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# SELECTION OF *Nothofagus* HOST TREES BY THE APHIDS *Neuquenaphis staryi* AND *Neuquenaphis edwardsi*

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**Abstract—**Leaf volatiles were collected from three *Nothofagus* species growing in close proximity in Los Ruiles National Reserve, Chile. The volatile preparation from leaves of *No. alessandrii* were attractive to the specialist aphid, *Neuquenaphis staryi*, but not to the generalist aphid, *Ne. edwardsi*, while the volatile preparations of *No. dombeyi* and *No. glauca* were attractive to *Ne. edwardsi*, but not to *Ne. staryi*. This reflects the pattern of aphid/host-plant associations. $\alpha$-Agarofuran was found to occur in all leaf volatile preparations and was shown by electroantennography and olfactometry to be attractive for both *Neuquenaphis* spp., suggesting it may be the *Nothofagus* host-recognition factor for *Neuquenaphis*. The factor(s) mediating *Ne. staryi*'s specialization on *No. alessandrii* remain to be identified.

**Key Words—***Nothofagus, Neuquenaphis*, leaf volatiles, $\alpha$-agarofuran, olfactometry, electroantennography.

## INTRODUCTION

There is ample evidence that the host-selection behavior of herbivorous insects is mediated primarily by secondary plant chemicals, although cues at other trophic levels, such as from natural enemies or competitors, may also be important in certain cases (Dicke, 2000). Southern beeches (*Nothofagus* spp.) in Chile are parasitized by the native aphid genus, *Neuquenaphis*. This genus is quite diverse and exhibits a wide range of specificity within *Nothofagus* hosts, from the specialist *Ne. staryi*, which is found only on *No. alessandrii*, to the generalist *Ne. edwardsi*, which has been found on eight host tree species (Quiroz et al., 1999, and

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unpublished results). The pattern of association between *Neuquenaphis* and *Nothofagus* probably arises from the capacity of *Neuquenaphis* to respond to chemical and physical features of the host plants. Selection and acceptance by aphids of their host plants is a complex and highly integrated process that occurs in four successive stages (Niemeyer, 1990). The first of these stages (landing on the plant) involves chemical attraction by volatiles emanating from the surface of the leaf. At each of the other stages, the aphid may find plant features that induce it to continue on the plant or to leave.

In earlier work (Quiroz et al., 1999), the distribution of four *Neuquenaphis* species on *Nothofagus* was reported, and a preliminary analysis of the leaf volatiles of six *Nothofagus* species was presented. A major component in the volatile profile of *No. glauca* was identified as the terpene, $\alpha$-agarofuran. This compound was attractive to alates of *Ne. sensoriata*. We wish to clarify here that the alates of *Ne. sensoriata* used in that study, were misidentified (C. C. Ramírez, personal communication) and that the aphid recorded as *Ne. sensoriata* in Quiroz et al., 1999, was, in fact, *Ne. edwardsi*. Therefore, the results reported in Quiroz et al., 1999, relate to the generalist aphid, *Ne. edwardsi* that may find its host plants by attraction to $\alpha$-agarofuran.

Los Ruiles National Reserve, 200 km south of Santiago, is an isolated coastal pocket where the last remaining stands of *No. alessandrii* are to be found. It occurs mixed with *No. glauca* and *No. dombeyi*. As reported previously (Quiroz et al., 1999), *Ne. staryi* was found only on *No. alessandrii* and not on the other two neighboring species in this reserve, whereas *Ne. edwardsi* was found on both *No. glauca* and *No. dombeyi* and not on *No. alessandrii*. There is almost certainly a specific attraction for *Ne. staryi* to *No. alessandrii* and an ability for it to survive on this plant. *No. alessandrii* has few associated insects and its leaf extracts show toxicity in several bioassays (Russell et al., 2000). By the same token, *Ne. edwardsi* must be attracted to, and have an ability to survive on, *No. glauca* and *No. dombeyi* rather than on *No. alessandrii*.

In order to extend our previous work (Quiroz et al., 1999) and to confirm the primary attraction of *No. alessandrii* for alates of *Ne. staryi*, and *No. glauca* and *No. dombeyi* for alates of *Ne. edwardsi*, we undertook further work with the leaf volatiles of *No. alessandrii*, *No. glauca*, and *No. dombeyi* from the Los Ruiles National Reserve.

## METHODS AND MATERIALS

*Plants and Insects*. Both plants and aphids were collected from Los Ruiles National Reserve (32°49′ S: 72°31′ W), Chile. Leafy stems (0.5 m) were cut from branches of *No. alessandrii* Ep., *No. glauca* (Phil.) Krasser, and *No. dombeyi* (Mirb.) Oerst., and stored in a cool-box during transportation to the laboratory.

Alates of *Ne. staryi* and *Ne. edwardsi* were collected from leaves of their host tree and kept on leaves in suitable tubes and at cool temperatures (4°C) until required.

*Entrainment of Leaf Volatiles*. The cut end of each stem was sealed with Teflon tape and the stems (4) placed into a 10-l bell-jar. Air was drawn through the jar by an oil-free pump at 1 l/min for 20 hr, and was purified by passage through an inlet filter containing activated charcoal and molecular sieves. The air exited from the jar through a Porapak Q (50/80 mesh, 30 mg) trap that entrained the leaf volatiles. These were desorbed from the Porapak Q with distilled dichloromethane (2 ml) and concentrated (200 $\mu$l) under a stream of nitrogen to give an extract containing the leaf volatiles. Several entrainments were carried out to acquire sufficient volatile concentration for the bioassays.

*Analysis of Volatiles*. Aliquots (1 $\mu$l) of the concentrated volatile extracts were analyzed by GC–MS. A capillary Supelco SPB-5, GLC column (30 m $\times$ 0.25 mm ID) was directly coupled to a mass detector with an integrated data system (GC model HP-56690, MD model HP-5972). Ionization was by electron impact at 70 eV and 280°C. The GC oven was programmed to remain at 40°C for 10 min and then increase at 5°C/min to 250°C. The helium carrier gas flow was 1 ml/min. The GC peaks of each volatile extract were identified by comparison of their retention times and mass spectra with commercial standards. When these were not available, mass spectra were compared with a computerized library data-base (NIST98).

*Electroantennogram Detection* (EAD). Aliquots (2 $\mu$l) of volatile extracts were injected into a Shimadzu GC equipped with a HP-5 MS (similar liquid phase and column dimensions as above) and a 1:1 effluent splitter that allowed simultaneous FI detection and electroantennogram detection. Nitrogen was used as the carrier gas (1 ml/min), and the oven was programmed as above. The outlet for the EAD was held in a humidified air-stream flowing at 5 ml/sec over a *Neuquenaphis* antennal preparation. A glass microcapillary indifferent electrode filled with Ringer solution and grounded with a silver wire was inserted into the aphid's head close to an antenna. A similar recording electrode connected to an amplifier was positioned in the distal end of the antenna. The signal was stored and analyzed on a PC with the EAD program from Syntech, The Netherlands.

*Olfactometry*. Behavioral studies were performed in an olfactometer as described by Pettersson (1970). The olfactometer consisted of a quadratic arena permeated by air (100 ml/min) coming from the stretched corners (arms) and drawn out through a hole above its center. Two glass tubes containing the same volatile extract were connected to the end of two consecutive arms and two tubes containing the competing stimulus or solvent control were connected to the other two arms. The observation arena was divided into four zones and one indifferent zone in the center. An aphid was placed onto the center of the arena and the time it spent in each arm was recorded during 15 min. Each experiment was replicated at least seven times and the results analyzed by nonparametric statistics (Wilcoxon

one-tailed rank-sum test for two groups). The mean times spent in each zone containing the volatiles sources were compared. Authentic $\alpha$-agarofuran was obtained from *No. glauca* and characterized as previously described (Quiroz et al., 1999).

## RESULTS AND DISCUSSION

The leaf volatiles from the three species of *Nothofagus* leaves were entrained from the head-space of several small leafy branches cut from the trees. This method differed from the preferred field-trapping method used in the previous study (Quiroz et al., 1999), but it enabled longer trapping times from multiple collections and gave greater yields of entrained volatiles for bioassay. *No. alessandrii* gave the poorest yield of volatiles with *No. dombeyi* giving 2×'s, and *No. glauca* 4×'s the yield of total volatiles on the basis of a common internal standard. This meant that while four trappings of *No. dombeyi* and *No. glauca* were sufficient for testing with aphids, several collections of *No. alessandrii* were combined to provide sufficient material. Each volatile preparation was analyzed by GC–MS and, although the same compounds were almost always present for a particular species, yields of the individual components varied markedly.

The identity and relative abundance of the entrained leaf volatiles collected from the three *Nothofagus* species are shown in Table 1, which represents a typical GC–MS profile of leaf volatiles collected in late November/early December. GC–MS traces showed typical atmospheric contaminants, such as alkanes and substituted benzenes, reflecting the long collection times employed, and in spite of having a carbon/molecular sieve filter on the inlet of the head-space apparatus. These contaminants and the siloxanes originating from the GC column liquid phase, have been eliminated from Table 1. All the compounds identified in the previous work (Quiroz et al., 1999) were found in this study, but we were able to identify a greater number (48 as opposed to 21) occurring in one or more species. This is a reflection of the methods used and the longer trapping times employed. Over the three species, 66 peaks were observed in the GC: 22 were identified with authentic compounds, 26 were provisionally identified from a mass spectral library match, 18 peaks remain unidentified. The identified compounds fall into three categories. Common monoterpenes found as constituents of many leaf volatiles (Knudsen et al., 1993), esters and aldehydes, also found in many leaf volatiles, and a significant group of sesquiterpenes in which cadinane and eudesmane structural-types predominate.

Compounds that are common to the three *Nothofagus* species are: $\alpha$-pinene (**3**), camphene (**4**), sabinene (**6**), $\alpha$-copaene (**33**), (*E*)-$\beta$-farnesene (**44**), germacrene D (**48**), $\delta$-cadinene (**56**), $\alpha$-agarofuran (**57**), and $\gamma$-eudesmol (**64**). *No. glauca* gave relatively high yields of the monoterpenes, $\alpha$-pinene and sabinene, whereas *No. dombeyi* gave high yields of $\alpha$-copaene. Compounds found only in *No. alessandrii*

TABLE 1. COMPOSITION OF LEAF VOLATILES FROM THREE *Nothofagus* SPECIES

| | Compound | Identification method[b] | Retention time (min) | Relative areas[a] (%) | | |
|---|---|---|---|---|---|---|
| | | | | *N. alessandrii* | *N. glauca* | *N. dombeyi* |
| 1 | Thujene | B | 12.54 | | | 0.9 |
| 2 | Tricyclene | B | 13.01 | 2.0 | | 2.8 |
| 3 | $\alpha$-Pinene | A | 13.79 | 2.2 | 18.4 | 2.9 |
| 4 | Camphene | A | 14.56 | 0.1 | 0.8 | 5.2 |
| 5 | Benzaldehyde | A | 15.23 | 0.1 | | |
| 6 | Sabinene | B | 16.02 | 8.0 | 52.1 | 1.3 |
| 7 | Phenol | A | 16.87 | 0.1 | | |
| 8 | 6-Methyl-5-hepten-2-one | A | 16.90 | 0.1 | | |
| 9 | (*Z*)-3-Hexenyl acetate | A | 17.85 | 5.0 | 0.5 | |
| 10 | $\alpha$-Terpinene | B | 18.11 | | 0.6 | |
| 11 | Hexanyl acetate | A | 18.14 | 0.6 | | |
| 12 | (*E*)-2-Hexenyl acetate | A | 18.23 | 0.8 | | |
| 13 | *p*-Cymene | A | 18.46 | 1.8 | 1.2 | |
| 14 | Limonene | A | 18.68 | 1.7 | 0.9 | |
| 15 | (*E*)-Ocimene | B | 19.59 | | 0.2 | 0.6 |
| 16 | $\gamma$-Terpinene | A | 19.95 | | 1.0 | |
| 17 | $\beta$-Terpineol | B | 20.27 | | 1.2 | |
| 18 | Terpineolene | A | 21.20 | | 0.3 | |
| 19 | Nonanal | A | 21.79 | 2.0 | | |
| 20 | Unknown 1 (M, 150) | | 22.76 | 9.7 | 21.0 | |
| 21 | Camphor | A | 23.09 | | 0.1 | 0.6 |
| 22 | Isocamphopinone | B | 24.14 | | 0.1 | |

TABLE 1. CONTINUED

| | Compound | Identification method[b] | Retention time (min) | Relative areas[a] (%) | | |
|---|---|---|---|---|---|---|
| | | | | *N. alessandrii* | *N. glauca* | *N. dombeyi* |
| 23 | 4-Ethylbenzaldehyde | A | 24.27 | 0.1 | | |
| 24 | 4-Terpineol | A | 24.28 | | 0.2 | |
| 25 | Unknown 2 (M, 146) | | 24.68 | 0.2 | | |
| 26 | Unknown 3 (M, 152) | | 24.86 | 0.1 | | |
| 27 | Decanal | A | 25.37 | 1.3 | 0.5 | |
| 28 | 4-Terpineol acetate | B | 25.71 | | 0.5 | |
| 29 | Unknown 4 (M, 136) | | 28.47 | 0.6 | | |
| 30 | $\alpha$-Cubebene | A | 29.73 | 2.5 | | 0.3 |
| 31 | $\alpha$-Muurolene | B | 30.23 | | | 1.0 |
| 32 | Unknown 5 (M, 174) | | 30.35 | 2.8 | | |
| 33 | $\alpha$-Copaene | A | 30.59 | 0.6 | 1.4 | 35.3 |
| 34 | Unknown 6 (M, 204) | | 30.77 | 0.7 | 0.4 | |
| 35 | $\beta$-Santalene | B | 30.91 | 1.2 | 0.2 | |
| 36 | $\alpha$-Cedrene | A | 30.59 | 0.2 | | |
| 37 | Caryophyllene | A | 31.70 | | 1.0 | 2.5 |
| 38 | $\alpha$-Humulene | B | 31.75 | 0.6 | | |
| 39 | $\alpha$-Santalene | B | 31.76 | | 0.4 | |
| 40 | Unknown 7 (M, 204) | | 32.02 | | 0.2 | |
| 41 | $\beta$-Bergmantene | B | 32.14 | 0.2 | 0.2 | |
| 42 | $\alpha$-Guaiene | B | 32.25 | 1.3 | | |
| 43 | Unknown 8 (M, 204) | | 32.41 | | 0.1 | 0.4 |
| 44 | (*E*)-$\beta$-Farnesene | B | 32.68 | 0.3 | 0.9 | 3.3 |

TABLE 1. CONTINUED

| | Compound | Identification method[b] | Retention time (min) | Relative areas[a] (%) | | |
|---|---|---|---|---|---|---|
| | | | | *N. alessandrii* | *N. glauca* | *N. dombeyi* |
| 45 | Aromadendrene | B | 32.86 | | 0.8 | 4.2 |
| 46 | Unknown 9 (M, 220) | | 33.15 | 0.2 | | 0.3 |
| 47 | $\alpha$-Curcumene | B | 33.29 | 0.7 | | 0.7 |
| 48 | Germacrene D | B | 33.43 | 2.6 | 5.3 | 1.5 |
| 49 | $\beta$-Selinene | B | 33.53 | | 0.4 | |
| 50 | $\gamma$-Cadinene | B | 33.69 | | | 0.5 |
| 51 | $\alpha$-Selinene | B | 33.75 | | 0.5 | |
| 52 | $\gamma$-Muurolene | B | 33.87 | | 0.6 | |
| 53 | $\alpha$-Farnesene | B | 34.00 | 3.2 | 0.3 | |
| 54 | Unknown 10 (M, 204) | | 34.15 | 9.7 | | |
| 55 | Unknown 11 (M, 204) | | 34.24 | | 0.4 | |
| 56 | $\delta$-Cadinene | B | 34.47 | 1.2 | 0.6 | 12.8 |
| 57 | $\alpha$-Agarofuran | A | 35.08 | 4.7 | 2.0 | 2.3 |
| 58 | Unknown 12 (M, 220) | | 35.32 | 1.4 | | |
| 59 | Nerolidol | B | 35.36 | | 1.6 | 1.2 |
| 60 | Unknown 13 (M, 220) | | 35.45 | 4.7 | | |
| 61 | Unknown 14 (M, 218) | | 35.67 | 1.0 | | |
| 62 | Unknown 15 (M, 220) | | 35.84 | 2.1 | | |
| 63 | Unknown 16 (M, 222) | | 36.62 | | 1.6 | 1.2 |
| 64 | $\gamma$-Eudesmol | B | 36.95 | 1.0 | 0.9 | 8.7 |
| 65 | Unknown 17 (M, 222) | | 37.40 | | 0.9 | 0.4 |
| 66 | Unknown 18 (M, 222) | | 38.16 | 0.7 | | |

[a] Calculated as a percentage of the total volatile peak area for that plant.
[b] A = comparison with authentic compounds; B = GC–MS comparison with the library database (NIST 98) with a similarity index >95%.

were: benzaldehyde (**5**), phenol (**7**), 6-methyl-5-hepten-5-one (**8**), hexanyl acetate (**11**), (*E*)-2-hexenyl acetate (**12**), nonanal (**19**), 4-ethylbenzaldehyde (**23**), $\alpha$-cedrene (**36**), $\alpha$-humulene (**38**), $\alpha$-guaiene (**42**), and several unknowns. Aldehydes and esters seem to be common in *No. alessandrii*, while a greater variety and yield of monoterpenes seem to occur in the volatile profile of *No. glauca*.

Results of olfactometry studies with solutions of entrained volatiles against *Ne. staryi* and *Ne. edwardsi* are shown in Figure 1. When *Ne. staryi* was given pair-wise choices between volatiles of *No. alessandrii* and volatiles of either *No. glauca* or *No. dombeyi* or of a solvent control, the aphid preferred to move toward the olfactometer arms containing the *No. alessandrii* volatiles, indicating that there is a specific attractant(s) for *Ne. staryi* in the leaf volatiles of *No. alessandrii*. When *Ne. staryi* was presented with a choice between volatiles of *No. glauca* and *No. dombeyi*, and between each of these volatile preparations and solvent, the aphid moved between both arms spending a similar time in each. This indicates that these volatile blends were no more attractive than the solvent controls, eliciting a neutral response from the aphid. When *Ne. edwardsi* alates were offered the same pair-wise choices, the aphid moved toward the arms containing either volatiles of *No. glauca* or *No. dombeyi*, indicating it was attracted to volatiles of these plants rather than the volatiles of *No. alessandrii*. When presented with a choice of *No. alessandrii* volatiles and solvent, it spent equal time in each arm unable to make a preference decision. Given *Ne. edwardsi*'s generalist nature and its known attraction for $\alpha$-agarofuran, a component in *No. alessandrii* volatiles, the volatile mixture from *No. alessandrii* either lacks an additional component(s) that will determine preference or there is a component(s) in the mixture that is deterring the aphid from settling at the *No. alessandrii* source.

Olfactometry studies support field observations for host associations of *Ne. staryi* and *Ne. edwardsi*, and indicate that the leaf volatiles are a source of primary host attraction. In order to delineate this source of attraction in the host plant volatiles, we carried out some experiments with an electroantennogram used as a secondary detector (EAD) to a GC. Achieving functional antennal preparations with aphids is known to be difficult, due to there being few olfactory sensilla and low response voltages (Pickett et al., 1992), and we had limited success with this technique. We were unable to achieve a successful functioning antennal preparation of *Ne. edwardsi*, but a preparation with an antenna of *Ne. staryi* gave two clear signals with *No. alessandrii* volatiles, which we were able to correlate with peaks in the GC–MS. One signal corresponded to the peak for $\alpha$-agarofuran (**57**). We were able to confirm this EAD response using authentic $\alpha$-agarofuran with *Ne staryi*; an EAD signal coincided with the FID peak for $\alpha$-agarofuran. The second signal corresponded to compound **54**, but we have been unable to identify this compound (unknown 10) as an attractant for *Ne. staryi*.

In the olfactometer bioassay, alates of *Ne. staryi* were attracted by authentic $\alpha$-agarofuran compared with the solvent control (Table 2). Both *Ne. staryi* and *Ne.*

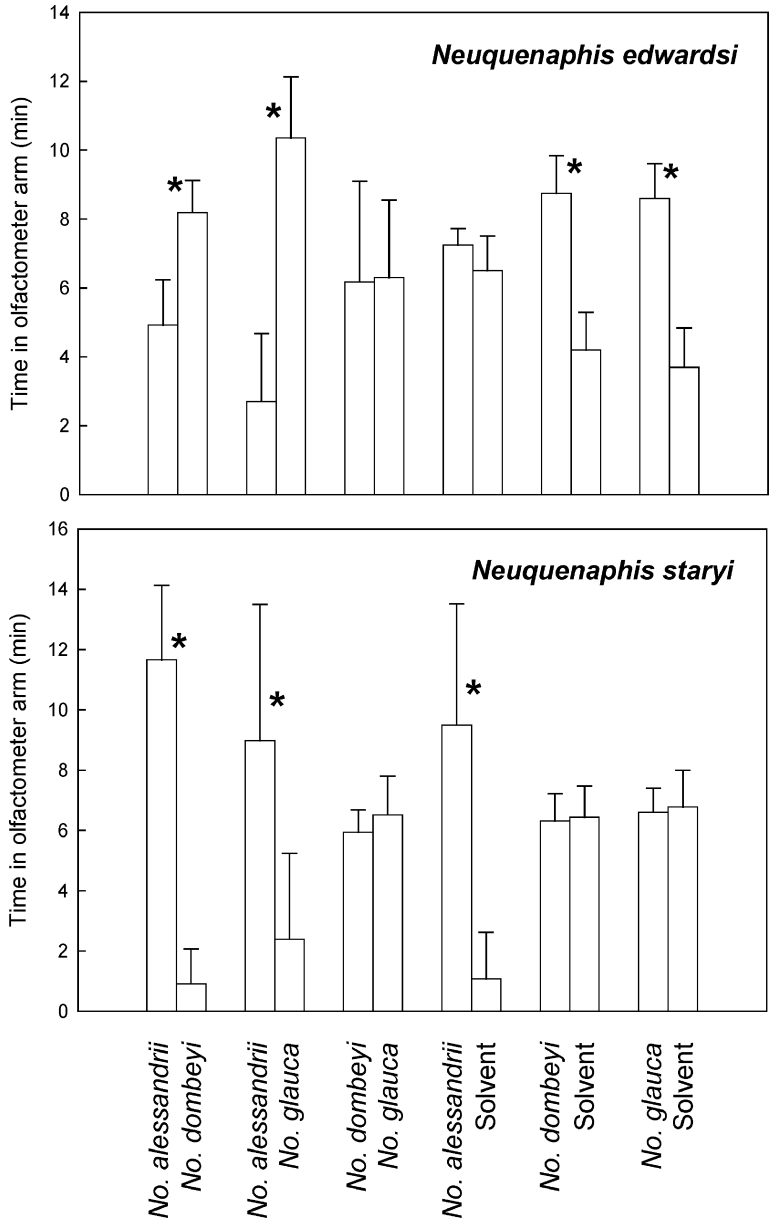


FIG. 1. Preferences of *Neuquenaphis edwardsi* and *Neuquenaphis staryi* for different stimuli offered pair wise in an olfactometer. Asterisks denote significant differences ($P < 0.05$, Wilcoxon one-tailed rank-sum test for two groups).

TABLE 2. RESPONSE OF *Neuquenaphis* INTRODUCED SINGLY INTO AN OLFACTOMETER AND EXPOSED TO $\alpha$-AGAROFURAN

| | Time spent (min)[a] | | |
|---|---|---|---|
| | Solvent[b] | 10 $\mu$g of $\alpha$-agarofuran | $P^c$ |
| *Ne. staryi* alatae | $3.2 \pm 2.4$ | $8.1 \pm 4.1$ | 0.02 |
| *Ne. edwardsi* alatae[d] | $4.9 \pm 1.7$ | $8.0 \pm 1.1$ | 0.01 |

[a]Mean $\pm$ standard error.
[b]Dichloromethane for *Ne. staryii* and hexane for *Ne. edwardsi*.
[c]Wilcoxon one-tailed rank-sum test for two groups.
[d]Data from Quiroz et al., 1999.

*edwardsi*, a specialist aphid and a generalist aphid, respectively, are attracted to $\alpha$-agarofuran. $\alpha$-Agarofuran is not a common terpene, but with this and previous work, we have now shown its occurrence in five *Nothofagus* species. This raises the possibility that $\alpha$-agarofuran may be found in most *Nothofagus* and may be the principal host-recognition factor for *Neuquenaphis*. If that is the case, then the question remains, what factor(s) determines *Ne. staryi's* selection of *No. alessandrii* as its only host plant and *Ne. edwardsi's* avoidance of this plant? This factor(s) may fulfill both functions, attracting *Ne. staryi* on the one hand and repelling *Ne. edwardsi* on the other, although the presence or absence of attractants in the volatile blends may be the more important principle. Del Campo et al. (2003), suggested that it was the recognition of host-specific chemicals rather than the avoidance of deterrents that determined the feeding behavior of the pea aphid, *Acyrthospiphon pisum*. Compound **54**, which occurs only in *No. alessandrii*, may be the other factor that allows *Ne. staryii* to recognize its host plant, but it has not been possible to confirm this. The leaf chemistry of *No. alessandrii* is quite different from the other Chilean *Nothofagus* (although it has similarities to the New Zealand *No. fusca*) and we have found the phytoalexin, pinosylvin, occurring only in *No. alessandrii* leaf extracts (Russell et al., 2000). However, we could not find pinosylvin or any related phenolics in the head space volatiles from leaves of *No. alessandrii*, ruling out the possibility that such phenolics may be the unique host-recognition factors for *Ne. staryi*. Olfactometer experiments with benzaldehyde, phenol, 4-ethylbenzaldehyde, nonanal, 2-hexenyl acetate, and hexanyl acetate, which occur only in *No. alessandrii* volatiles, also indicated that these compounds were unlikely attractants to *Ne. staryii* or repellants to *Ne. edwardsii*.

Primary host selection behavior by herbivorous insects is mediated mainly by plant volatiles. In this study, we have shown that leaf volatile chemicals (constitutive or induced) can be collected and influence the host recognition behavior of a specialist and a generalist *Neuquenaphis* in a manner that reflects the observed plant–insect associations in the natural environment. It appears that the principal

host-recognition factor for *Neuquenaphis* on *Nothofagus* is $\alpha$-agarofuran and that other factors play a role in the specialization of *Ne. staryi*.

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