

## Differential Susceptibility of Poplar Hybrids to the Aphid *Chaitophorus leucomelas* (Homoptera: Aphididae)

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**ABSTRACT** After its recent introduction to Chile, the aphid *Chaitophorus leucomelas* Koch is becoming a serious pest affecting commercial poplar, *Populus* spp., plantations. The pattern of natural infestation of *C. leucomelas* among poplar hybrids with different pedigrees and the aphid intrinsic rate of increase ( $r_m$ ), of *C. leucomelas* were assessed in the field. In most of the hybrids, aphid abundance peaked in March (late summer). Among 12 types of poplar crosses, [(*P. trichocarpa* Torr. & Gray × *P. deltoides* Bartram ex Marshall) × (*P. trichocarpa* × *P. deltoides*)] and [(*P. trichocarpa* × *P. maximowiczii* Henry) × *P. maximowiczii*] showed the highest and lowest aphid densities, respectively. A trend to find more aphids in branch bases was apparent. The intrinsic rate of *C. leucomelas* increase was higher in [(*P. trichocarpa* × *P. deltoides*) × *P. deltoides*] hybrids, and lower in [(*P. trichocarpa* × *P. maximowiczii*) × *P. trichocarpa*] hybrids. Aphid density and performance were higher in hybrids with *P. deltoides* parentage, whereas hybrids with *P. maximowiczii* parentage showed lower aphid densities and performance. Hybrids with *P. nigra* L. parentage, namely, [*P. trichocarpa* × *P. nigra*], also had high aphid density, but aphid performance was lower compared with hybrids with *P. deltoides* parentage. These results suggest that among poplar hybrids studied, susceptibility to *C. leucomelas* is inherited through *P. deltoides*, whereas resistance seems to be inherited through *P. maximowiczii*. Thus, *P. maximowiczii* hybrids are recommended for commercial or ornamental planting programs in zones where there is a high risk of aphid infestation.

**KEY WORDS** aphid, poplar, hybrid, infestation, susceptibility

INTERSPECIFIC HYBRIDIZATION, followed by clonal selection, is one of the methods for genetic improvement of commercial trees. In this process, fast-growing, short-rotation woody crops and productive woody biomass hybrids are selected. This has been the case for selected poplar hybrids (*Populus* spp.), which now have worldwide distribution (Stettler et al. 1996). Furthermore, poplar crops have been shown to reduce pollution, pesticide runoff, and erosion compared with agricultural systems (Stettler et al. 1996, Zsuffa et al. 1996, Newman et al. 1997), which has enhanced their value. However, interspecific hybridization may result in unexpected features in the progeny such as susceptibility to herbivorous insects (Whitham 1989, Fritz et al. 1999, Mattson et al. 2001).

For *Populus* spp., the existence of hybrids with increased susceptibility to pathogens, and particularly to phytophagous insects, has been described previously (Whitham 1989, Floate et al. 1993, Floate and Whitham 1993, Newcombe 1996, Whitham et al. 1996). Studies addressing natural resistance among

poplar hybrids to most phytophagous insects reveal that resistance depends on the pedigree and type of insect attack (Mattson et al. 2001). For instance, resistance to the leaf beetle *Phratora californica* Brown (Coleoptera: Chrysomelidae) likely comes from the *Populus trichocarpa* Torr. & Gray parent (James and Newcombe 2000). Hybrids between *Populus alba* L. and *Populus grandidentata* Michx. are more resistant to the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) (Robison and Raffa 1994). Hybrids between *Populus nigra* L. and *Populus maximowiczii* Henry are resistant to the gypsy moth, *Lymantria dispar* (L.) (Kruse and Raffa 1996), whereas larval performance of the cottonwood leaf beetle, *Chrysomela scripta* F. (Coleoptera: Chrysomelidae), is generally poorer on clones with higher *P. trichocarpa* parentage (Coyle et al. 2001). Hybrids with *Populus deltoides* Bartram ex Marshall parentage are also more susceptible to *C. scripta* (Bingaman and Hart 1992). High susceptibility to the sawfly *Nematus* sp. in *P. trichocarpa* and *P. deltoides* (T × D) hybrids has been described previously, whereas hybrids between *P. trichocarpa* × *P. maximowiczii* seem resistant to *Nematus* (U.S. EPA 1999). Among aphids, the spotted poplar aphid, *Aphis maculatae* Oustlund, has been shown to attack a wide range of poplar hybrids with an even larger variation in susceptibility between clones of similar parentage (Wilson and Moore 1986, Mattson

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et al. 2001). Another important aphid, the speckled poplar aphid, *Chaitophorus populicola* Thomas, has been described as producing serious injury on *P. deltoides* (Solomon 1985).

In Chile, commercial poplars generated from a small number of introduced hybrids are planted on nearly 6,000 ha. However, close to 2,500 poplar hybrids produced from interspecific hybridization of four *Populus* species (*P. trichocarpa*, *P. deltoides*, *P. maximowiczii*, and *P. nigra*) have been recently introduced to Chile, as part of an effort to increase the genetic diversity of the genus and select outstanding hybrids for commercial use (Zamudio et al. 2003). Few insects have been found to attack both recently introduced hybrids and preexisting poplar plantations (Sanhueza et al. 1998). However, a recent increase in infestations of the aphid *Chaitophorus leucomelas* Koch on established and introduced poplar hybrids is occurring among commercial plantings in the center of Chile. *C. leucomelas* was first reported in 1995 in northern Chile (Muñoz and Beeche 1995) and is quickly spreading to the south (Klein-Koch and Waterhouse 2000). During fall, sexual individuals of *C. leucomelas* mate and lay eggs that overwinter on poplar trees. In the spring, larvae (foundatrices) hatch from the eggs and initiate several alate parthenogenetic generations that extend throughout the summer, feeding on poplars. In the fall, sexual morphs are produced and the cycle starts again. However, nothing is known about the type and degree of susceptibility of poplar hybrids in Chile to *C. leucomelas*. Here, we report results obtained from monitoring the abundance of *C. leucomelas* on different poplar hybrids during one growing season, as well as *C. leucomelas* reproductive performance in a field assay. Our preliminary hypotheses were that 1) there are significant differences in the degree of susceptibility between poplar hybrids to *C. leucomelas* attack and 2) *C. leucomelas* reproductive performance is higher on susceptible hybrids. Results from our research are expected to be useful for clonal selection, either for commercial purposes or for ornamental plants.

### Materials and Methods

**Field Site and Procedures.** Between August 1999 and March 2001, the Poplar Research Centre, Universidad de Talca, imported two sets of poplar hybrids from the Poplar Molecular Genetics Cooperative, University of Washington (Seattle, WA). Each set was established in a specially conditioned greenhouse to follow a rigorous quarantine regime for 1 yr. Once the quarantine period was over, the new poplar germplasm was transferred to an experimental nursery located within the main Universidad de Talca campus (35° 30'S, 72° 30'W, elevation 90 m). Using a randomized complete block design, ≈6,000 cuttings from 12 crosses of *Populus* species were planted in this nursery. Cuttings were separated 60 cm from each other and fertirrigation was applied (mixture of 200 ppm N, 88 ppm P, and 166 ppm K, two times per week with daily water addition). In spring 2002, a total of 153 plants

were selected from this experimental nursery for monitoring the presence of *C. leucomelas*. Clones belonging to one family per interspecific cross of the following species were monitored: *P. trichocarpa* (T), *P. deltoides* (D), *P. maximowiczii* (M), and *P. nigra* (N). Crosses evaluated were T × D ( $n = 5$ ), T × M ( $n = 15$ ), T × N ( $n = 11$ ), T × T ( $n = 15$ ), TD × D ( $n = 15$ ), TD × T ( $n = 15$ ), TD × TD ( $n = 15$ ), TD × TN ( $n = 20$ ), TM × M ( $n = 6$ ), TM × T ( $n = 8$ ), TM × TM ( $n = 16$ ), and T ( $n = 12$ ).

**Aphid Density.** One branch was chosen at random from each of the trees selected for evaluation. The branch was initially tape-marked, and all existing aphids (including nymphs, winged and wingless morphs) in each leaf were visually counted monthly until May 2003 (mid-autumn). To estimate aphid density, the number of aphids per leaf was divided by the leaf area. Leaves were digitalized, and their area was calculated using the software SigmaScan 5.0.

**Aphid Performance.** From the trees used to assess *C. leucomelas* density described above, four trees per cross were used to assess *C. leucomelas* performance. Four leaves per tree were marked, and on each leaf, between three and five adult parthenogenetic *C. leucomelas* females, either wingless or winged, were enclosed in a clip-cage (1.5 cm in diameter). After 24 h, all adults were removed from the clip-cage, and one wingless nymph was subsequently monitored daily until adulthood, and the prereproductive period (T) was determined. The total number of new nymphs produced subsequently ( $Md$ ) were counted and removed daily. The intrinsic rate of increase,  $r_m$ , was determined using the equation of Wyatt and White (1977):  $r_m = 0.738 (\ln Md) / T$  correction factor. This equation has been used by several workers to calculate  $r_m$  for aphids (Legrand and Barbosa 2000, Stone et al. 2000, Miller et al. 2003).

**Data Analysis.** A one-way analysis of variance (ANOVA) was performed to compare aphid density among hybrids. The variation of aphid density over time on different hybrids was estimated by performing a repeated measures MANOVA with crosses and time (months) as between and within-subject factors, respectively. This test was chosen because univariate output fails to meet the assumption of circularity and sphericity (Vonesh and Chinchilli 1997). The significance of the maternal effect among different hybrids was tested by specific planned comparisons. Data were transformed using  $\log_{10}(X + 1)$  when normality assumptions of ANOVA were violated. One-way ANOVA also was performed to compare *C. leucomelas* aphid reproductive performance among hybrids. Fisher's least significant difference (LSD) test was used for all multiple comparisons. All statistical analyses were performed using Statistica 4.5 software (StatSoft, Inc. 1999).

### Results

*C. leucomelas* density was significantly different between poplar crosses ( $F_{11, 141} = 3.69$ ;  $P < 0.001$ ). Hybrids from the TD × TD and TM × M crosses had

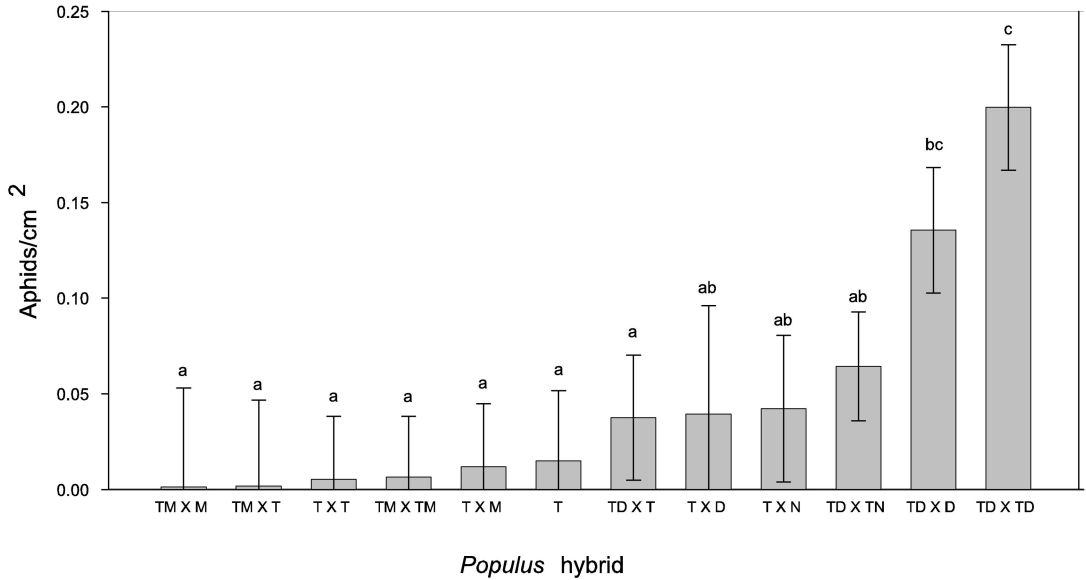


Fig. 1. Density (aphid/cm<sup>2</sup>, mean ± SE) of *C. leucomelas* on different poplar hybrids at Universidad de Talca, Chile. D, *P. deltoides*; M, *P. maximowiczii*; N, *P. nigra*; and T, *P. trichocarpa*. Different letters above bars indicate that differences between values are significant at  $P < 0.05$  (Fisher's LSD multiple comparison test).

the highest and lowest aphid densities, respectively (Fig. 1). The repeated measures MANOVA showed a significant effect of time, and significant time × cross interaction (time: Wilks'  $\lambda = 0.027$ ,  $F_{6, 139} = 778.5$ ,  $P < 0.0001$ ; and cross × time: Wilks'  $\lambda = 0.226$ ,  $F_{6, 701}$ ,  $P < 0.0001$ ). Crosses showing temporal variation in *C. leucomelas* density were T × D, T × N, TD × D, TD ×

T, TD × TD, and TD × TN (Fig. 2, A, C, E, F, G, and H, respectively). In contrast, crosses T × M, T × T, TM × M, TM × T, TM × TM, and T (Fig. 2, B, I, and J, respectively) showed almost no variation over time. *C. leucomelas* reached different abundance peaks during the growing season studied. For example, aphids reared on T × N and TD × D reached their peaks in

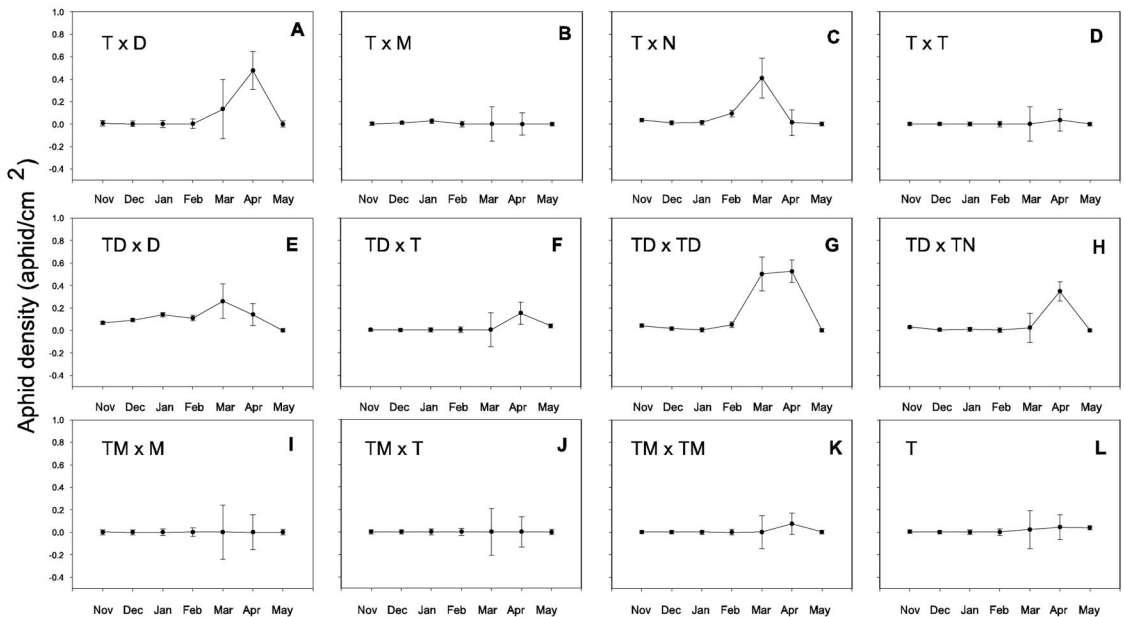


Fig. 2. Temporal variation (November 2002–May 2003) in *C. leucomelas* density (mean ± SE) in different poplar hybrids at Universidad de Talca, Chile. Letters at the upper left corner of each panel indicate hybrid. D, *P. deltoides*; M, *P. maximowiczii*; N, *P. nigra*; T, *P. trichocarpa*.

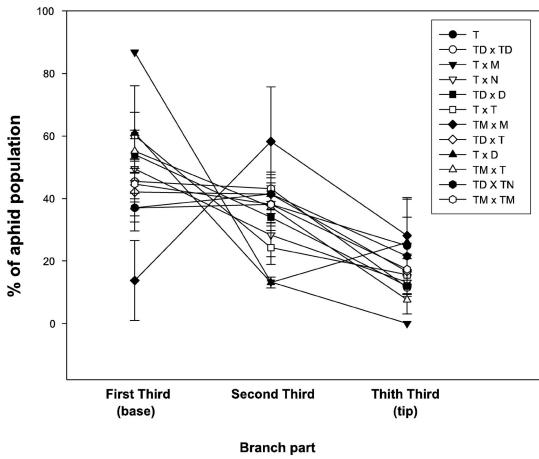


Fig. 3. Within-branch distribution of *C. leucomelas* (mean %  $\pm$  SE of the total aphid population) on poplar hybrids at Universidad de Talca, Chile.

March, whereas those on T  $\times$  D, TD  $\times$  T, TD  $\times$  TD, and TD  $\times$  TN reached a peak in April (Fig. 2). Interestingly, TD  $\times$  TD expressed the largest differences in aphid density compared with all other hybrids ( $P = 0.001$ , multiple comparison with Bonferroni's correction). Comparison between hybrids with TD as the maternal parent against all other hybrids showed that *P. deltooides* supported the growth of more aphids than all other hybrid parents (planned comparison:  $F_{1,141} = 21.74$ ;  $P < 0.00001$ ). The same was not true for contrast with *P. trichocarpa* maternal parentage (planned comparison:  $F_{1,141} = 2.58$ ;  $P = 0.11$ ), whereas the *P. maximowiczii* maternal parentage resulted in lower aphid density (planned comparison:  $F_{1,141} = 6.26$ ;  $P < 0.05$ ).

To explore the within-branch distribution of *C. leucomelas*, the proportion of aphids found in the

base, mid and tip parts of a tree branch was estimated. In most of the crosses, there were more *C. leucomelas* at the base of the branch (Fig. 3). Only on TM  $\times$  M hybrids was there a higher number of *C. leucomelas* in the middle part of the branches. The trend to find more aphids in the base of the branch also was found over time in all crosses (data not shown).

The intrinsic rate of increase of *C. leucomelas* varied significantly among crosses ( $F_{7,45} = 4.73$ ;  $P < 0.01$ ; Fig. 4). It is worth noting that many aphids, particularly those on crosses TM  $\times$  T, T  $\times$  T, TM  $\times$  TM, and T  $\times$  M, did not survive long enough to estimate  $r_m$ . In the case of those on T  $\times$  M, some parthenogenetic females were able to reproduce, but their nymphs did not survive for a time similar to the prereproductive period. Where  $r_m$  was estimated, aphids on TD  $\times$  D, TD  $\times$  T, and TD  $\times$  TD hybrids showed higher  $r_m$  values, whereas those on T and TM  $\times$  TM hybrids had lower  $r_m$  values (Fig. 4). Similar to the aphid density data, the  $r_m$  of aphids reared on hybrids with *P. deltooides* as maternal parent was higher than the  $r_m$  of aphids reared on hybrids with all other parents (planned comparison:  $F_{1,45} = 21.15$ ;  $P < 0.0001$ ). In contrast, hybrids with *P. trichocarpa* and *P. maximowiczii* in the maternal parentage supported the lowest *C. leucomelas*  $r_m$  values (planned comparison:  $F_{1,45} = 8.16$ ;  $P < 0.05$  and  $F_{1,45} = 4.97$ ;  $P < 0.05$ , respectively).

Discussion

In our study, *C. leucomelas* showed a nonrandom distribution over an experimental site where a number of interspecific crosses between four poplar species were grown in proximity. *C. leucomelas* was more abundant in hybrids with *P. deltooides* and *P. trichocarpa* in their parentage, but abundant in very low density in hybrids with *P. maximowiczii* parentage

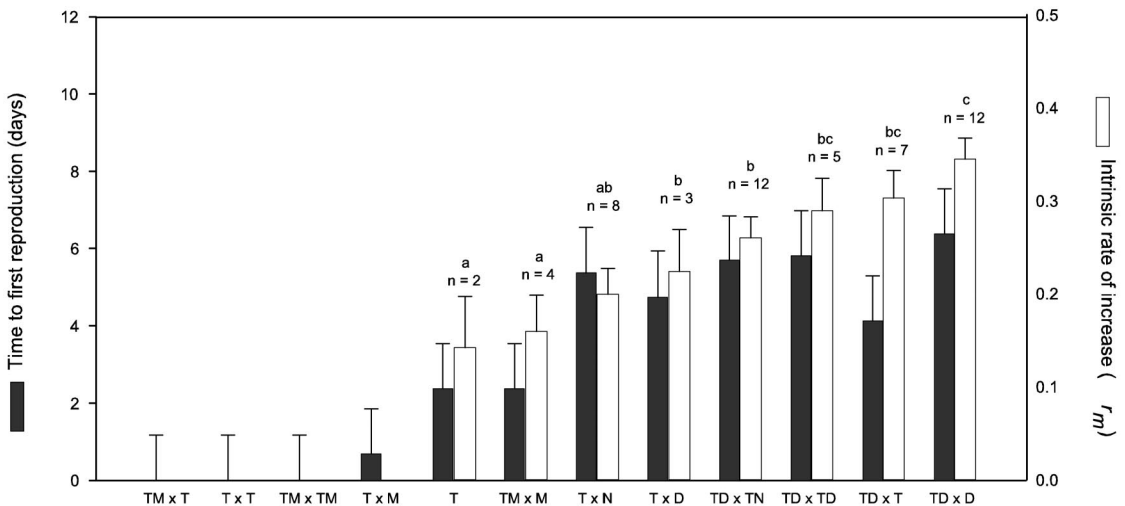


Fig. 4. Time to first reproduction (■) and  $r_m$  values (□) (mean  $\pm$  SE) of *C. leucomelas* on different poplar hybrids at Universidad de Talca, Chile. Different letters over  $r_m$  indicate that differences between values are significant at  $P < 0.05$  (Fisher's LSD multiple comparison test). Number of individuals surviving until  $r_m$  estimate is given.



(Fig. 1). Reproductive performance ( $r_m$ ) followed a similar trend (Fig. 4). Hybrids with *P. nigra* parents [*P. trichocarpa* × *P. nigra*], also supported high *C. leucomelas* density, although not as high as *C. leucomelas* on hybrids with *P. deltoides* parents. These results suggest that hybrids with *P. trichocarpa* or *P. deltoides* parent contain some physiological factors that allow aphids to develop large populations. Poplar hybrids with *P. deltoides* parentage also have been found to be susceptible to other pest Coleoptera (Bingaman and Hart 1992) and Lepidoptera (U.S. EPA 1999).

The low density of *C. leucomelas* found in the hybrids with *P. maximowiczii* parents (Fig. 1) may indicate that *P. maximowiczii* contain *C. leucomelas* resistance factors. Hybrids with *P. maximowiczii* parents are resistant to the gypsy moth (Kruse and Raffa 1996), but nothing is known about *P. maximowiczii* resistance to aphids. Trichomes (Goffreda et al. 1988, Johnson et al. 2002), epicuticular waxes (Powell et al. 1999, Shepherd et al. 1999), and plant allelochemicals (Glinwood and Pettersson 2000, Chaman et al. 2003) have all been associated with aphid resistance. Although not addressed in the current study, we observed that epicuticular waxes in *P. maximowiczii* give the lower leaf surface a pale appearance and a tougher surface. It is possible that these properties may inhibit *C. leucomelas* stylet penetration during feeding. This potential resistance mechanism needs further research.

It is worth noting that *C. leucomelas* density tended to peak in late summer (March and April; Fig. 2) and that aphids were more abundant on the base of branches (Fig. 3). This suggests that aphid distribution and abundance are correlated with leaf age. For example, galling aphids perform better in older cottonwood tissues than in juvenile tissues (Kearsley and Whitham 1998). In addition, plant defenses are usually lower and nutrients higher in the phloem of senescent leaves than in young leaves (Merritt 1996). Higher densities of *C. leucomelas* in older leaves (base of branches) may be the result of a nutritional enhancement of plant tissues, which has been described in other aphids (Telang et al. 1999, Sandstrom et al. 2000, Gonzales et al. 2002).

Other studies of aphids attacking poplar are very rare. The system of the galling aphids of the genus *Pemphigus* feeding on *Populus fremontii* S. Wats and *Populus angustifolia* E. James, and their hybrids is probably the best understood. In this system, aphid distribution shows within-plant variation (Kearsley and Whitham 1998) affected by leaf shape (Floate and Whitham 1993), plant architecture (Larson and Whitham 1997), and plant genotype (Paige and Capman 1993). Although *P. fremontii* and *P. deltoides* belong to the same section, Aigeiros, within the genus *Populus*, *P. fremontii* shows a relative higher resistance to aphids. This may be related with the differences in the type of aphid attack. *Pemphigus* spp. are galling aphids, whereas *C. leucomelas* is a free-living aphid. Solomon (1985) reported great susceptibility in *P. deltoides* infested by *C. populicola*, resulting in trees stem deformities. Other studies of free-living aphids attacking poplar have focused on honeydew compo-

sition in relation to ant-aphid mutualism (Fischer and Shingleton 2001, Wimp and Whitham 2001). Only one study assessed the environmentally mediated effect of host plant on the abundance of the aphid *C. populicola* (Coleman and Jones 1988), but no susceptibility or resistance conclusion was made. Thus, mechanisms underlying differential susceptibility of poplar trees to free-living aphids are a matter of further research.

In summary, we have found that poplar hybrids with *P. deltoides* in the parentage are more susceptible to the aphid *C. leucomelas*. Although in lesser extent, hybrids with *P. nigra* in the parentage are also susceptible to this aphid. In contrast, hybrids with *P. maximowiczii* in the parentage are clearly more resistant. Therefore, this last type of hybrids could be recommended for commercial or ornamental planting programs in zones where there is a high risk of aphid attack. Extrapolation of these results to other sites and climatic conditions should be made with caution. In other latitudes, the susceptibility resistance pattern, or both described herein may change considerably. We are currently addressing this issue by comparing poplar susceptibility and resistance to *C. leucomelas* along a latitudinal gradient in Chile.

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