
SHORT COMMUNICATION

Treating hop plants with (Z)-jasmone increases colonization by *Phorodon humuli* (Hemiptera: Aphididae) spring migrants**T.W. Pope^{1,2*}, C.A.M. Campbell¹, J. Hardie² and L.J. Wadhams³**

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Abstract

Hop plants were sprayed with (Z)-jasmone, at a rate of 50 g ha⁻¹, during the spring migration of the damson-hop aphid *Phorodon humuli* (Schrank) in 2002 and 2003. Numbers of *P. humuli* spring migrants colonizing hop plants, *Humulus lupulus* L., 2–6 and 7–11 days after applying this treatment were assessed in both years. During the first five-day period, significantly more spring migrants were found on hop plants treated with (Z)-jasmone, in comparison with control plants, in 2002. By contrast, no significant difference was evident in the second five-day period. Although the migration in 2003 was much lighter than in 2002, greater numbers of migrants were again removed from treated plants. Indeed, more spring migrants were removed from plants sprayed with (Z)-jasmone in this year during both five-day periods (11 and 44%, respectively) compared with the 23% greater numbers removed in the first five-day period in 2002. Therefore, unlike some other species of aphid, where numbers were consistently lower on plots sprayed with (Z)-jasmone, spraying the secondary host of *P. humuli* with this compound appears to increase colonization by spring migrants.

Keywords: Aphididae, host-finding, olfaction, semiochemical

Introduction

Plants attacked by herbivorous insects may release volatile signals, which cause neighbouring intact plants to

become 'repellent' to incoming herbivores and 'attractive' to predators and parasitoids (Pickett *et al.*, 2003). (Z)-Jasmone, which is associated with the stress-induced jasmonic acid or octadecanoid pathway, is one such compound (Loughrin *et al.*, 1995; Paré & Tumlinson, 1997). (Z)-Jasmone was identified initially from the volatile profile of the black currant, *Ribes nigrum* L., the primary host of the currant-lettuce aphid, *Nasonovia ribis-nigri* (Mosley) (Hemiptera: Aphididae). Behavioural assays, using a four-arm olfactometer, showed (Z)-jasmone to be repellent to spring and summer aphid morphs, which fly to secondary hosts

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including lettuce, *Lactuca sativa* L. (Birkett *et al.*, 2000). However, the effects of (Z)-jasmane were not restricted to *N. ribis-nigri*. In the same study, yellow water traps fitted with sachets releasing this compound caught significantly fewer spring migrants of the damson-hop aphid, *Phorodon humuli* (Schrank) (Hemiptera: Aphididae), than control traps. Similarly, plots of winter wheat, *Triticum aestivum* L., sprayed with (Z)-jasmane were infested by significantly fewer cereal aphids, including *Metopolophium dirhodum* (Walker), *Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (Linnaeus) (all Hemiptera: Aphididae) (Birkett *et al.*, 2000; Bruce *et al.*, 2003), than unsprayed plants. By contrast with the responses of these aphid species, in olfactometer and wind tunnel studies, (Z)-jasmane evoked positive behavioural responses in an aphidophagous, the seven-spot ladybird, *Coccinella septempunctata* Linnaeus (Coleoptera: Coccinellidae), and in an aphid parasitoid, *Aphidius ervi* Haliday (Hymenoptera: Braconidae) (Birkett *et al.*, 2000).

Intact bean plants (*Vicia faba* L.) treated with (Z)-jasmane, at an initial concentration of 0.1 ppm in a closed glass vessel, were found to produce increased levels of (*E,E*)- α -farnesene, β -caryophyllene, (*E*)-4,8-dimethyl-1,3,7-nonatriene and (*E*)- β -ocimene (Birkett *et al.*, 2000), compounds which have previously been shown to be released by plants attacked by herbivorous insects (Turlings *et al.*, 1995). This result suggests that (Z)-jasmane may act as a phytopheromone, influencing the release of volatiles from neighbouring intact plants (Birkett *et al.*, 2000; Chamberlain *et al.*, 2001). Interestingly, after about 24 h, no remaining (Z)-jasmane could be detected in the glass vessel; however, structurally similar and biosynthetically related contaminants of the commercial (Z)-jasmane used were still present. It has, therefore, been suggested that the (Z)-jasmane is taken up selectively by the bean plant (Chamberlain *et al.*, 2001). The aim of the present study is to assess whether *P. humuli* is inhibited from colonizing hop plants sprayed with (Z)-jasmane, as might be inferred by the negative response of several other aphid species to secondary host-plants sprayed with this compound.

Materials and methods

Randomized complete block experiments were conducted in plantations of dwarf hops, *Humulus lupulus* (L.), at East Malling Research in 2002 and 2003. Hops were grown in 30 m rows consisting of six 5 m panels and the hop stems (bines) were supported by a 2.4 m high trellis. The second and fifth panel formed the individual plots in each block. Three of the six blocks were on cv. Herald and three on cv. First Gold.

(Z)-Jasmane (Sigma-Aldrich, UK; purity 90%) was applied to all hop plants in a panel using an Oxford Precision Sprayer (MDM Engineering Ltd, UK) fitted with a fan nozzle (015 F110). Each treatment panel was sprayed with 0.125 g (Z)-jasmane solubilized in 0.5 l of water by means of a non-ionic surfactant (Ethylan BV, Akros Chemicals, UK, 0.1%), which is equivalent to 50 g (Z)-jasmane ha⁻¹. The control used the same formulation, minus the (Z)-jasmane, applied at the same rate. Random numbers were used to select which of the two panels received the (Z) Jasmane and which the control, in each block.

Six healthy hop bines in the centre of each hop panel were selected for aphid assessments. Twenty-four hours after treatment applications all spring migrants on the three

Table 1. Total numbers of *Phorodon humuli* spring migrants removed from hop bines during five-day periods after spraying the plants with (Z)-jasmane in 2002 and 2003.

Year	Days after treatment application	Treated bines	Control bines	Statistics
2002	2–6	1941	1576	$F_{1,5} = 23.91, P = 0.05$
	7–11	1776	1836	$F_{1,5} = 0.10, P = 0.77$
	12–16	158	174	$F_{1,5} = 0.98, P = 0.37$
2003	2–6	166	149	$F_{1,5} = 0.76, P = 0.42$
	7–11	174	121	$F_{1,5} = 2.39, P = 0.18$

apical leaf pairs on each of the bines were counted and removed. Thereafter, numbers of spring migrants were counted and removed daily. Aphid numbers were recorded between 1–15 June 2002, and 12–21 June 2003. In order to reduce the risk of missing transient effects from treating hop plants with (Z)-jasmane, each recording period was divided into five-day blocks.

Data were examined by analysis of variance (ANOVA) using GenStat 5 (Payne, 2000). In order to stabilize variances, the daily counts were transformed to square roots ($n^{0.5}$) and summed across three sampling periods, 2–6 days, 7–11 days and 12–16 days, after treatment application in 2002 and over the first two sampling periods in 2003.

Results and discussion

A total of 7461 *P. humuli* spring migrants was removed from assessed hop bines in 2002 and 610 in 2003 (table 1). In the first five-day period after treatment, significantly more spring migrants were removed from hop bines treated with (Z)-jasmane than controls in 2002 ($F_{1,5} = 23.91, P = 0.05$). However, that pattern was reversed in the second and third five-day sampling periods, but the differences were non-significant.

A similar increase in aphids on the treated plants was observed in 2003. However, because the migration to hop was much lighter than in 2002, the difference failed to achieve statistical significance by ANOVA in either five-day sampling period (although a contingency test between totals on treated and untreated bines in 2003 was significant; $\chi^2 = 8.03, P < 0.01$). Indeed, more spring migrants were removed from bines treated with (Z)-jasmane than from untreated bines in the first and second five-day periods (11 and 44%, respectively) in 2003. By contrast, greater numbers (23%) of aphids were removed from treated bines only in the first five-day period in 2002.

Jasmonic acid and its methyl ester are known to stimulate production of various defence-related secondary metabolites by plants in response to stress, such as attack by insect herbivores (Bleichert *et al.*, 1995). Furthermore, because methyl jasmonate is volatile, it can act as an airborne signal for such processes (Farmer & Ryan, 1990). Birkett *et al.* (2000) and Bruce *et al.* (2003) found that the biosynthetically related (Z)-jasmane is also involved in plant defence responses. In olfactometer studies, the aphids *N. ribis-nigri* (Birkett *et al.*, 2000) and *S. avenae* (Bruce *et al.*, 2003) responded negatively to (Z)-jasmane, and sprays of the compound significantly reduced numbers of colonizing cereal aphids on plants treated with (Z)-jasmane.

By contrast, although traps releasing (Z)-jasmone caught significantly fewer *P. humuli* spring migrants than controls (Birkett *et al.*, 2000), spraying the chemical on hop plants increased the numbers that settled on the treated plants. However, as (Z)-jasmone is highly volatile (Koch *et al.*, 1997), it is unlikely to have remained on the surface of the hop plants for long. Therefore, the results presented here are more likely due to the effects that (Z)-jasmone has on hops rather than to any direct effects of this compound on the behaviour of *P. humuli* spring migrants.

Bean plants appear to selectively take up (Z)-jasmone from the aerial phase (Chamberlain *et al.*, 2001), which may have resulted in the plants producing increased levels of compounds associated with insect damage (Birkett *et al.*, 2000). It is possible that (Z)-jasmone is also selectively taken up by hop plants and that this results in changes to the volatile profile produced by treated plants. Interestingly, changes to the volatile profile of bean plants treated with (Z)-jasmone lasted eight days (Birkett *et al.*, 2000). Similarly, in the present study, a significant difference in numbers of *P. humuli* spring migrants removed from hop bines was only recorded for the first five-day period after applying (Z)-jasmone in 2002. Further work is required to determine the effects of (Z)-jasmone on the volatiles produced by hop plants and, subsequently, to test the responses of spring migrants to these compounds.

Phorodon humuli spring migrants appear to respond positively to hop plants sprayed with (Z)-jasmone, which contrasts with the negative response of cereal aphids to winter wheat similarly sprayed with (Z)-jasmone (Birkett *et al.*, 2000; Bruce *et al.*, 2003). This may reflect the fact that *P. humuli* frequently over-exploits hop plants (Barber *et al.*, 2003) unlike some aphid species; *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), for example, characteristically occurs in sparse populations. For *M. persicae*, spacing out behaviour, sensitivity to food plant quality and ready induction of dispersive winged morphs in response to moderate crowding ensures that populations mostly remain at low densities (Way & Cammell, 1970). However, in *P. humuli* inherent qualities and dispersal behaviour are less effective at regulating populations, which allows a build-up to excessive and destructive numbers.

Acknowledgements

T.W.P. was funded by the East Malling Trust for Horticultural Research and C.A.M.C. by the Department for Environment Food and Rural Affairs. J.H. was funded by the Biotechnology and Biological Sciences Research Council (BBSRC). Rothamsted Research receives grant-aided support from the BBSRC.

References

- Barber, A., Campbell, C.A.M., Crane, H., Darby, P. & Lilley, R. (2003) Cost-benefits of reduced aphicide usage on dwarf hops susceptible and partially resistant to damson-hop aphid. *Annals of Applied Biology* **143**, 35–44.
- Birkett, M.A., Campbell, C.A.M., Chamberlain, K., Guerrieri, E., Hick, A.J., Martin, J.L., Matthes, M., Napier, J.A., Pickett, J.A., Poppy, G.M., Pow, E.M., Pye, B.J., Smart, L.E., Wadhams, G.H., Wadhams, L.J. & Woodcock, C.M. (2000) New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *Proceedings of the National Academy of Sciences, USA* **97**, 9329–9334.
- Blechert, S., Brodschelm, W., Hölder, S., Kammerer, L., Kutchan, T.M., Mueller, M.J., Xia, Z.-Q. & Zenk, M.H. (1995) The octadecanoic pathway: signal molecules for the regulation of secondary pathways. *Proceedings of the National Academy of Sciences, USA* **92**, 4099–4105.
- Bruce, T.J.A., Martin, J.L., Pickett, J.A., Pye, B.J., Smart, L.E. & Wadhams, L.J. (2003) *cis*-Jasmone treatment induces resistance in wheat plants against the grain aphid, *Sitobion avenae* (Fabricius) (Homoptera: Aphididae). *Pest Management Science* **59**, 1031–1036.
- Chamberlain, K., Guerrieri, E., Pennacchio, F., Pettersson, J., Pickett, J.A., Poppy, G.M., Powell, W., Wadhams, L.J. & Woodcock, C.M. (2001) Can aphid-induced plant signals be transmitted aerially and through the rhizosphere? *Biochemical Systematics and Ecology* **29**, 1063–1074.
- Farmer, E.E. & Ryan, C.A. (1990) Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. *Proceedings of the National Academy of Sciences, USA* **87**, 7713–7716.
- Koch, T., Bandemer, K. & Boland, W. (1997) Biosynthesis of *cis*-jasmone: a pathway for the inactivation and the disposal of the plant stress hormone jasmonic acid to the gas phase. *Helvetica Chimica Acta* **80**, 838–850.
- Loughrin, J.H., Manukian, A., Heath, R.R. & Tumlinson, J.H. (1995) Volatiles emitted by different cotton varieties damaged by feeding beet armyworm larvae. *Journal of Chemical Ecology* **21**, 1217–1227.
- Paré, P.W. & Tumlinson, J.H. (1997) *De novo* biosynthesis of volatiles induced by insect herbivory in cotton plants. *Plant Physiology* **114**, 1161–1167.
- Payne, R.W. (2000) *The guide to GenStat. Part 2: statistics*. Oxford, VSN International.
- Pickett, J.A., Rasmussen, H.B., Woodcock, C.M., Matthes, M. & Napier, J.A. (2003) Plant stress signalling: understanding and exploiting plant-plant interactions. *Biochemical Society Transactions* **31**, 123–127.
- Turlings, T.C.J., Loughrin, J.H., McCall, P.J., Röse, U.S.R., Lewis, W.J. & Tumlinson, J.H. (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences, USA* **92**, 4169–4174.
- Way, M.J. & Cammell, M.E. (1970) Self regulation in aphid populations. pp. 232–242 in den Boer, P.J. & Gradwell, G.R. (Eds) *Proceedings of the Advanced Study Institute on 'Dynamics of numbers in populations'* Oosterbeek, The Netherlands, 7–18 September 1970. Wageningen, The Netherlands, Centre for Agricultural Publishing and Documentation.

(Accepted 23 October 2006)

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