Life-history parameters and population dynamics of *Ericaphis fimbriata* (Hemiptera: Aphididae) on blueberry, *Vaccinium corymbosum*[1]

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Abstract—Development rate and age-specific fecundity and survival of *Ericaphis fimbriata* (Richards) virginoparae were determined during the spring on young leaves of blueberry, *Vaccinium corymbosum* L., as functions of temperature. The same traits were measured during the summer and the autumn on both young and mature leaves at 21.2 °C. The temperature threshold for development was 4.1 ± 0.5 °C (SE). For apterae, development time from birth to adult was 157.7 ± 5.9 day-degrees (dd). Proportional lengths of instars I–IV were 0.16, 0.14, 0.34, and 0.36, respectively. Adult life was 434.5 ± 17.5 dd and proportional lengths of the pre-reproductive, reproductive, and post-reproductive periods were 0.05, 0.74, and 0.21, respectively. Mean fecundity was 23.6 ± 1.0 nymphs per female. Mean survival was 602.9 ± 14.6 dd, and more than 80% of apterae survived the peak reproductive period. Alate fecundity was 16.5 ± 3.2 nymphs per female and alate survival was 460.9 ± 47.5 dd. Leaf type and season of measurement had significant effects on development time and fecundity: development time was 158.2 dd (+4.9 upper asymmetric SE) on young *V. corymbosum* 'Duke' leaves in the spring but 312.4 dd (–16.9 lower asymmetric SE) on mature 'Bluecrop' leaves, the dominant leaf type, from a commercial field in the summer. Fecundity for the respective leaf types and seasons was 16.7 (–1.6) and 1.4 (+ 0.5) nymphs per female. From summer to autumn, development time increased on young 'Duke' and 'Bluecrop' leaves but decreased on mature 'Bluecrop' leaves; fecundity decreased on young 'Duke' and 'Bluecrop' leaves but remained at low levels on mature 'Bluecrop' leaves. A simulation model showed that seasonal changes in development time and fecundity were capable of reducing population growth rates to near zero depending on aphid distribution with respect to young and mature leaves. The results support a combined bottom-up and top-down view of aphid population regulation and suggest that control efforts should focus on the spring, when the population growth rate is maximal.

Résumé—Nous avons déterminé le taux de développement, la fécondité en fonction de l'âge et la survie en fonction de l'âge des femelles virginipares d'*Ericaphis fimbriata* (Richards) au printemps sur de jeunes feuilles de l'airelle *Vaccinium corymbosum* L. en regard de la température. Nous avons répété les mêmes mesures en été et en automne sur des feuilles jeunes et matures à 21,2 °C. Le seuil thermique du développement est de 4,1 ± 0,5 °C (ET). Chez les aptères, la durée du développement de la naissance à l'état adulte est de 157,7 ± 5,9 jours-degrés (jd). Les durées proportionnelles des stades I–IV sont respectivement de 0,16, 0,14, 0,34 et 0,36. La vie adulte dure 434,5 ± 17,5 jd et les durées proportionnelles des périodes pré-reproductive, reproductive et post-reproductive sont respectivement de 0,05, 0,74 et 0,21. La fécondité moyenne est de 23,6 ± 1,0 larves par femelle. La survie moyenne est de 602,9 ± 14,6 jd et plus de 80 % des individus survivent à la période de reproduction maximale. La fécondité des femelles ailées est de 16,5 ± 3,2 larves par femelle et leur survie est de 460,9 ± 47,5 jd. Le type de feuille et la saison dans laquelle se font les mesures ont des effets significatifs sur la durée du développement et la fécondité; la durée du développement est de 158,2 jd (+4,9, ET asymétrique supérieure) sur de jeunes feuilles « Duke » de *V. corymbosum* au printemps, mais de 312,4 jd (–16,9, ET asymétrique inférieure) sur des feuilles matures « Bluecrop », le type dominant de feuilles, dans une

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bleuetière commerciale en été. Les fécondités sur les deux types de feuilles et les deux saisons sont respectivement de 16,7 (–1,6) et de 1,4 (+0,5) larves par femelle. De l'été à l'automne, la durée du développement augmente sur les jeunes feuilles de types « Duke » et « Bluecrop », mais elle diminue sur les feuilles matures « Bluecrop »; la fécondité diminue sur les jeunes feuilles « Duke » et « Bluecrop », mais elle reste faible sur les feuilles matures « Bluecrop ». Une modèle de simulation montre que les changements saisonniers de durée du développement et de fécondité sont capables de réduire les taux de croissance de la population à presque rien, selon la répartition des pucerons entre les feuilles jeunes et matures. Ces résultats incitent à invoquer une combinaison de contrôles ascendants et de contrôles descendants pour expliquer la régulation de la population et indiquent que les efforts de contrôle devraient s'exercer au printemps au moment où le taux de croissance de la population est maximal.

[Traduit par la Rédaction]

Introduction

Ericaphis fimbriata (Richards) (= *Fimbriaphis fimbriata*) (Hemiptera: Aphididae) (Remaudière and Remaudière 1997) is the dominant aphid on blueberry, *Vaccinium corymbosum* L. (Ericaceae), in southwestern British Columbia, Canada (Raworth 2004). Populations can increase to several thousand aphids per plant by the end of June in commercial fields. *Blueberry scorch virus* (BlScV) has been detected in 76 blueberry fields in southwestern British Columbia (Wegener *et al.* 2003). BlScV is a member of the carlavirus group and is transmitted by *E. fimbriata* in a nonpersistent fashion (Bristow *et al.* 2000). Symptoms depend on the virus strain and the blueberry cultivar and include severe blighting of flowers and young leaves, twig dieback, and yield reductions of more than 85% in the third year of symptom expression. Chemical aphid controls applied in June provide inconsistent results, yet populations consistently decline during July and August (Raworth 2004). Understanding the forces that drive the observed population dynamics is essential for developing rational aphid management strategies. This paper describes the basic life-history parameters of *E. fimbriata* (development rate and age-specific fecundity and survival) as functions of temperature and season. The data were modelled and the resulting rate of population increase was compared with field data. Implications for aphid population dynamics theory and management of aphids on blueberry are discussed.

Materials and methods

Development rate, fecundity, and survival versus temperature

A colony of the green form of *E. fimbriata* was initiated on 28 March 2003 from the progeny of 33 fundatrix aphids collected from potted blueberry plants that were naturally infested the previous autumn and subsequently maintained in a screenhouse (49°01′N, 122°21′W) at Abbotsford, British Columbia. The colony was maintained on potted plants, *V. corymbosum* 'Duke', in screened cages within a greenhouse (49°15′N, 121°46′W) at Agassiz, British Columbia. The greenhouse received natural lighting, was heated to 20 °C, and was vented for cooling as necessary. 'Duke' plants for the following studies were grown in 8 L pots, maintained under ambient conditions outside, and fertilized weekly with 20:20:20 N–P–K.

On 21 May, 128 adult aphids from the colony were placed on 18 young 'Duke' leaves (5 cm long) collected three to five leaves back from a growing tip. Aphids were held in seal-tight dishes (5 cm diameter) with filter paper moistened with distilled water on the bottom. After 19 h at 21 °C, 129 progeny were individually isolated in similar dishes and randomized among three environmental chambers. Temperatures were measured with calibrated Hobo® loggers (Onset Computer Corp., Bourne, Massachusetts) recording every 36 min. Chamber temperatures were 11.9 ± 0.43 °C (SD), 16.8 ± 0.19 °C, and 20.9 ± 0.27 °C, and temperatures within the dishes were 0.5 °C higher when the dishes were illuminated; lighting was 175 $\mu E \cdot m^{-2} \cdot s^{-1}$ (1 µE = 1 µmol of photons) and 16L:8D. Hereafter, experimental temperatures cited are those experienced by the aphids within the dish. Aphids at 12.2 and 17.1 °C were checked daily, and aphids at 21.2 °C were checked twice daily, for exuvia, progeny, and death. Leaves were replaced weekly with fresh young leaves and, because the lids on the dishes allowed some air exchange, distilled water was

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added to the filter paper every 3–6 days, depending on temperature, to maintain leaf turgidity.

Events were assumed to occur at the midpoint of the check interval. Complete developmental records from birth to death were obtained for 100 apterous aphids and 9 alatae; records for which a molt was missed were not utilized. The data were analyzed separately for apterae and alatae, using regression (Campbell *et al.* 1974; SAS Institute Inc. 1990), to determine the temperature threshold for each instar, the period from birth to adult, the pre-reproductive, reproductive, and post-reproductive periods, and adult life (molt to adult to death). Curvature was tested by adding x^2 to the regression. Duration of each life stage in day-degrees (dd) above a common threshold of 4.1 °C was determined by deducting the threshold from the temperature experienced by the aphids and forcing the regression through the origin. Instar durations were determined as proportions of the duration from birth to adult using ratio estimation based on the relative instar lengths in day-degrees above 4.1 °C. Similarly, the lengths of the pre-reproductive, reproductive, and post-reproductive periods were determined as proportions of adult life. Lifetime fecundity was regressed against temperature separately for apterae (n = 113, including those aphids for which a molt was missing) and alatae (n = 11). A curve of the form $y = a + b(1.0 - e^{cx})$, where x = 100/temperature, was fitted to the lifetime fecundity data for apterae using PROC NLIN in SAS® (SAS Institute Inc. 1990). Age-specific fecundity and survival curves were determined for apterae at each temperature on both calendar and physiological time scales, and for alatae on a physiological time scale, combining data from all temperatures. Aphid age on the physiological time scale was expressed as quarter-instar periods (quips) (Frazer and Gilbert 1976), where 1 quip = 5.9 dd above 4.1 °C.

Development rate, fecundity, and survival versus leaf type and season

Ericaphis fimbriata nymphs were set up in seal-tight dishes, as described above, on 28 July and 18 September. Nymphs were derived from 49 and 79 adults collected from a commercial 'Bluecrop' field (49°1′N, 122°16′W) at Abbotsford and the laboratory colony on the respective dates. For each date, 45 progeny were randomized among three treatments (leaf types): young leaves from potted 'Duke' plants at Agassiz; young leaves from the commercial 'Bluecrop' field at Abbotsford; and mature leaves from the same field. Aphids were maintained at 21.2 °C and checked twice daily for exuvia, progeny, and death. Measurements from the 21 May trial at 21.2 °C (young leaves from potted 'Duke' plants) were added to the data. Development time from birth to adult (dd above 4.1 °C), lifetime fecundity, and survival were analyzed by ANOVA (SAS Institute Inc. 1990) after log transformation of development time and fecundity to stabilize the variance (Southwood 1966). The model was y = leaf type, season, leaf type × season interaction. Means and SEs for development time and fecundity were back-transformed and plotted against the date the trial was initiated.

Availability of young and mature leaves in the field at Abbotsford was determined weekly from 23 July to 22 October. A leaf terminal was defined as a stem with leaves, produced from a bud. Leaf terminals were sorted into two categories, those having all mature leaves and those having some young leaves. The number of leaf terminals in each category was counted on 10 blueberry branches at each sampling. For each terminal with young leaves, the numbers of young and mature leaves were counted. The proportion of terminals with one or more young leaves and the proportion of young leaves on those terminals were calculated.

Modelling

Life-history data were modelled on a day-degree time scale using a "boxcar" simulation written in FORTRAN (Gilbert *et al.* 1976). Step length was one quip. Durations for instars I–IV were 4, 4, 9, and 10 quips, respectively. The model incorporated the age-specific fecundity and survival data for apterae obtained at 12.2 °C because that temperature best represented temperatures during April, May, and June; means of mean daily temperatures and SDs at the Abbotsford Airport for these months in 2001, 2002, and 2003 were 9.3 (±2.6), 12.4 (±3.0), and 16.1 (±2.8) °C, respectively. The model population was initiated with one newly emerged fundatrix aphid. Raworth (2004) indicated that fundatrices emerged between 17 February and 24 March 2003 at Agassiz, but most emerged in March. Time of emergence was set at 12 March. Day-degrees in the field from 1 January to 12 March were calculated above a threshold of 4.1 °C using the sine method (Raworth 1994). Daily minimum and maximum temperatures were obtained from the Environment Canada site at

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Agassiz, British Columbia. This timing suggested a duration of 153 dd (26 quips) after 1 January for fundatrix emergence. Developmental threshold and rate were assumed to be the same as for apterous virginoparae. Age-specific fecundity and survival of fundatrices were also assumed to be the same as for apterous virginoparae, but age-specific fecundity was reduced proportionally to the ratio of the lifetime fecundity of fundatrices and the lifetime fecundity of apterous virginoparae at 12.2 °C (19.4/26.6 = 0.73). The latter estimate (26.6) is discussed below; the former estimate (19.4 ± 3.27 (SE), n = 13) was measured during April 2003 on mature 'Bluecrop' leaves from a plant maintained in the greenhouse at Agassiz and fertilized weekly with 20:20:20 N–P–K; temperatures fluctuated between 12 and 20 °C (mean = 15.0 °C), and lighting was 15L:9D.

The model incorporated the production of fourth-instar alatae using a regression of ln(proportion of fourth-instar aphids that had wing pads) (y) against quips (x) ($y = 0.93 - 0.016x$; $r^2 = 0.41$, df = 50, $P < 0.001$). Data were obtained from aphid samples of nine field populations during 2001 to 2003 (Raworth 2004): 2001, Abbotsford south (49°01′N, 122°16′W) and Richmond (49°09′N, 123°04′W); 2002, Abbotsford south, Richmond, Cloverdale (49°05′N, 122°48′W), Pitt Meadows (49°18′N, 122°38′W), and Abbotsford north (49°06′N, 122°16′W); and 2003, Abbotsford south and Richmond. Quips were determined as described above, using minimum and maximum temperatures from the closest Environment Canada site: Vancouver International Airport, 49°12′N, 123°10′W; Abbotsford Airport, 49°01′N, 122°21′W; Pitt Meadows Campbell Scientific, 49°12′N, 122°40′W; and Cloverdale East, 49°06′N, 122°43′W. Developmental threshold and rate for alatae were not significantly different from the estimates for apterae, so the estimates for apterae were used to simulate alate development in the model. However, fecundity and survival for alatae were different from the estimates for apterae, so age-specific fecundity and survival for alatae in the model were derived from the combined data for alatae at all three temperatures.

Rates of population increase during the spring, in the nine field populations described above, were compared with simulated rates after the age distribution stabilized (quip 80), with and without alate emigration. The rate of population increase was calculated as the slope of the regression of ln(number of aphids) versus quip. Slopes were determined separately for each field population during April, May, and June, when aphid numbers on a log scale increased approximately linearly with physiological time (quips), and aphidophagous predators and parasitoids either were not detected or were detected in low numbers. The rates of increase were weighted by the reciprocal of the variance of the estimate, and the mean was calculated.

An important practical concern for pest managers relates to the sample size needed to determine aphid density in early April, after egg hatch (Raworth 2004). The model and the sample data from the nine field populations during spring were used to estimate fundatrix density in each field. Mean quip and aphid density were calculated for each field population, and the model was run to determine fundatrix densities that would provide equivalent model densities at the appropriate quip. Probabilities of detecting aphids in samples of 50, 100, 500, and 1000 terminals were then calculated for a series of aphid densities that bounded the fundatrix density estimates, assuming that in early April each infested terminal is occupied by only one developing fundatrix: probability of detection = $1.0 - (1.0 - \text{infestation rate})^{\text{no. of terminals}}$. Probabilities were plotted against infestation rate, and sampling strategies were evaluated with respect to estimated fundatrix density and sample size.

The maximum effects of leaf type and season (spring versus summer) on the life-history parameters were simulated by assuming that aphids living on young leaves in the spring would be found on mature leaves in the summer. Development time, fecundity, and survival were interpolated linearly between the spring measurements on young leaves and the summer measurements on mature leaves. The timings of the development time measurements were taken as the approximate dates when the nymphs were in third instar (28 May (quip 111) and 10 August (quip 288) for spring and summer, respectively), and the timings of the fecundity and survival measurements were taken as the approximate dates when the peak reproductive period was complete (24 June (quip 166) and 24 August (323) for spring and summer, respectively). These changes in development time, fecundity, and survival were added to the model sequentially and the simulated population growth curves were plotted to illustrate the effects graphically. The same approach was taken to simulate changes in development time,

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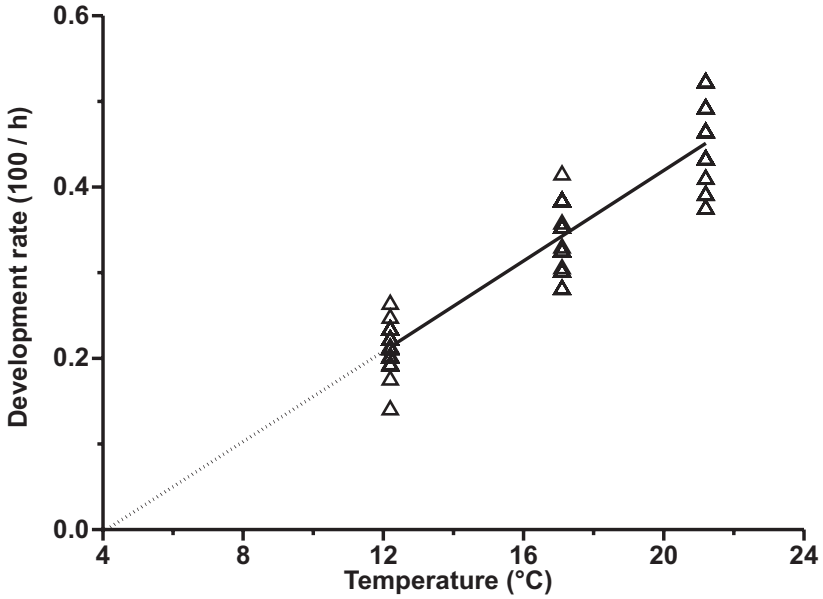
Fig. 1. Development rate of *Ericaphis fimbriata* from birth to adult versus temperature; $y = -0.11 + 0.026x$; $r^2 = 0.88$, df = 98, $P < 0.001$.



fecundity, and survival of aphids living continuously on young leaves, but the parameters were added simultaneously and a single curve was generated.

Results

Development rate, fecundity, and survival versus temperature

The development rate of apterous *E. fimbriata*, instars I–IV, from birth to adult (Fig. 1), and during adult life increased linearly with temperature ($P < 0.001$), but there was no relationship between temperature and the pre-reproductive, reproductive, or post-reproductive development rates ($P > 0.05$). Temperature thresholds for instars I–IV, from birth to adult, and during adult life revealed no pattern, but the threshold for birth to adult, 4.1 ± 0.5 °C (SE), was the most accurate and was adopted for all subsequent calculations. Development time from birth to adult was 157.7 ± 5.9 dd (SE) above 4.1 °C. Proportional lengths of instars I–IV, based on a threshold of 4.1 °C, were 0.16, 0.14, 0.34, and 0.36, respectively. Mean adult longevity required 434.5 ± 17.5 dd above 4.1 °C and proportional lengths of the pre-reproductive, reproductive, and post-reproductive periods above the same threshold were 0.05, 0.74, and 0.21, respectively. Developmental parameters for alatae were not well estimated, there being only three, one, and five aphids with complete records at 12.2, 17.1, and 21.2 °C, respectively, but the estimates were not significantly different from those for apterae ($P > 0.05$).

The mean number of nymphs per apterous female from all temperatures was 23.6 ± 1.0 (SE). Age-specific fecundity, plotted on a calendar time scale, increased rapidly to a maximum soon after the molt to adult and then gradually declined; reproduction started later and continued longer at lower temperatures (Fig. 2A). The differences in timing among temperatures were virtually eliminated by consolidating the data on a physiological time scale, which removes the effects of temperature on timing, but there was clearly a trend for reduced peak fecundity as temperature increased (Fig. 2B). Verifying this trend, total fecundity of apterae decreased with increasing temperature (Fig. 3). The asymptote of the fitted curve (Fig. 3) was 26.7 nymphs per adult aphid, very close to 26.6 ± 1.6, the mean value measured at 12.2 °C. Lifetime fecundity of alatae was 16.5 ± 3.2 nymphs, significantly lower than that of apterae ($t = 2.12$, $P < 0.05$). There was no relationship between total fecundity and temperature for alatae ($P > 0.05$). The age-specific pattern for alatae, based on all temperatures, was similar to that for apterae but peak fecundity was lower and the decline was more erratic (Fig. 4A).

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Fig. 2. Age-specific fecundity (A, B) and survival (C, D) of apterous *Ericaphis fimbriata* at 12.2 °C (●), 17.1 °C (□), and 21.2 °C (+) on both calendar (A, C) and physiological (B, D) time scales, where 1 quip = 5.9 day-degrees above 4.1 °C.

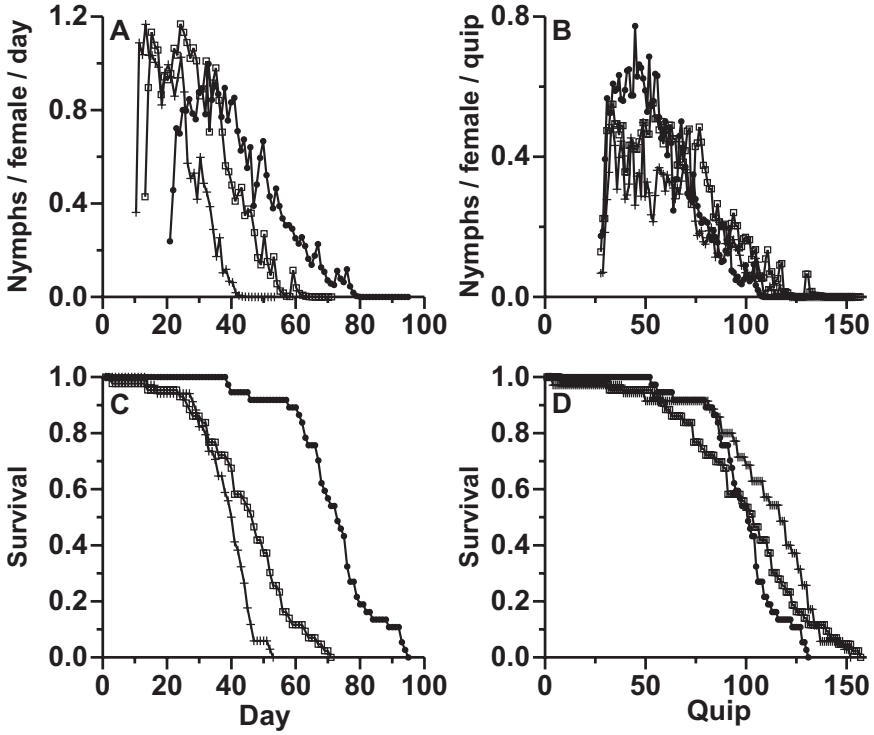

Fig. 3. Mean (±SE) fecundity of apterous *Ericaphis fimbriata* versus temperature; $y = -1957.8 + 1984.5(1.0 - e^{-1.19x})$, where $x = 100/\text{temperature}$; df = 110, $P < 0.01$.

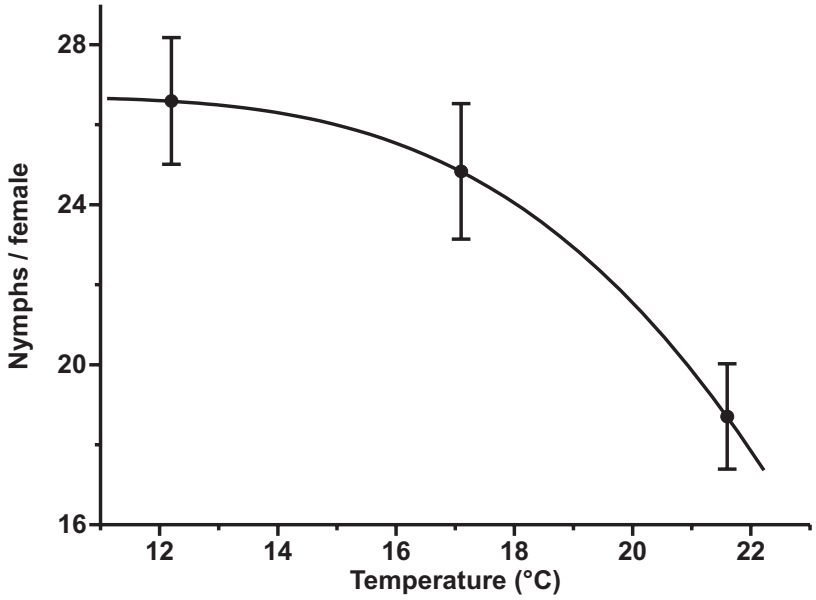

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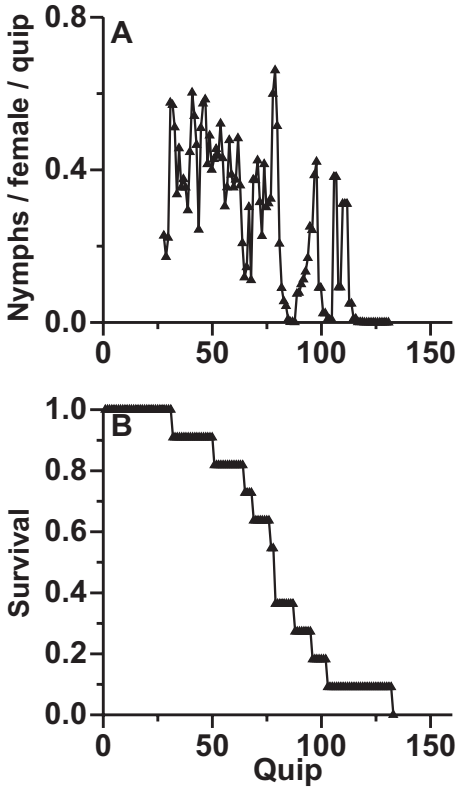
Fig. 4. Age-specific fecundity (A) and survival (B) of alate *Ericaphis fimbriata* on a physiological time scale, where 1 quip = 5.9 day-degrees above 4.1 °C.



Age-specific survival of apterae, plotted on a calendar time scale, decreased earliest at the highest temperature and later as temperature decreased (Fig. 2C). On a physiological time scale, survival was similar among the three temperatures (Fig. 2D); more than 80% of apterae survived until quip 75, when the major part of the reproductive effort was complete (Figs. 2B, 2D). Mean survival was 602.9 ± 14.6 dd above 4.1 °C. There were insufficient data to determine an age-specific pattern for alatae at each temperature, but the combined data on a physiological time scale showed that survival was high during aphid development and much of the reproductive period (Fig. 4B). Mean survival of alatae was 460.9 ± 47.5 dd above 4.1 °C, significantly less than that of apterae (t = 2.86, $P < 0.05$).

Development rate, fecundity, and survival versus leaf type and season

The leaf type × season interaction was significant for development time and fecundity ($P < 0.001$). From summer to autumn, development time increased on young 'Duke' and 'Bluecrop' leaves but decreased on mature 'Bluecrop' leaves (Fig. 5A); fecundity decreased on young 'Duke' and 'Bluecrop' leaves but remained at low levels on mature 'Bluecrop' leaves (Fig. 5B). The main effects, leaf type and season, were significant for both development time and fecundity ($P < 0.001$), and all main-effects means differed ($P < 0.05$). Survival varied significantly only among seasons ($P < 0.001$), being longer in the spring (650.2 ± 25.2 dd) and the summer (578.8 ± 41.0 dd) than in the autumn (375.9 ± 36.7 dd).

The proportion of leaf terminals with young leaves was 0.078 ± 0.0089 (SE) on 23 July. This decreased to 0.028 ± 0.0056 on 30 July and declined steadily thereafter to zero on 22 October. For leaf terminals that had young leaves, the proportion of leaves that were young was constant at 0.34 ± 0.030. Although no counts of terminals with young leaves were made prior to 23 July, previous observations indicated that buds break in March and leaf terminals grow actively until fruit set in May. Therefore, the proportion of leaf terminals with young leaves must decline from 1.0 some time in May or June to low levels near the end of July.

Modelling

Modelled rates of population increase, assuming either no emigration or 100% emigration, were 0.070 ± 0.00010 and 0.067 ± 0.00044 ln(aphids) per quip, respectively. Neither rate was significantly different from the rate of increase in the spring, 0.072 ± 0.0041, determined from nine field populations during 2001 to 2003 (t = 0.48 and t = 1.2, $P > 0.05$; Fig. 6). The abrupt increase in aphid density at quip 50 denotes the point at which the fundatrix aphid in the model began reproducing. The increase would be more gradual had fundatrix emergence been modelled over a period of time, as it occurs in the field (Raworth 2004).

Seasonal changes in the life-history parameters severely affected the population growth rate (Fig. 7). Changes in development time and fecundity each produced large effects, whereas changes in survival had little effect. Overall, the population growth rate was reduced to near zero. These results probably overestimate the effects of plant quality because it was assumed that all aphids would be found on mature leaves when the summer measurements of development

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Fig. 5. Mean (±SE) development time of *Ericaphis fimbriata* from birth to adult (A) and fecundity (B) measured at different times during the 2003 field season on leaves from different sources: young leaves from *Vaccinium corymbosum* 'Duke' plants maintained in 8 L pots (●); young leaves from 'Bluecrop' plants in a commercial field (▲); and mature leaves from 'Bluecrop' plants in a commercial field (■).

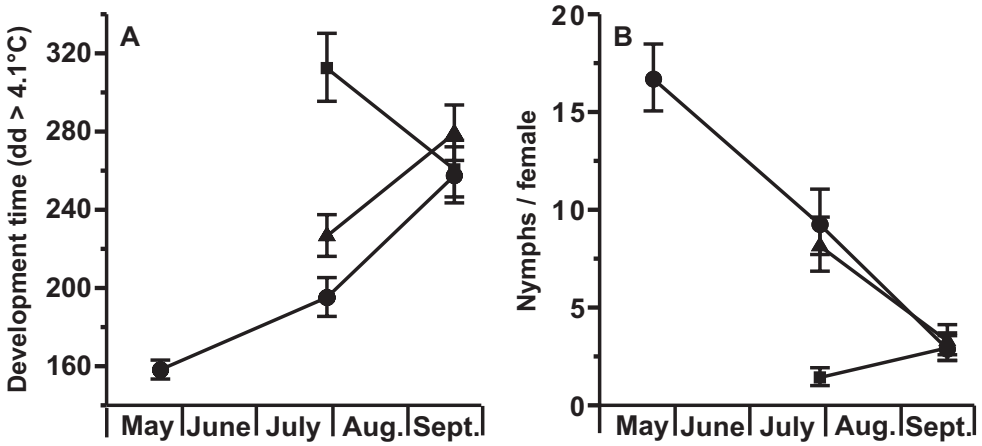
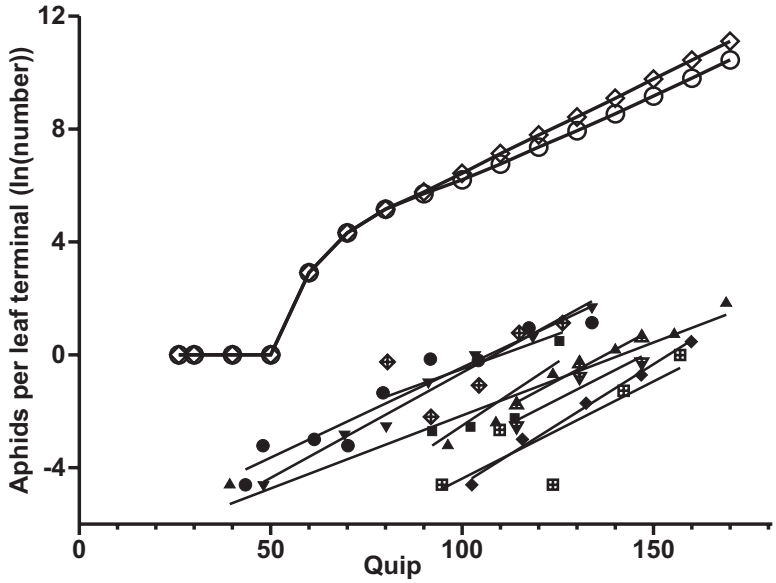


Fig. 6. Simulated population trends for *Ericaphis fimbriata* on a physiological time scale, where 1 quip = 5.9 day-degrees above 4.1 °C and development time and age-specific fecundity and survival were measured on young *Vaccinium corymbosum* 'Duke' leaves during May and June 2003: ◇, no emigration of alatae; ○, emigration of alatae. Other symbols represent aphid sample data from nine field populations during 2001 to 2003. Linear regressions were fitted to the data separately for each field and year.



time, fecundity, and survival were made. A small proportion of leaves during the summer were young. No data are available on aphid distribution with respect to young and mature leaves, but aphids were found on both leaf ages when samples were collected during 2001 to 2003. If the aphids always lived on young leaves, changes in plant quality would still affect the population dynamics (Fig. 7). The actual effect of the plant must fall between the simulated effects of young and mature leaves (Fig. 7, + versus △).

Estimated fundatrix densities in the nine commercial field populations varied from 0.000074 to 0.0040 fundratrices per leaf terminal. Fields with densities above 0.00061

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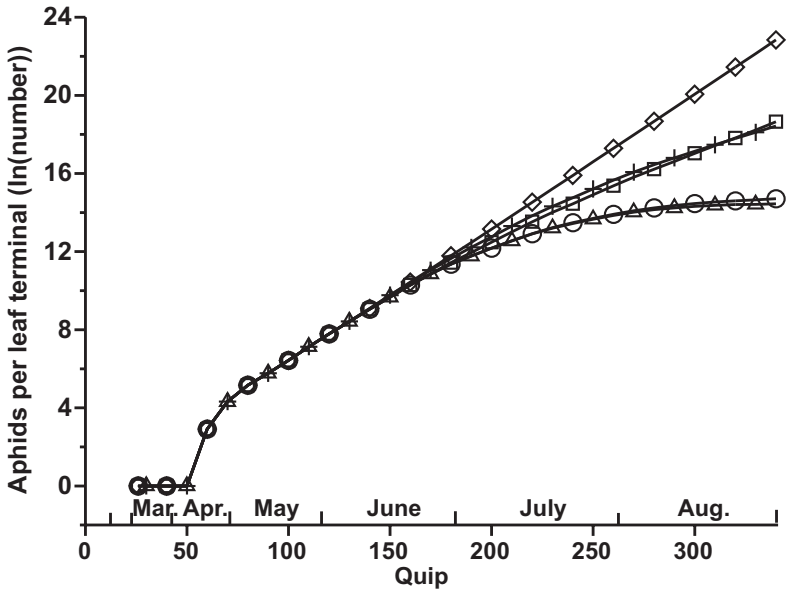
Fig. 7. Simulated population trends for *Ericaphis fimbriata* on a physiological time scale, where 1 quip = 5.9 day-degrees above 4.1 °C: development time and age-specific fecundity and survival measured on young *Vaccinium corymbosum* 'Duke' leaves during May and June 2003 (◇); population trends obtained by sequentially adding seasonal changes in development time (□), fecundity (○), and survival (△) measured on mature 'Bluecrop' leaves from a commercial field in August and interpolated between the June and August measurements; and population trends obtained by simultaneously adding seasonal changes in the same variables measured on young 'Bluecrop' leaves from a commercial field in August (+). Calendar time was based on temperatures at the Abbotsford Airport, 2003.



fundatrices per terminal had peak population densities above 4.0 aphids per terminal during the summer, whereas fields with densities below 0.00040 fundatrices per terminal had peak population densities below 1.6 aphids per terminal. The probability of detecting aphids at densities of 0.00061 fundatrices per terminal in a sample of 1000 terminals was 0.46 (Fig. 8); therefore, aphids would be missed about 55 times in 100 samples of 1000 terminals. The probability of detection dropped to 0.26 for a sample of 500 terminals, in which case aphids would be missed about 75 times in 100 samples of 500 terminals. Given that commercial pest managers may sample 100 terminals, it appears that they will detect few of the cases that lead to high densities in June. Their samples will become reliable when densities reach 0.02 or 0.03 aphids per terminal, some time in late April or May.

Discussion

The developmental temperature threshold for *E. fimbriata* virginoparae was 4.1 °C, and it was assumed for modelling purposes that the same threshold applied to egg and fundatrix development. This assumption is reasonable because in insects generally, the thresholds for post-diapause emergence and non-diapause development are similar (Gilbert 1988). In addition, the threshold is usually equal to the average field temperature on emergence, being selected to be as high as possible but low enough to allow emergence at a time when adequate food is available. In our case, the mean daily temperatures for January, February, and from 1 March to the estimated date of emergence at Abbotsford were 4.8 ± 2.8 (SD), 4.6 ± 2.0, and 5.0 ± 3.2 °C, respectively (means of means and SDs for 2001, 2002, and 2003), which is consistent with Gilbert (1988). The thermal requirement for development in day-degrees should be minimal (Gilbert 1988); therefore, it is not unreasonable to assume that both fundatrices and subsequent virginoparae have similar heat requirements, but this should be checked. With respect to fundatrix fecundity, Raworth (1984) showed that the use of ratio estimation to determine age-specific fecundity from a known pattern produces a biassed

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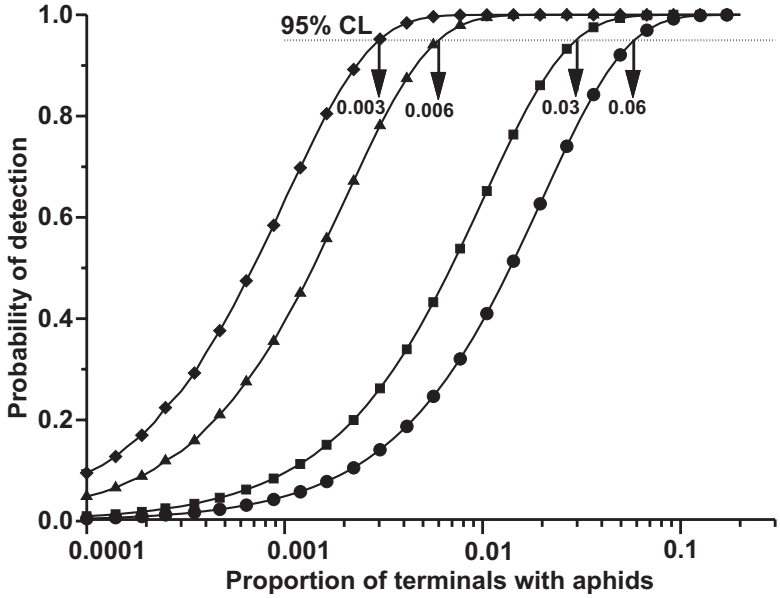
Fig. 8. Probability of detecting *Ericaphis fimbriata* fundatrices versus fundatrix density, assuming that in late March and early April there is only one fundatrix per infested terminal. Number of terminals sampled: ◆, 1000; ▲, 500; ■, 100; and ●, 50.



estimate of peak fecundity that greatly affects population growth rates; however, changing fundatrix fecundity in the model had little effect on the subsequent population growth rate because that rate is determined mainly by later generations of apterous virginoparae.

Development rate and age-specific fecundity for apterous virginoparae were similar to published data for other aphids (*cf.* McCornack *et al.* 2004). However, we must ask whether these measurements accurately reflect what would be found on commercial blueberry in the field. The question applies whether the measurements are made on excised leaves in dishes, in clip cages on small plants in growth chambers, or in clip cages on commercial plants in the field — all experimental conditions that change the environment and behaviour of the aphids. The question is complicated by many possible effects, including reduced antibiotic effects on excised leaves (Montllor *et al.* 1990; Robinson 1992), release of nutrients during leaf aging (Scholze 1992), and reduced turgor pressure in excised leaves, which could have both positive and negative effects on aphid development and reproduction (Wearing 1972). It is tempting to interpret the decrease in total fecundity with increasing temperature as indicating a problem with the use of excised leaves; however, the results of other workers suggest that this generalization may be unfounded. Raworth (1984) observed no relationship between total fecundity and temperature between 8 and 23 °C when trials were conducted with *Brevicoryne brassicae* (L.) on whole kale (*Brassica oleracea* L.) (Brassicaceae) plants. However, McCornack *et al.* (2004) observed decreased total fecundity at 30 °C, compared with fecundity at 20 and 25 °C, for *Aphis glycines* Matsumura on whole soybean (*Glycine max* L.) (Fabaceae) plants. Asin and Pons (2001) observed decreasing fecundity for *Sitobion avenae* (Fabr.) and *Metopolophium dirhodum* (Walker) on excised corn (*Zea mays* L.) (Poaceae) leaves between 18 and 25 °C when leaves were changed every 2 days, but increasing fecundity for *Rhopalosiphum padi* (L.) at temperatures up to 27.5 °C before a large decline at 30 °C. Likewise, various authors have observed an increase then a decrease in fecundity with increasing temperature for the following aphids: *Lipaphis erysimi* (Kaltenbach) on cabbage (*B. oleracea*) leaf disks replaced at the first sign of deterioration, with peak fecundity at 20 °C (Liu and Yue 2001); cotton aphid, *Aphis gossypii* Glover, on excised cotton (*Gossypium hirsutum* L.) (Malvaceae) leaflets replaced every 12 h at 25, 30, and 35 °C and every 24 h at 10, 15, and 20 °C, with peak fecundity at 25 °C (Xia *et al.* 1999); and *A. gossypii* on whole cucumber

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(*Cucumis sativus* L.) (Cucurbitaceae) plants, with peak fecundity at 17.5 °C (Kim and Kim 2004). In general, the response of total fecundity to temperature is similar between studies using excised leaves or whole plants, but the optimum temperature depends uniquely on the aphid–host-plant system. However, the question still remains, how do these measurements relate to field conditions? It is not possible to make measurements in the field without modifying the aphid's environment or behaviour; therefore, we answered the question indirectly by comparing simulated rates of population increase, based on laboratory measurements, with rates observed in the field during the spring when population growth was exponential and few predators and parasitoids were present. We used the fecundity and survival data obtained at 12.2 °C for the model because that temperature corresponded best with average field temperatures; however, it also corresponded to the maximum fecundity possible, as defined by the asymptotic relationship between fecundity and temperature measured in the laboratory.

We expected a negative relationship between total fecundity and temperature for alatae, similar to that for apterae (*cf.* Liu and Yue 2001), but it was not observed, perhaps because there were too few individuals. The age-specific reproductive pattern for alatae was similar to that for apterae but was more variable, again probably because of low sample size. Total fecundity of alatae was lower than that of apterae, in agreement with the results of other workers (*cf.* Liu and Yue 2001).

The simulated population growth rate, which included only aphid life-history parameters, was not significantly different from the observed population growth rate in nine field populations from 2001 to 2003. We can use this to validate the life-history data in the model, but only if factors such as predators and parasitoids that can depress population growth rate in the field were not significant; if they were significant, then the model could be "right" for the wrong reason, the effects of predators masking negatively biassed estimates of development rate and fecundity. The various life stages of aphidophagous predators (coccinellids, chrysopids, syrphids, and cecidomyiids) and parasitoids (unemerged aphid mummies) were not observed in the field until 22 May 2001, 28 May 2002, and 10 June 2003. Predators were observed sporadically, whereas parasitoid numbers increased gradually through June, July, and early August and then declined (unpublished data). Although a few of the sample points used to determine the spring rate of increase occurred when predators and parasitoids were observed, there was no obvious departure from the linear model when the data were plotted on a log scale with physiological time on the *x*-axis. Therefore, from mid-March to early June, aphid mortality due to predators and parasitoids was probably not significant and the life-history data in the model can be validated by the field data. Although alatae production is high in the spring (Raworth 2004), it appears to be a dispersive strategy that has little effect on the population dynamics, apterae being largely responsible for the rate of population increase.

Changes in development time and fecundity as a function of leaf type and season had significant effects on the rate of population increase and must have played an important role in the mid-season declines that were observed in all nine field populations (Raworth 2004). Consistent population declines in all fields and years may not be expected if natural enemies were the sole regulating factor. Regular and important, negative plant quality effects on development time and fecundity, probably associated with fruit development and the production of sugars rather than nitrogen-rich compounds, would substantially increase the probability of consistent population declines when combined with natural enemies and other mortality factors. Similar seasonal changes in population parameters of other aphid species have been described by other authors (Raworth 1984; Day *et al.* 2004; Dixon 2005), but details differ among systems. For example, Day *et al.* (2004) found that fertility decreased during the summer and that this change was most likely to drive population change in the green spruce aphid, *Elatobium abietinum* (Walker); however, development time actually decreased in the summer, when nutrients were scarce. In contrast, we report decreased fertility and increased development time in summer, both factors seriously impacting the population dynamics. In a review, Karley *et al.* (2004) concluded that for aphids on agricultural crops in temperate regions, and possibly for aphids on grasses and forbs in natural vegetation, mid-season population crashes result from a combination of slow-acting, non-catastrophic processes, including emigration of alatae, depressed birth rates, and enhanced mortality from natural enemies. Our results support this conclusion and add

increased development time to the list of factors. Small changes in development time can seriously affect population growth rates (Lewontin 1965); in our case, changes in development time are as important as changes in fecundity. Unfortunately, we did not obtain nutritional information from the leaves to provide a causal link at the molecular level.

Dixon (2005) argued for bottom-up regulation of aphid abundance for tree-dwelling aphids. Karley *et al.* (2004) argued for a combination of top-down and bottom-up regulation (mid-season crash) for aphids on agricultural crops and proposed that this may also apply to aphids on grasses and forbs in natural vegetation. The work of Gilbert and Raworth (1998) refutes Karley *et al.* (2004) and supports Dixon (2005) for the thimbleberry aphid, *Masonaphis maxima* (Mason), on thimbleberry, *Rubus parviflorus* Nutt. (Rosaceae), a nonagricultural herbaceous plant (not a forb). However, the work of Charnov *et al.* (1976) lends support to the top-down view for the pea aphid, *Acyrthosiphon pisum* (Harris), on a forb, alfalfa (*Medicago sativa* (L.) 'Lucerne') (Fabaceae). Our work on *E. fimbriata* supports Karley *et al.* (2004), but we suspect that knowledge of the biological details and the interactions between biotic and abiotic factors such as predation and weather, or plant quality (for the aphids) and weather, will be necessary to understand the dynamics of each system (*cf.* Clutton-Brock and Coulson 2002). Furthermore, predictability will be limited to the extent that weather and the movement of aphidophagous arthropods from outside a system are unpredictable (*cf.* Frazer and Gilbert 1976).

Raworth (2004) argued that growers should shift chemical aphid controls from postbloom to prebloom in April, after the aphids have hatched. The current work supports that conclusion, finding that several natural factors are already acting to slow the rate of population increase during June, July, and August, whereas population regulation during the spring is minimal. However, the approach to pest management must change. Previously, growers utilized sample data gathered by pest managers to determine the necessity of aphid controls postbloom, in June, but the low density of fundatrices prebloom presents sampling problems. Reliable estimates of aphid density would require too many samples; therefore, in most cases, growers will need to make a decision about the use of chemical controls without current sample data. This is contrary to integrated pest management practices. However, given the importance of BlScV and the knowledge that *E. fimbriata* is found in most if not all blueberry fields in southwestern British Columbia, growers will probably adopt a single "calendar" chemical application for aphids in April. Such an application may reduce peak aphid populations in late June proportionally to the reduction in April. For example, given a rate of increase of 0.072 ln(aphids) per quip, 130 quips from 1 April to 30 June, and pre- and post-chemical-treatment densities of 0.001 and 0.0001 aphids per terminal on 1 April, the respective population densities on 30 June would be 10.9 and 1.1 aphids per terminal. A reduction in the transmission rate of BlScV would also be expected, unless transmission is caused predominantly by migrant alatae of other species. Further work is needed to confirm the usefulness of prebloom chemical treatments in regulating aphid populations and to determine the respective roles of *E. fimbriata* and migrant alatae of other species in the spread of BlScV.

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