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Behavior and Population Development of *Phorodon humuli* (Schrank) (Homoptera: Aphididae) on Two Hop Cultivars of Different Susceptibility

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The two hop cultivars "Hallertauer Magnum" (HM) and "Spalter Select" (SE) are regarded by growers as extremely different in their susceptibility to the damson-hop aphid Phorodon humuli *(Schrank). To investigate these anecdotal observations, spring migration and initial population development of* P. humuli *were monitored on the two cultivars in 1998 and 1999 in an experimental hop garden. Numbers of migrant aphids on SE were significantly lower, comprising 18.8 and 30.2% as compared to HM in 1998 and 1999, respectively. Population development of apterous aphids on these two cultivars differed significantly. At the end of the monitoring period numbers of aphids on SE were 7.5 and 14.2% as compared to HM in 1998 and 1999, respectively. In behavioral studies of* P. humuli *alates released on glasshouse plants, those on SE spent significantly more time in motile behavior patterns than aphids on HM. In the glasshouse, population development also differed significantly and the number of aphids developing on SE was 12.9% of that on HM after 28 days. It is concluded that SE exhibits a certain repellent effect on* P. humuli *and, compared to HM, is possibly nutritionally less suitable to the aphid.*

KEY WORDS: aphid migration; aphid resistance; damson-hop aphid; hops; *Humulus lupulus*; *Phorodon humuli*.

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INTRODUCTION

The damson-hop aphid *Phorodon humuli* (Schrank) is a major pest of hops in the northern hemisphere. It is an obligate holocyclic/heteroecious species with four *Prunus* spp. serving as primary hosts and the hop *Humulus lupulus* L. as its sole secondary host (Eppler, 1986). The aphid can cause serious losses of yield up to the complete destruction of a crop, and even light infestations of the harvested cones can damage their quality and reduce their economic value (Barber *et al.*, 2003). Farmers usually control *P. humuli* with the prophylactic use of insecticides. This has stimulated the development of resistant aphid genotypes within the hop-growing regions, where hops are usually concentrated in a comparatively small area (Hrdý *et al.*, 1986). An integrated approach to pest management in hops is needed badly in order to break this cycle and to prevent the selection of strains resistant to new insecticides in the future. One cornerstone of such an integrated strategy consists in the breeding of hop cultivars (cvs) at least partially resistant to *P. humuli* infestation. Differences in varietal susceptiblity to this species have been demonstrated previously (Hornung, 1975; Campbell, 1983; Darby and Campbell, 1988; Dorschner and Baird, 1988; Kralj *et al.*, 1998).

A hop-breeding program for aphid-resistant genotypes was initiated in the UK in the 1980s (Darby and Campbell, 1996; Campbell, 2001; Barber *et al.*, 2003). In Germany, hop breeding has hitherto focused on genotypes resistant to fungal diseases, but resistance to aphids is now also seen as a challenge for future hop research. According to the experience of farmers in the Hallertau hop-growing region, the bitter cultivar (cv.) Hallertauer Magnum (HM) seems to be most susceptible to *P. humuli*, whereas the aroma cv. Spalter Select (SE) suffers few problems from aphid infestation. The aims of the present study were to investigate and verify these anecdotal observations, and to find clues to explain the obvious aphid tolerance of SE by studying the behavior of *P. humuli* on both cvs. Such knowledge is important for the future breeding of less susceptible hop genotypes and should facilitate a more successful integrated pest management approach in hop growing.

METHODS

Field Study Site and Experimental Design

Field investigations were carried out in 1996, 1998 and 1999 in a 2.2 ha private hop garden in Oberulrain near Neustadt a.d. Donau, Kelheim district, Bavaria, Germany (11°49′E, 48°48′N) at approximately 385 m above sea level. Plants were spaced 1.5 m apart within rows and 3.2 m between rows. Every third row contained poles to support the 7-m high trellis. Part

Fig. 1. Scaffold tower for the field monitoring of aphid migration and aphid population development. Oberulrain, Bavaria, Germany, May 1996.

of this hop garden (0.45 ha) contained 48 plots of 12 different cvs, originally planted for investigations of the resistance of cvs to hop downy mildew, *Pseudoperonospora humuli* (Miyabe et Takahashi) Wilson. Plots comprising 12 plants of the 12 cvs were arranged randomly in non-pole rows. The pole rows and the rest of the garden were planted with cv. Northern Brewer. Two support strings were provided for each plant and two stems (bines) were trained up each support string.

Aphid population development was monitored from eight scaffold towers that were erected on 22 May 1996, 15 May 1998 and 12 May 1999 centrally within in four plots of cvs HM and SE. Two platforms were erected on each tower 2.5 and 5 m above ground (Fig. 1). The platforms served as permanent observation points for monitoring the aphid migration and population development while minimizing the disturbance of insects on foliage. Both bines on 12 support strings of the six central plants in each plot were accessible and could be inspected easily from the platforms on each tower up to the trellis at 7 m. No insecticides or acaricides were applied during the monitoring period, which extended until 14 June 1996, 9 June 1998 and 11 June 1999. Weather data were recorded with a Thies (Göttingen, Germany) eprom-version weather station sited centrally in the experimental part of the hop garden.

Field Monitoring

After the towers were erected, the garden was monitored daily by one person until the first migrant *P. humuli* was detected. Thereafter, observations were made daily by three people. The total number of alate

P. humuli present on both bines of each of the 12 support strings was recorded two to four times (usually three) per day, depending on weather conditions and aphid migratory activity. Observations were discontinued only on rainy days. Monitoring was conducted following a standardized circuit of the eight plots, with two persons counting arthropods and the third taking the records. The duration of each circuit was approximately 2–2.5 h. Counts were made of all living and dead alatae and their exact positions from the shoot tip to the seventh apical pair of leaves on each of the two bines on a string. Records were also made of the numbers of aphids observed taking flight and of predation, e.g., by spiders or ladybirds. Daily counts were also made of the numbers of apterous morphs on both bines on each support string.

At the end of each monitoring period, all of the bines were inspected for growth. Any mechanical damage caused for example by abrasion with the scaffolding or by the daily work program was noted. The two strings of the 12 monitored in each replicate that were most strongly effected by mechanical damage were rejected prior to data analysis.

All counts (n) that were obtained during field monitoring were $\ln (n+1)$ transformed to create normal distribution and/or homogeneity of variances of the data set. The total numbers of unwinged aphids (young larvae, older larvae and adult exsules) on bines in each of the four replicates with ten support-strings per cv. on each date were subjected to repeated measures ANOVA and then compared with a t-test [least significant difference (LSD), $df = 1.6$; $P < 0.05$]. For alate aphids, the results with the highest numbers of aphids from each day's monitoring circuit were analyzed. The mean numbers of aphids in each replicate with ten strings per cv. on each date were subjected to repeated measures ANOVA and then compared with a t-test (LSD, $df = 1.6$; $P < 0.05$).

Glasshouse Experimental Design and Monitoring

The experiments were conducted on 30 pot-grown hop plants of HM and SE, respectively. Plants were approximately 120–150 cm high at the start of the experiment. Early in the aphid migration, alate *P. humuli* were collected in the field from young hops of the two cvs and transported to the glasshouse on the leaves on which they were found. In a parallel series of observations, two aphids per cv. were transferred carefully with a fine brush to plants of the same cv., respectively, and their behavior on the two cvs was observed synchronously by two persons for 30 min with a magnifying glass (5×). The actions of six clearly differentiated patterns of behavior or the time spent on them were recorded: We distinguished the behavior of the

transferred aphids into probing (repeated vigorous penetration of leaf tissue with the stylet, antennae waving), phloem ingestion (stylet inserted in leaf tissue, antennae not waving and swung backwards to a position parallel with the abdomen), horizontal motion on the leaf, vertical motion on the bine, change of leaf side, and change of leaf storey (Table II). The replicates were run over four consecutive days with usually eight parallel series observed per day. Altogether, we obtained 60 series of observations on both cvs, respectively. Differences in the behavior on the two cvs were analyzed using the Wilcoxon-test.

Aphid population development in the glasshouse was monitored on 29 plants of HM and SE, respectively. The numbers of apterous aphids on each plant were counted on days 2, 5, 9, 18, and 28 after the initial release of two alate *P. humuli* per plant. The counts (n) were ln ($n + 1$) transformed and compared by repeated measures ANOVA.

RESULTS

Aphid Migration

Monitoring of alate aphids failed completely in 1996, as only four migrants were detected in the experimental plots during the entire monitoring period. Therefore, evaluation of the 1996 data was not possible and the year served mainly as a test stage while the monitoring routine was established.

In both 1998 and 1999, aphid migration rates changed during the season, were higher in HM as compared to SE, and the differences between cvs were different at different dates (Table I, Fig. 2a and b).

The aphid migration to hops started on 19 May in 1998, and first significant differences were found on 20 May between the numbers of aphids that settled on the two cvs. The numbers of winged aphids reached a maximum on HM between 28 May and 3 June and differences between the cvs remained significant until 5 June. When summarized over all 19 monitoring days (using data from the monitoring circuit on each day with maximum numbers of aphids), 1201 alate aphids were recorded on HM and 226 (18.8% compared to HM) on SE (Fig. 2a).

The first migrants of *P. humuli* were recorded on both cvs on 20 May in 1999. After three rainy days, when observations were discontinued, the number of aphids that had settled on the two cvs was first significantly different on 24 May. The number of winged aphids settling on HM reached a maximum on 30 May, and differences between the two cvs remained significantly different from 27 May until 6 June. The numbers of alate aphids

Table I. Effects of Hop cvs HM and SE and Sampling Date in the Field on Aphid Migration and Aphid Population Development Rates in 1998 and 1999[a]

Source	df	SS	*F*	*P*
Aphid migration 1998				
Cultivar	1.6	79.37	49.72	<0.001
Sample date	18.108	28.58	7.89	<0.001
Sample date × Cultivar	18.108	7.52	2.08	<0.05
Aphid migration 1999				
Cultivar	1.6	39.09	33.77	<0.01
Sample date	18.108	55.38	20.43	<0.001
Sample date × Cultivar	18.108	5.15	1.90	<0.05
Aphid field population development 1998				
Cultivar	1.6	130.55	61.62	<0.001
Sample date	17.102	245.24	26.73	<0.001
Sample date × Cultivar	17.102	51.16	5.58	<0.001
Aphid field population development 1999				
Cultivar	1.6	62.79	47.47	<0.001
Sample date	18.108	455.87	58.30	<0.001
Sample date × Cultivar	18.108	25.99	3.32	<0.001

[a]Degrees of freedom (df), sum of squares (SS), *F*-value (*F*), and *P*-value (*P*) from repeated measures ANOVA.

recorded in 1999 were slightly higher than in 1998 with 1462 on HM and 441 (30.2% compared to HM) on SE (Fig. 2b) when summarized over all 19 monitoring days.

Aphid Population Development in the Field

In both 1998 and 1999, aphid population development rates changed during the season, were higher in HM as compared to SE, and the differences between cvs were different at different dates (Table I, Fig. 3a and b).

The first unwinged larvae were found on 20 May in 1998 on HM. Significant differences between cvs in unwinged aphid numbers were first recorded on 26 May and, except on 28 May, remained significant until the end of the monitoring period on 9 June, when there was a peak mean number of 173.3 ± 122.6 per replicate on HM and 13.0 ± 9.6 on SE (7.5% of HM mean) (Fig. 3a).

The first unwinged larvae were found on 25 May on both cvs in 1999. Significant differences between cvs in numbers of unwinged aphids became first visible on 27 May. Differences remained significant from 4 June until the end of the monitoring period on 11 June, when there was a peak mean number of 333.8 (SE ± 150.7) per replicate on HM and 47.5 (SE ± 24.8) on SE (14.2% of HM mean) (Fig. 3b).

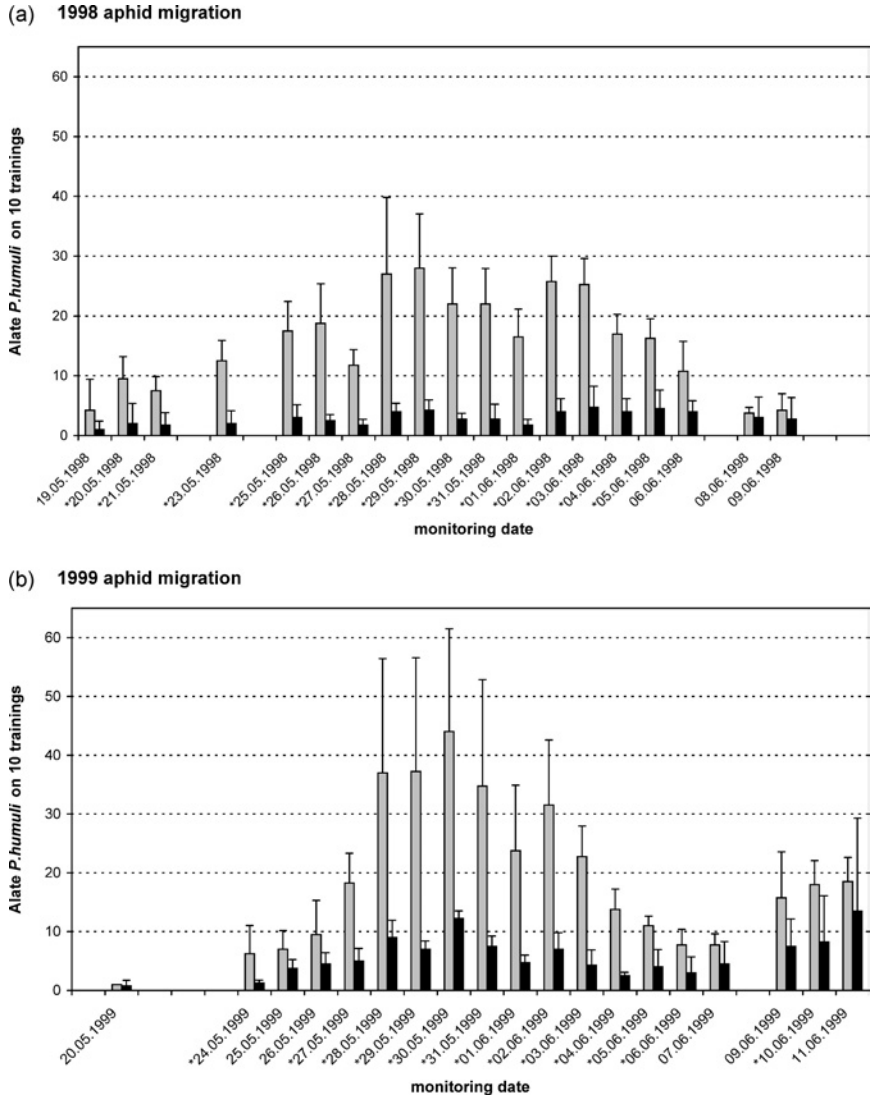

Fig. 2. (a) Daily records of alate *Phorodon humuli* on cvs Hallertauer Magnum (grey bars) and (b) Spalter Select (filled bars) in Oberulrain during 1998 and 1999 (highest counts from two to four monitoring circuits per day are presented). Means and SE of four replicates with 10 strings, respectively. Dates with significant differences between the cvs (*t*-test, LSD, $df = 1.6$, $P < 0.05$) are marked by an asterisk.

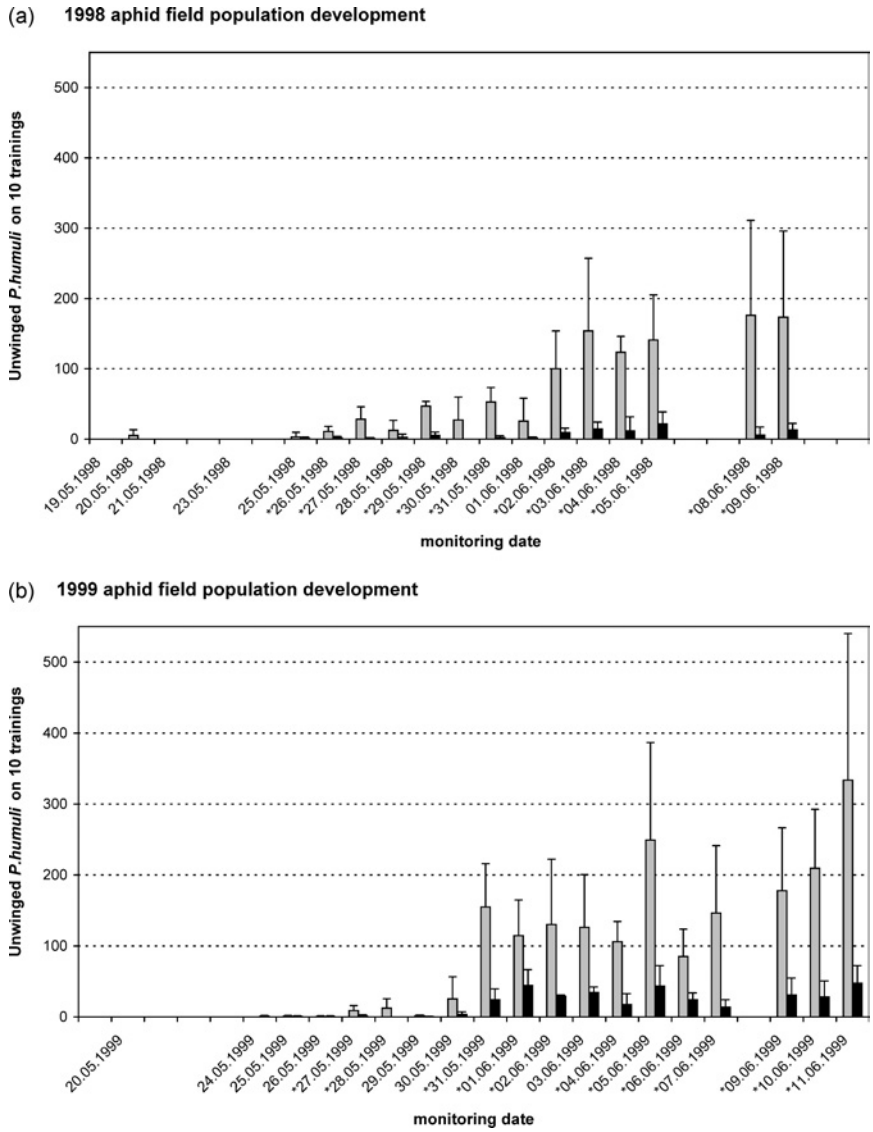

Fig. 3. (a) Daily counts of unwinged *Phorodon humuli* on cvs Hallertauer Magnum (grey bars) and (b) Spalter Select (filled bars) in Oberulrain during 1998 and 1999. Means and standard error of four replicates with 10 strings, respectively. Dates with significant differences between the cvs (t-test, LSD, $df = 1.6$, $P < 0.05$) are marked by an asterisk.

Predation of Alate Aphids

During the monitoring periods, three groups of predators of *P. humuli* were recorded in the field: adult ladybirds (Coccinellidae), larvae of green and brown lacewings (Chrysopidae and Hemerobiidae), and spiders (Araneida). Predation of alate aphids by ladybirds and lacewings occurred rarely, but considerable predation by spiders was observed. In 1998, 39 of 228 (17.1%) migrant *P. humuli* were caught by spiders on SE and 78 of 1200 (6.5%) on HM. Predation of alate aphids by spiders was less in 1999. Only eight of 441 (1.8%) were recorded dead in spider webs on SE and 27 of 1462 (1.8%) on HM. Summarized over both cvs and years, the predation rate by spiders was 152 of 3330 alate aphids (4.6%). No spiders were removed for identification during the field trials, but judging from the shape of the webs, the main species of importance were from the genus *Dictyna* (Dictynidae).

Aphid Behavior and Population Development in Greenhouse Trials

Alate *P. humuli* spent more time in motile behavior patterns on SE than on HM, with significant differences in horizontal motion on the leaves and vertical motion on the bines. In contrast, the aphids spent less time probing and ingesting phloem sap on average on SE, but these differences, however, were not statistically significant (Table II). The development rate of populations of unwinged progeny was significantly higher on HM as compared to SE ($F = 66.09$, $df = 1.56$, $P < 0.001$; repeated measures ANOVA). After 28 days, the mean aphid numbers on SE was only 12.9% of that on HM (Table III).

Table II. Behavioral patterns for individual alate *Phorodon humuli* within the first 30 minutes after release on leaves of hop cvs HM and SE[a,b]

Behavioral pattern	HM	SE
Probing (min)	0.85 ± 2.11	0.26 ± 0.54 ns
Phloem sap ingestion (min)	2.67 ± 6.92	0.39 ± 1.26 ns
Horizontal motion on the leaf (min)	3.37 ± 4.67	4.55 ± 4.28*
Vertical motion on the bine (min)	0.00 ± 0.00	1.00 ± 2.60***
Change of leaf side (n)	0.90 ± 0.83	1.37 ± 1.66 ns
Change of leaf storey (n)	0.12 ± 0.37	0.27 ± 0.65 ns

[a]Mean time (min) or mean number of events (n) ±standard error ($N = 60$, respectively).
[b]Differences between cvs (Wilcoxon-Test): ns: no significance.
*$P < 0.05$, ***$P < 0.001$.

Table III. Aphid Population Development After 28 Days on Hop Cvs HM and SE, in a Glasshouse Arising from the Release of Two Alate *Phorodon humuli* Per Plant[a]

Day	HM	SE
2	2.1 ± 3.39	2.8 ± 2.91
5	10.6 ± 9.32	6.7 ± 5.11
9	15.6 ± 9.23	7.8 ± 5.19
18	167.5 ± 147.52	17.7 ± 21.03
28	2598.3 ± 2206.39	334.2 ± 332.34

[a]Means ± SE of apterous aphids per plant ($N = 29$, respectively).

DISCUSSION

Phorodon humuli colonizing *Humulus lupulus* may encounter plant genotypes varying in their susceptibility—resistance spectrum to the aphid. The identification of suitable host plants by an aphid involves four basic components: visual, olfactory, mechanical and gustatory stimuli, with any combination of these being possible. Thus, Dorschner and Baird (1989) list a wide range of possible plant defense barriers against being colonized by aphids. These include volatile substances, leaf pubescence, the chemical composition or amount of epicuticular waxes, and leaf tissues resistant to stylet penetration by mechanical means or by resisting depolymerization by aphid salivary enzymes. Furthermore, aphid colonization may be inhibited by the presence of chemical antifeedants or the lack of feeding stimulants, by mechanisms which alter the aphid's path to the phloem and make that cell type difficult to locate, and by the composition of the phloem sap itself, making it nutritionally inadequate for the aphid.

Our results indicate that at least two mechanisms are involved which in combination produce significant differences in the susceptibility of HM and SE to *P. humuli*: Firstly, our monitoring of migrant aphids showed that SE was colonized by 70–80% fewer alate *P. humuli* than was HM. This observation indicates that SE exhibits a certain repellent effect on *P. humuli*. Secondly, the significantly different aphid population development that occurred between these indicates that the phloem sap taken up on SE was nutritionally less suitable for *P. humuli*. A possible explanation could be some difference in the amino acid composition affecting aphid fertility (Hornung, 1975). On the other hand, we actually evidenced significant differences in aphid behavior and aphid reproduction rates on these two cvs, but no data was collected on the real mechanisms responsible. Thus, the discussion of mechanisms accounting for the recorded varietal differences in the susceptibility of HM and SE to *P. humuli* is merely a hypothetic one, and may be regarded as a challenge for extensive further studies.

One reason for the different levels of colonization may be a difference in leaf color between cvs, with SE possessing the darker green foliage. Campbell (1991) recorded 1.5 times more migrant *P. humuli* on a yellow-foliaged variant of cv. Brewer's Gold than on the green variant of that cv., thus providing evidence of visual selection during landing. Another possible reason contributing to the difference may be the release of semiochemicals by "pioneer colonizers" of *P. humuli* on a hop plant leading to the aggregation of migratory morphs on this plant (Campbell *et al.*, 1993), possibly with the honeydew of feeding aphids as a source of chemical cues (Dorschner and Kenny, 1992). However, we believe that the most important factor that would account for the significantly higher number of aphid migrants on HM may be differences in volatiles released by the cvs themselves, and their affect on aphid behavior. Lösel *et al.* (1996) found that a number of components identified in the headspace odors from hop, presented both as simple compounds and as relatively simple mixtures, modified the landing behavior of *P. humuli* in the field. Methyl salicylate, butyl isothiocyanate and 4-pentenyl isothiocyanate reduced the numbers landing. Unfortunately, assumed differences in the headspace volatiles of HM and SE have not been investigated yet.

Our behavioral observations from the glasshouse also support the repellency hypothesis for SE. Aphids spent significantly more time in motile behavior patterns on SE than on HM and less average time with ingesting phloem sap, although, contrary to our expectations, the latter behavior in our experiment was not significantly different. However, comparable significant differences between aphids on resistant and susceptible hops were observed by Paul *et al.* (1996) who found that >20% of aphid time on the susceptible selection was taken up with phloem sap ingestion, whereas <4% of time was spent on that activity on a resistant experimental genotype. Dorschner and Baird (1989) found similar differences in time spent with phloem ingestion on resistant and susceptible selections but, contrary to our results, they recorded a significant increase in the frequency of probing on resistant hops.

Paul *et al.* (1996) concluded from their studies that resistance to aphids in hops was associated with the phloem and did not involve surface features of the leaves. Among possible resistance mechanisms, they discuss mechanical factors, e.g., as the blocking of aphid stylets, the presence of antinutritional compounds or simply an inadequate supply of nutrients. This interpretation accords with Dorschner and Baird (1989) who found that the resistance of two experimental accessions to hop aphids apparently did not involve volatiles or surface features common to those genotypes, such as cuticular or epidermal layers. They recommended that future

efforts concerning the nature of hop aphid resistance should center on phloem physiology and the biochemistry of hops.

Other factors that influence the pattern of aphid infestation, such as the preference of migrants for plants along the edges of hop gardens (Eppler, 1989) or local patterns of wind shelter (Campbell, 1977), were excluded by the experimental layout. The positive correlation between average bine height and migrant aphid numbers reported by Campbell (1977) would suggest a likely preference for SE bines by migrating aphids as the rapid vertical growth of SE clearly surpassed that of HM during May and June.

Generally, our results confirm that SE ranks among the resistant hop cvs with respect to infestation by *P. humuli*. This finding agrees with the results of Kralj *et al.* (1998) who found that resistance to *P. humuli* was related to a combination of three volatile compounds in hop essential oil, viz. alpha-pinene, beta-pinene, and an unidentified third compound. In a list of damage scores from 1 to 10 for more than 100 accessions, Kralj *et al.* (1998) gave SE a score of 3, thus categorizing it among eight cvs least susceptible. For future hop breeding, the option of producing genotypes with similar partial aphid resistance to that of SE would provide a useful foundation for an integrated pest management strategy in hop growing. This strategy would not only allow reduction of pesticide and application costs (Barber *et al.*, 2003), it would also help minimize the ever-present risk of aphids developing resistance to insecticides.

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REFERENCES

Barber, A., Campbell, C. A. M., Crane, H., Darby, P., and Lilley, R. (2003). Cost-benefits of reduced aphicide usage on dwarf hops susceptible and partially resistant to damson-hop aphid. *Ann. Appl. Biol.* **143:** 35–44.

Campbell, C. A. M. (1977). Distribution of damson-hop aphid (*Phorodon humuli*) migrants on hops in relation to hop variety and wind shelter. *Ann. Appl. Biol.* **87:** 315–325.
Campbell, C. A. M. (1983). Antibiosis in hop (*Humulus lupulus*) to the damson-hop aphid, *Phorodon humuli*. *Entomol. Exp. Appl.* **33:** 57–62.
Campbell, C. A. M. (1991). Response of *Phorodon humuli* to yellow and to green hop foliar colours. *Entomol. Exp. Appl.* **60:** 95–99.
Campbell, C. A. M. (2001). Integrated management of damson-hop aphid on dwarf hops. Proceedings of the Scientific Commission of the International Hop Growers' Convention. Canterbury, Kent, England, 5–7 August 2001, pp. 61–65.
Campbell, C. A. M., Pettersson, J., Pickett, J. A., Wadhams, L. J., and Woodcock, C. M. (1993). Spring migration of damson-hop aphid, *Phorodon humuli* (Homoptera, Aphididae), and summer host plant-derived semiochemicals released on feeding. *J. Chem. Ecol.* **19:** 1569–1576.
Darby, P., and Campbell, C. A. M. (1988). Resistance to *Phorodon humuli* in Hops. *IOBC/WPRS Bull.* **5:** 56–63.
Darby, P., and Campbell, C. A. M. (1996). Aphid-resistant hops—The key to integrated pest management in hops. *Brighton Crop Prot. Conf. Pests Dis.* **1996:** 893–898.
Dorschner, K. W., and Baird, C. R. (1988). Susceptibility of hop to *Phorodon humuli*. *Entomol. Exp. Appl.* **49:** 245–250.
Dorschner, K. W., and Baird, C. R. (1989). Electronically Monitored Feeding Behavior of *Phorodon humuli* (Homoptera: Aphididae) on Resistant and Susceptible Hop Genotypes. *J. Insect Behav.* **2:** 437–446.
Dorschner, K. W., and Kenny, S. T. (1992). Occurrence of hop aphid phagostimulants in the honeydew of aphids. *Entomol. Exp. Appl.* **65:** 49–55.
Eppler, A. (1986). Untersuchungen zur Wirtswahl von *Phorodon humuli* Schrk. I. Besiedelte Pflanzenarten. *Anz. Schädlingskde.* **59:** 1–8.
Eppler, A. (1989). Settling behaviour of *Phorodon humuli* in relation to virus spread. Proc. Intern. Workshop Hop Virus Dis. Rauischholzhausen 1988, pp. 113–120.
Hornung, U. (1975). Zum Einflußder Wirtspflanze auf ihren Parasiten am Beispiel *Humulus lupulus* L.—*Phorodon humuli* Schrank. *Angew. Bot.* **49:** 45–53.
Hrdý, I., Kremheller, H. T., Kuldová, J., Lüders, W., and Ula, J. (1986). Insektizidresistenz der Hopfenblattlaus, *Phorodon humuli*, in böhmischen, bayerischen und baden-württembergischen Hopfenabaugebieten. *Acta Entomol. Bohemoslov.* **83:** 1–9.
Kralj, D., Kač, M., Dolinar, M., Žolnir, M., and Kralj, S. (1998). Marker-assisted hop (*Humulus lupulus* L.) breeding. *Monatsschr. Brauwissensch.* **1998:** 111–119.
Lösel, P. M., Lindemann, M., Scherkenbeck, J., Maier, J., Engelhard, B., Campbell, C. A. M., Hardie, J., Pickett, J. A., Wadhams, L. J., Elbert, A., and Thielking, G. (1996). The Potential of Semiochemicals for Control of *Phorodon humuli* (Homoptera: Aphididae). *Pestic. Sci.* **48:** 293–303.
Paul, T. A., Darby, P., Green, C. P., Hodgson, C. J., and Rossiter, J. T. (1996). Electrical penetration graphs of the damson-hop aphid, *Phorodon humuli* on resistant and susceptible hops (*Humulus lupulus*). *Entomol. Exp. Appl.* **80:** 335–342.