to water losses by the plant (Fig. 4.4).

A large proportion of the sugars (40–50%) formed by photosynthesis are used by plants for respiration. Respiration fulfills two vital roles: it generates energy for various functions (stomatal control, translocation of substances, etc.) and it produces the building blocks for the various compounds required by the plant (proteins, hormones, pigments, regulatory and defence compounds, etc.).

Two basic types of respiration have been defined (Fig. 4.5): maintenance (R_m; destined to secure the functioning of the existing plant processes and systems) and growth (R_g; linked to the increase in plant size). A basic axiom is that the plant must always secure enough substrate for R_g; thus, if the carbohydrate supply is reduced due to deleterious environmental conditions or management practices, R_g would have a greater chance to be affected as compared with R_m (Loomis and Connor, 1992).

The final product of photosynthesis is glucose, which through respiration is converted into the other substances needed by the plant. The biochemical efficiency of the transformation of glucose into other compounds is defined as the production value (V_p) or efficiency of conversion (Table 4.5). Thus, from the same amount of initial compound (glucose), almost two times more cellulose or starch will be obtained than protein. Hence, if the plant has to form
Chapter 4

Solar energy absorbed through chloroplasts

\[ \text{CO}_2 + \text{water} \]

Respiratory energy

Given off

Photosynthesis

Carbohydrates + O\(_2\)

Respiration

Taken in

Fig. 4.4. General scheme of photosynthesis and respiration, indicating fluxes of oxygen, carbohydrates, carbon dioxide and water between the plant and the environment. (Adapted from Weinbaum, 1978.)

1 gram CO\(_2\)

Mature (carbon exporting) leaf

0.62 gram carbohydrate

Glucose pool

0.28 gram dry matter

New leaf

CO\(_2\) Maintenance respiration

CO\(_2\) Growth respiration

Fig. 4.5. Scheme of growth and maintenance respiration in fruit crops, including carbon cost of leaf construction. (Adapted from Weinbaum, 1978.)
Table 4.5. Production values (V_p), defined as the efficiency of converting 1 g of glucose into different plant components. (Adapted from Loomis and Connor, 1992.)

<table>
<thead>
<tr>
<th>End product</th>
<th>V_p (g/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sucrose</td>
<td>0.92</td>
</tr>
<tr>
<td>Cellulose, starch</td>
<td>0.86</td>
</tr>
<tr>
<td>Lignin</td>
<td>0.52</td>
</tr>
<tr>
<td>Protein</td>
<td>0.45</td>
</tr>
<tr>
<td>Lipid</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Tissues with a high proportion of compounds with high V_p (such as shoots), its growth potential will be higher than if the tissues to be formed have a low V_p (such as fruits). The global energy efficiency of blueberries is unknown, but it is expected that the efficiency of conversion should be high, since a high proportion of plant tissues contain compounds with high V_p.

The overall efficiency of photosynthesis for agricultural plants is low, since out of a total of 100 units of energy that reach agricultural land in a given period, less than 4 units end up being stored in the different tissues produced by the plant (Long et al., 2006). This occurs because: (i) a large amount of this energy is lost in winter and early spring because there is no leaf tissue to trap solar radiation (a situation that in blueberries can be partially overcome though the use of tunnels or greenhouses); (ii) another part of the energy is reflected from leaves (because a large portion of the light has a quality that does not interact with blueberry leaf pigments); (iii) another proportion of the solar energy is lost due to saturation of the leaf by the radiation (in blueberries the photosynthetic rate reaches a maximum at 40–50% of full sunlight; Fig. 4.6); and (iv) an important proportion is ‘lost’ as heat (due to inefficiency in the conversion of glucose into other compounds through respiration). Thus, even though growers optimize management of blueberries in the field (irrigation, nutrition, use of shading nets, phytosanitary controls, etc.), the maximum amount of the solar energy that a blueberry field can capture approaches only 4% of the total incoming solar energy.

Variables that affect the photosynthetic rate

In any process that requires the participation of different components, the velocity or rate of the process will depend on the level of the variable or component that is the farthest from its optimum value; this concept is known as the Law of the Minimum.
Even though photosynthesis cannot occur without light, excess light can damage plant tissues. The extra light energy that reaches a blueberry leaf must be rapidly dissipated through transpiration to avoid reduction of photosynthetic rates. In blueberries, leaf temperatures at full sun can reach up to 15°C above those of the air. High temperature and drought have deleterious effects on blueberries. It has been reported that rabbiteye types tolerate heat and drought stress better than highbush (Galletta and Ballington, 1996). In their screening of wild species germplasm, Erb et al. (1988a,b) found Vaccinium elliottii, Vaccinium darrowii and Vaccinium ashei to be the most drought-tolerant species and that this trait was transmitted to the hybrid progeny.

Successful adaptation to heat and drought in blueberry may depend on how rates of CO₂ assimilation, transpiration and water-use efficiency are affected by changes in leaf temperatures (Hancock et al., 2008). Studies on Vaccinium corymbosum showed that the temperature optimum was 18–26°C for ‘Jersey’ and 14–22°C for ‘Bluecrop’, while for V. darrowii it was 25–30°C (Moon et al., 1987a). As temperature was increased from 20 to 30°C, the photosynthetic rate was decreased by 30% in ‘Bluecrop’ but only by 20% in ‘Jersey’ and 9% in V. darrowii (Moon et al., 1987a). The authors concluded that ‘Jersey’ and V. darrowii possess a greater tolerance to high temperature and drought conditions, which operates through restriction of water loss by decreasing stomatal aperture via high epicuticular wax deposition (Moon...
et al., 1987b). Considering that the condition favouring survival at higher temperature of V. darrowii is heritable, southern highbush blueberry cultivars, which have a high V. darrowii component in their background (Hancock et al., 2008), may have a greater tolerance to higher temperature than northern highbush blueberry cultivars. It would also indicate that in certain growing regions highbush blueberries are under temperature stress during typical summer days.

As in other fruit crops, photosynthetic rates in blueberries increase as light reaches higher intensities (Fig. 4.6). In dim light, the CO₂ released by respiration exceeds the small amounts of CO₂ fixed by photosynthesis. Further increases in light intensity will eventually allow fixation to begin compensating the loss by respiration. The light intensity at which carbon formation equals expenditure is known as the 'light compensation point' (Fig. 4.6), which for V. darrowii and V. corymbosum is about 50 μmol/m²/s (Moon et al., 1987a). Photosynthesis is eventually saturated as light intensity increases; in blueberry (rabbiteye, northern highbush and V. darrowii), this occurs at about 700–800 μmol/m²/s (Teramura et al., 1979; Moon et al., 1987a) and corresponds to 40–50% of maximum light intensity.

The maximum net photosynthetic rate measured in highbush blueberries (11.5–11.9 μmol/m²/s) is 25–35% higher than that for V. darrowii (Moon et al., 1987a) and double those reported for excised shoots of rabbiteye blueberries (Teramura et al., 1979) and those growing in the field (Andersen, 1989); however, research on potted ‘Tifblue’ rabbiteye blueberries showed rates of 9.0 μmol/m²/s (Wright et al., 1993). As reported by Singsaas et al. (2001), the difference could be due to genetic variability, different environmental conditions or type of plant material used (excised shoots versus plants). Recent experiments on the ‘Elliott’ highbush blueberry in Chile (Lobos et al., 2011) have shown that: (i) the photosynthetic rates in open-field plants are similar to those published previously for this species; and (ii) the presence of fruit generally increases the rate of photosynthesis of nearby leaves by about 20% (probably due to higher demand for carbohydrates).

Since stomatal closure during water stress impedes the diffusion of one of the compounds (CO₂) needed for photosynthesis, water-deficient plants have reduced photosynthetic rates. The photosynthetic rate generally shows a midday depression (Li et al., 2009), which can be explained by: (i) an accumulation of photosynthates in the leaf that stops the photosynthetic process (feedback inhibition); (ii) stomatal closure because transpiration exceeds water absorption and conduction, and thus the leaves undergo temporary water stress; and (iii) a low CO₂ concentration, since the plant has to process a large air volume to obtain the carbon (CO₂) needed for photosynthesis and, if the air is still, the CO₂ available within the leaf (intercellular CO₂) can be a limiting factor (Li et al., 2009).
Chapter 4

Variables affecting respiration

Temperature is the most important environmental factor influencing respiration. Respiration is very low at 0°C (which is used in postharvest handling to extend the life of the fruit) and increases up to a maximum near 38°C. At higher temperatures, the respiratory rate is dramatically reduced due to damage to the enzymes that catalyse the processes. The effect of temperature on the rate of any biological process can be measured through a concept known as $Q_{10}$ (increase in the rate of a process when the temperature is raised by 10°C). The respiratory process has a $Q_{10}$ near 2; this means that the rate of respiration doubles when temperature is increased by 10°C (Fiore and Layne, 1999).

HARVEST INDEX (PROPORTION OF DRY MATTER ALLOCATED TO HARVESTABLE ORGANS), $H$

The total production of dry matter in a plant is a function of the total radiation intercepted (mainly by the leaves). In other words, the plant will increase in size as the leaves are able to intercept more radiation during the season (Green et al., 2003). However, the goal in a blueberry planting is to have a high and sustained production of quality fruit; therefore, management practices must be developed to channel a high proportion of the dry matter produced to the fruit, and this has to be done without altering the long-term productivity of the plant. There are providers or ‘sources’ of carbohydrates and receivers or ‘sinks’ of carbohydrates. In the summer, the most important sources for the plant are the leaves, but in the spring during bud opening and early leaf and floral expansion, the most important sources are the reserve tissues (older shoots, buds, structural roots) (Fiore and Lakso, 1986). Thus, if there are two sinks with similar priority and distance to a given source, the one that has the greatest strength will receive a higher proportion of the carbohydrates and, hence, will have the highest growth potential.

Throughout the life of a blueberry planting, the sinks vary in their importance (Fig. 4.7). Initially there is a greater proportion of carbohydrates assigned to vegetative organs (roots, canes and leaves); the fruit gains increasing importance later on until the productive life of the orchard is complete (usually around 20–30 years after planting). From that point, the relative importance of the fruit as a sink for carbohydrates decreases and this
Yield in Blueberries

Fig. 4.7. Distribution of dry matter in wild highbush blueberries to various organs throughout plant life. (Adapted from Pritts and Hancock, 1985.)

implies that an important part of the resources is assigned to the foliage and, to a lesser extent, to canes and roots (following the priority mentioned above). Retamales and Hanson (1989) found that field-grown 22-year-old "Bluecrop" northern highbush blueberry plants had accumulated a total of 10.1 kg of dry matter and this was partitioned 96.3% to vegetative and 3.7% to reproductive tissues. The distribution among vegetative tissues was: leaves, 7.3%; 1-year-old shoots, 10.7%; 2- to 3-year-old shoots, 13.8%; >3-year-old shoots, 17.0%; crown, 36.3%; and roots, 11.2%.

In order to respond to market requirements, there has been a steady increase in fruit size through breeding; however, there has not been a similar increase in yield, as fruit numbers per plant have reduced concomitantly (Fig. 4.8). This is known as a compensatory effect, which means that yield cannot expand indefinitely, and that for every increase in one variable (in this case, fruit size) another is reduced (in this case, the fruit number per plant has decreased), although not proportionally.

When there is a need to establish the impact of various cultural practices on yield, it is useful to utilize the concept of yield components. The influence of a cultural practice can be evaluated by examining the effects it has on the component parts of yield. In the case of blueberries, these yield components are:

\[
\text{Yield} = \text{Number of canes/plant} \times \text{number of fruit/cane} \times \text{weight/fruit} \quad (4.2)
\]

Statistical methods (path analysis) have been used to define the interactions among these components and between them and yield (Fig. 4.9). In Jersey highbush blueberry, the results of such analysis indicate that the number of fruits/cane is the component with highest incidence on yield (the one that has
Chapter 4

Fig. 4.8. Effect of date the variety was released in highbush blueberry ('Rubel'=1912, 'Jersey'=1928, 'Berkeley'=1949, 'Earliblue'=1952, 'Bluecrop'=1952, 'Blueray'=1955, 'Elliott'=1973 and 'Spartan'=1977) on the size, fruit number and yield. (Adapted from Siefer and Hancock, 1986; Ehlenfeldt and Martin, 2002.)

Fig. 4.9. Representation of the yield components in blueberry cv. Jersey. (Adapted from Siefer and Hancock, 1986.)

the largest positive coefficient assigned in its relationship with yield), followed in descending order by cane number/plant and weight/fruit. Compensatory effects were apparent, as increased fruit numbers negatively impacted on all other yield components.

In the future, market requirements might demand cultural practices focused on greater profitability, including the possibility of producing larger
fruit at the expense of yield. If this becomes the case, it will be beneficial to better understand the impact of various management practices on the yield components in different varieties and productive regions.

CONCLUSIONS

Photosynthesis (the conversion of light energy into chemical energy stored in plant tissues) sustains life on Earth and is fundamental for agricultural productivity. The yield of a crop depends on various factors: capture of solar energy (mainly by leaves), the transformation of this energy into various compounds required by the plant for its activities, and finally the distribution of these compounds among diverse plant organs.

In the different blueberry regions around the world, the availability of radiation is quite variable. This has an impact on cultural practices, particularly pruning and the use of shading nets. Judging from the diverse responses to the use of shading nets in highbush blueberries in Chile and the USA, levels of natural light are excessive for blueberries in Chile, but not in the USA. The colour of the nets is also important, with black nets having (at the same level of shading) more detrimental effects (such as reduced soluble solids and delayed colour development) than white, grey or red nets.

Most of the carbohydrates required for fruit production (85%) come from the radiation intercepted by leaves, which depends, among other factors, on: (i) plant density; (ii) early cropping; (iii) rate of foliage expansion; (iv) duration of leaf area; (v) rate of leaf area removal; and (vi) plant architecture. The capacity of a plant to capture light can be estimated by calculating the leaf area index (LAI) and the relationship between number of leaves and fruits (LF ratio). Even though LAI is very important in evaluating crop development and defining management practices, this variable has not been studied in blueberries. The availability of radiation influences both the quality of the current year crop (colour and level of anthocyanins) as well as flower induction for next year’s crop. A value of 25% of full sun has been established as the critical minimum value to trigger flower induction in rabbiteye blueberries. There is a need to have more studies on this topic in order to define light capture and distribution within the crop throughout the season.

The amount of compounds available for plant growth is a function of the total amount of photosynthesis at a certain period, as well as how much glucose is used through respiration. The rate of photosynthesis depends on various factors, among which are genotype, light intensity and temperature. The photosynthetic rate saturates (reaches its highest level) at 40–50% of maximum light intensity; the rest of the energy must be dissipated through transpiration in order to maintain leaf temperature and, along with it, avoid damage to leaf structures. Photosynthetic rates and temperature optima are similar for highbush and rabbiteye blueberries.
Temperature is the factor with the greatest effect on respiratory rate; the \( Q_10 \) value for respiration is near 2. Two types of respiration have been defined: growth and maintenance. The plant must always secure enough carbohydrate for maintenance respiration. The transformation of glucose into other compounds has specific efficiencies of conversion. As a corollary, since the formation of various compounds has different efficiencies of conversion, the growth capacity of a plant will depend not only on its photosynthetic capacity but also on the proportion of different compounds in its tissues.

In order to maintain the productivity of a plant over the long term, carbohydrates must be provided to its various organs in the quantity and timing that the various organs require. A relationship is established between sources (leaves and reserve organs) and sinks (flowers, fruits, roots, etc.). In the plant, the carbohydrates are distributed according to distance, priority (fruits have the highest priority) and sink strength (joint effect of sink activity and sink size). The sinks vary in their importance throughout the lifespan of a blueberry planting and according to the management practices used (pruning, thinning, nutrition, irrigation, etc.). Through breeding and management practices, strong efforts have been made to increase fruit weight. Even though yield has also increased, due to compensatory effects, it has increased in a lower proportion than fruit size. The effect of management practices on yield can be analysed through the concept of yield components, which for blueberries are canes/plant, fruits/cane and weight/fruit.

There is a close relationship between solar radiation, photosynthesis and yield, but there is a need to conduct research in order to improve our understanding of the interaction among these factors, as well as to obtain a greater knowledge on the effect of various cultural practices performed in different environmental conditions and on different plant materials.

**REFERENCES**


Yield in Blueberries


Yield in Blueberries


INTRODUCTION

The nutrient demand of blueberries is low compared with fruit trees (Table 5.1). Some authors have reported adequate growth and fruiting in rabbiteye blueberries grown for several seasons in low-fertility soils with no fertilizer application (Austin and Brightwell, 1977; Austin and Gaines, 1984). However, in most situations, regular fertilizer applications are usually needed for commercial fields (Hanson and Hancock, 1996; Krewer and NeSmith, 1999). There are various conditions, both in the plant and the soil, which explain the low nutritional requirements of blueberries compared with other fruit crops. Blueberries are said to be calcifuge plants, which means they are adapted to acidic soil conditions. Best growth and productivity are obtained when blueberries grow with soil pH in the range of 4.0 to 5.5. At this pH, the availability of most soil nutrients is limited and this reduces the amount of mineral elements that are absorbed by the plant (Korcak, 1989; Hanson and Hancock, 1996). Blueberry roots are shallow and devoid of hairs (which limits the surface area in contact with the soil), and in natural habitats they are colonized by a specialized type of fungus called ericoid mycorrhizae. Studies on northern highbush showed that increasing fertilization rates decreased ericoid mycorrhizae colonization of ‘Duke’ and had little influence on colonization of ‘Reka’ (Golldack et al., 2001). This type of cultivar-specific response in sensitivity to ericoid mycorrhizae colonization by nutrient availability may be responsible for some of the differences in the frequency and intensity of colonization that were detected among different highbush blueberry cultivars (Scagel, 2005). In addition, the fine root hair system of blueberries demands a loose soil, which makes sandy loams high in organic matter preferable for their cultivation.

There has been a significant expansion in the amount of land planted to blueberries across the world, and as a result soils that are less optimal for blueberry production are often being used. In many cases, amendments such as organic mulches and acidification are needed to provide adequate conditions for plant growth and development.
Table 5.1. Sufficient or normal foliar concentrations of nutrients for highbush blueberries and apple (dry weight basis).

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Highbush blueberry</th>
<th>Apple</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Macroelements (‰)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>1.70–2.10</td>
<td>2.20–2.40</td>
</tr>
<tr>
<td>P</td>
<td>0.08–0.40</td>
<td>0.13–0.33</td>
</tr>
<tr>
<td>K</td>
<td>0.40–0.65</td>
<td>1.35–1.85</td>
</tr>
<tr>
<td>Ca</td>
<td>0.30–0.80</td>
<td>1.30–2.00</td>
</tr>
<tr>
<td>Mg</td>
<td>0.15–0.30</td>
<td>0.35–0.50</td>
</tr>
<tr>
<td>S</td>
<td>0.12–0.20</td>
<td>–</td>
</tr>
<tr>
<td><strong>Microelements (ppm)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>25–70</td>
<td>35–50</td>
</tr>
<tr>
<td>Cu</td>
<td>5–20</td>
<td>7–12</td>
</tr>
<tr>
<td>Fe</td>
<td>60–200</td>
<td>&gt;150</td>
</tr>
<tr>
<td>Mn</td>
<td>50–350</td>
<td>50–150</td>
</tr>
<tr>
<td>Zn</td>
<td>8–30</td>
<td>35–50</td>
</tr>
</tbody>
</table>

aData from Hanson and Hancock (1996).

bData from Stiles and Reid (1991).

In many growing areas, N is the most frequent, if not the only, mineral nutrient that must be applied to blueberries (Hanson and Hancock, 1996). Soils high in organic matter have a greater N supply and fertilization rates can be lower. However, when organic mulches are added, additional N needs to be provided, as N is used by microbes to decompose these materials (Eck et al., 1990). Ca is another important nutrient because it impacts on fruit quality. Several characteristics of the soil and the blueberry plant influence the Ca supply to the fruit.

Once the amount of nutrient to be applied is defined, there is a need to establish the method of fertilizer application. Fertilizers can be broadcast, applied through fertigation or sprayed on the leaves. A combination of methods is commonly used. The decision to use a certain type of application will depend on technical and economic factors (Hart et al., 2006).

In this chapter we examine some fundamental concepts of plant nutrition and then describe the critical factors influencing blueberry nutrition. These factors include: (i) the supply of nutrients from the soil (substrate); (ii) soil pH; (iii) the role of ericoid mycorrhizae; (iv) determination of nutrient status; (v) absorption and translocation of nutrients within the plant; and (vi) the application of nutrients.

FUNDAMENTAL CONCEPTS OF MINERAL NUTRITION

The goal of fertilization is to remove limitations to yield and quality by supplying the blueberry crop with ample nutrition in advance of demand. A fertilizer application should be based on soil and plant analysis, information on
environmental conditions, plant performance and management, and grower experience. A fertilizer application should produce a measurable change in plant growth, plant performance or nutrient status. Results from nutrient applications can vary from year to year and from field to field. The use of fertilizers must be a part of a complete management package. If some parts or components of the blueberry growing system are not working properly, they cannot be substituted by additional fertilization. Soil properties such as pH, moisture and organic matter influence the nutritional status of the orchard. Increasing fertilizer rates will not correct other limiting factors (Hart et al., 2006).

To obtain optimum yields, plants must have sufficient nutrient levels at all times. Nutrient deficiencies (or excesses) will have an impact on both yield and fruit quality. The importance of the impact will depend on the magnitude, opportunity and duration of the deviation from optimum (Marschner, 1986). In commercial plantings, the high yield and quality required by the market impinges on the need by the grower to monitor the crop constantly. This will allow satisfying the nutrient requirements in the amount and opportunity needed to avoid nutrient deficiencies or excesses (Hart et al., 2006).

Plants interact with the environment (nutrients, light, water and biotic factors) to generate growth. The amount of growth and the balance between reproductive and vegetative growth determines yield. Adequate nutrition is based on the interaction between the soil and the plant (Marschner, 1986). There are specific conditions that maximize root growth and absorption of water and nutrients. For plant growth to occur, the soil must satisfy certain biological, physical and chemical conditions. Plants contain mineral elements that are 'essential' for their metabolism, growth and development, which includes reproduction (flower formation and fruit development). The definition of ‘essentiality’ implies that such an element is required by the plant to complete its cycle and that it cannot be replaced by another element. The essential elements are classified as ‘macroelements’ or ‘microelements’, based on their proportion in plant tissues and not on their relative importance (Lawlor, 1991). Plants are fairly selective in the absorption of mineral elements from the soil, so they usually take what they need and not necessarily what the soil offers.

Soils have the three states of matter: solid, liquid and gas. The solid phase is constituted by organic and inorganic materials. The organic component consists of the residues of plants and animals in various stages of decomposition and a stable part called humus. The inorganic fraction is composed of primary and secondary minerals with different particle sizes. The fractions of the soil that participate in the ionic exchange are those components with particle diameters less than 0.02 mm and are called colloids. Colloids are particles which have a large surface area and if suspended in water will not settle. The particle sizes in the soil are the following: sand, ≤0.12 mm; silt, ≤0.02 to 0.002 mm; clay, ≤0.002 mm (Loomis and Connor, 1992).
Colloids (organic and inorganic) develop negative charges on their surfaces. The cations (with positive charge: K⁺, Na⁺, H⁺, Ca²⁺, Zn²⁺, Mg²⁺, Cu²⁺, Al³⁺) are attracted and retained by these surfaces, while the anions (with negative charge: NO₃⁻, OH⁻) are not retained so firmly. The amount of cations (expressed as milliequivalents per 100 g of dry soil, meq/100 g) is called cation exchange capacity (CEC). CEC is one of the most important chemical properties of soils. It represents the amount of cations that are easily exchangeable with other cations and as a result are available for the plant. Thus, the CEC of a soil represents the total amount of exchangeable cations that the soil can retain. Representative CEC values for clay range from 30 to 100 meq/100 g, while for organic matter CEC may be as great as 300 meq/100 g (Loomis and Connor, 1992).

The CEC associated with soil acidity is called pH-dependent CEC. This means that the actual CEC of the soil depends on the pH of the soil. Given the same amount of organic matter, a neutral soil (pH around 7) will have a higher CEC than an acid soil (e.g. with pH around 5). In other words, the CEC of a soil with a pH-dependent charge will increase with a rise in pH. Since blueberries are adjusted to acid soils, the pH-dependent CEC in this crop tends to be lower than in most fruit crops. This is one of the reasons why blueberries have low nutrient requirements.

As seen in Table 5.2, the CEC in soils planted to blueberries ranges from 1 to 25 meq/100 g soil. The higher the CEC, the more clay or organic matter present in the soil (and the higher the water-holding capacity). The ability to change the soil pH also depends on the CEC. High-CEC soils require more elemental S to change their pH. Low-CEC soils are more prone to develop cation deficiencies. So for sandy soils, more frequent additions of small amounts of fertilizer are better. In these soils a large one-time addition of cations can lead to large leaching losses, because the soil is not able to hold on to the excess cations.

THE NITROGEN CYCLE

In most blueberry cropping situations, N is the nutrient most commonly applied and whose deficiency is most prevalent (Hanson and Hancock, 1996). Soil N is in a constant state of flux, moving and changing chemical forms (Subbarao et al., 2006). The nitrogen cycle is mediated by microorganisms whose activity is dependent on the chemical and physical conditions of the soil (Fig. 5.1). There are processes that increase the N availability for plants (nitrification and mineralization), while others reduce the N availability for the crop (immobilization, denitrification, volatilization and leaching). The main characteristics of these processes are now explained and their impact on N nutrition in blueberries is addressed.

Nitrification, defined as the biological oxidation of ammonium (NH₄⁺) to nitrate (NO₃⁻) (Subbarao et al., 2006), is the process by which decomposing proteins, inorganic N and other nitrogenous substances that originate from
Table 5.2. Characteristics of soils planted to blueberries.

<table>
<thead>
<tr>
<th>Site and source</th>
<th>Latitude</th>
<th>Depth (cm)</th>
<th>Texture</th>
<th>Organic matter (wt%)</th>
<th>pH</th>
<th>CEC (meq/100 g)</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>Bases (% of CEC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>USA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oregon</td>
<td>44°34'N</td>
<td>&gt;200</td>
<td>Clay loam</td>
<td>3-4</td>
<td>5.0-5.6</td>
<td>11-20</td>
<td>57-66</td>
<td>9-11</td>
<td>11-17</td>
<td></td>
</tr>
<tr>
<td>Michigan</td>
<td>42°24'N</td>
<td>40-70</td>
<td>Sandy loam</td>
<td>7-10</td>
<td>4.5</td>
<td>22-25</td>
<td>&gt;60</td>
<td>&gt;15</td>
<td>&gt;10</td>
<td></td>
</tr>
<tr>
<td>Georgia</td>
<td>31°28'N</td>
<td>60</td>
<td>Loamy</td>
<td>1.0</td>
<td>4.7-5.1</td>
<td>3-10</td>
<td>50-62</td>
<td>9-12</td>
<td>12-20</td>
<td></td>
</tr>
<tr>
<td>Europe</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Spain, Huelva</td>
<td>37°17'N</td>
<td>25-250</td>
<td>Sandy</td>
<td>0.4-0.7</td>
<td>4.8-5.4</td>
<td>2-5</td>
<td>37-55</td>
<td>33-48</td>
<td>2-4</td>
<td></td>
</tr>
<tr>
<td>South America</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Chile, Collipulli</td>
<td>37°57'S</td>
<td>20</td>
<td>Clay loam</td>
<td>3.3</td>
<td>5.3</td>
<td>9</td>
<td>72</td>
<td>20</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Chile, Osorno</td>
<td>40°36'S</td>
<td>60-120</td>
<td>Loamy, clayey silt</td>
<td>13.4</td>
<td>5.0</td>
<td>11</td>
<td>67</td>
<td>15</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Argentina, Concordia</td>
<td>31°13'S</td>
<td>40-60</td>
<td>Sandy loam, sand</td>
<td>0.2-5.2</td>
<td>4.6-5.7</td>
<td>1-22</td>
<td>63</td>
<td>12</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Argentina, Buenos Aires</td>
<td>34°40'S</td>
<td>40-60</td>
<td>Clay loam</td>
<td>1.5-4.7</td>
<td>5.4-6.1</td>
<td>17-24</td>
<td>62</td>
<td>14</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

CEC, cation exchange capacity.
aData from W.Q. Yang (Oregon, 2011, personal communication).
bData from Hanson (1987).
aData from H.D. NeSmith (Georgia, 2011, personal communication).
Data from Vadillo (2006).
Data from Tosso (1985).
Data from R.S. Lavado (Buenos Aires, 2010, personal communication).
organic matter are transformed to nitrate by microorganisms. It has been estimated that 75% of inorganic N may be nitrified in cultivated soils. In acid soils, such as those planted to blueberries, the microbes responsible for most nitrification are inhibited; consequently, the rate of nitrification could be reduced (Hanson, 2006).

Nitrate-N is subject to leaching and can also escape into the environment as gaseous molecules (N₂O, NO and N₂). Most of the fertilizer-N is applied in
the NH$_4^+$ form, which in Michigan blueberry soils was nitrified mostly within 4 weeks of application (Retamales and Hanson, 1990). The rapid conversion of NH$_4^+$ to NO$_3^-$ in the soil limits the effectiveness of much of the applied N fertilizer. Ammonium is held by electrostatic forces to negatively charged clay surfaces and functional groups of organic matter. This binding is sufficient to limit N losses by leaching (Subbarao et al., 2006). Thus nitrification of ammonium-N results in the transformation of N from a relatively soil-immobile form (NH$_4^+$) into a highly mobile form (NO$_3^-$). Management practices can increase the potential for nitrification. It is generally agreed that the population of nitrifying organisms increases rapidly upon moderate addition of ammonium to the soil. In Michigan, soil nitrifier populations and nitrification rates were higher in old blueberry fields than in adjacent, undisturbed forest soils (Hanson et al., 2002). This could be due to ammonium applications, improved drainage or alterations in soil chemistry or structure. Organic matter composition, soil texture, CEC, drainage and pH can also affect the rate of nitrification (Subbarao et al., 2006). However, research in blueberry has shown that nitrification rates are not related to soil pH (Hanson et al., 2002). Blueberry production practices (application of ammonium-containing fertilizers, addition of P and K fertilizers, cultivation, composition and quality of litter, and drainage) lead to a greater number of nitrifying bacteria and increased nitrification capacity. The practical significance of these findings is that the optimum timing of fertilizer application depends on the specific nitrification capacity of the site. On soils that nitrify readily, NO$_3^-$ is formed rapidly and multiple applications of lower N rates should be used to reduce leaching losses and increase fertilizer use efficiency (Subbarao et al., 2006). Growers have observed that plants grow more slowly when replanted on old blueberry sites compared with virgin soils. Perhaps a factor contributing to this slow growth on replanted sites is that they have higher nitrification rates which increase N loss through leaching and reduce efficiency of fertilizer use. Nitrate leaching can be measured in the field by placing porous ceramic capsules beneath the rooting depths of blueberries (i.e. >80 cm; Eck et al., 1990). A vacuum pump connected to the samplers via flexible polyethylene tubing can be used to collect the samples.

Blueberries absorb nitrate less readily than ammonium, and this has an important impact on N nutrition in blueberries (Eck et al., 1990). For this reason, it is desirable to reduce the nitrification rate in order to improve the nitrogen-use efficiency of blueberries and limit the potential leaching of nitrate into soil water. Nitrification rates and N recovery by 3-year-old `Bluecrop' were measured after applications of ammonium sulfate with or without the nitrification inhibitor dicyandiamide (DCD) on sandy loams with pH 4.8. Concentrations of fertilizer-derived nitrate were significantly lower in DCD-treated soils 2 weeks following application, but DCD had no effect on total nitrate levels or fertilizer-derived nitrate later in the season. DCD had no effect on fertilizer-derived or total N levels in plants. It seems that the effect of DCD
on nitrate levels is short-lived and, when the whole season is considered, the impact would be minimal or negligible (Throop and Hanson, 1998).

Denitrification is the transformation of nitrate or nitrite (NO$_3^-$) to gaseous nitrogen either as molecular nitrogen (N$_2$) or an oxide of nitrogen (NO or N$_2$O). The escape of these gases from the soil would represent a net loss of N from the field. The bacteria involved in this transformation use oxygen from nitrate for their respiration. The populations of these bacteria increase with the organic matter content of the soil (Loomis and Connor, 1992). Wetting and drying cycles change the oxygen availability in the soil and have major effects upon soil microbial processes. Nitrification and denitrification rates increase dramatically after wetting of air-dried soils. In order to reduce the impact of denitrification, growers should avoid marked fluctuations in soil water content, especially when high levels of nitrate are present in the soil.

Volatilization is the loss of N through the conversion of ammonium to free ammonia (NH$_3$) gas, which is then released to the atmosphere. Free ammonia increases about tenfold with each unit increase in pH. Thus about 0.004% of the N is present as free NH$_3$ at pH 5 and nearly 0.04% at pH 6 (Loomis and Connor, 1992). Hot and windy conditions also favour volatilization losses. Additions of ammonium fertilizers can lower the pH in localized areas and reduce the rate of N loss. When ammonium fertilizers are broadcast, volatilization losses can be reduced by irrigating shortly after application. Up to 20% of the applied fertilizer can be lost due to volatilization from blueberry fields if rain is not received, or the field is not irrigated in a timely fashion (Krewer and NeSmith, 1999).

Leaching of nitrate is often the main cause of N loss and is of high concern to water quality (Subbarao et al., 2006). Environmental agencies in many places have set standards for the maximum amount of nitrate permitted in drinking water; the level is 10 ppm in the USA. The rate of leaching depends on soil drainage, rainfall, quantity of nitrate present in the soil and rate of crop uptake. Well-drained soils, low crop yield, high N inputs (especially when roots are not active) and high rainfall are all conditions that increase the potential for nitrate leaching (Loomis and Connor, 1992; Subarao et al., 2006). The coarse, porous soils which are common to blueberry croplands may facilitate leaching (Hanson, 2006). In commercial highbush blueberry fields, measurements taken 2–3 months after fertilization have shown a decline in topsoil (0–30 cm) NO$_3^-$ and NH$_4^+$ and an increase in subsoil (30–60 cm) NO$_3^-$ and NH$_4^+$, which was probably due to leaching (Retamales and Hanson, 1990).

Immobilization refers to incorporation of inorganic N into microbial biomass, and then more permanently to humus (Myrold and Bottomley, 2008). All living organisms require N and soil microorganisms compete with crops for N. Immobilization occurs through the incorporation of N (NO$_3^-$ or NH$_4^+$) into the microbial biomass with resultant resistance to further availability for plant use. Substantial proportions of applied N may be incorporated into the microbial biomass within 24 h of application of
ammonium sulfate and near-complete immobilization may occur within 1 week after application of N fertilizer. The immobilized N is incorporated into proteins, nucleic acids and other organic N constituents of microbial cells and cell walls; as such, it becomes part of the biomass. As the microbes die and decay, some of the biomass N is released as NH$_4^+$ through the process of mineralization; the remainder undergoes conversion to more stable organic N compounds, ultimately becoming part of soil organic matter. The stabilized organic compounds are not readily available to plants; therefore, the net result of immobilization–mineralization is a decrease in the availability for the crop of the N added to soil as fertilizer, and also the partial conversion of this N to a form (NO$_3^-$) that is not subject to loss from most soils (Mulvaney et al., 1993).

Of particular importance for N availability is the C/N ratio or the ratio of available C to mineral N (NH$_4^+$ and NO$_3^-$). When C/N ratio ≤20, mineralization exceeds immobilization, whereas at C/N ratios ≥30, immobilization exceeds mineralization. The C/N ratio of the materials incorporated into the soil determines if N will be immobilized (tied up) or mineralized (available) (Yang et al., 2002). The C/N ratio of the residues declines as they decay (Loomis and Connor, 1992). As explained in the section on mulches in Chapter 6, the incorporation of materials with high C/N ratio (e.g. sawdust, straw, bark, etc.) will cause greater demand for N, and thus result in N immobilization. In these cases, extra N has to be added to compensate for microbial immobilization (including mycorrhizal fungi) and leave N available for the blueberry crop (Yang et al., 2002; Hanson, 2006). Immobilization locks up N temporarily. When the microorganisms die, the organic N in their cells becomes available for plant uptake through mineralization.

Mineralization is the process by which microbes decompose organic N from manure, dead microbes, organic matter and crop residues to produce ammonium. Since mineralization is a biological process, its rate varies with factors that affect microbial activity, such as soil temperature, moisture and the amount of oxygen in the soil (aeration). Mineralization occurs readily in warm soil (20–35°C). Between 1 and 10% of the soil organic reserves may be mineralized within a year (Loomis and Connor, 1992). Assuming as an average that each 1% of organic matter content releases about 7 kg N/year, in most blueberry soils this would amount to 30–120 kg N/ha per annum (Krewer and NeSmith, 1999). It is important to estimate mineralization and immobilization potentials of a given soil when determining N application rates. In some cases native inorganic N released from organic matter may be considerable and sufficient to satisfy plant requirements.

SOIL pH REQUIREMENTS OF BLUEBERRIES

The soil pH range recommended for highbush blueberry is between 4.5 and 5.5, and 4.2 to 5.0 for rabbiteye blueberry. The pH of the soil influences the
availability of nutrients for plants (Fig. 5.2). High soil pH is a common problem encountered in new blueberry sites. When blueberries are grown in soil with high pH, their leaves turn yellow with green veins or are completely yellow. These leaves are small and often turn brown and fall from the plant before the season is over. Little growth occurs, and some plants may die. Plants stunted by high soil pH usually do not recover, even when soil pH is reduced (Hart et al., 2006). Plants established in high pH soils often require replanting to obtain a uniform and vigorous stand. Fe, Mn and Cu deficiencies are common in soils with high pH; thus, rather than application of these elements to the soil, correcting pH will usually be more helpful.

Soils are acidified either with elemental S incorporated before planting or with sulfuric acid applied through the irrigation system. In the case of soil S application, since the transformation of S into acid is a process mediated by microorganisms, it requires time, moisture and warm temperatures for pH change. As a result, soil pH should be corrected at least one year before planting. Table 5.3 provides estimates of the amount of elemental S required to shift the pH to a final pH of 5.0.

Fig. 5.2. Effect of soil pH on availability of nutrients for crops. (Adapted from web1.msue, 2011.)
As shown in Table 5.3, there are two variables that affect the amount of elemental S needed to drop the pH. The first is the initial pH of the soil; the second is the CEC of the soil. The higher the difference between the initial pH and the desired pH, the more elemental S will be required to adjust soil acidity. Also, the higher the CEC (or the buffer capacity of the soil), the more elemental S will be needed to reach the target pH. If more than 3.4 t of S are needed per hectare, the dosage should be split. The elemental S needs to be thoroughly mixed and incorporated in the first 15–20 cm of the soil. Studies done over two years on half-high 'Northblue' blueberries showed that, only when peat was used either as soil amendment or mulch, the impact on soil pH during the first year was significant on the top 5 cm of the soil (4.3–4.5 versus 5.9 for control). On the other hand, sawdust caused little change in pH on the top 5 cm (5.7 versus 5.9 for control). Mulching treatments or soil amendments did not alter pH at 5–15 cm depth (Karp et al., 2006). When the effects of hardwood woodchip fines (2–5 cm length) were studied for 3 years in southern highbush blueberries 'Star' planted in three sites, soil pH dropped in the first season between 0.4 and 0.7 units; however, in the second season this pH level raised on average by 0.2 units (Cox, 2009). After one season, experiments on 'Pioneer' and 'Concord' highbush blueberries by Kramer et al. (1940) reported no change in pH with respect to control soil (pH 4.5) with various mulches (peat–sawdust, pine leaves, oak leaves, straw) and lespedeza cover.

The most common fertilizer forms of N fertilization (urea, ammonium sulfate) acidify the soil. A survey done in Oregon blueberry fields showed that the average soil pH was 5.46 when 45–110 kg N/ha were used, and 4.92 when 340–500 kg N/ha were applied (Scagel and Yang, 2005). Sulfuric acid, incorporated through drip irrigation, acidifies soils more quickly than elemental S, especially in weakly-buffered soils (sandy, low in organic matter). However, this material is hazardous and difficult to use (Horneck et al., 2004). The application of 1.6 litres of sulfuric acid is equivalent to 1 kg of elemental S.

Table 5.3. Estimated levels of elemental sulfur (t/ha) required to change the pH of soil from 6.5, 6.1 or 5.7 to a desired pH of 5.0 according to the soil’s cation exchange capacity (CEC) ranging from <14 to >25 meq/100 g soil. (Adapted from Horneck et al., 2004.)

<table>
<thead>
<tr>
<th>Desired soil pH</th>
<th>CEC (meq/100 g)</th>
<th>Current soil pH</th>
<th>Amount of elemental S to apply (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>&lt;14 (sandy)</td>
<td>6.5</td>
<td>2.02–2.35</td>
</tr>
<tr>
<td>5.0</td>
<td>14–25 (silt loam)</td>
<td>6.1</td>
<td>1.23–1.68</td>
</tr>
<tr>
<td>5.0</td>
<td>&gt;25 (clay loam)</td>
<td>5.7</td>
<td>0.56–0.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.02–2.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.23–1.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.56–0.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.69–3.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.79–2.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.90–1.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4.03–4.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.80–3.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.35–1.68</td>
</tr>
</tbody>
</table>
ROLE OF MYCORRHIZAL FUNGI IN BLUEBERRY NUTRITION

Ericoid mycorrhizal fungi form symbiotic associations with blueberry roots and help them prosper in soils with low pH, low nitrate, low Ca and high organic matter (Vega et al., 2009). Mycorrhizal inoculation has increased plant, root and shoot dry weight, without influencing shoot/root ratios. Leaf photosynthetic rate, transpiration and water-use efficiency were not affected by mycorrhizal inoculation in blueberries (Yang et al., 2002). Mycorrhizae increase the uptake of soil nutrients and efficiency of fertilizer application, improve water use and protect the blueberry plant from toxic elements such as Al, whose concentration increases as pH decreases (Scagel and Yang, 2005). Mycorrhizal associations also increase the ability of ericaceous plants to tolerate high Cu and Zn concentrations.

The ability of these fungi to enhance the uptake of soluble inorganic N and P and utilize organic or insoluble N and P substances in the soil can be important in the nutrition of blueberries. These fungi can assimilate both ammonium and nitrate ions and transfer them to the host plant. These mycorrhizae can also use organic compounds such as amino acids, peptides, proteins and polymers such as chitin and lignin to transfer substantial amounts of N to the plant host. Ericoid mycorrhizae are capable of transferring C and N simultaneously to the host plant when organic sources of N are applied, therefore offsetting a portion of the carbon drain required to sustain fungal growth (Yang et al., 2002). In highbush blueberries, Valenzuela-Estrada et al. (2008) established similar colonization by mycorrhizae in the first two root orders (finer: < 50 µm, absorptive roots) and the decline in colonization in third and fourth root branching orders.

Mycorrhizal associations are most prevalent in natural environments, but can be important in nursery and commercial plantings. Surveys of highbush blueberry farms in Oregon have shown large variations in mycorrhizal infection levels (0.5 to 44% of total root length), with most colonization occurring in the top 15 cm of the soil profile (Scagel and Yang, 2005). Levels of root colonization can be doubled if plants are inoculated in the nursery. Inoculation in the nursery of container-grown blueberry plants increased total plant biomass in six of the seven highbush blueberry cultivars studied (Scagel, 2005). The colonization of blueberry roots by ericoid mycorrhizae may have some level of host–fungus specificity, as there have been reports of variation among mycorrhizal isolates in their ability to increase nutrient solubility or uptake. Roots on highbush blueberry cultivars that fruit early in the season tended to have higher levels of colonization than cultivars that fruit later in the growing season (Scagel and Yang, 2005). Mycorrhizal colonization of blueberry varies significantly with cultivar, rate of fertilizer application, and the amount and type of soil organic matter present in the soil. Usually, increasing amounts of fertilizer decreases mycorrhizal colonization and the
effects are cultivar-specific (Hanson, 2006). Soil amendment of blueberry sites with organic materials (rotted sawdust, peat) also reduces mycorrhizal infection.

**ESTIMATING THE NUTRIENT NEEDS OF BLUEBERRIES**

The total fertilizer needs of a blueberry planting can be determined by calculating the demand as well as the supplies of each element. The relationship between demand, supplies and fertilization needs is established through the equation:

\[
\text{Fertilizer need} = \frac{\text{nutrient demand} - \text{nutrient supplies}}{\text{efficiency}}
\]

(5.1)

In the case of young blueberry plantings which have not yet reached maturity, their vegetative mass as well as fruit production is expanding each year. During this period, the balance between vegetative and reproductive growth changes from one season to the next, which has to be considered in estimating the amount of fertilizer needed to satisfy nutrient needs. For this reason, age-based fertilizer recommendations that are considered appropriate for the typical growth patterns and yields at each location have been developed in different regions of the world (Tables 5.8 and 5.9). These data reflect the large differences in soil nutrient supply, plant growth and expected yields that exist in different blueberry-producing regions.

In the case of a mature blueberry planting, the fertilizer needs will be determined by the amount of nutrients extracted from the planting, which is a function of the nutrient content in the fruit harvested plus the material removed by pruning (assuming it is not re-incorporated into the orchard) (Tables 5.4 and 5.5). The total nutrient supply in a planting is dependent on the natural fertility of the soil, the nutrient content of the irrigation water, and the addition of any nutrient-containing material (organic or inorganic, such as mulch).

Equation (5.1) provides the basis for a gross estimation of the total amount of each nutrient that would need to be added as fertilizer. As an example, if for a mature 'Elliott' planting we assume a yield of 10 t, the nutrient extraction by the fruit will be the highest for N and K (10.8 and 11.2 kg of N and K₂O, respectively); while the extraction of P, Ca and Mg will be the lowest (Table 5.6). On the other hand, if we assume that the grower removes 20% of 1- to 4-year-old-wood by pruning and this material is taken out from the field, this would amount to an extraction of 2.27 kg N, 0.17 kg P₂O₅ and 0.76 K₂O (Table 5.6). The fruit would then, in this scenario, represent 82.6, 93.9 and 93.6% of the annual removal of N, P and K from this field.

The efficiency of N fertilization for mature highbush blueberry plants cv. 'Bluecrop' was estimated at 32% in Michigan (Retamales and Hanson, 1989) and 22–43% in Oregon (Bañados et al., 2006b). The quantities of fertilizers that need to be applied must be increased in order to compensate for nutrient
Table 5.4. Nitrogen, potassium and phosphorus concentrations (percentage of dry weight) in different plant parts of mature (8- to 10-year-old) blueberry cultivars during mid-winter. (Adapted from Bañados et al., 2006a.)

<table>
<thead>
<tr>
<th>Plant part</th>
<th>'O'Neal'</th>
<th>'Bluejay'</th>
<th>'Brigitta'</th>
<th>'Elliott'</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>K</td>
<td>P</td>
<td>N</td>
</tr>
<tr>
<td>Bud, flower</td>
<td>2.7</td>
<td>0.85</td>
<td>0.26</td>
<td>2.6</td>
</tr>
<tr>
<td>Bud, vegetative</td>
<td>2.0</td>
<td>0.47</td>
<td>0.18</td>
<td>2.0</td>
</tr>
<tr>
<td>Wood, 1-year-old</td>
<td>0.9</td>
<td>0.36</td>
<td>0.07</td>
<td>1.0</td>
</tr>
<tr>
<td>Wood, 2-year-old</td>
<td>0.9</td>
<td>0.30</td>
<td>0.06</td>
<td>1.0</td>
</tr>
<tr>
<td>Wood, 3-year-old</td>
<td>0.7</td>
<td>0.19</td>
<td>0.05</td>
<td>0.7</td>
</tr>
<tr>
<td>Wood, 4-year-old</td>
<td>0.7</td>
<td>0.15</td>
<td>0.05</td>
<td>0.6</td>
</tr>
<tr>
<td>Crown</td>
<td>0.7</td>
<td>0.19</td>
<td>0.05</td>
<td>0.7</td>
</tr>
<tr>
<td>Roots</td>
<td>1.6</td>
<td>0.19</td>
<td>0.20</td>
<td>1.2</td>
</tr>
</tbody>
</table>

Significance of means in each column: **P<0.005; ***P<0.001.
Table 5.5. Dry matter (g) and dry matter partitioning (percentage of total) in different plant parts of mature (8- to 10-year-old) blueberry cultivars during mid-winter. (Adapted from Bariados et al., 2006a.)

<table>
<thead>
<tr>
<th>Plant part</th>
<th>‘O’Neal’</th>
<th>‘Bluejay’</th>
<th>‘Brigitta’</th>
<th>‘Elliott’</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry weight (g)</td>
<td>% of total</td>
<td>Dry weight (g)</td>
<td>% of total</td>
</tr>
<tr>
<td>Bud, flower</td>
<td>42.5</td>
<td>0.50</td>
<td>10.2</td>
<td>0.15</td>
</tr>
<tr>
<td>Bud, vegetative</td>
<td>9.6</td>
<td>0.11</td>
<td>0.9</td>
<td>0.01</td>
</tr>
<tr>
<td>Wood, 1-year-old</td>
<td>551.2</td>
<td>6.41</td>
<td>127.6</td>
<td>1.89</td>
</tr>
<tr>
<td>Wood, 2-year-old</td>
<td>658.9</td>
<td>7.66</td>
<td>198.4</td>
<td>2.94</td>
</tr>
<tr>
<td>Wood, 3-year-old</td>
<td>882.3</td>
<td>10.26</td>
<td>223.0</td>
<td>3.30</td>
</tr>
<tr>
<td>Wood, 4-year-old</td>
<td>2097.4</td>
<td>24.37</td>
<td>2815.6</td>
<td>41.68</td>
</tr>
<tr>
<td>Crown</td>
<td>2758.6</td>
<td>32.06</td>
<td>1833.7</td>
<td>27.15</td>
</tr>
<tr>
<td>Roots</td>
<td>1602.7</td>
<td>18.63</td>
<td>1545.6</td>
<td>22.88</td>
</tr>
<tr>
<td>Total plant</td>
<td>8603.2</td>
<td>100.0</td>
<td>6755.0</td>
<td>100.0</td>
</tr>
</tbody>
</table>
loss due to runoff, weed uptake, volatilization and immobilization. In order to account for various factors that influence the rate of fertilizers to apply, Hirzel (2008) established a ‘dosage factor’ which varies according to the nutrient, the supply of the nutrient from the soil and reserves, the efficiency of application, the degree of fixation (for P and K) and the presence of weeds (Table 5.6).

The amount of N fertilizer calculated in this exercise is much lower than the 185 kg N/ha per annum suggested for Oregon by Hart et al. (2006) and lower than the 73 kg N/ha per annum recommended for mature blueberry fields (>8-year-old) by Hanson and Hancock (1996) in Michigan (Table 5.8). Even though some fields in Oregon have been reported to reach 44.8 t/ha, which would remove 48.4 kg N/ha per annum and according to our calculations would require 103–206 kg N/ha per annum to be applied as fertilizer, a survey of 100 fields in Oregon, of which 56% of the plantings were <8 years old, showed that highbush blueberry growers apply an average of 193 kg N/ha per annum (Scagel and Yang, 2005). Most growers surveyed (96%) used overhead irrigation, while the calculations in Table 5.6 were based on fertigated plantings, which have been reported to make more efficient use of fertilizers. The survey also found that the N fertilization rate increased annually by 6 kg/ha for every year of age (Scagel and Yang, 2005).

In the case of P2O5, the estimations from the data provided in Table 5.6 (10–25 kg/ha) cover levels recommended for soil tests, in the range >30 ppm for mineral soil and >20 ppm for organic soils (see Table 5.10; Hanson and Hancock, 1996). For K2O, only fertilizer rates suggested for the 0–10 ppm range by Hanson and Hancock (1996) would not be covered with rates calculated using Table 5.6.

SOIL AND FOLIAR ANALYSIS

Several tools are used to establish the nutrient status of blueberry fields, including soil analysis, foliar analysis and visual symptoms. Soil analysis is commonly used about a year before planting a new field in order to establish the initial fertility of the soil, the organic matter content and especially the pH. If pH is above 5.5 it should be corrected at least a year before planting. Applications of elements such as K and Mg are also more available to roots if applied before planting and mixed with the soil, rather than broadcast over the surface after planting. Once the blueberries are planted, the use of soil analysis is usually restricted to checking soil pH and salinity (Hart et al., 2006).

Soil samples should be obtained between the canopy drip line and the plant crown (Hart et al., 2006). The area sampled should be restricted to a uniform soil type and condition within the field (Stiles and Reid, 1991). The area included should not exceed 5 ha. The surface 2–3 cm of soil must be scraped away, and then samples collected from the 2–40 cm depth. Each soil sample submitted for analysis should be a composite of 20 to 40 subsamples taken from throughout the area (Hanson and Hancock, 1996).
Table 5.6. Estimation of nutrients extracted in a mature blueberry field cv. 'Elliott' by the fruit (yield=10 t) and wood (20% of above-ground wood removed by pruning), as well as the amount of nutrients applied through fertigation needed to replace that extraction.

<table>
<thead>
<tr>
<th>Item</th>
<th>N</th>
<th>P&lt;sub&gt;2&lt;/sub&gt;O&lt;sub&gt;5&lt;/sub&gt;</th>
<th>K&lt;sub&gt;2&lt;/sub&gt;O</th>
<th>CaO</th>
<th>MgO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Concentration in fruit (mg/100 g fresh fruit)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>108</td>
<td>26</td>
<td>112</td>
<td>13.5</td>
<td>9</td>
</tr>
<tr>
<td>Nutrient removed (kg/ha) for 10 t of fruit&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.8</td>
<td>2.6</td>
<td>11.2</td>
<td>1.35</td>
<td>0.9</td>
</tr>
<tr>
<td>Removed by pruning 20% of &gt;1-year-old wood (kg)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2.27</td>
<td>0.17</td>
<td>0.76</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total removed: fruit + wood (kg/ha)</td>
<td>13.07</td>
<td>2.77</td>
<td>11.96</td>
<td>1.35</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Fertilizer dose (kg/ha) according to soil fertility

<table>
<thead>
<tr>
<th>Soil Type</th>
<th>Dosage factors&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Estimated rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium-fertility soil</td>
<td>3.1–3.4   5.4–6.5 4.2–5.0  8.9–11.1  6.7–8.9</td>
<td>40–45  15–18  50–60  12–15  6–8</td>
</tr>
<tr>
<td>High-fertility soil</td>
<td>2.3–2.7   3.6–5.1 2.9–3.3  5.9–7.4  4.4–5.6</td>
<td>30–35  10–14  35–40  8–10  4–5</td>
</tr>
</tbody>
</table>

<sup>a</sup>In order to obtain elemental levels (P, K, Ca and Mg) the values of P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O, CaO and MgO must be divided by 2.29, 1.2, 1.4 and 1.67, respectively.

<sup>b</sup>Data from Hirzel (2008); low-fertility soils correspond to sandy soils and low organic matter.

<sup>c</sup>Data from Bariados et al. (2006a).

<sup>d</sup>Data from Hirzel (2008); considers the soil supply, supply from reserves, efficiency of application, fixation (for P and K) and presence of weeds.

Leaf foliar analysis is used to determine the concentration of elements in the plant at a certain moment in the season. They can be used to predict fertilizer needs, diagnose deficiencies and evaluate the performance of fertilizer programmes. Annual foliar analysis is recommended. In highbush blueberries, Hanson (1987) found that the nutrient levels in soil samples had weak correlation with leaf nutrient concentrations. In samples from plants of various ages these correlations were 0.084 for P, 0.239 for K, 0.088 for Ca and 0.132 for Mg. For plants <7 years old, correlations were somewhat higher: 0.333 (K), 0.228 (Ca) and 0.94 (Mg).

In order to be useful, tissue collection must follow strict procedures including timing, type of tissues and number of plants to be sampled. Standards have been developed for a period when leaf nutrient levels are
stable (first two weeks of harvest), which in the case of blueberries is usually in late July to mid-August in the northern hemisphere; late January to mid-February in the southern hemisphere. Fully expanded leaves from the mid portion of current-season shoot should be collected. Usually two to five leaves are collected from 10–50 plants that are distributed randomly in the field (avoiding borders). The plants should represent a uniform condition (age, variety, soil, irrigation system, etc.). If a nutritional disorder is suspected, leaves from affected plants should be collected as one sample and compared with samples of ‘normal’ plants. Only one variety should be included in a sample. The sample should not represent a field larger than 5 ha (Krewer and NeSmith, 1999; Hart et al., 2006).

Recommended levels for foliar nutrients have been developed for different producing regions (Table 5.7). In general, the recommended ranges for the various elements are usually, but not always, similar. For example, recommended levels of P, B and Fe in Missouri are lower than in other regions, and recommended Mn levels are higher in Michigan than elsewhere (Table 5.7). These differences demonstrate the need to develop and use local standards. Weather (high and low temperatures, rainfall), fruit load, shoot

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Highbush blueberry</th>
<th>Rabbits eye</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Oregon&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Michigan&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Macroelements</strong> (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>1.76–2.00</td>
<td>1.70–2.10</td>
</tr>
<tr>
<td>P</td>
<td>0.10–0.40</td>
<td>0.08–0.40</td>
</tr>
<tr>
<td>K</td>
<td>0.41–0.70</td>
<td>0.40–0.65</td>
</tr>
<tr>
<td>Ca</td>
<td>0.41–0.80</td>
<td>0.30–0.80</td>
</tr>
<tr>
<td>Mg</td>
<td>0.13–0.25</td>
<td>0.15–0.30</td>
</tr>
<tr>
<td>S</td>
<td>0.11–0.16</td>
<td>0.12–0.20</td>
</tr>
<tr>
<td><strong>Microelements</strong> (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cu</td>
<td>5–15</td>
<td>5–20</td>
</tr>
<tr>
<td>Fe</td>
<td>61–200</td>
<td>60–200</td>
</tr>
<tr>
<td>Mn</td>
<td>30–250</td>
<td>50–350</td>
</tr>
<tr>
<td>Zn</td>
<td>8–30</td>
<td>8–30</td>
</tr>
</tbody>
</table>

<sup>a</sup>Data from Hart et al. (2006).
<sup>b</sup>Data from Hanson and Hancock (1996).
<sup>c</sup>Data from Fuqua et al. (2005).
<sup>d</sup>Data from Owen Plank and Tucker (2000).
<sup>e</sup>Data from Krewer and NeSmith (1999).
growth, soil data, soil moisture, pruning intensity, yield, fruit quality, insect and disease load can all affect plant functioning and the nutrient status of the plant (Stiles and Reid, 1991).

METHODS OF APPLYING FERTILIZERS

Soil application

Until the last decade, most fertilizer applied to blueberry plantings was broadcast on the soil surface. In most instances, the applications were concentrated at the beginning of the season when root growth was scarce and the chances of nutrient losses were high. In the case of N, it was shown that despite the low pH (which would reduce nitrification rates) nitrate formation was high and an important proportion of the N applied in ammonium form was lost through leaching (Retamales and Hanson, 1990). Studies demonstrating the inefficiency of this system have induced growers to incorporate changes to this practice. Among the innovations are the use of controlled-release fertilizers, the use of split applications during the growing season and fertigation.

In the case of young plantings, these are expanding their vegetation as well as the production of fruit. In this period the balance between vegetative and reproductive growth changes from one season to the next, so it is difficult to estimate the amount of fertilizer required to satisfy these needs. Some guidelines published in the literature show the wide range of recommended rates in different zones (Table 5.8). The data reflect the large differences in soil nutrient supply, plant growth and expected yields.

Table 5.8. Recommended rates of nitrogen application for highbush blueberry orchards of different ages in Michigan and Oregon.

<table>
<thead>
<tr>
<th>Years in the field</th>
<th>Michigana</th>
<th>Oregonb</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>kg/ha</td>
<td>g/plant</td>
</tr>
<tr>
<td>2</td>
<td>16.8</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>–</td>
<td>22.7</td>
</tr>
<tr>
<td>4</td>
<td>33.6</td>
<td>25.5</td>
</tr>
<tr>
<td>5</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>50.4</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>72.9</td>
<td></td>
</tr>
</tbody>
</table>

aData from Hanson and Hancock (1996).

bData from Hart et al. (2006).
The use of fertigation (the application of fertilizers through pressure irrigation systems) has increased markedly in blueberry production in the last years. In many producing regions, blueberries are established on ridges with drip irrigation beneath sawdust or bark chip mulch. Advantages of fertigation include improved efficiency of fertilization, minimal losses due to leaching, optimization of the nutritional balance of the plant by supplying nutrients directly to the root zone, reduced potential for fertilizer burn and greater control of nutrient concentration in soil solutions.

In fruit crops, dramatic increases in nitrogen-use efficiency have been measured using fertigation versus surface application. Uptake efficiency was increased two to three times over previous surface fertilizer applications. A study was conducted on highbush (‘Duke’, ‘Blueray’) and half-high (‘Northblue’) blueberries planted in a silt loam soil where equivalent rates of N, P, K and Mg were applied through fertigation or granular surface application. After 3 years, greater fruit yield and plant volume were obtained under the fertigation regime, without any difference in N leaf levels between the two treatments. Apparently, greater plant volume from fertigation resulted in higher yields. Since N levels were not affected by fertilization regime, but plant volume and fruit load were greater with fertigation, N uptake on a per plant basis was likely higher in fertigated plants. A more consistent availability of N in the root zone may have allowed plants with fertigation to utilize N more efficiently (Finn and Warmund, 1996).

The suggested fertilizer rates to be supplied through fertigation are shown in Table 5.9. The following fertilizer split within the season has been recommended (Hirzel, 2008): bud break to fruit set (10%), fruit set to pink fruit (30%), pink fruit to harvest (40%) and postharvest (20%).

The performance of controlled-release N fertilizers was equivalent to regular fertilizers in highbush blueberry (Hanson and Retamales, 1992), but sulfur-coated urea had the greatest and ammonium sulfate the lowest plant growth (urea was intermediate) when applied to 1-year-old ‘Tifblue’ rabbiteye blueberries (Patten et al., 1988). The main advantages of slow-release fertilizers are that they have reduced risk of fertilizer burn to the plants and that they require less frequent applications to satisfy nutrient needs (Krewer and Ruter, 2009); however, their higher cost may offset these benefits.

Table 5.9. Suggested fertigation rates for blueberries. (Adapted from Krewer and NeSmith, 1999.)

<table>
<thead>
<tr>
<th>Plant diameter (cm)</th>
<th>Fertilizer dose (g/plant/week)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
</tr>
<tr>
<td>30</td>
<td>1.0</td>
</tr>
<tr>
<td>60</td>
<td>1.5</td>
</tr>
<tr>
<td>90</td>
<td>2.0</td>
</tr>
<tr>
<td>120 and up</td>
<td>2.5</td>
</tr>
</tbody>
</table>
Foliar applications

Foliar application of nutrients is a means to rapidly supply nutrients directly to tissues (foliage, flowers or fruit) at times when a quick response is needed. Even though soil treatments last longer, soil-applied micronutrients are tied up under some conditions and would be unavailable to the plants; therefore, foliar sprays could be necessary (Strik et al., 2010). For example, low air temperatures and cold soils in the spring often reduce nutrient availability. In certain seasons and production areas, the demand for certain elements required for rapid development of leaves and shoots can exceed the supply from roots and reserves. Soil pH can decrease nutrient availability and foliar nutrient application could ameliorate the deficit faster than correction of soil pH. Foliar sprays may end up as the best way to supply a given element because either the soil supply is insufficient or there is a need to precisely control the time and rate that the element is available to the plant. Foliar applications are often timed to coincide with specific vegetative or fruiting stages of growth, and the fertilizer formula is adjusted accordingly. Applications may also be used to aid plants in recovery from transplant shock, hail damage or the results of other weather extremes (Kuepper, 2003). However, foliar applications are more expensive than soil fertilization on a nutrient unit base and usually must be repeated several times to be effective for an entire season (Hart et al., 2006). Therefore, foliar sprays should be aimed at accomplishing a particular outcome in response to a specific need. As a result, foliar sprays should be considered as supplements to and not replacements for soil fertilization (Stiles and Reid, 1991).

A detailed discussion on foliar application is presented in Chapter 7. In general terms, to get the most efficient results from nutrient sprays and avoid damage to the crop, three considerations must be followed: (i) the proper application rates must be established; (ii) the modes of application must be considered (adjuvants, volume, moment of the season, time of the day, droplet size, etc.); and (iii) the effectiveness of the foliar application must be evaluated based on target tissues and specific environmental conditions at the time of application.

Certain micronutrients such as B and Cu can injure plants if applied foliarly at higher amounts than necessary for plant growth, and can cause extensive damage to blueberries (Strik et al., 2010). Research has shown that foliar sprays can damage leaves and are an inefficient way to apply N to highbush blueberries. No more than 5% w/v urea, the equivalent to 16 kg N/ha, can be applied to blueberry plants without burning leaves. Because of the waxy cuticle of blueberry leaves, they are not very effective in taking up N. Less than 50% of the applied N would enter the plant via the leaves (Hart et al., 2006). A study on highbush blueberries in which N-enriched potassium nitrate was applied foliarly to 3-year-old 'Jersey' potted plants and a liquid NPK (10-10-10 liquid formulation; Nachurs Alpine Solutions, Marion, Ohio, USA)
was sprayed for four seasons on mature commercial plantings of 'Jersey', 'Rubel' and 'Bluecrop' showed the following: (i) the foliar N obtained from spray amounted to only 0.7% (single application) and 1.2% (double) of the total elemental N in leaves; (ii) the contribution of foliar-derived translocated N on the N status of the new leaf growth was minimal (<0.3% of total leaf N); and (iii) foliar sprays increased NPK leaf levels but had no effect on yield, berry weight or soluble solids (Widders and Hancock, 1994).

Studies at full canopy development in various fruit crops have shown that, depending on the volume of water used, 44 to 58% of the spray ends up in leaves, and only about 2% of the water applied reaches the fruit (Hall, 1991). However, to be effective, the nutrient has to penetrate the leaf. This reduces even further the efficiency of foliar sprays. If the application aims to deposit nutrients on fruits, such as the case of Ca, the efficiency of a foliar spray is expected to be very low.

**ORGANIC MANAGEMENT OF NUTRITION**

Growers with organic fields utilize a ‘feed-the-soil’ system that incorporates cover crops, peat, compost, fish meal, humus, and manures rich in naturally produced N. These natural nutrients promote the growth of beneficial soil microorganisms and supposedly do not harm the symbiotic endomycorrhizal fungi associated with the blueberry root system. These decomposers process biomass materials and indirectly relay N, P, K and other available plant nutrients through the crop rhizosphere (Wang et al., 2008).

In organic production of blueberry, high levels of soil organic matter are especially important not only for their contribution to the soil’s ability to retain and supply moisture to the crop, buffering pH and releasing nutrients through decay, but also because they are a desirable environment for symbiotic mycorrhizal fungi that assist blueberry roots in absorbing water, N, P and other minerals (Yang et al., 2002). Green manures in advance of planting can play an important role in cycling organic matter into the soil system, as can applications of composts and livestock manures (Kuepper and Diver, 2004). Livestock manure and manure/bedding mixtures can be adequate sources of nutrients for blueberries. The nutrient content of manure needs to be known in order to estimate the application rates; however, they have great variability depending on animal species and feed, presence of bedding or other additions, and handling procedures (Hanson and Hancock, 1996).

Once a blueberry planting is established, supplemental N is the greatest concern in organic production, followed by K. Fertilizer recommendations are based on foliar analysis. Organic fertilizers are usually less soluble than inorganic ones. It has been suggested that these fertilizers should be applied from 1 to 4 weeks ahead of the recommended schedule for soluble fertilizers (Kuepper and Diver, 2004). Generally all of the ammonium-N and 25–50% of
the organic N will be available for the blueberry plant in the year of application. Usually N rates should be increased by 50–100% for organic materials because the microorganisms will tie up the N (Hanson and Hancock, 1996). Other authors state that despite the slower release of organic-based N, the carryover from previous seasons probably results in roughly the same amount of N released each season as is being applied (Kuepper and Diver, 2004).

Even though fertilization practices vary greatly among growers, for highbush blueberries grown under mulch, application rates equivalent to 158–170 kg N/ha in the establishment year and 238–257 kg N/ha for subsequent years have been estimated. They are usually split into two or three applications (Kuepper and Diver, 2004). In a trial to compare organic and conventional nutrient management of highbush and rabbiteye blueberry nursery stock, the authors concluded that it was more difficult to supply enough nutrients for optimal growth using organic formulations, and they recommended a constant and steady input of low concentrations of a balanced nutrient mix (Miller et al., 2006).

K for blueberries grown under organic management is often adequately provided through decaying mulches. The need for further supplementation should be determined by soil and/or tissue testing. Where additional K is needed, it can be applied in a number of mineral forms – including sulfate-of-potash-magnesia, granite meal and greensand. Some forms of potassium sulfate are also allowed in organic production (Kuepper and Diver, 2004).

Fertigation – the practice of injecting soluble fertilizers through drip irrigation lines – is a common practice in conventional blueberry production. Some materials accepted in organic production, such as spray-dried fish protein and poultry protein, as well as several organic liquid fertilizers derived from fish emulsion, seeds, kelp or seaweed, satisfy the requirement of complete water solubility of fertilizers (Kuepper and Diver, 2004).

Foliar feeding of blueberries is practised by some organic growers and is especially helpful when plants are stressed. Foliar fertilization programmes usually employ seaweed and fish emulsion.

**REQUIREMENTS FOR SPECIFIC ELEMENTS AND THEIR DEFICIENCY SYMPTOMS**

**Macronutrients**

In this section we analyse the different nutrients needed in blueberry production. For each of them, the symptoms of deficiency and/or toxicity are described and the rates of application are suggested, as well as the timing and application method. Greater coverage is given to N and Ca because of their importance in yield and fruit quality.
Nitrogen

Deficiencies in N are the most frequently reported nutrient deficiency in blueberries worldwide. Plants deficient in N are commonly stunted, with low vigour and pale green to chlorotic (yellow) leaves. The chlorosis is uniform across the leaf, with no mottling or pattern. Fewer canes are initiated. Symptoms appear first on lower (older) leaves and will eventually include the entire plant if N is not applied. Leaves drop early and yields are usually reduced (Hanson and Hancock, 1996; Hart et al., 2006).

Excessive N results in plants with numerous, vigorous shoots and large, dark green leaves. During the season, plants may produce several growth flushes. Growth occurring at the end of the season may not harden properly before winter. The tips of those shoots are often killed by low winter temperatures. Plants with excessive N have reduced yields, smaller berries and ripen later (Hanson and Hancock, 1996; Hart et al., 2006).

As discussed above, proper timing of fertilizer applications may increase N use by plants and avoid waste. Urea is one of the most commonly used fertilizers in blueberries. After urea is applied, N levels in the root zone increase for only 6–8 weeks after application, suggesting that multiple applications may be necessary to maintain sufficient soil N levels throughout the period of high demand (bloom to harvest) (Retamales and Hanson, 1990).

As shown previously (Table 5.8), recommended rates of N application vary greatly among various producing regions. While 73 kg N/ha is recommended for mature orchards (>7-year-old fields) in Michigan (Hanson and Hancock, 1996), 185 kg N/ha is suggested in Oregon (Hart et al., 2006). These differences reflect variations in crop demand (vegetative and reproductive tissue), soil supply and fertilizer efficiency.

It is generally accepted that fertilizers supplying N as ammonium (urea, ammonium sulfate) are preferable for blueberries. Blueberries are adapted to acidic soils that contain NH$_4^+$ as the predominant N form. There has been considerable research on the preference of blueberries for NO$_3^-$ or NH$_4^+$. While some studies establish the preference of blueberries for NH$_4^+$, in others no differences in vegetative growth due to N form have been observed (Hanson, 2006).

Differences in response to N form may be due to variability in rhizosphere pH (the pH in the immediate vicinity of roots). Absorption of NO$_3^-$ is accompanied by a net release of excess OH$^-$ which will increase the rhizosphere pH; while the uptake of NH$_4^+$ requires net release of H$^+$ with a concomitant drop in rhizosphere pH (Merhaut and Darnell, 1995). In leguminous crops it was found that the acidification in NH$_4^+$ occurred in the presence of light (Rao et al., 2000). When exposed to equal concentrations, blueberries absorb NH$_4^+$ more rapidly. Less energy is necessary to assimilate NH$_4^+$ than NO$_3^-$ (Merhaut and Darnell, 1995).
Nitrate reductase, the enzyme that mediates $\text{NO}_3^-$ transformation in the plant, has been found in stems, leaves and roots of blueberries, but the activity in blueberry is very low compared with other crops (Merhaut, 1993). This in part may be due to the fact that the enzyme contains Fe in one of its subunits, an element which is little available in acid soils (Poonnachit and Darnell, 2004). There is controversy on the effect of N source ($\text{NH}_4^+$ versus $\text{NO}_3^-$) on the level of enzyme activity. However, the lower uptake rate of $\text{NO}_3^-$, as well as the need for its transformation within the plant, may lead to slower growth rates when this compound is the primary source of N (Poonnachit and Darnell, 2004; Hanson, 2006).

Blueberries recover relatively low percentages of soil-applied N, depending on environmental conditions and cultural practices. Mature bushes treated with labelled urea (to track N fate) at bud break recovered only 32% of applied N by the end of the season. The remaining N was still in the root zone (15%) or unaccounted for (53%) (Retamales and Hanson, 1989). Lower N rates (100 versus 200 kg N/ha) had greater N recovery (Bañados et al., 2006b).

In fruit crops, the greatest amount of N is absorbed when their leaf mass is highest (Weinbaum et al., 1978). In highbush blueberries it was found (Bañados et al., 2006b) that fertilizer recovery was greater as plants developed along the season and with denser planting within the row (0.45 versus 1.2 m). High N demand and absorption capacity in blueberries occur from late bloom until the end of fruit harvest. Fertilization practices that maintain sufficient N in the root zone during this 2- to 3-month period likely optimize nitrogen-use efficiency. In 3-year-old ‘Bluecrop’ blueberry plants, it was found that application timing greatly affected the amount of fertilizer absorbed by blueberry plants. Plant uptake appeared to be most influenced by plant demand and growth. Efficient uptake occurred only after shoots and leaves had begun growth, while absorption decreased as growth ceased late in the season (Throop and Hanson, 1997).

Precise assessment of N demand is complicated in perennial plants such as blueberries, because N absorbed one year may be retained in the plant and used during subsequent seasons. Increasing plant N reserves late in the season may benefit bushes during the following year. In potted 2-year-old rabbiteye blueberries, reserves supplied 90% of the N required by reproductive tissues at bloom and 50% as late as fruit maturity. Under field conditions only 6% of the N content of mature bushes at the end of the season was derived from fertilizer applied that spring (Birkhold and Darnell, 1993).

Since N is retained in bushes for use during subsequent seasons, increasing plant N reserves late in the season likely benefits bushes during the following year and, as a result, late-season fertilization can be beneficial. However, late applications can promote a greater number of actively growing shoots which can be damaged by cold at the end of the season due to insufficient hardening (Smolarz and Mercik, 1989).
Phosphorus
As in the case of other fruit crops, symptoms of deficiency for this nutrient are rarely seen (Stiles and Reid, 1991); however, there are some conditions where P deficiency can occur. P deficiencies are associated with lower availability of P in very acid soils, possible leaching of P in very sandy soils and the fact that some virgin blueberry sites are naturally very low in P. Effects of excessive P are rarely seen in the field, although high pH can interfere with absorption and metabolism of Fe, Zn and Mn (Stiles and Reid, 1991; Krewer and NeSmith, 1999). Leaf P levels are highest at the beginning of the season and lowest at harvest. Tissue concentrations are little affected by variations in crop load and moisture status. Threshold foliar P levels to establish deficiency vary. It was defined as 0.07% in Michigan, 0.05% in Massachusetts, and 0.09% in Wisconsin and Minnesota (Hart et al., 2006).

Under P deficiency, plants can be stunted and leaves are unusually small. Another common symptom is a purplish coloration on older leaves and stems, although this symptom may also be caused by other factors such as low soil temperatures and water-saturated soils. Leaves may lie unusually flat against the stems (Hanson and Hancock, 1996; Hart et al., 2006).

Fertilizer P added to soils undergoes various adsorption, absorption and precipitation reactions with soil components. The end result is that most fertilizer P adds to the soil reserves, and solution P levels are increased only slightly (Hanson, 2001). Recommended P applications are based on soil and leaf tests. However, the low pH and high Fe and Al concentrations in most blueberry soils might not allow traditional soil tests to accurately reflect plant-available P (Roper and Schmitt, 2007). This might be the reason for the low correlation between soil and leaf P levels that Hanson (1987) found for 539 leaf and soil samples collected from highbush blueberries of various ages in Michigan. In Oregon, applications of P are only recommended if soil test (Bray) readings are below 50 ppm and leaf P is below 0.10%. At 26–50 ppm soil P and 0.08–0.10% leaf P, up to 45 kg P2O5/ha is recommended. When soil P is below 25 ppm and leaf P is below 0.07%, 45–67 kg P2O5/ha is recommended (Hart et al., 2006). In Michigan, although recommendations are based on soil P levels, they suggest P application only when tissue P levels fall below 0.08% (Table 5.10).

Many virgin fields benefit from a pre-plant application of P. It has been estimated that it takes 8 kg of phosphate to increase the P level in the soil by 1 kg. In pine bark bed culture, it may be necessary to apply P three or four times a year. This is necessary as pure pine bark has poor P-holding capacity (Krewer and NeSmith, 1999).

Potassium
Levels of K are rarely low in blueberries, except on sandy soils. As with other fruit crops, chlorosis of leaf margins in older leaves is the first detectable
Table 5.10. Recommended potash and phosphate application rates for highbush blueberries. (Adapted from Hanson and Hancock, 1996.)

<table>
<thead>
<tr>
<th>Soil test (ppm)</th>
<th>K\textsubscript{2}O</th>
<th>P\textsubscript{2}O\textsubscript{5}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All soils</td>
<td>Mineral soils</td>
</tr>
<tr>
<td>0-10</td>
<td>101</td>
<td>168</td>
</tr>
<tr>
<td>10-20</td>
<td>84</td>
<td>140</td>
</tr>
<tr>
<td>20-30</td>
<td>67</td>
<td>112</td>
</tr>
<tr>
<td>30-40</td>
<td>34</td>
<td>56</td>
</tr>
<tr>
<td>40-50</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td>&gt;50</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Symptom of K deficiency. This symptom can lead to scorched along the margin, cupping, curling, and necrotic spots and dieback of shoot tips (Hart et al., 2006). Younger leaves (near shoot tips) may develop interveinal chlorosis similar to symptoms of Fe deficiency (Hanson and Hancock, 1996). Excessive K (leaf K >0.9%) can result in nutrient imbalances, particularly Mg and Ca deficiencies (Stiles and Reid, 1991). Krewer and NeSmith (1999) reported that in Georgia significant amounts of K can leach from soils. Low leaf K can be due to a number of factors: reduced root function, flooding, poor drainage, high N levels, drought and very acid soils (Stiles and Reid, 1991). Root growth is important for K nutrition. In clayey or compacted soils, root proliferation will be reduced; in these conditions, soil nutrient analysis can show high K, but leaf K could be low (Shaw, 2008). Since fruit is an important sink for K in the plant, leaf K levels are also greatly influenced by fruit load. K levels increase strongly as fruit matures; averaging around 60 mg/berry when fruit is ripe (Hart et al., 2006).

When leaf K levels are below normal, fruit yields have been increased with K fertilization on a range of soil types. In Oregon, K fertilizers are not recommended if soils levels are above 150 ppm and leaf K concentration is higher than 0.40%. Excess K can interfere with Mg uptake, so it should not be applied unless a foliar analysis indicates a deficiency (Pritts, 2000). Up to 84 kg K\textsubscript{2}O/ha is suggested if soil tests readings are between 101 and 150 ppm and tissue K is 0.21–0.40%. An application of between 84 and 112 kg K\textsubscript{2}O/ha is advised when soil levels are 0–100 ppm and leaf K is <0.2% (Hart et al., 2006). Similar application levels are recommended in Michigan (Table 5.10), but it is suggested that if crop load is high, leaf K levels between 0.35 and 0.40% would be adequate (Hanson and Hancock, 1996). In general, on light-textured soils where leaching readily occurs, one or two applications of K are needed annually on bearing plants (Krewer and NeSmith, 1999). Potassium chloride (muriate of potash) is preferred by growers because it is cheaper, but
blueberries are sensitive to the chloride in this material. Damage can occur when high rates are used or the material is applied to young plants or not spread uniformly (Pritts, 2000). K can be applied any time of the year.

Calcium
Blueberries are said to be calcifuges that thrive in low pH, are efficient in Ca$^{2+}$ uptake and have low Ca requirements relative to other temperate fruit crops. Healthy bushes typically have 0.3–0.8% Ca in leaf tissue (Eck, 1988) compared with 1–3% in temperate tree crops (Shear and Faust, 1980). Considering foliar levels, blueberries are seldom deficient in Ca (Hanson and Hancock, 1996; Hart et al., 2006); however, Ca nutrition has recognized effects on the quality of various fruits (fruit texture, firmness and ripening rate), even when leaf levels indicate that plants are adequately supplied with Ca (Hanson et al., 1993). Even though deficiencies have not been reported in the field, due to the slow translocation of Ca within the plant, deficiency symptoms should tend to occur on the younger plant tissues (Hirschi, 2004). Intervinal chlorosis and/or browning (scorched-looking) in the edges of newly formed leaves has been characteristic of Ca deficiency in other crops (Hanson and Hancock, 1996). High K and N supply, as well as wide fluctuations in moisture during the season, can accentuate the severity of low plant Ca levels (Hirschi, 2004). Low leaf Ca levels can also occur in heavily fertilized, vigorously growing plants (Stiles and Reid, 1991). Ca deficiency symptoms are most common in plants growing in lower pH soils which also tend to have low Ca levels. Plants living in calcareous areas generally contain much more Ca than those, such as blueberries, which are adapted to acidic conditions (Demarty et al., 1984). In the presence of high substrate Ca$^{2+}$, calcifuges cannot regulate Ca$^{2+}$ influx and accumulate excessive amounts. Ca serves various roles within plant cells, among which are structural, defense and communication among tissues and organs. To accomplish these roles, narrow concentration ranges must be maintained within the cells. When Ca uptake exceeds the needs, part of the Ca can be sequestered by forming calcium oxalates, which also helps in defense and detoxification of heavy metals (Franceschi and Nakata, 2005). This can, in part, explain the weak relationships that are usually found between Ca applications and changes in Ca-related processes such as firmness and decay prevention. Wright et al. (1995) found that high levels of supplemental soil Ca$^{2+}$ led to greater uptake of Na$^+$ and concluded that, when the calcifuge blueberry was exposed to salinity, high Ca$^{2+}$ accentuates the detrimental effects of Na$^+$ on cell metabolism. Low pH soils also have abnormally high Mn levels. As a benchmark, if Mn leaf levels are above 450 ppm, soils are likely to have low pH and low soil Ca (Hart et al., 2006).

High leaf Ca can be due to low crop load or high soil Ca (Hart et al., 2006; Strik et al., 2010). Excessive Ca can reduce Fe absorption by plant roots, as well as interfere with Mg and K metabolism in plants. Ca and Mg are elements
that should be in balance with each other. Normally a ratio of 8–10 units of soil Ca to Mg is desirable. Since most virgin blueberry soils are low in Mg, it is often included in small amounts for balanced blueberry fertilizer (Krewer and NeSmith, 1999).

Ca is absorbed preferentially by young roots. Soil ammonium, K and Mg interfere with Ca absorption by roots, and high levels of these nutrients will reduce fruit Ca levels. Ca moves to the fruit through transpiration. Because leaves transpire more than fruits, they accumulate more Ca (White and Broadley, 2003). Fruits tend to accumulate most of their Ca when shoot growth is limited. Low levels of Ca in the fruit are more critical than leaf concentrations. The ratio of leaf Ca/fruit Ca concentrations (dry weight basis) is indicative of the Ca partitioning among reproductive and vegetative organs. Leaf/fruit Ca ratio in 'Elliott' was 1.3 at 18 days after full bloom, increased to 3.6 by 65 days after full bloom and finished at 11.0 at 134 days after full bloom (Stückrath et al., 2008).

Seeds in the fruit are involved in fruit Ca accumulation (Buccheri and Di Vaio, 2005). Fruit of varieties that regularly produce low numbers of seeds or grown in seasons with poor environmental conditions at pollination are expected to have lower fruit Ca levels.

Even though no studies have been done on Vaccinium species to establish the functionality of the xylem during the season, in other fruit crops (apples, grapes, kiwifruit), Ca tends to accumulate in the fruit during the first half of its growth when the xylem (conducting tissue) is functional (Creasy et al., 1993; Dichio et al., 2003; Drazeta et al., 2004); later in the season the translocation of Ca would be limited to the phloem and the build-up of Ca in the fruit should be strongly reduced.

Ca levels decrease by dilution (Fig. 5.3). Ca must be present in the tissue where it is needed, as there is little retranslocation of Ca within the plant (Hirschi, 2004).

![Fig. 5.3. Changes in calcium concentration during the season (days after bloom) in fruits of 'Elliott' highbush blueberry. (Adapted from Stückrath et al., 2008.)](image-url)
As in other fruit crops, fruit Ca levels in blueberries influence fruit firmness and postharvest life (Hanson et al., 1993). However, these relationships have been difficult to document. In one study, soil applications of lime and gypsum to highbush blueberries for 5 years had limited impact on fruit Ca levels and no effect on yield, fruit size or firmness (Hanson and Berkheimer, 2004). Ca sprays (0–24.2 kg Ca/ha) as calcium chloride or calcium trihydroxyglutarate (commercial name: Nutrical) applied for two seasons to ‘Bluecrop’ highbush blueberries failed to alter the proportion of soft or rotten berries, as well as berry firmness and berry Ca levels (Hanson, 1995). Studies done on the effect of three foliar applications of either calcium chloride or calcium nitrate at 15, 30 and 45 days after fruit set on ‘Bluecrop’, ‘Blueray’ and ‘Ivanhoe’ showed modest impacts on leaf Ca levels at four rates (0, 47.5, 90 and 180 g Ca/100 l water). The lowest Ca rate (47.5 g Ca/100 l) increased Ca levels in fruit skin and seeds, but 90 g Ca/100 l were required to increase Ca levels in the pulp. Both Ca sources (chloride and nitrate) had similar effects on fruit Ca levels. Sensory evaluation of firmness determined a greater proportion of firm fruit only for ‘Bluecrop’ and ‘Blueray’ (Retamales and Arredondo, 1995). Stickrath et al. (2008) applied foliar Ca fertilizers (120 g Ca2+ l) twelve times during the season and determined significantly higher Ca fruit levels at harvest of ‘Elliott’ with the 5 ml/l but not with 0.5 or 3.0 ml/l. Texture and the levels of pectic substances were not affected by Ca sprays. Hanson et al. (1993) showed that fruit firmness was increased using Ca dips from 30 to 240 s (1–4% w/v calcium chloride); however, the fruit had a saline taste that was unacceptable for tasters in a panel (Hanson et al., 1993).

There have been reports of scorching of young leaves after Ca sprays in studies done in the USA with preharvest applications of calcium chloride at 0.08% w/v (Hanson, 1995), but not in Chile at double the rate (Retamales and Arredondo, 1995). Foliar Ca sprays should be avoided in conditions of high humidity and temperatures above 25°C, especially when leaves are young (Stiles and Reid, 1991).

Magnesium
Deficiencies in Mg have been reported in field planting in many blueberry-growing areas (Eck et al., 1990). Mg deficiencies are seen occasionally in Georgia (Krewer and NeSmith, 1999) and periodically in Michigan (Hanson and Hancock, 1996). Lower Mg levels are common in low pH fields. Mg deficiencies are most severe on rapidly growing plants or those with heavier fruit loads. An interveinal chlorosis is most characteristic of Mg deficiencies; although Krewer and NeSmith (1999) state that the most common symptom they have observed in young rabbiteye blueberries is leaves that are pink on the edges and yellowish between the veins. Eventually these leaf areas turn yellow to bright red, while the tissue adjacent to the main veins remains green (Hanson and Hancock, 1996). Leaves may eventually turn red, yellow or brown and prematurely drop from the plant as the deficiency becomes
more severe. Basal (lower) leaves of shoots and canes are the first to show symptoms. Leaves on shoot tips usually stay symptomless (Hanson and Hancock, 1996).

Although the leaf deficiency level is generally thought to be below 0.1%, there have been reports of Mg deficiency in bushes with leaf levels as high as 0.2% (Hanson and Hancock, 1996). Higher optimum Mg levels occur when leaf K levels are also high. High Ca and/or K reduces Mg absorption and may also indicate a need for Mg. Desirable ranges of the percentage of bases (as a proportion of the CEC) in soil samples are 60–80% Ca, 15–30% Mg and 10–15% K. If in the soil analysis Mg is less than 4% of the bases or if K exceeds Mg as a percentage of the bases, Mg applications should be done (Hanson and Hancock, 1996). For practical purposes in fruit crops in general, a ratio of the percentages of K to Mg greater than or equal to 4:1 in foliar samples usually indicates that the Mg supply is inadequate (Stiles and Reid, 1991). Excessive tissue Mg (above 0.4%) commonly indicates that soil pH is too high (Hart et al., 2006).

If foliar levels indicate a deficiency, the decision on what fertilizer to use should be based on soil pH. If the soil pH is above 4.5, magnesium sulfate (Epsom salts) or SulPoMag (21–24% K2O, 21% S, 10–18% MgO) are recommended. Epsom salts can be supplied through the irrigation system. However, if pH is below 4.0 or 4.5, dolomitic lime at a rate of 1 t/ha should be the choice (Hart et al., 2006). Mg deficiency can be corrected by applying 17–56 kg Mg/ha (Hanson and Hancock, 1996; Krewer and NeSmith, 1999). All soil applications should be done in autumn (Hart et al., 2006). Water quality should be tested to determine the quantities of Mg that could be supplied through the water supply.

**Sulfur**

Deficiencies in S are rare in blueberries. Deficiency symptoms of S are often confused with N deficits. Low S plants are stunted and their leaves are light-green with no pattern or mottling. The first symptoms appear in younger tissues. S is routinely applied when the soil pH is too high (Table 5.3). Since S deficiencies are rare, S is seldom applied to correct a deficiency of this element, although blueberries have responded to S applications (Beaton, 1966). If S is low, S-containing-materials such as ammonium sulfate, ordinary superphosphate, potassium-magnesium sulfate or magnesium sulfate could be used in the fertilization programme (Owen Plank and Kissel, 2010).

**Aluminium**

Under soil acidification, toxic Al³⁺ ions are released into the soil solution (Reyes-Díaz et al., 2010). Organic matter mineralization also results in a release of H⁺ ions, decreasing soil pH (Reyes-Díaz et al., 2009); however, the organic amendments and mulches may mediate fluctuations in soil moisture and temperatures and also bind active forms of Al that are released when
the mineral soils are acidified before planting (Yang and Goulart, 1997). These ions accumulate in the roots and inhibit root expansion, but also have been found to produce a deleterious effect on shoot physiology, including chloroplast functioning, total chlorophyll content, photosynthetic rates, canopy development and yields (Yang and Goulart, 1997; Reyes-Diaz et al., 2010). The toxic effects of Al are largely associated with its interference in P and N metabolism, since the symptoms were reversed by foliar P and N application as ammonium polyphosphate to highbush blueberries. Ericoid mycorrhizal infection could ameliorate Al toxicity, but once Al binding and accumulation sites in mycorrhizal-infected roots are fully occupied, excessive Al may be transported into leaves of the mycorrhizal-infected plants and cause damage (Yang and Goulart, 1997).

Studies on highbush blueberries found that 'Brigitta' was least affected by high Al³⁺ substrate levels, with 'Legacy' being intermediate and 'Bluegold' most susceptible; 'Brigitta' accumulated more Al in roots and leaves and had a faster recovery of photochemical parameters (Reyes-Diaz et al., 2009).

**Micronutrients**

**Iron**

Fe deficiencies are common in blueberries. The margins of young leaves in Fe-deficient plants become chlorotic while the veins remain green. As the deficiency progresses, leaves become brown or bronze-gold and may drop. Fe deficiency symptoms differ from those caused by Mg deficiency in that the main veins and many minor veins remain green in Fe-deficient leaves (Hanson and Hancock, 1996). Shoot growth and leaf size are often reduced. Symptoms of Fe deficiency are generally the first indicator of high soil pH (>5.5) (Hanson and Hancock, 1996). Rather than lack of Fe in the soil, it is the high pH which makes Fe unavailable to the plant (Hart et al., 2006). The deficiency has also been associated with soils that are saturated, poorly drained, or have very high Mn or P level (Stiles and Reid, 1991).

Leaf Fe levels are not always a reliable indicator of plant Fe status, as symptoms may appear over a wide range of leaf Fe concentrations, but the problem is that part of the Fe is unavailable for metabolism (Krewer and NeSmith, 1999). In fact, plants with leaf levels in what is considered the deficiency range may sometimes exhibit no symptoms of deficiency. Soil applications of Fe sources seldom benefit Fe-deficient bushes (Hanson and Hancock, 1996). Then, the most effective and efficient means to correct Fe deficiencies is to adjust soil pH. Notwithstanding, if leaf foliar levels are in the deficiency range, two foliar applications of iron chelate (10% Fe) at a rate of 1 kg/400 l water per hectare have been recommended. A surfactant is necessary to enhance penetration through the waxy cuticle of blueberry leaves (Krewer and NeSmith, 1999). Iron chelate at a rate of 17–34 kg/ha
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Iron can alternatively be applied to the soil (Hart et al., 2006). Since there are many formulations of iron chelate, the rate must be adjusted according to product concentration. Iron sulfate can also be used where pH is high, as it lowers the pH and supplies Fe. A suggested rate is three teaspoons per metre of bush height spread evenly under the bush (Krewer and NeSmith, 1999).

Manganese

Unless the pH exceeds the recommended range, Mn deficiencies are rarely found in most blueberry-growing areas (Hanson and Hancock, 1996; Fuqua et al., 2005; Hart et al., 2006). With Mn deficiency, sectors near the leaf margin may die. There could also be isolated dead spots throughout the leaf. Leaves are smaller and interveinal chlorosis of young leaves has been found to be associated with Mn deficit (Fuqua et al., 2005). The primary effect of Mn deficiency would be through reduced photosynthesis (Stiles and Reid, 1991).

Tissue Mn levels increase as pH drops. Thus tissue Mn levels can serve as an indicator of soil pH levels. Tissue levels above 450 ppm are considered excessive, especially if they are present for long periods. However, there are reports that highbush blueberry plants can grow normally with leaf Mn concentrations as high as 650 ppm, since they have mechanisms for Mn tolerance (Hart et al., 2006). Cultivars may differ in their response to Mn. No detrimental effects were reported by Korcak (1989) with plants of ‘Dente’ rabbiteye blueberries at soil pH 5.1 (1175 ppm foliar Mn) or at pH 6.9 (994 ppm Mn) or ‘Tifblue’ plants at soil pH 5.1 (531 ppm Mn) or pH 6.9 (343 ppm Mn). ‘O’Neal’ has been found to be especially susceptible to high Mn levels. Abnormalities due to high Mn in ‘O’Neal’ include multiple flushes of growth over the season, multiple laterals arising from a single position on the shoots (often called ‘witches broom’) and small, crinkled leaves with a reddish colour in the margins. Leaf levels for mild and severe symptoms are very similar in ‘O’Neal’, with mild symptoms present when foliar levels were 426 and 111 ppm for first and second flush of growth, while severe symptoms occurred when 476 and 151 ppm were measured for the first and second flush, respectively. Mn toxicity symptoms (abnormal shoot growth) in ‘O’Neal’ were correlated with low pH, high Mn in the sawdust and manure applied as mulch and before planting. It is recommended to measure Mn levels in organic soil amendments before application (Bañados et al., 2009).

High soil water content resulting in low oxygen availability has also been found to induce Mn toxicity in blueberries. Under these conditions (low oxygen, high Mn levels, low pH), the more mobile Mn$^{2+}$ form is more available for root uptake than Mn$^{3+}$ (Bañados et al., 2009). High Mn also induces Ca deficiency, resulting in small, crinkled, malformed leaves. The foliar application of various fungicides increases surface levels of Mn; however, most of these materials do not penetrate the leaves and can lead to spurious leaf Mn readings (Stiles and Reid, 1991). If Mn is found deficient, two foliar applications of manganese chelate (2–8% Mn) at 7 kg/ha or manganese
Chapter 5

sulfate (32% Mn) at 2.2 kg/ha during the summer have been recommended (Hanson and Hancock, 1996).

**Boron**

Tip dieback is the most prevalent symptom of B-deficient blueberry tissues. Leaves close to aborted shoot tips develop a mottled chlorosis and cupped shape. Internodes tend to be shorter in affected shoots (Hanson and Hancock, 1996). Flower and vegetative buds may fail to open or develop in severely affected plants. Winter injury in B-deficient plants tends to be greater (Hart et al., 2006). Deficiency is aggravated by dry weather and a heavy crop load. B deficiencies are more prevalent in coarse-textured soils. Low plant B may accentuate deficiencies of other nutrients because of impaired root function. In fruit crops in general, low B is often associated with Ca deficiency problems (Stiles and Reid, 1991). Its incidence varies across the blueberry-producing regions; while common in Oregon (Hart et al., 2006), it has not been found in Michigan (Hanson and Hancock, 2006).

If B is deficient, 11–22 kg borax/ha (11% B) can be applied in the autumn or early spring prior to rain. Alternatively 0.9–2.7 kg Solubor (20% B) in 950 l water per hectare can be sprayed before bloom or after harvest and before leaf senescence. An annual application of 560 g B/ha has been suggested (Hart et al., 2006). Foliar and soil treatments of B (four applications of 0.2 kg B/ha between early bloom and 6 weeks after bloom) to ‘Bluecrop’ highbush blueberries increased leaf and flower B levels, as well as fruit soluble solids, but failed to alter plant vigour, number of flowers per cane, fruit set or yield (Wojcik, 2005). Contrarily, a 4-year-study on the effect of autumn and spring B foliar applications to ‘Collins’ and ‘Blueray’ highbush blueberries grown in Missouri increased yield by an average of 10% for the four seasons, which was mostly due to increased number of berries per plant. B sprays also reduced tip dieback symptoms (Blevins et al., 1998). The foliar B levels need to be monitored carefully, as toxic levels of B can be reached rapidly (Hanson and Hancock, 2006).

**Zinc**

Symptoms of Zn deficiency include short internodes and small leaves. Low Zn causes a uniform yellowing of young leaves early in the season with no interveinal pattern. Affected leaves can fold upward along the midrib. The importance of Zn deficiency varies across productive regions. Symptoms have been reported in Oregon (Hart et al., 2006), but not in Michigan (Hanson and Hancock, 1996) or Missouri (Fuqua et al., 2005). Zn deficiency is accentuated at high pH (>6.0) and low soil temperature. Excessive use of P might also lead to Zn deficiency (Stiles and Reid, 1991).

If plants are deficient in Zn, a foliar spray of 454 g Zn chelate (14% Zn) is recommended after harvest and before leaf fall in a volume of 935 l per
hectare. Another option is a soil application of Zn chelate at a rate of 11–34 kg/ha (Hart et al., 2006).

**Copper**

Cu deficiencies are rarely seen in rabbiteye or highbush blueberry fields (Hanson and Hancock, 1996; Krewer and NeSmith, 1999; Hart et al., 2006), although deficiencies have been reported on high-organic blueberry soils in North Carolina (Krewer and NeSmith, 1999). In other areas, symptoms have been induced experimentally by removing this nutrient from the substrate. Cu deficiency symptoms are similar to those associated with insufficient Mn (Hanson and Hancock, 1996). They include interveinal chlorosis of young leaves and, in severe cases, shoot dieback. Cu deficiency may be more severe in soils high in organic matter (>25%) (Hart et al., 2006). Coarser-texture soils, high soil pH and high soil P levels tend to accentuate low tissue Cu levels (Stiles and Reid, 1991).

In North Carolina, 6 kg of elemental Cu is applied before planting on sites with high organic matter and repeated every 5 years. A trial application is suggested if Cu leaf levels are <3 ppm (Krewer and NeSmith, 1999). When needed, a broadcast application of copper sulfate (25% Cu) has been recommended at a rate of 34–56 kg/ha. Another option is a foliar spray of 0.5 kg of copper sulfate in a volume of 900 l per hectare any time leaves are present (Hanson and Hancock, 1996; Hart et al., 2006).

**CONCLUSIONS**

Blueberries grow on low pH soil. They require less mineral fertilizer than most fruit crops. The CEC is associated strongly with the fertility of the soil and with the buffer capacity for changes in soil pH. Soil pH must be adjusted to the range of 4.5–5.5 in order to avoid nutrient imbalances and deficiencies. Usually, S applied one year before planting is used to adjust pH. Most blueberry roots are confined to the top 30 cm of the soil. They are colonized by a special type of mycorrhizae. These ericoid mycorrhizae reduce their infection with the application of mineral fertilizers and with root age. They protect the plant from Al toxicity which is prevalent in low pH soils. Soil analysis is recommended before planting to determine nutritional status and pH. Once the field is planted, leaf analysis should be the basis for nutrient management, along with soil pH monitoring. In order to be useful, strict procedures must be followed for leaf sample collection. Normal foliar levels vary somewhat in P, B, Fe and Mn across production regions which may reflect environmental conditions for best performance. The fertilizer need is based on nutrient demand and supply, but the efficiency of fertilizer use has to be considered. The most common method for fertilizer application has been broadcast; however, fertigation has increased in acceptance due to higher efficiency and ease of application. Organic
nutrient management is also expanding for blueberries. Whatever the method, efficiency usually increases as the number of applications increase. Except for some micronutrients and specific occasions, foliar fertilization is not very efficient and has proved costly. After correction of pH and P levels at planting, N and sometimes K are the nutrients that usually require annual applications in blueberry fields. Deficiency symptoms have been described for each of the major blueberry nutrients, along with specific fertilization practices to restore sufficiency.

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Nutrition


BLUEBERRY FIELD MANAGEMENT AND HARVESTING

INTRODUCTION

Once a grower has selected both the site and the plant material (varieties), it is time to get involved in the management of the crop. The goals of blueberry management are: (i) to avoid or minimize stressful conditions to the plant; (iii) to optimize plant function in relation to the environmental conditions; and (iii) to properly balance growth among the various parts of the plant. To be cost-effective, these interventions must increase plant growth and yield sufficiently to justify the cost involved. Since blueberry varieties have different parents and are planted in widely different environments, their response to stress and their response to horticultural practices vary widely. Because environmental stress is not constant throughout the season, it is important to consider not only the degree of intervention but also when it is needed.

In this chapter we cover several management practices of utmost importance in blueberry cultivation, including mulching, irrigation, pruning, pollination and harvesting. In the case of mulching, the characteristics, considerations and effects of both organic and plastic materials are presented. The impact of insufficient or excess water is explained. The methods to determine water status in blueberry fields are discussed and the most important irrigation systems compared. The timing, intensity and effects of pruning are presented, along with the reproductive biology of blueberries and the most effective planting designs. We also discuss mechanical harvesting.

FUNDAMENTAL CONCEPTS OF IRRIGATION

Water has several functions within the plant: (i) it is the milieu for transporting nutrients and growth substances to the various parts of the plant; (ii) it is necessary for the plant to regulate the temperature of its tissues, especially when plants are grown in hot environments; and (iii) it is necessary to maintain normal physiological activity, since water is the driving force for
growth. In fruit crops, such as blueberry, there is often a premium price for fresh fruit where water content is maximized.

Water stress can be due to either excess or deficit. Excesses normally occur in blueberries when the plant is in dormancy or during bud break. Deficits usually happen during the middle of the growing season, when temperatures are high and demand for water is maximum (Darnell, 2006). There are various techniques to alleviate water-related stress. They can be classified as either: (i) strategic, which are undertaken before planting, and comprise variety selection, plant density, use of mulch, trellising, irrigation and drainage system selection and design; or (ii) tactical, which are the opportunistic implementation of strategies once the crop is planted, and include fertilizers (dose, method, timing), pruning (timing and intensity), weed control, management of irrigation and drainage systems (Daebke and Aboudrare, 2004).

To provide an adequate water supply to plants, it is important that: (i) the soil root zone be large enough to supply the plant; (ii) the soil water supply be replenished frequently enough to avoid water stress; (iii) the water freely infiltrates the soil without leaching nutrients to depths below the root zone; and (iv) an effective water-absorbing root system is maintained throughout the plant’s life cycle.

The low root density of blueberries leads to slow water movement within the soil profile and consequently, under moderate to high evaporative demand on the canopy, water stress is developed within the plant. Due to this, the capacity of the water to move within the plant is controlled more by the transpiration induced by the environment than by soil moisture. This places great emphasis on understanding canopy microclimate and stomatal behaviour (the pores in leaves where plants exchange water and gases with the environment) as a means to control not only water loss, but also water potential.

Before discussing the irrigation of blueberries, it is important to understand some basic concepts regarding water relationships in fruit crops.

**FUNDAMENTAL CONCEPTS IN WATER RELATIONSHIPS**

Water is essential for plant growth and development. The soil must supply large quantities of water to meet the transpiration demands of growing plants. The behaviour of water in the soil and the plant has been unified in a single energy concept: the water potential or \( \Psi \). This concept considers the soil–plant–atmosphere chain as a continuum. Although \( \Psi \) is usually expressed in units of pressure (megapascal, MPa), it indicates the energy of the water in a given part of the system.

The energy concept is used to explain why water enters the soil, is absorbed and transported through plants, and then evaporates into the
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atmosphere through transpiration. Under most conditions (relative humidity somewhat less than 100%), water potential ($\Psi_w$) is highest in the soil and lowest in the atmosphere, with intermediate values in the plant. There is then a gradient from the soil through the plant to the atmosphere. Water potentials in the soil and the plant are related (although not linearly), as can be seen in water-stressed blueberries (Table 6.1).

The capacity of a soil to store water is the result of the attraction of the soil matrix (solids) for water. Water interacting with the soil loses energy, so the water potential (or energy) of the water retained by the soil is lower than that of pure water. The interaction of ions (salts, fertilizers, etc.) and other solutes with water (called osmotic forces) further reduces the energy level (or potential) of water in the soil. The gravitational forces also affect the energy or potential of soil water, particularly under saturated moisture conditions. A major consequence of this low energy status (or potential) of soil water is that the removal of water from the soil matrix by a plant root requires the expenditure of energy, which is ultimately supplied by sunlight through photosynthesis. Various forces act on the water in the system. The relationship among the various energies required to move water from the soil and within the plant is expressed by the water potential ($\Psi_w$). The water potential is the result of the gravitational potential ($\Psi_g$), the matric potential ($\Psi_m$) and the osmotic potential ($\Psi_s$):

$$\Psi_w = \Psi_g + \Psi_m + \Psi_s$$

(6.1)

As equation (6.1) states, the three components are additive. $\Psi$ has a negative sign representing the energy difference between different components of the system. Under normal field conditions, after free drainage of water has occurred (24–72 h after rain or irrigation), the gravitational potential ($\Psi_g$) is considered insignificant relative to the other components.

Table 6.1. Soil and leaf water potential in well-watered (daily irrigated) and water-stressed (not irrigated for the designated number of days) 2-year-old ‘Rancocas’ highbush blueberry plants. Values are means of four replicates ±standard error. (Adapted from Lee et al., 2006.)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Day</th>
<th>Soil</th>
<th>Leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td>Well watered</td>
<td>1</td>
<td>-0.20±0.013</td>
<td>-1.01±0.033</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-0.18±0.021</td>
<td>-0.99±0.024</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.20±0.010</td>
<td>-1.00±0.054</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-0.22±0.031</td>
<td>-1.07±0.023</td>
</tr>
<tr>
<td>Water stressed</td>
<td>1</td>
<td>-0.21±0.027</td>
<td>-1.02±0.056</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-0.33±0.017</td>
<td>-1.42±0.049</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.83±0.068</td>
<td>-1.58±0.075</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-0.99±0.045</td>
<td>-1.79±0.038</td>
</tr>
</tbody>
</table>
The central importance of $\Psi$ in water relationships arises because differences in total $\Psi$ provide the driving force for water movement and therefore determine the direction of water movement in any system. Water moves freely into the root. Water is then going from an area of high water potential (the soil) into the root, which is an area of low water potential. Then water crosses through various tissues until it reaches the vascular cells (xylem). Transpiration provides the pulling force for drawing water up into the shoot of the plant. It is assumed that the gaseous areas of plants including the stomatal cavity are saturated with water vapour and the relative humidity is 100% (Salisbury and Ross, 1991).

The matric potential ($\Psi_m$) not only gives the soil its water-storing ability but also functions to determine water movement. In agricultural situations, the matric potential is measured with a soil tensiometer. $\Psi_m$ is always negative. Water always moves down its water potential gradient from areas of higher water potential (higher water concentration) to areas of lower water potential. In the soil, the osmotic potential, which also is negative, originates from the presence of solutes. The most obvious plant osmotic adjustment in fruit crops is by the fruit that accumulate large quantities of soluble solids (mostly sugars) over the season through photosynthesis (the transformation of solar energy into carbohydrates; see Chapter 4).

Unlike the matric potential, the osmotic potential of a soil does not affect the movement of soil water, nor does it influence the retention of water by the soil matrix. Its main effect is the influence on water uptake by plant roots. A soil solution with a high solute content (such as when high dosages of fertilizers are applied) effectively restricts water movement through the root cells because the presence of salts lowers the energy level in the plant root.

As water is removed from the soil, the remaining water is held at a more negative potential indicating that the water is under tension and that work must be done to extract water from the soil (Fig. 6.1). The relationship between the matric potential (related to water-storing ability and water movement within the soil) and the moisture content for soils of different textures is called the soil moisture characteristic curve. Under normal (non-saline) conditions, such as those that commonly occur in blueberry fields, the matric potential dominates the availability and movement of soil water. At a given matric potential, the heavier textured soils (with finer particles, such as clay) hold more water than the lighter textured (sandy) soils. After free drainage has occurred in a saturated soil ($\Psi_m=0$), the moisture content of the soil is said to be at ‘field capacity’. Depending on the soil texture this free drainage would occur in 24 (sandy) to 72 h (clayey soil). At this point pores are filled with water. Plants remaining in this condition may have insufficient oxygen for normal respiration. For most soils this point is about $-0.033$ MPa or $-0.33$ bar (Fig. 6.1).

The matric potential decreases (it becomes more negative) as water is removed from the soil, until this potential is equal to that of the plant. At that
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Fig. 6.1. Water-holding properties for various soil textures. For each soil, the available water supply is the difference between the field capacity (FC) and the wilting point (WP); retained water volumes correspond to the range between FC and WP. (Adapted from Shan, 2011.)

point the plant can no longer remove water from the soil. In that moment, the turgor or water pressure in the plant cells (which is responsible to keep cells firm) drops to zero and the plant wilts. If water is not replenished the plant will wilt permanently and will not recover even if put in an atmosphere having 100% relative humidity.

Plant species can have different water potentials before permanent wilting occurs. For most species, it is reached at a water potential of −1.5 MPa or −15 bars. The amount of water retained in a given soil at −1.5 MPa is referred to as the ‘permanent wilting point’. The amount of water held between field capacity and permanent wilting point is known as ‘available water’ (Fig. 6.1).

The water potential in a non-transpiring plant approaches the water potential in the soil, but through transpiration, a gradient in water potential develops from the soil, to and through the plant; thus water moves from the soil, through the plant and out to the external atmosphere. The water potential can then be assessed in different parts of the plant (leaf, shoot). Plant water status depends on a combination of soil, atmospheric and crop factors (Jones and Tardieu, 1998).

Evapotranspiration is defined as crop water losses both by evaporation from the soil and transpiration from the plants. Evaporation is the term
used to describe the change from the liquid state to a gaseous state, purely a physical process. The level below that of soil water potential, to which plant water potential falls during the day, depends on the magnitude and duration of the lag of absorption behind transpiration. Transpiration is governed by atmospheric factors such as radiation, air temperature, relative humidity and wind speed, while water absorption is governed partly by soil factors, including water content and unsaturated conductivity (capacity of water to move within the soil between field capacity and permanent wilting point). Water absorption is also a function of plant factors, such as the amount of absorbing root surface and permeability of the roots (Salisbury and Ross, 1991).

Transpiration is a biophysical process involving soil moisture content, the passage of water throughout the plant, movement of water from leaf stomata and the transport of water in the atmosphere by processes of diffusion (movement from higher to lower solute concentration) and turbulence (air movement that normally cannot be seen). Transpiration involves the physical change of state of water (liquid to gas). The propensity of plants to lose water through the leaves (transpiration) depends on the activity of the stomata. These orifices allow photosynthesis and transpiration to occur simultaneously. The degree of stomatal opening is measured as the stomatal conductance. The degree of stomatal opening is to a large part related to the gradient of vapour pressure between the plant and the environment. Increased transpiration rates are generally associated with higher photosynthetic rates and dry weight accumulations (Loomis and Connor, 1992).

The amount of fruit harvested can strongly influence the water status of the plant if it results in a reduction in root growth. This relationship is especially important in recently established plants, where high crop loads can severely reduce root growth. A reduced root volume lessens the total soil water availability and results in low water potential over the entire season. It can also impact on plant size, reducing future yield potentials.

WATER STRESS IN BLUEBERRIES

Water is the most abundant component in all plants. Depending on the tissue, water encompasses as much as 70% (canes) to 85% (fruit) of the weight of organs in blueberries (Retamales and Hanson, 1989). As a result, all plant processes are eventually affected by water stress with diverse magnitudes. In general, water deficits reduce transpiration the most, followed by photosynthesis and to a much more limited extent respiration. A strong reduction in leaf area coupled with reduced photosynthesis results in major reductions in dry weight accumulation. Heavy cropping accentuates leaf area reduction, but increases transpiration rates per leaf area. Water stress reduces mineral availability and water uptake, but specific elements can be affected differently. For example, water-stressed 2-year-old ‘Bluecrop’ and ‘Jersey’
Field Management and Harvesting

Plants allocated a higher percentage of dry matter to their root system at the expense of above-ground growth (Cameron et al., 1989).

There is a differential tolerance to water stress among blueberry species. Rabbiteye blueberries are generally more tolerant than highbush (Eck, 1988). Highbush blueberry is a shallow-rooted crop that is highly sensitive to soil water deficit. However, the impact of water stress on plant functioning depends on the level of stress, the time of the season and the variety. When highbush blueberries are exposed to even mild episodes of drought, vegetative growth of the plant is rapidly reduced and fruit development is often diminished. When Améglio et al. (2000) subjected 9-year-old 'Bluecrop' highbush plants in containers to 10 days of water deficit in the middle of the growing season, they found that water potential, embolism, transpiration (leaf and plant) and stomatal conductance were highly sensitive to drought (as judged by rapid stomatal closure and reduction in transpiration). The rapid drop in stomatal conductance effectively restricted water loss and prevented tissue death. Five days after irrigation was initiated water-stressed plants had similar transpiration levels to control plants.

In another experiment, 7-year-old 'Bluecrop' highbush blueberries were grown in peat–pine bark (50:50) substrate in containers and were subjected during the growing season to mild (replacement of 65% of the water transpired by well-watered plants) or severe water stress (replacement of 35% of the water transpired by well-watered plants) (Mingeau et al., 2001). This water stress was imposed for 3 weeks in four different periods: fruit growth (weeks 7 to 4 before peak harvest), ripening (weeks 4 to 1 before peak harvest), harvest (with week 2 defined as peak harvest) and postharvest (weeks 4 to 7 after peak harvest). The highbush blueberries exhibited a marked sensitivity to water stress, in particular between fruit formation and maturation.

The magnitude of the plant response was related to phenological stage. Plants were able to recover control levels of transpiration faster under mild stress than under severe stress. The periods of maximum water requirement were the first two weeks after petal fall and the two weeks before and after harvest. In control plants (no water stress), most shoot elongation occurred during the green fruit stage, but stressed plants had negligible shoot elongation during this period. After rehydration, their shoot elongation rate was greater than control plants, particularly in those that had been under severe stress. For all water stress periods during the vegetative season, stem diameter did not increase while under water stress. Severe water restriction reduced yields by 31% in plants stressed during initial fruit growth and by 49% in plants stressed near harvest. The effect of stress on yield was mainly due to a reduction in fruit size and not fruit number (Table 6.2).

Mingeau et al. (2001) also studied the effects of water stress during the postharvest period, at the time when blueberries would be expected to initiate flower buds. Severe stress restricted to this period did not have a significant impact on yield the following year. Although severe stress reduced fruit
Table 6.2. Effects of time and intensity of water stress on yield and its components in 7-year-old ‘Bluecrop’ highbush blueberries. (Adapted from Mingeau et al., 2001.)

<table>
<thead>
<tr>
<th>Stress period</th>
<th>Stress intensity (% of transpiration)</th>
<th>Yield/bush (g)</th>
<th>Fruit/bush (g)</th>
<th>Fruit weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>100</td>
<td>2850&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3150&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.92&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Fruit growth</td>
<td>65</td>
<td>2225&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2961&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.76&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>28 May–16 June</td>
<td>35</td>
<td>1965&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3181&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.64&lt;sup&gt;abc&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ripening</td>
<td>65</td>
<td>2250&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2992&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.77&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>18 June–7 July</td>
<td>35</td>
<td>1450&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2667&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.56&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Harvest</td>
<td>65</td>
<td>2100&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2835&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.76&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a,b</sup>Mean values within a column with unlike superscript letters were significantly different at \( P<0.05 \) level (Newman-Keuls test).

number per bush by generating a lower number of flower buds per bush (53% of control plants), there was a compensatory effect due to increased size per fruit (59% greater than control). This suggests that water stress during flower induction might have a similar effect to winter pruning on subsequent fruit production. However, the authors cautioned that water stress imposed at this time to obtain large size fruit could jeopardize plant architecture by encouraging the formation of saplings from the crown. Water stress at this period could also cause early defoliation which would reduce the level of reserves and, with this, the development of leaf and flower buds in the following season.

Sensitivity to short-term water deficits varies among cultivars. As soil water was depleted ‘Duke’ maintained, on average, significantly higher stem water potentials and greater stomatal conductance than ‘Elliott’, while ‘Bluecrop’ appeared to be less tolerant to short-term water deficits (Bryla and Strik, 2006).

**WATER EXCESS (FLOODING)**

Even though wild highbush blueberries are found growing on hummocks in wetlands, flooded areas are not recommended for plantations, as blueberries perform much better on dry land. It has been suggested that the fibrous root system of blueberries may aid the plant in surviving flooding, since higher oxygen levels, necessary for root growth, frequently occur close to the soil surface in poorly aerated soils. The oxygen concentration adequate for optimum plant growth has been established at 0.01 kg/m<sup>3</sup>; these levels were detected at 30 cm depth (Topp et al., 2000).

Flooding stress is primarily due to a deficiency in soil oxygen, as oxygen in soil pores is depleted by microbial and root respiration (Darnell, 2006). Soil oxygen levels can drop from 20% to less than 5% within 2 days of flooding.
The effects of flooding on cultivated blueberries vary with the duration, the time of the season and perhaps species. Rabbiteye blueberries are reported to be more flood-tolerant than highbush (Davies and Flore, 1986a; Eck, 1988), but these differences appear slight. It is possible that the perceived differences in flooding tolerance might be due to the increased sensitivity of most highbush blueberry cultivars to *Phytophthora* root rot, rather than to physiological factors (Davies and Flore, 1986a; Crane and Davies, 1988).

Blueberry plants respond to flooding by stomatal closure, which reduces transpiration and slows damaging reductions in water potentials. However, stomatal closure limits gas exchange, which decreases photosynthesis and eventually may lead to growth cessation and death. Stomatal conductance and transpiration decreased significantly after 4 to 5 days of flooding during the growing season. Photosynthetic rates in highbush blueberries decreased to 60% of non-flooded control within 2 days of flooding (Davies and Flore, 1986a). After 1 day of flooding, rabbiteye blueberries in containers had net photosynthetic rates that were 64% lower than non-flooded control plants (Davies and Flore, 1986b). Carbon assimilation (photosynthesis minus respiration) in highbush blueberries became negative after 11–19 days of flooding due to decreased photosynthesis, reduced stomatal conductance to CO₂ and high leaf temperatures, which increased respiration (Darnell, 2006).

It has been reported that the cultivated highbush blueberry can survive extended periods of flooding, if it occurs at times other than the spring period of active growth; however, growth and plant development can be severely impacted at any time during the season (Darnell, 2006). Flooding of highbush blueberries reduces water and nutrient uptake, suppresses plant growth and reduces yield and quality (Abbott and Gough, 1987a). The reduction in water uptake under flooded conditions has been attributed to the adverse effects of high CO₂ and low O₂ concentrations on the permeability of root cells to water.

Flooding highbush blueberries for 4 months at different stages reduced both vegetative and growth (Abbott and Gough, 1987b). The flooding reduced shoot and internode length, leaf size and root dry weight, and plants had fewer flower buds, fewer flowers per bud, delayed bloom, reduced fruit set and weight and less soluble solids in the fruit (Table 6.3). Highest damage occurred when flooding started at bud break. The negative effects on reproductive development could have been partially due to a reduction in the production and/or translocation of hormones such as cytokinins and gibberellins which promote bud activity.

Flooding duration also affects the responsiveness of blueberry plants to environmental stimuli. Davies and Flore (1986a) found that stomatal conductance and carbon assimilation declined during the first four or five days of flooding, although stomata were still responsive to changes in vapour pressure gradient. As flooding was prolonged, stomatal conductance declined and carbon assimilation became negative. After 24 days of flooding, the
Table 6.3. Effect of 4 months of root-zone flooding on reproductive growth in 2-year-old container-grown ‘Bluecrop’ highbush blueberry. (Adapted from Abbott and Gough, 1987b.)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Flower buds/ shoot</th>
<th>Flowers/ bud</th>
<th>Full bloom</th>
<th>Fruit set</th>
<th>Fruit weight</th>
<th>Soluble solids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17 May</td>
<td>87.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>11.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Flooded</td>
<td>1.7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>21 May</td>
<td>55.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.10&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.9&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Mean values within columns with unlike superscript letters were significantly different at P<0.05 level (Duncan's test).

<sup>b</sup>Data on flower buds/shoot, flowers/bud, date of full bloom and fruit set are means of one year.

<sup>c</sup>Data on flower buds/shoot, flowers/bud, date of full bloom and fruit set are means of two years.

Stomatal conductance was near zero and stomata did not respond to changes in the environment. Carbon assimilation continued with negative values and, depending on the variety, the leaves became red or chlorotic. Recovery after 24 days of flooding to pre-flood stomatal conductance and transpiration values required 16–18 days for rabbiteye blueberries, while highbush blueberries had recovered only 64% of the levels of control plants by that time.

**IRRIGATION**

In many blueberry-producing regions rain and/or the water table do not provide all water requirements of the plants (Williamson et al., 2006). Blueberries are shallow-rooted plants that are rapidly subject to drought injury (Spiers, 1986). The cultivated highbush blueberry root and conduction systems have minimal lateral transport. It has been demonstrated that providing irrigation to one side of the plant (as in drip irrigation) can result in extreme differential growth and disrupted fruit production (Abbott and Gough, 1986). Care should be taken in the design, operation and maintenance of irrigation equipment to ensure that it provides even distribution of water for plant use.

Under most commercial production conditions, irrigation is economically justified because of its positive impact on plant growth, yield and fruit quality. The demand for irrigation is greatest and most critical when full foliage is present, maximum berry growth is occurring and rain is scarce or non-existent (Williamson et al., 2006). The main issue with irrigation management is to determine the frequency, quantity and timing of irrigation in order to optimize both water-use efficiency and crop growth and productivity. Once the grower has decided that irrigation is profitable, it is important to consider that there are some plant characteristics that impact on water application.
Irrigation scheduling

To avoid drought stress, irrigation, rain and/or the water table must be adequate to provide sufficient water for plant transpiration and evaporation. There are various ways to schedule irrigation. The most commonly used are: (i) determination of orchard water status; and (ii) moisture accounting. In the water status method, tensiometers or other devices are used to measure availability of water in the soil. A certain criterion or threshold is defined to start irrigation (Williamson et al., 2006). When tensiometers are used, readings are provided in centibars (cb). A reading of 10–20 cb reflects a soil that is at field capacity (i.e. water availability is at its maximum). Readings from 20 to 85 cb indicate the need for irrigation, with 20–40 cb and 60–80 cb usually indicating the need to irrigate in light- and heavy-textured soils, respectively. However, reports from Florida indicate that in sandy soils irrigation should be scheduled when soil water tension reaches 10–20 cb (Smajstrla and Harrison, 2008). In research done on southern highbush blueberries grown in sandy soils in Florida (Table 6.4), in the first three years after establishment, it was found that the highest plant volume was obtained when a 10 cb threshold was used for scheduling drip irrigation in comparison with 15 or 20 cb. With 10 cb scheduling, average fruit yield for years 2 and 3 was 68 and 394% higher than scheduling with 15 or 20 cb, respectively (Haman et al., 2005).

The moisture accounting method balances soil moisture gains from rainfall and irrigation against soil moisture losses from evaporation and transpiration (crop water productivity or CWP). The moisture accounting method has been reported to work well on soils that do not have a high water table. When a water table is present, it can be measured simply by digging a

<table>
<thead>
<tr>
<th>Month</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>64.4</td>
<td>26.5</td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>60.6</td>
<td>34.1</td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>71.9</td>
<td>56.8</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>53.0</td>
<td>87.1</td>
<td>177.9</td>
</tr>
<tr>
<td>May (harvest)</td>
<td>56.8</td>
<td>117.3</td>
<td>310.4</td>
</tr>
<tr>
<td>June</td>
<td>124.9</td>
<td>147.6</td>
<td>344.5</td>
</tr>
<tr>
<td>July</td>
<td>128.7</td>
<td>196.8</td>
<td>393.7</td>
</tr>
<tr>
<td>August</td>
<td>121.1</td>
<td>193.1</td>
<td>367.2</td>
</tr>
<tr>
<td>September</td>
<td>109.8</td>
<td>166.6</td>
<td>336.9</td>
</tr>
<tr>
<td>October</td>
<td>87.1</td>
<td>143.8</td>
<td>200.6</td>
</tr>
<tr>
<td>November</td>
<td>75.7</td>
<td>90.8</td>
<td>174.1</td>
</tr>
<tr>
<td>December</td>
<td>53.0</td>
<td>53.0</td>
<td>174.1</td>
</tr>
</tbody>
</table>
post hole in the row between bushes and installing a piece of drainage tubing (Williamson et al., 2006). The key to successful use of moisture accounting is the estimation of CWP (Byers and Moore, 1987). A widely accepted method for estimating CWP is the use of evaporation pans. In this method, the evaporation from a standardized evaporation pan (Class A Weather Bureau) is related to CWP. The pan is 1.2 m (4 ft) in diameter and 250 mm (10 in) deep and should be installed 150 mm off the ground. The normal operating water level is specified at 175–200 mm of water depth. In many producing regions, evapotranspiration data can be obtained through the internet from meteorological web sites. Crop CWP and evaporation from the Class A pan are related by the crop coefficient (K or Kc). In other words, to assess the water that a blueberry field has consumed, the water evaporated from the pan has to be multiplied by the Kc.

Research in Florida established that crop coefficients varied from 0.10 to 0.24 for 1-year-old rabbiteye blueberry plants (Haman et al., 1997b). In the case of 2- and 3-year-old plants Kc ranged from 0.10 to 0.49. In both cases, highest values were for summer months. Research in Arkansas estimated the Kc value for young highbush blueberry to be 0.75, even though there were no significant differences in total vegetative growth, yield or quality with Kc values of 0.5 and 1.0 (Byers and Moore, 1987). Based on lysimeter studies (a lysimeter is a container of soil in which measurements of gains and losses of soil water can be made; e.g. by weighing), in 5- to 6-year-old 'Bluecrop' plants, it was determined that crop coefficients increased during leaf expansion to 0.19 for 5-year-old plants and 0.27 for 6-year-old plants; these crop coefficients remained at these levels until leaf senescence. Assuming a cylindrical bush shape, the maximum crop coefficient was equal to 1.5 times the measured canopy coverage (measured in m²). Canopy coverage was equal to 18% of the total cultivated area.

A problem with the moisture accounting method is that precise Kc values are often difficult to establish due to regional and site-specific variability in climate, soil characteristics, crop physiology and cultural practices. A grower using the moisture accounting method for scheduling irrigation should use a conservative crop coefficient value, frequently check soil water availability with soil probes, and look for stress symptoms in plants (reduced shoot and leaf growth, alteration of leaf angles and wilting). Crop coefficients should then be adjusted until adequate moisture levels are reached.

**Determining soil moisture**

There is a great range in the characteristics of the methods used to determine water status in agricultural situations. Some of them determine the availability of water in the soil while others measure the status of water in the plant.
In recent years, there has been increasing availability of devices and sensors for automatic measurement of soil and crop water (Jones and Tardieu, 1998). Measurement of soil water potential and soil water content provide an index of the rate at which water is taken up by the plant or lost from the root zone. Data on soil water content and potential are therefore most useful in conjunction with information about the soil–plant–atmosphere system. Although climate- and soil-based methods provide a means for estimating irrigation amount and timing, they do not take into account the variability among cultivars, growth stages and the response of plants to soil moisture deficit. The water refill point, which is the lowest possible soil water content with no decrease in yield or fruit quality, varies among varieties, soils, management practices and seasons. An integrated approach utilizing both soil and plant factors for irrigation scheduling is often beneficial (Al-Yahyai, 2006). Physiological variables (plant water potential and gas exchange), as well as plant growth and fruit production and quality, should be correlated with soil water content prior to determining the appropriate amount and timing of water to apply to a blueberry field.

Among the methods used to determine soil water, the simplest one is 'feel and appearance'. Field samples are taken which the operator feels by hand. The great advantages of this approach are its low cost, rapidity and the possibility to assess multiple locations. Among the disadvantages of 'feel and appearance' are that considerable experience is required and it has low accuracy (Williamson et al., 2006). The gravimetric method measures mass water content. Field samples are collected, weighed, oven dried, and again weighed. The advantages to this approach are its accuracy and that multiple locations can be measured. However, the process is labour-consuming and there is a time delay between sampling and results.

Electrical resistance blocks (gypsum blocks) and granular matrix sensors (GMS) measure soil water potential. They tend to work better at higher tensions (lower water contents). They can be set to turn on irrigation automatically when a certain level is reached. GMS technology reduces the problems inherent in gypsum blocks (slow response time and dissolution of the block) by using a mostly insoluble granular fill material. Like gypsum blocks, GMS sensors operate on the principle of variable electrical resistance (Shock, 2008). A major difficulty is the representativeness of site sensor placement (Améghlo et al., 1999). To date, gypsum blocks and GMS have been rarely employed in blueberry fields.

Tensiometers have been widely used in blueberry management. A tensiometer consists of a porous cup, connected through a rigid body tube to a vacuum gauge, with all components filled with water. They measure soil water potential (tension) which is directly related to the ability of plants to extract water from soil. This reading is a measure of the energy that would need to be exerted by the plant to extract water from the soil (Smajstrla and Harrison, 2008).
The way tensiometers work is that a partial vacuum is created as water moves from the sealed tensiometer tube to the surrounding soil. The change in vacuum is translated into a reading which is a direct indication of the attractive forces between the water and soil particles. As the soil dries, the water potential decreases (tension increases) and the tensiometer vacuum gauge reading increases. Conversely, an increase in soil water content (from irrigation, water table or rainfall) decreases tension and lowers the vacuum gauge reading. In this way, a tensiometer continuously records fluctuations in soil water potential under field conditions. A tensiometer indicates only when irrigation should be scheduled, and not how much water should be applied. Digital tensiometers can be set up to turn on irrigation systems when a previously defined threshold is reached. Tensiometers are placed below the plant canopy in positions where they will receive typical amounts of rainfall and irrigation. The porous ceramic of the device should be set in the blueberry root zone (usually 30 cm depth) with the ceramic cup firmly in contact with the soil.

Growers often use tensiometers for irrigation scheduling because of their several advantages: (i) they provide direct measurements of soil moisture status; (ii) they are easily managed; and (iii) they can be automated to control water applications when the soil water potential decreases to a predetermined critical value. Among the drawbacks are: (i) they need careful placement and constant maintenance; (ii) they are useful only under mostly uniform soil texture; (iii) their practical operating range is about 0 to 0.75 bar (Fig. 6.2), which is a range that usually excludes its use for medium- and fine-textured soils; and (iv) they are not appropriate to use if soils are saline, or if saline irrigation water is being used, because in those conditions the osmotic potential will be a large portion of the total soil potential (Wilk et al., 2009).

**Determining plant water status**

In general, the establishment of water status through plant measurements is more frequently used for research purposes than to schedule irrigation in commercial fields. One exception is the visible symptoms of water stress (Loomis and Connor, 1992; Darnell, 2006), but in this case the assessment is too late since the productive potential of the plant has already been reduced by the stress experienced. If symptoms of water stress are observed in blueberry plants during fruit growth, the yield potential has already been reduced (Mingeau et al., 2001).

Methods of measuring water status in plants can be classified as: (i) direct or (ii) indirect. The measurement of relative water content (RWC) is one of the direct methods which estimate the current water content of the sampled leaf tissue relative to the maximal water content it can hold at full turgidity. Normal values of RWC range from 98% in turgid and transpiring leaves to
Fig. 6.2. Effect of irrigation on soil water potential as measured by tensiometers placed at 30 cm (12 in) or 60 cm (24 in). (Adapted from Smajstrla and Harrison, 2008.)

about 40% in severely desiccated and dying leaves. In most crop species the typical RWC around wilting is about 60 to 70%. This method has not been used in commercial blueberries to schedule irrigation, but Davies and Johnson (1982) have reported that for rabbiteye blueberries, the relative water content changed 6.4% per 1.0 MPa change in water potential.

Another direct method of water status measurement is the water potential, which measures the energy (tension) status in either the leaf or the stem. This has not been used to schedule irrigation in blueberries, but has been used by some elite tree fruit growers. A fully matured leaf or a stem is enclosed in a reflective plastic bag for 1 h to suppress transpiration and allow stem water potential to equilibrate with leaf water potential. Measurements are taken near noon with a pressure chamber (Al-Yahyai, 2006). Stem water potential, which corresponds to the tension of the xylem vessels in the trunk, is representative of the whole plant and is a reliable plant-based water status indicator for irrigation scheduling in fruit trees (Moriana et al., 2010). Within the plant the microclimate is not uniform, and this will generate a range of water potentials reached by organs of different type (leaves, fruits, shoots and canes of different ages).

In fruit trees it has been reported that there is a 35% differential in leaf water potentials between outer exposed and shaded leaves. No data on the variability of this characteristic are available for blueberries. In fruit trees, the stem water potential has been found to be a good indicator of water stress for crops in conditions of heterogeneous soil humidity, particularly when
only a small part of the soil contains easily available water (e.g. limited drip or minisprinkler irrigation, a patchy root system). In such cases, the use of complementary stress indicators such as sap flow, which are not biased by the spatial distribution of soil water and which therefore are more specific to the actual water stress, would overcome the uncertainty that can arise from the use of stem water potential values alone (Améglio et al., 1999). Another negative issue associated with water potential measurements in plant tissues is that these measurements do not consider internal osmotic adjustment, which corresponds to the active accumulation of solutes in the cell sap. However, since blueberries are not drought-tolerant plants, their ability for osmotic adjustment is minimal (Muralitharan et al., 1992).

The indirect methods of measuring plant water status include: (i) crop canopy temperature; (ii) changes in trunk or stem diameter; (iii) stomatal conductance; and (iv) sap flow. An infrared thermometer (IRT) is used to determine crop canopy temperature. A general problem often encountered in assessing plant water stress by canopy temperature is the representativeness of the target area. The inclusion of non-transpiring surfaces (soil, branches, etc.) inside the IRT field of view generates unwanted shifts in the temperature readings. At present, affordable and portable thermal imaging devices with high resolution are available; these have solved the problem of discriminating between foliage and non-transpiring surfaces (Testi et al., 2008).

The trunk diameter fluctuations (TDF) sensor measures the daily cycle of shrinking and swelling in the trunk/stem of the crops. This cycle is produced owing to the lag between transpiration and root uptake that is partially compensated with the water of the trunk. Therefore, the trunk is a water reservoir in the soil-plant-air continuum. The approach has been used successfully in almond and lemon trees, but not in olive trees (Moriana et al., 2010). TDF was not useful as a permanent system in plums due to temporal changes as trees aged (Bonet et al., 2010). TDF has not been tried in blueberries and the growth pattern of blueberries with multiple shoots would complicate these measurements.

The basic principle of sap flow is that transpiration occurs as a continuum from soil to plant to atmosphere and it may be measured or estimated as moisture loss from the soil, liquid flow through the plant stem (xylem sap flow) or vapour loss to the surrounding atmosphere. The stem of a woody plant is a convenient place to measure xylem sap flow and ultimately, transpiration. If measured over a sufficiently long period to negate changes in stem storage, speed of transport in the xylem sapwood of a woody plant stem can be established if a heat pulse is applied to the trunk and the change in temperature is measured at a given distance from that heat source (Swanson, 1994).

Sap flow measurements give reliable, direct estimates of plant or shoot water loss without disturbing the conditions of the leaf environment. In irrigated grapevines, sap flow measurements have been shown to be good
estimators of canopy transpiration (Cifre et al., 2005); to our knowledge these measurements have not been made in blueberry.

Stomatal conductance (i.e. the ability of these pores to open or close in response to environmental conditions) is used to quantify gas diffusion processes, such as transpiration, between plants and the atmosphere (Byers et al., 1988). Stomatal closure is among the first processes occurring in the leaves in response to drought. Diurnal changes in stomatal conductance, leaf water potential and transpiration have been shown to be closely related in blueberries (Bryla and Strik, 2006; Fig. 6.3 and Table 6.5) and thus it is difficult to isolate one factor from another (Davies and Darnell, 1994). A moderate correlation has also been found in both highbush and rabbiteye blueberries between stomatal conductance and leaf water potential (Davies and Darnell, 1994), and the various plant parameters of water status are related (Fig. 6.3). Regardless of cultivar or in-row spacing, stomatal conductance decreases rapidly as stem water potential approaches -0.6 MPa (Fig. 6.3).

There is variability among cultivars in their response to soil water loss (Bryla and Strik, 2006). 'Duke' maintained, on average, significantly higher

![Graph showing stomatal conductance as a function of stem water potential for highbush blueberry cultivars ('Duke', 'Bluecrop' and 'Elliott') spaced 0.5 or 1.2 m apart within rows. Each symbol represents one measurement. The relationship was fitted with an inverse second-order polynomial (y = 6.10/x^2 - 25.82/x + 25.38, with r^2=0.57 and P<0.001).]
stem water potentials (less negative) and greater stomatal conductance than ‘Elliott’ and ‘Bluecrop’ as soil water was depleted (Table 6.5), which may indicate that this cultivar has the highest tolerance to short-term soil water deficits. ‘Bluecrop’, on the other hand, had the lowest stem water potentials and stomatal conductance, and thus may be more sensitive to water deficits than the other two cultivars. The authors speculated that ‘Duke’ may require less frequent irrigation than the others because it produced the deepest root system and extracted more water at depths below 0.6 m.

Work by Byers et al. (1988) on young ‘Bluecrop’ highbush blueberry showed that leaf stomatal conductance values were high in early morning, remained high throughout the day and decreased in late evening. Stomata in highbush blueberry were not as sensitive to water deficits as those of rabbiteye blueberries (Davies and Johnson, 1982). Byers et al. (1988) concluded that the root system of highbush blueberries is inefficient in water uptake; so, even if soils water levels are adequate, temporary drought stress during midday is likely. Considering that young, fully expanded leaves generally have lower stomatal conductivity than old, mature ones (Davies and Darnell, 1994), if this method is going to be used to monitor water status there is a need to carefully select leaves that will adequately represent the whole plant.

Accessing the water status of a blueberry plantation is very important to maximize yield and fruit quality. A combination of methods will likely provide more reliable information than the use of individual techniques.
Digital tensiometers or electrical resistance blocks (gypsum or GMS sensors) combined with sap flow meters and TDF sensors appear the most promising techniques.

**Calculating water needs**

Once a method to determine the water status of the crop has been selected, there is a need to calculate the amount of water to be applied. Blueberry cultivars vary in size and shape of their plant canopy and root system, as well as the timing of harvest, which influence biomass production/partitioning and water requirements. There is considerable variation in the morphological and physiological adaptations of cultivars to tolerate short-term episodes of water deficits, such as deeper root systems, greater water-use efficiency (relationship between net photosynthesis and transpiration) and the ability to maintain higher plant water status (Erb et al., 1991). Since most water is lost through the leaves, some authors found that crop water was strongly correlated with canopy size (Wang et al., 2007), while Bryla and Strik (2007) reported that although percentage canopy cover in highbush blueberries was up to 246% greater at 0.45 m planting distance within the row than at 1.2 m, water use increased by no more than 10%.

Various cultural practices also affect crop water use, such as mulching, type of irrigation system, ground cover, cultivation practices and planting density (Allen et al., 1998). In highbush blueberries, close spacings (0.5 m within row) had significantly higher water uptake per hectare at 0-0.6 m soil depth than wider spacings (1.2 m) (Bryla and Strik, 2006, 2007). Bryla and Strik (2007) found that water use in highbush blueberry was related to ripening period, with highest water use for ‘Duke’, which ripened first, and lowest in ‘Elliott’, which ripened last. Mulching has been shown to conserve soil moisture and prevent weed growth, which can alter water availability for blueberry plants (Eck et al., 1990; Haman et al., 2005). The effect of mulching can be greater in soils of low water-holding capacity. Part of the effects of mulching on soil moisture could be attributed to reduced soil temperature in the top 10 cm (Haman et al., 1988).

In the literature, there is large variability in the recommended amounts of water that should be applied to blueberries. The water requirement of an adult blueberry field in the area of New South Wales in Australia has been calculated to be about 25 mm per week during the growth period and up to 40 mm per week in the final two weeks of fruit growth (Ireland and Wilk, 2006). Brightwell and Austin (1980) indicated that water requirements for rabbiteye blueberries in Georgia are in the range of 25.5 to 44.5 mm per week to obtain a large root development during the growing season. In the north-eastern USA, 5 l/bush per day is recommended for 3- to 4-year-old highbush blueberry plants, and 14 to 27 l/bush per day for mature plants (Kender and Brightwell,
1966). In New Jersey, water use in sunny days during June–August was calculated to be 3.5 to 4 l/bush per day for 5-year-old plants and 4 to 4.5 l/bush per day on 6-year-old ones (Storlie and Eck, 1996). In Arkansas, the general recommendation is to apply 3.8 l/bush per day in young plants and 7.6 l/bush per day in adult plants. However, in an experiment on 3-year-old 'Bluecrop', Byers and Moore (1987) used a K of 0.74 and tensiometer readings at 15 cm depth (indicating that average soil matric potentials were maintained at levels higher than 0.012 MPa in the intervals between irrigations), and were able to reduce water applied by 68% to 1.3 l/bush per day.

Water stress can be alleviated by increasing the amount of water retained in each portion of the soil profile through added irrigation and also soil modification. Research done in rabbiteye blueberries showed that plants receiving more than one water-supplementing treatment (irrigation, peat moss incorporation and mulch) had greater root weight than those receiving only one (Patten et al., 1989). Total root weight correlated strongly and positively with plant height and yields. In well-aerated sandy soils, where moisture can be limiting, roots are concentrated in areas where, through various cultural practices, soil moisture is most prevalent. For plants having greater root depths, growers should avoid concentrating soil moisture near the soil surface.

Water quality

Low water quality can have short- and long-term effects on crop performance (Ayers and Westcot, 1985), particularly in blueberries. Some blueberry-growing areas (Texas, Alabama, Mississippi and northern Chile) have particularly low water quality. Good quality water should have low salts: total sodium (Na⁺) <2 mM, total bicarbonate (HCO₃⁻) <1.5 mM and total chloride (Cl⁻) <4.0 mM (Haby and Pennington, 1988).

Salinity problems related to water quality can also occur if the total quantity of salts in the irrigation water is high enough that salts accumulate in the crop root zone to the extent that yields are affected. If excessive quantities of soluble salts accumulate in the root zone, the crop has extra difficulty in extracting enough water from the salty soil solution (Ayers and Westcot, 1985). The maximum salt content tolerated in water by blueberries is in the range of 250–300 ppm (Bell, 1982; Freeman, 1983). The most helpful salinity hazard indicator is electrical conductivity (EC). At high electrical conductivity the infiltration rate of water in the profile is affected (Loomis and Connor, 1992). Water for blueberry irrigation is generally recommended to have an EC below 0.45 mmho/cm or 0.45 dS/m (Ireland and Wilk, 2006); although other authors establish a 1.0 dS/m threshold (Himelrick and Curtis, 1999).

To some extent, modification of irrigation geometry can mitigate the effects of salty water. Research on rabbiteye blueberries showed that root-zone salinity was greatest and plant growth least when the wetting front of the
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emitter focused salt directly under the plant (Patten et al., 1989). To reduce salt build-up near the root system, water should be applied in smaller amounts to a greater volume of soil and more frequently. Mulch can also reduce root-zone salinity by decreasing surface evaporation and improving infiltration.

Water with a pH lower than 6.5–7.0 is also desirable. Alkaline (high pH) irrigation water will eventually raise the soil pH to a level harmful to blueberries, and high pH water is more likely to contain potentially harmful levels of salts, sodium and carbonates. The pH of irrigation water can be adjusted with phosphoric, hydrochloric or sulfuric acid. Sulfuric acid is usually cheaper. Addition of 1.66 l of sulfuric acid is equivalent to 1 kg of elemental sulfur. Well water treated at a rate of 21 ml sulfuric acid per litre of water changed its pH from 8.7 to 5.0–5.4 (Malik and Cawthon, 1977). An injector pump is used to force the acid into the main irrigation line to be thoroughly mixed with water (Williamson et al., 2006). These acids should be handled with extreme care, as they are very toxic and can irritate the respiratory and digestive tract, as well as eyes and skin.

Irrigation systems

Various irrigation systems have been used in blueberry including furrow, sprinkler, microjet and drip (surface or buried emitters). Each of the different irrigation systems has advantages and disadvantages. When selecting an irrigation system, economic and technical parameters such as field size, need to control frosts, topography, availability and quality of water, type of soil, human resources and costs should be considered (Loomis and Connor, 1992; Holzapfel, 2009). The decision as to which irrigation system to use should be made before the field is planted.

Over-the-canopy sprinkler systems are relatively simple to install and maintain, and have been widely used to irrigate blueberries. In a survey done in Oregon, 96% of the blueberry fields had overhead and 4% used drip irrigation (Scagel and Yang, 2005). Overhead is also commonly used in Florida and Michigan. Overhead sprinklers can serve for frost control if enough water can be delivered during the event (Haman et al., 1997b). Unlike surface irrigation, sprinklers require moderately clean water so that the sprinkler nozzles are neither blocked nor damaged by suspended sediment. Sprinklers provide even wetting and hence water moves uniformly through the soil profile (Loomis and Connor, 1992). Sprinklers deliver water on the canopy top and this can increase disease problems. Also, a portion of the water is deposited between rows where it is unavailable to the crop (Bryla, 2008).

Furrow is a type of surface irrigation that requires flat land or gentle slopes. Soil physical properties determine infiltration rate and the slope defines the period that water remains on the surface for irrigation. Furrow irrigation is not suitable for soils with high infiltration (sands and sandy loams).
Moisture levels are quite variable within the field and between periods of irrigation. Water-use efficiency is lower in furrow irrigation than pressurized systems. Erosion can be a problem if slopes are not appropriate or the volumes of water are excessive (Loomis and Connor, 1992). Furrow irrigation has been used with good results in some areas (Lyrene and Muñoz, 1997). A study done nearly 30 years ago to compare the costs of various irrigation systems established that the total cost of furrow was 29% cheaper than drip and overhead irrigation (Fereres et al., 1981).

Drip irrigation is used widely in many growing regions. Drip systems are somewhat more expensive to install and more difficult to maintain than furrow and sprinkler systems, but offer better water control and higher distribution uniformity. Drip irrigation has been used most commonly in soils with a high water-holding capacity (Holzapfel et al., 2004). In some areas (such as Florida), the use of drip irrigation has resulted in salinity problems around the superficial root system and crown due to a high concentration of calcium carbonate and magnesium in the irrigation water. If rainfall has been sufficient to permit roots to extend beyond the soil volume typically wetted by the emitter, water stress occurs more often during dry periods with drip than with overhead or microsprinklers irrigation (Patten et al., 1989).

Drip emitters are best suited to young plants with limited root systems, giving better water-use efficiency. If drip emitters are used for mature plants, the wetted area should cover 50% of the root zone. When drip is used in lighter texture soils, two lines of emitters, one on each side of the plant, are probably needed to provide adequate coverage.

A trial comparing drip emitters that were: (i) buried 0.1 m deep on each side of the plants; (ii) on one line suspended at 1.2 m above the plants; or (iii) placed on the soil surface at each side of the plants was performed for 2 years on newly planted 'Duke' highbush blueberries in Oregon (Bryla, 2006). During the first two years after planting, plants irrigated with buried drip were larger and produced significantly more whips than the other systems. Subsurface drip had the extra advantages of eliminating water runoff and bed erosion that were observed with both surface drip treatments. It also maintained lower soil water content near the crown, which may have reduced rots due to Phytophthora and Pythium (Bryla, 2006). However, research on alfalfa in Australia has demonstrated that whitefringed weevils (Naupactus leucoloma) can damage subsurface drip irrigation lines (Nicholas, 2010).

Microspray irrigation is a low-pressure irrigation system that is only rarely used with blueberries, but offers advantages similar to drip. As with drip irrigation water application can be directed to areas were blueberry roots are growing, which will save water compared with overhead sprinklers (Holzapfel et al., 2004). Microspray is preferred for irrigation on sandy soils because its greater wetting pattern reaches a larger percentage of the root system. Because microsprays wet more soil volume than drip, plants tend to produce a larger root system, which may provide an advantage in a shallow, densely
rooted crop such as blueberry. Both microspray and drip allow fertigation, but microspray is not compatible with plastic mulch. Growers who use microsprinklers in Florida have reported better fruit quality and fewer disease problems than with overhead sprinklers (Haman et al., 1997a).

A system called sub-irrigation has been widely used for irrigation of field crops and vegetables during the last 20 years (Qiaoosheng et al., 2007), and has been adapted to blueberries (Hanson, 2006). Although many fields are suited to the system (requires specific soil and topography characteristics), it currently amounts to only 4% of the acreage in Michigan. In sub-irrigation water is pumped into a tile drain system to elevate the water table. In blueberries it can be economical if the field needs tiling anyway. The system that several growers have been operating in Michigan includes the typical tile drain system, with water table management boxes at various locations. The boxes contain sliding gates that allow the grower to back the water table up behind the box. Fields are ‘zoned’ based on elevation differences, and a control box is positioned between the zones.

Among the advantages of sub-irrigation for crops in general are labour, water and nutrient savings, more uniform plant growth, lower air humidity, less foliar disease and fewer environmental problems from nutrients and chemicals leaching (Qiaoosheng et al., 2007). Some specific advantages to this system in blueberry fields are: (i) drainage can be managed so there can be irrigation advantages even if no water is pumped into the system (controlled drainage); (ii) the plants and sometimes the soil surface stay dry which would reduce disease and some weeds; (iii) there is potential to reduce pollutant movement out of fields, since the water is retained; and (iv) maintaining a saturated anaerobic zone can also help control nitrification and loss of nitrogen (Hanson, 2006).

A comparative study was established in a silty clay loam on ‘Elliott’ blueberries in Oregon to evaluate irrigation systems (sprinkler, microspray and drip) and water application levels (50, 100 or 150% of estimated crop evapotranspiration, ET). During the first year after planting it was found that soil water content was significantly higher when plants were irrigated by drip (29.7%) and lowest when they were irrigated by sprinklers (24.9%). In the second year, microspray had the lowest water content (20.4%) and drip had the highest (31.6%). Soil water content, however, did not differ significantly among the different irrigation levels until the second year after planting, with 150% ET, having the highest (28.4%) and 50% ET, having the lowest (22.0%). Overall, shoot dry weight was highest in plants irrigated at 100% ET, by drip or at 150% by microspray. The authors attributed the benefit of these two treatments to higher soil water content and/or higher irrigation frequency, which probably enhanced plant water status over the other treatments (Bryla, 2008). Other work done in Oregon showed that young plants under drip irrigation had longer roots and higher colonization of mycorrhizae in the upper 15 cm than plants under overhead irrigation (Scagel and Yang, 2005).
Another comparison of irrigation methods was done for 6 years (2- to 7-year-old plants) in south central Chile (latitude 36°30'S) on highbush blueberry ‘Bluetta’ planted in a loamy-clay soil with good internal drainage. Levels of water application, from 20 to 133% of reference evapotranspiration, under microjet and drip irrigation were evaluated. With drip and microjet irrigation, fruit yield increased with higher amounts of water. During the first two years of harvest, plants under drip irrigation produced higher yields compared with those with the microjet system, at all levels of water application. However, in the fourth and subsequent seasons, plants irrigated with microjets surpassed those drip irrigated. In the last season, a 7-year-old blueberry had the highest yield of 10,300 kg/ha with microjet irrigation and a level of water replacement of 6200 m³/ha, compared with 6800 kg/ha for drip irrigation with the same amount of water applied (Fig. 6.4).

**MULCH**

The increasing popularity of blueberries has brought about attempts all across the world to grow the species outside its natural habit of the native lowland (acid soils, high organic matter, loose soil), to a range of different soil conditions. In addition to modifying soil acidity, the maintenance of moisture near the soil surface is of great importance because of the extreme shallow rooting of blueberries. Among the various amendments and practices that can

![Fig. 6.4. Yield (kg/ha) of 7-year-old ‘Bluetta’ highbush blueberry with varying amounts of water applied under drip and microjet irrigation. (Adapted from Holzapfel et al., 2004.)](image-url)
enhance soil moisture, the most successful and widespread has been the use of mulch. Mulches also control weeds and, in the case of plant-derived materials, supply organic matter (Clark and Moore, 1991; Himelrick et al., 1995).

The use of mulches is common across the blueberry industry. A survey done in Oregon showed that 58% of the blueberry growers used some type of mulch (Scagel and Young, 2005). The types of mulches used cover a wide range, depending on the particular needs of the grower, economic considerations and availability of materials within the area of the blueberry field. The types of mulch most commonly used in blueberry cultivation include peat moss, pine bark, sawdust, straw, hay, manure, paper, leaf litter, plant residues, compost and plastic films (Himelrick et al., 1995; Hart et al., 2006; Cox, 2009). The performance of blueberry plants under these mulches is site-dependent since it varies according to various factors, including amount applied, ageing of the material, content of toxic substances, C/N ratio of the materials, mulch placement (on the surface or incorporated), colour and thickness.

Plastic mulches

Plastic mulches are used in many blueberry-growing regions. Most benefits from plastic mulches occur in the first years after planting, since this is the period when competition for water, light and nutrients is strongest. Depending on the type and quality of the mulch, they can last from 2 to 7 years, with weed mats (plastic woven sheets) having the longest active life (Cox, 2009). Growing crops on plastic mulch affects energy balances of both the mulch and the bare soil between rows, and this will alter the exchange of energy (i.e. heat) between the plant and its environment. The optical properties of the mulch (i.e. colour) and the extent of mulch–soil contact determine the effect of the plastic on both the above-ground and below-ground environment (Tarara, 2000; Cox, 2009).

If the mulch has been installed tightly and is in direct contact with the soil, the layer of air between plastic and soil is minimized and heat will be transferred readily by conduction (movement of energy by molecular vibrations in a solid or between a solid and a motionless fluid), leading to a rise in soil temperature. Alternatively, if plastic mulch is laid loosely, leaving an air gap between the plastic and the soil, then heat first must be conducted from the plastic to the still air layer before diffusing through the air gap and being transferred to the soil. Air has much lower thermal diffusivity than soil and heat transfer from the mulch in this case is slowed down. If the plastic is not contacting the soil, most energy at the hot plastic surface will then be transferred by convection (vertical transfer of energy to or from a surface by a moving fluid) to the atmosphere (Tarara, 2000). The increase in soil temperature associated with plastic mulches also brings along higher water
demands (Larco et al., 2009). Black plastic mulch can be sprayed with a mixture of water and brightly-coloured latex paint to reduce soil temperatures. The extent of soil warming is affected by the colour of the plastic. Plastic mulches with high shortwave absorbance (black) or high shortwave transmittance (clear) are expected to generate the highest soil temperatures and have the greatest impact on root growth in the top layers of the soil. Since woven weed mats allow some air movement, they have less impact on soil temperature than plastic films. Maximum temperatures are higher but minimum temperatures are lower under woven plastic mulch, as compared with wood chips, in blueberries (Table 6.6).

Plastic mulches also affect the light environment of the plants whose soil is covered by them. No reports of studies on blueberries were found, but in pepper, twice as much reflected PAR was measured above clear plastic mulch than above black plastic and bare soil. Both red and black plastic reflect about the same amount of PAR, but red plastic increases the ratio of red to far-red (R/FR) in the reflected light. The R/FR ratio is critical for various characteristics of the plant, such as leaf size, root/shoot ratio and cuticle thickness (Liu et al., 2009). In bell peppers, it was found that the percentage of PAR reflected from the mulches was highest in silver mulches and lowest in black mulches (Diaz-Perez, 2010). Additionally, it has been shown in watermelons that planting holes cut through plastic mulches potentially direct CO₂ (a gas needed for photosynthesis) towards the canopy of plants, the so-called ‘chimney effect’. As much as double ambient concentrations have been measured above holes cut for transplants (Soltani et al., 1995). Since most of the canopy of blueberries develops at greater distances than those of vegetables, most of the effect of this reflected light and CO₂ levels would be expected to occur in young plants and in lower portions of the canopy.

Woven black weed mats are used in many blueberry production regions. Reports from Australia state that weed mats are successful in weed control, protection of soil from erosion and hand picking disturbance. In contrast with polyethylene films, mats allow rainfall and irrigation water to permeate once the material has aged (Ireland and Wilk, 2006). A problem with plastic

<table>
<thead>
<tr>
<th>Season</th>
<th>Mulch treatment</th>
<th>Maximum daily range (°C)</th>
<th>Maximum (°C)</th>
<th>Minimum (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>Weed mat</td>
<td>13.2</td>
<td>36.5</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td>Wood chip</td>
<td>5.5</td>
<td>30.7</td>
<td>9.9</td>
</tr>
<tr>
<td>2007</td>
<td>Weed mat</td>
<td>13.5</td>
<td>33.3</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td>Wood chip</td>
<td>5.7</td>
<td>28.4</td>
<td>8.4</td>
</tr>
</tbody>
</table>

Table 6.6. Maximum and minimum soil temperatures (°C) at 2 cm depth over two years in a site planted to ‘Star’ southern highbush blueberries (loam soil) under woven plastic (weed mat) or wood chip mulch at Corindi, Australia (latitude 30°8′S). (Adapted from Cox, 2009.)
mulch is the cost and environmental nuisance of its disposal once its active life has ended (Cox, 2009). In blueberries, plastic mulches should be used in combination with fertigation, since the fertilizer placed under the plastic is often depleted after one or two years (Williamson et al., 2006).

**Organic mulches**

In areas where blueberries have not been planted in naturally acidic high-organic soils (>3%), mulching with organic mulches provides many benefits. Organic mulches increase plant size, berry yield, soil moisture, root weight, organic matter, soil structure, reduce frost damage, reduce weed growth, delay vegetative bud opening, reduce soil temperature in the summer and minimize soil temperature fluctuations (Patten et al., 1989; Clark and Moore, 1991; Williamson et al., 2006). Part of the effect of organic mulches on soil temperature is due to increased soil moisture (Haman et al., 1988; Ireland and Wilk, 2006); however, factors other than water relationships contribute significantly to the enhanced performance of highbush blueberries under mulch (Clark and Moore, 1991). Sawdust or bark mulch increased photosynthetic and respiration rates of ‘Bluecrop’ plants by 32–59%, which was partly explained by a 60–69% rise in chlorophyll levels (Wu et al., 2006). However, there has been little or no effect observed of mulch on fruit size or weight.

Rabbiteye blueberries appear to respond less to mulch than northern and southern highbush (Haman et al., 1988; Clark and Moore, 1991) and mulches are not commonly used in commercial rabbiteye plantings (Himelrick et al., 1995). However, research on rabbiteye (Patten et al., 1989) reported a reduction in frost damage in mulched plants, which contradicts previous research in fruit trees where it was reported that mulch increased frost damage by lessening the transfer of heat from the soil during the frost (Hogue and Neilsen, 1987). The decrease in frost damage in the blueberry study was attributed to a delay by the mulch in dormancy release and retardation in rate of spring bud opening or to reduced nitrogen levels in plants under mulch (Patten et al., 1989).

The ideal mulching material is one that disintegrates slowly, thus placing less strain on the nitrogen supply of the soil and requiring less frequent reaplication (Eck et al., 1990). Sawdust and pine bark are the most widely used mulching materials. A 50:50 mixture of these materials provides most benefits (Himelrick et al., 1995). Aged or rotted sawdust has been commonly shown to increase growth and yield of blueberries. This effect is thought to be due mainly to physical improvement of the soil, as evidenced by greater root growth under decomposed mulch in highbush (Gough, 1980; Odneal and Kaps, 1990) and rabbiteye blueberry (Spiers, 1986), and greater numbers of fine roots in the top 15 cm (Scagel and Yang, 2005). Application for 11 years
of wheat straw to silt loam soils without cultivation in Ohio at 0, 2, 4, 8 or 16 t/ha per annum increased available water capacity by 18–35%, total porosity by 35–46% and soil moisture retention by 29–70% (Mulumba and Lal, 2008). Sawdust mulch increased oxygen diffusion rates and porosity, and reduced soil bulk density at the end of the second season in groundnut (Khan et al., 2000).

Fresh sawdust should never be used because it can release toxic compounds and will tie up more nitrogen. Red maple and beech have had negative impacts, and use of cedar, oak and walnut has been associated with chlorotic leaves and poor growth. Compost should be applied early in the season and not in the autumn, as it tends to promote vigour and increase chances of winter injury. Straw can be used if locally available, but needs to be reapplied more frequently as it decomposes faster. Peat moss can also be used, but is expensive and tends to dry out in the surface and is difficult to rewet (Demchak, 2003).

Within the soil profile, roots will grow primarily where the organic matter is present. Among the amendments used for increasing organic matter in the planting hole, peat moss has been shown to provide the most consistent benefit. Aged sawdust (either hardwood or softwood) or compost can also be used in the planting hole (Williamson et al., 2006). However, the C/N ratio of sawdust and compost must be measured to determine if they have enough nitrogen available for the crop (see below). If nitrogen is needed it should not be supplied directly to the planting hole as young roots are very susceptible to salt damage (Himelrick et al., 1995).

Incorporation of organic material can more frequently cause detrimental impacts or have little effect as compared with surface placement of these materials. Sawdust has decreased root length when incorporated in highbush blueberries at planting (Yang et al., 2002). In Oregon, sawdust incorporated prior to planting did not improve plant growth in well-drained sandy loam, loam or silt loam soils compared with heavier soils (Hart et al., 2006).

Plantings perform better when mulching is continuous versus only 1, 2 or 3 years after planting (Spiers, 1982, 1986). Once the decision to use mulches has been taken they should not be discontinued. The rate of deterioration of pine bark in Georgia was estimated to be 2.5 cm/year (1 in/year). As degradation of the organic mulch proceeds, weed control declines, some blueberry roots become exposed, can dehydrate, and are subject to herbicide toxicity or physical damage if weeds are controlled with hand tools (Krewer et al., 1997).

The depth of the organic mulch should be 10–20 cm. Approximately 3–8 cm should be added every other year (Himelrick et al., 1995; Williamson et al., 2006). If depth is increased, roots will tend to grow higher in the crown and only within the mulch or in the interface with the soil. The pH of the source and the soil should be monitored annually in the planting (Demchak, 2003). The C/N ratio, chemical composition, particle size and degree of decomposition of organic materials affect their performance when used as mulches. There is considerable variability in these factors among mulches.
and unfortunately few studies have described these characteristics, making it difficult to provide precise directions and specify the impact of organic mulches on blueberry performance. However, it is known that the C/N ratio in the organic matter added will determine nitrogen availability. Sources with a C/N ratio >30:1 will tie up (immobilize) nitrogen (Yang et al., 2002). If C/N ratio is <20:1, the organic matter will mineralize and supply nitrogen to the blueberry. Residues with C/N ratios between these values will neither tie up nor release nitrogen (Table 6.7). The C/N ratio for any material decreases as it decomposes. Before a mulch is used, its C/N ratio should be determined to make the necessary adjustments (Demchak, 2003).

Recommendations have been provided on how much extra nitrogen should be applied when mulches are used. As a general rule, it is suggested that when mulches are used the nitrogen rate should be increased by 30%. The rate can then be adjusted according to leaf analysis and subsequent plant growth and appearance (Williamson et al., 2006). In Oregon, where it is recommended to incorporate 9 cm of Douglas-fir sawdust in 30 cm of soil within the row prior to planting, the addition of 107 kg N/ha is suggested to avoid immobilization of nitrogen for blueberry plants (Hart et al., 2006).

Mulch can neutralize poor quality water better than peat moss applied at the planting hole. This was demonstrated by Malik and Cawthon (1977) when high pH, salty water (pH=8.7, Na+=129 mM, total HCO₃⁻=258 mM and Cl⁻=25 mM) was applied as drip irrigation to recently planted rabbiteye blueberries. Pine bark mulch at the base of each plant (28 dm³ of medium size) buffered soil pH, electrical conductivity and sodium in the soil, but no

Table 6.7. C/N ratios for various organic materials used for mulching and soil amendments in blueberries, and their propensity to supply or tie up nitrogen. (Data from Demchak, 2003; Whatcom, 2005.)

<table>
<thead>
<tr>
<th>Organic material</th>
<th>C/N ratio</th>
<th>Nitrogen supplied (+) or tied up (−)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Legumes</td>
<td>9:1 to 19:1</td>
<td>+</td>
</tr>
<tr>
<td>Peat moss</td>
<td>45:1 to 58:1</td>
<td>−</td>
</tr>
<tr>
<td>Farm manure</td>
<td>90:1</td>
<td>−</td>
</tr>
<tr>
<td>Rotted manure</td>
<td>20:1</td>
<td>+</td>
</tr>
<tr>
<td>Grass clippings</td>
<td>19:1</td>
<td>+</td>
</tr>
<tr>
<td>Straw</td>
<td>20:1 to 80:1</td>
<td>−</td>
</tr>
<tr>
<td>Alfalfa hay</td>
<td>18:1</td>
<td>+</td>
</tr>
<tr>
<td>Douglas-fir bark</td>
<td>491:1</td>
<td>−</td>
</tr>
<tr>
<td>Aged hardwood sawdust</td>
<td>60:1</td>
<td>−</td>
</tr>
<tr>
<td>Fresh sawdust</td>
<td>300:1 to 700:1</td>
<td>−</td>
</tr>
<tr>
<td>Sawdust weathered for 2 months</td>
<td>625:1</td>
<td>−</td>
</tr>
<tr>
<td>Sawdust weathered for 3 years</td>
<td>142:1</td>
<td>−</td>
</tr>
<tr>
<td>Douglas-fir sawdust</td>
<td>800:1</td>
<td>−</td>
</tr>
</tbody>
</table>
effect was found with the incorporation of 18.7 dm$^3$ peat moss per planting hole. Mulch may reduce soil salinity by decreasing surface evaporation and by allowing greater infiltration (Patten et al., 1989).

In the lower south-eastern USA southern highbush blueberries are grown in a system called ‘pine bark culture’. The pine bark is used to construct beds 20–30 cm deep. Plants are planted with most of their root system in this bark bed. Providing plants receive adequate water and nutrients, they are vigorous and productive as the decomposing bark generates a proper environment for root growth. Although the cost of implementation is high, the premium price growers receive for the early fruit justifies the investment (Williamson et al., 2006).

**PRUNING**

Highbush blueberry bushes need regular pruning for sustained productivity. Most pruning in northern highbush is done during the winter when canes are dormant, while southern highbush are often pruned both in summer after harvest and during the dormant season (see details below). Pruning can reduce the overall plant size and crop yield in the following season, but if properly conducted, the overall effects of pruning are larger fruit, earlier ripening and greater stability of yields. Pruning to regulate crop load can ultimately lengthen the life of bushes and increase the number of productive harvests. Regular pruning allows light to travel deeper into the canopy and stimulate the formation of more flower buds. Pruning also reduces the conditions favourable for disease development by increasing air circulation and removing diseased canes.

Yield in blueberries is a complex interaction between several different yield components including canes per bush, flower buds per cane and fruit weight. When Siefker and Hancock (1987) studied yield component variation in nine highbush cultivars, they found that canes per bush and berries per cane were generally stronger determinants of yield than berry weight. However, a strong negative relationship was found between berry numbers and berry weight, which could partially compensate for yield losses due to reduced berry numbers. This is called ‘component compensation’ and is why berry size is responsive to pruning intensity. In the different cultivars, overall component interactions ranged from slightly additive in ‘Bluecrop’ and ‘Spartan’ to highly compensatory in ‘Rubel’ and ‘Berkeley’. ‘Blueray’, ‘Earliblue’, ‘Elliott’, ‘Jersey’ and ‘Northland’ showed intermediate compensatory responses.

**Pruning young plants**

Fruit yield in young plants needs to be reduced to encourage vegetative growth. It is recommended that flower buds be removed on newly set
highbush blueberries by rubbing them off by hand or pruning off the tips of shoots. Canes on plants in the second and third year are also commonly prevented from bearing more than two clusters of fruit, although this practice is dependent on the overall vigour of the plants. Reducing yield in young plants allows a mature bearing surface to develop as quickly as possible.

Strik and Buller (2005) measured the effect of removing flower buds for two years on the growth and yield of young 'Duke', 'Bluecrop' and 'Elliott' bushes over a 4-year period. They found that early cropping significantly reduced the dry weight of roots, crowns and young shoots in all cultivars. Early cropping reduced yield in the fourth year by 44% in 'Elliott', 24% in 'Duke' and 19% in 'Bluecrop'. Cumulative yields were similar in the early cropped versus de-budded 'Duke' and 'Bluecrop', while in 'Elliott' early cropping reduced cumulative yield by 20 to 40%.

Highbush blueberries grown in warm southern climates can reach mature size in as little as 3 to 4 years, while those grown in colder northern cold climates take as many as 6 to 8 years to reach full maturity. As a result, overall pruning strategies differ somewhat for southern and northern highbush blueberries. In northern highbush, it is generally recommended that growers keep only about two of the new canes produced each year until the bushes reach maturity. In southern highbush, young vigorous bushes are commonly left unpruned for the first two to four years or thinned to the strongest three or four new canes each year. Well-pruned mature bushes of both northern and southern highbush will have ten to 20 canes of varying ages, depending on the cultivar's ability to produce renewal canes.

Pruning mature bushes

Annual pruning is recommended for long-term stability of yield. If bushes are pruned only occasionally, an uneven balance of very old and young canes is produced. The highest-yielding bushes contain about 15–20% young canes (<2.5 cm), 15–20% old canes (>3.5 cm) and 50–70% middle-aged canes. The most productive canes are 2.5–3.5 cm wide at their base and 4 to 6 years old, but some younger canes are needed for renewal and a few older canes for support.

During each dormant season, the largest canes should be removed at their base to let as much light as possible into the centre of the bush. The overall condition of canes should be considered when deciding which to remove; weak or diseased canes should receive the highest priority along with those that are low-spreading or mechanically damaged. Many growers in the coldest regions wait until the late winter so they can remove canes that have been damaged by extreme cold. The cuts should be as close to the main cane as possible, so that short stubs are not left. In Michigan, most pruning is focused on whole cane removal, while in Chile and the Pacific Northwest more effort is focused on the top of bushes to balance floral and vegetative growth.
Siefker and Hancock (1987) compared berry weight, berry number and yield per bush in mature 'Jersey' bushes for three years after removing 20 to 40% of the total base area. Pruning significantly reduced berry number in the first year, but not in the second and third, while berry weight was significantly increased by pruning in years 1 and 3. Pruning intensity had a negative impact on yield per plant in the first year, but had no effect in years 2 and 3. Pruning also significantly increased the number of renewal canes formed. They concluded that moderate pruning may reduce yields in the first year but it generally increases fruit weight and may act to prevent an eventual decline in productivity by stimulating the production of new vigorous canes.

Strik et al. (2003) compared the effect of pruning intensity on berry weight, yield and harvest efficiency in mature 'Bluecrop' and 'Berkeley' plants in Oregon over a 5-year period. They compared three treatments: (i) conventional pruning with the removal of the most unproductive canes, thinning of 1-year-old shoots and removal of weak and excessively fruiting shoots from the top of bushes; (ii) 'speed pruning' where only one or two of the most unproductive canes were removed at their base; and (iii) unpruned. Yields were highest in the unpruned controls, but the conventionally pruned bushes had 27% larger fruit and could be harvested in about half the time. Fruit began to ripen on the conventionally pruned bushes about 5 days earlier than on the unpruned ones. The speedily pruned bushes were intermediate for all these characteristics.

Summer pruning in southern highbush

In addition to winter pruning, southern highbush are also commonly hedged at 100 to 122 cm (40 to 48 in) after the fruiting season using a sickle mower or hedge trimmer. This practice is much faster than detailed hand pruning and is done to maintain bush size, reduce disease and pest pressure, prevent over-bearing and achieve some drought tolerance. In a study on a mature planting of 'O'Neal' in North Carolina, Mainland (1993) compared seven different pruning treatments conducted in mid-June: (i) no pruning; (ii) removal of weak and damaged canes and bush shaping (lop); (iii) removal of weak and damaged canes, bush shaping and removal of twigs that were damaged or flowering excessively; (iv) hedged flat at 100 cm (40 in) with no cane pruning; (v) similar to (iv) but with removal of weak and damaged canes and bush shaping; (vi) hedged at an angle with the peak at 122 cm (48 in) and the edges at 61 cm (24 in) with no cane pruning; and (vii) similar to (vi) but with removal of weak and damaged canes and bush shaping. Yield was highest in those bushes that were not pruned; however, fruit weight was highest in all treatments that were hedged and they stored longer (Table 6.8). The various treatments had little influence on harvest date.
Table 6.8. Yield, berry weight and percentage of firm and non-diseased berries after 7 weeks of storage in the first season after harvest in 1989, 1990 and 1991 from various pruning treatments on mature ‘O’Neal’ plants in North Carolina. (Adapted from Mainland, 1993.)

<table>
<thead>
<tr>
<th>Pruning treatment</th>
<th>Yield (kg/bush)</th>
<th>Weight/berry (g)</th>
<th>% Good berries</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>4.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.69&lt;sup&gt;b&lt;/sup&gt;</td>
<td>22.4&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lop</td>
<td>3.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.80&lt;sup&gt;b&lt;/sup&gt;</td>
<td>23.1&lt;sup&gt;abc&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lop and detail</td>
<td>3.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.87&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>27.2&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Top (flat)</td>
<td>3.6&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>2.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>36.0&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Top (flat) and lop</td>
<td>3.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>40.0&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Top angle</td>
<td>3.9&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.96&lt;sup&gt;a&lt;/sup&gt;</td>
<td>33.1&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Top angle and lop</td>
<td>3.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>38.2&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

See text for details on pruning treatments.

<sup>a,b,c</sup>Mean values within columns with unlike superscript letters were significantly different at P<0.05 level (Waller-Duncan test).

Experiments have also been conducted on cane removal during the summer in both southern and northern highbush. The primary objective of this practice is to stimulate laterals to break, while reducing excess plant vigour. The time when this is done is critical, as the number and length of laterals is dependent on how early pruning is done. The goal is to prune on the date that allows good laterals to break and induces sufficient flower bud development for good yields the following season. While summer pruning is typically done soon after harvest, vegetative bud development should be evaluated, since advanced shoot and bud development will reduce the response. Cultivars differ greatly in their response to summer pruning date.

Bañados et al. (2009) studied the effect of summer pruning on lateral shoot growth, flower bud formation, harvest date and fruit weight in the southern highbush cultivars ‘O’Neal’ and ‘Star’ and the northern highbush ‘Elliott’. Shoots were cut back to 20–30 cm at monthly intervals during the growing season from 15 December to 15 March (dates for the southern hemisphere). Pruning in mid-December resulted in the highest number and longest shoots in ‘O’Neal’ and ‘Star’, and the highest number of flower buds per new shoot in these cultivars (Table 6.9). The largest fruit were produced in ‘O’Neal’ and ‘Star’ after pruning in December or January compared with the plants that received no pruning (2.0 versus 1.5 g) or were pruned too late. The harvest season the following year was also delayed by 14 days in these two cultivars after all pruning treatments. The northern highbush cultivar ‘Elliott’ was less responsive to pruning than ‘O’Neal’ and ‘Star’. ‘Elliott’ plants pruned after December did not produce any laterals. However, fruit were significantly larger in the pruned ‘Elliott’ plants (1.7 versus 2.0 g) and pruning delayed harvest by 7 days. The authors concluded that summer pruning can increase
### Table 6.9. The effect of summer pruning on lateral length, number of laterals per shoot and number of flower buds per shoot on ‘O’Neal’ and ‘Star’ after different monthly pruning dates. (Adapted from Bañados et al., 2009.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Pruning date</th>
<th>Laterals/ shoot</th>
<th>Lateral length (g)</th>
<th>Flower buds/ lateral</th>
</tr>
</thead>
<tbody>
<tr>
<td>O’Neal</td>
<td>15 December</td>
<td>3a</td>
<td>19.0a</td>
<td>19.4ab</td>
</tr>
<tr>
<td></td>
<td>15 January</td>
<td>3a</td>
<td>20.4a</td>
<td>17.4ab</td>
</tr>
<tr>
<td></td>
<td>28 February</td>
<td>1b</td>
<td>9.5b</td>
<td>4.1d</td>
</tr>
<tr>
<td></td>
<td>15 March</td>
<td>0b</td>
<td>3.7b</td>
<td>5.2bc</td>
</tr>
<tr>
<td></td>
<td>None</td>
<td>2b</td>
<td>10.3b</td>
<td>11.4bc</td>
</tr>
<tr>
<td>Star</td>
<td>15 December</td>
<td>3a</td>
<td>15.5a</td>
<td>11.5a</td>
</tr>
<tr>
<td></td>
<td>15 January</td>
<td>3a</td>
<td>17.4a</td>
<td>12.7a</td>
</tr>
<tr>
<td></td>
<td>28 February</td>
<td>2ab</td>
<td>12.5ab</td>
<td>7.8ab</td>
</tr>
<tr>
<td></td>
<td>15 March</td>
<td>0b</td>
<td>1.2b</td>
<td>5.2b</td>
</tr>
<tr>
<td></td>
<td>None</td>
<td>0b</td>
<td>13.5ab</td>
<td>7.6ab</td>
</tr>
</tbody>
</table>

Notes: Mean values within columns with unlike superscript letters were significantly different at \( P<0.05 \) level (Waller–Duncan test).

yield and fruit quality in ‘O’Neal’ and ‘Star’ if they are pruned early in the season; otherwise the effect can be the opposite. If summer pruning is done in ‘Elliott’, it should be restricted to the most vigorous canes and done very early. They also speculated that the dormancy status of the vegetative buds greatly affected the response.

### Renewal pruning and mechanical harvesting

If an old planting has not been pruned in years, a drastic amount of pruning may be necessary to recover high yields. One strategy that has been employed is to remove all canes except the most productive few. This drastically reduces yields, but at least some fruit is produced on the remaining canes. A large flush of new canes appears in the following year, which must be thinned annually until a productive ratio of young to old canes is produced. Another strategy that has been effective is to cut all of the canes to ground level and sacrifice almost the entire yield the following year. Howell et al. (1975) found that when large, unthrifty ‘Jersey’ bushes were sawed off at ground level, their yields surpassed those of unpruned controls at the second harvest season by 15,353 to 3363 kg/ha.

To obtain high yields through mechanical harvesting, it is critical to maintain narrow crown widths so that fruit do not miss the harvester collection plates. This is particularly important in old plantations where crown width gradually expands over the years. In the study of Howell et al. (1975), they maintained 20, 25 and 30 cm crown widths by controlling suckers with
dinitrophenol, paraquat and flame, and found that ground losses of fruit after mechanical harvesting decreased as the crown width was narrowed. The paraquat treatment at the rate of 1.13 kg/ha was most effective at sucker control.

**POLLINATION**

**Reproductive biology**

Because blueberries are not completely self-fertile, cross-pollination generally results in higher seed set, fruit set and larger fruit (Morrow, 1943; Darnell and Lyrene, 1989). Overall, rabbiteye cultivars are less self-fertile than highbush, and cross-pollination between cultivars with an overlapping bloom is critical to adequate fruit set (Brevis and NeSmith, 2005). El-Agamy *et al.* (1981) found fruit set in selfed versus outcrossed cultivars to be reduced by an average of 30% in rabbiteye and 15% in southern highbush. Seed number per fruit in selfed cultivars was reduced by about 97% in rabbiteye and 66% in southern highbush. Selfing reduced fruit set and seeds per fruit in northern highbush by 1–58% and 36–823%, respectively, across several studies (Table 6.10). Selfing also reduced fruit weight in northern highbush by 4–35%.

The level of self-fertility is highly variable across rabbiteye and highbush cultivars. In southern highbush, El-Agamy *et al.* (1981) found that reductions in fruit set due to selfing ranged from 11% ('Sharpblue') to 50% ('Avonblue'), and reductions in seed per fruit ranged from 65% ('Flordablue') to 70% ('Sharplblue'). In rabbiteye, they found reductions in fruit set due to selfing varied from 24% ('Climax') to 60% ('Beckyblue') and reductions in seed per fruit ranged from 77% ('Climax') to 100% ('Aliceblue'). In northern highbush, reductions in seed numbers per fruit due to selfing varied from 36% ('Nelson') to 89% ('Aurora') and reductions in fruit set varied from 0 ('Liberty' and 'Ozarkblue') to 58% ('Bluegold'). Reductions in berry weight ranged from 2% ('Draper') to 35% ('Sierra') (Table 6.10).

Most of the highbush cultivars that had limited fruit size reduction due to self-pollination ('Draper', 'Duke', 'Legacy', 'Nelson', 'Rubel') also had high fruit set. Likewise, all the ones which had the most dramatic reductions in fruit weight due to selfing also had low fruit set ('Sierra', 'Sunrise' and 'Toro'). However, several with average to high reductions in fruit weight after selfing still had excellent fruit set ('Aurora', 'Bluecrop', 'Liberty' and 'Ozarkblue'). 'Jersey' was intermediate for both fruit fertility and fruit set after selfing. 'Bluegold' and 'Brigitta' were unusual in that they had a minimal fruit reduction due to selfing, but poor fruit set.

Similar effects of self-pollination have been observed in southern highbush. Lang and Dunka (1991) compared bee-mediated cross-versus self-pollination in 'Sharpblue' and 'Gulfcoast' southern highbush, and found that
Table 6.10. The effect of self-pollination on seed per fruit, fruit weight and fruit set in cultivars of highbush blueberry. Data from Ehlenfeldt (2001) (study 1), Krebs and Hancock (1988) (study 2) and J.F. Hancock and G.A. Lobos (unpublished results) (study 3). The studies of Krebs and Hancock and Hancock and Lobos were conducted in the field, while that of Ehlenfeldt was done in the greenhouse.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Study</th>
<th>Seed</th>
<th>Outcross</th>
<th>Difference (%)</th>
<th>Fruit weight (g)</th>
<th>Difference (%)</th>
<th>Fruit set (%)</th>
<th>Difference (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Aurora'</td>
<td>3</td>
<td>4.7</td>
<td>43.4</td>
<td>823</td>
<td>1.35</td>
<td>1.89</td>
<td>28</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>10.7</td>
<td>26.7</td>
<td>149</td>
<td>1.87</td>
<td>2.36</td>
<td>21</td>
<td>77</td>
</tr>
<tr>
<td>'Bluecrop'</td>
<td>1</td>
<td>9.5</td>
<td>36.5</td>
<td>284</td>
<td>1.55</td>
<td>1.93</td>
<td>25</td>
<td>77</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>10.7</td>
<td>41.8</td>
<td>290</td>
<td>1.15</td>
<td>1.14</td>
<td>14</td>
<td>50</td>
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<tr>
<td>'Bluegold'</td>
<td>2</td>
<td>6.2</td>
<td>9.8</td>
<td>58</td>
<td>1.09</td>
<td>1.14</td>
<td>4</td>
<td>40</td>
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<tr>
<td>'Bluejay'</td>
<td>3</td>
<td>1.3</td>
<td>20.4</td>
<td>1469</td>
<td>1.69</td>
<td>2.06</td>
<td>18</td>
<td>30</td>
</tr>
<tr>
<td>'Brigitta'</td>
<td>3</td>
<td>22.1</td>
<td>34.4</td>
<td>96</td>
<td>1.77</td>
<td>1.80</td>
<td>2</td>
<td>90</td>
</tr>
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<td>'Draper'</td>
<td>3</td>
<td>15.3</td>
<td>40.7</td>
<td>166</td>
<td>1.70</td>
<td>1.80</td>
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<td>76</td>
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<tr>
<td>'Duke'</td>
<td>1</td>
<td>14.7</td>
<td>20.5</td>
<td>39</td>
<td>1.42</td>
<td>1.55</td>
<td>9</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>7.7</td>
<td>43.7</td>
<td>467</td>
<td>1.60</td>
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<td>21</td>
<td>20</td>
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<td>'Elliott'</td>
<td>2</td>
<td>7.7</td>
<td>43.7</td>
<td>467</td>
<td>1.60</td>
<td>2.03</td>
<td>21</td>
<td>20</td>
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<tr>
<td>'Jersey'</td>
<td>1</td>
<td>15.1</td>
<td>48.4</td>
<td>220</td>
<td>1.16</td>
<td>1.64</td>
<td>29</td>
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<td>'Legacy'</td>
<td>1</td>
<td>13.5</td>
<td>30.1</td>
<td>123</td>
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<td>1.89</td>
<td>19</td>
<td>78</td>
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<td>'Nelson'</td>
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<td>17.1</td>
<td>36</td>
<td>1.49</td>
<td>1.71</td>
<td>15</td>
<td>64</td>
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<td>'Ozarkblue'</td>
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<td>311</td>
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<td>2.10</td>
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<td>24.7</td>
<td>61</td>
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<td>0.85</td>
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<td>49</td>
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<tr>
<td></td>
<td>2</td>
<td>11.8</td>
<td>22.7</td>
<td>92</td>
<td>0.82</td>
<td>0.96</td>
<td>15</td>
<td>60</td>
</tr>
<tr>
<td>'Sierra'</td>
<td>1</td>
<td>4.9</td>
<td>29.1</td>
<td>494</td>
<td>1.10</td>
<td>1.69</td>
<td>35</td>
<td>41</td>
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<td>9.5</td>
<td>630</td>
<td>1.91</td>
<td>2.51</td>
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<td>'Sunrise'</td>
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<td>27.1</td>
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<td>1.72</td>
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<td>'Average'</td>
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<td>31.8</td>
<td>221</td>
<td>1.31</td>
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cross-pollination increased fruit size by about 14% but did not influence fruit set. Seed count was 58% lower in selfed plants and the harvest percentage of early-ripening fruit was significantly reduced. In another study, Huang et al. (1997) found that significantly more ovules aborted after self-pollination of 'Sharpblue', 'O’Neal' and 'Gulfcoast' than after cross-pollination. El-Agamy et al. (1981) discovered that fruit set in selfed southern highbush cultivars averaged 67%, while cross-pollinated ones averaged 82%. Seeds per berry averaged 3.9 in self-pollinated cultivars versus 11.2 in outcrossed ones. The relative ranking in self-fertility among cultivars (low to high) was 'Avonblue', 'Sharpblue' and 'Flordablue'.

Meader and Darrow (1943) found self-pollination also reduces seed set, fruit set and fruit weight in potted rabbiteye blueberries. In a comparison of ten old cultivars that are no longer grown, they discovered that the cultivars fell into three groups: (i) those that were mostly self-sterile; (ii) those that set about a third of their fruit when self-pollinated; and (iii) one ('Blueboy') which set fruit equally well whether self- or out-crossed. Berry weights after self-pollination versus cross-pollination were reduced from 29 to 82%, and seed numbers per berry were reduced from 10 to 75%. In more recent work, Mainland et al. (1979) found that fruit set in plants of ‘Tifblue’ averaged only 16% when caged versus 78% when open pollinated. El-Agamy et al. (1981) found fruit set to average 18% in selfed rabbiteye cultivars versus 47% in outcrossed ones, while seed numbers per fruit averaged 1.5 in selfed plants versus 8.5 in outcrossed ones. The relative ranking in self-fertility among cultivars (lowest to highest) was 'Aliceblue', 'Tifblue', 'Beckyblue', 'Climax' and 'Bluebelle'.

**Planting designs**

For those cultivars that will benefit from cross-pollination, it is recommended that two different varieties with similar flowering dates be planted in alternate rows. In those fields where machine harvesting prohibits alternate row spacings, our experience suggests that the number of rows of interspersed varieties should not exceed ten, with closer proximities being better (Hancock et al., 1989). Several growers have indicated that four row blocks is the smallest workable size that can be machine-harvested.

**Pollination requirements**

All blueberry varieties require a pollinator to undergo fertilization. Growers commonly place hives of honey bees into the field to ensure adequate pollination. Bee density is a critical factor in determining fruit set, berry weight and rate of ripening (Dogterom and Winston, 1999; Dedej and Delaplane,
Chapter 6

2003), with the goal being to have four to eight bees working each blueberry plant during the hottest part of the day (Pritts and Hancock, 1992). Different densities of beehives are recommended, depending on the attractiveness of different blueberry varieties to honey bees. Recommendations range from 2.5 beehives per hectare for ‘Weymouth’, ‘Bluetta’ and ‘Rubel’, to 4.0 for ‘Bluecrop’, 5.0 for ‘Elliott’ and ‘Coville’, and 6.0 for ‘Jersey’. Hives should contain at least 45,000 honey bees.

It is unclear why blueberry varieties vary in their attractiveness to bees (Eck, 1986). Marucci (1965) suggested that the difference in attractiveness was more related to differences in the volume of nectar production than sugar content. However, Brewer and Dobson (1969) found no difference in the nectar production of unattractive ‘Jersey’ versus attractive ‘Rubel’, and the nectar of ‘Jersey’ had a higher sugar concentration than ‘Rubel’. Vincent (1971) found that it took bees much longer to fill their honey stomach with nectars at higher sugar content, reducing the time for floral visitations. Flowers with short, broad corollas such as ‘Bluecrop’ are thought to be more easily pollinated by honey bees than those with longer, narrow corollas such as ‘Earliblue’, ‘Coville’, ‘Berkeley’ and ‘Jersey’ (Eck and Mainland, 1971; Pritts and Hancock, 1992). Corollas of rabbiteye ‘Tifblue’ flowers are too long to make nectar readily accessible to short-tongued honey bees (Dedej and Delaplane, 2003).

Nectar robbery has been a concern among blueberry growers, where honey bees obtain nectar through slits cut into blueberry blossoms by carpenter bees (Xylocopa virginica L.). While nectar robbers are less effective at pollination than legitimate bee visitors, the impact of corolla slitting by carpenter bees does not appear to be significant on overall fruit set in rabbiteye fields (Sampson et al., 2004).

It is recommended that bees should be placed in the field at the very beginning of bloom (5–25% of flowers open) and kept in the field until petal drop. The hives should be spread out across the farm, with no more than 300 m between hives. The maximum pollination activity is ensured by: (i) removing competing flowers in the field; (ii) placing bees into fields at 5% bloom; (iii) spreading the hives evenly throughout the field; (iv) facing hives to the east; and (v) avoiding toxic pesticides while bees are in the field (Pritts and Hancock, 1992).

In general, bumble bees are more efficient at pollination than honey bees (Javorek et al., 2002; Sampson and Spiers, 2002; Heinrich, 2004). Bumble bees and other wild solitary bees ‘sonicate’ pollen from the anther, which honey bees cannot do (Delaplane and Meyer, 2000). Bumble bees also tend to work under cooler, wetter and windier conditions than honey bees and they carry more pollen. Javorek et al. (2002) estimated that bumble bees deposit 43.1 pollen grains per visit, while bumble bees deposit only 11.5, plus they visit more flowers per minute.

Natural populations of bumble bees are generally not high enough to provide for the pollination needs of a typical blueberry plantation, but colonies
can be purchased to increase bumble bee numbers during bloom (http://www.extension.org/pages/Pollinating_Northern_Highbush_Blueberries). A density of two quads per acre (eight colonies) is recommended when bumble bees are going to be the primary pollinator, but combinations can also incorporate honey bees, to diversify the sources of pollination. When this is done, the bumble bee quads should be placed away from honey bee hives.

Numerous other wild bee species are important pollinators and growers should make every effort to protect them (Tuell et al., 2009). Over 150 native (wild) bee species have been found in Michigan blueberry fields, and ten of these are considered to have a significant impact on the pollination of blueberries. The bulk of these bees are solitary ground-nesting digger bees (Andrea spp.) which need undisturbed soil for nesting. In Georgia rabbiteye blueberries, the most numerous bee visitors are honey bees (Apis mellifera L.), bumble bee queens (Bombus spp.), bumble bee workers, carpenter bees and south-eastern blueberry bees (Habropoda laboriosa [E]) (Delaplane, 1995). The south-eastern blueberry bee and bumble bee queens were found to be the most efficient pollinators on 'Tifblue' (Cane and Payne, 1990). Sampson and Cane (2000) have suggested that Osmia ribifloris Cockerell, which is native to the western USA, could also be used as an effective pollinator of rabbiteye blueberry.

In large plantings of blueberries, too few native bees generally exist for full pollination, so the addition of honey or bumble bee hives is necessary; however, it is still beneficial to create natural bee habitats with a mix of plants that bloom before and after blueberries (see Fielder et al., 2008 for more details). To protect bee populations, broad-spectrum insecticides should not be applied when blueberry flowers are open, and applications should be made when bees are not foraging. A late evening application is more desirable than a morning application, so that the insecticide residue can dry before the bees are active. More information on how to protect bees from toxic chemicals can be found in Riedl et al. (2006).

MECHANICAL HARVESTING

The development of blueberry harvesters began in the USA soon after World War II when increased industrialization sharply reduced the amount of labour available for blueberry picking (Dale et al., 1994). The first harvesters were hand-held vibrators. A gasoline-powered air compressor was developed in 1957 consisting of a small cart and up to eight vibrators. This allowed harvesting four rows at a time, with two pickers per row. The system was noisy and not very practical. It was promptly replaced by rechargeable battery units on small pull carts. The vibrators contained individual electrical motors and a fabric on a metal structure was used to collect the berries.

It has been estimated than more than 2600 electrical shakers have been sold (Brown et al., 1996). In 1963, up to 35% of Michigan and 20% of Jersey
berries were harvested with these devices. Electrical shakers are still being used in small operations across the USA and new improved models are being evaluated for the fresh market in Chile and Argentina, due to rising costs of labour for picking fruit. An air-blast sorter has been added to remove all non-desirable plant tissues (leaves, twigs, and overripe or unripe fruits). Most fruit picked with vibrators is channelled to processing.

In 1959, agricultural engineers of the USDA at Michigan State University started to develop the first over-the-row harvester. The goal was to produce a machine that removed mature, blue fruit selectively and had an efficient collection system. Over-the-row harvesters were soon being developed by several other companies and institutions. During the 1960s, several models emerged that were self-propelled or tractor-pulled. Some of the tractor-pulled ones were used to harvest bushes of small stature.

All current commercial models straddle the row, but several different picking mechanisms are used (Dale et al., 1994). The 'slapper' mechanism consists of bars mounted on a vertical plane. Two sets of bars are staggered on either side of the equipment and swing like gates that independently 'slap' the bushes as the harvester moves down the row. In some harvesters there is a 'sway' mechanism, which is a variation of a slapper. In this case, 'swinging gates' are also located on each side of the harvester, but the gates are opposite to one another and work in tandem. The bush is then 'swayed' from one side to the opposite. A horizontally vibrating 'finger' mechanism is available in some machines. A variation of this is the so-called 'vertirotor' which consists of numerous horizontal 'fingers' arranged around two vertical axes on either side of the equipment. The fingers 'roll through' the plants as the harvester advances through the row. Since the fingers in the vertirotor vibrate in a vertical direction, a similar displacement along the fingers is obtained (Dale et al., 1994).

These different mechanisms have their positive and negative points. The 'slapper' usually removes large numbers of fruit and is particularly effective for late-season 'remove all' tasks. However, the vigorous action of this system usually causes greater damage to the bushes and removes a larger proportion of immature fruit. The 'sway' mechanism is generally gentler, removing a high proportion of ripe fruit with less damage to plant structures. The finger system and its variation (the vertirotor) are probably the most delicate, but are not appropriate for clean-up harvests (Dale et al., 1994).

In the 1990s, the USDA developed the V45 harvester which has 45°-angled, spiked-drum shakers, a cane dividing and positioning system, and cushioned catching surfaces (Peterson and Brown, 1996). The cane dividing system bends the canes away from the crown and over unto the elevating catching surface. The cane dividing system greatly reduces the amount of fruit dropping on the crown rather than catch frames. Most recently, a forced air concept has been developed that may further reduce damage by better directing and cushioning the falling berries.
Hand harvesting of highbush blueberries is labour-intensive and requires as many as 1150 hours of labour per hectare (Brown et al., 1983). Comparatively, the use of mechanical vibrators nearly tripled worker productivity and reduced harvesting cost by 55%. The over-the-row harvesters have cut harvest labour to 22 worker-hours per hectare for berries used in processing (Gough, 1994). Other researchers have reported that the over-the-row harvester increased worker productivity by nearly 60 times and reduced harvesting cost by 85% (Brown et al., 1996). Estimates done in the 1970s established that the cost for mechanically harvesting of 1 kg of blueberries was US$0.164 compared with US$0.215 for hand picking (Dale et al., 1994). Recent estimates are that hand harvesting raises the cost of harvesting from US$1.10 to 1.50/kg for southern highbush blueberries and from US$0.86 to 1.10/kg for rabbiteye blueberries (Salley et al., 2007).

Even though the picking cost is lower for mechanically harvested fruit, more berries are picked per hectare by hand and they have a higher value. An evaluation of mechanical harvesting of highbush blueberries in British Columbia (Canada) established a 14–16% yield reduction compared with hand harvest. The green fruit harvested was 4.0% of the mechanically harvested yield and 0.35% of hand-harvested yield over the three years of study (van Dalfsen and Gaye, 1999). Harvesting machines not only bruise the fruit, but cause visible damage to plant structures making the plants more susceptible to diseases. Mainland et al. (1975) found that only 0.04 canes/bush were damaged by hand pickers compared with 2.20 canes/bush by over-the-row harvesters. The harvester broke nine times as many canes as did commercial hand pickers.

In the 1980s it was estimated that 60% of the highbush blueberries of the east coast of the USA were mechanically harvested, while by the 1990s machines were used to harvest 70% of Michigan’s berries and about half of the New Jersey crop (Dale et al., 1994). As the supply of labour for hand picking fresh fruit continues to decrease and the market demand for fresh blueberries increases, there is the requirement that: (i) the fruit harvested with mechanical harvesting systems have postharvest quality that is similar to hand-harvested fruit; (ii) there is a major improvement in mechanical harvesting systems to reduce postharvest handling and sorting operations to separate defective fruit; and (iii) new cultural practices are developed that increase the yield of high-quality fruit (Takeda et al., 2008). Perhaps major changes in bush architecture could enhance harvest efficiency and fruit quality (Dale et al., 1994).

CONCLUSIONS
A number of management practices are of utmost importance in blueberry cultivation, including mulching, irrigation, pruning, pollination and harvest.
Irrigation is economically justified in most situations, as rain and/or water table are usually not able to supply water needs of blueberries. Blueberries have a shallow root system (20–30 cm deep) and are susceptible to water stress due to either excess or deficit. Rabbiteye blueberries are generally more tolerant to water stress than highbush. The behaviour of water in the soil and the plant has been unified in a single energy concept: the water potential or \( \Psi \), which considers the soil–plant–atmosphere as a continuum. Even though wild highbush blueberries are found growing on hummocks in swamps, flooded areas should not be used to grow blueberries. Flooding stress is mainly caused by lack of soil oxygen, which closes stomata and reduces transpiration.

To determine adequate amount and timing of water to supply to a blueberry field, physiological variables (plant water potential, gas exchange) should be determined, as well as plant growth, fruit production and quality. To monitor water status in blueberry fields, digital tensiometers or electrical resistance blocks (gypsum or GMS sensors) combined with sap flow meters and TDF sensors appear the most promising techniques. Various cultural practices (mulching, type of irrigation system, ground cover, cultivation practices and planting density) as well as characteristics of blueberry cultivars (canopy size and shape, root system, timing of harvest) affect their water use and needs. Good quality water (low salts; EC <0.45 mmho/cm) will allow maximum yield under good soil and water management practices. The most common irrigation systems used in blueberries are drip and overhead sprinklers.

The use of mulches is widespread among blueberry growers. This practice brings about many benefits, among which weed control and moisture retention are paramount. There are many different materials that can be used depending on availability and specific needs. Plastic mulches increase soil temperature and the effect varies according to type of material (film or woven mat), colour and degree of contact with the soil. Plants under mulch show greater root growth which might be a consequence of improved soil structure as determined by improved porosity and oxygen availability. Usually 10–20 cm of organic mulch is applied at planting. Considering degradation of the material, 3–8 cm should be added annually to maintain the benefits. Once the practice of organic mulch has been initiated it should not be interrupted in order to avoid damage to the root system. If the C/N ratio of the organic material used as mulch is >30, it will tie up nitrogen and leave it unavailable for blueberry plants. To avoid this it is recommended to increase nitrogen rates by 30% when organic mulching is used.

Highbush blueberry bushes need regular pruning for sustained productivity. Most pruning in northern highbush is done during the winter when canes are dormant, while southern highbush are often pruned both in summer after harvest and during the dormant season. Fruit yield in young plants needs to be reduced to encourage vegetative growth. Annual pruning is recommended in mature plantings for long-term stability of yield. The most productive canes are 2.5–3.5 cm wide at their base and 4–6 years old, but
some younger canes are needed for renewal and a few older canes for support. In Michigan, most pruning is focused on whole cane removal, while in Chile and the Pacific Northwest more effort is focused on the top of bushes to balance floral and vegetative growth. In addition to winter pruning, southern highbush are also commonly hedged at 100 to 122 cm (40 to 48 in) after the fruiting season using a sickle mower or hedge trimmer.

Because blueberries are not completely self-fertile, cross-pollination generally results in higher seed set, fruit set and larger fruit. Overall, rabbiteye cultivars are less self-fertile than highbush, and cross-pollination between cultivars with an overlapping bloom is critical for adequate fruit set. For those cultivars that will benefit from cross-pollination, it is recommended that two different varieties with similar flowering dates be planted in alternate rows. All blueberry varieties require a pollinator to undergo fertilization. Growers commonly place hives of honey bees into the field to ensure adequate pollination.

The high cost of labour and the inability to obtain sufficient numbers of pickers have forced many growers to mechanize their harvest operation. This has some trade-offs as machine-harvested blueberries generally are softer, have higher incidence of decay, a greater rate of weight loss and lower postharvest life than hand-harvested berries. However, new machines are being developed that are much gentler on the fruit and could be used for the fresh market.

REFERENCES


Chapter 6


GROWTH REGULATORS

INTRODUCTION

Blueberries are a perennial crop that, when well managed, can produce for 25 years or more in some locations. In order to stay in business, growers need to efficiently manage their plantings. Hand labour can reach up to 80% of the operational costs in a mature blueberry field (Takele et al., 2007). Labour management is the key to blueberry crop profitability (Plattner et al., 2008). This not only involves constant monitoring but also timely intervention and detailed assessment of the cost/benefit ratio of management practices. Fruit crop performance can be significantly controlled through genetic and management practices.

Once plants have been established, growers usually find traits that are less than desirable or environmental factors that reduce crop productivity, diminish quality, or somehow affect profitability of the blueberry field. Among the myriad of management tools available for blueberry culture, plant growth regulators (PGRs) offer opportunities to solve specific problems. They can then become part of the management package and applied whenever the cost/benefit ratio is adequate. The cost of these compounds is generally high so they have to be effective and their impact on plant processes needs to be confirmed (Greene, 2002).

Plant growth regulators should probably be called plant bioregulators, since they not only affect growth. They are ‘natural or synthetic compounds applied to plants or plant organs to regulate growth and development’ (Petracek et al., 2003). PGRs are generally effective in low concentrations (dose), have a narrow optimum concentration–response range and must be absorbed by the plant tissue (usually leaves) to induce the desired physiological response. PGRs not only affect the process they are targeted for, but alter the overall physiology of the plant. As a result, there is the need to look for collateral effects or changes, both in the developmental or research phase as well as during application in a commercial setting (Bukovac, 2005).
PGRs have been used in all stages of fruit production, including nursery, canopy development and growth control, flowering and fruiting, alteration of fruit quality and ripening, and stress tolerance and plant–environment interactions. PGRs are usually applied as foliar sprays using water as the carrier solvent. PGR performance not only depends on the compound applied, but also, very importantly, there is a need to provide proper conditions for the compound to reach the target at a level that can cause changes in plant physiology. For that, adequate consideration must be given to environmental conditions before, during and after the application (Stover and Greene, 2005), plant condition and physiological stage, and application techniques, spray additives and equipment (Bukovac et al., 2002; Bukovac, 2005). Under the optimum environmental and plant cultural conditions, the performance of the most active and effectively formulated PGR is determined primarily by the quality of the spray application practice (Bukovac, 2005).

In this chapter we examine the most important considerations regarding the spray application of PGRs, as well as review the factors that affect their performance. The most important current or potential uses of PGRs in highbush blueberry production are presented, considering not only their desired response but also the most relevant side or collateral effects on plant functioning or fruit quantity/quality. Most emphasis is on the research that has been done on highbush blueberry (both southern and northern), but where appropriate, research on related species (lowbush and rabbiteye blueberry, and cranberry) is presented.

**APPLICATION OF PLANT GROWTH REGULATORS**

Efficient and uniform delivery of the desired dose to the intended target is central to maximizing the performance of systemic compounds (Bukovac et al., 2002). Spray application of foliarly applied PGRs is dependent on a wide range of interacting variables or events. Among these, the most important are: (i) effectiveness of the application equipment; (ii) chemical and physical characteristics and formulation of the active ingredient; (iii) atomization of the spray solution/emulsion/suspension; (iv) delivery of the spray uniformly over the intended target; (v) interaction between spray droplet and plant surface, which leads to retention, droplet drying and residue formation; (vi) penetration and transport of the active ingredient to the active site; (vii) environmental factors, mainly temperature and relative humidity, before, during and immediately after spray application; and (viii) plant condition, particularly foliage, with regard to stresses, diseases or inadequate nutrition. All of these stages and events are interrelated, in the sense that a change in one will usually have a profound effect on another, and may be affected by application variables, plant factors or environmental conditions (Bukovac, 2005). Even though this discussion is focused mainly on the application of
PGRs, most of the principles should be generally appropriate to the application of pesticides and nutrients to the canopy of blueberries.

**Formulation**

The main objective in formulating a systemic ingredient is to structure the compound in a manner that can be readily applied by the spraying systems in an aqueous carrier to obtain maximum biological activity. An additional objective in formulating systemic ingredients is to improve plant wetting, coverage and penetration (Bukovac et al., 2002). Most PGRs are commercially available in one formulation. Water is the most commonly used carrier, since it is inexpensive, readily available and is an excellent solvent for most PGRs in a wide range of conditions. However, aqueous base solutions have high surface tension and, because of this, are generally ineffective in wetting and spreading compounds across waxy leaves and fruit surfaces.

**Atomization**

Atomization corresponds to the conversion of the spray liquid into a cloud of droplets. Orchard sprayers usually atomize the liquid using nozzles which force the spray liquid through an orifice by high-velocity air or high pressure after passing the spray liquid through a cylinder or a preformed plate or disc. Other nozzle systems (air inclusion, electrostatic, rotary sleeve and spinning disc) have been developed, but they have not been widely adopted by the industry (Bukovac, 2005).

The droplet size population produced by most orchard sprayers ranges from >100 µm to <500 µm in diameter. In most droplet spectra there are a large number of small droplets which contribute little to the total spray volume but significantly to the spray drift. In order to accommodate for variability in plant size and density, training systems, leaf development during the season and for different varieties, growers usually adjust the flow rate to deliver the desired spray volume per tree or hectare. As flow rate is altered, the droplet size of the spray is changed. Such changes might influence spray penetration into the canopy, retention and coverage.

**Spray deposition**

Uniform delivery of sprays is difficult to achieve because many factors (planting systems, plant volumes and densities, seasonal changes in canopy development, surface characteristics) affect the quality and performance of the spray. Spray deposition is a complex process that can be viewed as
Chapter 7

consisting of the following stages: (i) delivery or transport of the atomized spray; (ii) impaction of spray droplets with the plant surface; and (iii) retention by the plant organs.

The most common orchard sprayers are air-blast or axial fan sprayers. In most cases, the same sprayer is used for different crops and for applying a range of different chemicals to blueberries throughout the season. In Michigan, blueberry growers commonly use air-blast sprayers that propel spray up and through the bushes. Cannon sprayers that project spray across the tops of several blueberry rows are also popular because their field capacity (ability to treat large areas quickly) is high, and, since fewer passes along the field are needed, the potential for mechanical damage of developing fruit is reduced (Hanson et al., 2000). However, cannon sprayers may result in irregular deposition and/or off-target drift during windy conditions (VanEe et al., 2000). In a study to evaluate the effect of sprayer type (conventional air-blast sprayer versus multi-fan/nozzle, above-row sprayer) on control of fruit rots in mature ‘Jersey’ highbush blueberries, the nozzle pressures were set at 1.0 and 1.2 kPa for the air-blast and above-row sprayers, respectively. The above-row sprayer provided fruit rot control at least equivalent to the air-blast sprayer even though less chemical was applied (Hanson et al., 2000).

Air volume and velocity have a pivotal role in the delivery of the spray cloud. Greater canopy penetration and uniformity of deposition were obtained with air-blast sprayers which delivered high volume and low-velocity air. Unfortunately, both the air and the spray are delivered mainly from a point source and this is the main factor leading to non-uniform spray distribution over the plant (Hanson et al., 2000). Besides, growers usually have limited time to cover their fields and, if high volumes are used, the time employed in covering the whole field is increased and this implies that part of the spray cannot be done within the optimum window for maximum effect of the applied compound. When spraying has to be done near harvest, fruit damage and drop by physical contact with the sprayer also need to be taken into consideration.

Research on spray deposition in blueberries is scarce. VanEe et al. (2000) divided the canopy of 40-year-old ‘Jersey’ highbush blueberries in four sections (top, interior, side close to sprayer, side distant from sprayer). A black die and collecting targets were used to measure spray deposition patterns. Their findings confirmed results previously reported for fruit trees (Bukovac, 2005), in the sense that areas of the bushes closer to the spraying equipment received greater coverage than those that were more distant. The effect was more pronounced as season progressed and more foliage was present on the plant (Fig. 7.1).

A marked decrease in the uniformity of spray coverage occurred during the season near bloom. This change in spray uniformity was correlated with leaf development as measured in the above-mentioned experiment through the proportion of sunlight available in different sections of the canopy throughout the season (Fig. 7.2).
Fig. 7.1. Spray coverage (percentage of surface area of card targets) at different positions in mature ‘Jersey’ blueberry canopies following application with an air-blast sprayer (SP) on four dates between pink bud (13 May) and green fruit (11 July). Data are means across three pruning treatments. LSD (least significant difference) value refers to comparisons between dates and positions. (Adapted from VanEe et al., 2000.)

Fig. 7.2. Changes in light levels (percentage of full sun) in the top third, middle and bottom third of mature ‘Jersey’ blueberry canopies between the first open flowers and the first fruit harvested. Data are means across three pruning treatments. (Adapted from VanEe et al., 2000.)
When different pruning severities were imposed (removal of 0, 20 or 40% of the largest canes at the base of the bush), more severe winter pruning increased deposition in areas of the canopy which received the least overall coverage. However, pruning tended to have less effect in sections where overall coverage was high (e.g. bottom and near side of the bush) (Fig. 7.3). Since growers commonly apply compounds to alternate rows in order to cover greater area in less time, the impact of this practice was analysed in the study. As expected, it was found that the section of the row furthest from the application point of the sprayer had significantly lower amount of residues. This amounted to about a fifth of the equivalent section in areas of the field that were sprayed in every row (Fig. 7.4).

PGRs are somewhat slightly mobile in plant tissues. The lack of uniformity in spray delivery to fruit crops acquires paramount importance in the case of less mobile compounds such as pesticides and nutrients. This non-uniform distribution raises questions about the merit of sprayer calibration where the focus is placed only on the amount of spray solution delivered through the nozzles under some prescribed sprayer settings and not the uniformity of the spray received by plant organs. This situation might provide a false sense of security, since some sections of the plant may actually be overdosed while others may be undersprayed. In a more general view, when the compound has been applied at the proper timing and dose but has not produced the desired effects, non-uniform application might be one of the explanations to be considered. Studies in a range of crops have found that about 60% of tested sprayers had calibration errors greater than 10% (Ayers and Bosley, 2005).

The current practice of recommending a constant dose per unit ground area ignores the quantity and quality of the target and the biological requirement that PGRs must be absorbed by plant tissues before a response.

Fig. 7.3. Effect of pruning severity (light, medium or heavy) on spray coverage (percentage of surface area of card targets) at different positions in mature 'Jersey' blueberry canopies following application with an air-blast sprayer (SP). Data are means of four treatment dates between pink bud (13 May) and green fruit (11 July). LSD (least significant difference) value refers to comparisons across pruning treatment and position. (Adapted from VanEe et al., 2000.)
Growing Regulators

Fig. 7.4. Spray coverage (percentage of surface area of card targets) in different positions of mature ‘Jersey’ blueberry canopies following application with an air-blast sprayer driven down each row middle or alternate row middles on two dates. Data are means across three pruning treatments. LSD (least significant difference) value refers to comparisons across spray treatment, date and position. (Adapted from VanEe et al., 2000.)

can be induced. Growers recognize that for most PGRs an optimum response is obtained with dilute sprays. However, for a number of practical and economic considerations, dilute spraying is being replaced with lower volumes than required for full plant retention. In high volume spraying, retention volume is not critical in determining performance of the active ingredient, since any additional volume applied will run off. As carrier volume is progressively reduced, spray volume eventually becomes limiting because of inadequate coverage and uniformity, which affects penetration and may lead to phytotoxicity (Bukovac, 2005).

Impaction

The impaction of spray droplets on plant tissues results in either reflection or retention by the surfaces. If not lost to the surrounding environment, droplets that are initially reflected may impact again one or more times and eventually be retained. The energy of the movement (kinetic energy) of the impacting droplet will cause it to spread; its surface area will increase, as will the wetting of the plant surface. Part of the kinetic energy is stored in the new liquid-air
surface formed. This new surface area tends to return to its lowest state of
energy and the droplet retracts. If the kinetic energy exceeds a critical value,
the deformed droplet will retract completely, become extended perpendicular
to the target surface and then will be reflected from the plant surface.
Impaction is an extremely rapid process. The total droplet–surface residence
time for a reflecting droplet may be less than 1/1000 of a second. Studies done
on different fruit tree crops have found that droplet reflection from leaves is
not a significant limitation in spray application to fruit trees (Looney, 1993;
Greene, 2002). No data are available on blueberries.

Retention

Spray retention is a defining event in foliar application of compounds, since
only the portion that is retained will be available for penetration and subsequent
biological effect. In the case of PGRs, retention is perhaps the most important
event in the PGR spraying process, for it determines the dose available for
penetration. The total spray retained from a high volume application is
determined by the total target area wetted and the retention factor (volume/
unit area) characteristic of the spray/fruit crop. In low volume spraying, the
volume retained for a given species is linearly related to the volume applied. In
both cases, total spray retained per plant increases with the rapid increase in
leaf area during the cropping season (see Fig. 7.2). For sprays applied at low
volumes, where the spray is retained and remains as discrete droplets on the
plant surfaces, reductions in surface tension did not change total retention,
but significantly increased the affinity of droplets for the surface. Accumulated
residues from previous sprays and the presence of some natural product on
plant surfaces modify spreading and retention (Bukovac, 2005).

Estimates of the full retention value for a given crop and planting system
vary widely. Numerous factors and their interactions make it difficult to
estimate the retention accurately. Among these are: (i) composition of the
spray solution (e.g. spray additives) may strongly alter plant surfaces and
retention; (ii) spray equipment design and calibration; and (iii) changes in
quantity and quality of the surface area during the season.

Surfactants dramatically alter the form of the deposit. All surfactants lower
spray surface tension and improve wetting. Surfactants, when used, reduce
reflection, increase spreading and, at high volume spraying, reduce the total
dose retained per unit surface area. Another important use of surfactants is
to enhance penetration of the active ingredient. They can do this by altering
the solubility of the active ingredient in the spray solution, and hence its
sorption into the cuticle, and increasing the droplet–plant surface contact. The
surfactants most commonly used for application of PGRs to blueberries are
non-ionic, among which are X-77, Silwet L-77, Kinetic and Flood (Krewer et
al., 2007).
Droplet drying and deposit formation

Any non-volatile compound and spray additive present precipitates out as a residue of varying size, form and consistency as the carrier phase (water) of the droplet evaporates. Rapid drying, particularly of small droplets in low volume application, may reduce spreading and penetration. However, it appears that a higher concentration of active ingredient in the spray solution compensates by providing a greater driving force for penetration. The active ingredient may be distributed uniformly over the original droplet/plant surface interface or as masses of various sizes over veins, stomatal cells, damaged areas or specialized structures. Spray additives that are hygroscopic increase the hydration of the deposit, and the active ingredient can more readily diffuse to the active-ingredient-depleted deposit/surface interface and replace the active ingredient diffusing into the plant. This can maintain a positive driving force for penetration after the deposit has apparently dried (Bukovac, 2005).

Environmental factors that affect the performance of plant growth regulators

There are various factors that can dramatically alter the degree of plant response to PGRs. Knowledge of these factors is necessary to adjust the spray application in order to obtain the desired degree of response. Changes in the environmental conditions in the field, such as temperature and humidity, result in simultaneous modification of multiple parameters. This situation often makes it difficult to translate results from controlled experiments into protocols that can assure a given response in the field and provide growers with tools to make adequate decisions at the appropriate time. For ease of discussion, the factors can be chronologically separated into before application, during application and after application. Most of the research on these matters has been done on fruit trees, particularly in apples; however, when data are available, information on blueberries or related species is provided.

Conditions before application

Fruit tree thinners, particularly naphthaleneacetic acid (NAA), have been the most extensively studied PGRs. There are a number of environmental factors previous to the application of fruit thinners that can alter plant response. Among these are some factors that increase the response, such as low light intensity, high humidity, frost damage and low temperatures during leaf growth. Conversely, high temperature and dry conditions prior to thinner application reduce the effectiveness of thinners. Part of the effect is due to the influence of environmental conditions on leaf growth, cuticle development and deposition of epicuticular waxes. In European wild blueberries (Vaccinium
myrtillus, Vaccinium uliginosum and Vaccinium vitis-idaea), it was found that cuticle thickness was almost double in the adaxial (upper) surface of leaves (Semerdjieva et al., 2003). The epicuticular structures of rabbiteye blueberry leaves were dense in new leaves, but absent in mature leaves (Freeman et al., 1979).

**Conditions during application**

Many label recommendations for PGRs regarding environmental factors (rain, temperature and times of application), as well as the use of surfactant, are based on results from controlled laboratory studies, and are supported by anecdotal field observations. Even though this gives a general trend, the actual situation in the field may differ from these theoretical models.

The impact of environmental conditions during application has been studied using leaf discs. It was shown that penetration of NAA into pear leaf discs increased with temperature, with a marked increment above 25°C. The change was attributed to decreases in the cuticular viscosity (Bukovac, 2005). No report on these matters was found for blueberries.

**Conditions after application**

The effect of environmental conditions after application usually includes a combination of factors. The effect of environment on plant response to PGRs may result from uptake effects, influence of PGR conversion to the active form, and/or physiological processes through which PGR action is mediated.

Applications of growth regulators are often made under adverse conditions with growers debating whether to spray with rainfall being imminent. Field observations suggest that if a spray droplet dries before rain occurs, there is likely to be a substantial amount of PGR activity retained, which in part is due to enhanced uptake as the droplet dries. Wash-off studies typically reveal that PGR activity is reduced if residues are washed from the leaves too soon after application. One such study was done on 'Tifblue' rabbiteye blueberry (NeSmith and Krewer, 1997a). Data on the occurrence of simulated rainfall after 1–72 h of gibberellic acid (GA₃) application to 1-year-old plants in the greenhouse showed that there was a rapid GA₃ uptake (as indicated by the effect of GA₃ on fruit set) in 1 to 4 h, with a more gradual uptake over the next 68 h (Fig. 7.5). Thus, if rain occurs after 4 h following the application of GA₃ to rabbiteye blueberries, it can be assumed that uptake was mostly completed and there would be no need to reapply the compound.

Most PGRs do not require chemical conversion to be effective, since the compound is already in the active form. The most obvious exception is ethephon (2-chloroethylphosphonic acid; a compound assayed for bloom delay in southern highbush blueberries), which has to decompose and release ethylene to become physiologically active. Plant response to ethephon is
Fig. 7.5. Fruit set of ‘Tifblue’ rabbiteye blueberry in response to wash-off time following an application of gibberellic acid. Spray was applied to the point of drip at a concentration of 251 mg GA₃/L⁻¹. (Adapted from NeSmith and Krewer, 1997a.)

especially temperature-dependent, since temperature influences both uptake and rate of ethephon decomposition to release ethylene. It has been observed that the thinning response to ethephon in apples increases linearly with temperature from 8 to 24°C with virtually no thinning at ≤8°C (Stover and Greene, 2005).

CURRENT AND POTENTIAL USES OF PLANT GROWTH REGULATORS IN BLUEBERRY PRODUCTION

In the following sections a review of the main current and potential uses of PGRs in blueberry production is provided. When existing, both positive and negative collateral effects of their application are provided.

Vegetative growth

Mature blueberry plants, especially rabbiteye, can reach heights in excess of 2.5 m, making management difficult, particularly application of agrichemicals and mechanical or hand harvesting. Hence, practices that reduce shoot growth but do not adversely affect fruit yield and quality would be helpful for management of these species.

Paclobutrazol (chemical name (2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1-yl)pentan-3-ol), known commercially as PP333® or Cultar®, is a very potent triazole compound and an inhibitor of
an early step in the gibberellin biosynthetic pathway (Rademacher, 2000). Paclobutrazol has a relatively long half-life, limited phloem mobility and its inhibitory effects can be overcome with exogenous applications of gibberellins. The compound reduces vegetative growth in several tree fruit and nut species (apple, pear, grape, walnuts), and is regularly used by avocado growers in Chile (Jorquera et al., 2006). The compound is readily translocated through the xylem, which makes it possible to apply it as a soil drench or trunk injection or spray. Among the secondary effects of paclobutrazol application to fruit trees are increased flower bud initiation, increased fruit colour, reduced fruit acidity in cherry and pear but not in apple, and lower fruit firmness in cherry but no change in apple and greater firmness in pears (Curry and Williams, 1986).

Initial trials were done in the 1980s on rabbiteye blueberries. This species is characterized by its vigorous growth and tall size, which in commercial plantings can commonly exceed 3.5 m. A single application of paclobutrazol (1, 2, 4 or 8 g active ingredient per plant; Mainland, 1989) was done in 0.5 l of water in a circle 15 cm from the bush around the time of bud break. In another trial, soil applications of paclobutrazol (3, 6 or 12 g active ingredient per plant; Spiers, 1988) were done at the end of harvest. In the season of application there were no detectable effects of the treatments. In the following season, both floral and vegetative bud break were delayed from 10 to 15 days by rates greater than 2 g per bush. At 4 and 8 g/bush the plant growth pattern was altered since many buds remained inactive or began growth at unpredictable times during the season. Cane response on individual bushes was markedly irregular. Rates of 2 g/bush or higher reduced yield, while berry size was reduced at 8 g/bush. In the second season after application, the effect of paclobutrazol was more uniform among canes within a plant, but again all rates that had an effect on vegetative growth caused deleterious effects on the reproductive components. At rates lower than 2 g active ingredient per plant, there was no effect of paclobutrazol on leaf area, floral or vegetative bud development, and rates of photosynthesis or transpiration. Paclobutrazol had no influence on leaf mineral content of N, P, Ca, Mg, Fe or Cu. Mn was increased by all levels of paclobutrazol, but only the highest level (12 g active ingredient per plant) increased leaf levels of K and Zn.

Experiments in highbush blueberry have been focused on the effect of paclobutrazol on hastening fruit production for more rapid evaluation in breeding programmes (Ehlenfeldt, 1998). Soil drenches of 25 ppm of paclobutrazol done after harvest inhibited shoot elongation and stimulated earlier and greater flower bud production of 3-year-old 'Bluetta', 'Bluecrop' and 'Jersey' plants. Treatments increased bud numbers by 359–797%, while reducing vegetative bud formation (Table 7.1). This effect caused overcropping and reduced fruit size.

Foliar treatments of paclobutrazol at the end of the growing season to mature 'Bluecrop', 'Blueray' and 'Duke' plants resulted in a more moderate effect than the drench (Table 7.2). Flower bud numbers were increased without
Table 7.1. Floral bud production in highbush blueberry cultivars in response to a soil drench of paclobutrazol at 25 ppm. (Adapted from Ehlenfeldt, 1998.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Paclobutrazol</th>
<th>Total</th>
<th>Simple</th>
<th>Total as % of control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bluetta</td>
<td>−</td>
<td>16.7</td>
<td>15.8</td>
<td>−</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>65.1***</td>
<td>51.3***</td>
<td>389***</td>
</tr>
<tr>
<td>Bluecrop</td>
<td>−</td>
<td>19.0</td>
<td>18.5</td>
<td>−</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>68.1***</td>
<td>54.5***</td>
<td>359***</td>
</tr>
<tr>
<td>Jersey</td>
<td>−</td>
<td>7.6</td>
<td>7.6</td>
<td>−</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>60.6***</td>
<td>58.1***</td>
<td>797***</td>
</tr>
</tbody>
</table>

***Mean values were significantly different compared with no paclobutrazol at P<0.001 level (Student's t test).

affecting vegetative growth. Although bud numbers increased with dose, flowers per bud were not affected by the treatments. 'Bluecrop' and 'Blueray' responded similarly to paclobutrazol applications, while 'Duke' showed no significant response to any treatment. Part of the lower response of 'Duke' plants might be due to their lower stature in this trial, since the researchers found that better response was obtained when the compound was applied to

Table 7.2. Floral buds per plant and number of flowers per bud of 'Bluecrop', 'Blueray' and 'Duke' highbush blueberries treated with foliar applications of paclobutrazol. (Adapted from Ehlenfeldt, 1998.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment (mg/l)</th>
<th>Floral buds/plant</th>
<th>Flowers/bud</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bluecrop</td>
<td>0</td>
<td>11.5</td>
<td>8.9</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>17.2</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>17.8</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>20.1</td>
<td>9.8</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>33.0</td>
<td>8.5</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>31.4</td>
<td>8.9</td>
</tr>
<tr>
<td>Blueray</td>
<td>0</td>
<td>7.2</td>
<td>8.3</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>13.1</td>
<td>7.1</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>11.8</td>
<td>7.8</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>15.8</td>
<td>7.2</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>30.6</td>
<td>7.9</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>23.2</td>
<td>8.6</td>
</tr>
<tr>
<td>Duke</td>
<td>0</td>
<td>3.5</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>4.8</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>9.5</td>
<td>5.6</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>7.5</td>
<td>5.4</td>
</tr>
</tbody>
</table>

a,b,c,d Mean values within a column for a variety with unlike superscript letters were significantly different at P<0.001 level (Fisher's protected LSD test);
plants growing vigorously and in which the inhibition of shoot elongation, to
favour carbohydrate accumulation, would trigger flower bud induction.

In the case of soil applications, variable movement of the chemical
within the soil profile, due to water movement or soil binding or location of
the chemical with respect to the active roots, might explain the differences in
response among canes within a bush.

In summary, paclobutrazol may have the potential to be used in com-
cmercial blueberry settings for plant size reduction and increased yields,
but insufficient data have been generated to rigorously test this possibility.
Experimental results have been quite variable and much longer-term studies
are needed.

Enhancement of leaf development

Deciduous fruit crops, including blueberries, undergo every year a physio-
logical stage of development known as dormancy. The release from dormancy
and subsequent bud development (flower and vegetative) requires a period of
exposure to low temperatures (under 7.2°C) followed by a subsequent rise in
spring temperatures (Stringer et al., 2004). In highbush blueberry, vegetative
buds usually open about 2 weeks before floral buds; however, some rabbiteye
and southern highbush blueberries have the tendency to open leaf buds after
flower buds.

Under climatic conditions in certain blueberry-producing regions (i.e.
south-eastern USA, northern Chile, southern Spain and Portugal), marginal
winter chilling occurs. This results in delayed canopy development, and
may cause early growth cessation and inhibition of shoot, flower and leaf
development. Carbohydrate supply at bloom is heavily dependent on the
previous season’s reserves, but if heavy fruit set occurs before leaf emergence,
carbohydrate supply may be restricted and the development of leaf buds will
often be suppressed, resulting in low leaf/fruit ratios. Under these conditions,
accelerated spring leaf development prior to, or concomitant with, flower
opening may increase fruit size and reduce fruit development period of some
poor-leafing cultivars, particularly under marginal chilling (Stringer et al.,
2002; Williamson et al., 2002).

Utilization of chill compensation chemicals provides a management
option to avoid the effects of insufficient chilling. These chemicals aid in
breaking dormancy and promote earlier and greater leaf development.
Hydrogen cyanamide or HCN (commercially known as Dormex®) has been
studied and used extensively in several fruit crops (peaches, apples, grapes,
raspberries) for these purposes. When applied at proper rate and timing to
blueberries, it can promote leaf development and avoid deleterious effects on
floral buds (Williamson et al., 2001).

Research done on ‘Misty’ southern highbush in the southern USA
(Williamson et al., 2002) demonstrated that HCN, applied when 36–40
chilling-hours (hours between 0 and 7.2°C) had been accumulated,
accelerated vegetative bud break. In control plants (no HCN), the percentage of vegetative buds that grew remained low throughout the season. HCN-treated plants had a large and rapid increase in vegetative bud break (Table 7.3). The response to HCN was linear, which implies that vegetative bud break increased proportionally to the rise in HCN rate.

As a secondary effect, HCN advanced fruit ripening. Significantly more fruit were harvested from HCN-treated plants before 1 May. This has great implications in the market price per kilogram of fruit, since fruit marketed before 1 May has almost double the price of fruit marketed in late May. Besides, the nearly 0.3 g difference in fruit weight for HCN-treated fruit harvested before 1 May also has practical and economic significance. The fruit number was significantly reduced when plants were treated with 1.5% v/v HCN (52% of non-treated control), which might have influenced fruit weight. However, HCN at 0.75% v/v had similar fruit size to the 1.5% v/v HCN rate, but fruit load was similar for 0.75% v/v to the non-treated control. This would imply that most of the effect of HCN on fruit size was probably not due to reduced fruit load but to earlier and greater expansion of leaf area (Table 7.4).

Table 7.3. Effect of hydrogen cyanamide (HCN) spray concentration on vegetative bud break of mature ‘Misty’ southern highbush blueberry following treatment on 17 December and 6 January (50% flowering=20 February). (Adapted from Williamson et al., 2002.)

<table>
<thead>
<tr>
<th>HCN concentration (% v/v)</th>
<th>Vegetative buds growing (% of total)</th>
<th>29 DBF (22 Jan)</th>
<th>14 DBF (6 Feb)</th>
<th>14 DAF (6 Mar)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>0.75</td>
<td>33</td>
<td>40</td>
<td>54</td>
<td></td>
</tr>
<tr>
<td>1.5</td>
<td>71</td>
<td>74</td>
<td>71</td>
<td></td>
</tr>
</tbody>
</table>

Significance of trend (linear) *** *** ***

DBF, days before flowering; DAF, days after flowering.
Trend significant at ***P ≤ 0.001.

Table 7.4. Effect of hydrogen cyanamide (HCN) spray concentration applied on 17 December 1997 on time of harvest, fruit yield (number and weight) of mature ‘Misty’ southern highbush blueberry following treatment (full bloom=20 February). (Adapted from Williamson et al., 2002.)

<table>
<thead>
<tr>
<th>Harvest period</th>
<th>1–30 April</th>
<th>1–31 May</th>
<th>1–31 May</th>
<th>No. of fruit</th>
<th>Total yield (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Total yield</td>
<td>Mean berry weight (g)</td>
<td>% Total yield</td>
<td>Mean berry weight (g)</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>30.8</td>
<td>1.61</td>
<td>69.2</td>
<td>1.31</td>
<td>3582</td>
</tr>
<tr>
<td>0.75</td>
<td>52.3</td>
<td>1.93</td>
<td>47.7</td>
<td>1.51</td>
<td>3467</td>
</tr>
<tr>
<td>1.5</td>
<td>71.5</td>
<td>1.96</td>
<td>28.5</td>
<td>1.13</td>
<td>1861</td>
</tr>
</tbody>
</table>
In summary, if properly used, Dormex applied at 0.75% v/v to some poor-leafing southern highbush and rabbiteyes can stimulate more rapid leaf development in the spring, resulting in increased fruit size and more concentrated ripening on the first two harvests in blueberry cultivars, particularly under marginal chilling.

Reproductive growth

Bloom delay

Spring freeze damage is a major problem for blueberries in different regions of the world. Even though there have been efforts to breed for varieties with a shorter span from bloom to harvest, earliness in harvest season usually is associated with early blooming. Thus, growers focusing on producing fruit for the early market are more prone to suffer frequently from spring freezes. Ethephon or Ethrel® is a growth regulator that upon contact with plant tissues releases ethylene, the ripening hormone (Howell et al., 1976). Ethephon was studied for several years and localities to determine if its application in the previous autumn might delay bloom of southern highbush blueberries in the following season (Krewer et al., 2005; NeSmith, 2005). Ethephon significantly delayed bloom in southern highbush varieties (Table 7.5). When measured at bloom (22 February), selection ‘FL 86-19’ and cv. ‘O’Neal’ were delayed 1.2 and 1.1 flower bud stages (which would correspond to 8–11 days), respectively, by one application of 400 ppm ethephon the previous autumn (early October). Moreover, ethephon doubled flower density in ‘O’Neal’ and increased flower density by over 40% in ‘FL 86-19’.

In ‘Sharpblue’ southern highbush, bloom delay from ethephon was estimated to be 0 to 6 days, depending on spray concentration and stage of

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment</th>
<th>Flower bud stage</th>
<th>Flower bud density (no. of buds/cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘FL 86-19’</td>
<td>Control</td>
<td>5.3</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Ethephon</td>
<td>4.1**</td>
<td>0.55**</td>
</tr>
<tr>
<td>‘O’Neal’</td>
<td>Control</td>
<td>3.5</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Ethephon</td>
<td>2.6**</td>
<td>0.61**</td>
</tr>
</tbody>
</table>

Stage 3 = bud scales separated, flower apices visible; stage 4 = individual flowers distinguishable, buds scales abscised; stage 5 = individual flowers distinctly separated, corollas unexpanded and closed (Spiers, 1978).

Value was significantly different from that of the control at **P ≤ 0.01 level.
flower development in control plants (Table 7.6). At the beginning of bloom (10% anthesis for control), 400 ppm resulted in nearly 6 days delay in bloom development. By late bloom (90% anthesis for control), the highest rate (400 ppm ethephon) was nearly 3 days behind the control plants in flower development. The estimated delay in bloom was greater as ethephon rates increased regardless of the level of bloom in the controls. Ethephon-treated plants continued to show delayed blooming with respect to controls in late stages of flower development (>60% flowers open in all treatments). Similar results were obtained with ethephon sprays to ‘Climax’ rabbiteye blueberries (NeSmith, 2005).

A 2- to 4-day delay in ripening was observed for treatments that had a 7- to 10-day delay in flowering (NeSmith, 2005). In some trials, cumulative harvest dates were delayed by between 5 and 9 days for plants treated with the highest ethephon rate (400 ppm) when compared with control plants (Table 7.7). No harvest delay, relative to controls, was detected for the 100 and 200 ppm rates (Krewer et al., 2005). A negative association between total yield and ethephon rate (Table 7.7) was found in one of the two seasons (Krewer et al., 2005). The authors attribute yield reduction to poor bloom overlap between treated ‘Sharpblue’ and untreated ‘Misty’ pollinizers, as well as very poor pollination weather during the period when plants of the treatments were blooming heavily.

Current recommendations for usage of ethephon in south Georgia are to apply two sprays of 400 ppm, with the first application in mid-October and the second in early November (NeSmith, 2005). The studies in Georgia indicate that ethephon can effectively delay bloom (7–10 days) in different blueberry varieties with no apparent phytotoxicity. Depending on temperatures during

<table>
<thead>
<tr>
<th>Open flowers ( % of control )</th>
<th>Ethephon concentration ( ppm )</th>
<th>100</th>
<th>200</th>
<th>400</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>2.5</td>
<td>4.8</td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>2.0</td>
<td>4.3</td>
<td>5.4</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>1.7</td>
<td>3.9</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>1.5</td>
<td>3.6</td>
<td>4.8</td>
<td></td>
</tr>
<tr>
<td>50</td>
<td>1.2</td>
<td>3.3</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>0.9</td>
<td>3.0</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>70</td>
<td>0.7</td>
<td>2.7</td>
<td>3.9</td>
<td></td>
</tr>
<tr>
<td>80</td>
<td>0.4</td>
<td>2.4</td>
<td>3.6</td>
<td></td>
</tr>
<tr>
<td>90</td>
<td>0.0</td>
<td>1.8</td>
<td>3.1</td>
<td></td>
</tr>
</tbody>
</table>
Table 7.7. Effect of autumn ethephon applications to ‘SharBlue’ blueberry plants on cumulative percentage of total yield by harvest date on the year after application. (Adapted from Krewer et al., 2005.)

<table>
<thead>
<tr>
<th>Ethephon rate (ppm)</th>
<th>Cumulative yield (% of total)</th>
<th>Total yield to 3 June (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>26 April</td>
<td>3 May</td>
</tr>
<tr>
<td>0</td>
<td>10.6</td>
<td>35.6</td>
</tr>
<tr>
<td>100</td>
<td>7.8</td>
<td>30.5</td>
</tr>
<tr>
<td>200</td>
<td>7.8</td>
<td>30.4</td>
</tr>
<tr>
<td>400</td>
<td>4.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Significance of trend
- Linear: **, *, ***
- Quadratic: NS

<table>
<thead>
<tr>
<th>Significance of trend</th>
<th>26 April</th>
<th>3 May</th>
<th>12 May</th>
<th>19 May</th>
<th>3 June</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear</td>
<td>**</td>
<td>*</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Quadratic</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS, not significant.

<sup>a</sup>Value was significantly different from that of the control at P < 0.05 level (Dunnett's test).

Trend significant at *P < 0.05, **P < 0.01 or ***P < 0.001.

fruit development, this may translate into a 2- to 4-day delay in fruit ripening date. This smaller impact on harvest date is probably because heat unit accumulation that controls fruit development is slow early in the season. For growers who get a premium price for early fruit, a few days of delay in harvest can have a marked impact (NeSmith, 2005). Individual growers would need to assess the situation in their particular condition (variety, weather, market) and balance the potential impact of spring frost versus possible delay in harvest due to ethephon sprays. However, this decision is difficult as the ethephon must be sprayed before the risk of frost is known.

The application of ethephon could have some added benefits. Ethephon application has increased flower bud density both in highbush (Robbins and Doughty, 1984) and rabbiteye blueberries (Krewer et al., 2005). This increase in flower bud numbers may have potential to increase yields if percentage fruit set is not altered. To rigorously test this possibility, it would be important to determine if other varieties respond similarly. Ethephon applications may also be useful to synchronize the bloom stages of blueberries for improved pollination and fruit set (Krewer et al., 2005; NeSmith, 2005).

**Inhibition of flower bud formation or elimination of flowers in nursery plants**

In some conditions, it is desirable to completely eliminate reproductive buds of blueberry plants. It has been demonstrated that young plants often do not establish well if they bear fruit in the first two or three years after planted (Strik and Buller, 2005). Also, pollen-transmitted viruses (Blueberry leaf mottle virus and Blueberry shock I larvirus; Sandoval et al., 1995) can infect these young
blueberry plants and decrease permanently their fruiting potential and vigour. Growers can reduce fruit load manually through pruning and fruit thinning. However, this is usually cost-ineffective, does not totally prevent viral infection and has less impact on the vegetative/reproductive balance. GA₃ has effectively inhibited flower bud formation in various fruit species (apple, pear, peach, grapes, sour and sweet cherry; Retamales et al., 2000).

Early studies showed that GA₃ could reduce flower bud formation in blueberry. When 5 to 500 ppm GA₃ was sprayed at bloom to increase fruit set on rooted cuttings of ‘Coville’ highbush blueberries, return bloom was decreased (between 60 and 96% of non-sprayed controls) with increasing GA₃ levels (Mainland and Eck, 1969a). However, when similar GA₃ levels were sprayed also at bloom to 5-year-old ‘Coville’ field plants, there was no effect of GA₃ on return bloom (Mainland and Eck, 1969b). When 2-year-old ‘Bluecrop’ and ‘Elliott’ nursery plants grown in containers were treated with 0, 150 or 300 ppm GA₃ at 7, 9, 11 or 13 WAFB, it was found that 300 ppm GA₃ reduced flower bud initiation by as much as 60%. Greater effect was found with latest application (13 WAFB) and higher GA₃ dose (150 versus 300 ppm). GA₃ reduced the total number of flowers per bush rather than the number of flowers per bud (Retamales et al., 2000).

Black and Ehlenfeldt (2007) tested different types of gibberellins (GA₃, GA₄, GA₅, GA₇, GA₁₇) on flower bud suppression in 1-year-old rooted cuttings of ‘Bluecrop’ and ‘Duke’ highbush blueberries. The concentrations ranged from 50 to 600 ppm and they were applied during the summer (early July to mid-September in the northern hemisphere). If it is assumed that full bloom would occur during the first week of May, these dates would correspond to between 11 WAFB (for early July) and 23 WAFB (for mid-September). When GA₁₇ was trialled in ‘Bluecrop’, the greatest degree of flower bud suppression (90%) resulted from applications of 400 ppm repeated weekly from 11 to 21 WAFB. However, these treatments also reduced total vegetative bud number (by 40%) and plant height. There was a dose effect, with greatest effect from 400 or 600 ppm (average 72 or 73% flower bud suppression for the various timings) versus 42% suppression for 200 ppm GA₁₇.

When the effect of timing of GA₁₇ sprays was evaluated (two sprays/week), the period that would correspond to 13 WAFB was the most effective (71% flower bud suppression), as compared with 53 to 67% suppression in other timings. This would correspond with the period of greatest effect of GA₃ in experiments reported by Retamales et al. (2000). The latest GA₁₇ applications (early to mid-September in the northern hemisphere, which would correspond to 21–22 WAFB) were more effective on ‘Duke’ than ‘Bluecrop’, indicating that flower bud suppression treatments were more effective on the more precocious variety, or that a greater proportion of flower buds was being induced at that moment in ‘Duke’ compared with ‘Bluecrop’. When GA₃, GA₄, GA₅, and GA₁₇ were compared in ‘Bluecrop’ at similar rates (200 ppm) and timing (18–25 August to 1 September), GA₃ appeared to be
somewhat more effective than the other GAs; however, the overall effect of treatments was low (versus control), which might be due to the low rate used (Black and Ehlenfeldt, 2007).

In summary, these experiments with young plants indicate that GA$_3$ and GA$_4+7$ have a similar effect on suppressing flower bud induction, but in the areas where highbush blueberries are grown, the flower induction process would occur over a long period and, under these conditions, only repeated GA sprays at 400 ppm for nearly 3 months would assure the complete suppression of flower bud formation; however, these applications could reduce total vegetative bud number and plant height.

An alternative option to eliminate flower buds in nursery plants may be the use of HCN. Research done mainly with rabbiteye and southern highbush blueberries has shown that flower buds in the Spiers scale stage 3 (Spiers, 1978) or beyond (bud scales separated, apices of flowers visible) will be killed by HCN sprays. Experiments on southern highbush 'Misty' have shown that 2% (v/v) HCN can kill between 19 and 38% of flower buds if applied when 10–30% of flower buds are in stage 3. Bud mortality was related to chilling, with highest bud mortality for plants that received no chilling (Table 7.8). Again, it appears difficult to eliminate all flower buds in nursery plants since on a given date many buds are not at the most susceptible stage to be affected by HCN sprays.

### BALANCING REPRODUCTIVE AND VEGETATIVE GROWTH IN MATURE PLANTS

#### Inhibition of flower bud formation

In certain growing conditions, fruit thinning might be needed to enlarge fruit size or balance fruit load once the plants are established. Since fruit are

<table>
<thead>
<tr>
<th>HCN spray concentration (% v/v)</th>
<th>Pre-treatment chilling (h at &lt;7.2°C)</th>
<th>Significance of trend (linear)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>150</td>
</tr>
<tr>
<td>0</td>
<td>1.0</td>
<td>1.5</td>
</tr>
<tr>
<td>1</td>
<td>20.0</td>
<td>11.0</td>
</tr>
<tr>
<td>2</td>
<td>38.0</td>
<td>26.0</td>
</tr>
</tbody>
</table>

Significance of trend (linear)

NS, not significant.

Trend significant at **$P<0.01$ or ***$P<0.001$.  

Table 7.8. Effect of hydrogen cyanamide (HCN) spray concentration (0, 1 or 2%, v/v) and pre-treatment chilling levels (0, 150 or 300 h at <7.2°C) on the percentage of flower bud mortality of 2-year-old container-grown 'Misty' blueberry. (Adapted from Williamson et al., 2001.)
competing with vegetative growth for the resources (nutrients, carbohydrates) which are available, it would be convenient to remove the fruit at the earliest possible date (Looney, 1993). In this context, rather than waiting for the complete expression of reproductive growth at bloom time or thereafter, the idea is to intervene during the induction of reproductive buds which would occur near the end of summer. As was evident from research done with GA in nursery plants, the application of this compound would only partially reduce the number of flower buds in blueberry plants. Although this is insufficient for nursery plants, it might be adequate for managing crop load in mature field plants. Experiments done on 4-year-old field ‘Bluecrop’ plants (Table 7.9) showed that two GA₃ applications of 300 ppm done 15 and 18 WAFB markedly reduced the number of fruit (45% less than non-sprayed control) in the following season and significantly increased fruit size (38% greater than control). Yields would be reduced by 30%, but the greater size might prove advantageous for growers in areas with low frost risk at bloom and who are focused on hand picking for the fresh market, since both harvest efficiency and fruit price should be improved (Strik et al., 2003). Before commercial utilization of this practice, this type of grower should develop trials in different varieties to establish the best timing and rates for their specific conditions.

**Flower and fruit thinning**

Larger fruit size is often an advantage for fruit destined for the fresh market and the economic benefits of treatments that reliably improve average fruit size may be substantial. Part of the reduction of fruit load is usually done at pruning, although both vegetative and reproductive buds are removed with this practice (Strik et al., 2003). The other classical approach to improve

<table>
<thead>
<tr>
<th>No. of GA₃ sprays</th>
<th>Buds/shoot</th>
<th>Fruit at harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Number</td>
</tr>
<tr>
<td>0</td>
<td>16.6ᵃ</td>
<td>606ᵇ</td>
</tr>
<tr>
<td>1</td>
<td>15.7ᵃ</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>17.7ᵃ</td>
<td>332ᵃ</td>
</tr>
</tbody>
</table>

Applications were done 15 and 18 weeks after full bloom; buds/shoot was measured on 16 October 1996; fruit at harvest was measured between 17 December 1996 and 16 January 1997.

ᵃᵇMean values within a column with unlike superscript letters were significantly different at P<0.01 level (Least Significant Difference test).
average fruit size at harvest has been to reduce the flower and/or fruit number early in the season. Since, in most situations, the use of hand labour implies high cost or delays in implementing the reduction in flower/fruit load, this is an area where growth regulators have been intensively investigated and used in many fruit crops. Considering that commercially beneficial flower and fruit thinning usually reduces total crop load (both number of fruit and total weight of the harvest), the improvement of fruit size at harvest is accounted for by reduced competition among fruit for various resources (water, nutrients and carbohydrates). Depending on intensity and opportunity of the operation, crop reduction might produce larger fruit size and higher return bloom (Looney, 1993).

In the case of blueberries, there have been very few trials on thinning agents. Perhaps this is partly due to the recent expansion of the industry where the supplies usually have not been able to satisfy the demand and the market has put less emphasis on fruit quality. However, the situation has been changing rapidly in the last few years as small berries are being directed to the lower-price processed market and growers are getting higher prices for larger berry sizes (fruit diameter: 18–21 mm = large, 22–25 mm = extra large).

The first thinning trials were done on rabbiteye blueberries, since they commonly produce small-sized fruit. Several compounds that have successfully thinned flower and/or fruitlets in tree fruits (mainly apples) were assayed on cv. 'Tifblue' both in the greenhouse and in the field (Cartagena et al., 1994). In the greenhouse, benzyladenine (BA) at 25 and 75 ppm had 40 and 43% fruit set, GA₃ at 25 and 50 ppm had 67 and 38% fruit set, NAA at 7.5 and 15 ppm had 55 and 53% fruit set and 1-naphthyl N-methylcarbamate (carbaryl) at 400 and 600 ppm had 40 and 31% fruit set, respectively.

These same compounds were then trialled for two seasons on field-grown 8-year-old 'Tifblue' plants in Mississippi (Cartagena et al., 1994). Applications were done either 10 or 20 days after corolla drop, when berries were on average 5.2 and 8.5 mm in diameter. In these studies, BA at 75 ppm reduced fruit set in 1991 and 1992 (39 and 77%), also the combination of carbaryl (400 ppm) and BA at 25 ppm reduced fruit set (55 and 87%), versus 76 and 97% fruit set for the control in 1991 and 1992, respectively. Overall, combinations of carbaryl and GA₃ reduced fruit set, but the response depended on GA₃ concentration and varied from year to year. GA₃, NAA and carbaryl also reduced fruit set, but the results were inconsistent (Table 7.10).

In 1991 greater thinning occurred when sprays were done 10 days after corolla drop. Regarding fruit quality, BA at 25 ppm increased fruit diameter at first harvest in 1991 (15.6 versus 14.1 mm for control), and carbaryl at 400 ppm increased fruit size in 1991 (15.3 versus 14.1 mm for control) as well as in 1992 (17.1 versus 16.3 mm for control). Increase in fruit diameter was not always related to the degree of thinning, and varied depending on year and application time (Table 7.10). Yield and return bloom were not influenced
Table 7.10. Fruit set and fruit diameter (first harvest) of mature 'Tifblue' blueberry plants as affected by chemical thinners sprayed 10 days after corolla drop in 1991 and 1992. (Adapted from Cartagena et al., 1994.)

<table>
<thead>
<tr>
<th>Chemical</th>
<th>Concentration (ppm)</th>
<th>Year</th>
<th>Year</th>
<th>Year</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0</td>
<td>76.0d</td>
<td>96.6d</td>
<td>14.1de</td>
<td>16.3bc</td>
</tr>
<tr>
<td>BA</td>
<td>25</td>
<td>64.9bcd</td>
<td>86.6bc</td>
<td>15.6ab</td>
<td>16.2cd</td>
</tr>
<tr>
<td></td>
<td>75</td>
<td>38.7a</td>
<td>77.1ab</td>
<td>14.4cd</td>
<td>15.9d</td>
</tr>
<tr>
<td>GA₃</td>
<td>25</td>
<td>74.2d</td>
<td>78.0ab</td>
<td>14.4cd</td>
<td>16.7abcd</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>73.1cd</td>
<td>95.5bc</td>
<td>14.7bcde</td>
<td>16.4abcd</td>
</tr>
<tr>
<td>NAA</td>
<td>7.5</td>
<td>68.7bcd</td>
<td>97.2fg</td>
<td>14.8bcde</td>
<td>16.6abcd</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>69.6bcd</td>
<td>90.8de</td>
<td>15.1bcd</td>
<td>16.4abcd</td>
</tr>
<tr>
<td>Carbaryl</td>
<td>400</td>
<td>68.8bcd</td>
<td>92.4de</td>
<td>15.3bc</td>
<td>17.1a</td>
</tr>
<tr>
<td></td>
<td>600</td>
<td>66.1bcd</td>
<td>90.3de</td>
<td>15.9a</td>
<td>16.7abc</td>
</tr>
<tr>
<td>Carbaryl + BA</td>
<td>400 + 25</td>
<td>54.7abc</td>
<td>87.4bc</td>
<td>13.9a</td>
<td>16.6abcd</td>
</tr>
<tr>
<td></td>
<td>400 + 75</td>
<td>63.9bcd</td>
<td>96.3de</td>
<td>14.6cde</td>
<td>16.2cd</td>
</tr>
<tr>
<td>Carbaryl + GA₃</td>
<td>400 + 25</td>
<td>71.2cd</td>
<td>92.9de</td>
<td>14.5cde</td>
<td>16.3bcd</td>
</tr>
<tr>
<td></td>
<td>400 + 50</td>
<td>51.7b</td>
<td>98.0ef</td>
<td>14.2de</td>
<td>17.0bc</td>
</tr>
</tbody>
</table>

BA, benzyladenine; GA₃, gibberellic acid; NAA, naphthaleneacetic acid.

Means within a column with unlike superscript letters were significantly different at P≤0.05 level (t-test).

by any of the treatments. Results from this study indicate that BA alone or combined with carbaryl could be potentially used as a fruit thinner, but the dose and timing need to be refined in further trials done in other growing regions and with various plant materials.

Studies done recently in Slovenia on highbush blueberries (Koron and Stopar, 2006) tested the efficacy of ammonium thiosulfate (ATS), Armothin® (active ingredient: alkoxylated fatty alkylamine polymer) at 1.5% v/v, BA at 200 ppm and CPPU (N-(2-chloro-4-pyridyl)-N'-(phenylurea) at 10 or 20 ppm applied to mature 'Rancocas' and 'Elliott' plants. ATS and Armothin were applied at full bloom, while BA and CPPU were sprayed 14 days after full bloom. In most treatments, there were strong phytotoxic effects with injury to flowers, fruits, shoots and leaves, evidenced by leaf, flower and fruit drop and reductions in plant growth rate and yield (total fruit number, weight and size). CPPU delayed fruit ripening by 3 (10 ppm) or 4 weeks (20 ppm). Although fruit number was significantly reduced in several treatments (Table 7.11), the fruit remaining on the plant could not benefit because leaves and shoots were damaged and the ability of the plants to generate carbohydrates was significantly reduced, an effect which in some treatments lasted for several weeks.
Table 7.11. Effect of application of various thinning agents on fruit weight, fruit number, proportion of fruit as related to control and total yield of ‘Rancocas’ and ‘Elliott’ highbush blueberries. (Adapted from Koron and Stopar, 2006.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment</th>
<th>Fruit weight (g)</th>
<th>Fruit number</th>
<th>Fruit number (% of control)</th>
<th>Total yield per bush (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elliott</td>
<td>Control</td>
<td>0.96&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3815</td>
<td>100</td>
<td>3662&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>ATS 1% v/v</td>
<td>0.90&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>2588</td>
<td>67.8</td>
<td>2329&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Armothin 1.5% v/v</td>
<td>0.65&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2123</td>
<td>55.6</td>
<td>1380&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>BA 200 ppm</td>
<td>0.77&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>1705</td>
<td>44.7</td>
<td>1313&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>CPPU 10 ppm</td>
<td>0.99&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3564</td>
<td>93.4</td>
<td>3528&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>CPPU 20 ppm</td>
<td>1.02&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2943</td>
<td>77.1</td>
<td>3002&lt;sup&gt;b,c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Rancocas</td>
<td>Control</td>
<td>0.85&lt;sup&gt;b,c,d&lt;/sup&gt;</td>
<td>2540</td>
<td>100</td>
<td>2150&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>ATS 1% v/v</td>
<td>0.82&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>1718</td>
<td>67.6</td>
<td>1409&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Armothin 1.5% v/v</td>
<td>0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1622</td>
<td>63.9</td>
<td>892&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>BA 200 ppm</td>
<td>0.74&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1624</td>
<td>63.9</td>
<td>1202&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>CPPU 10 ppm</td>
<td>0.97&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1476</td>
<td>58.1</td>
<td>1432&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>CPPU 20 ppm</td>
<td>0.91&lt;sup&gt;c,d&lt;/sup&gt;</td>
<td>457</td>
<td>18.0</td>
<td>416&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

ATS, ammonium thiosulfate; BA, benzyladenine; CPPU, N-(2-chloro-4-pyridyl)-N'-phenylurea.

<sup>a,b,c</sup>Mean values within a column for each cultivar with unlike superscript letters were significantly different at P<0.05 level (Duncan’s multiple range test).

A further trial done by the same researchers in Slovenia on ‘Elliott’ and ‘Bluecrop’ utilized lower rates of BA (20 or 50 ppm) and CPPU (2 or 5 ppm) applied at late bloom. No effect on total yield was observed. CPPU at 5 ppm increased fruit diameter and height, but not weight in ‘Elliott’. At these rates, CPPU did not alter the ripening period in either variety (Koron and Stopar, 2006).

Preliminary trials on the effect of soybean oil (Golden Natur’1®; GN) applied at bud break (10–11 February) at 0, 6, 9, 12 and 15% v/v were done on 3-year-old ‘Legacy’ in Tennessee (Deyton et al., 2005). Soybean oil has been assayed for thinning fruit trees and its application found to increase internal CO2 in shoots and fruits, which decreased respiration rates, probably due to feedback inhibition (Myers et al., 1996). Bloom opening was delayed by 2–6 days with sprays greater than 9% v/v GN, with higher concentration causing greater bloom delay. Rates of 0, 6 and 9% v/v oil had 0, 30 and >70% flower bud mortality, respectively, at 36 days after treatment. Plants treated with 12 and 15% v/v oil sprays had an estimated 24 and 13%, respectively, of a normal crop load (compared with untreated control plants). A similar trial of soybean oil used young plants of various southern highbush cultivars in North Carolina. Treatments of 0, 6, 9 and 12% v/v GN were sprayed on 5 March. These rates of GN did not affect flower bud mortality, crop load or berry...
size across several southern highbush cultivars (Deyton et al., 2005). From these preliminary trials it would appear that concentrations between 6 and 9% v/v could be adequate for flower bud delay and thinning. High bud mortality will, of course, reduce yield, but determination of an oil dose-response (bud mortality) relationship may provide a means of chemically thinning blueberries in the future.

In conclusion, further trials need to be developed in a range of varieties with different compounds and rates before some recommendation can be established for the use of thinning agents in blueberries. The need to increase fruit size for the fresh market should activate research in this area in the near future.

Fruit set improvement

Adequate commercial yields in blueberry would require at least 60% fruit set (Eck, 1988). Rabbiteye blueberries often exhibit poor fruit set in low-chill regions (NeSmith, 2005). Less than 40% fruit set has been measured in 'Climax', 'Brightwell' and 'Tifblue' in Georgia (Davies and Buchanan, 1979; NeSmith and Adair, 2004) as well as 'Bluegem' in Florida (Davies and Buchanan, 1979). GA₃ has been extensively studied to increase fruit set in rabbiteye blueberries (NeSmith and Krewer, 1992, 1997b; Cano-Medrano and Darnell, 1998; NeSmith et al., 1999; Merino et al., 2002; NeSmith, 2002, 2005).

The current recommendation for Georgia is to make two GA₃ applications of 150–200 ppm, the first one at floral stage 6 of the Spiers (1978) scale of flower development (corollas completely expanded and open; when 40–50% of blooms would be open and about 10% of petals should have fallen), followed by a second application 14 days later (Krewer et al., 2007). If application is made too early (flower stage 5), bee activity and pollination are reduced, and flowers do not open normally. This scheme should increase fruit set in most rabbiteye blueberry varieties from 0–9% up to a level of 30–75% (NeSmith, 2005).

GA₃ has also been used to set rabbiteye blueberry fruit following a freeze. Freeze-damaged flowers may never open properly or be receptive to bee pollination, so the application of GA₃ can save a harvest. The impact of a freeze on fruit set will vary with stage of bloom, cultivar, wind and temperature conditions, and duration of low temperature (NeSmith et al., 1999). A bloom temperature below −3.3°C will likely kill flowers at stage 5 and 6. Blossom temperatures in the range of 0 to −3.3°C will cause partial damage to flowers at floral stages 5 and 6. At this stage of development, it has been shown that fruit set can be increased significantly (2% versus 38%) if GA₃ is applied at 250 ppm immediately after the freeze and a second application made 10 to 18 days later (Krewer et al., 2007). Under these conditions, fruit size in
GA3-treated plants was 66% ('Brightwell') and 75% ('Tifblue') of open pollinated controls. The reduction of fruit size caused by GA3 sprays was partially due to increased fruit set (i.e. increased competition for carbohydrates) and reduced seed number within GA3-treated fruits (NeSmith et al., 1995). Some of the problems encountered with the use of GA3 for these purposes are: (i) there is some variability in response among seasons and varieties; (ii) the application of GA3 can result in a high number of pigmy fruit (<1 g), a problem that is especially marked when GA3 is applied to 'Climax' rabbiteye and some southern highbush varieties; and (iii) in some cases, stressed plants set too much fruit, which causes them to have poor vegetative growth and low return bloom (Krewer et al., 2007).

Even though research on both lowbush and highbush blueberries has shown that GA3 (50-500 ppm) can allow development of seedless (parthenocarpic) berries (Barker and Collins, 1965; Mainland and Eck, 1969a), no field studies have been published regarding the application of GA3 to improve fruit set in highbush blueberry plants after a freeze. Fruit set levels similar to, or slightly higher than, those of hand-pollinated treatments (62%) were obtained with 500 ppm GA3 or the combination of an auxin (50 ppm NAA) and 50 ppm GA3. Parthenocarpic fruit were about 60% of the size of pollinated (seeded) berries (Mainland and Eck, 1969b).

Even though some southern highbush blueberries have shown low fruit set (19% in ‘Millennia’ and 22% in ‘Bluecrisp’), other cultivars (‘O’Neal’, ‘Bladen’, ‘Revelle’, ‘Sharpblue’ and ‘Palmetto’) are reported to have fruit set >50% (Lang and Danko, 1991; Williamson and NeSmith, 2007). Fruit set in northern highbush varieties was found to be 56 and 66% for ‘Bluecrop’ and ‘Patriot’, respectively (MacKenzie, 1997). Given this situation, GA3 applications to increase fruit set in highbush fields could only be needed when conditions such as low bee activity or spring freeze damage to flowers generate low fruit set. Otherwise, the heavier fruit load in the season when GA3 is applied would tend to produce small fruit and may reduce flowering the following year.

**Fruit size enlargement**

Considering that research in the 1990s proved that GA3 did increase fruit set in rabbiteye blueberries but had a deleterious impact on fruit size, there was a need for another compound that could enlarge fruit size with a neutral or small effect on fruit set. Previous trials in other fruit crops (kiwifruit, apples, table grapes, olives, persimmon) had demonstrated that a synthetic cytokinin known as CPPU (N-(2-chloro-4-pyridyl)-N'-phenylurea) could markedly enhance fruit size when applied near bloom (Greene, 1989; Reynolds et al., 1992; Antognozzi et al., 1993a,b; Sugiyama and Yamaki, 1995). This compound has now been tested extensively on rabbiteye blueberries both
in the greenhouse and field in different seasons, varieties and rate/timing combinations (Merino et al., 2002; NeSmith and Adair, 2004; NeSmith, 2005, 2008; Serri and Hepp, 2006; Williamson and NeSmith, 2007). In some trials, large increases in fruit set (up to three times) and size (up to 35%) were found. The optimum window of application of CPPU for rabbiteye blueberries was 7 to 21 days after 50% bloom (stage 6), with the highest success being from an application made at 14±3 days after 50% bloom (NeSmith, 2008). In rabbiteye varieties (‘Brightwell’, ‘Climax’, ‘Bluebelle’, ‘Powderblue’, ‘Premier’ and ‘Tifblue’) this application caused an average increase of 5–25% in berry size and a nearly 20% increase in fruit set (NeSmith and Adair, 2004; NeSmith, 2005, 2008). The effect on fruit set was more pronounced in poor fruit set situations, such as when there was little overlap in bloom date among varieties and low bee activity (NeSmith, 2008).

On southern highbush blueberries, different combinations of CPPU (5, 10 or 15 ppm) applied 7, 10, 14 and/or 20 days after stage 5 (or after 50% bloom) have been tried in several varieties: ‘Bladen’, ‘Bluecrisp’, ‘Georgiagem’, ‘Legacy’, ‘Magnolia’, ‘Millennia’, ‘O’Neal’, ‘Palmetto’, ‘Revelle’, ‘Santa Fe’, ‘Sharpblue’ and ‘Star’ (Williamson and NeSmith, 2007). CPPU field applications increased fruit set in Georgia (15–100%) but not in Florida, although in Georgia fruit set was reduced in ‘Bladen’ (30%) and no effect was found in some CPPU treatments applied to ‘Revelle’ and ‘O’Neal’. Individual berry weight was generally increased (10–40%) (Table 7.12), although no effect of CPPU sprays on fruit size was obtained in Georgia for ‘Palmetto’ and ‘Georgiagem’ and for

| Table 7.12. Effect of CPPU applied to mature plants on fruit yield and mean berry fresh weight of three southern highbush blueberry cultivars grown in Florida. (Adapted from Williamson and NeSmith, 2007.) |
|---------------------------------|-----------------|-----------------|
| **CPPU treatment**              | **Yield (g/plant)** | **Berry weight (g/berry)** |
|                                 | ‘Sharpblue’ | ‘Star’ | ‘Santa Fe’ | ‘Sharpblue’ | ‘Star’ | ‘Santa Fe’ |
| Control                         | 2750<sup>a</sup> | 3656<sup>d</sup> | 2066<sup>a</sup> | 1.21<sup>b</sup> | 1.04<sup>b</sup> | 1.18<sup>b</sup> |
| 5 ppm, 14 DAFB                  | 2479<sup>b</sup> | 5259<sup>a</sup> | 2013<sup>a</sup> | 1.46<sup>a</sup> | 1.57<sup>a</sup> | 1.48<sup>b</sup> |
| 5 ppm, 14 DAFB + 5 ppm, 20 DAFB | 1873<sup>a</sup> | 4911<sup>b</sup> | 1282<sup>a</sup> | 1.34<sup>b</sup> | 1.53<sup>a</sup> | 1.36<sup>b</sup> |
| 10 ppm, 14 DAFB                 | 1895<sup>b</sup> | 4089<sup>d</sup> | 1848<sup>a</sup> | 1.47<sup>a</sup> | 1.46<sup>a</sup> | 1.47<sup>b</sup> |
| 10 ppm, 14 DAFB + 10 ppm, 14 DAFB | 1520<sup>b</sup> | 4443<sup>b,c</sup> | 2007<sup>a</sup> | 1.51<sup>a</sup> | 1.59<sup>a</sup> | 1.50<sup>c</sup> |

CPPU, N-(2-chloro-4-pyridyl)-N-phenylurea; DAFB, days after full bloom. Control plants were sprayed with water and surfactant (Triton B 1956, 0.05 % (v/v)) at 14 DAFB.

<sup>a,b,c,d</sup> Mean values within a column with unlike superscript letters were significantly different at P<0.05 level (Duncan’s multiple range test).
some CPPU treatments in 'Milennia' and 'O'Neal' (Williamson and NeSmith, 2007).

When fruit number was calculated based on yield per plant and berry size, it was found that varieties reacted differently to CPPU application. In 'Star', fruit number was little affected, with the lowest fruit number reaching about 80% that of control plants for 10 ppm treatments, while in 'Sharpblue' and 'Santa Fe' the CPPU treatments reduced fruit count by 25–56% and 54–78%, respectively. Highest fruit drop was obtained with two applications (10 and 20 days after flowering), with most responsive dose being 5 ppm for 'Santa Fe' and 10 ppm for 'Sharpblue' (Williamson and NeSmith, 2007).

The delay in fruit ripening that had been previously reported on rabbiteye blueberries (NeSmith and Adair, 2004) was also observed in southern highbush. Since southern highbush are aimed at early markets, this delay in harvest could reduce profitability. The proportions of ripe berries before 10 May in control treatment (no CPPU) in 'Reveille', 'Bladen', 'Georgiagem' and 'Palmetto' were 1–3%, 10–15%, 35% and 72%, respectively; while in the plants treated with 10 ppm CPPU applied 10 to 14 days after 50% bloom those proportions were <1%, 1–5%, 27% and 53%, respectively. The greatest delay in fruit harvest appeared to be associated with those treatments that increased mean berry weight the most. Field observations indicated that the delay was most noticeable when young emerging leaves were burned by spray applications (Williamson and NeSmith, 2007).

The inclusion of a surfactant (Silwet L-77, 0.5% (v/v)) did not seem to consistently affect the level of fruit set in response to CPPU applications in southern highbush. In general, the addition of a surfactant had greater negative than positive impact on fruit set, size and phytotoxicity (Williamson and NeSmith, 2007).

Serri and Hepp (2006) conducted trials in Chile on ‘Elliott’ and ‘Lateblue’ northern highbush blueberries. They applied 10 ppm CPPU at 10 to 15 days after 50% bloom, and obtained a 20 and 50% increase in fruit weight, respectively. Within each variety, fruit numbers were similar in the CPPU and control treatments (no CPPU applied), which suggests that there were similar increases in yield for both varieties in response to CPPU. The CPPU-treated plants had a 3- and 15-day delay in reaching 50% fruit harvested for 'Elliott' and 'Lateblue' respectively, perhaps due to higher fruit numbers. The authors did not report any phytotoxicity derived from CPPU sprays.

Considering that several localities in Chile have an extended bloom season, there was a need to study the effect of repeated CPPU sprays. Trials were done in the 2008/9 season in south-central Chile (latitude 36°S) on ‘Duke’, in which the number of applications (one, two or three), dose (0, 5 or 10 ppm CPPU) and time of application (3, 10 and/or 17 DAFB) were trialled. The results (Table 7.13) show that CPPU treatments did not affect individual fruit weight (control was 1.14 g, while CPPU was 1.11–1.15 g) or fruit weight loss in postharvest after 20 days at 4°C. Only the application of 10 ppm CPPU
Table 7.13. Effect of the application of CPPU, in different dosages, times and number of applications, on mature ‘Duke’ plants. (Adapted from Retamales and Romero, unpublished results.)

<table>
<thead>
<tr>
<th>Treatment (date/dose)</th>
<th>Yield/plant (g)</th>
<th>Fruit diameter (% of control) (mm)</th>
<th>Soluble solids (% of control) (°Brix)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>5745&lt;sup&gt;b,c,d&lt;/sup&gt; 0.0</td>
<td>13.2&lt;sup&gt;g&lt;/sup&gt;</td>
<td>0.0 11.0&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>1/5 ppm</td>
<td>6172&lt;sup&gt;a,b,c&lt;/sup&gt; 7.5</td>
<td>13.2&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.2 10.8&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
<tr>
<td>2/5 ppm</td>
<td>6873&lt;sup&gt;k,b,c&lt;/sup&gt; 19.6</td>
<td>13.1&lt;sup&gt;h&lt;/sup&gt;</td>
<td>-0.2 10.3&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>3/5 ppm</td>
<td>7081&lt;sup&gt;k,b&lt;/sup&gt; 23.3</td>
<td>13.3&lt;sup&gt;ef&lt;/sup&gt;</td>
<td>1.1 10.9&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 2/5 ppm</td>
<td>6978&lt;sup&gt;kb&lt;/sup&gt; 21.5</td>
<td>13.5&lt;sup&gt;de&lt;/sup&gt;</td>
<td>2.5 10.7&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 3/5 ppm</td>
<td>5948&lt;sup&gt;kb,c&lt;/sup&gt; 3.5</td>
<td>13.6&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>3.2 11.2&lt;sup&gt;b,c&lt;/sup&gt;</td>
</tr>
<tr>
<td>2 &amp; 3/5 ppm</td>
<td>5161&lt;sup&gt;c,d&lt;/sup&gt; -10.2</td>
<td>13.4&lt;sup&gt;de&lt;/sup&gt;</td>
<td>1.6 10.7&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 2 &amp; 3/5 ppm</td>
<td>6449&lt;sup&gt;kb,c&lt;/sup&gt; 12.3</td>
<td>13.0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-1.4 10.7&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>1/10 ppm</td>
<td>5722&lt;sup&gt;b,c,d&lt;/sup&gt; -0.4</td>
<td>12.9&lt;sup&gt;h&lt;/sup&gt;</td>
<td>-2.2 10.8&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>2/10 ppm</td>
<td>6120&lt;sup&gt;kb,c&lt;/sup&gt; 6.5</td>
<td>14.2&lt;sup&gt;*&lt;/sup&gt;</td>
<td>7.5 10.8&lt;sup&gt;de&lt;/sup&gt;</td>
</tr>
<tr>
<td>3/10 ppm</td>
<td>5342&lt;sup&gt;b,c,d&lt;/sup&gt; -7.0</td>
<td>13.3&lt;sup&gt;def&lt;/sup&gt;</td>
<td>1.2 11.8&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 2/10 ppm</td>
<td>5851&lt;sup&gt;c,d&lt;/sup&gt; 1.8</td>
<td>13.6&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>3.3 11.1&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 3/10 ppm</td>
<td>7614&lt;sup&gt;a&lt;/sup&gt; 32.5</td>
<td>13.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.7 11.2&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>2 &amp; 3/10 ppm</td>
<td>6118&lt;sup&gt;kb,c&lt;/sup&gt; 6.5</td>
<td>13.2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.4 9.8&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>1 &amp; 2 &amp; 3/10 ppm</td>
<td>4177&lt;sup&gt;d&lt;/sup&gt; -27.3</td>
<td>12.8&lt;sup&gt;h&lt;/sup&gt;</td>
<td>-3.2 11.5&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Significance of trend (linear) ** *** *** ***

CPPU, N-(2-chloro-4-pyridyl)-N'-phenylurea; DAFB, days after full bloom.

Treatment: application dates = 1, 2, 3 correspond to 3, 10, 17 DAFB, respectively; dose = 5 or 10 ppm.

Mean values within a column with unlike superscript letters were significantly different at P≤0.05 level (Duncan’s multiple range test).

Trend significant at **P ≤ 0.01 or ***P ≤ 0.001.

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both at 3 and 17 DAFB significantly increased fruit yield per plant with respect to control (32.5% greater). Fruit diameter was both positively and negatively affected by CPPU treatments compared with control, with highest positive impact over the control with the application of 10 ppm applied 10 DAFB (7.5% greater than control) and 10 ppm CPPU applied 3 and 17 DAFB (4.7% greater than control). There were also positive and negative impacts on soluble solids, with the highest positive effect over the control with the use of 10 ppm CPPU applied at 17 DAFB (7.3% greater than control) and the application of 10 ppm CPPU sprayed 3, 10 and 17 DAFB (5.0% greater than control). Overall, the treatment of 10 ppm applied both at 3 and 17 DAFB to ‘Duke’ appears as the most promising, since it increased both fruit yield and diameter, and had soluble solids and postharvest behaviour similar to control plants.
In general, both in southern highbush trials done in the USA and experiments on ‘Duke’ in Chile, the inclusion of two application dates would be beneficial, probably because this allows for a greater proportion of the flowers to be at the proper stage for maximum CPPU effect. However, it appears (at least for ‘Duke’ under the growing conditions in central Chile) that three applications of 10 ppm CPPU would be excessive since it reduced yields by 27.3% with respect to control, which is due to both lower number of fruit (17.0%) and smaller fruit size (12.4%) with respect to control plants. The fact that CPPU treatments did not have deleterious effects on postharvest weight loss (6.0% loss for control, 5.0–6.6% for CPPU-treated fruit) is interesting since there was, in some cases, a greater fruit expansion (diameter) which could have reduced epidermal wax density and might have had an effect on this barrier to water loss from the fruit.

Some detrimental effects observed when using CPPU in blueberry are: (i) some inconsistent responses to the PGR in different seasons, zones and varieties; (ii) foliage and blossom/fruit burn have been observed under some circumstances; (iii) shorter internodes have occurred in some cases; and (iv) delayed fruit maturity which generally is in the range of 3 to 7 days. In the case of southern highbush, reduced spray volumes seem to avoid or minimize phytotoxicity (NeSmith, 2005; Williamston and NeSmith, 2007).

In summary, CPPU is advancing towards commercial use in blueberry management in different countries. Research has shown that for most varieties and producing regions both fruit size and set benefit the most when CPPU is applied at 5–10 ppm between 7 and 21 days after bloom. However, any use should be on a trial basis until more research is done in different conditions and with various plant materials.

Harvest regulation: advanced maturity and enhanced abscission

A concentrated harvest period is a beneficial trait for machine harvesting and is a criterion in breeding blueberry varieties. The harvest period for individual blueberry varieties ranges from 3 to 6 weeks. This prolonged harvest period for any given variety presents a problem for the mechanical harvesting of the fruit. Plant structures (including immature fruit) are damaged with each pass of the harvester and green fruit are removed. Even when fruit is hand harvested, greater efficiency in labour could be obtained if more fruit would be available to harvest at a given time. Thus, it would be convenient to find management practices that concentrate fruit ripening in highbush blueberries (Eck, 1970).

Application of ethephon to several fruit crops (sour cherries, apples) has enhanced ripening. Fruit drop in ‘Tifblue’ rabbiteye blueberry was increased with 100 ppm ethephon applied when first berries were maturing. Four days after treatment, control plants had 2% of berries drop versus 26% in ethephon-treated plants. By 8 days after treatment the control had doubled the proportion of fruit drop, while ethephon-treated plants reached 33% of fruit drop (Ban et al., 2007).
Experiments done in highbush blueberries showed that at first picking, all rates of ethephon resulted in a greater proportion of total ‘Weymouth’ fruit harvested compared with non-sprayed control (Table 7.14). Within 72 h after the application, a marked influence upon ripening was noticeable to the eye. In ‘Blueray’, ethephon treatments did not differentiate from the control in the first picking and there was a clear dose–response in this cultivar. Applications of 1920 ppm ethephon resulted in a greater percentage of fruit harvested at first picking than at 480 ppm. In both varieties, the ripening effect seemed to disappear after the second picking (Eck, 1970).

For the first two pickings fruit size was significantly reduced by the ethephon applications, where fruit with the two highest doses (1920 and 3840 ppm) had 20–21% less weight than control fruits in ‘Weymouth’. The two highest ethephon rates were also detrimental for fruit size in ‘Blueray’; however, fruit weight was affected only in the second harvest and the reduction amounted to 17% with respect to untreated control.

Internal fruit quality of both highbush blueberry varieties was affected by ethephon sprays. While pH was increased and titratable acidity decreased significantly by all ethephon rates, only the highest dose of ethephon reduced soluble solids upon application (Eck, 1970). Research done on 'Tifblue' rabbiteye blueberries has shown that fruit firmness was reduced from 220 to 50 g/mm² after 4 days of treatment with 100 ppm ethephon.

In another trial, aimed at establishing the joint influence of ethephon concentration and time of application (Warren et al., 1973), fruit of

<table>
<thead>
<tr>
<th>Ethephon rate (ppm)</th>
<th>0</th>
<th>240</th>
<th>480</th>
<th>960</th>
<th>1920</th>
<th>3840</th>
</tr>
</thead>
<tbody>
<tr>
<td>cv. ‘Weymouth’</td>
<td>18a</td>
<td>30b</td>
<td>32b</td>
<td>34bc</td>
<td>40bc</td>
<td>46c</td>
</tr>
<tr>
<td>cv. ‘Blueray’</td>
<td>45a</td>
<td>30b</td>
<td>20c</td>
<td>23bc</td>
<td>27bc</td>
<td>18c</td>
</tr>
<tr>
<td>Harvests</td>
<td>First</td>
<td>Second</td>
<td>Third + four</td>
<td>First</td>
<td>Second</td>
<td>Third</td>
</tr>
<tr>
<td>cv. ‘Weymouth’</td>
<td>37</td>
<td>40</td>
<td>48</td>
<td>43</td>
<td>33</td>
<td>36</td>
</tr>
<tr>
<td>cv. ‘Blueray’</td>
<td>47ab</td>
<td>47ab</td>
<td>41a</td>
<td>64ab</td>
<td>70a</td>
<td>69a</td>
</tr>
<tr>
<td>Significance of trend (linear)</td>
<td>**</td>
<td>**</td>
<td>NS</td>
<td>**</td>
<td>**</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS, non significant.
Trend significant at **P<0.01.
abc Mean values within a column with unlike superscript letters were significantly different at P<0.05 level.
greenhouse-grown ‘Morrow’ highbush blueberry fruit were dipped directly into ethephon (2000, 4000 or 8000 ppm) at different stages of growth (8, 22, 28, 36, 43 and 48 days after bloom). Earliest ripening was obtained with 8000 ppm applied late in stage II (28 DAFB). Harvest period was shortest, less than a week, when treatments were done in stage III (starting at 36 DAFB). As in the previous study, berry weight decreased with higher ethephon rates, but little difference was noted with respect to stage of development at time of treatment. An increase in ethephon concentration resulted in greater acidity, reduction in soluble solids and decrease in soluble solids/acid ratio at each time of application until stage III of development. The researchers concluded that the optimum time of application was near the end of stage II and beginning of stage III (Warren et al., 1973).

Experiments done in the 1960s and 1970s demonstrated that ethephon at 1.12 kg/ha applied foliarly two weeks before harvest would, on most occasions, double the anthocyanin levels in cranberries (Eck, 1972). The changes in anthocyanin levels were fully expressed 8 days after treatment. Those trials also showed that final yield was not affected by ethephon applications.

Fig. 7.6. Effect of ethephon (I) on anthocyanin content (as determined by optical density at 525 nm) of ‘Tifblue’ rabbiteye blueberry compared with non-sprayed control (E). Values are means with standard error represented by vertical bars. Mean value was significantly different from that of the control at *P<0.05 or **P<0.01 level. (Adapted from Ban et al., 2007.)
Recently, research on ‘Tifblue’ rabbiteye blueberry showed that 100 ppm of ethephon applied at the onset of first berry coloration increased anthocyanin levels by similar magnitudes to those reported in the cranberry experiments (Fig. 7.6) (Ban et al., 2007).

It has been suggested that ethephon could be useful when sprayed after large fruit is hand harvested as a means to promote more uniform ripening of the fruit left on the plant (Ban et al., 2007). Trials on ‘Bluecrop’ and ‘Stanley’ highbush blueberries by Robbins and Doughty (1984) showed that applications of 2000 ppm ethephon done immediately following first harvest increased the number of flower buds and number of flowers for the next season in ‘Bluecrop’ but not in ‘Stanley’.

Studies on the use of ethephon in blueberries were initiated nearly 30 years ago. Despite this long history of research, this management tool has not been implemented commercially. The increasing emphasis on blueberries as a source of anthocyanins and the need for greater efficiency in blueberry production might provide a new opportunity to this compound. The results presented in this section demonstrate that ethephon is capable of advancing maturity in highbush blueberry but its influence appears to be dependent on variety and of limited duration. The internal quality of the berry was also altered. The changes that ethephon cause in the acidity, pH and firmness, and the possible reduction in size, would be disadvantageous, but on the other hand, the increase in anthocyanin is a beneficial effect that might warrant further study. Since the varieties that have been studied had dissimilar behaviour, information will be needed on the response to ethephon in a greater number of cultivars including some recently released commercial varieties.

CONCLUSIONS

The application of PGRs to blueberries is an issue that has received less attention than for other fruit crops. The data available suggest there is uneven distribution of sprayed compounds within the canopy. This might lead to ineffectiveness of the PGRs applied or phytotoxicity due to overdose in certain areas of the plant. Various environmental factors (temperature, light quality and intensity, rain and relative humidity) influence the effectiveness of PGRs.

The characteristics and effects of various PGRs applied for different purposes were reviewed. The main and collateral effects, both positive and negative, were presented. It can be concluded that growth regulators can be a valuable tool in blueberry management and that their use should acquire greater importance as blueberry planting expands into areas less ideal for the crop and as the markets increase the quality standards for the fruit. Such is the case of the effect of CPPU on fruit size and ethephon on anthocyanins. The various growth regulators that have been tested to overcome deficiencies in the management of blueberries fall into three classes: (i) those that are used
commercially on a regular basis; (ii) those that show promise but will need further trials in different growing regions and with a greater diversity of plant materials; and (iii) those that have been investigated but have not produced adequate results. In the first group, the application of GA₃ for improving fruit set or to set fruit after a frost can be included. Along with this, the use of HCN for leaf development is a tool that has been adopted with adequate results in different regions, and the use of ethephon to enhance leaf development can, in most conditions, be safely adopted by growers. In the second group, the use of gibberellins, particularly GA₃, for inhibition of flowering will require further trials. A similar situation exists with the application of HCN for flower thinning. Finally, the use of CPPU for fruit enlargement, along with some collateral effects on fruit abscission, needs additional research. These applications focus on crop load regulation and fruit size, a subject that should demand greater attention from the blueberry industry in coming years. The third group includes those applications that have been tested in other species or for other purposes, but when trialled in highbush blueberries have not produced adequate results. In this group can be included fruit thinners (NAA, BA, ATS, Armothin, soybean oils and others), paclobutrazol for reducing plant size as well as ethephon for maturity enhancement.

REFERENCES


of four seedless grape selections. Journal of the American Society for Horticultural Science 117, 85–89.


INTRODUCTION

Blueberries are routinely subject to a wide array of diseases (Caruso and Ramsdell, 1995; Cline and Schilder, 2006). Probably the most widespread problems in blueberry are mummy berry (Monilinia vaccinii-corymbosi (Reade)), blueberry stunt phytoplasma, Blueberry shoestring virus (BBSSV), Blueberry shock virus (BlShV), Tomato ringspot virus (TmRSV), Blueberry scorch virus (BlScV), stem blight (Botryosphaeria spp.), stem canker (Botryosphaeria corticis Demaree and Wilcox), phytophthora root rot (Phytophthora cinnamomi Rands), phomopsis canker and twig blight (Phomopsis vaccinii Shear), botrytis (Botrytis cinerea Pers.; Fr.), alternaria fruit rot (Alternaria spp.) and anthracnose fruit rot (Colletotrichum gloeosporioides (Penz.) Penz. and Sacc.).

Most of the above diseases are widespread, although mummy berry and the virus diseases are most prevalent in areas that grow northern highbush, and stem blight, cane canker and phytophthora root rot are most common in rainy, hot climates where southern highbush are grown. Leaf spots and fungal-induced defoliation are also a problem in the south-eastern USA. Rabbit-eye blueberries have somewhat different disease susceptibilities from highbush, but can be affected by botrytis blossom and twig blight, stem blight, blueberry stunt and mummy berry, and several defoliating fungus diseases. For many of these diseases, resistant cultivars are available (Table 8.1).

Two new diseases have recently emerged in the south-eastern USA that have become widespread there, bacterial scorch (Xylella) and blueberry necrotic ring blotch. Little is known about cultivar resistance to these, but it is clear that the planting of clean stock is critical to minimizing spread.

A number of insects and arthropods do significant damage to highbush blueberries including the blueberry maggot (Rhagoletis mendax Curran), blueberry gall midge (Dasineutum oxycoecum Johnson), blueberry bud mile (Acalitus vaccinii Keller), flower thrips (Frankliniella spp.), Japanese beetle (Popillia japonica Newman), sharp-nosed leaf hopper (sten vector) (Scaphytopius magdalensis Prov.), blueberry aphid (shoestring and blueberry scorch...
Table 8.1. Reported resistance in highbush and rabbiteye cultivars to various diseases; see text for more details and references.

<table>
<thead>
<tr>
<th>Disease or pest</th>
<th>Most resistant cultivars</th>
<th>Level of resistance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alternaria fruit rot</td>
<td>NH: 'Aurora', 'Brigitta', 'Draper', 'Elliott'</td>
<td>High</td>
</tr>
<tr>
<td>Anthracnose fruit rot</td>
<td>NH: 'Aurora', 'Bluejay', 'Brigitta', 'Draper', 'Legacy', 'Toro'</td>
<td>Moderate to high</td>
</tr>
<tr>
<td>SH: 'Bluerridge', 'Sharpblue'</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>RE: 'Bluebell', 'Centurian', 'Homebell', 'Powderblue', 'Southland'</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Blueberry scorch – eastern strain</td>
<td>NH: 'Jersey'</td>
<td>High</td>
</tr>
<tr>
<td>Blueberry scorch – western strain</td>
<td>NH: see Table 8.2</td>
<td>High</td>
</tr>
<tr>
<td>Blueberry shoestring</td>
<td>NH: 'Bluecrop', 'Bluejay', 'Northland'</td>
<td>Moderate</td>
</tr>
<tr>
<td>Blueberry stunt</td>
<td>RE: 'Premier', 'Tifblue'</td>
<td>High resistance to vector</td>
</tr>
<tr>
<td>Fusicoccum canker</td>
<td>NH: 'Anna', 'Bluettia', 'Goldtraube', 'Hardyblue', 'Heerma', 'Patriot', 'Spartan'</td>
<td>High</td>
</tr>
<tr>
<td>Leaf spots</td>
<td>SH: 'Bladen', 'Reveille'</td>
<td>High</td>
</tr>
<tr>
<td>Mummy berry shoot blight</td>
<td>NH: 'Jersey', 'Duke', 'Bluejay', 'Elliott', 'Lateblue', 'Spartan'</td>
<td>Moderate to high</td>
</tr>
<tr>
<td></td>
<td>SH: 'Reveille'</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td>RE: 'Coastal', 'Delite', 'Centurion', 'Walker'</td>
<td>Moderate</td>
</tr>
<tr>
<td>Mummy berry fruit rot</td>
<td>SH: 'Bluejay', 'Brigitta', 'Rubel', 'Reka'</td>
<td>High</td>
</tr>
<tr>
<td>Necrotic ringspot</td>
<td>SH: 'Bluettia', 'Cape Fear', 'Reveille'</td>
<td>Moderate</td>
</tr>
<tr>
<td>Phomopsis twig blight and canker</td>
<td>NH: 'Bluecrop', 'Elliott', 'Bluettia', 'Rubel'</td>
<td>Moderate to high</td>
</tr>
<tr>
<td>Phytophthora root rot</td>
<td>SH: 'Emerald', 'Primadonna', 'Santa Fe', 'Springhigh'</td>
<td>High</td>
</tr>
<tr>
<td>Powdery mildew</td>
<td>NH: 'Berkeley', 'Bluecrop', 'Coville', 'Earliblue', 'Rancocas'</td>
<td>Moderate to high</td>
</tr>
<tr>
<td>Stem blight</td>
<td>NH: 'Weymouth'</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>SH: 'Cape Fear', 'Murphy', 'O'Neal', 'Springhigh', 'Santa Fe'</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td>RE - 'Premier', 'Powderblue'</td>
<td>Moderate</td>
</tr>
<tr>
<td>Stem or cane canker</td>
<td>SH: 'Croatan', 'Emerald', 'Jewel', 'Millennia', 'O'Neal', 'Primadonna', 'Reveille', 'Santa Fe', 'Sapphire', 'Schrin', 'Springhigh', 'Springwide', 'Windsor'</td>
<td>High, depending on race of fungus</td>
</tr>
<tr>
<td>Red ringspot</td>
<td>NH: 'Bluecrop', 'Jersey', 'Rubel'</td>
<td>Moderate to high</td>
</tr>
<tr>
<td></td>
<td>RE: 'Woodard'</td>
<td>High</td>
</tr>
</tbody>
</table>

^NH, northern highbush; SH, southern highbush; RE, rabbiteye.
Pests, Their Management and Resistance

virus vector) (*Illinoia pepperi* Mac. G.), cranberry fruit worm (*Acrobasis vaccinii* Riley), cherry fruit worm (*Grapholita packardi* Zell) and the plum curculio (*Conotrachelus nenuphar* Herbst).

Flower thrips, blueberry bud mite and the blueberry gall midge are particular problems in the south-eastern USA. Rabbiteye blueberries generally suffer from fewer major pests than highbush types; however, significant damage is caused by cranberry fruit worm, blueberry gall midge and blueberry bud mites in rabbiteye blueberry. The spotted-wing drosophila has become a major problem in California and the Pacific Northwest, and is becoming of industry-wide concern.

A number of weed species compete with blueberries for water, light and nutrients. Annual weeds tend to be most troublesome in new plantings. Some common annual weeds include pigweeds (*Amaranthus* spp.), common ragweed (*Ambrosia artemisifolia*), common lambsquarters (*Chenopodium album*) and various annual grasses (*Digitaria sanguinalis*, *Setaria* spp.). Perennial weeds become more troublesome as plantings age. Examples include Canada thistle (*Cirsium arvense*), field bindweed (*Convolvulus arvensis*), field horsetail (*Equisetum arvense*) and quackgrass (*Agropyron repens*), as well as woody species such as blackberry (*Rubus* spp.), poison ivy (*Toxicodendron radicans*) and Virginia creeper vine (*Parthenocissus quinquefolia*).

**MOST COMMON FUNGAL DISEASES OF HIGHBUSH AND RABBITEYE BLUEBERRY**

Primary data sources on symptoms and spread are Pritts and Hancock (1992) and Cline and Schilder (2006). Pictures of these diseases are available online (http://www.blueberries.msu.edu/diseases.html).

**Fungi primarily affecting fruit**

**Alternaria fruit rot**

Alternaria fruit rot (*Alternaria* spp.) causes a fruit rot that begins at the blossom end of the berries as sunken lesions covered by blackish, dark-green sporulations. It is the most common postharvest rot of blueberries. The fungus overwinters on old, dried-up berries and peduncles, and its spores are dispersed by wind-blown rain and splashing. Fungicides help control this disease, but the most effective methods of control are cultural, including removal of infected wood, harvesting dry fruit before they are overripe and rapid cooling after harvest. Most alternaria rot occurs at the stem scar after harvest. Hancock et al. (2008) found the most resistant northern highbush cultivars to be 'Brigitta', 'Aurora', 'Elliott' and 'Draper'.
**Anthracnose fruit rot or ripe rot**

Anthracnose fruit rot or ripe rot (*Colletotrichum acutatum*) is a widespread problem wherever blueberries are grown. As diseased fruit ripen, their blossom end softens and puckers with orange spore masses. The spores are readily transferred by rainfall and where fruit touch. The fungus overwinters on twigs, canes and on bud scales, and sporulates in the spring during bloom. Fungicide sprays are commonly used to control this disease, beginning at bloom and continued at 7- to 14-day intervals throughout the green fruit stage. Pruning can help reduce contamination by removing diseased twigs and opening the canopy. Disease levels are also reduced by the timely harvesting of ripe berries and cooling fruit immediately after harvest. Postharvest rots can be severe when fruit is not handled properly after harvest.


**Botrytis fruit rot**

Botrytis fruit rot (*B. cinerea* Pers.: Fr.) is a widespread disease in highbush and rabbiteye blueberries. Infected berries are covered by a fluffy grey mould, which develops pre- and postharvest. The fungus also causes a blossom cluster blight where flowers turn brown and are covered by a grey mould (see section on botrytis blossom and twig blight (p. 235) for more details on disease development and spread). Disease is favoured by freeze injury to flowers and cool wet weather during bloom. Effective fungicides are available. Little information is available on the resistance of northern and southern highbush blueberries to botrytis fruit rot; however, Smith *et al.* (1996) found ‘Menditoo’ and ‘Premier’ to be among the most susceptible rabbiteye cultivars, while ‘Southland’, ‘Woodard’ and ‘Tifblue’ were the most resistant.

**Mummy berry**

Mummy berry (*M. vaccinii-corymbosi* (Reade)) is probably the most common disease of highbush and rabbiteye blueberries. Infected floral inflorescences are purple-brown; whitish-grey spore masses are found on the midrib of
infected leaves and at the base of infected blossoms. Berries shrivel and turn a pinkish colour as they ripen. These 'mummy berries' fall to the ground, and mushroom-like apothecia (brown and cup-shaped) germinate the following spring and produce ascospores. The spores are discharged during wet weather and are dispersed by wind to new leaf and flower shoots. These shoots become blighted and produce conidia that are spread to open flowers by wind and insects. Fungicides are effective against this disease, with sprays being applied from bud break through bloom on a 7- to 14-day cycle. Overwintering mummies can also be eliminated by hand raking or by burying them with a 2.5 cm (1 in) layer of mulch in the autumn or winter. Dedej et al. (2004) found that honey bee hives equipped with dispensers containing the biocontrol agent, *Bacillus subtilis*, significantly reduced the amount of mummy berry disease.

Cultivars vary widely in their susceptibility to mummy berry, and there is no strong association between resistance to the shoot blight and fruit infection stages. Stretch et al. (1995) found among highbush cultivars that 'Jersey', 'Duke', 'Bluejay' and 'Elliott' were the most resistant to the shoot blight stage. Ehlenfeldt and Stretch (2000) found resistance to shoot blight to be weaker in rabbiteye than highbush, but they deemed the rabbiteyes 'Coastal', 'Delite', 'Centurion' and 'Walker' to be the least susceptible. Stretch and Ehlenfeldt (2000) found the most resistant highbush cultivars to the fruit infection stage to be 'Reka', 'Bluejay' and 'Brigitta'. Cline and Schilder (2006) suggested that 'Croatian' and 'Jersey' are highly susceptible to both phases of the disease, while 'Reveille' is quite resistant. They described 'Rubel' as being very susceptible to shoot blight, but relatively resistant to fruit infection. Wise et al. (2010) list 'Bluejay', 'Duke', 'Elliott', 'Lateblue', 'Northblue' and 'Northsky' as resistant, and 'Jersey' and 'Spartan' as moderately resistant.

**Fungi primarily affecting canes**

**Botrytis blossom and twig blight**

Botrytis blossom and twig blight (*B. cinerea*) is widespread in highbush and rabbiteye blueberries, with rabbiteye generally being more severely affected (particularly 'Tifblue'). It begins as a blossom cluster blight where flowers turn brown and are covered by a grey mould. About 1–2 weeks after blossom infection, leaves can develop irregular necrotic areas. Berries also can become infected. Infected berries are covered by a fluffy grey mould (see p. 234 for more details on botrytis fruit rot). The fungus overwinters on infected plant material, and is spread by airborne spores. Cool wet conditions favour the spread of this disease.

Protective fungicide sprays can be used to reduce botrytis infection when long periods of cool, moist weather are predicted; however, such control is often unsatisfactory (Smith, 2011). Fungicides have to be applied at the
proper stage of flower development for effective control. 'Tifblue' flowers are most susceptible when they are in full bloom (Smith, 1998). Two strategies that help reduce disease incidence are to prune off infected twigs in the winter and make sure the bush canopy is open. The use of bumble bees as vectors of the fungicidal biological control agents Prestop® \( (Gliocladium catenulatum) \) and Mycostop® \( (Streptomyces griseoviridis) \) has also been shown to be useful against blueberry blossom blight.

A limited amount of information is available on cultivar susceptibility to botrytis blossom blight. Smith (1998) determined that 'Tifblue' and 'Gulfcoast' were generally more susceptible than 'Climax' and 'Premier'. In another study, Smith (1999) determined that 'Magnolia' and 'Tifblue' were more susceptible than 'Premier', 'Climax' and 'Jubilee'. In both of these studies, susceptibility was positively associated with floral development (Smith et al., 2011). Of the three rabbiteye cultivars most often grown in North Carolina ('Powderblue', 'Premier' and 'Tifblue'), 'Powderblue' is notably more susceptible to botrytis outbreaks during bloom, and is routinely sprayed with fungicides.

Phomopsis canker and twig blight

Of phomopsis canker and twig blight \( (P.\ vaccinii\ Shear) \), phomopsis canker is most common in the cooler production regions like Michigan, while twig blight is most prevalent in hotter, moist production regions such as North Carolina. Phomopsis canker appears first on young stems as 2.5-5 cm (1-2 in) long reddish-brown areas that develop into elongated, flattened cankers that are covered by small, pimple-like pycnidia. Infected stems typically wilt and their leaves turn brown during the heat of summer. Winter injury and harvester damage offer the most common entry points for infection. In phomopsis twig blight, flower buds are infected as they open, leaving a trail of brown, dead blossoms down the fruiting shoot. The symptoms are most visible at the green fruit stage. This fungus also causes a fruit rot distinguished by very soft berries that split and leak juice, but most cultivars are resistant to this phase of the disease (unless fruit are allowed to hang too long).

\( P.\ vaccinii \) overwinters on dead twigs and canes, and splashing rain spreads the conidiospores. Fungicides can be used to control twig blight; they are usually sprayed from bud break to bloom, on a 7- to 14-day schedule. Disease spread is minimized by removal of diseased canes during the winter.

There is wide variation among highbush and rabbiteye cultivars in resistance to phomopsis canker and twig blight. Baker et al. (1985) found 'Elliott' and 'Bluettta' to be the least susceptible of nine highbush cultivars to phomopsis canker. In a screen of 50 blueberry cultivars, Polashock and Kramer (2006) found 'Northsky' and 'Chippewa' to be the most resistant to phomopsis canker. In a screen of 50 blueberry cultivars, Polashock and Kramer (2006) found by far the strongest resistance to twig blight in half-high ('Northsky' and 'Chippewa') and lowbush ('Blomidon', 'Chignecto' and 'Cumberland') cultivars. Among the rabbiteye and highbush cultivars they screened, 'Rubel' was the least susceptible and 'Emerald', 'Powderblue',}
'Legacy', 'Hannah’s Choice' and 'Duke' were the most susceptible. Cline and Schilder (2006) suggest that the highbush cultivars 'Murphy', 'Harrison' and 'Jersey' are highly susceptible to twig blight, while 'Croatan' and 'O’Neal' are moderately susceptible and 'Reveille', 'Cape Fear' and 'Bluechip' are relatively resistant. Wise et al. (2010) list 'Bluetta' and 'Elliot' as being resistant to phomopsis twig blight and canker, and 'Bluecrop' and 'Rubel' as moderately resistant.

**Fusicoccum (godronia) canker**
Fusicoccum (godronia) canker (*Fusicoccum putrefaciens*) is a serious disease in the cooler production areas. Symptoms generally appear on the lower third of 1- to 2-year-old stems, first as small, reddish areas (like a bull's-eye), which then develop into elliptical, brownish-purple lesions 2.5 to 15 cm (1 to 6 in) long. Infected canes wilt and die back. The fungus overwinters in diseased wood and new infections occur throughout the growing season whenever it rains. Wounds are not necessary for infection. To control disease spread, infected canes should be removed and destroyed, and monthly applications of fungicides made throughout the growing season.

In a survey of 31 highbush cultivars in Norway, Stromeng and Stensvand (2001) found 'Goldtraube' and 'Hardyblue' to be the most resistant cultivars, 'Ama', 'Bluetta', 'Heerma', 'Patriot' and 'Spartan' had low to moderate susceptibility, 'Berkeley', 'Bluecrop', 'Duke' and 'Ivanhoe' had moderate to high susceptibility, and 'Blueray', 'Collins', 'Earliblue' and 'Jersey' were most susceptible. Wise et al. (2010) rated 'Rancocas' as resistant in Michigan and 'Coville' and 'Rubel' as moderately resistant.

**Stem blight**
Stem blight (*Botryosphaeria* spp.) is most common in rainy, hot climates where southern highbush and rabbiteye are grown. It is the most important disease limiting establishment of blueberries in the south-eastern USA (Cline and Schilder, 2006). *Botryosphaeria dothidea*, *Botryosphaeria obtusa* and *Botryosphaeria ribis* are the species most commonly associated with stem blight. The disease enters young canes through wounds and results in the death of canes and ultimately the whole bush; young plants are most susceptible. It begins as a rapid wilt-down of leaves on individual branches and spreads downwards until the whole cane is dead. An infected stem cut longitudinally displays a light brown discoloration under the bark. Symptoms usually appear soon after harvest and get worse as the season progresses.

The fungus overwinters in dead and dying canes of a wide range of woody host plants. Spores are carried by wind and rain from infected wood throughout most of the year, except in mid-winter. The removal of diseased canes is the most effective method of reducing spread of the disease in
established plantings. It is also important to avoid droughty, sandy soils and heavy muck soils. Fungicides are of only limited value in controlling this disease.

There appears to be a wide range in resistance among blueberries to stem blight. In a survey of 50 blueberry cultivars, Polashock and Kramer (2006) found using an attached stem assay that half-high (‘Northsky’, ‘Northblue’ and ‘Chippewa’) and lowbush cultivars (‘Putte’) had much higher resistance to stem blight than highbush cultivars. ‘Weymouth’ was the most resistant highbush, while ‘Ozarkblue’, ‘Bluecrop’, ‘Duke’ and ‘Blueray’ were among the most susceptible. The rabbiteye cultivar ‘Powderblue’ was also highly susceptible. In detached stem assays conducted by Smith (2004, 2009) of mostly southern highbush and rabbiteye cultivars, ‘Bluecrisp’, ‘Brightwell’, ‘Star’, ‘Ozarkblue’, ‘Sapphire’, ‘Misty’ and ‘Emerald’ were among the most resistant, while ‘Alapaha’, ‘Austin’, ‘Legacy’, ‘O’Neal’, ‘Reveille’ and ‘Tifblue’ were highly susceptible.

Cline and Schilder (2006) indicate that some of the most susceptible southern highbush cultivars are ‘Bluechip’ and ‘Bounty’, while ‘Murphy’, ‘O’Neal’ and ‘Cape Fear’ are very resistant. They also suggest that the southern highbush cultivars ‘Croatan’, ‘Reveille’, ‘Harrison’ and ‘Bladen’, and the rabbiteyes ‘Premier’ and ‘Powderblue’, are susceptible, but losses of plants to disease are low enough (10–20%) that fields can be successfully established. In various patent descriptions, Lyrene indicates that his southern highbush releases ‘Springhigh’ and ‘Santa Fe’ have high resistance to stem blight, while ‘Emerald’ and ‘Primadonna’ are medium to high.

**Stem or cane canker**

Stem or cane canker (*B. corticis* Demaree and Wilcox) is a significant problem in rainy, hot climates where cultivated blueberries are grown. The disease attacks only young, vigorously growing shoots. Spores are released when it is wet from April to September. Disease symptoms first appear as raised, red bumps and develop over 4–6 months into cankers that are swollen and have deep cracks running through them. The most susceptible cultivars (‘Weymouth’, ‘Wolcott’ and ‘O’Neal’) can have a series of these cankers running the whole length of the stem.

Fungicides are not particularly effective in controlling this disease, making clean propagation, sanitation, maintenance of high plant vigour and the use of resistant cultivars critical. It is also highly beneficial to plant in areas isolated from infected plantations. Diseased canes should be religiously removed and extreme care taken to propagate from only healthy sources. Even visibly clean stems can be infected if taken from fields where the disease is present.

There are multiple races of stem canker. ‘Croatan’ is resistant to most of the races found in North Carolina, while ‘O’Neal’ and ‘Reveille’ are resistant
to some of them (Ballington et al., 1993). In his patent applications, Lyrene indicates that 'Emerald', 'Millennia', 'Primadonna', 'Santa Fe', 'Sapphire', 'Sebring', 'Springhigh', 'Springwide' and 'Windsor' are highly resistant to the races found in Florida. All rabbiteye cultivars are very susceptible to cane canker, although their high vigour makes them tolerant.

Fungi affecting leaves

Leaf spots
Several leaf spot diseases infect blueberries in the south-eastern USA, with the most serious being anthracnose leaf spot (Gloeosporium minus) and septoria leaf spot (Septoria albobipunctata).

Gloeosporium or anthracnose leaf spot (G. minus) is an extremely common foliar disease of blueberries in the south-eastern USA and often results in defoliation and reduced yield. Symptoms appear first as small reddish flecks of colour and develop into large brown lesions 1 to 2.5 cm in diameter (1/2 to 1 in), with a bull's-eye pattern. Stems with infected leaves eventually turn brown, then grey and die. In some cultivars such as 'Jersey', stem dieback of up to 50 cm (20 in) can occur (Cline and Schilder, 2006).

Septoria leaf spot is a widespread problem in highbush and rabbiteye blueberries across all of the south-eastern USA. Infected leaves have numerous small, purple spots from 3 to 6 mm (1/8 to 1/4 in) in diameter, with white to tan centres. Stem lesions can also be found, primarily on young plants and at the base of mature bushes. Plants can be completely defoliated by septoria leaf spot in wet years.

Some southern highbush cultivars such as 'Reveille' and 'Bladen' are resistant to these two diseases, although fungicide applications are required with most cultivars. Others, like 'Star', are quite susceptible. At least one fungicide application is generally recommended before harvest and then every two weeks until the end of summer. The common practice of summer topping of bushes also helps control these diseases (see Chapter 6) by removing older infected leaves and stimulating the growth of new, vigorous shoots.

Leaf rust
Leaf rust (Naohidemyces vaccinii, formerly Pucciniastrum vaccinii) is common in the south-eastern USA and is observed occasionally in the eastern USA, Argentina, New Zealand, Spain and Australia (Cline and Schilder, 2006). It is the primary defoliating fungus in Florida. The disease appears as reddish-brown spots on leaves that become yellow and drop prematurely. The underside of leaves have yellow and orange clusters of spores. The disease is most severe in areas where its alternative host the hemlock tree lives; however,
the disease can successfully overwinter on evergreen blueberry leaves in warm climates where there are no hemlocks. Levels of disease are generally not sufficient to warrant fungicide sprays, but in areas of heavy disease pressure fungicides can be used to help retain leaves after harvest. The northern highbush cultivars ‘Bluecrop’, ‘Collins’, ‘Earliblue’ and ‘Weymouth’ are resistant (http://www.fruit.cornell.edu/).

**Powdery mildew**

Powdery mildew (Microsphaera vaccinii) is widespread and attacks all cultivars of highbush and rabbiteye blueberries, but its overall economic impact is probably minimal. As the season progresses, small (3 to 6 mm; 1/8 to 1/4 in), irregular reddish-brown spots covered with a faint white mould appear on leaves that become somewhat distorted. In the late summer and autumn, round black fruiting bodies (0.8 to 1.6 mm; 1/32 to 1/16 in) develop in the web-like structures. These ‘cleistothecia’ are where the causal fungus overwinters. Fungicides can be used to control this disease, although the economic benefit of spraying for powdery mildew is suspect. The fungicides applied for control of fruit rots and other leaf diseases are also effective against powdery mildew. Wise *et al.* (2010) rate ‘Berkeley’, ‘Earliblue’ and ‘Rancocas’ as being resistant, and ‘Bluecrop’ and ‘Coville’ as moderately resistant.

**Fungal and bacterial diseases primarily affecting roots**

**Armillaria root rot**

Armillaria root rot (Armillaria mellea) is a common disease of woody plants all across the world. Diseased bushes are low in vigour and generally decline gradually, although they die very fast after their trunks are girdled by the disease. The most obvious symptoms are mushrooms that appear along the base of crowns and white, fan-shaped fungal growth under the bark at soil level. The disease spreads down rows as healthy roots come in contact with diseased ones. Armillaria root rot is most important where new blueberry fields are planted in old, diseased woodlots with stumps and roots, and in plantings mulched with infected wood chips. Fungicides are poor at controlling this disease; the best defence is to plant on sites without old tree stumps and roots, or to wait until they decay naturally.

**Phytophthora root rot**

Phytophthora root rot (*P. cinnamomi* Rands) is most common in rainy, hot climates where southern highbush are grown. Rabbiteye are generally more
tolerant than highbush, but are still affected; ‘Tifblue’ is one of the most tolerant. The disease is often associated with heavy soils on sites with poor drainage. Diseased bushes characteristically have reduced vigour with wilting leaves, premature yellowing and reddening of leaves, and eventually shoot dieback and defoliation. The disease is spread by zoospores that swim to root tips and invade them. The best control is to avoid soils with very poor drainage and the use of raised beds. Phytophthora root rot has been a particular problem in southern highbush grown in pine bark beds that are saturated with water.

In one study, Smith (2006) found ‘Star’, ‘Bluecrisp’, ‘O’Neal’, ‘Jewel’, ‘Jubilee’, ‘Southmoon’ and ‘Misty’ to be more vigorous in infested soil than other southern highbush cultivars. In another study by Smith (2011), ‘Southmoon’, ‘Gulfcoast’ and ‘Springhigh’ were the most vigorous in diseased soil, although no cultivar thrived. Lyrene indicates in his patent applications that ‘Emerald’, ‘Primadonna’, ‘Santa Fe’ and ‘Springhigh’ have high resistance to phytophthora root rot.

MOST COMMON BACTERIAL DISEASES OF HIGHBUSH AND RABBITEYE BLUEBERRIES

Bacterial leaf scorch
Bacterial leaf scorch (Xylella fastidiosa) was recently identified in Georgia and has the potential to become a major problem elsewhere (Brannen et al., 2007). It is caused by the same organism producing Pierce’s disease of grapes. The first symptom is a burn at the tips of leaves that resembles drought damage or fertilizer burn. The symptoms are caused by a blockage of the xylem by the bacteria and induced plant products. The scorching can start on individual stems, but eventually becomes uniformly distributed throughout the bush. Leaves eventually abscise and young stems take on a yellow colour. Stem dieback does not occur until the later stages of disease. The plant eventually dies when its leaves drop. It is likely that insect vectors transmit the bacterium, perhaps sharpshooters and spittle bugs.

Little research has been conducted on how to control the disease but it is clear that care should be taken to propagate only from Xylella-free plants. Once diseased plants are identified in the field they should be removed and destroyed. Insecticides are available that can be used against leaf hoppers, and soil-applied neonicotinoid products may also help in the spring. Among southern highbush varieties, ‘V1’ appears to be the most susceptible, although ‘Star’ and numerous other varieties readily get the disease (Brannen et al., 2007). ‘V5’ may have at least field resistance to this bacterium. It is not known how susceptible rabbiteye cultivars are.
Crown gall
Crown gall (Agrobacterium tumefaciens) enters the roots through wounds and forms tumours or galls on roots and sometimes the crown. Infected plants can be stunted. It is generally associated with diseased nursery stock. Infected plants should be removed and destroyed by burning, and grasses should be grown in diseased fields for 2–3 years before replanting.

MOST COMMON VIRAL DISEASES OF HIGHBUSH AND RABBITYE BLUEBERRY

Primary sources on symptoms and spread are Pritts and Hancock (1992), Cline and Schilder (2006) and Schilder and Miles (2008). Pictures of these diseases are available online (http://www.blueberries.msu.edu/diseases.html).

Blueberry leaf mottle
Blueberry leaf mottle (BBLMV) is locally important in Michigan and is most prevalent in the highbush cultivars ‘Jersey’ and ‘Rubel’. In ‘Rubel’, the tops of bushes are killed back by the disease and there is little renewal growth. Leaves become deformed and mottled. ‘Jersey’ bushes also have a stem dieback but it is less severe and little leaf deformity occurs, although the leaves are smaller and paler green. This disease can be confused with necrotic leafspot, as both diseases cause shoot diebacks, but leaves of mottle-diseased bushes do not have necrotic spots. The disease is spread between bushes by infected pollen, and it can take up to 3 to 4 years for symptoms to appear.

Mosaic
Mosaic (unknown virus) is found to a limited extent in most northern highbush production areas, but is considered of little concern. The causal agent is unknown but is suspected to be viral. The symptoms are bright yellow and green mottling of leaves with some red streaking. Symptoms can disappear and reappear on stems across years.

Blueberry shoestring
Blueberry shoestring (BBSSV) is most prevalent in areas that grow northern highbush. Diseased bushes have strap-like leaves that are often misshapen into twisted and crescent shapes. New stems also have narrow, elongated reddish streaks that are 0.6 to 2.5 cm (1/4 to 1 in) long (or sometimes longer). Fruit on infected canes has a reddish-purple colour; flowers can have a pink tinge or reddish streak. The disease is vectored by the blueberry aphid, I. pepperi. The disease has a 2- to 4-year latent period and symptoms
are often distributed haphazardly within the bush. Wise et al. (2010) describe 'Bluecrop', 'Bluejay' and 'Northland' as resistant. Hancock et al. (1986) found all highbush were susceptible to rub-inoculation with the shoestring virus.

**Blueberry scorch**

Blueberry scorch (B1ScV) is most prevalent on the coasts of North America, but reports have also come from Michigan, Italy and the Netherlands. In New Jersey, it is referred to as Sheep Pen Hill disease and is caused by a strain unique to the Pacific Northwest. In the most susceptible cultivars, the primary symptom is a sudden necrosis of both flowers and leaves during bloom (although a few leaves survive in the infected zone). As leaves yellow in the autumn, they can display reddish areas around their veins. The most tolerant cultivars show mild chlorosis and some distortion of new shoots, or no symptoms at all (Table 8.2). Only one or two shoots per bush show symptoms initially before the virus spreads throughout the plant. Significant yield declines and death occur over 3 to 5 years.

Scorch is vectored by aphids and spreads in a circular pattern from the original point of infection; it does not take more than a few years before all plants in a field are infected. Infected bushes should be removed and burned and insecticides applied to control the aphid vector. Cultivars show a wide range of responses to the north coast strain of B1ScV (Table 8.2), whereas 'Jersey' is the only cultivar that appears unaffected by the east coast strain (Martin, 2006).

**Table 8.2. Reaction of different highbush blueberry cultivars to the western and eastern scorch virus strains. (Adapted from Bristow et al., 2000; http://www.blueberries.msu.edu/virus.)**

<table>
<thead>
<tr>
<th>Level of reaction</th>
<th>West coast strain</th>
<th>East coast strain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower and leaf necrosis, general decline</td>
<td>'Berkeley', 'Bluejay', 'Collins', 'Darrow', 'Earliblue', 'Elliot', 'Jersey', 'Northland', 'Pemberton', 'Rubel', 'Spartan'</td>
<td>All cultivars except 'Jersey'</td>
</tr>
<tr>
<td>Marginal chlorosis and/or pale green leaves</td>
<td>'Bluecrop', 'Legacy', 'Olympia'</td>
<td>'Jersey'</td>
</tr>
</tbody>
</table>
Blueberry shock
Blueberry shock (BlShV) is generally restricted to the Pacific Northwest, with a few reports in Michigan. The primary symptom, similar to blueberry scorch, is a sudden necrosis of flowers and leaves during bloom. Unlike scorch, a second flush of leaf growth occurs that appears normal, although there are no fruit. Symptoms disappear in subsequent years and crops become normal. The virus can be spread by pollen. The rate of spread across a field varies with cultivar, but all bushes eventually become infected. The virus spreads rapidly in 'Berkeley', 'Bluegold', 'Bluetta', 'Duke', 'Earliblue' and 'Liberty', and slowly in 'Bluecrop' and 'Blueray'.

Blueberry necrotic ring blotch
Blueberry necrotic ring blotch (BNRBaV) has appeared very recently in the south-east USA. Infected plants develop irregular red or brown ring spots on the upper and lower surfaces of leaves, with or without green centres, depending on cultivar. Eventually the rings join together and cover the entire leaf surface, possibly leading to defoliation. The virus is already widespread in the south-eastern USA, and most likely has been distributed on nursery stocks. The vector for this virus is unknown at this time.

Red ringspot
Red ringspot (BRRV) is found mostly in the eastern USA. The most apparent symptoms are reddish-brown ringspots with green centres (3 to 6 mm in diameter; 1/8 to 1/4 in) on stems and red to purple spots on the upper surfaces of leaves. Fruit can also have red blotches. Mealybug is thought to be the vector of BRRV in Michigan (Schilder and Miles, 2008). Diseased bushes should be removed and destroyed.

The highbush cultivars 'Bluetta', 'Blueray', 'Coville', 'Darrow', 'Earliblue' and 'Rubel' are known to be susceptible, while 'Bluecrop' and 'Jersey' are resistant (Pritts and Hancock, 1992). The rabbiteye 'Woodard' is also likely to be resistant (Ehlenfeldt et al., 1993).

Tomato ringspot
Tomato ringspot (ToRSV) is an important disease in the north-western USA and has been found in Michigan, New York, Canada and Chile. Leaves appear malformed with small circular, necrotic spots ranging from 1.6 to 4.7 mm (1/16 to 3/16 in) in diameter. These spots are also found on young stems, and flower clusters sometimes appear deformed. Shoots gradually die back and the bushes slowly decline until death. ToRSV is spread by the dagger nematode at a rate of about 1 m per annum. The virus has a wide array of hosts, including apples, grapes and raspberries. Weeds such as
dandelion, chickweed and narrow-leaved plantain can act as hosts of ToRSV. Control consists of removing diseased bushes and fumigating before planting new fields.

**Necrotic ringspot**
Necrotic ringspot (TRSV) is found occasionally in the northern USA, Canada and Chile. It causes brown necrotic spots on older leaves (1.6 to 3.1 mm wide; 1/16 to 1/8 in); these spots can fall out, leaving ‘shot-holes’. In some highbush cultivars, leaves may also be smaller with shorter internodes, and stem dieback can occur. Diseased bushes become stunted, and gradually decline in yields over several years. The disease is spread gradually by the dagger nematode in a circular fashion. Weeds such as dandelion, chickweed and narrow-leaved plantain can act as hosts of TRSV. The highbush cultivar ‘Jersey’ is resistant, while most other cultivars are not. If diseased fields are replanted, fumigation is recommended.

**COMMON PHYTOPLASMA DISEASES OF HIGHBUSH AND RABBITEYE BLUEBERRIES**

**Blueberry stunt phytoplasma**
Blueberry stunt phytoplasma is a widespread problem in northern highbush and rabbiteye. Leaves on diseased plants are smaller and cup downwards with yellowish margins, but have veins that remain green. The disease causes a severe stunting of bushes and fruit ripen slowly, with reduced size. The sharp-nosed leaf hopper (S. magdalensis) vectors the disease. The leaf hopper overwinters in roots and stems. For control, all infected plants should be removed and destroyed, and leaf hopper activity should be monitored so that insecticides can be applied when they become active. The rabbiteye cultivars ‘Premier’ and ‘Tifblue’ are resistant to the vector (Ballington et al., 1993).

**OTHER LOCALLY IMPORTANT DISEASES OF HIGHBUSH AND RABBITEYE BLUEBERRY**

**Alternaria leaf spot**
Alternaria leaf spot (Alternaria tenuissima) is somewhat common in the southeastern USA and Argentina. The leaf spots are circular to irregular shaped, brownish-grey lesions that have red borders; they are most common on the lower leaves of bushes. The same fungus causes a twig blight in Argentina (Wright et al., 2004) and one of the most important, worldwide fruit rots (see p. 233). Fungicides are available to control this disease.
Bacterial canker
Bacterial canker (*Pseudomonas syringae*) is found primarily in the Pacific Northwest of the USA. Diseased canes have reddish-brown (to black) cankers that can extend the full length of a cane and girdle stems. The cane dies above the canker. Diseased stems should be pruned out and excessive autumn growth prevented by proper fertilization. Copper fungicides can be used in the spring and autumn to help control this disease.

Cylindrocladium rot
Cylindrocladium rot (*Calonectria illicicola*) is a pathogen sometimes important in propagation beds in the south-eastern USA. It is often called ‘peanut blight’ because the same pathogen affects groundnuts. The fungus kills softwood and hardwood cuttings in a circular fashion. There are orange, spherical fruiting bodies on the dead stems. The use of clean rooting media is the most effective preventive measure.

Neofusicoccum stem canker
Neofusicoccum stem canker (*Neofusicoccum spp.*) is a disease of growing importance in all of the blueberry production regions in Chile. Diseased plants have reddish-brown necrotic lesions that extend the full length of canes, often on only one side of the bush. Twigs above the lesions die back and the whole cane eventually succumbs. Pruning wounds are thought to be an important entry point for the disease. Fungicides probably can be used to protect wounds against the pathogen. A number of highbush and rabbiteye cultivars are known to be susceptible, including ‘Brigitta’, ‘Bluecrop’, ‘Brightwell’, ‘Duke’, ‘Elliott’, ‘Misty’ and ‘O’Neal’ (Espinoza et al., 2009). ‘Elliott’ may be the most susceptible.

Phomopsis soft rot
Phomopsis soft rot (*Phomopsis vaccinii*) is of minor importance, except on the highbush cultivar ‘Harrison’, which is no longer planted. Infected berries split open and leak juices primarily during postharvest handling. This is the same fungus that causes blueberry twig blight and cane canker, and the fungicides used to control these diseases have some efficacy against the fruit rot stage.

Pestalotiopsis cane canker
Pestalotiopsis cane canker (*Pestalotiopsis spp.* and *Truncatella angustata*) is a common problem in Chile (Espinoza et al., 2008). Diseased plants have light-brown necrotic lesions on canes that are ringed with a reddish line. Twigs
die back and eventually the whole plant collapses. Pruning wounds are a key entry point for the disease and fungicides could help control these pathogens, although recommendations have not been developed. After twig inoculations ‘Brightwell’ and ‘O’Neal’ appeared to be the most susceptible cultivars, ‘Bluecrop’ and ‘Misty’ the least susceptible, and ‘Brigitta’, ‘Duke’ and ‘Elliott’, were in the middle.

**Red leaf**
Red leaf (*Exobasidium vaccinii*) is found mostly on lowbush blueberries but occasionally appears in highbush grown in the mid-western and eastern USA. The primary symptoms are terminal leaves that pucker and turn red in mid-summer; the underside of these leaves is covered by cream-coloured layers of spores. Eventually the affected areas dry up. Infected bushes do not recover and should be destroyed. Fungicides can be used to protect healthy bushes if a high level of disease is present.

**Exobasidium fruit spot or green spot**
Exobasidium fruit spot or green spot (*Exobasidium vaccinii*) is recognized as a serious disease of blueberry fruit in the south-eastern USA on northern highbush, southern highbush and rabbiteye blueberry. Affected berries develop green unripe spots that do not ripen, producing a highly visible green or pink spot on an otherwise ripe berry. In severe cases, the crop has been rendered unharvestable and abandoned in the field.

**Witches broom**
Witches broom (*Pucciniastrium goepperti*um) is a minor disease of highbush blueberries and is usually found in northern temperate regions near fir trees. It is much more common in lowbush blueberries. Diseased plants have broom-like masses of spongy shoots with short internodes and small leaves. The most effective control measures are to plant at least 500 m from fir trees and kill diseased plants with herbicide.

**INSECT PESTS OF HILGHBUS AND RABBITEYE BLUEBERRIES**

Primary sources for this section are Pritts and Hancock (1992), Liburd and Arevalo (2006) and Isaacs (2010). Pictures of these pests are available online (http://www.blueberries.msu.edu/diseases.html).
Insect pests of flowers and fruit

Flower thrips
Flower thrips (Frankliniella bispinosa (Morgan) and Frankliniella tritici (Fitch)) are particular problems in the south-eastern USA on southern highbush and rabbiteye blueberries. These species are most active during bloom, feeding on ovaries, pollen and corollas of the flowers and resulting in reduced pollination and seed set. Their damage on fruit appears as small round necrotic areas. Chilli thrips (Scirtothrips dorsalis Hood) have recently been recorded attacking southern highbush and rabbiteye blueberries in Florida. They feed on young green tissues, leaves and fruits. Thrips belonging to the genera Frankliniella and Scirtothrips have a wide range of hosts and they travel in wind currents. They can be monitored by tapping flowers over white boards or using white sticky traps (Liburd et al., 2009). Biological control agents have been used to control thrips in other crops, but their effectiveness has not been demonstrated in blueberry (Arevalo et al., 2009). A number of biologically based pesticides are available for their control.

Blueberry maggot
Blueberry maggot (R. mendax Curran) is the most serious pest of blueberries in the eastern half of the USA. Eggs are generally laid under the skin of ripening or ripe berries, although some females oviposit into ‘full green’ fruit. Only one egg is laid per fruit and the maggot hatches 2 to 7 days later. The maggots are initially colourless and become whitish. The fruit with maggots are very soft and often have a small hole where the eggs were inserted. After feeding in the fruit for about 20 days, the larvae fall on to the ground to pupate.

The blueberry maggot overwinters in the soil under bushes for 1 to 2 years, depending how much chilling the pupae receive over the winter. The adult is a little smaller than a housefly and has a black and dark grey body; there are distinctive black bands on its wings. It also has whitish markings on its thorax and thin bands of white on its abdomen.

The blueberry maggot is commonly monitored using yellow sticky traps baited with ammonium acetate. When flies are detected, insecticides are generally applied every 7 to 10 days throughout the season to prevent egg laying. Integrated pest management programmes have also been developed where pesticide application ceases after two applications, if no additional flies are detected (Burrack and Littlejohn, 2011).

Liburd et al. (1998) evaluated 18 highbush cultivars for infestation by the blueberry maggot fly over three seasons. They found significantly lower numbers of maggots in berries of the early-ripening cultivars, ‘Earliblue’ and ‘Bluette’. Of the later ones, ‘Northland’ and ‘Herbert’ had the lowest number of maggots in their berries.
Cherry fruit worm
Cherry fruit worm (*Grapholitha packardi* Zeller) is a major pest in the mid-Atlantic and mid-western USA. Eggs are laid on to developing berries and leaves at about petal drop. The larvae enter the berries at the calyx cup and feed within them. They may move between berries but do not web them together. The larvae are initially white with black heads, and become pink with brown heads. After larval development, the larvae leave the berries and hibernate in burrows on weed stems or pruned blueberry stubs. They pupate in the early spring and emerge during bloom. The adult is a dark-grey moth with a wingspan of about 9.5 mm (3/8 in); the wings have chocolate-brown bands. Traps can be used to track emergence and the abundance of adults. Insecticide sprays are commonly applied in areas where infestations are common.

Cranberry fruit worm
Cranberry fruit worm (*A. vaccinii* Riley) is a widespread problem in the eastern half of North America. Eggs are deposited in the calyx cup of berries and, upon hatching, the larvae bore into the fruit, usually near the stem. The larvae are green with a dark head and feed on multiple berries, webbing the berries together and leaving their frass behind. The presence of the frass and webbing can be used to separate cranberry fruit worm from cherry fruit worm damage. The insect overwinters in a cocoon made of silk and soil particles; the larvae pupate in the spring. Adults are small with dark greyish-brown wings with two distinctive white patches on each forewing. Traps are used to monitor for this pest, two per acre. Pesticides are applied when the moths begin flight, and a degree-day model has recently been developed for Michigan for timing these sprays.

In a 6-year field trial of ten highbush cultivars in which infestation by cranberry fruit worm was assessed, ‘Duke’ had the highest percentage of fruit clusters with larvae in three of the six years, perhaps because it was the earliest cultivar evaluated (Van Timmeren and Isaacs, 2009). ‘Toro’, ‘Rubel’ and ‘Legacy’ had the lowest levels of infestation in two of the six years.

Cranberry weevil or blueberry blossom weevil
Cranberry weevil or blueberry blossom weevil (*Anthonomus musculus* Say) is most serious in New Jersey and Massachusetts, but is only a sporadic problem. The weevils sometimes feed on developing buds, but they are most active when inflorescences begin to open. They sometimes clip the flower pedicel, which dangles and eventually drops off the bush. Their damage also appears as tiny holes drilled into flower buds and corollas; infected flowers do not open and turn purple before falling to the ground. Leaf buds can also be attacked, completely destroying the buds or leaving small round holes in the earliest-developing leaves.
The grub is small, legless, white and C-shaped with a brown head. The adult weevil is small (1.5–2.5 mm; 1/16 to 3/32 in) and brown with whitish markings. Weevils are monitored by the beating tray method or counting the number of individual punctures in flower clusters. Control methods are required if there are more than five adults per bush or more than one puncture is found per five flower clusters (Liburd and Arevalo, 2006).

**Plum curculio**
Plum curculio (C. nenuphar Herbst) is an important pest of fruit crops that occasionally causes economic damage in blueberry, primarily in the mid-Atlantic and southern USA. The oviposition wound on the fruit is a diagnostic crescent-shaped scar that remains visible throughout the season. The larva is a white grub, 6 mm (1/4 in) long, with no legs and a brown head. It feeds on a single fruit, which may fall to the ground. The larvae leave the fruit after feeding and pupate in the ground. Early varieties are most likely to be harvested while larvae are still in the fruit; however, fruit infested with plum curculio is usually so badly damaged that the berries drop prematurely rather than getting harvested along with sound fruit.

Adults emerge in the mid-summer to autumn, and overwinter under debris. The adult is rarely seen, but can be identified as a small weevil 6 mm (1/4 in) long with a long snout. The surface of the insect is predominantly brown and wrinkled, with grey, white and black specks. The adults 'play dead' when disturbed. Traps are available to monitor plum curculio and help time insecticide sprays.

**Japanese beetle**
Japanese beetle (P. japonica Newman) is a major pest of blueberries in the eastern USA where it is an introduced pest. It is a shiny deep-green beetle, with dark-brown wing covers and an abdomen with white tufts along its sides. Damage appears as skeletonized leaves and scarred fruits. Leaf feeding is generally not a significant concern unless population numbers are extremely high; however, fruit feeding can significantly reduce quality and serve as an entry point for disease. These beetles also hang tightly on to berries and can ultimately contaminate packaged fruit.

The larvae prefer to feed on roots of grasses, and as a result are more common in sodden fields. The grubs are C-shaped, cream-coloured with brown heads and have three pairs of legs. Adults emerge in the summer as berries are beginning to ripen and are active for 6 to 12 weeks. Adults can be monitored beginning in mid-May with traps baited with pheromone, although placement of traps in crop fields can actually attract more beetles to a field.

The grubs are the most susceptible stage for control using insecticides. Removal of grassy areas in and around fields during July and August can
significantly reduce populations (Szendrei et al., 2005). Biological control agents are also available to help suppress populations such as the nematode, *Heterorhabditis bacteriophora*, and the bacteria, *Bacillus thuringiensis* (Bt) and *Bacillus popillae* (milky spore).

There may be some difference among cultivars in susceptibility to Japanese beetle damage. When Van Timmeren and Isaacs (2009) evaluated the susceptibility of ten highbush cultivars to Japanese beetle feeding in laboratory and field trials, they found ‘Brigitta’ to be the most susceptible to fruit feeding, while ‘Elliott’ and ‘Legacy’ were the least susceptible to foliage feeding.

### Insect pests of buds

#### Blueberry gall midge or cranberry tip worm

Blueberry gall midge or cranberry tip worm (*D. oxycoccana* Johnson) is a widespread pest of highbush and rabbiteye blueberries, and can become particularly problematic in the south-eastern USA (Lyrene and Payne, 1995). The adult is a tiny fly, with long legs, transparent wings and globular antennae. Larvae go through several colour changes from transparent to orange. Females lay eggs in floral and vegetative buds. Flower buds dry up and fall apart soon after infestation. Developing vegetative shoots are killed, resulting in a tip-burn that can be confused with frost damage. Mature larvae fall to the ground to pupate. There can be several generations produced each year. This pest can be monitored by examining shoots for the percentage of buds infested or by placing shoot tips into zip-locked bags and monitoring for larval emergence (Sarzynski and Liburd 2003; Yang, 2005). For control, insecticides can be sprayed during early bud development.

The rabbiteye cultivars ‘Powderblue’ and ‘Brightwell’ are highly resistant to flower bud damage; ‘Climax’, ‘Aliceblue’, ‘Beckyblue’, ‘Bonita’, ‘Tifblue’ and ‘Woodard’ are moderately susceptible and ‘Premier’ and ‘Windy’ are highly susceptible (Lyrene et al., 1995). Most southern highbush blueberry (*Vaccinium corymbosum* L.) cultivars are highly resistant to flower bud damage, although they do suffer considerable vegetative damage (Lyrene, 2007). ‘Climax’ is one of the most susceptible cultivars to vegetative bud damage; infested plants can be almost leafless in the spring.

#### Blueberry bud mite

Blueberry bud mites (*A. vaccinii* Keifer) are a particular problem in the south-eastern USA on rabbiteye and southern highbush, but are found in most blueberry production regions. The blueberry bud mite is too tiny to be seen by the naked eye, but is whitish, elongate and conical with eight legs near its head. Heavily infested buds are reddish in colour and have rough bumps
on their outer scales. As the buds open, the flowers desiccate and become distorted with distinctive red blisters (Weibelzahl and Liburd, 2010). The resulting flowers often do not set fruit and the fruit that do develop have rough skins. Bud mites do not cause the vegetative tip-burn associated with gall midge damage.

Epizootics by the acarine fungal parasite, *Hirsutella thompsonii* (Fisher), are at least partially responsible for the decline of blueberry bud mite during the summer and early autumn in the south-eastern USA (Weibelzahl and Liburd, 2009).

Timely pruning of old canes helps control this disease along with horticultural oils and miticides. In southern states, the practice of hedging (mowing) bushes after harvest significantly reduces bud mite damage the following year. Some varieties, particularly ‘Rubel’, are sensitive to the mite’s feeding; others show few symptoms. Among four highbush cultivars in the field, Isaacs and Gajek (2003) found ‘Burlington’ and ‘Rubel’ to be the most highly infested, while ‘Bluecrop’ and ‘Jersey’ were the least susceptible.

Insect pests of foliage

Blueberry aphid

Blueberry aphid (*I. pepperi* Mac. G.) is bright green and usually found on new succulent leaves and stem tips. It is of greatest importance in Michigan due to its role as a vector of BBSSV. The largest individuals can be 4 mm (1/8 in) in length. The adults give birth to live young without mating, and several generations of live-bearing females are produced each year, leading to very high densities by mid-season. Aphids overwinter as eggs on bushes. The feeding activity of the aphids produces honeydew which supports the growth of a black sooty mould. The primary economic damage of the blueberry aphid is as a vector for BBSSV. Aphids can be monitored by searching the succulent lower shoots on bushes weekly after bloom. Natural enemies usually keep aphid populations suppressed, but if fields are infected with virus or are composed of susceptible varieties, both broad-spectrum and selective insecticides are available for their control. Several species of parasitic wasps (*Praon* and *Aphidius* species) and predatory insects attack aphids and their eggs (Isaacs et al., 2008), so insecticides should be used that have lower toxicity to beneficial insects.

A wide range of densities of blueberry aphids was found on 18 northern highbush cultivars, but no immunity was identified (Hancock et al., 1982). ‘Bluejay’, ‘Northland’, ‘Bluett’ and ‘Bluehaven’ supported the lowest numbers, while ‘Spartan’, ‘Darrow’, ‘Lateblue’, ‘Coville’ and ‘Jersey’ carried the highest numbers.
Leaf rollers
Three species of leaf roller are common in the USA – red-banded (*Argyrotaenia velutinana* Walker), fruit-tree (*Archips argyrospilus* Walker) and oblique-banded (*Choristoneura rosaceana* Harris) – while the orange tortrix (*Argyrotaenia citrana*) is most common in the Pacific Northwest. The fruit-tree leaf roller adult is metallic brown with dark-brown spots on its wings. The oblique-banded leaf roller is tan with chocolate-coloured bands on its wings. The red-banded leaf roller has a complex pattern of colours on its wings including patches of brown, orange, tan and silver. The orange tortrix moth has wings that are pale yellowish-brown to grey in colour with darker mottling.

Leaf rollers construct a shelter by rolling leaves with silk and pupate within their shelters. They sometimes tie flowers and green fruit together with silk. The larvae feed on flowers and the surface of berries, although their major importance is as a contaminant of harvested blueberries. They are easily dislodged from their shelters. Natural predators normally keep leaf roller numbers in check, although chemical insecticides are an option if numbers are too high. Pheromone traps are available to determine adult emergence, and growing-degree models have been developed to predict egg hatch, larval development and optimal timing for control (Isaacs, 2010).

Sharp-nosed leaf hoppers
Sharp-nosed leaf hoppers (*S. magdalensis* Prov., *Scaphytopius acutus* and *Scaphytopius frontalis*) are widespread pests that do not cause direct injury to blueberry bushes, but they vector the protoplasma that causes blueberry stunt disease. The sharp-nosed leaf hopper overwinters in blueberry leaves on the ground as an egg. Eggs hatch in the spring and the insect goes through five sedentary nymphal instars before becoming an adult in mid-summer. The dark brownish-black adults can travel great distances. Insecticides are available for leaf hopper control and their activity periods can be tracked using yellow sticky boards.

Resistance to the vector of blueberry stunt, the sharp-nosed leaf hopper, has been found in *Vaccinium ashei* and *Vaccinium elliottii*, but not in wild or cultivated *V. corymbosum* (Meyer and Ballington, 1990). The rabbiteye cultivars ‘Premier’ and ‘Tifblue’ are resistant to the vector (Ballington et al., 1993).

White-marked tussock moth
White-marked tussock moth (*Orgyia leucostigma* (J.E. Smith)) is most common as a pest in the north-eastern USA and Canada near woodlots. Mature larvae are large (30 mm; 1 1/4 in) with distinctive coloration and hairs. They have a bright-red head with a yellowish body, a pair of upright pencil tufts of black
hairs on the prothorax, and four white to yellowish brush-like tufts of hairs on the back towards the head. The hairs can irritate the skin of the harvesting crew. Female moths lay large, hairy masses of eggs on blueberry branches. Frequent pruning and good weed management reduce the numbers of these moths, but if populations reach damaging levels, monitoring and control guidelines are now available (Isaacs and Van Timmeren, 2009).

**Other locally important insect pests of highbush and rabbiteye blueberry**

**Blueberry leaf beetle**
Blueberry leaf beetle (*Colaspis pseudoflavosa* Riley) is most commonly found in the southern USA in poorly managed fields. The adults are shiny black and 4 mm (3/16 in) long. Adults feed on leaves and skeletonize them, but they do most of their damage to younger leaves. High infestation during a cropping season can interfere with next year’s yield. After several seasons of high infestations, bushes can be killed. Insecticides can help control this insect, but well-maintained fields rarely have significant infestations.

**Blueberry span worm**
Blueberry spanworm (*Itame argillacearia* Packard) is a minor pest, most commonly found in the northern USA on lowbush blueberries. Adult blueberry spanworms have grey-brown wings; females have dark spots on the wings, while males are mostly uniform in colour. First instar larvae are tan or grey with black spots and mature larvae are yellow-orange with a line of black spots. In the early season, larvae feed on flower buds and blossoms, and then move to leaves. They feed at night and hide in leaf litter during the day. Lowbush blueberries can be monitored for this insect by sweeping the foliage with nets; insecticides are sprayed when population numbers are high.

**Citrus thrips**
*Citrus thrips* (*Scirtothrips citri* (Moulton)) have become a problem in California where blueberries are planted next to citrus. Citrus thrips feed on the new flush growth of blueberry plants, which causes stunting and likely affects yield and fruit quality. They are found in the blueberry canopy from May to early October. Regular insecticide sprays are being developed to control this insect (http://cekern.ucdavis.edu/index.cfm).

**Leaf-footed bugs**
Leaf-footed bugs (*Leptoglossus* spp.) are common in the southern USA, generally where little pesticide is being sprayed. They are usually controlled by
natural enemies. These bugs are brown, about 2 cm (4/5 in) long, and their hind legs are shaped like a leaf. They damage fruit by poking holes into them. If population numbers become problematic, insecticides can be used to control them.

**Scale**

Scale (several species) is generally found in older fields on old wood, and can reduce bush vigour. They feed on the phloem and produce honeydew that supports sooty moulds. The scales are small waxy dots, 2 to 3 mm (1/12 to 1/8 in) wide, on stems that cover a yellow insect. Population sizes are generally held in check by good pruning practices and several natural enemies.

**Spotted-wing drosophila**

Spotted-wing drosophila (SWD; *Drosophila suzukii*) is a small vinegar fly that is a new pest of blueberries, primarily in the central coast of California and the Pacific Northwest (but now reported in Florida, North Carolina and the Great Lakes region). Its spotted wings are characteristic of the species. They oviposit into intact fruit prior to harvest, and within a few days the fruit flesh starts to break down, leading to collapse of the fruit. The adult SWD lives for about 2 weeks and can lay more than 100 eggs in a day. Key factors in its control are monitoring and the timely application of insecticides with knockdown activity (Isaacs et al., 2010).

**White grub**

White grubs (*Cyclocephala longula*) have recently become a major problem in southern highbush blueberries in California (Haviland and Hernandez, 2011). They feed on plant roots, stunt plants and sometimes kill young newly planted bushes. The grubs pupate in May, and fly at dark from mid-June to mid-July; egg hatch occurs in mid-July. The nematode *H. bacteriophora* and the insecticide imidacloprid are effective in controlling the grub.

**NEMATODE PESTS OF HIGHBUSH AND RABBITEYE BLUEBERRIES**

The most common nematodes found on blueberry plants are the root-lesion (*Pratylenchus* spp.), dagger (*Xiphinema* ssp.) and stubby-root (*Pratylenchus* ssp.). The dagger nematode vectors the disease necrotic ringspot. All the nematodes are unsegmented roundworms that are almost invisible without magnification. They range in size from 2.5 mm (1/10 in – dagger nematodes) to 1 mm (1/25 in – stubby-root nematodes). Specialized laboratory procedures
are necessary for their isolation and identification. To test for nematodes, soil samples should be taken during June and July (Pritts and Hancock, 1992).

The impact of nematodes in established plantings is not generally thought to be great; however, high nematode populations likely slow the growth of new plantings. It is not known what nematode levels cause economic damage, but pre-plant fumigation is recommended in the late summer or early autumn the year before planting.

MOST COMMON WEEDS OF Highbush AND RABBIT-EYE BLUEBERRY FIELDS

Pictures of the most serious weed problems of blueberries are available online (http://www.blueberries.msu.edu/diseases.html).

There are numerous weeds regularly found in blueberry fields (Table 8.3). Weeds can be divided into three groups: (i) annuals, which live less than 1 year; (ii) biennials, which live up to 2 years; and (iii) perennials, which live more than 2 years. Within these broad categories are grasses (monocots), broadleaf plants (dicots), sedges and horsetails. There are both herbaceous and woody perennials.

<table>
<thead>
<tr>
<th>Type</th>
<th>Common name</th>
<th>Scientific name</th>
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<tbody>
<tr>
<td>Annual broadleaves</td>
<td>Annual sow thistle</td>
<td>Sonchus oleraceus</td>
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<tr>
<td></td>
<td>Barnyard grass</td>
<td>Echinochloa crus-galli</td>
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<td></td>
<td>Black nightshade</td>
<td>Solanum ptycanthum</td>
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<td></td>
<td>Chickweed</td>
<td>Stellaria media</td>
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<td></td>
<td>Cocklebur</td>
<td>Xanthium strumarium</td>
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<td></td>
<td>Fall panicum</td>
<td>Panicum dichotomillorum</td>
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<td></td>
<td>Galinsoga</td>
<td>Galinsoga quadriradiata</td>
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<td></td>
<td>Giant foxtail</td>
<td>Setaria faberi</td>
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<td></td>
<td>Jimsonweed</td>
<td>Datura stramonium</td>
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<td></td>
<td>Lambsquarter</td>
<td>Chenopodium album</td>
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<td></td>
<td>Pigweed</td>
<td>Amaranthus spp.</td>
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<td></td>
<td>Purslane</td>
<td>Portulaca oleracea</td>
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<td>Ragweed</td>
<td>Ambrosia artemisiifolia</td>
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<td></td>
<td>Shepherd's purse</td>
<td>Capsella bursa-pastoris</td>
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<td></td>
<td>Smooth hawksbeard</td>
<td>Crepis capillaris</td>
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<td></td>
<td>Velvetleaf</td>
<td>Abutilon theophrastii</td>
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<tr>
<td>Biennial broadleaves</td>
<td>Bull thistle</td>
<td>Cirsium vulgare</td>
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<tr>
<td>Perennial broadleaves</td>
<td>Bindweed, field</td>
<td>Convolvulus arvensis</td>
</tr>
<tr>
<td>Type</td>
<td>Common name</td>
<td>Scientific name</td>
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<tr>
<td>Perennial grasses</td>
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<td></td>
<td>Bindweed, hedge</td>
<td><em>Calystegia sepium</em></td>
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<td></td>
<td>Bittersweet, oriental</td>
<td><em>Celastrus orbiculatus</em></td>
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<td></td>
<td>Canada thistle</td>
<td><em>Cirsium arvense</em></td>
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<td></td>
<td>Cinquefoil</td>
<td><em>Potentilla spp.</em></td>
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<td></td>
<td>Common catsear</td>
<td><em>Hypochaeris radicata</em></td>
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<td></td>
<td>Crabgrass</td>
<td><em>Trifolium repens</em></td>
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<td></td>
<td>Creeping buttercup</td>
<td><em>Ranunculus repens</em></td>
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<td></td>
<td>Dandelion</td>
<td><em>Taraxacum officinale</em></td>
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<td></td>
<td>Dock</td>
<td><em>Rumex crispus</em></td>
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<td></td>
<td>Goldenrod</td>
<td><em>Solidago canadensis</em></td>
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<td></td>
<td>Hemp dogbane</td>
<td><em>Apocynum cannabinum</em></td>
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<td>Horse nettle</td>
<td><em>Solanum carolinense</em></td>
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<td></td>
<td>Marestail</td>
<td><em>Coryza canadensis</em></td>
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<td></td>
<td>Milkweed, common</td>
<td><em>Asclepias syriaca</em></td>
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<td></td>
<td>Nightshade, bitter</td>
<td><em>Solanum dulcamara</em></td>
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<td></td>
<td>Pokeweed</td>
<td><em>Phytolacca americana</em></td>
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<td>Red sorrel</td>
<td><em>Rumex acetosella</em></td>
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<td></td>
<td>Smartweed</td>
<td><em>Polygonon pensylvanicum</em></td>
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<td>Smilax (greenbriar)</td>
<td><em>Smilax spp.</em></td>
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<td></td>
<td>Stinging nettle</td>
<td><em>Urtica dioica</em></td>
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<td></td>
<td>Trumpet creeper</td>
<td><em>Campsis radicans</em></td>
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<td></td>
<td>Virginia creeper</td>
<td><em>Pathenocissus quinquefolia</em></td>
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<td></td>
<td>White clover</td>
<td><em>Trifolium repens</em></td>
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<td></td>
<td>White heath aster</td>
<td><em>Aster pilosus</em></td>
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<td>Woody perennials</td>
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<tr>
<td></td>
<td>Blackberry</td>
<td><em>Rubus spp.</em></td>
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<td></td>
<td>Dewberry</td>
<td><em>Rubus spp.</em></td>
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<tr>
<td></td>
<td>Elderberry</td>
<td><em>Sambucus canadensis</em></td>
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<tr>
<td></td>
<td>Grapevine</td>
<td><em>Vitus spp.</em></td>
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<tr>
<td></td>
<td>Himalayan blackberry</td>
<td><em>Rubus discolor</em></td>
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<tr>
<td></td>
<td>Poison ivy</td>
<td><em>Toxicodendron radicans</em></td>
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<td></td>
<td>Sassafras</td>
<td><em>Sassafras albidum</em></td>
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<td></td>
<td>Sumac</td>
<td><em>Rhus spp.</em></td>
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<tr>
<td>Other</td>
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<td></td>
<td>Horsetail</td>
<td><em>Equisetum arvense</em></td>
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<tr>
<td></td>
<td>Yellow nutsedge</td>
<td><em>Cyperus esculentus</em></td>
</tr>
</tbody>
</table>
There are two types of annuals: (i) cool season (or winter) annuals that germinate in late summer or autumn, are dormant during the winter, flower in spring or early summer and then die (e.g. chickweed); and (ii) warm season (or summer) annuals that germinate during spring or summer, flower and then die at the end of that growing season (e.g. crabgrass and foxtail). Biennials remain in a vegetative stage during the first season and after the winter, they bolt, flower, set seed and then die (e.g. wild carrot and bull thistle). Perennial weeds live for many seasons and flower more than once. Their perennial structures (rhizomes, stolons, crowns, entire plants, nutlets and/or roots) survive from year to year (e.g. nutsedge, quackgrass, dandelion and dewberry). Sedges are perennial and while they look superficially like grasses, they belong to the family Cyperaceae rather than Poaceae, and have stems with three vertical rows. Horsetails are not flowering plants. They belong to the ancient family Equisetum and reproduce asexually via spores.

Management of weeds in blueberries is important for a number of reasons: (i) they compete with plants for water, nutrients and light; (ii) some serve as alternative hosts for insects and diseases; (iii) weeds growing close to blueberries reduce air flow which can favour fungal growth and harbour insects; (v) they provide habitat for vertebrate pests such as voles; (vi) they can compete for pollinators during bloom; and (vii) some produce fruit that can contaminate harvested blueberries.

Probably the most important weed management strategy is to eliminate all perennial weeds before planting. Once perennial weeds become established in a blueberry field, they become extremely difficult to remove. The key to perennial weed control is to eliminate them as much as possible during the year prior to planting, using a combination of cultivation and herbicide application (before they go to seed!). Growing rye or other cover crops for one or two years prior to planting blueberries will also reduce the number of weeds.

Weeds can be controlled by cultivation, mulching and herbicide sprays (Majek, 2006; Wise et al., 2010). Shallow cultivation can be used to control weeds in the row middles, although perennial grass sods such as tall or hard fescue are often planted instead to suppress weeds. Fabric weed barriers are often used to control weeds in the first few years after planting. Mulches are commonly employed within the rows to smother emerging weeds and prevent germination. Heavy mulches such as sawdust or wood chips are applied annually at depths of 7.5 to 10 cm. Straw mulches are not used, as they decompose quickly and provide favourable environments for field mice and voles. Perennial ryegrass is sometimes planted within rows for weed suppression.

The herbicides employed and their time of application depend on the weed species present. Some pre-emergence herbicides are used in the spring before the weed seeds germinate; other post-emergence ones are used in the middle and latter part of the season. Pre-emergence herbicides are applied to the soil surface, and rainfall or irrigation is necessary to move the herbicide into the
soil. Post-emergence herbicides kill weeds through the leaves and must be carefully applied to avoid contact with the blueberry. They work best when the weeds are actively growing, and most need a rain-free period of at least 1 to 8 h after application to do their work. Some post-emergence herbicides kill only the tissues that come in contact with them (e.g. paraquat), while others are translocated in the plant (e.g. glyphosate).

It is critical that established fields are scouted regularly during the season to remove perennial weeds before they become established. It is also important to avoid using single herbicides repeatedly, as it can lead to an increase in resistant weeds. Specific herbicide recommendations can be found on local extension web sites (e.g. http://edis.ifas.ufl.edu/wg016, http://whatcom.wsu.edu/ipm/manual/blue/weed-management.html and http://www.blueberries.msu.edu/).

REFERENCES


Chapter 8


Szendrei, Z., Mallampalli, N. and Isaacs, R. (2005) Effect of tillage on abundance of


APPENDIX 8.1 SYMPTOMS OF MAJOR BLUEBERRY DISEASES

**Fruit rots**

Fruit have sunken lesions at the blossom end that are covered by dark, greenish-black masses of spores; widespread problem – alternaria fruit rot

Fruit have sunken lesions at the blossom end that are covered with orange spore masses; widespread problem – anthracnose fruit rot

Fruit shrivel and turn a pinkish colour as they ripen; widespread problem – mummy berry

Fruit are covered by a fluffy grey mould; widespread problem – botrytis fruit rot

**Spring shoot blights**

Infected floral inflorescences are purple-brown; whitish-grey spore masses are found on the midrib of infected leaves and at the base of infected blossoms; widespread problem – mummy berry

Flowers turn brown and are covered by a grey mould; stems initially are not affected, later becoming dark brown or black, noticeably darker than phomopsis twig blight; widespread problem – botrytis blossom and twig blight
Trail of brown, dead blossoms and leaves along the fruiting shoot, all leaves are dead in infected zone, wood around bud is brown and necrotic; most common in hotter, moister production regions – phomopsis twig blight

Sudden, complete necrosis of both flowers and leaves during bloom; some leaves are still alive in the infected zone; no fungal masses; most prevalent on the coasts of North America, but reports have also come from Michigan, Italy and the Netherlands – blueberry scorch

Sudden, complete necrosis of flowers and leaves during bloom; some leaves are alive in infected zone; no fungal masses; second flush of leaf growth occurs that appears normal; generally restricted to the Pacific Northwest but also reports from Michigan – blueberry shock

**Cane diebacks/reduced bush vigour**

Dead canes have elongated, flattened cankers that are covered by small, pimple-like pycnidia; most common in cooler production regions – phomopsis canker

Lower third of 1- to 2-year-old stems have small, reddish areas (like a bull’s-eye) that develop into elliptical, brownish-purple lesions 2.5 to 15 cm (1 to 6 in) long; most common in the coolest production regions – fusicoccum canker

No apparent canker but infected, dying stems show a pecan-brown discoloration under the bark; widespread problem in highbush and rabbiteye in rainy, hot climates – stem blight

Raised, red bumps appear and develop over 4 to 6 months into cankers that are swollen, with deep cracks running through them; most common in rainy, hot climates – stem canker

Bushes have reduced vigour with wilting leaves that prematurely yellow and redden; most common in hot, moist climates where southern highbush are grown – phytophthora root rot

Bushes are low in vigour and have mushrooms at the base of crowns, as well as fan-shaped fungal growth under the bark at soil level; locally important worldwide in replanted woodlots – armillaria root rot

Extensive dieback of stems and little or no crop; leaves appear malformed with small circular, necrotic spots ranging from 1.5 to 4.5 mm (1/16 to 3/16 in) in diameter; spots are also found on young stems and flower clusters sometimes appear deformed; most important in the north-western USA and found in Michigan, New York, Canada and Chile – tomato ringspot

Extensive dieback of stems and little or no crop; leaves have brown necrotic spots on older leaves 1.5 to 3 mm (1/16 to 1/8 in) wide that fall out, leaving
‘shot-holes’: locally important in the northern USA, Canada and Chile – necrotic ringspot

Extensive dieback of stems and little or no crop; leaves are reduced in size, cup downward with yellowish margins, but have veins that remain green; widespread problem in northern highbush and rabbiteye – blueberry stunt

Leaves abscise and young stems take on a yellow colour; earlier symptoms are a leaf burn that first appears on individual stems, but eventually effects all canes; stem dieback does not occur until the later stages of disease – bacterial leaf scorch

**Leaf discolorations and distortions**

Irregular reddish-brown spots on leaves that are covered with a faint white mould; infected leaves are somewhat distorted; common worldwide problem – powdery mildew

Reddish-brown spots on leaves that become yellow and drop prematurely; the underside of leaves have yellow and orange spores associated with the lesions; whole plant can be defoliated; common in the south-eastern USA and found in the eastern USA, Argentina, Spain and Australia – leaf rust

Small reddish flecks of colour appear initially and develop into large brown lesions 1.25 to 25 mm (1/2 to 1 in) in diameter, with a bull’s-eye pattern; whole plant can be defoliated; widespread problem in the south-eastern USA – gleosporium or anthracnose leaf spot

Numerous small, purple spots, 1.5 to 4.5 mm (1/8 to 1/4 in) in diameter, on leaves that have white to tan centres; whole plant can be defoliated; widespread problem in the south-eastern USA – septoria leaf spot

Leaves are strap-like and often misshapen into twisted and crescent shapes; new stems have narrow reddish streaks; most important in Michigan but found elsewhere in northern highbush – blueberry shoestring

Leaves appear malformed with small circular, necrotic spots ranging from 1.6 to 4.7 mm (1/16 to 3/16 in) in diameter; spots are also found on young stems, and flower clusters sometimes appear deformed; leads to extensive shoot dieback; most important in the north-western USA, but found elsewhere in highbush blueberries – tomato ringspot

Leaves have brown necrotic spots on older leaves 1 to 3 mm (1/16 to 1/8 in) wide that fall out, leaving ‘shot-holes’; leaves may become rosetted and stem dieback can occur; leads to extensive shoot dieback; occasionally found in the northern USA, Canada and Chile – necrotic ringspot

Reddish-brown ring spots 3 to 6 mm (1/8 to 1/4 in) in diameter on stems and red to purple spots on the upper surfaces of leaves; most common in eastern USA – red ringspot
Irregular red or brown ring spots on the upper and lower surfaces of leaves, with or without green centres; rings can join together and cover the entire leaf surface leading to defoliation; widespread in south-eastern USA – blueberry necrotic ring blotch

Leaves are mottled and often malformed; leaves can be strap-like or rosetted; most important in Michigan – blueberry leaf mottle

Bright yellow and green mottling of leaves with some red streaking; found to a limited extent in most northern highbush production areas – mosaic

Leaves are reduced in size, cup downward with yellowish margins, but have veins that remain green; leads to extensive shoot dieback; widespread problem in northern highbush and rabbiteye – blueberry stunt

Leaves have a scorching at their tips, resembling drought or fertilizer burn; the scorching starts on individual stems, but eventually becomes uniformly distributed throughout the bush; leaves eventually abscise and young stems take on a yellow colour – bacterial leaf scorch

**APPENDIX 8.2 CHARACTERISTIC SYMPTOMS OF BLUEBERRY PEST DAMAGE**

**Flowers**

Brown feeding damage on corollas and ovaries by tiny insects; reduced pollination and fruit set; most important in the eastern USA – flower thrips

Flower pedicels are clipped and dangling; tiny holes are drilled into flower buds and corollas; adult weevil is small, 1.5–2.5 mm (1/16 to 3/32 in), with a pronounced snout and brown with whitish markings; sporadic problem in mostly New Jersey and Massachusetts – cranberry weevil

**Fruit**

Larvae begin colourless and turn to whitish; no webbing attached to fruit; adult fly has distinctive black bands on its wings; the most serious pest of blueberries in the eastern half of the USA – blueberry maggot

Larvae enter berries at the calyx cup; they are initially white with black heads and become pink with brown heads; no webbing attached to fruit; adult is a dark-grey moth with chocolate-brown markings; major pest in the mid-Atlantic and mid-western USA – cherry fruit worm

Fruit have a diagnostic crescent-shaped scar where the eggs were laid; no webbing attached to fruit; larva is a white grub, 6 mm (1/4 in) long, with no
legs and a brown head; adult is a small weevil with a long snout; primarily a problem in the southern USA – plum curculio

Larvae bore into the fruit near the stem; they are green with a dark head and feed on multiple berries; berries are webbed together and covered with frass; adults have dark, greyish-brown wings and two white markings on each forewing; widespread problem in the eastern half of North America – cranberry fruit worm

Fruit collapse due to the feeding of small white maggots; primarily in the central coast of California and the Pacific Northwest (but now reported in Florida, North Carolina and the Great Lakes region) – spotted-wing drosophila

**Leaves and buds**

Leaves are skeletonized and covered with clusters of shiny, deep-green beetles with dark-brown wing covers and abdomens with white tufts along their sides; major pest of blueberries in the eastern USA – Japanese beetle

Flower buds dry up and disintegrate; terminal vegetative buds are killed and blacken, or produce very short shoots with only a few highly distorted leaves; southern highbush plants in the south-eastern USA may be almost leafless in the spring; a widespread pest of highbush and rabbiteye blueberries, particularly in the south-eastern USA – blueberry gall midge

Heavily infested flower buds are reddish in colour and have rough bumps on their outer scales; they desiccate and produce distorted flowers with distinctive red blisters; vegetative buds are not attacked; more of a problem in the south-eastern USA on rabbiteye and southern highbush, but widely distributed – blueberry bud mite

Young leaves and succulent new stems are covered with small, bright-green aphids; feeding activity produces honeydew which supports the growth of a black sooty mould; vector of blueberry shoestring virus; of greatest importance in Michigan – blueberry aphid

Leaves are rolled together with silk; flowers and green fruit can also be tied together with silk; common problem in eastern and north-western USA – leaf rollers

Leaves show feeding damage; very distinctive larvae are present that have a bright-red head, a yellowish body, and tufts of hairs that project out from the head and line both sides of the body; the hairs can irritate the skin; female moths lay large, hairy masses of eggs on blueberry branches; most common as a pest in the north-eastern USA and Canada near woodlots – white-marked tussock moth
INTRODUCTION

About two-thirds of the highbush blueberry world production is marketed as fresh fruit, and the consumption of blueberries has doubled in the last 12 years. This expansion was triggered, at least in part, by the discovery in the 1990s that blueberries are one of the fruit species with highest antioxidant content (Prior et al., 1998). Antioxidants have been found to generate diverse positive impacts on human health and the highest benefits are obtained by the consumption of fresh fruit. Consequently, the concept of quality in blueberries has changed to include not only size, sugar (soluble solids, SS), acids (titratable acidity, TA) and firmness, but also the concentration of antioxidants.

The growth in demand for fresh blueberry fruit has not only required greater production of fruit during the summer, but also year-round supply from the southern hemisphere. To meet this demand, the postharvest life of the fresh fruit has had to be expanded from days to weeks. Numerous management practices have a marked effect on the quality and postharvest life of the fruit, from site selection to the choosing of varieties and the types of cultural practices. In this chapter we define the attributes of fruit quality, followed by an analysis of the factors that affect quality before harvest. At the end of the chapter, we describe the main factors that influence the postharvest life of the fruit and the approaches that can be used to maintain fruit quality, with a focus on the fresh market.

FRUIT MATURATION AND QUALITY

Maturity at harvest is the most important factor that determines fruit quality and postharvest life. The quality of blueberry fruit cannot be improved after it is picked; therefore, it is important to harvest the fruit when its development is optimum for handling and consumption. Generally, fruit develop the highest sugar and most intense flavours if allowed to ripen fully on the plant (Beaudry,
Blueberries generally ripen rapidly on the plant, usually going from 50% pink to fully blue in 2–3 days, and then require only several more days to develop full flavour and sweetness (Forney, 2009). As a rule, immature fruit are more subject during handling and storage to dehydration and bruising, and present inferior quality when they turn blue. On the other hand, overripe fruit are likely to become soft and mealy soon after harvest, with an insipid flavour, and they are more prone to decay. Woodruff et al. (1960) showed that less mature highbush blueberries have a greater storage potential than more mature fruit. Thus, any fruit picked too early or too late is more susceptible to physiological disorders and will have a shorter postharvest life than fruit harvested at proper maturity (Kader, 1999). As shown below, the optimal time to pick blueberries is at most a few days after they turn blue.

**MEASURING FRUIT QUALITY**

Quality is defined as the degree of excellence or superiority in a combination of attributes, properties or characteristics that give each commodity value in terms of human food (Kader, 1999). The relative importance of each quality component depends upon the commodity and its intended use (e.g. fresh or processed) and varies among producers, retailers and consumers. To the producers, it is important that a certain commodity has high yield, is easy and cheap to harvest, and must withstand in good condition long-distance shipping to markets. Appearance, quality, firmness, uniformity, susceptibility to decay and shelf-life are important to wholesale and retail marketers.

In general, consumers’ initial purchase is based on fruit appearance (including freshness) and firmness (texture). However, subsequent purchases are dependent upon the consumer’s satisfaction given mainly by flavour and quality, which are related to the fruit’s soluble solids (mainly sugars), titratable acidity (organic acids), sugar/acid ratio, flesh firmness and nutritional quality (Kader, 1999). Beaudry (1992) suggested the following overall set of quality standards for blueberries (Table 9.1).

**Table 9.1.** Recommended quality standards for blueberry fruit. (Adapted from Beaudry, 1992.)

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Level or range</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>2.25 to 4.25&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Acidity (primarily citric acid)</td>
<td>0.3 to 1.3% w/w</td>
</tr>
<tr>
<td>Soluble solids</td>
<td>&gt;10% w/w</td>
</tr>
<tr>
<td>Sugar/acid ratio</td>
<td>10 to 33</td>
</tr>
<tr>
<td>Firmness</td>
<td>&gt;70 g for a 1 mm deformation</td>
</tr>
<tr>
<td>Size</td>
<td>&gt;10 mm</td>
</tr>
<tr>
<td>Colour</td>
<td>Blue, &lt;0.5% w/w anthocyanin</td>
</tr>
</tbody>
</table>

<sup>a</sup>Perkins-Veazie et al. (1995) established a pH level of <3.5.
Saftner et al. (2008) developed different groups of visual, textural and flavour-related quality parameters in a sensory evaluation of ten highbush and two rabbiteye blueberries. Visual quality comprised appearance, blue colour and fruit size. Textural quality included bursting energy, skin toughness, texture during chewing and juiciness. Finally, flavour-related quality was broken down into sweetness, tartness, sweet/tart balance, blueberry flavour and overall eating quality. According to Beaudry (1992), the eating texture of the blueberry is affected by a number of factors including skin thickness, pulp firmness and presence of stone cells.

Flavour-related characteristics better predict consumer preferences for overall quality than the other parameters (Saftner et al., 2008), although textural and visual characteristics also contribute. In general, cultivars with lower compression firmness had low sensory scores for bursting energy and texture during chewing. For the 12 cultivars used in the study, overall eating quality was most highly correlated with flavour acceptability ($r = 0.87$) and blueberry-like flavour intensity ($r = 0.85$). Within the range of fruit size and colour evaluated, their results indicate that fruit size is a better indicator of sensory visual quality than the acceptability and intensity of fruit colour. In a 3-year study that evaluated southern highbush blueberry varieties for quality attributes that included both instrumental analyses and sensory evaluation, Bremer et al. (2008) concluded that blueberries with very low titratable acidity (0.3% w/w), despite high soluble solids concentrations between 10 and 12% w/w, were not acceptable to consumers.

Fruit quality is commonly established by instrumental assessment of each characteristic of the fruit (size, colour, soluble solids, pH and acidity), as well as sensory evaluation including taste panels. However, there are some drawbacks in measuring individual quality parameters. The methods often require sample preparation, are destructive, time-consuming and expensive, and generally focus on only a few aspects of fruit quality. Particular care must also be taken to analyse samples under the same conditions. For example, when fruit temperature (4.4 to 38°C) was studied for its effect on firmness readings independent of maturity stage, the firmness of berries decreased when they were warmed and increased when they were cooled (16% difference between the extreme temperatures). There is also inherent variability among plants in a field and within each bush, and sample collection may not appropriately estimate the population of fruit within a field.

Systems have been developed to measure simultaneously a number of fruit maturity variables. Guidetti et al. (2009) used visible–near infrared spectroscopy (Vis-NIR; 450–980 nm) to evaluate correlations between soluble solids, firmness, ascorbic acid and total content of anthocyanins and polyphenols from fresh and homogenized samples of ‘Brigitta’ and ‘Duke’ highbush blueberries. Correlation coefficients between Vis-NIR predicted values and instrumental levels ranged from 0.80 and 0.92 for predictive models that were established using fresh samples. The highest correlations between
predicted and instrumental values were for flavonoid and anthocyanin contents
\((r>0.90)\), while for fresh samples the highest correlations were for anthocyanin
content in ‘Duke’ and soluble solids and firmness in ‘Brigitta’.

Studies using Vis-NIR for evaluating the impact of artificially induced
changes in source–sink relationships (through leaf girdling and leaf plucking)
on the maturation of intact fruit of southern highbush blueberry showed that
Vis-NIR, in conjunction with statistical methods, was able to detect changes
in pigmentation, soluble solids, water and reflective index (Mowat and Poole,
1998). After studying the use of NIR (750–2500 nm) and mid-infrared (MIR;
4000–400 cm\(^{-1}\)) spectroscopy in highbush varieties ‘Brigitta’ and ‘Duke’,
Sinelli \textit{et al.} (2008) concluded that ascorbic acid concentrations could not be
adequately assessed through NIR nor MIR. However, both NIR and MIR were
adequate for estimating soluble solids concentrations. Besides, NIR models
adequately predicted total content of phenols, flavonoids and anthocyanins.

Alterations in volatiles assessed by gas chromatography–mass spec-
trometry (GS–MS) have been used to detect and discriminate among diseases
of several crops. An electronic nose (E-nose) is an array of electronic gas
sensors tuned to a cross-section of volatiles that is capable of indirectly
measuring volatiles emanating from the fruit. This technique was applied
successfully to detect the presence and differentiate among three postharvest
diseases (\textit{Botrytis cinerea}, \textit{Colletotrichum gloeosporioides} and \textit{Alternaria spp.}) of
‘Brightwell’ rabbiteye blueberries with 90% overall correct classification (Li \textit{et
al.}, 2010).

**INDIVIDUAL FACTORS INFLUENCING FRUIT QUALITY**

**Fruit size**

Large fruit are easier and cheaper to harvest (Strik \textit{et al.}, 2003) and have
greater consumer appeal than small fruit. Saftner \textit{et al.} (2008) found that
individual fruit weight values were highly correlated with scores for panel
acceptability of size \((r=0.67)\), appearance \((r=0.62)\) and overall eating quality
\((r=0.47)\). These results indicate that larger berries are preferred for fresh
consumption.

**Weight loss**

The maximum weight loss that can occur during storage before blueberries
become unsalable has been estimated to be 5–8\% (Sanford \textit{et al.}, 1991).
Machine-harvested rabbiteye blueberries stored at 3°C had a weight loss of
0.2\% per week, which was about double the rate of change in weight loss of
hand-harvested fruit. When Perkins-Veazie \textit{et al.} (1995) evaluated eight
southern highbush blueberry clones (plus the northern highbush 'Bluecrop' and rabbiteye 'Climax'), the weight loss after 21 days of storage at 5°C ranged from 3.6% (in clone ‘A109’) to 6.6 or 6.7% (in ‘Gulfcoast’ and ‘Climax’). Miller et al. (1993) showed a marked effect of packing material on weight loss of ‘Sharpblue’ southern highbush blueberry. After 3 weeks at 1°C plus 2 days at 16°C, fruit packed manually in fibre-pulp cups had significantly higher weight loss than those packed automatically in polystyrene cups (7.4 versus 1.0%). In controlled atmosphere storage, Alsmairat et al. (2011) found that moisture loss was only 0.6 to 2.3% over an 8-week storage period and it was dependent upon cultivar and storage atmosphere.

**Aroma**

Blueberries do not have as strong a characteristic aroma as do strawberries and apples. However, over a hundred volatile compounds have been identified in highbush blueberries, including low-molecular-weight esters, alcohols, aldehydes, acylc terpenes and cyclic terpenes (Hirvi and Honkanen, 1983). As fruit ripen, the concentration of aroma volatiles increases rapidly, closely following pigment formation. Several volatiles are common to highbush and rabbiteye blueberries, as well as bilberry (Vaccinium myrtillus).

In a study on instrumental and sensory quality characteristics of rabbiteye and highbush blueberries, Saftner et al. (2008) found that total aromatic volatile concentrations (Table 9.2) were not correlated with sensory scores for flavour, overall eating quality or with any other sensory characteristic. Thus volatile concentration, at least when analysed using the procedures and technique (solid-phase microextraction, SPME) employed in that study, was not a good indicator of blueberry taste or overall eating quality.

**Scar**

The size and wetness of the scar is a very important attribute in blueberries, as it is considered to be the principal point of entry of microorganisms and is associated with about 90% of fruit decay (Cappellini and Ceponis, 1977). Blueberries do not present an abscission zone and final fruit separation from the pedicel is brought about by mechanical rupture of the vascular system and the epidermis. As a consequence, when fruit is removed from the plant at harvest, there is a wound in both the vascular tissue and epidermis (Gough and Litke, 1980).

The scar size is to a large extent a genetically controlled trait; therefore, a dry and small scar is a highly desirable characteristic in a cultivar. The stem scar diameter varied as much as 50% among eight clones of southern highbush blueberries (range from 1.46 mm in ‘A109’ to 2.20 mm in ‘MS108’).
Table 9.2. Surface colour (L, a and b), fruit weight in fresh fruit and aromatic volatile concentration of blueberry extracts from ten highbush and two rabbiteye blueberry varieties (‘Coastal’ and ‘Montgomery’) listed by harvesting season. (Adapted from Saftner et al., 2008.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Surface colour</th>
<th>Aromatic volatile concentration (pA)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L</td>
<td>a</td>
</tr>
<tr>
<td>‘Chanticleer’</td>
<td>24.52</td>
<td>-0.09</td>
</tr>
<tr>
<td>‘Duke’</td>
<td>27.21</td>
<td>-0.13</td>
</tr>
<tr>
<td>‘Hannah’s Choice’</td>
<td>26.28</td>
<td>-0.03</td>
</tr>
<tr>
<td>‘Weymouth’</td>
<td>21.94</td>
<td>-0.04</td>
</tr>
<tr>
<td>‘Berkeley’</td>
<td>30.84</td>
<td>-0.70</td>
</tr>
<tr>
<td>‘Bluecrop’</td>
<td>27.33</td>
<td>0.09</td>
</tr>
<tr>
<td>‘Blugold’</td>
<td>30.12</td>
<td>-0.66</td>
</tr>
<tr>
<td>‘Coville’</td>
<td>27.51</td>
<td>-0.01</td>
</tr>
<tr>
<td>‘Elliott’</td>
<td>31.73</td>
<td>-0.78</td>
</tr>
<tr>
<td>‘Lateblue’</td>
<td>26.16</td>
<td>-0.32</td>
</tr>
<tr>
<td>‘Coastal’</td>
<td>20.29</td>
<td>0.11</td>
</tr>
<tr>
<td>‘Montgomery’</td>
<td>27.73</td>
<td>-0.37</td>
</tr>
</tbody>
</table>

See section on ‘Colour’ below for explanation of surface colour variables (L, a and b); total volatile concentration is reported in detector area response units of picoamps (pA).

\[ab,c,d,e,f,g\]

Mean values within a column with unlike superscript letters were significantly different at \(P<0.05\) level (Tukey’s Honestly Significant Difference test).

(Perkins-Veazie et al., 1995). From field observations there is the perception that within a cultivar scar size would be positively correlated with fruit size (i.e. bigger fruit usually have larger scars). However, Ballington et al. (1984) reported no association between scar diameter and fruit size among various cultivars and Vaccinium species. The data of Perkins-Veazie et al. (1995) indicate little relationship between fruit size and scar diameter.

**Colour**

Highbush blueberry colour is a highly complex attribute affected by chemical and physical parameters. The light blue colour of fresh blueberries is determined by the amount of waxy ‘bloom’ (quantity and structure) and the anthocyanin content of the skin. Most of the anthocyanin pigments are formed during the 6 days following the development of red colour (Woodruff et al., 1960). Blue colour development can take place off the plant, but further sugar accumulation is very limited.

The wax reflects and refracts light, causing the light-coloured appearance on the skin surface (Albrigo et al., 1980). Sapers et al. (1984) studied the wax
ultrastructure of ripe highbush blueberries under the electron microscope and distinguished two types of variety: one, represented by ‘Blueray’ and ‘Burlington’, that had upright and flat wax platelets over a layer of continuous wax or annealed patches of wax; the other, typified by ‘Elliott’, which had few if any platelets and instead had an extreme degree of patchiness.

The whitish material or ‘bloom’ on the surface of the fruit is a rather loose, thin and fragile wax deposit. The fragile nature of the wax makes it sensitive to even gentle rubbing, brushing and bouncing of the fruit. This relationship has made preservation of the waxy bloom during handling an important goal.

To get objective colour measurements of blueberry fruit a colorimeter is commonly used. The instrument provides three variables: $L$ (with lower values provided by darker fruit), $a$ (where negative and positive values indicate predominance of green and red, respectively) and $b$ (expressing the blue component or blueness). In a study on ten highbush and two rabbiteye blueberry cultivars, Saftner et al. (2008) found that variations in green (negative $a$) and red (positive $a$) chromas were not as large as that of the blue chroma (Table 9.2). Research on 11 highbush varieties showed that in fresh blueberries there was a close relationship between the $L$ value and visual assessments of waxy bloom. When numerical scores where assigned to bloom, a regression analysis of this relationship yielded a correlation coefficient of $r=0.75$ (values can range from $-1$ to $1$). Samples that scored high for bloom also tended to have slightly higher negative values of $b$ (an indication of greater blueness), the correlation coefficient being $r=-0.62$ (Supers et al., 1984). The surface $L$ values were also negatively correlated with sensory scores for intensity of blue colour ($r=-0.62$) and significantly, albeit rather weakly, correlated with sensory scores for acceptability of appearance ($r=0.46$). Chromaticity $b$ values were correlated with sensory scores for intensity of blue colour ($r=0.48$) and negatively correlated to sensory scores for acceptability of appearance ($r=-0.41$). These results would indicate that consumer preferences are for brighter, less intensively blue-coloured fruit.

**Firmness**

Fruit firmness is an important characteristic in blueberries, since it relates to consumer appeal and to postharvest decay of the fruit (NeSmith et al., 2002). Fruit with higher firmness can better withstand harvest (especially mechanical) and subsequent shipping. Fruit of firmer cultivars can be left on the bush longer (hanging potential), allowing more flexibility in timing of harvests (Ehlenfeldt, 2005).

Most of the mechanical methods used to measure firmness determine the force needed to puncture, penetrate or deform the fruit (Chiabrando et al., 2009). In blueberry, the softening that occurs at ripening is linked with the enzymatic digestion of cell wall components such as pectin, cellulose and
hemicellulose. Blueberry seems to be unusual in the sense that fruit softening occurs without substantial modifications in the size of pectin molecules. In contrast, hemicellulose levels decrease in blueberry as ripening progresses (Vicente et al., 2007). Total water-soluble pectin, which constitutes much of the middle lamella, decreases linearly as fruit passes from green to blue. This degradation of the middle lamella and cell wall is directly responsible for the loss of firmness.

In blueberry, species ancestry has not been consistently related to firmness; however, cultivars with higher firmness often possess a greater percentage of *Vaccinium darrowii*. Conversely, varieties with softer fruit often have a higher percentage of lowbush (*Vaccinium angustifolium*) ancestry (Ehlenfeldt and Martin, 2002). Saftner et al. (2008) reported that the highbush blueberry cultivars ‘Lateblue’, ‘Weymouth’ and ‘Chanticleer’ were softer than nine other highbush varieties and they also had low sensory scores for bursting energy and texture during chewing. The largest difference (16–24%) was between ‘Hannah’s Choice’ (the firmest cultivar) and ‘Coastal’, ‘Lateblue’, ‘Weymouth’ and ‘Chanticleer’ which were the softest. In general, compression firmness values were most tightly correlated with sensory scores for juiciness (r = 0.48) followed by bursting energy (crispness, r = 0.44) and texture during chewing (r = 0.33), and were not significantly associated with sensory scores for intensity of skin toughness. The rather weak correlation between compression firmness and sensory scores for texture during chewing might be due to the abundance and/or size of stone cells and seeds, which were not considered in that study.

Blueberry firmness is more greatly affected by changes in maturity than by differences among cultivars (Beaudry, 1992), and slight differences in maturity can have profound influences on the relationship between instrumental firmness and sensory textural scores. Ballinger et al. (1973) measured firmness (resistance to compression) of ‘Berkeley’ highbush blueberries at different maturity stages. They showed that small, green, unripe fruit were extremely firm (57.8 g/0.1 mm of compression) and that firmness dropped sharply up to the red colour stage; however, firmness varied little as berries passed from the red-purple (9.6 to 9.8 g/0.1 mm of compression) to the completely blue stage (7.6 to 8.8 g/0.1 mm of compression). Similar trends were observed by Vicente et al. (2007) in ‘Duke’ highbush blueberry fruit. Research of Ballinger et al. (1973) showed that fruit from later harvests had lower firmness readings. When the highbush cultivars ‘Wolcott’, ‘Croatan’, ‘Morrow’ and ‘Murphy’ were harvested 11 days apart, the firmness was, on average, from 7.8 to 6.4 g/0.1 mm of compression lower in later than in earlier harvests.

In a 3-year-trial done in California to evaluate instrumental and sensory quality of southern highbush blueberry varieties, Bremer et al. (2008) reported (Table 9.3) that ‘Jewel’ and ‘O’Neal’ had the lowest average firmness (13.6 g/0.1 mm deformation), while ‘Revelle’ and ‘Misty’ had the highest (18.1 g/0.1 mm deformation), and ‘Emerald’ and ‘Star’ were intermediate (17.0 g/0.1 mm deformation). As with other quality attributes (soluble solids,
Table 9.3. Ranges in quality attributes of six southern highbush blueberry cultivars grown in the San Joaquin Valley (California) for three seasons, 2005-2007. (Adapted from Bremer et al., 2008.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Soluble solids, SS (%) w/w</th>
<th>Titratable acidity, TA (%) w/w</th>
<th>SS/TA ratio</th>
<th>Firmness a (g/0.1 mm deformation)</th>
<th>TEAC b (µmol TE/g FW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Emerald'</td>
<td>11.6-12.3</td>
<td>0.60-0.90</td>
<td>13.2-20.0</td>
<td>16.2-18.2</td>
<td>13.2-19.1</td>
</tr>
<tr>
<td>'Jewel'</td>
<td>10.9-12.3</td>
<td>0.67-1.00</td>
<td>11.4-18.1</td>
<td>12.1-14.8</td>
<td>10.3-11.7</td>
</tr>
<tr>
<td>'Misty'</td>
<td>11.1-13.7</td>
<td>0.57-0.83</td>
<td>16.6-20.6</td>
<td>15.5-21.2</td>
<td>17.4-21.9</td>
</tr>
<tr>
<td>'O'Neal'</td>
<td>10.8-11.8</td>
<td>0.27-0.77</td>
<td>14.5-40.5</td>
<td>12.8-14.8</td>
<td>11.7-13.6</td>
</tr>
<tr>
<td>'Revelle'</td>
<td>13.3-15.8</td>
<td>0.70-0.80</td>
<td>18.1-22.9</td>
<td>15.9-21.6</td>
<td>13.8-20.7</td>
</tr>
<tr>
<td>'Star'</td>
<td>11.1-12.9</td>
<td>0.67-0.77</td>
<td>16.4-17.4</td>
<td>17.0-19.7</td>
<td>12.1-12.7</td>
</tr>
</tbody>
</table>

Firmness was converted from initial readings of lb per 4 mm deformation.

bTEAC, Trolox equivalent antioxidant capacity (oxygen radical absorbance capacity assay; TE, Trolox equivalents; FW, fresh weight).

Firmness was a significant interaction between cultivars and season, meaning that for a given characteristic the variability for a certain cultivar was dependent upon the environmental conditions of the specific growing season. Differences in climate, soils, cultural practices and other environmental factors may cause firmness of some cultivars to vary from region to region and from season to season. Ballinger et al. (1973) showed that firmness varied by 14.6% in successive seasons and that five out of six highbush blueberry cultivars showed the same trend. Donahue et al. (2000) reported in lowbush blueberry that smaller fruit always had higher firmness readings.

Ehlenfeldt (2005) found the following when the firmness and holding ability of 19 highbush blueberry cultivars were studied during postharvest: (i) the seven softest cultivars were released before 1953, which he partially attributed to the incorporation of firmer-fruited species material into Vaccinium corymbosum; (ii) at weekly intervals, most cultivars showed single digit decreases in firmness from the first harvest, except for 'Legacy' which had a 15% increase; (iii) when harvest was delayed to wait for a greater proportion of blue fruit, firmness in all cultivars decreased (ranging from -1 to -15%) at week 2, and decreased even further at week 3 (by as much as ~23% for 'Chanticleer'), with 'Legacy' again departing from the rest as it showed almost no decrease; and (iv) holding ability cannot be predicted based solely on initial firmness, as 'Legacy' was not the firmest fruit initially, but showed a better ability to hold and possibly increase in firmness.

Fruit firmness can be reduced dramatically by how the fruit is handled. When 'Wolcott' highbush blueberry fruit were dropped upon hard boards, they softened (bruised) in proportion to the distance of fall. Multiple drops of small distances (10.2 cm) softened blueberries as much as large distances...
(40.8 cm), if the total distance of the increments was the same. Regardless of cultivar, size, ripeness or initial firmness, the firmness of blueberries after a standard fall can be predicted if their initial firmness is known (Ballinger et al., 1973). Similarly, when lowbush blueberries were dropped on to a moving smooth conveyor belt from heights of 40, 80, 120 or 160 cm, increasing height resulted in greater loss of fruit firmness as measured by instrumental and sensory methods. Studies on ‘Brightwell’ rabbiteye blueberries established that the greatest loss in firmness was caused by machine harvesting (20–30%), followed by a 10–15% loss in firmness due to grading and sorting.

Miller et al. (1993) found that fruit firmness declines during the postharvest storage of ‘Sharpblue’ southern highbush blueberry. Since blueberries from later harvests have a more rapid decrease in fruit quality during storage than the fruit from earlier harvests, Miller et al. (1993) suggested that fruit from this cultivar should be picked as soon as possible after reaching marketable maturity. Sanford et al. (1991) concluded that in lowbush the storage temperature had a greater influence on fruit firmness than bruising at harvest. Berries held at 0°C were the firmest and fruit held at 5°C showed disproportional decrease in firmness, and each additional rise in storage temperature (up to 20°C) resulted in incremental decreases in fruit firmness.

Perkins-Veazie et al. (1995) have shown that fruit firmness at harvest is not a good indicator of firmness after storage. For example, compared with the other clones, ‘O’Neal’ southern highbush had high epidermal and stem scar firmness before storage but was intermediate to low in firmness after storage. Fruit from ‘G616’ southern highbush clone were of similar firmness to ‘Bluecrop’ highbush and ‘Climax’ rabbiteye before storage, but were the softest fruit of all clones after storage (Table 9.4). For all clones, epidermal firmness decreased after storage (average 25.4% for southern highbush clones). Except for rabbiteye ‘Climax’ and ‘A109’ southern highbush, all clones had reduced firmness at the stem scar following storage.

Seediness

The degree of seediness tends to be higher in rabbiteye than highbush blueberries. In a comparison of three rabbiteye cultivars (‘Climax’, ‘Premier’ and ‘Tifblue’) and two highbush (‘Bluecrop’ and ‘Jersey’), a sensory panel gave higher scores to highbush varieties on this character. Within the highbush varieties, no difference was found among varieties (Silva et al., 2005).

Soluble solids

As berries approach maturity and pass from the red stage to the blue stage, the total sugars increase, mainly due to an increase in reducing sugars. Woodruff
<table>
<thead>
<tr>
<th>Clone</th>
<th>Epidermal firmness (g/0.1 mm) Before storage</th>
<th>Epidermal firmness (g/0.1 mm) After storage</th>
<th>Firmness change (%)</th>
<th>Stem scar firmness (g/0.1 mm) Before storage</th>
<th>Stem scar firmness (g/0.1 mm) After storage</th>
<th>Firmness change (%)</th>
<th>Average firmness (g/0.1 mm) Before storage</th>
<th>Average firmness (g/0.1 mm) After storage</th>
<th>Firmness change (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘A109’</td>
<td>5.9b</td>
<td>4.3b</td>
<td>27b</td>
<td>4.1f</td>
<td>4.0bc</td>
<td>2c</td>
<td>5.0d</td>
<td>4.2b</td>
<td>17b</td>
</tr>
<tr>
<td>‘Cape Fear’</td>
<td>6.1b</td>
<td>4.9a</td>
<td>20b</td>
<td>6.0b</td>
<td>5.1a</td>
<td>5bc</td>
<td>6.1b</td>
<td>5.0a</td>
<td>17b</td>
</tr>
<tr>
<td>‘Cooper’</td>
<td>6.1b</td>
<td>4.1bc</td>
<td>33b</td>
<td>5.5b</td>
<td>4.5b</td>
<td>18b</td>
<td>5.8bc</td>
<td>4.3b</td>
<td>26b</td>
</tr>
<tr>
<td>‘Gulfcoast’</td>
<td>6.8a</td>
<td>4.8a</td>
<td>29b</td>
<td>6.4a</td>
<td>5.2a</td>
<td>19b</td>
<td>6.6a</td>
<td>5.0a</td>
<td>24b</td>
</tr>
<tr>
<td>‘G616’</td>
<td>5.1c</td>
<td>3.7c</td>
<td>27b</td>
<td>4.7bc</td>
<td>3.6c</td>
<td>23bc</td>
<td>4.9d</td>
<td>3.7c</td>
<td>26b</td>
</tr>
<tr>
<td>‘MS108’</td>
<td>5.9b</td>
<td>4.9a</td>
<td>17b</td>
<td>5.9bc</td>
<td>5.2a</td>
<td>12bc</td>
<td>5.9bc</td>
<td>5.1a</td>
<td>14b</td>
</tr>
<tr>
<td>‘O’Neal’</td>
<td>6.7a</td>
<td>4.4b</td>
<td>34e</td>
<td>6.4a</td>
<td>4.4b</td>
<td>31e</td>
<td>6.6a</td>
<td>4.4b</td>
<td>33e</td>
</tr>
<tr>
<td>‘Sierra’</td>
<td>5.8b</td>
<td>4.9a</td>
<td>16b</td>
<td>5.5a</td>
<td>4.9b</td>
<td>11bc</td>
<td>5.7c</td>
<td>4.9b</td>
<td>13b</td>
</tr>
<tr>
<td>‘Bluecrop’</td>
<td>5.1c</td>
<td>4.3b</td>
<td>16b</td>
<td>4.8b</td>
<td>4.3b</td>
<td>10bc</td>
<td>5.0d</td>
<td>4.3b</td>
<td>13b</td>
</tr>
<tr>
<td>‘Climax’</td>
<td>5.8b</td>
<td>4.4b</td>
<td>24b</td>
<td>4.3c</td>
<td>4.4b</td>
<td>2c</td>
<td>5.1d</td>
<td>4.4b</td>
<td>13b</td>
</tr>
</tbody>
</table>

Epidermal/stem scar firmness was measured with a gram gauge penetrometer adapted with a 0.3 mm wire; firmness was converted from initial readings of g/0.1 mm deformation.

\(a,b,c\) Mean values within a column with unlike superscript letters were significantly different at \(P \leq 0.05\) level (Least Significant Difference test).
et al. (1960) established that the largest increase occurs in the first six days after red coloration of the berries. Soluble solids levels tend to vary from year to year and among different locations.

Beaudry (1992) suggested that perception of sweetness may be affected by other factors, such as titratable acidity. Highbush blueberry cultivars such as ‘Bluegold’ and ‘Chanticleer’ with high soluble solids (13.0 to 13.2% w/w) were not perceived as particularly sweet in sensory evaluation, while the opposite occurred with cultivars having low soluble solids such as ‘Lateblue’, ‘Coville’ and ‘Duke’ (Saftner et al., 2008). This may indicate that a difference in soluble solids by itself does not have practical importance regarding the perception of fruit sweetness.

Fader et al. (2003) have shown in strawberries that anthocyanins and phenolic compounds, which are even more prominent in blueberries, strongly refract light and contribute up to 32% to soluble solids readings from a refractometer. They found that removal of anthocyanins and phenolic compounds before measuring soluble solids with a refractometer increases the reliability of soluble solids as an indicator of sweetness.

After evaluating southern highbush varieties in California for 3 years, Bremer et al. (2008) reported that soluble solids values tended to be more stable than titratable acidity or firmness (Table 9.3). When comparing highbush cultivars, they found that ‘Reveille’ had the highest average in soluble solids (14.4% w/w), ‘O’Neal’ had the lowest (11.4% w/w), and the other cultivars were intermediate (11.7 to 12.3% w/w). Hancock et al. (2008) found average content of soluble solids among highbush cultivars to range from 9.5 % w/w (‘Bluecrop’) to 12.7 % w/w (‘Brigitta’).

When Kushman and Ballinger (1963) studied different harvest schedules (3-, 6-, 9- and 12-day intervals) in ‘Wolcott’ highbush blueberry they found that harvest interval had little influence on soluble solids levels, although an increase in sugars (mainly reducing) was obtained with longer intervals. In their study on the effect of storage on the quality of southern highbush blueberries, Perkins-Veazie et al. (1995) found that levels of soluble solids did not differ greatly among clones and between fresh fruit and that stored for 21 days at 5°C plus 1 day at 20°C, except for fruit of the ‘Climax’ rabbiteye blueberry (included as standard), which increased significantly after storage. Although weight loss can concentrate sugars, the magnitude of weight loss of ‘Climax’ fruit was less than that of ‘Gulfcoast’ southern highbush, which showed no change in soluble solids.

Titratable acidity

Organic acids are important to flavour. The composition of organic acids is a distinguishing characteristic among the Vaccinium species. In highbush blueberries, the predominant organic acid is usually citric (average 75%:
range 38–90% w/w), while the proportions of malic, quinic and succinic acids are 3, 5 and 17%, respectively. In the case of rabbiteye fruit the most important organic acids are succinic and malic (50 and 34%, respectively), while citric accounts for only 10% (Ehlenfeldt et al., 1994).

As reported by Bremer et al. (2008), the composition of organic acids affects sensory quality, since the combination of citric and malic acid gives a sour taste, and succinic acid provides a bitter taste. Acid profile differences may also have a bearing on other important factors such as fruit colour development, decay susceptibility, and insect and bird predation (Ehlenfeldt et al., 1994). Greater fruit acidity enhances the colour strength of anthocyanins, as was observed by Sapers et al. (1984) in samples of 'Coville' and 'Elliott'.

Both environmental and developmental factors affect acidity levels in blueberry fruit. Research on highbush blueberries established that acidity falls sharply in the first six days after fruit reach red coloration (Woodruff et al., 1960). Kushman and Ballinger (1963) studied different harvest schedules (3-, 6-, 9- and 12-day intervals) in 'Wolcott' highbush blueberry and found that total titratable acidity tended to decrease as the season progressed and as the harvest interval was lengthened. In the case of southern highbush blueberries, a 3-year evaluation in California (Bremer et al., 2008) determined that titratable acidity varied by up to 50% among seasons for 'Emerald', 'Jewel' and 'O'Neal'. 'O'Neal' had a significantly lower average (0.55% citric acid) than the rest, which averaged 0.70–0.80% citric acid (Table 9.3).

Statistical analysis of samples collected at different maturity stages in 11 highbush cultivars showed that 86% of the total variability in titratable acidity among cultivars could be explained by genetic differences (Sapers et al., 1984). Perkins-Veazie et al. (1995) found that titratable acidity values of southern highbush cultivars ranged from 0.54 to 1.13%, with an average of 0.84%. Hancock et al. (2008) found titratable acidity in highbush cultivars to range from 0.90% ('Jersey') to 2.10% ('Bluegold').

When the association between instrumental and sensory quality was studied by Saftner et al. (2008) in highbush and rabbiteye blueberries it was found that titratable acidity was inversely correlated with pH ($r = -0.76$), but as reported also by Rosenfeld et al. (1999), it was not related to scores of tartness or to any other flavour-related sensory evaluation. The authors concluded that the apparent lack of correlation between titratable acidity and flavour-related evaluations may suggest that there is an optimal acid concentration needed in blueberry fruit for enhanced flavour. However, part of the explanation might be related to the type of acid present in each cultivar.

During storage, the average acidity dropped slightly in four out of eight southern (Perkins-Veazie et al., 1995) and in northern highbush blueberries (Perkins-Veazie et al., 1995; Chiabrando et al., 2009). Similar decreases of acidity during storage were found by Smittle and Miller (1988) in 'Woodard' rabbiteye blueberry during 21 days of storage at 5°C; however, Miller and Smittle (1987) found little change in acidity of 'Climax' and 'Woodard'
rabbits eye blueberries during 21 days of storage at 3°C. Acids are one of the energy reserves of the fruit, being used in respiration and converted to simpler molecules such as CO₂ and water. Acids decrease as a result of respiration, but water loss in the fruit might increase the concentration of acids (Echeverria et al., 2009). As a consequence, titratable acidity would change during storage depending on the rates of respiration and water loss.

**Ratio of soluble solids to titratable acids**

Low SS/TA ratios have been associated with good keeping quality (Ballinger and Kushman, 1970). An SS/TA ratio of 6.5 or lower has been recommended as desirable in highbush blueberry cultivars for resistance to postharvest decay organisms (Galletta, 1975). Based on the relationship between SS/TA ratios and relative keeping quality of blueberries, Galletta et al. (1971) established three classes: (i) cultivars having SS/TA values lower than 18 possess good keeping quality; (ii) those cultivars having SS/TA values between 18 and 32 have medium keeping quality; and (iii) the keeping quality would be low for cultivars having SS/TA values higher than 32.

Evaluation of six southern highbush varieties in California showed that there was high variability among seasons in SS/TA ratio (near 50%) for ‘Emerald’, ‘Jewel’ and ‘O’Neal’ (Bremer et al., 2008). Perkins-Veazie et al. (1995) studied southern highbush blueberry clones in Arkansas; their results indicated that at harvest most of the clones, excluding ‘Cape Fear’ (SS/TA=18.7), had SS/TA ratios lower than 18, which is recommended for longest storage life. Following 21 days of storage at 5°C plus 1 day at 20°C, only ‘O’Neal’ (SS/TA=22.9) and the rabbits eye ‘Climax’ (SS/TA=26.2) had an SS/TA ratio higher than 18 (Perkins-Veazie et al., 1995). Hancock et al. (2008) found SS/TA ratios in highbush blueberry to range from 5.9 (‘Bluegold’) to 12.8 (‘Jersey’).

The SS/TA ratio increases from unripe green (<=2) to the fully blue stage (>=20) and then remains at that level (Castrejón et al., 2008). This is because titratable acidity declines from the unripe green (about 3% w/w) to the fully blue stage (near 0.5% w/w), while soluble solids increase from the unripe green (about 9% w/w) to the 100% ripe stage (about 15% w/w), and both sugars and acidity change little later on.

SS/TA ratios differ among blueberry types; the highbush blueberries (‘Weymouth’, ‘Morrow’, ‘Croatan’ and ‘Bluecrop’) had an average value of 4.7, while the rabbits eye blueberries (‘Tifblue’, ‘Garden Blue’, ‘Homebell’ and ‘Callaway’) reached 10.5 (Ballington et al., 1984). The values for SS/TA ratio in various southern highbush blueberries and across three seasons varied from 11.4 to 40.5 (Table 9.3).

There seems to be a strong environmental effect on SS/TA ratios as Saftner et al. (2008) reported values of 20.1 and 24.9 for ‘Weymouth’ and
'Bluecrop' highbush blueberries (Table 9.5), while the SS/TA ratios published by Ballington et al. (1984) were 3.7 for 'Weymouth' and 2.6 for 'Bluecrop'. Part of the difference might be due to the fact that the latter researchers collected all of their fruit in one pass including all stages of ripeness. Research comparing successive harvests of different highbush blueberry varieties showed that 'Elliott' and 'Coville' were consistently high in acidity; the SS/TA ratio and anthocyanins remained constant for successive harvests. On the other hand, first harvests of 'Berkeley', 'Bluetta', 'Collins' and 'Earliblue' were higher in acidity than second harvests, although SS/TA ratios were still within the ripe range (Sapers et al., 1984).

The organic acid concentration influences the perception of sweetness. Each reduction of 0.1% (as a proportion of total fruit weight) is equivalent to an increase of 1% in the perceived sweetness. During the ripening of highbush blueberry, citric acid declines from about 1.2 to 0.6% of total fruit weight, corresponding to a perceived sweetness increase of 6% (Beaudry, 1992).

**pH**

Saftner et al. (2008) found that the pH values of blueberry extracts were correlated with scores for intensity of flavour ($r=0.56$) and acceptability of flavour ($r=0.51$), as well as overall eating quality ($r=0.48$). The pH values

### Table 9.5. Compression firmness of whole fruit and soluble solids, titratable acidity and pH from ten highbush and two rabbiteye blueberry varieties ('Coastal' and 'Montgomery') listed by harvesting season. (Adapted from Saftner et al., 2008.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Compression firmness (N)</th>
<th>Soluble solids, SS (% w/w)</th>
<th>Titratable acidity, TA (% w/w)</th>
<th>SS/TA ratio</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Chanticleer'</td>
<td>1.56bc</td>
<td>13.0a</td>
<td>0.40bc</td>
<td>32.3b</td>
<td>3.4a</td>
</tr>
<tr>
<td>'Duke'</td>
<td>1.67abc</td>
<td>10.9bcd</td>
<td>0.43bc</td>
<td>25.5bcd</td>
<td>3.0bcd</td>
</tr>
<tr>
<td>'Hannah's Choice'</td>
<td>1.86a</td>
<td>12.3a,b</td>
<td>0.45bc</td>
<td>27.3bcd</td>
<td>3.3ab</td>
</tr>
<tr>
<td>'Weymouth'</td>
<td>1.51cd</td>
<td>11.2bcd</td>
<td>0.56bc</td>
<td>20.1cd</td>
<td>2.8bc</td>
</tr>
<tr>
<td>'Berkeley'</td>
<td>1.54cd</td>
<td>11.5bcd</td>
<td>0.44bc</td>
<td>26.6bcd</td>
<td>3.1ab</td>
</tr>
<tr>
<td>'Bluecrop'</td>
<td>1.64abcd</td>
<td>11.5bcd</td>
<td>0.46bc</td>
<td>24.9bcd</td>
<td>3.1ab</td>
</tr>
<tr>
<td>'Bluegold'</td>
<td>1.71abcd</td>
<td>13.2a</td>
<td>0.64b</td>
<td>20.9cd</td>
<td>3.1abc</td>
</tr>
<tr>
<td>'Coville'</td>
<td>1.66abcd</td>
<td>10.8c</td>
<td>0.58bc</td>
<td>18.7d</td>
<td>3.0abc</td>
</tr>
<tr>
<td>'Elliott'</td>
<td>1.64abcd</td>
<td>11.3bcd</td>
<td>1.27a</td>
<td>9.0e</td>
<td>2.5c</td>
</tr>
<tr>
<td>'Earliblue'</td>
<td>1.40d</td>
<td>10.6d</td>
<td>1.22a</td>
<td>8.9e</td>
<td>2.5c</td>
</tr>
<tr>
<td>'Coastal'</td>
<td>1.37d</td>
<td>12.2abcd</td>
<td>0.35c</td>
<td>35.6e</td>
<td>3.0abc</td>
</tr>
<tr>
<td>'Montgomery'</td>
<td>1.76ab</td>
<td>11.3bcd</td>
<td>0.58bc</td>
<td>19.5cd</td>
<td>2.8bc</td>
</tr>
</tbody>
</table>

$^{a,b,c,d}$Mean values within a column with unlike superscript letters were significantly different at $P \leq 0.05$ (Tukey's Honestly Significant Difference test).
for highbush blueberries fall in a range from 2.5 for ‘Elliott’ and ‘Lateblue’ to 3.4 for ‘Chanticleer’ (Table 9.5). Chiabrando et al. (2009) determined that the pH of ‘Coville’ and ‘Bluecrop’ highbush blueberry fruit increased from 2.8 at harvest to 3.3 after 35 days of cold storage. Good storage quality is associated with pH values lower than 3.5 (Perkins-Veazie et al. 1995).

When evaluating the relationship between pH and acidity for a range of blueberry progenies, Galletta et al. (1971) established that for a change of one pH unit, the acidity reflected a fourfold change in concentration.

There does not appear to be a consistent pattern of change in pH values during storage. Perkins-Veazie et al. (1995) reported that fruit pH values at harvest were in the range of 3.01 (for southern highbush ‘MS108’) to 3.43 (for ‘Cape Fear’ southern highbush) with an average of 3.24. When these fruits were again measured after 21 days of storage at 5°C plus 1 day at 20°C, it was found that the average pH had increased slightly and the range varied from 3.12 (for ‘MS108’) to 3.47 (for ‘G616’ southern highbush). The fruit pH of the northern highbush blueberry ‘Bluecrop’ changed from 3.39 at harvest to 3.51 after storage (Perkins-Veazie et al., 1995). Smittle and Miller (1988) for rabbiteye blueberries ‘Climax’ and ‘Woodard’ and Echeverría et al. (2009) for the southern highbush ‘O’Neal’ reported that pH decreased after cold storage at 5 and 3°C. Echeverría et al. (2009) attributed this drop in pH in fruit stored under modified atmosphere to CO2 diffusion into fruit tissues.

Antioxidant capacity

There is strong evidence that the antioxidants present in fruits and vegetables protect lipids, proteins and nucleic acids against oxidative damage initiated by free radicals. It has been established that free radicals play a major role in cancer, heart, vascular and neurodegenerative diseases (Howard et al., 2003).

Among 41 fruits and vegetables tested for their antioxidant capacity using an assay for oxygen radical absorbing capacity (ORAC), blueberries had the highest value. Although various kinds of antioxidants have been identified in fruit, anthocyanins and other phenolic compounds have received the greatest attention (You et al., 2011). Blueberry fruits contain an array of phenolics, including anthocyanins, quercetin, kaempferol, myricetin, chlorogenic acid and procyanidins, which contribute to antioxidant capacity. Up to 60% of the total phenolic content in highbush blueberries is accounted for by anthocyanins (Kalt et al., 2003). Anthocyanins are responsible for the bright orange, red and blue colours in fruit and are dependent on environmental pH values (You et al., 2011). Indeed, anthocyanins change their colour with pH: they appear red in acidic, violet in neutral and blue in basic aqueous solution (Yoshida et al., 2009).

Blueberry fruit have the highest concentration of antioxidants and phenolics in the skin, more than double those of the seeds (Table 9.6). For a
Table 9.6. ORAC, phenolic and anthocyanin levels in different parts of southern highbush blueberries 'Reveille' and 'Bladen'. (Adapted from Mainland and Tucker, 2002.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Berry part</th>
<th>ORAC (µmol TE/g FW)</th>
<th>Phenolics (mg/g)</th>
<th>Anthocyanins (mg/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Reveille'</td>
<td>Whole berry</td>
<td>16</td>
<td>2.9</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>Seeds</td>
<td>28</td>
<td>5.6</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Skin</td>
<td>66</td>
<td>9.8</td>
<td>9.1</td>
</tr>
<tr>
<td>'Bladen'</td>
<td>Whole berry</td>
<td>34</td>
<td>5.2</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>Seeds</td>
<td>59</td>
<td>14.2</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Skin</td>
<td>166</td>
<td>27.4</td>
<td>12.7</td>
</tr>
<tr>
<td>Overall average</td>
<td>Whole berry</td>
<td>25</td>
<td>4.1</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Seeds</td>
<td>44</td>
<td>9.9</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>Skin</td>
<td>116</td>
<td>18.6</td>
<td>10.9</td>
</tr>
</tbody>
</table>

ORAC, oxygen radical absorbing capacity; TE, Trolox equivalents; FW, fresh weight.

given weight, the total amount of skin or surface area increases as the berry size decreases. Various authors have found a highly inverse relationship between fruit size and antioxidant activity (Connor et al., 2002b; Moyer et al., 2002; Howard et al., 2003).

There is considerable variation among blueberry cultivars in antioxidant capacity. Ehlenfeldt and Prior (2001) determined the ORAC, phenolic and anthocyanin concentrations in fruit of 87 highbush blueberry cultivars and found in southern highbush that values ranged from 4.6 ('Avonblue') to 22.3 ('Sharpblue') µmol Trolox equivalents (TE)/g fresh weight (FW). In northern highbush the range was 5.5 ('Berkeley') to 30.5 ('Elliott') and 31.1 ('Rubel'). Heritability estimates in blueberry progenies were 0.43, 0.46 and 0.56 for antioxidant capacity, total phenolics and total anthocyanins, respectively (Connor et al., 2002a).

Besides genotype, the antioxidant capacity can be affected by location, growing season, cultural management, maturity, and postharvest handling and storage. Howard et al. (2003) found significant main effects for growing season and genotype × growing season for ORAC, total antioxidants and fruit weight. Similarly, Connor et al. (2002b) evaluated nine highbush blueberry cultivars in three locations (Michigan, Minnesota and Oregon) for two seasons and found a significant genotype × environment interaction for antioxidant activity. Although differences in overall mean antioxidant activity among locations occurred, there was no significant change in rank among locations. In contrast, in a 3-year evaluation of southern highbush in California, Bremer et al. (2008) found that antioxidant capacity varied significantly among cultivars but not among seasons (Table 9.3). 'Misty' had the highest ORAC (19.6 µmol TE/g FW) and 'Jewel' the lowest (11.0 µmol TE/g FW).
Delaying fruit harvest can have a marked positive influence on levels of anthocyanins in blueberry fruit. Fruit maturity had a significant effect on antioxidant activity, total phenolic content and anthocyanin content, and bush ripeness x fruit maturity interactions were significant (Connor et al., 2002c). Similar results were reported by Prior et al. (1998) who found that when the fruit of the rabbiteye cultivars 'Brightwell' and 'Tifblue' were left on the bush for an extended time (49 days) after first becoming blue, the antioxidant activity was much higher (124% for 'Brightwell' and 64% for 'Tifblue') than when the berries had first become blue (Table 9.7). In another study done by Mainland and Tucker (2002), the levels of antioxidants in highbush blueberry remained constant or decreased from the ripe to the overripe stage, while harvesting overripe berries in rabbiteye caused a 10% increase in ORAC values (Table 9.8).

Levels of antioxidant capacity are not always tightly associated with phenolic or anthocyanin content. Studies on highbush blueberries 'Brigitta', 'Bluegold' and 'Nelson' showed that anthocyanin content was substantially higher in fruit of more advanced stages of ripeness (fully blue versus 5–50% or 50–95% blue). In contrast, the phenolic content and ORAC were lower in riper fruit (Kalt et al., 2003). On the contrary, Castrejón et al. (2008) found in highbush blueberries ('Reka', 'Puru', 'Bluecrop' and 'Berkeley') that ORAC and phenolic contents were higher in early maturation (100% whitish green) and stabilized from 60% blue on. In another experiment, berries of 'Elliott' highbush blueberry were harvested from plants at two levels of bush ripeness (30–50% and 60–80% of ripe berries on plants) and separated into three maturity classes on the basis of percentage fruit colour. The authors found that the level of bush ripeness had no significant effect on antioxidant activity, total phenolic content and anthocyanin content; however, fruit maturity as well as bush ripeness x fruit maturity interactions had a significant effect on these three traits (Connor et al., 2002c).

Kalt et al. (1999) found that there was a slight increase in both anthocyanins and ORAC at 20°C, but not at other temperatures (0, 10 or 30°C). Anthocyanins continued to be synthesized during storage at 20°C.

Table 9.7. ORAC, phenolic and anthocyanin levels in rabbiteye blueberries 'Tifblue' and 'Brightwell' for two stages of maturity (just ripe = just blue; overripe = beginning to soften). (Adapted from Prior et al., 1998.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Maturity stage</th>
<th>ORAC (μmol TE/g FW)</th>
<th>Phenolics (mg/100 g FW)</th>
<th>Anthocyanins (mg/100 g FW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tifblue</td>
<td>Just ripe</td>
<td>23.0</td>
<td>3.6</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>37.8</td>
<td>4.1</td>
<td>1.5</td>
</tr>
<tr>
<td>Brightwell</td>
<td>Just ripe</td>
<td>15.3</td>
<td>2.7</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>34.3</td>
<td>4.6</td>
<td>1.6</td>
</tr>
</tbody>
</table>

ORAC, oxygen radical absorbing capacity; TE, Trolox equivalents; FW, fresh weight.
Table 9.8. ORAC, phenolic and anthocyanin levels in highbush (‘Croatan’, ‘Reveille’, ‘Bladen’) and rabbiteye (‘Tifblue’, ‘Powderblue’) blueberries of three stages of maturity (pre-ripe = slight red on scar; ripe = full ripe; overripe = beginning to soften). (Adapted from Mainland and Tucker, 2002.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Maturity stage</th>
<th>ORAC (μmol TE/mg FW)</th>
<th>Phenolics (mg/g)</th>
<th>Anthocyanins (mg/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘Croatan’</td>
<td>Pre-ripe</td>
<td>24</td>
<td>3.6</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>Ripe</td>
<td>26</td>
<td>3.6</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>23</td>
<td>3.8</td>
<td>1.4</td>
</tr>
<tr>
<td>‘Reveille’</td>
<td>Pre-ripe</td>
<td>12</td>
<td>1.9</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Ripe</td>
<td>16</td>
<td>2.6</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>15</td>
<td>2.5</td>
<td>0.6</td>
</tr>
<tr>
<td>‘Bladen’</td>
<td>Pre-ripe</td>
<td>24</td>
<td>3.3</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Ripe</td>
<td>43</td>
<td>5.2</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>34</td>
<td>4.1</td>
<td>2.0</td>
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<tr>
<td></td>
<td>Average highbush</td>
<td>Pre-ripe</td>
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<td>2.9</td>
</tr>
<tr>
<td></td>
<td>Ripe</td>
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<td>3.5</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
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<td>3.5</td>
<td>1.3</td>
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<td>1.2</td>
<td>0.2</td>
</tr>
<tr>
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<td>Ripe</td>
<td>16</td>
<td>2.5</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>21</td>
<td>3.2</td>
<td>0.9</td>
</tr>
<tr>
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<td>Pre-ripe</td>
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<td>2.1</td>
<td>0.3</td>
</tr>
<tr>
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<td>Ripe</td>
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<td>1.0</td>
</tr>
<tr>
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<td>Overripe</td>
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<td>4.6</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Average rabbiteye</td>
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<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Ripe</td>
<td>23</td>
<td>3.0</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Overripe</td>
<td>25</td>
<td>3.9</td>
<td>1.2</td>
</tr>
</tbody>
</table>

ORAC, oxygen radical absorbing capacity; TE, Trolox equivalents; FW, fresh weight.

although the rate of pigment formation declined after about 4 days. Less anthocyanin pigment was formed in the least ripe fruit. After 8 days of storage at 20°C, the anthocyanin content of fruit harvested at 5–50% or 50–95% blue exceeded that of ripe fruit (Kalt et al., 2003). Berries of ‘Liberty’, ‘Brigitta’, ‘Legacy’, ‘Bluegold’, ‘Elliott’, ‘Nelson’, ‘Jersey’ and ‘Little Giant’ highbush blueberry were stored from 3 to 7 weeks at 5°C and none of the cultivars showed a significant change in antioxidant activity during storage (Connor et al., 2002c). However, berries of ‘Elliott’ highbush blueberry with 50–75% fruit coloration, harvested from bushes with 60–80% of mature fruit, showed a significant increase in antioxidant activity, total phenolic content and anthocyanin content during the first three weeks of storage (Connor et al., 2002c). In contrast, Remberg et al. (2003) reported that antioxidant capacity (ferric reducing antioxidant power, FRAP values) of ‘Bluecrop’, ‘Hardyblue’, ‘Patriot’, ‘Putte’ and ‘Aron’ blueberry decreased considerably (by 24 to 34%) during 4 weeks of cold storage (1 or 8°C) and controlled atmosphere (10% CO₂).
and 10% O₂; note that CO₂ and O₂ concentrations in this chapter are expressed in percentages on a v/v basis and they are assumed to be equivalent to kPa or kilopascals. It appears that increases in anthocyanins can be obtained only at high temperatures (20°C) which are not compatible with optimization of other quality parameters during postharvest that are important for consumers.

The impact of cultivation type on antioxidants is controversial. While Wang, S.Y. et al. (2008) found that highbush ‘Bluecrop’ fruit grown organically yielded significantly higher total phenolics, total anthocyanins and antioxidant activity (ORAC) and that the cultural method changed the concentrations of the antioxidants present in the fruit, You et al. (2011) reported that although there were significant differences among various rabbiteye cultivars (‘Powderblue’, ‘Climax’, ‘Tifblue’ and ‘Woodard’) in total phenolics, total anthocyanins and ORAC values, the levels of these compounds did not differ significantly between organic and conventional cultivation. Similarly, Sablani et al. (2010) compared organic and conventional cultivation of ‘Reka’ and ‘Duke’ highbush blueberries, and found that total antioxidant content, phenolic content and total antioxidant activity of berries were not altered by the agricultural production system.

**Fruit decay**

Fresh fruits are prone to fungal contamination in the field, during harvest, transport and retail, and in the consumer’s hands. Fruits contain high levels of sugars and other nutrients which support microbial growth, and their low pH makes them particularly susceptible to fungal spoilage because a large proportion of the bacterial competition is eliminated since most bacteria prefer near neutral pH (Almenar et al., 2007). Some fungi cause spoilage within the field while others proliferate and cause most of their damage after harvest. Fungal spoilage of fruits depends on variety, as well as methods of harvesting, handling, transport and postharvest storage. Woodruff and Dewey (1959) described the deterioration events for the highbush blueberry and concluded that most fruit breakdown during storage was physiological, with fungal infection and growth occurring adventitiously on the debilitated tissues.

Blueberries are more resistant to fungal spoilage than the other berry crops. In a study on the level of contamination in fresh samples of berries and citrus, Tournas and Katsoudas (2005) found that the contamination level (percentage of contaminated berries per sample) differed among the various berry types. The highest mean contamination level of 8.2% was observed in raspberries, closely followed by blackberries and strawberries, while the lowest percentage (38%) occurred in blueberries. The lower contamination level in blueberries may be related to their smooth, hard skin, which makes them less susceptible to many fungi.

The most common moulds isolated from blueberries are *B. cinerea* Pers: Fr. and *Alternaria*, followed by *Fusarium, Penicillium*, yeasts, *Cladosporium*,...
Trichoderma and Aureobasidium (Tournas and Katsoudas, 2005). For more information on the organisms causing fruit spoilage in blueberries see Chapter 8.

FACTORS THAT INFLUENCE STORAGE LIFE OF BLUEBERRIES

Cultivar

Prange and DeEll (1997) stated that virtually all postharvest quality factors are under genetic control. Therefore, from a quality and postharvest standpoint, cultivar selection is the most important management decision in blueberry production. The variable storage life among and within cultivars is a result of inherent factors determining fruit quality as well as their interaction with the growing conditions and the storage environments (Forney, 2009). Fruit of different cultivars differ in size, colour, texture and flavour as well as storage potential (Connor et al., 2002b). For instance, in blueberries, wet stem scars and the development of blue pigments before sugar build-up are undesirable characteristics that affect both fruit quality and postharvest life (Forney, 2009).

In one comparison of the long-term storability (0–5°C; 2% O₂ and 8% CO₂) of nine northern highbush cultivars, Hancock et al. (2008) found that ‘Bluegold’, ‘Brigitta’ and ‘Legacy’ were the best in storage, reaching 4–7 weeks. In another comparison of 17 cultivars, they found ‘Brigitta’ to store the longest (8 weeks) followed by ‘Aurora’ and ‘Draper’.

Climate

The factors that control photosynthesis (i.e. light, temperature, CO₂ and rainfall) are the major environmental controllers of berry fruit quality. Once the site has been selected, there is little control on these external variables, except where protected blueberry cultivation is realized. However, the microclimate can be controlled by various practices: planting density, training, pruning, irrigation, application of growth regulators and fertilization (Prange and DeEll, 1997). These variables can affect air movement and solar penetration within the plant. As explained in Chapter 4 on photosynthesis, the goal is to capture a large proportion of sunlight during the season and partition an important amount of carbohydrates towards reproductive growth.

Sudden or excess exposure to sun can cause sunburn. Sunburn may either produce evident damage to the fruit that will render them unsuitable for marketing or will alter their physiology and diminish their storage potential.
Light intensity above photosynthetic saturation levels can increase fruit temperature and may result in fruit damage and loss of firmness (Sams, 1999).

High temperatures during ripening can have various undesirable effects. Hot berries are softer than cool berries (Sams, 1999) and more readily become dark during handling (Lyrene, 2006). The force needed to detach a ripe berry from the plant is lower when the temperatures are cool and the berry is fully turgid. Hot weather during harvest makes the berries of some highbush blueberry varieties taste bland, but the same high temperatures may make rabbiteye berries sweeter (Lyrene, 2006).

Rain during harvest can adversely affect fruit quality of highbush blueberries because it delays harvest, washes off fungicides, moistens stem scars, splits and softens berries, all of which can also impact the incidence of fungal diseases. The problem is exacerbated if high temperatures occur concurrently with rain (Pritts and Hancock, 1992). Frequent rains during harvest may dilute flavours and reduce berry sweetness (Lyrene, 2006).

**Nutrition**

Even though all essential elements are needed for adequate yield and high fruit quality, N, K and Ca are the nutrients most often linked with fruit quality in blueberries.

Ballinger and Kushman (1969) found that the application of N to highbush blueberry increased the fruit/leaf ratio and decreased fruit size and acidity. High levels of N can indirectly influence fruit quality by increasing shoot growth, which will reduce pesticide distribution within the canopy, increase risk of disease on fruit, delay maturation and delay fruit drying after a rain (Hart et al., 2006). Excess N has been associated with softer fruit (Sams, 1999).

Even though P deficiencies are rare in blueberries (Hart et al., 2006), low levels of P in highbush blueberry have been associated with fewer leaves, a high fruit/leaf ratio and small fruit size (Ballinger and Kushman, 1969). Low P has been reported to result in a loss of firmness, particularly in fruit that are low in Ca (Sams, 1999). Townsend (1973) observed that in one of three years fruit size in highbush blueberry decreased with application of P fertilizers.

Adequate K nutrition has been associated with increased yields, fruit size, soluble solids and ascorbic acid concentrations, improved fruit colour, increased shelf-life and better shipping quality of many horticultural crops (Lester et al., 2010). However, like N, K fertilization can result in a decrease in firmness or crispness, as measured by a decrease in resistance to compression (Sams, 1999). In fruit crops in general, an association has been found between pH regulation, organic acid levels and K content of fruit. Being the most abundant and mobile cation, K is generally associated with high fruit
acidity (Prange and DeEll, 1997). Ballinger and Kushman (1969) found that titratable acidity increased in highbush blueberry with higher K levels.

Ca is the element that has received most attention with regard to its beneficial impact on fruit quality and postharvest life of the fruit (Sams, 1999). However, the experimental effects of Ca sprays on fruit quality have been inconsistent. Ballinger and Kushman (1969) found that soil applications of Ca actually increased the fruit count to leaf count and decreased fruit size, while Hanson (1995) found no effects of preharvest Ca sprays on fruit quality. Stückrath et al. (2008) reported that 30 ml/l of a fertilizer containing 1.20 g Ca2+/l applied 12 times in the season at 4- to 19-day intervals to ‘Elliott’ highbush blueberries significantly improved fruit Ca levels and texture (as measured by presence of low-methoxyl pectins) and influenced fruit colour measurements (Hunter L, b, and chroma). Hanson and Berkheimer (2004) applied calcitic limestone (1100 kg/ha) or calcium sulfate (550 kg/ha) for five seasons to mature ‘Jersey’ highbush blueberries. The treatments increased soil pH and Ca levels, but had inconsistent effects on Ca levels in leaves and fruit. Ca applications did not alter berry yield, size, firmness or fruit rot incidence. Angeletti et al. (2010) applied 600 kg calcium sulfate/ha for one season to ‘O’Neal’ and ‘Bluecrop’ highbush blueberries and found reduced fruit softening, which was attributed to a 10% increase in Ca content in cell walls. Ca treatments also lowered the fruit respiration rate and weight, but did not affect colour, anthocyanins, acidity or sugar levels compared with control plants (no Ca).

It has been shown that Ca supply to the fruit not only depends on the provision of the element by the soil, but perhaps more importantly also on the capacity of the plant to capture the element (root growth) and the competition for Ca between reproductive and vegetative tissues (dry matter partitioning). This model fits with the observation that the removal of excess vegetation (i.e. summer pruning) can shift more water, and with it more Ca, to the fruit and fruit quality could then be improved.

**Plant water status**

A deficiency or excess of water can influence postharvest quality of berry crops. Management of water often poses a dilemma between yield and postharvest quality (Prange and DeEll, 1997). Since 80 to 90% w/w of the blueberry fruit is water, fruit growth is highly dependent upon water availability (Sargent et al., 2006). The grower has to establish an adequate level of water that will allow normal fruit growth, without reaching levels of excess water with the consequent reduced oxygenation of the root system. A mild water shortage can reduce crop yield and fruit size, but may benefit some quality attributes such as concentration of antioxidants, which are highest in the skin of the fruit (Mainland and Tucker, 2002). Monitoring and maintenance of adequate water levels are discussed in Chapter 6.
Canopy management

Ballinger and Kushman (1969) concluded that fruit count/leaf count ratio (F/L) influences highbush fruit quality to a greater degree than mineral nutrition. A high F/L results in later ripening, lower soluble solids, and smaller berries. During the harvest season, as berries are harvested, the soluble solids increase when the F/L ratio drops to a level of 1 to 2. These authors suggested that this was due to fewer fruit competing for carbohydrates from the sources (leaves). As mentioned in Chapter 4, light availability not only affects flower bud induction but also fruit quality. In rabbiteye blueberries, it has been found that fruits picked from shaded parts of the canopy have similar weight but are less blue than those exposed to the sun (Patten et al., 1987).

Harvest method

In general, machine-harvested blueberries are softer, have higher incidence of decay, greater rate of weight loss and shorter postharvest life than hand-harvested berries. Berries may be bruised at numerous points in the commercial mechanical harvesting and handling operation. Fruit are first removed from the plant by vigorous shaking, which can result in contact with neighbouring stems and other berries. The detached berries then fall as much as 1.5 to 2.5 m to the catching plates at the bottom of the harvester. On their way, they impact on plant structures and/or components of the machine. The berries then roll off the catching plates to a conveyor, which usually moves the fruit through a forced-air system to separate fruit from other plant tissues. Berries are then dropped at different heights on to other berries in a fruit lug. This lug may be transferred a few times before arriving at the packing shed (Dale et al., 1994).

The proportion of marketable fruit is generally much lower for mechanically harvested than hand-harvested fruit. Research with over-the-row harvesters done by Mainland et al. (1975) in North Carolina determined that machine harvesters operating in mature highbush blueberries decreased yield of marketable ripe fruit by 19 to 44%. Compared with commercially hand-harvested fruit, machine-harvested fruit was 10–30% softer, and when held for 7 days at 21°C the fruit developed 11–41% more decay. In the case of rabbiteye blueberries, Austin and Williamson (1977) reported hand-harvested fruit were 29 to 37% firmer, and after 7 to 11 days at 15.5°C, machine-harvested lots had more than twice the amount of soft and unmarketable fruit. In rabbiteye blueberries, respiration rates at ambient temperature were 31.1% higher for machine-harvested berries than for hand-harvested fruit (Nunez-Barrios et al., 2005). Additional research in rabbiteye blueberries (Miller and Smittle, 1987) showed that the magnitude of the effect of machine harvesters was dependent upon variety. The berries of ‘Climax’, which at harvest were firmer, less acidic and had lower SS/TA ratio than
'Woodard', developed less decay and had longer inherent shelf-life than those of 'Woodard' after machine harvest. These findings are basically inconsistent with the work of Galletta et al. (1971), which in highbush blueberry related higher SS/TA ratio to decreasing shelf-life.

Shaker-bar frequencies and harvest time during the day have a marked influence on harvested fruit quality. Howell et al. (1976) reported that, by decreasing vibration frequency, the amount of bruising on highbush blueberries was reduced. A decrease in shaker-bar frequency during high-turgor harvest times (night and early morning) has been found to foster improved fruit quality of blueberries. When 'Tifblue' rabbiteye blueberries were machine-harvested at different times of the day (06.00, 09.00, 12.00 or 15.00 hours), it was found that the number of mature berries remaining on the plants decreased with later harvest times during the day (Patten et al., 1988). Harvesting in early morning when there was dew on the fruit did not have detrimental effects on fruit storability relative to fruit harvested dry. However, the authors did not evaluate the possible negative impact of wet surfaces on fruit waxy 'bloom'. The effect of harvest time during the day on pack out and fruit quality after storage (14 or 28 days at 5°C) was inconsistent between and within years.

A harvester (V45) from the USDA that required bushes to be divided into a V shape during the shaking operation was studied for its effects on fruit quality. Trials on 'Elliott' and 'Bluecrop' blueberries harvested with the V45 showed that internal quality and firmness were better than those of the commercial rotary harvester and as good as the hand-harvested fruit (Brown et al., 1996; Peterson et al., 1997). Based on these promising results, the V45 was evaluated in 6-year-old 'Brightwell' and 'Powderblue' rabbiteye blueberries, as well as in 3-year-old 'FL-86-19' and 'Star' southern highbush blueberries. Plants had to be pruned to remove 30–50% of the canopy and open the middle, resulting in V-shaped plants. The V45 caused little cane damage. In rabbiteye blueberries, internal fruit damage and skin splitting were less in V45-harvested fruit than in fruit harvested by a sway harvester and nearly the same as those of hand-harvested fruit. However, in 'FL-86-19' southern highbush blueberry, the V45 detached a lower proportion of blue fruit and excessive amounts of immature and stemmed fruit. Percentage bloom coverage in the fruit harvested with V45 was intermediate between hand-harvested and sway-machine-harvested fruit for both rabbiteyes ('Brightwell') and southern highbush blueberry ('FL-86-19') (Takeda et al., 2008).

POSTHARVEST CONDITIONS

Maximizing quality and extending market life of fresh blueberries adds value to the fruit by enabling access to new markets (Forney, 2009). The maximum quality and storage life of the fruit have already been determined
when the fruit are harvested. Success in achieving the maximum storage life of blueberry fruit is dependent upon slowing down the degradative processes following ripening (senescence) and limiting the progress of decay. Two principles can be used to guide postharvest decision making: (i) the fruit is alive and responsive to the environment; and (ii) the fruit’s quality potential never increases after the fruit has been picked (Sargent et al., 2006).

Fruit quality loss during postharvest handling is primarily the result of decay, physiological breakdown, physical abuse and dehydration. Fruit must be of high initial quality to maximize postharvest life. Following harvest, blueberry fruit must be cooled and held near 0°C and at a relative humidity of about 95% for maximum storage life (Forney, 2009). Controlled or modified atmospheres are techniques that can be used in conjunction with low temperatures to enhance storage life and reduce decay of blueberries. With the expansion of the blueberry industry and the increased demand for high-quality fresh fruit, the use of postharvest technologies to optimize marketing of high-quality fresh fruit is of utmost importance.

Cooling after harvest

Harvested blueberries should be cooled as soon as possible. Sargent et al. (2006) recommended that if blueberries are going to be shipped, they should be cooled to 1°C within 4 h of harvest. Beaudry (1992) reported that reducing temperatures rapidly from field levels to 0°C increases shelf-life of highbush blueberries as much as eight- to tenfold relative to non-cooled fruit (Table 9.9) and causes an eightfold reduction in respiration rate. Research on rabbiteye blueberries has shown that immediate refrigeration at 1°C for hand-harvested fruit will give a gain of 35% in firmness compared with fruit left at 22°C for 8 days. Surprisingly, refrigeration had a marginal effect for machine-harvested fruit with 9% gain in firmness compared with ambient temperature (Nunez-Barrios et al., 2005). After 8 days, machine-harvested fruit and hand-harvested fruit stored at 22°C had equivalent firmness.

A reduction in respiratory rate signals a slowdown in the overall metabolism of the fruit, which influences softening, tissue breakdown and pigment synthesis. At a temperature of 26.7°C, blueberry respiration can produce as much as 6100 kcal of heat per ton per day. Unless this heat is removed by cooling, it can elevate fruit temperature as much as 14.4°C (Boyette et al., 1993). The respiration rate of blueberries at 26.7°C is nearly 20 times the rate at 4.5°C. In other words, blueberries held at 4.5°C have nearly 20 times the shelf-life of those held at 26.7°C.

Pallets of fruit need to be cooled as soon as possible, preferably through forced-air cooling. In still air, the average cooling rate of pallets of blueberries is slow because heat is transferred from the interior only by conduction and all of the materials surrounding the fruit reduce the cooling rate (Boyette et al.,
1993). It requires more than 36 h to cool blueberries in the centre of a pallet to 4.5°C with room cooling alone. Forced-air cooling can rapidly drop fruit temperature and reduce the metabolic activity of the fruit, delay the softening and thus reduce decay susceptibility. Depending on the circumstances, the rate of cooling has been found to be four to ten times (Vicente et al., 2005) or 16 to 20 times (Boyette et al., 1993) faster with forced cooling.

Forced-air cooling is accomplished by exposing packages (field lugs or trading packages) to higher air pressure on one side than on the other. This pressure differential forces the cool (1°C) and moist air (90–95% relative humidity) through the packages, which removes heat more effectively from the berries. To obtain proper air movement, it is necessary to adequately stack the packages in order to minimize any spaces that might force the air to pass around rather than through the containers, reducing cooling efficiencies. Recommendations call for 5% to 8% of the lateral surface and 3% to 5% of the total surface in the bottom to remain void in order to ensure adequate air movement through the packages (Vicente et al., 2005). Cooling with chilled water (hydrocooling) is very effective for blueberries that will be processed. However, it damages the bloom of the fruit, making it impractical for the fresh market (Sargent et al., 2006).

### Cooling during storage

After berries have been cooled, it is recommended that they be held at 0–1°C and 85–95% relative humidity (Vicente et al., 2005). Under these conditions blueberries can maintain an acceptable condition for two (Vicente et al., 2005) to three weeks (Schotsmans et al., 2007). The critical temperature for freezing blueberries is −1.3°C. Overall, berries with higher soluble solids content are less likely to freeze.

The effect of storage temperature differs among cultivars. For instance, Bounous et al. (1997) found that mass loss of highbush blueberries stored at 1°C for 3 weeks was 2.5% for 'Dixi', 21% for 'Darrow' and 25% for 'Coville'. On the other hand, firmness at harvest was 28% greater for 'Climax' than 'Woodard' rabbiteye blueberry, and the difference increased to 38% after 2 weeks of storage at 3°C (Miller and Smittle, 1987). Cultivars can vary in their response to cooling. NeSmith et al. (2005) found that the rate of firmness loss was similar among rabbiteye blueberry cultivars at 1°C and 12°C, except for 'Premier', which lost firmness more rapidly. At 22°C 'Brightwell' had the lowest rate of firmness drop. The greatest difference in rate of firmness loss among varieties was found at 32°C, where 'Powerblue' had a sixfold increase over 'Brightwell'. The extent of mass loss in response to temperature increases followed a similar trend to firmness loss, but there were fewer differences among cultivars (NeSmith et al., 2005).

Storing pallets of fruit at the optimal temperature of 0°C can sometimes
result in condensation forming inside the overwrapped package, which is unacceptable for most receivers (Beaudry, 1992). This condensation can be reduced by maintaining the fruit temperature at or above the dew point. The condensation can influence fungal decay, although its impact is generally thought to be minimal. However, some containers allow greater moisture loss than others. Almenar et al. (2008) compared decay levels of ‘Elliott’ highbush blueberries packed in the standard commercial clamshells made of polyethylene terephthalate (PET) or of the experimental biodegradable polylactide (PLA), and found that fungal development after 18 days at 10°C was lower in PET than in PLA containers (5% versus 11%). The effect could be attributed to the greater moisture loss in PET containers (Beaudry, 1992). Tasting panels showed that based on flavour, texture, external appearance and overall quality, consumers could distinguish between blueberries from different packages and they preferred those packaged in PLA containers (Almenar et al., 2010).

Nunes et al. (2004) studied the effects of various temperatures (0, 5, 10, 15 or 20°C) on the quality of ‘Patriot’ highbush blueberries and concluded that: (i) a single quality factor cannot be used to express loss of quality of blueberries over the normal physiological range of temperatures; and (ii) prediction of blueberry shelf-life calculated from data from the literature on respiration rates at various temperatures is not precise unless the type of cultivar and the quality of the fruit at harvest, as well as environmental factors involved, are well known and the limiting quality factor is closely related to the overall metabolic rate.

Controlled and modified atmospheres

Modified atmosphere (MA) and controlled atmosphere (CA) are used as supplements to temperature management for extending the postharvest life of berries (Vicente et al., 2005). This technology involves altering the normal concentrations of O₂ and CO₂. The difference between MA and CA is that the control of O₂ and CO₂ levels is active under CA while the control is passive under MA (Sargent et al., 2006). O₂ and CO₂ are biologically active molecules important in metabolic processes in plants. In the case of many climacteric fruits, O₂ and CO₂ act to delay ripening not solely through their influence on respiration per se, but largely through their inhibitory effects on the action of ethylene, the ripening hormone (Beaudry, 1999). Conditions of low O₂ and high CO₂ slow the decline in quality by inhibiting ripening and, at sufficiently high CO₂ concentrations, by suppressing decay organism’s activity (Beaudry, 1992) (Table 9.9). For blueberry, the impact of CO₂ on decay suppression tends to be of greater importance than the effects of reduced O₂.

The primary use of MA/CA for blueberries is in long-distance marine transport. A wide array of systems is available, from a simple one that keeps
Table 9.9. The effect of O₂ concentration and temperature on the shelf-life of ‘Bluecrop’, ‘Jersey’ and ‘Elliott’ highbush blueberry fruit stored in modified-atmosphere packages, as judged by visual rating only. CO₂ levels, while not reported, would be approximately a quarter of the gradient in O₂ between the package interior and air. (Adapted from Beaudry, 1992.)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Temperature (°C)</th>
<th>Average postharvest life (days)</th>
</tr>
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<tr>
<td></td>
<td>Air*</td>
<td>Intermediate</td>
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<tr>
<td>‘Bluecrop’</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>5</td>
<td>16</td>
</tr>
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<td>25</td>
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<tr>
<td>‘Target’</td>
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<tr>
<td></td>
<td>5</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>6</td>
</tr>
</tbody>
</table>

*Target O₂ concentrations referred to by ‘air’, ‘intermediate’, ‘optimal’ and ‘anaerobic’ are 21%, 15%, the lowest O₂ tolerated without causing fermentation (-2 to 4%) and levels that induce fermentation (<2%), respectively.

the fresh-air exchange gate closed if the CO₂ concentration is below a certain set limit (Thermo King AFAM+) to more sophisticated systems that have an initial gas flush followed by active ventilation controls (TransFresh Tectrol CA) or membrane separation systems with supplemental CO₂ injection (Carrier EverFresh). Another system consists of a large bag that is wrapped around a pallet and sealed with tape (TransFresh Tectrol MA); the bag is then pierced with a nozzle through which CO₂ can be injected to attain an atmosphere of 5–10% O₂ and 10–15% CO₂. The nozzle is then removed and the perforation is sealed (Bounous et al., 1997; Sargent et al., 2006).

One problem that faces the industry is the deleterious effects that occur once the CA containers are open and fruit is subject to dramatic changes in temperature and gas composition. Modified-atmosphere packaging (MAP) has the potential to provide low O₂/high CO₂ regimes similar to those of CA storage, but throughout the marketing chain. A package should maintain the atmospheric composition over the range of temperatures commonly encountered between harvest and consumption. Poor temperature control, however, can cause package O₂ levels to drop low enough to induce anaerobic respiration and generate off-flavours. MAP is designed to generate a physiologically adequate O₂ partial pressure inside the package by matching total respiratory O₂ uptake of the packaged product to the total permeation through the film (Beaudry et al., 1992).

The most appropriate concentrations of CO₂ to store blueberries range from 10 to 12% (Sargent et al., 2006), as decay organisms are controlled
and the physiological breakdown is slowed down (Beaudry, 1992). Sargent et al. (2006) reported that lowering the O₂ concentration would have little benefit in extending storage life and too low O₂ (<2% O₂) may inhibit flavour development or cause the development of off-flavours. The atmosphere surrounding the fruit during storage can have marked effects on fruit quality and condition depending upon Vaccinium species, cultivar, harvest date, handling immediately after harvest, storage conditions and packaging (Schotsmans et al., 2007).

Alsmairat et al. (2011) tested the impact of storage atmospheres on nine highbush cultivars in which the CO₂ and O₂ percentages summed to 21%. Fruit firmness, skin reddening and decay declined and the proportion of fruit with internal discoloration tended to increase as CO₂ concentrations increased. Cultivar effects were far more pronounced than atmospheric effects. ‘Duke’, ‘Toro’, ‘Brigitta’, ‘Liberty’ and ‘Legacy’ appeared well suited to extended CA storage, ‘Elliott’ stored moderately well and ‘Ozarkblue’, ‘Nelson’ and ‘Jersey’ stored poorly.

Work on five highbush blueberry cultivars (Remberg et al., 2003) found lower decay levels after 4 weeks under CA storage (10% O₂; 10% CO₂) when fruit were stored at 1°C, but the opposite trend was observed in two of those cultivars (‘Hardyblue’ and ‘Patriot’) when fruit were at 8°C. Rabbiteye blueberries stored for 28 days at 1.5°C had 5% decay in both regular storage (RS) and CA (2.5% O₂ + 15% CO₂) for ‘Maru’, but in ‘Centurion’ CA storage significantly decreased the incidence of decay from 8% to 1.5% (Schotsmans et al., 2007).

Schotsmans et al. (2007) found no effect of storage conditions (RS versus CA) on weight loss and shrivelling of ‘Centurion’ and ‘Maru’ rabbiteye blueberries after 6 weeks at 1.5°C. Beaudry et al. (1998) reported that mass loss of ‘Bluecrop’ and ‘Berkeley’ highbush blueberries was reduced by CA storage (2% O₂ and 8% CO₂, 21 days) compared with RS. After 6 weeks of storage at 1°C, weight loss was 10% lower in ‘Darrow’ and 25% lower in ‘Coville’ highbush blueberries stored under modified atmosphere (19% CO₂) compared with RS (Bounous et al., 1997).

Forney et al. (2003) found that firmness increased in ‘Burlington’ highbush blueberry fruit when stored at 0% CO₂, and that softening was slight at 10% CO₂ and increased at greater CO₂ levels (15, 20 or 25%) after 3 and 6 weeks at 0°C. Softening occurred concomitant with flesh discoloration. Schotsmans et al. (2007) found greater softening of ‘Centurion’ and ‘Maru’ rabbiteye blueberries in CA storage (2.5% O₂ + 15% CO₂) than RS (1.5°C).

Smittle and Miller (1988) reported that total sugar accumulation for rabbiteye cultivars ‘Climax’ and ‘Woodard’ decreased in storage, with a higher decrease in RS compared with CA storage. Similar trends were found by Schotsmans et al. (2007) for ‘Maru’ and ‘Centurion’ rabbiteye blueberries.

Remberg et al. (2003) found after 4 weeks that the changes in acidity were not consistent among highbush blueberry cultivars stored in RS or CA (10%
Pre- and Postharvest Management of Fruit Quality

02; 10% CO₂). Titratable acidity of ‘Centurion’ rabbiteye blueberry changed little during RS, whereas a significant increase occurred during CA storage of this variety. On the contrary, Smittle and Miller (1988) reported that pH and acidity of rabbiteye blueberries were not affected by storage duration or atmosphere composition.

Alternative methods for reducing postharvest spoilage

Currently the most common approaches taken to reduce postharvest spoilage of blueberries are based on controlling the rate of fruit ripening and pathogen growth using low temperatures, preventive fungicide applications and MA storage (Vicente et al., 2005). Fruit rot diseases are best controlled by using several integrated strategies. Success is reached when all the tools available are used to produce and maintain a quality berry. These include preharvest, harvest and postharvest procedures. Among the preharvest control methods are cultivar selection, fungicide applications, and pruning to open the canopy to allow better air circulation and fungicide coverage. Frequent harvesting to remove all ripe fruit will drastically reduce fruit rots (Cline, 1997) and prevention of infection through proper sanitation is effective to control decay.

Among the postharvest measures to reduce microbial spoilage of fruits are careful culling, storage at low temperatures or under controlled or modified atmospheres, and application of various chemicals and physical treatments (Miller et al., 1994). The most common postharvest method to reduce or slow down decay is cooling. ‘Bluetta’ and ‘Bluecrop’ highbush blueberries pre-cooled at 2°C had 60–80% less decay than berries that were not pre-cooled when held for 24 h at 21°C following a 3-day simulated transit period at 10°C (Hudson and Tiedjen, 1981). Even though the growth of many fungi is slower at 1°C, postharvest decays such as anthracnose (Gloeosporium spp.), grey mould rot (B. cinerea Pers. Ex Fr.) and alternaria (Alternaria spp.) result in spoilage (Miller et al., 1994).

In the last few years emphasis has been focused on developing alternatives to fungicide sprays. There has been increasing concern regarding the use of synthetic fungicides in fruit production and their presence in the environment due to health risks (Sharpe et al., 2009; Wang et al., 2010). These alternatives can be classified as chemical or physical treatments. Among the chemical treatments, the trend is towards the use of natural products. In blueberries there are reports on the effects of isothiocyanates, ozone, high-oxygen atmospheres, essential oils and hexanal. Allyl isothiocyanate (AITC) is a natural volatile compound that is present in plants belonging to the Brassicaceae family and is responsible for the pungent taste of mustard and horseradish. Application of AITC to ‘Duke’ highbush blueberries retarded blueberry decay by nearly 90% during storage at 10°C, but the treatment decreased total phenolics, total anthocyanins and reduced antioxidant
activities (Wang et al., 2010). The sensory quality of the fruit was not evaluated. Ozone has been reported to have strong antimicrobial effects against fungi and other pathogens. It rapidly inactivates microorganisms by reacting with intracellular enzymes, nucleic acids and components of cell envelopes and spore coats. In 2001, the US Food and Drug Administration approved ozone for use on food. In blueberry, ozone treatments (450 or 6000 ppb ozone for 48 h at 20°C) reduced growth of fungal spores of B. cinerea without deleterious effects on fruit quality; however, ozone had little effect on growth of Sclerotinia sclerotiorum and the overall incidence of decay was not reduced (Sharpe et al., 2009). The authors attributed this result to the high susceptibility of blueberries to fungal infection, and to the presence of latent infections that occurred at bloom and were not affected by the low penetration of gaseous ozone treatment.

'Duke' highbush blueberry fruit placed for 9 to 35 days at 5°C in high-oxygen atmospheres (40%, 60%, 80% or 100% O₂) showed decreased incidence of decay with increasing O₂ concentrations >40%. Titratable acidity, soluble solids and surface colour were little affected. O₂ levels between 60% and 100% promoted increases of total phenolics and total anthocyanins (Zheng et al., 2003).

Essential oils are aromatic oily extracts obtained from plant tissues. Various components of essential oils have been identified to be effective in inhibiting microbial growth. Increasing evidence has shown that some essential oils also possess antioxidant properties (Ruberto and Baratta, 2000). All seven essential oils tested inhibited 'Duke' highbush blueberry fruit decay development (16 to 72%) after 4 weeks at 10°C compared with control. The effect was attributed to the antimicrobial capability of these compounds, which would act through disruption of cellular membrane functions and interference with active sites of enzymes and cellular metabolism. Sugar and organic acid components were improved by oil applications. Even though there was usually an increment in antioxidant activity, the reduction in decay was not correlated with a promotion of antioxidant activity. This suggests that potential antimicrobial activity against pathogens causing spoilage is largely dependent upon the potency of a particular compound in inhibiting the microbes and not as much on its effects on antioxidant promotion (Wang, C.Y. et al., 2008).

Hexanal, or hexanaldehyde, is an alkyl aldehyde used in the flavour industry to produce fruity flavours. It is a natural plant volatile with antifungal properties that have been reported to reduce postharvest diseases. When 'Duke', 'Brigitta' and 'Burlington' highbush blueberry fruit were treated with hexanal vapour at 0.9 µl hexanal/l air for 24 h, there was a 50–70% reduction in decay in treated fruit compared with the control. Marketable fruit in all three cultivars was 20–40% greater in hexanal treatments after 12 weeks of storage compared with controls (Song et al., 2010). Considering that its volatile nature complicates the commercial use of hexanal, Almenar
et al. (2007) developed a method to encapsulate hexanal into cyclodextrins (naturally occurring molecules produced from starch) in order to control *in vitro* postharvest pathogens of berry fruits. They found that 1.1, 1.3 and 2.3 µl hexanal/l air was necessary to prevent growth of *Colletotrichum acutatum*, *B. cinerea* and *Alternaria alternata*, respectively.

The physical treatments trialled to control decay in blueberries include gamma and ultraviolet radiation and hot-water dips. When various doses (0 to 3 kGy) of gamma radiation were tried on 'Climax' rabbiteye blueberries it was found that irradiation generated softer berries and greater decay as dose was increased. The irradiated berries had lower consumer preference and reduced fresh market quality (Miller et al., 1994). Alternatively, ultraviolet radiation (UV-C at 0–4 kJ/m²) was tested as a means to extend shelf-life of 'Collins' and 'Bluecrop' highbush blueberries: while weight loss and firmness were found not to be affected by light treatment, decay incidence of ripe rot was decreased by 10% with 1–4 kJ/m² while antioxidants (total, anthocyanins, total phenolics and FRAP) were usually higher in treated fruit of both cultivars, with higher radiation levels needed to obtain significant effects on 'Bluecrop' (Perkins-Veazie et al., 2008). Hot-water dips are effective physical treatments for fungal pathogen control in various fruit species since most fungal spores and latent infections are either on the surface or in the first few layers under the epidermis of the fruit. Fan et al. (2008) found that *B. cinerea* and *Colletotrichum* spp. were the main spoilage microorganisms in ‘Burlington’ highbush blueberries. These fungi were effectively controlled by hot-water treatments (60°C for 15 or 30 s). Even though heat treatments diminished weight loss and the proportion of shrivelled and split berries, they also reduced the bloom of fruit most likely by melting the surface wax (Fan et al., 2008). This would limit the chances for this technique to be used in decay control of fresh fruit.

In summary, although there are some emerging technologies that could complement the benefits of low-temperature storage, fungicides and modified atmospheres, there are still many aspects that should be understood before these are adopted extensively. The feasibility and limitations of these options must be evaluated on a commercial scale (Vicente et al., 2005).

**CONCLUSIONS**

Blueberry production and marketing have increased markedly in the last decade. Maturity at harvest is the most important factor that determines postharvest life and final fruit quality. The highest quality fruit (higher sugar, better postharvest, maximum health benefits and more intense flavours) are those allowed to ripen fully on the plant. Fruit quality can be established by external appearance, sensory attributes, nutritional contents and microbiological condition.

Sensory studies have determined that the overall eating quality of blueberries is most tightly correlated with flavour acceptability and blueberry-like
flavour intensity. Blueberries do not possess a characteristic aroma, but over a hundred volatile compounds have been identified in their fruit. The size of the stem scar explains about 90% of fruit decay. Fruit colour depends upon components on and within the fruit skin and is determined primarily by the extent of the waxy bloom (quantity and structure).

Fruit firmness also relates to consumer appeal and to postharvest decay of the fruit. Even though soluble solids levels vary among seasons and locations, their values were more stable than titratable acidity or firmness. SS/TA values can predict postharvest life of the fruit. The keeping quality will be good for clones with SS/TA <18 and low for fruit with SS/TA >32. The pH values of blueberry extracts were correlated with scores of intensity of flavour and acceptability of flavour, as well as overall eating quality.

Blueberry fruits contain various phenolics, mainly anthocyanins, which contribute to antioxidant capacity. Anthocyanins account for up to 60% of total phenolic content in highbush blueberries. Besides genotype, the antioxidant capacity could be affected by location, growing season, maturity, and cultural and postharvest handling. There are contrasting results on the impact of cultivation type on antioxidants.

The variable storage life among and within cultivars is a result of inherent factors determining fruit quality, as well as their interaction with growing conditions and storage environments. Light, temperature, nutrients (especially K and Ca), CO₂ and water are the major environmental controllers of berry fruit quality. Fruit quality loss during postharvest handling is mainly the result of decay, physiological breakdown, physical abuse and dehydration.

Harvested blueberries should be cooled as soon as possible with forced air to reduce the respiration rate and slow the ripening process and the decline in quality. Berries stored at 0 to 1°C and 85 to 95% relative humidity can maintain an acceptable condition for several weeks. Controlled or modified atmospheres used in conjunction with low temperatures enhance storage life and reduce decay of blueberries. The most appropriate concentrations to store blueberries range from 10 to 12% CO₂ and 2 to 3% O₂. Lowering O₂ beyond <2% may cause the development of off-flavours.

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