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Alate Production of Soybean Aphid (Homoptera: Aphididae) in Minnesota

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ABSTRACT The soybean aphid, *Aphis glycines* Matsumura, is a serious pest in Midwestern soybean, *Glycine max* L. Merrill, and has the potential to colonize a large geographic range throughout a single growing season. Our objectives were to describe colonization patterns on a statewide spatial and temporal scale, examine the changing proportion of winged forms throughout a season, and assess photoperiod as a potential trigger for alate production. In Minnesota, we define initial colonization as the period of time during the early vegetative growth when alates were present and alatoid nymphs were absent on soybean. Initial colonization during 2002 and 2003 was ~2 wk. On average across Minnesota, summer migrants were first produced when most fields were at the initial flowering stages in 2002. In 2003, an outbreak year, initial detection of summer migrants occurred earlier during vegetative stages before flowering. The significant increase in the proportion of all potential migratory forms (i.e., alatoid nymphs and adults) occurred during the beginning of seed set for both years. During seed set, the mean proportion of alate *A. glycines* was 0.15 ± 0.04 (SE) in 2002 and 0.16 ± 0.06 in 2003. The mean proportion of alatoid nymph *A. glycines* was 0.14 ± 0.04 in 2002 and 0.29 ± 0.04 in 2003 during seed set. The total mean proportion of migratory forms was higher when the critical L:D photoperiod was 14.5:9.5 h/d. A regression analysis also indicated the proportion of winged *A. glycines* increased with decreasing photoperiod.

KEY WORDS *Aphis glycines*, alatoid production, soybean, colonization

THE SOYBEAN APHID, *Aphis glycines* Matsumura (Homoptera: Aphididae), was recently discovered in the United States and Canada. The date and source of its introduction from Asia are unknown, but the aphid was discovered infesting soybean, *Glycine max* L. Merrill, fields in 10 midwestern states in 2000 (Venette and Ragsdale 2004). In Minnesota, *A. glycines* was initially restricted to several southeastern counties; however, *A. glycines* migrated west and north and was collected from all soybean-producing areas by August 2001 (Venette and Ragsdale 2004). The movement of this new exotic pest across the United States and Canada was rapid, and establishment of *A. glycines* was confirmed in 20 U.S. states as of 2002 (Venette and Ragsdale 2004).

The economic impact of this invasive pest has been severe and has changed soybean production practices in the Midwest. Soybean grown in Minnesota was rarely damaged by insects before the discovery of *A. glycines* and was considered to be a low-risk crop to use in rotation with corn (Pedigo et al. 1981). Since 2000, heavy infestations of *A. glycines* have caused economic yield loss up to 45% in some untreated fields (Ostlie 2001). The recommended economic threshold for *A. glycines* is 250 individuals (all stages) per plant

through pod set (UMES 2005). Even with this threshold, an estimated 2.1 of the total 4.2 million hectares of soybean grown in Minnesota were treated in 2003 (Landis et al. 2003).

Aphis glycines is heteroecious (uses primary and secondary host plants during winter and summer, respectively) and holocyclic (sexual morphs produce overwintering eggs on the primary host) (Dixon 1973), but reproduction in the spring and summer is strictly by parthenogenic viviparae (no males produced and females larviposit). Two morphological forms, apterae (wingless) and alate (winged) adults, are present during the growing season in Minnesota when soybean is at risk of damage by *A. glycines* (June–August). The factors that influence the production of *A. glycines* alates during the growing season are not fully understood.

Summer migrants are likely formed because of a combination of several stimuli. Factors that induce alate production in other aphids include temperature and host plant quality (Johnson and Birks 1960, Johnson 1965, 1966), diet composition (Sutherland and Mittler 1971), photoperiod (Lees 1966a, 1966b), and crowding (Dixon 1985, Lü and Chen 1993). Roitberg et al. (1979) showed that natural enemies, fungal pathogens, and plant viruses can also increase alate production. The actual density required for crowded

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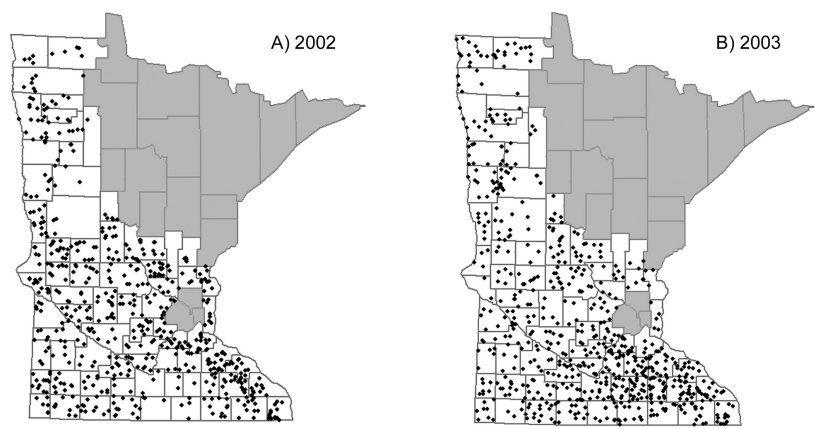


Fig. 1. *Aphis glycines* on *G. max* leaflet samples taken within Minnesota (circles indicate fields with *A. glycines*). (A) Summation of all fields sampled during 2002. (B) Summation of all fields sampled in 2003. Shaded counties do not have any *G. max* production.

conditions is species specific and can also be altered when in combination with other biotic and abiotic factors (Johnson 1965, 1966).

Colonization patterns for *A. glycines* in individual fields ranging from 4 to 20 ha have been described (Hodgson 2005, Hodgson et al. 2005); however, the distribution pattern on a larger scale is not well understood for this new pest. Here we describe the relative changes in the proportion of alates sampled from soybean fields during the growing season. The objectives of this paper were to describe the spatial and temporal population dynamics of alates in Minnesota, correlate spring and summer alate production with plant growth, and evaluate the critical photoperiod of summer migrants on a macro scale.

Materials and Methods

During 2002–2003, every soybean producing county in Minnesota (71 of 89 total counties) was randomly sampled from the early vegetative stage through seed set (Fig. 1). Sampling began on 27 May in 2002 and 28 May in 2003, which corresponded to 8 and 15%

average soybean emergence in Minnesota (UDSA 1997). Fields were chosen arbitrarily (i.e., only sampled once per year), and 30 plants from each field were sampled at random for *A. glycines*. As the first plant with *A. glycines* was observed, one leaflet with aphids was selected and placed in a 15-ml vial containing 70% ethanol. Each vial was labeled with the date, plant stage (see Fehr and Caviness 1977 for symbols and definitions), and geo-referenced. A total of 560 and 786 samples were collected in 2002 and 2003, respectively. In the laboratory, all aphids were carefully transferred with a fine camel hair brush into a 1.5-ml vial with 70% ethanol and later sorted under a stereomicroscope.

Key characteristics used for identifying instars were determined by observing *A. glycines* from a laboratory colony (Table 1) and using characters described by Zhang (1988). In alcohol-preserved specimens, we were unable to determine if first and second instars were developing wingpads. As a result, first and second instars were categorized as small instars and were not included in any analyses. The remaining aphids were categorized as large instars (third and fourth

Table 1. Identification of *A. glycines* life stages and morphological form

| Life stage | Ocular tubercles | No. antennal segments | Cauda size | Wing pads/wings |
|---|------------------|-----------------------|----------------------------|---------------------|
| Small nymphs, ^a morphological form not yet distinguishable | | | | |
| First instar | Absent | 4 (III ≈ IV) | Very reduced | Absent |
| Second instar | Present | 5 (III ≈ IV) | Somewhat apparent | Absent |
| Large apterous nymphs and apterae adults | | | | |
| Third instar | Present | 6 (III ≈ IV) | Apparent, wider than wide | Absent |
| Fourth instar | Present | 6 (III ≈ IV) | Apparent, longer than wide | Absent |
| Adult | Present | 6 (III > IV) | Apparent, very extended | Absent |
| Large alatoid nymphs and alatae adults | | | | |
| Third instar | Present | 6 (III ≈ IV) | Apparent, wider than long | Small pads apparent |
| Fourth instar | Present | 6 (III ≈ IV) | Apparent, wider than long | Large pads apparent |
| Adult | Present | 6 (III > IV) | Apparent and extended | Present |

^a Small nymphs refer to first and second instars, whereas large nymphs refer to third and four instars.

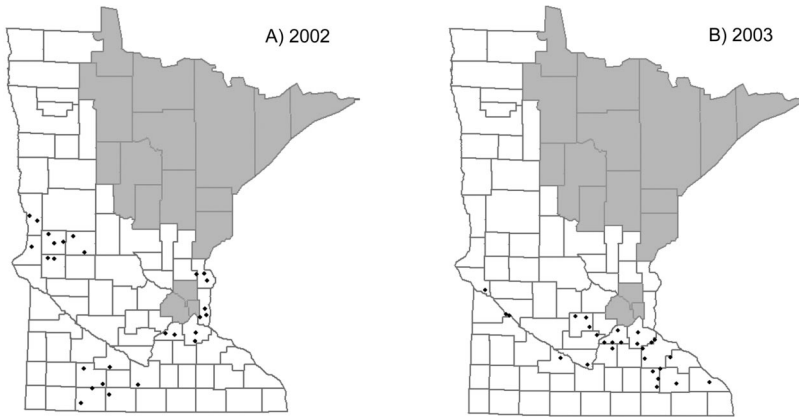


Fig. 2. First appearance of *A. glycines* on *G. max* leaflet samples within Minnesota (circles indicate fields with *A. glycines*). (A) 23–29 June 2002 with plants in the V3–V4 stages. (B) 15–21 June 2003 with plants in the V1–V2 stages. Shaded counties do not have any *G. max* production.

instars) with wingpads (alatoid nymphs) or without wingpads (apterous nymphs) or apterae or alate adults. Voucher specimens are located in the Department of Entomology, St. Paul, MN.

Samples were grouped by week, and the proportion of each age category and body morph was calculated so that seasonal differences of migratory forms could be compared. In addition to analyzing separate age categories and body morphs, the total proportion of alatoid nymphs and alates were combined to reflect all potential migratory individuals. The mean proportion and weighted SE were calculated by the following equations:

$$\bar{p} = \frac{\sum \alpha_i n_i}{N}$$

and

$$SE = \frac{\sqrt{\frac{\sum (p_i - \bar{p})^2}{N - 1}}}{\sqrt{N}}$$

where \bar{p} is the mean proportion of each category (i.e., alatoid nymphs, alates, or both), i is a sampled field, n is the number of aphids in each sample, N is the total number of samples for each week, and p_i is equal to α_i/n_i . The mean proportion of alatoid nymphs, adults, and both were averaged by the total number of samples per week because of the variation of aphids in each sample and total number of samples for each week. The proportions, p_i , were arc-sine square root transformed and analyzed using analysis of variance (ANOVA) and the Ryan-Einot-Gabriel-Welsch multiple range test (PROC GLM; SAS Institute 2001). Untransformed means of weekly proportions are reported here.

To evaluate photoperiod as a potential trigger for the development of migratory forms on a statewide scale, the proportion of light hours for each sample

week for Minnesota was calculated for 2002 and 2003 using the Sunrise Sunset Calculator (Edwards 1999). The average proportion of light hours in Minnesota was calculated for the northern and southern borders (≈ 645 km from Iowa to Canada) to estimate the variation of photoperiod within Minnesota during June–August. In addition, the average proportion of light per week for Minnesota was calculated using a geographical location (N 46.01974, W 95.03316). A linear regression analysis between the average proportion of light per week and the total proportion of alatoid nymphs and alates was performed (PROC REG; SAS Institute 2001).

Results and Discussion

In 2002, *A. glycines* was absent from all fields sampled throughout Minnesota the first 4 sampling wk. The first week with *A. glycines* was 23–29 June (Fig. 2), when the average plant stage throughout Minnesota was V3–V4 and $\approx 98\%$ of plants had emerged (MASS 2002). In 2003, *A. glycines* was absent the first 3 sampling wk; however, initial colonization occurred 1 wk earlier (15–21 June) than in 2002 when 94% of plants had emerged and the average plant stage was V1–V2 (MASS 2003). The alates captured in soybean in early June represent either local spring migrants coming from *Rhamnus* spp. or possibly long distant migrants from other regions. Analyses of variance for *A. glycines* between weeks were significant in 2002 (alatoid nymphs: $F = 7.56$; $df = 8,498$; $P < 0.0001$; alates: $F = 8.61$; $df = 8,498$; $P < 0.0001$) and in 2003 (alatoid nymphs: $F = 29.45$; $df = 8,674$; $P < 0.0001$; alates: $F = 2.64$; $df = 8,764$; $P < 0.0074$).

At initial detection in 2002, *A. glycines* was found in 15 counties throughout southern Minnesota (Fig. 2). The proportion of alates was low in 2002 (0.01 ± 0.01 SE) and continued to be a small proportion (0.01 ± 0.01) during 30 June to 6 July (Fig. 3). During 7–13 July, the proportion of alates was nearly zero (0.001 ± 0.001) and represented one alate from 93 samples

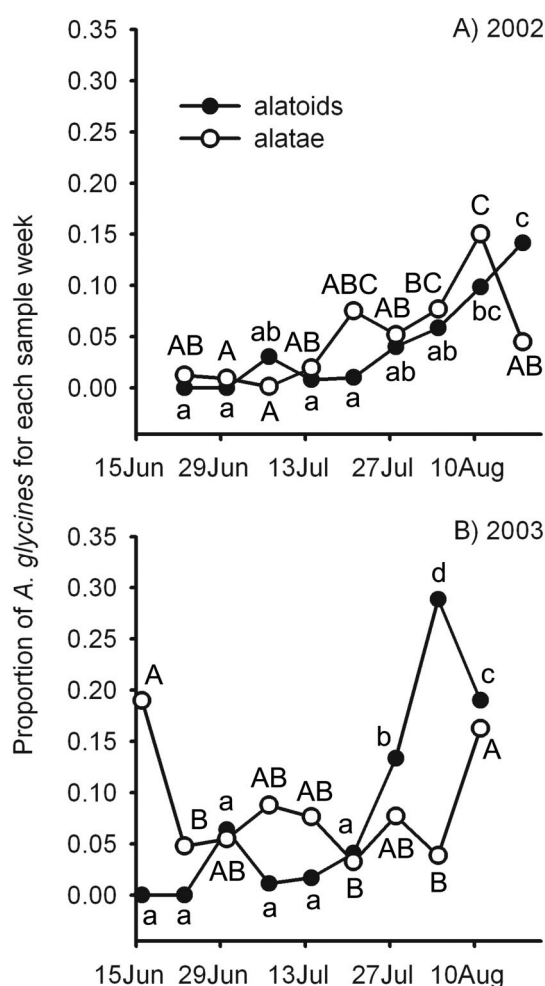


Fig. 3. The proportion of *A. glycines* alate nymphs and alates; means with same letter are not significantly different using GLM-REGWQ ($\alpha = 0.05$).

containing 383 total aphids (Fig. 3). When plants were at R3 (i.e., beginning pod set) during 21–28 July, the proportion of alates increased to (0.08 ± 0.03) ; Fig. 3). This midseason increase may represent summer migrants and is likely a result of individual apterous females responding to environmental conditions such as the declining host plant quality, crowding, or other stimuli (Blackman 1974, Dixon 1985). A significant increase in the proportion of alates (0.15 ± 0.04) occurred during 11–17 August when plants were at the R5 stage (i.e., beginning seed set; Fig. 3). During this week, 33 alates were found from 57 samples containing 393 total aphids. The alates may be a mixture of summer and fall migrants; however, gynoparae cannot be distinguished morphologically from summer migrants (Voegtlin et al. 2004a).

The proportion of alate nymphs in 2002 was zero during the 2-wk initial colonization period (Fig. 3). Alate nymphs were first detected during 7–13 July at a low proportion (0.03 ± 0.01) , and plants with alateoid

nymphs were in growth stage R1 (i.e., beginning flowering; Fig. 4). These alateoid nymphs developed into summer migrants within a few days. There was a significant increase in the proportion of alateoid nymphs (0.14 ± 0.04) during 18–24 August (Figs. 3 and 5), during which time plants were in the R5 growth stage (full size beans in green pods). These alateoid nymphs represent 45 aphids from 30 samples containing 253 total aphids. From the week of initial detection, alateoid nymphs were a consistently increasing proportion of the total number of aphids until that week.

At initial detection in 2003, *A. glycines* was found in 15 counties throughout southern Minnesota. Alates comprised 0.19 ± 0.06 of the total population (Fig. 3) at which time soybeans were in the early vegetative stage (V1–V2). During the last sample week of 10–16 August, the proportion of alates increased (0.16 ± 0.06) ; Fig. 3) when plants were in the R5 stage. In the last sample, 40 alates were found in 28 samples containing 1,116 total aphids (Table 2).

An absence of alateoid nymph production was observed in the first 2 wks after aphid detection (Fig. 3). Alateoid nymphs (0.06 ± 0.01) first appeared during the 29 June to 5 July with soybeans at the V4 plant stage (Figs. 3 and 4). Summer migration started 2 wk before flowering soybeans in Minnesota. There were no significant differences in the proportion of alateoid nymphs during the first 5 sampling wk; however, alateoid nymphs were detected in samples beginning the third week after aphids were first found. There was a significant increase of alateoid nymphs (0.29 ± 0.04) during 27 July to 2 August when soybeans were at the R5 plant stage (Figs. 3 and 5). These alateoid nymphs represent 808 aphids from 48 samples containing 2,070 total aphids.

On average, daylength in Minnesota reached its maximum of 16.0 light h during the summer solstice, and by 18 August, had declined to 13.8 light h (Fig. 6). In 2002 and 2003, the total proportion of potentially migratory aphids (alateoid nymphs and alates) was significantly higher during August (Fig. 6) when there was a L:D photoperiod of 14.5:9.5 h/d. Laboratory data are needed to confirm this observation, but it that seems significantly more alates are produced when the daylength drops to under 14.5 h of light. Regression analysis also indicated decreasing photoperiod was related to increasing proportions of alates in 2002 [$r^2 = 0.88$; $y = (-3.02 \pm 0.42)x + (1.97 \pm 0.26)$; $F = 50.73$; $df = 8,1$; $P < 0.0001$] and in 2003 [$r^2 = 0.69$; $y = (-4.35 \pm 1.11)x + (2.21 \pm 0.70)$; $F = 15.42$; $df = 8,1$; $P = 0.006$].

Based on cold temperature compatibility and host plant availability, *A. glycines* could successfully overwinter in some regions of Minnesota. McCornack et al. (2005) estimated the supercooling point of *A. glycines* eggs to be about -34°C , which suggests that survivorship is possible in southern regions of Minnesota. Temperatures routinely drop below -34°C in northern Minnesota, likely limiting the northern range of overwintering survivorship for *A. glycines*. For example, in years when winters are mild or when snow cover is deep, *A. glycines* might survive and be able to colonize

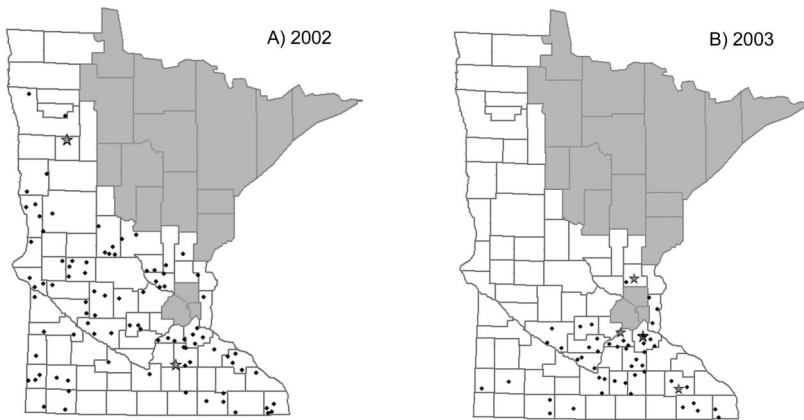


Fig. 4. First appearance of *A. glycines* alataid nymphs (circles indicate fields with *A. glycines* and stars indicate alataid nymphs) on *G. max* leaflet samples within Minnesota. (A) 7–13 July 2002 with plants in the R1 (i.e., flowering) stage. (B) 29 June to 5 July 2003 with plants in the V4–V5 stages. Shaded counties do not have any *G. max* production.

early vegetative soybean instead of migrating from other overwintering regions. However, if temperatures approach the lower lethal range for *A. glycines* eggs, survivorship will be decreased and colonization may be delayed.

Aphis glycines also have suitable primary host plants available in Minnesota. *Rhamnus cathartica* L., the most common overwintering host for *A. glycines*, is abundant in southeastern Minnesota and scattered throughout the state and is not a limiting overwintering factor (Ragsdale et al. 2004, Voegtlin et al. 2004b). In Minnesota during 2002 and 2003, apterous aphids were found in early vegetative commercial soybean fields and on *Rhamnus* spp. plants during the same sampling period (Ragsdale et al. 2004). Initial colonization from local *A. glycines* populations is possible with overwintering sites and favorable temperatures, and we consider the initial colonization on soybean from local sources but long distance migration is clearly possible.

Aphid species respond differently to light intensity, temperature, and host quality; however, accidental dispersal is rare, and most alates are obligatory migrants (Dixon 1985). Daily flight activity has not been determined for *A. glycines* but is probably similar to other aphids that prefer to fly during high light intensity and temperature periods. Most alates are in flight during the day when most of the samples are typically taken, and as a result, plant samples to estimate alate abundance often underestimate this morph. Nonattractive pan traps can be an effective way to collecting alates, although this type of sampling is a far more time-consuming way to sample migratory forms (Hodgson et al. 2005). The number of alates collected in 2002 and 2003 was always a small proportion of the total number of aphids (Fig. 3). Although the offspring of these alates were not reared for morph determination, the absence of alataid nymphs for the first 2 sampling wk implies that, in both years, alates could not directly produce alataid offspring. For most aphid

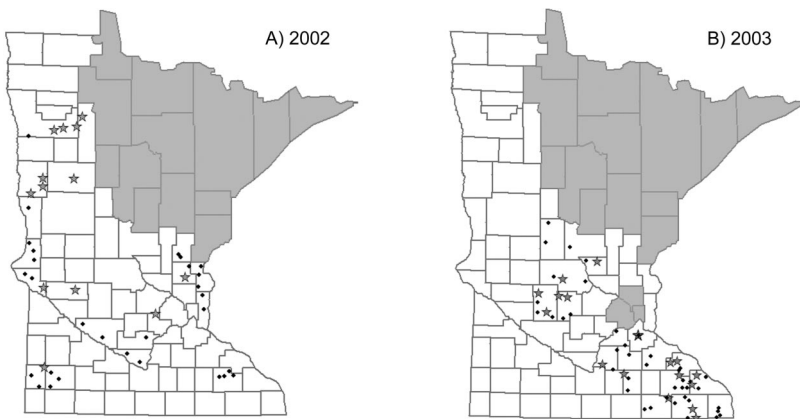


Fig. 5. Peak proportion of *A. glycines* alataid nymphs (circles indicate fields with *A. glycines* and stars indicate alataid nymphs) on *G. max* leaflet samples in Minnesota. (A) 18–24 August 2002 with plants at R5 (i.e., seed set) stage. (B) 3–9 August 2003 with plants at R5 stage. Shaded counties do not have any *G. max* production.

Table 2. Summary of *A. glycines* data collected in 2002 and 2003

| Sample week ^{a,b} | N ^c | n ^d | P (alatoids) ± SE ^e | p (alates) ± SE ^f |
|----------------------------|----------------|----------------|--------------------------------|------------------------------|
| 2002 | | | | |
| 23 June | 28 | 246, 49 | 0 ± 0 | 0.01 ± 0.01 |
| 30 June | 83 | 1,489, 215 | 0 ± 0 | 0.01 ± 0.01 |
| 7 July | 110 | 2,565, 383 | 0.03 ± 0.01 | 0 ± 0 |
| 14 July | 80 | 2,325, 446 | 0.02 ± 0.01 | 0.01 ± 0.00 |
| 21 July | 43 | 2,552, 516 | 0.01 ± 0.01 | 0.07 ± 0.02 |
| 28 July | 57 | 4,619, 890 | 0.04 ± 0.01 | 0.05 ± 0.01 |
| 4 Aug. | 52 | 5,850, 1,135 | 0.05 ± 0.02 | 0.07 ± 0.01 |
| 11 Aug. | 63 | 2,001, 393 | 0.09 ± 0.03 | 0.15 ± 0.04 |
| 18 Aug. | 32 | 1,559, 253 | 0.14 ± 0.04 | 0.04 ± 0.01 |
| 2003 | | | | |
| 15 June | 42 | 735, 170 | 0 ± 0 | 0.19 ± 0.06 |
| 22 June | 56 | 1,359, 352 | 0 ± 0 | 0.04 ± 0.02 |
| 29 June | 80 | 3,061, 1,352 | 0.06 ± 0.01 | 0.05 ± 0.02 |
| 6 July | 131 | 1,675, 503 | 0.01 ± 0.01 | 0.08 ± 0.02 |
| 13 July | 180 | 4,089, 1,240 | 0.01 ± 0.01 | 0.07 ± 0.01 |
| 20 July | 138 | 6,406, 1,814 | 0.04 ± 0.01 | 0.03 ± 0.01 |
| 27 July | 82 | 5,516, 1,597 | 0.13 ± 0.02 | 0.07 ± 0.02 |
| 3 Aug. | 48 | 4,846, 2,070 | 0.28 ± 0.04 | 0.03 ± 0.02 |
| 10 Aug. | 28 | 3,686, 1,116 | 0.19 ± 0.04 | 0.16 ± 0.05 |

^a Sampling for *A. glycines* started on 27 May 2002 and 28 May 2003.
^b Beginning of sample week.
^c Total no. of samples (vials) for each sampling week.
^d Total no. of aphids, total no. of large alatoid nymphs and adults.
^e Proportion of alatoid nymphs.
^f Proportion of alate adults.

species, alates cannot directly produce alatoid nymphs because offspring production is based on a physiological clock rather than on external pressures (Lees 1960, Dixon 1985).

Overall, *A. glycines* populations in 2002 were relatively low, and initial colonization was somewhat delayed compared with 2003 (Fig. 3). Soybean fields were occasionally treated for high populations of *A. glycines* in 2002, and economic loss was sporadic. In comparison, 2.1 million hectares of soybean were treated in 2003 in Minnesota alone, and aphid populations were severe and widespread (Landis et al. 2003). The life cycle of *A. glycines* is compatible with the seasonal patterns in the soybean-producing regions of Minnesota. In 2002 and 2003, initial colonization of *A. glycines* on soybean was characterized by the absence of aphids during late May and early June followed by the presence of alates for 2 wk. We observed a statewide absence of alatoid nymphs in the first 2 sample wk after initial detection of alates (Figs. 2 and 3). We interpret these data to mean that initial colonization on soybean in Minnesota is 2 wk in duration.

The first detection of alatoid nymphs may signify the development of summer migrants that can only develop on soybean in Minnesota. Summer migrants were first detected at the onset of soybean flowering (R1) in 2002 and during the mid-vegetative stage during 2003 (Fig. 2). An early indicator of potentially high populations of *A. glycines* may be the presence of summer migrating adults before flowering. The difference in the population dynamics of *A. glycines* between years may be triggered by an early initial col-

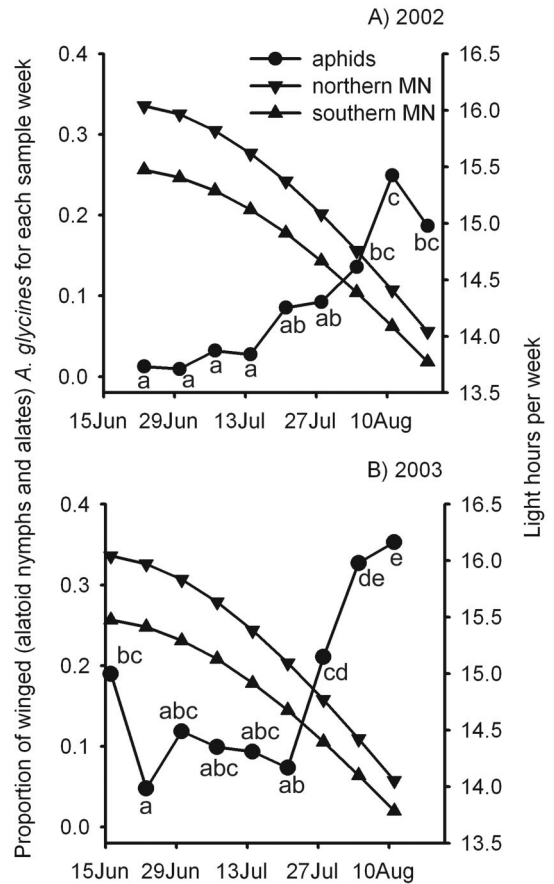


Fig. 6. The total proportion of *A. glycines* alatoid nymphs and alates compared with photoperiod in light hours for northern and southern Minnesota (to show statewide variation); means with same letter are not significantly different using GLM-REGWQ ($\alpha = 0.05$).

onization period because the number of potential generations (i.e., colonizing V1 versus V4 plants).

Factors that induce or suppress alate production are variable for each species. The timing of environmental triggers can be critical for the morphological determination of an aphid. In other aphid species, declining host plant quality, day length, and other physiological triggers have been described for development of summer migrants and decreasing day length combined with cool temperatures for development of sexuales (Lees 1966a, Blackman 1974, Dixon 1985, Mondor and Roitberg 2003, Ramos et al. 2003). Photoperiod does seem to affect alatoid production for *A. glycines* on a relatively large scale, although there is also likely a low temperature requirement that accompanies decreasing light availability. The proposed critical photoperiod of *A. glycines* is similar to the vetch aphid, *Megoura viciae* Buckton (14.5 h; Lees 1966a), and the black bean aphid, *Aphis fabae* Scopoli (13.5 h; Hardie 1987). However, Hardie (1987) proposed scotophase (i.e., dark periods) may actually be more significant than photophase (i.e., light periods).

Future research is needed to determine what factors trigger development of *A. glycines* migrants. Most literature supports nutrition and crowding as summer alate triggers; alternatively, other factors can inhibit alate production. Stress caused by extreme starvation may outweigh the cost of producing alatoid offspring, where adults only produce apterous individuals (Lees 1966b). Mutualistic relationships with ants can also develop on plants, where ants inhibit wing production in aphids by secreting dendrolasin, a compound found in the mandibular glands (Lees 1966b, Kleinjan and Mittler 1975, Müller et al. 2001).

The potential of initial colonization by *A. glycines* in Minnesota soybean is variable depending on overwintering conditions, proximity of spring host plants, and a suite of other unknown factors not discussed in this paper. *A. glycines* is present on early vegetative soybean and *Rhamnus* spp. at the same time, and initial colonization to soybean is ≈ 2 wk. Soybeans throughout Minnesota will likely be colonized during the mid-vegetative through the reproductive plant growth stages in a typical growing season because of the continuous production of alates throughout the summer.

Acknowledgments

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