Mini Risk Assessment
Silver Y Moth, *Autographa gamma* (L.)
[Lepidoptera: Noctuidae]

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Introduction
*Autographa gamma* is a polyphagous pest in much of Europe, Asia, and northern Africa. The likelihood and consequences of establishment by *A. gamma* have been evaluated in a pathway-initiated risk assessment. *Autographa gamma* was considered highly likely of becoming established in the US if introduced; the consequences of its establishment for US agricultural and natural ecosystems were also rated high (i.e., severe); (Lightfield 1997). In some parts of the world, this pest is also called beetworm (Zhang 1994).

*Figure 1.* Larval and adult stages of *Autographa gamma*
[Larval image from (CAB 2003); adult image from http://cgi.ukmoths.force9.co.uk/show.php?id=1134].

CAPS PRA: *Autographa gamma*
1. Ecological Suitability. Rating: High. *Autographa gamma* is found throughout the Palearctic. This region largely has a dry or temperate climate (CAB 2003). The currently reported global distribution of *A. gamma* suggests that the pest may be most closely associated with deserts and xeric shrublands; montane grasslands [not in the US]; and temperate broadleaf and mixed forests. Consequently, we estimate that approximately 48% of the continental US would be suitable for *A. gamma* (Fig. 2). See Appendix A for a more complete description of this analysis. In suitable areas, *A. gamma* should sustain populations by reproducing locally and overwintering successfully. However, *A. gamma* is a highly mobile pest, capable of both northerly and southerly migrations (Hill and Gatehouse 1992). If this pest migrated as far in the US as it does in Europe and Asia, all potential hosts would be in jeopardy of attack during particular times of the year.

![Figure 2. Predicted distribution of *A. gamma* in the continental US.](image_url)

2. Host Specificity/Availability. Rating: Low/High. This pest feeds on more than 200 different plant species, many of which are either low growing weeds or commonly cultivated crops (CAB 2003, Nash and Hill 2003). Notable host plants include: alfalfa/lucerne (*Medicago sativa*), alpine lady-fern (*Athyrium distentifolium*), artichoke (*Cynara scolymus*), arugula/ salad rocket (*Eruca sativa*), beet (*Beta vulgaris*), borage (*Borago officinalis*), Canada thistle (*Cirsium arvense*), Carnation (*Dianthus spp.*), carrot (*Daucus carota ssp. sativus*), chickpea (*Cicer arietinum*), chicory (*Cichorium intybus*), Chrysanthemum (*Chrysanthemum spp.*), corn (*Zea mays*), cotton (*Gossypium spp.*), cowpea (*Vigna unguiculata*), cruciferous crops (cabbage, kale, etc.) (*Brassica spp.*), dandelion (*Taraxacum officinale*), elderberry (*Sambucus nigra*), flax (*Linum usitatissimum*), geranium (*Pelargonium zonale*), grapevine (*Vitis vinifera*), green

See Appendix B for maps showing where various hosts are grown commercially in the US.

3. Survey Methodology. Rating: Medium. USDA (1986) provides some considerations for visual inspections of host plants for the presence of eggs, larvae, or pupae. In general, eggs may be found on the lower and upper surfaces of leaves. Larvae are likely to be found, if left undisturbed, on leaves that have been skeletonized or that have holes in the interior. Pupae may be found on the lower leaf surface (USDA 1986).

The sex pheromone, (Z)-7-dodecenyl acetate and (Z)-7-dodecenol in ratios from 100:1 to 95:5, has been used to attract and monitor male flight of A. gamma (Tóth et al. 1983, Mazor and Dunkelblum 1992, Dunkelblum and Mazor 1993). In field applications, the pheromone may be dispensed from rubber septa at a loading rate of 1 mg (Tóth et al. 1983, CAPS 1996). Lures should be replaced every 30 days (CAPS 1996). Newly-emerged adult males of A. gamma are not attracted to the pheromone; 3-d old males are most responsive to the lure (Szöcs and Tóth 1979). The pheromone of A. gamma may also attract other Lepidoptera in the US such as Anagapha ampla, Anagapha falcifera, Autographa ampla, Autographa biloba, Autographa californica, Caenurgia spp., Epismus argutanus, Geina periscalcidactyla, Helvitobys helvialis, Lacinipolia lutura, Lacinipolia renigera, Ostrinia nubilalis, Pieris rapae, Polia spp., Pseudoplusia includens, Rachiplusia ou, Spodoptera ornithogalli, Syngrapha falcifera (CAPS 1996, Cooper 1998), and Trichoplusia ni (Mazor and Dunkelblum 1992, Dunkelblum and Mazor 1993).

Sticky traps (i.e., Traptest traps) are relatively ineffective at capturing A. gamma; modified versions of an inverted cone trap (similar to Hartstack traps) baited with 0.1 mg of (97:3) E:Z-11-tetradecenyl acetate, a general attractant of several pest species of moths, captured 30-135 times more A. gamma than did sticky traps (Burgio and Maini 1995).
Adult males and females have also been collected using Robinson black-light traps (Craik 1979), but these traps attract moths non-discriminately. Such traps, placed 3m above the ground, have been used to successfully monitor the dynamics of *A. gamma* and other Noctuid moths (Zanaty et al. 1984-1985).

4. **Taxonomic Recognition. Rating: Low.** Several life stages of three Noctuid pests can be confused with *Autographa gamma*, of these, the most important species is *Trichoplusia ni* (Ronkay 1982, Nash and Hill 2003), as it is already present in the continental US (CAB 2003). The other easily confused species are *Cornutiplusia circumflexa* (Essex Y) which is geographically distributed in Europe, Asia and Africa (CAB 2003) and *Syngrapha interrogationis* (Scarce Silver Y) which is established in the United Kingdom (Nash and Hill 2003). Adults of *A. gamma* are grey to grayish brown in color with a “Y mark or gamma [γ] on the forewing” (Fig 1., Nash and Hill 2003). Nazmi et al. (1981) compare similarities and differences between closely related species. Species are most reliably identified by close examination of the genitalia (Nazmi et al. 1980-81, USDA 1986).

See Appendix C for a more complete taxonomic and morphological description of *A. gamma*.

5. **Entry Potential. Rating: Medium.** Interceptions of *Autographa gamma* or “*Autographa* sp.” have been reported 469 times since 1985 on vegetables, cut flowers, ornamentals, and other miscellaneous plants (USDA 2003). Annually, about 26 (±4 standard error of the mean) interceptions of *A. gamma* or “*Autographa* sp.” have been reported (USDA 2003). Historically, the majority of *Autographa* interceptions had been from European cut flowers and vegetables in ship’s stores (USDA 1986). From the mid-1980’s to the present, interceptions came more frequently from permit cargo. Specifically, the majority of interceptions were associated primarily with permit cargo (74%), general cargo (13%), and airline passengers (6%). Most interceptions have been reported from JFK International Airport (44%), Boston (10%), Elizabeth [New Jersey] (7%), Los Angeles (5%), Atlanta (5%), Dallas (4%), Miami (4%), and Memphis (4%). These ports are the first points of entry for cargo or airline passengers coming into the US and do not necessarily represent the intended final destination of infested material. Movement of potentially infested material is more fully characterized later in this document.

Interceptions of *A. grapha* have been reported from approximately 130 plant taxa.

6. **Destination of Infested Material. Rating: High.** When an actionable pest is intercepted, officers ask for the intended final destination of the conveyance. Cargo or passengers carrying materials infested with *A. gamma* or “*Autographa* sp.” were destined for 25 states, including the District of Columbia (USDA 2003). The most commonly reported destinations were New York (39%), Massachusetts (11%), California (9%), Texas (8%), New Jersey (6%), Florida (5%), and Georgia
(5%). We note six of these seven states have climate and hosts that may be suitable for establishment by *A. gamma* (Fig. 2).

7. **Potential Economic Impact. Rating: High.** *Autographa gamma* is pest of economic importance whose outbreaks damage many vegetable, flower, and greenhouse crops in Europe (Scopes and Biggerstaff 1973, Burges and Jarrett 1976, USDA 1986, Monnet 1997, INRA 2003). It is also an economically important pest of flax, sugarbeet, tobacco, and fruit and vegetable crops in Africa and the former Soviet Union (Dochkova 1972, Vasilev and Todorovski 1974, Harakly 1975, USDA 1986, CAB 2003). This pest damages sugarbeets by defoliating plants and, subsequently, reducing yields (Novák 1975). On all hosts, mature larvae cause the most damage (Dochkova 1972, Szöcs and Tóth 1979, Radin and Tošev 1983, INRA 2003). Feeding damage includes skeletonizing, or feeding on the leaf epidermis, as well as on the petiole (leaf stalk), leaving a cut leaf appearance (Harakly 1975, INRA 2003). First and second instar larvae feed on the leaf surface while third instar larvae will eat through the entire leaf (Novák 1975, USDA 1986). With respect to injury levels, an economic threshold of 25% loss in leaf area has been suggested, though a 60% loss of leaf area can be sufficient to destroy an entire crop (Novák 1975).

8. **Establishment Potential. Rating: High.** No US occurrences of establishment of the pest have been reported. A survey in Idaho found no moths in 188 traps (Cooper 1998). The pest was not detected in pheromone traps in South Carolina (CAPS 1996), nor Connecticut (Ellis 1998). Evaluation of the results of some of these surveys is complicated by the fact that not all portions of the states involved are equally suitable for establishment by *A. gamma*. However, the broad host range of the species, the availability of a suitable climate in portions of the US, and the strong dispersal capacity of adults (Macaulay 1972, Pedgley and Yathom 1993, Palmqvist 2001), contribute to its high potential for establishment in the US.

See Appendix D for a more complete description of the biology of *A. gamma*.

References:

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Appendix A. Comparison of climate zones. To determine the potential distribution of a quarantine pest in the US, we first collected information about the worldwide geographic distribution of the species (CAB 2000). We then identified which biomes
(i.e., habitat types), as defined by the World Wildlife Fund (Olson et al. 2001), occurred within each country or municipality reported for the distribution of the species. Biomes were identified using a geographic information system (e.g., ArcView 3.2). An Excel spreadsheet summarizing the occurrence of biomes in each nation or municipality was prepared. The list was sorted based on the total number of biomes that occurred in each country/municipality. The list was then analyzed to determine the minimum number of biomes that could account for the reported worldwide distribution of the species. Biomes that occurred in countries/municipalities with only one biome were first selected. We then examined each country/municipality with multiple biomes to determine if at least one of its biomes had been selected. If not, an additional biome was selected that occurred in the greatest number of countries or municipalities that had not yet been accounted for. In the event of a tie, the biome that was reported more frequently from the entire species’ distribution was selected. The process of selecting additional biomes continued until at least one biome was selected for each country. The set of selected biomes was compared to the occurrence of those biomes in the US.
Appendix B. Commercial production of hosts of *Autographa gamma* in the continental US.

Map 1. Alfalfa/lucerne (*Medicago sativa*)

Map 2. Artichoke (*Cynara scolymus*)

Map 3. Beet (*Beta vulgaris*)

Map 4. Carnation (*Dianthus spp.*)

Map 5. Carrot (*Daucus carota ssp. sativus*)
Map 6. Chicory (*Cichorium intybus*)

Map 7. Chrysanthemum; cut (*Chrysanthemum* spp.)

Map 8. Chrysanthemum; potted (*Chrysanthemum* spp.)

Map 9. Corn (*Zea mays*)

Map 10. Cotton (*Gossypium hirsutum*)

Map 11. Cowpea; dry (*Vigna unguiculata*)
Map 12. Cowpea; green (*Vigna unguiculata*)

Map 13. Cruciferous crops (broccoli-*Brassica oleracea* var. *botrytis*)

Map 14. Cruciferous crops (brussels sprouts-*Brassica oleracea* var. *gemmifera*)

Map 15. Cruciferous crops (cabbage-*Brassica oleracea*)

Map 16. Cruciferous crops (mustard cabbage-*Brassica* sp.)

Map 17. Cruciferous crops (cauliflower-*Brassica oleracea* var. *botrytis*)
Map 18. Cruciferous crops (pak choi-Brassica chinensis)

Map 19. Cruciferous crops (kale-Brassica spp.)

Map 20. Flax (Linum usitatissimum)

Map 21. Grapevine (Vitis spp.)

Map 22. Green bean/dry edible bean (Phaseolus spp.)

Map 23. Green bean/dry edible bean (Phaseolus spp.)
Map 24. Lettuce (*Lactuca* spp.)

Map 25. Onion; dry (*Allium cepa*)

Map 26. Onion; green (*Allium* spp.)

Map 27. Pea; dry (*Pisum* spp.)

Map 28. Pea; green (*Pisum sativum*)

Map 29. Pepper; hot (*Capsicum* spp.)
Map 30. Pepper; sweet (*Capsicum* spp.)

Map 31. Potato (*Solanum tuberosum*)

Map 32. Soybean (*Glycine max*)

Map 33. Spinach (*Spinacia oleracea*)

Map 34. Sugarbeet (*Beta vulgaris* var. *saccharifera*)

Map 35. Sunflower (*Helianthus annuus*)
Map 36. Tobacco (*Nicotiana tabacum*)

Map 37. Tomato (*Lycopersicon esculentum*)

Map 38. Wheat (*Triticum aestivum*)
Appendix C. Taxonomy of *Autographa gamma* (L.)

**Synonyms**
At the generic level:

*Autographa* (L.)
- *Phytometra* (L.)
- *Plusia* (L.)

At the species level:

*gamma* (Linnaeus) 1758
- *messmeri* Schadewald, 1992, Atalanta 23(3|4):577-580
- *voelkeri* Schadewald, 1992, Atalanta 23(3|4):577-580

**Description**

**Head:** [Quoted from Nazmi et al. (1981)] Vertex and frons with densely brownish grey erect hairs. Eyes naked, large, obscure, and densely lashed. Antennae filiform, brownish, about three-fourths of fore-wing, scape lighter than shaft; labial palpi strong, well developed and upturned with densely rough brownish scales. Tongue developed and coiled.

**Wings:** Adults of *A. gamma* can differ in appearance, depending on generation. “Specimens of the spring generation are oftensmall, with a more grayish colour, and the later generations are often brownish and with a larger wingspan” (Fibiger 1993). Wings are 20 mm from mid-thorax to wing tip (USDA 1986).

[Quoted from Nazmi et al. (1981)] Forewing large, dorsally with median area purplish grey, marked with golden gamma shapes, subterminal line dentated with dark shades; orbicular and reniform oblique, constructed on middle; ventrally paler.

![Figure C1. Wing venation patterns in *Autographa gamma*](Reproduced from Nazmi (1981))
Venation: [Quoted from Nazmi et al. (1981)] See Fig. C2 for general description of forewing. Sc reaching costal margin at about eight-elevenths length of wing; R₁ from cell at about seven-twelfths length of cell; R₂ from end of accessory cell; R₃ and R₄ stalked at about one-half way to margin, spaced distally; R₅ connate basally with the stem of R₃+R₄; M₁ free, M₂, M₃ Cu, proximated basally, spaced distally; Cu₂ from cell at about five-sixths length of cell; 2A and 3A complete.

![Figure C2. General diagram of forewing venation [Reproduced from Pogue (2002)]](image)

Ovum [Quoted from Carter (1984)]
Hemispherical; strongly and irregularly ribbed and reticulated; whitish, blue-grey around micropyle.

Larva:
[Quoted from Emmett (1980)]
Larvae with three pairs of prolegs only. Head with dark patch below ocelli or entirely black, glossy. Body varies from green with pale erratic longitudinal markings to almost black. Length [of late instar larve] variable, 30-30 mm.

[Quoted from Carter (1984)]
Head green, often with a conspicuous black streak extending posteriorly from ocellar region; in dark specimens, the black streak may be expanded to form a large blotch; body tapered towards head; prolegs present on abdominal segments 5, 6, and 10 only; body varying in color from yellowish green to greenish grey; dorsal line green bordered on either side by a sinuous, narrow, white line; irregular, narrow subdorsal line white; a white or yellowish white band between subdorsal and dorsal marginal lines; spiracles white, peritreme narrow, dark green or black; pinacula white, slightly raised; prothoracic and anal plates concolorous with integument; thoracic legs varying in colour from greenish brown to black.

Pupa: [Quoted from Sannino and Espinosa (2000)]
Pale green when just formed, gradually turning darkish starting from dorsum; black just before adult emergence. Cuticle generally rugose, granulose on head thorax and appendages, smooth on the rest of body. Dorsal cephalic margin of A1-7 finely punctate by very small papilliform reliefs [Fig C3]. Body cephalic end squat, little prominent and flattened. Lanceolate portion of the labium long a little more than half of the total length. Prothoracic femora length, 8-10 times prothoracic femora width. Caudal end of wings and maxillae extending to caudal margin of A6. Maxillae very long, circling forewing
tips. Metathoracic legs not visible. Abdominal spiracles elliptical (ratio length/width ca. 3-3.5/1), rather elevated and, on A3-6, with the cephalic margin prominent with respect to the caudal. Vice-like structures with the caudal jowl regularly rounded and provided with uniformly distributed papilliform reliefs; cephalic jowl in the middle prominent. Semiannular structures, with 6-8 transversal linear thin ridges, of which the inferior and the superior ones are only sketched. Some papilliform reliefs are present underlying the prominent caudal margin. The area beneath the said structures is little rounded and has some papilliform reliefs. Cremaster as typical in the group, with a ratio length/width ca. 1/1 and the basal portion wide twice the apical. It is dorsally canaliculated at the base and irregularly rugose moving towards the posterior end (particularly on the swelling).

Body length 17.4 ± 0.2 mm (range 16.0-18.8, No. = 34); body width (across the thorax) 5.3 ± 0.1 mm (r. 5-6.2, No. - 34).

**Figure C3.** Lateral view of stylized Plussinae pupa [Reproduced from Sannino and Espinosa (2000)] A, antenna; A1-A10, abdominal segments; C, cremaster; E, eye, F, frons; F1, femur of prothoracic leg; H, head; L, labium; L1, prothoracic leg; L2, mesothoracic leg; MS, mesothorax; MT, metathorax; MX, maxilla; P, prothorax; PS, prothoracic spiracle; S, abdominal spiracle; W1, mesothoracic wing; W2, metathoracic wing; WP, wing projection.
Male genitalia: [Quoted from Nazmi et al. (1981)] Male genitalia with uncus well developed, hairy, and curved with hook end; tegument elongate and moderately broad, vinculum moderately narrow; saccus well developed and elongate; valves elongated and broad apically; costa moderately sclerotized; cucullus moderately broad without corona, but with moderately large setae; clasper attached to the middle of valve far from clavus, elongate, finger-like with 6 small setae apically; clavus present, rounded apically and setose; aedeagus large, vesica moderately chitinized and armed with well sclerotized thorn-like cornutus.

Figure C4. Male genitalia of *Autographa gamma* [Reproduced from Nazmi (1981)]

Female genitalia: [Quoted from Nazmi et al. (1981)] Female genitalia with anal lobes moderate, triangular and clothed with longsetae, anterior apophysis shorter than posterior apophysis; ostium moderate, colliculum large and well chitinized, ducta bursa moderately long, tubular and somewhat chitinized; corpus bursa large, elongate and well chitinized at the entrance; ductus seminalis present near the top of the ductus bursa.

Figure C5. Female genitalia of *Autographa gamma* [Reproduced from Nazmi (1981)]
Appendix D. Biology of Autographa gamma

Population phenology

*Autographa gamma* typically has 2-3 generations annually, but under optimal conditions a fourth generation can occur (Dochkova 1972, CAB 2003). In Bulgaria, the species has three generations and initiates a fourth, incomplete generation each year (Dochkova 1972). In the laboratory, *A. gamma* will complete four generations per year (Rashid et al. 1971, Harakly 1975). *Autographa gamma* generally overwinters as a late-instar larva or as a pupa (Dochkova 1972), but it is not able to overwinter in all areas where it is a pest (Macauley 1974, Szöcs and Tóth 1979).

*Autographa gamma* is capable of long distance dispersal, and this high dispersal capability allows it to remain a pest in areas where populations cannot persist year round. The pest spends the winter months (until March) in the Black Sea and Mediterranean regions, and the early spring (April and May) along the northern Mediterranean, and the summer and fall in central and northern Europe (Szöcs and Tóth 1979, USDA 1986, Hill and Gatehouse 1992, INRA 2003). In autumn, adults migrate to North Africa and the Middle East to overwinter (Hill and Gatehouse 1992, INRA 2003). The arrival of *A. gamma* from southerly locations is consistently observed throughout northern and central Europe (Tóth et al. 1983). In northern Europe, temperatures are too cold for populations to persist through the winter (Hill and Gatehouse 1992) and in the Middle East it may be too hot for populations to withstand the summer (Pedgley and Yathom 1993). Cues that trigger a migration event are not clear but are probably related to food availability, temperature, moisture, and photoperiod (Novák 1976, Hill and Gatehouse 1992). Under shortened photoperiods, *A. gamma* has a longer adult pre-reproductive period, and a longer pre-reproductive period provides greater opportunity for migration (Hill and Gatehouse 1992).

Migration patterns vary widely from season to season, so there is no consistent, predictable pattern to population development in much of Europe (INRA 2003).

Climate, host plant type and availability, the ability to migrate, and the effects of parasites and diseases most affect the population dynamics of *A. gamma* (Maceljski and Balarin 1974).

Stage specific biology

The entire lifespan of *A. gamma* is 28-65 days, depending mainly on temperature (Rashid et al. 1971). Longevity is greater at lower temperatures than at higher temperatures (Harakly 1975).

**Adults.** *Autographa gamma* is active primarily at night (Macauley 1972, 1974, Harakly 1975, INRA 2003). Flight activity is greatest within three days after emergence (Macauley 1972) and before oviposition (Hill and Gatehouse 1992). During migrations, moths fly singly, or in groups ranging in size to several million individuals (INRA 2003). Moths can travel hundreds of kilometers (Macauley 1974, INRA 2003). During migration the moth flies during the day and night (Macauley 1972, Taylor et al. 1973).
In laboratory experiments, “...the moth flies spasmodically throughout the first few days and nights after emergence; subsequently, it flies only at night” (Taylor et al. 1973). During the night, *A. gamma* utilizes wind currents to facilitate dispersal; however, during the day, wind seems to have little influence on flight patterns (Taylor et al. 1973).

Mating occurs 1-2 days after eclosion and lasts 20-50 minutes (Harakly 1975). The preoviposition period depends on climate, but generally lasts 1-3 days (Harakly 1975). Moths begin egg-laying 1-5 days after mating (Rashid et al. 1971, Macaulay 1972).

The egg laying process starts off slowly and increases after the first day (Harakly 1975). Female moths can lay up to 1484 eggs but usually lay an average of 146-639 eggs (Dochkova 1972). Normally, about 500-600 eggs are laid (Harakly 1975, USDA 1986, CAB 2003). Under laboratory conditions, more eggs were laid between 13-16°C, and fewer eggs were laid at temperatures higher than 16°C (Hill and Gatehouse 1992). Eggs most often are laid singly but can rarely occur in groups of 2 or 3 (Vasilev and Todorovski 1974, CAB 2003). The adult moth lives 3-19 days and, this lifespan is longer in female moths than in males (Rashid et al. 1971, Harakly 1975).
**Eggs.** Eggs develop at temperatures of between 20-27°C (Dochkova 1972, USDA 1986) and hatch after 3-4 days (Rashid et al. 1971, Amate et al. 2000). Egg incubation may require 10-12 days under cooler temperatures (CAB 2003).

**Larvae.** *Autographa gamma* typically has 5-6 instars (Rashid et al. 1971, Dochkova 1972), however as few as 4 and as many as 7 instars have been reported under laboratory conditions (Harakly 1975). In general, higher temperatures lead to a shorter larval stage and food also largely affects the rate and thus, duration of development (Honek et al. 2002). In the field, larval develop in just under a month (CAB 2003, INRA 2003). More specifically, larvae require 21-25 days to develop during the summer; however, in the laboratory, larval development is complete in approximately 13 days (Vasilev and Todorovski 1974). In a separate laboratory study, the larval stage was reported to last an average of 20.6 ±1.70 days (Rashid et al. 1971). Some of this difference might be attributable to differences in food quality. Development on a suboptimal food source can take three times as long as development on optimal foods (Honek et al. 2002).

Larval activity occurs primarily at night (INRA 2003). In daytime, the larvae remain on the underside of the leaves (INRA 2003). Under laboratory conditions, “newly hatched” larvae moved around the surface of the host plant for 35-55 minutes when they then began feeding (Harakly 1975). In preparation for overwintering, larvae will move into soil (Vasilev and Todorovski 1974) or will reside on the underside of leaves (USDA 1986).

**Pupae.** Typically, the pupal stage lasts between one and two weeks (Rashid et al. 1971, Vasilev and Todorovski 1974); the duration is greatly influenced by climatic conditions (Harakly 1975). After the larva spins a cocoon, pupation occurs above-ground on host plants (Hill and Gatehouse 1992, CAB 2003) in leaf-folds or on other surfaces (INRA 2003).

**Interactions**

**Temperature and Relative Humidity**
Climate most directly affects the egg and larval developmental stages (Maceljski and Balarin 1974). Temperature greatly affects larval development; higher temperatures positively influence development while lower temperatures inhibit growth (Harakly 1975). Higher humidity and wet conditions positively affect the egg and larval stages (Maceljski and Balarin 1974).

Several studies have described the developmental threshold and accumulated degree days necessary for the completion of each phenological stage (Table 1).
<table>
<thead>
<tr>
<th>Stage</th>
<th>Developmental threshold (°C±SE)</th>
<th>Degree Days (±SE)</th>
<th>Notes</th>
<th>Reference</th>
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<tr>
<td>Egg</td>
<td>8.6 ± 0.14</td>
<td>56.6 ± 1.0</td>
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<td>Larva</td>
<td>5.9</td>
<td>374.4 ± 17.6</td>
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<td>(Dochkova 1972)</td>
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<td>6.5</td>
<td>261.6 ± 28.4</td>
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<td></td>
<td>7.6</td>
<td>282.6 ± 4.4</td>
<td>From authors’ Table 1</td>
<td>(Hill and Gatehouse 1992)</td>
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<tr>
<td>Pupa</td>
<td>9.9 ± 0.2</td>
<td>NA</td>
<td>From authors’ Table 1</td>
<td>(Honek et al. 2002)</td>
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<td></td>
<td>8.9 ± 0.4</td>
<td>127.2 ± 1.9</td>
<td></td>
<td>(Dochkova 1972)</td>
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<td>9.2</td>
<td>129.6 ± 1.9</td>
<td>From authors’ Table 1</td>
<td>(Hill and Gatehouse 1992)</td>
</tr>
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**Water**
Drought conditions limit population growth of *A. gamma* (Dochkova 1972). Rainy seasons increase *A. gamma* populations (Radin and Tošev 1983).

**Biotic Factors**
In years with high precipitation, parasites and viral infections can also limit population growth of *A. gamma* (Dochkova 1972). Parasites attack *A. gamma* during the larval stage; 88% of specimens collected from one field study were parasitized by *Apanteles ruficrus* (Harakly 1975). Viral diseases can so greatly impact the first generation that a second generation can be reduced to insignificant numbers (INRA 2003).