Olfactory and Feeding Preferences of *Cryptorhynchus lapathi* L. (Coleoptera: Curculionidae) Among Hybrid Clones and Natural Poplars

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ABSTRACT Hybrid poplar clones show varying levels of attack by *Cryptorhynchus lapathi* (L.), a wood-boring weevil. We studied differences in olfactory and feeding behavior among four different hybrid poplars in a series of laboratory bioassays. Weevils did not discriminate between resistant and susceptible clones based on olfaction in pitfall bioassays or antennal responses but did discriminate against the most resistant hybrid, NM 6 (*P. nigra* L. × *P. maximowiczii* Henry), in choice and no-choice paired-twig feeding bioassays. In addition, the susceptible hybrid, TN 302–9 (*P. trichocarpa* Torrey and Gray × *P. nigra*), was preferred for feeding over *Salix scouleriana* Barratt *ex* Hooker, a preferred host in the wild. We conclude that resistance among hybrid poplars is in part based on antixenotic cues before oviposition.

KEY WORDS hybrid poplar, *Cryptorhynchus lapathi*, resistance, *Populus maximowiczii*, host selection

THE POPLAR AND WILLOW borer, *Cryptorhynchus lapathi* (L.) (Coleoptera: Curculionidae), primarily attacks hosts in the family Salicaceae, but it may also infest several *Alnus* and *Betula* spp. (both Betulaceae) (Harris and Coppel 1967). Throughout most of British Columbia, adult emergence begins in July and peaks in mid- to late August, although there is considerable longevity and asynchrony in the lifecycle (Smith and Stott 1964) such that adults are present year round. The majority of weevils emerge in summer and oviposit throughout late summer and early fall. Females oviposit into niches created in the bark where larvae hatch and first mine before moving into the xylem. Damage includes decreased wood quality, stem breakage, and mortality (Broberg et al. 2001), and pathogen entry (Primm 1918, Abebe and Hart 1990).

This exotic weevil (Juelich 1887, Caesar 1916) is still expanding its range northward in North America (Broberg et al. 2002); it already covers the entire southern half of Canada and most of the continental United States, extending south into California (Furniss and Carolin 1977, Morris 1982, Garbutt and Harris 1991). Weevil attack is devastating to native North American *Salix* spp. (Salicaceae) (Broberg et al. 2001) and plagues many *Populus* spp. and commercially grown hybrids (Salicaceae) (Cadahia 1965, Dafauce 1976, Morris 1981, Moore et al. 1982, Abebe and Hart 1990, Johnson and Johnson 2003).

There are records of unequal incidence of *C. lapathi* attack among hybrid poplar clones in North America (Morris 1981, Moore et al. 1982, Abebe and Hart 1990, Johnson and Johnson 2003); however, the mechanisms for these apparent resistance phenomena among clones are unknown. There are two potential mechanisms to explain this phenomenon, antixenosis (non-preference) and antibiosis (Painter 1951, Kogan and Ortman 1978). Antixenosis indicates that the plant either lacks attractant stimuli or contains deterrent stimuli and is consequently not preferred behaviorally by herbivores. In antibiosis, the host plant contains compounds that adversely affect herbivore fitness at a physiological level, i.e., herbivores suffer decreased fecundity, longevity, and/or developmental rate. The third method of resistance (Painter 1951), tolerance, does not explain the absence of attack and was not considered further.

To date, only Cadahia (1965) and Dafauce (1976) have tried to determine the underlying mechanism(s) of resistance to *C. lapathi* in poplars. Dafauce (1976) focused on preoviposition resistance to adult weevils by European-grown clones, and his experiments were not conclusive. Feeding and oviposition were generally lower in clones derived from parent *P. alba* L., *P. simonii* Carrière, and *P. nigra* L. compared with clones of parent lines involving *P. deltoides* Bartram *ex* Marshall or *P.* × *euramericana* Dode (Guinier) (*P. deltoides* × *P. nigra*) (Dafauce 1976).

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ble 1. Parentage of the four hybrid poplar clones used in this study

brid	Maternal parent	Paternal parent	Breeding information
02-9	*P. trichocarpa* 95-925 from Hoh Valley, Washington	*P. nigra* L. 71.049/21 from V. Steenackers, Poplar Research Center, Geraardsbergen, Belgium	Bred by R.F. Stettler in 1988 at the University of Washington
52-226	*P. trichocarpa* 93-968 from Granite Falls, Washington	*P. deltoides* 101 from Illinois	Bred by R.F. Stettler in 1981 at the University of Washington
256-28	*P. trichocarpa* 95-877 from Hoh Valley, Washington	*P. maximowiczii* Henry 11863 from Japan	Bred by R.F. Stettler in 1987 at the University of Washington
6	*P. nigra*	*P. maximowiczii*	Bred in Germany

Our ultimate goal was to determine the mecha-m(s) of resistance among hybrid poplar clones cur-ly grown in North America. In this study, we ed the hypotheses that, compared with resistant es, susceptible clones lacking antixenosis would more attractive through olfaction and would sus-more feeding damage.

Materials and Methods

General Strategy. Weevils were given a choice be-en two potential hosts and were also exposed in choice experiments to a single host type in a series laboratory olfactory and feeding bioassays. Because quantitative information on resistance to *C. lapathi* available for commercially planted clones when study began in 2001, initial experiments compared onses by weevils to commercial clones versus nat-ly occurring (susceptible) black cottonwood, *ulus trichocarpa* Torrey and Gray. To maximize the lihood of encountering varying levels of resistance susceptibility, four clones were chosen from dif-nt breeding backgrounds: TN 302-9; TD 52-226; 256-28; and NM 6 (for parentage, see Table 1). eafter, these clones are referred to as TN, TD, TM, NM, respectively. Later experiments used infor-ion from field observations and compared re-ses among native willows and two clones that ed apparent resistance and susceptibility, respec-ly (Broberg and Borden 2005).

Plant Material. Clonal material for testing was ed current year's growth obtained from several ous coppiced ramets grown at Scott Paper's nurs-in Harrison Mills, British Columbia (49°15′ N, 8′ W) and pooled. The *P. trichocarpa* test mate-came from a single population in Langley, British mbia (49°5′ N, 122°42′ W), and consisted of 1-yr-material on individuals coppiced 2 yr previously. *scouleriana* Barratt *ex* Hooker stems of assorted growing from previously coppiced clumps, were cted from the Simon Fraser University campus, aby, British Columbia (49°17′ N, 122°56′ W). es were from determinate branches (i.e., lacking e apical meristems).

Weevil Colonies. To obtain adult *C. lapathi*, infested willow stems were collected in mid-July and kept ntilated 30 by 35 by 50-cm^3 bins in an outdoor ound at Simon Fraser University. In 2001, mate-was collected from Coquitlam, BC (49°20′ N, 9′ W); in 2002, near Hope, British Columbia (49°33′ N, 121°26′ W); and in 2003, from the Coquihalla summit area (49°59′ N, 121°00′ W). Emergent adults were manually removed from bins, sexed, and placed in 25 by 35 by 50-cm^3 ventilated containers with willow stems, water, and occasionally sliced apple fruit. Weevils for bioassays were held at 4°C.

Pitfall Olfactometer Bioassays. Pitfall olfactometers used to examine weevil responses to volatile stimuli were larger versions of those described by Prokopy et al. (1995). We used a 14 by 2.5-cm petri dish fitted with two open 1.8-ml Eppendorf centrifuge tubes, spaced 8 cm apart. The bottoms of the Eppendorf tubes were opened with a 5-mm-diameter drill, so they formed a tube through which weevils could pass into a pit below, from which escape was unlikely. Pits were glass jars 4.5 cm diameter and 6 cm high for stems alone or 4.3 cm diameter and 8.5 cm high when both stems and leaves were tested. Beetles were acclimated in the pitfall olfactometer for ≥10 min under the overturned bottom of a 3.5 by 1-cm petri dish before the start of a bioassay. Bioassays ran overnight, ≈18 h, in the dark with one female or male weevil per dish. Weevils were starved for 24 h before experiments in 2003, but in 2001 and 2002, small colony size and concern for increased mortality precluded using this procedure.

In choice bioassays, both pits contained stem sections cut to 3 cm in length. Diameters were matched between treatment and control pits and ranged from 7 to 20 mm. In no-choice bioassays, i.e., when only one pit contained plant material, both pits contained a 1-cm-long section of water-saturated dental wick. In this manner, once beetles made a choice to enter a pit, there was stimulus for them to stay (Pierce et al. 1988). In experiments that included leaf material, a single leaf was placed in a small vial of water in addition to the stem material. We placed a vial of water in the control pit in the corresponding no-choice bioassays. Treatments were applied in a completely randomized design and were repeated until sufficient response rates for statistical analysis were obtained.

We first tested responses to stem sections of each of the four clones paired with sections from *P. trichocarpa* or an empty (i.e., containing a wet dental wick) pit. After field-caging experiments (Broberg and Borden 2005) suggested that, among the four clones, TN was highly susceptible and NM was most resistant, we repeated pitfall olfactometer bioassays using NM, TN, and *S. scouleriana*, a preferred host in the field.

Table 2. Pitfall bioassay results of four hybrid poplar clones, *P. trichocarpa* (TT), and *S. scouleriana* (SS)

Dates performed	Plant material used	Weevil's choice (side 1 versus side 2)	Tails	Females		Males	
				N	Proportion entering side 1	*N*	Proportion entering side 1
20 Aug., 22 Sept., and 12 Oct. 2001	Stems alone	TN versus TT	2	20	0.55	15	0.50[a]
		TD versus TT	2	19	0.53	17	0.47
		TM versus TT	2	30	0.70[a]	27	0.78[b]
		NM versus TT	2	16	0.56	16	0.50
29 Aug. and 7 Sept. 2001 and 3 Oct. 2002	Stems alone	TT versus empty pit	1	14	0.93[c]	18	0.89[c]
		TN versus empty pit	1	12	0.83[a]	13	0.85[a]
		TD versus empty pit	1	14	0.79[a]	18	0.78[a]
		TM versus empty pit	1	13	0.85[a]	18	0.83[b]
		NM versus empty pit	1	15	0.87[b]	20	0.85[c]
30 Aug. and 25 Sept. 2003	Stems and leaves	NM versus TN	2	19	0.53	20	0.55
		NM versus SS	2	21	0.29	20	0.40
		TN versus SS	2	20	0.35	19	0.42

Distributions that differed significantly from the binomial distribution (with $p = 0.5$) indicated by [a] $P < 0.05$; [b] $P < 0.01$; and [c] $P < 0.001$.

Gas Chromatographic–Electroantennographic Detection Analysis. Leafy shoots from the terminals of hybrid poplars were collected in late August 2001, returned to the laboratory, placed in water, and aerated (Rudinsky 1974). Volatiles were captured on Porapak-Q (Byrne et al. 1975), eluted under pressure (N_2 gas) with 2 ml of distilled pentane. Both male and female adult *C. lapathi* were subjected to gas chromatographic–electroantennographic detection (GC-EAD) analysis of the captured volatiles (Arn et al. 1975). Captured volatiles (1 μl) were injected splitless (Hewlett–Packard 5890 gas chromatograph, injector port 250°C, detector port 260°C, temperature program: held 1 min at 50°C, increased 10°C/min to 280°C; DB-5 fused silica column, 30 m by 0.32 mm ID; J & W Scientific, Folsom, CA) and passed over an electrophysiological antennal preparation (Arn et al. 1975) or a flame ionization detector. Antennally active compounds were identified by GC-mass spectrometry (Varian Saturn 2000 Ion Trap, DB-5 column as above, electron impact mode) and confirmed by coelution with synthetic standards.

Paired-twig Feeding Bioassays. Paired-twig bioassays (Tomlin and Borden 1996) were performed to determine feeding preferences using 5-cm-long cut stem sections suspended on a central ≈2 by 2 by 2-cm^3 wax block. The exposed ends were sealed with paraffin wax, and each paired-twig assembly was placed in a 14 by 2.5-cm petri dish. Dishes were arranged in a completely randomized design, and individual nonstarved male or female weevils were allowed to feed for 3 d. Feeding was assessed by number of feeding punctures (determined under a dissecting microscope) and weight of frass (dried to constant mass) collected from under each of the twigs.

As in the pitfall bioassays, we first tested each of the four clones against *P. trichocarpa* ($n = 15$). No-choice experiments were also run on the four clones and *P. trichocarpa* ($n = 12$), in which the same material was placed on both sides of the paired-twig set up. Next, we used paired-twig bioassays to compare feeding responses among NM, TN, and *S. scouleriana* in choice ($n = 15$) and no-choice ($n = 12$) situations.

Statistical Analyses. In all cases, $\alpha = 0.05$. For pitfall olfactometer bioassays, responses were tested against the binomial distribution with $p = 0.5$ (Daniel 1995). Data from paired-twig feeding bioassays were tested with a series of paired *t*-tests (Daniel 1995). Data from no-choice feeding bioassays were analyzed by analysis of variance (ANOVA) using PROC GLM, and when significant differences were found, the REGWQ test was used for means separation (SAS Institute 1990). If necessary, data were transformed ($x^{1/2}$) before analyses to correct for non-normality and heteroskedasticity.

Results and Discussion

Pitfall Olfactometer Bioassays. Weevils of both sexes responded strongly and consistently to pits containing poplar stems of any origin when the alternative was an empty pit (Table 2). These results suggest the presence of attractive volatiles in all five types of poplar and absence of a repellent. In choice bioassays, male *C. lapathi* preferred cut stem sections of TN and TM, and females preferred TM to sections of susceptible *P. trichocarpa* stem (Table 2). This discrimination was absent in late October (data not shown). There was also no evidence of preference among TN, NM, and *S. scouleriana*, which included leaf material as well as stems (Table 2). Additional pitfall experiments including stem and leaf material during this same time period (C.B., unpublished results) showed that weevils preferred pits containing *S. scouleriana* over a series of field-collected alternate hosts and nonhosts: *P. trichocarpa*, *Populus tremuloides* Michaux, *Alnus rubra* Bongard, *Acer macrophyllum* Pursh (Aceraceae), and *Picea abies* L. Karsten (Pinaceae). Clearly, olfactory discrimination does not explain resistance among hybrids. Dafauce (1976) also found no olfactory discrimination between susceptible *P. deltoides* cultivar Missouriensis Zeeland and resistant *P. alba* L. cultivar bolleana Lauche in the laboratory. It is probable that the volatile profiles of hybrid poplars are very similar and discrimination is not possible.

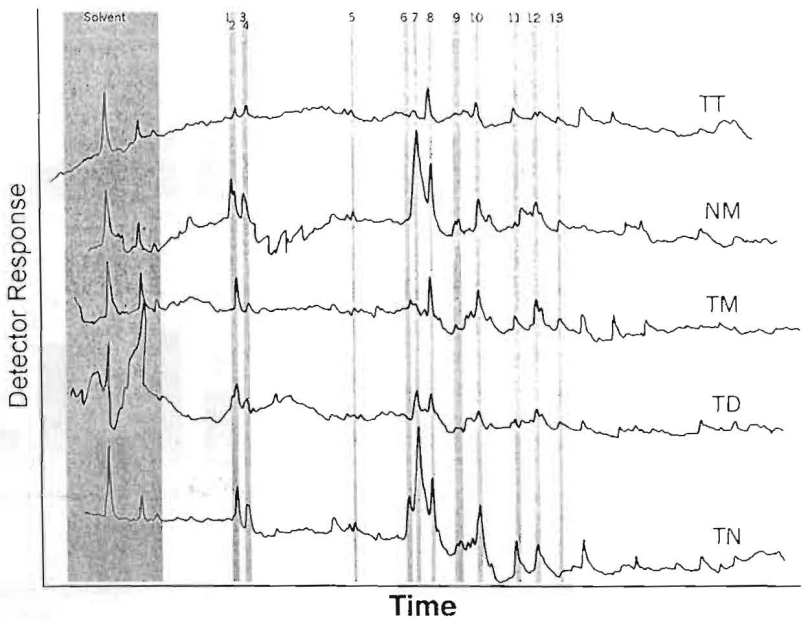

Fig. 1. Male GC-EAD responses to five different *Populus* sources. Peaks identified as follows: 1 = (*E*)-hex-2-en-1-al; 2 = hex-3-en-1-ol; 3 = (*E*)-hex-2-en-1-ol; 4 = hexanol; 5 = 1-octen-3-ol; 6 = benzyl alcohol; 7 = salicylaldehyde; 8 = conophthorin; 9 = mixture of (*E*)- and (Z)-chalcogran and guaiacol; 10 = nonanal; 11 = unknown; 12 = nonanol; 13 = methyl salicylate.

GC-EAD Analysis. A lack of olfactory discrimination is supported by comparative GC-EAD analysis that showed very similar volatile profiles and antennal responses among clones (Fig. 1). Male and female antennal responses were nearly identical, thus only males are shown. Antennal responses were primarily elicited by six-carbon alcohols, benzaldehyde, salicylaldehyde, conophthorin, nonanal, nonanol, methyl salicylate, and several unknown compounds. Low or high response to prominent volatiles were inconsistent with responses in the pitfall bioassays; e.g., response to salicylaldehyde was low in TM and high in NM, but both clones were preferred in pitfall experiments (Table 2). The strong antennal response to conophthorin by *C. lapathi* antennae despite its nearly undetectable level in the flame ionization detector of the mass spectrometer supports its earlier discovery in *P. trichocarpa* (Huber et al. 1999) and reflects a new finding in willows (Broberg et al. 2005). It further suggests that conophthorin may have behavioral activity for *C. lapathi*. In the closely related family Scolytidae, conophthorin acts as a repellent nonhost kairomone (Huber et al. 1999, Zhang et al. 2001), a repellent or attractive pheromone (Kohnle et al. 1992, Dallara et al. 2000, Rappaport et al. 2000), and a synomone for competing congenerics (Dallara et al. 2000). Other known bark beetle pheromones detected in the plant volatile profiles were 1-octen-3-ol (Pureswaran and Borden 2004) and chalcogran (Byers et al. 1989, 2000), which also occurs in *Salix* spp. (Broberg et al. 2005).

Paired-twig Feeding Bioassays. Weevils fed on the inner bark at the cut ends of stem sections despite sealing with paraffin, making estimation of puncture numbers difficult. However, data on frass production and feeding punctures were generally consistent (Table 3; Figs. 2–4).

Table 3. Results from paired-twig bioassays of four hybrid poplar clones and *P. trichocarpa* (TT)

Weevil's choice (side 1 versus side 2)	Tails	Mean no. feeding punctures ± SE				Mean amt of frass produced ± SE (mg)			
		Side 1	Side 2	*t*	*P*	Side 1	Side 2	*t*	*P*
TN versus TT	2	20.0 ± 4.6	14.3 ± 3.2	0.91	0.38	1.6 ± 0.5	1.4 ± 0.3	0.68	0.51
TD versus TT	2	10.4 ± 1.7	26.6 ± 4.2	−3.52	0.004	0.6 ± 0.1	1.2 ± 0.2	−2.57	0.02
TM versus TT	2	20.1 ± 3.9	19.7 ± 3.8	0.08	0.94	1.0 ± 0.2	1.3 ± 0.3	−0.59	0.57
NM versus TT	2	12.7 ± 1.8	22.9 ± 4.0	−2.58	0.02	1.2 ± 0.2	2.2 ± 0.3	−2.58	0.02
TN versus TT	2	15.6 ± 3.8	6.5 ± 2.3	2.00	0.07	1.5 ± 0.3	1.0 ± 0.2	1.40	0.18
TD versus TT	2	9.9 ± 3.6	13.0 ± 2.8	−0.65	0.52	0.7 ± 0.2	0.8 ± 0.2	−0.32	0.76
TM versus TT	2	21.1 ± 3.2	17.9 ± 6.4	2.01	0.07	1.0 ± 0.1	0.8 ± 0.1	1.75	0.10
NM versus TT	2	13.2 ± 3.1	12.7 ± 3.3	0.09	0.93	0.9 ± 0.2	1.0 ± 0.2	−0.71	0.49

Differences between side 1 and side 2 means were compared using a paired *t*-test.

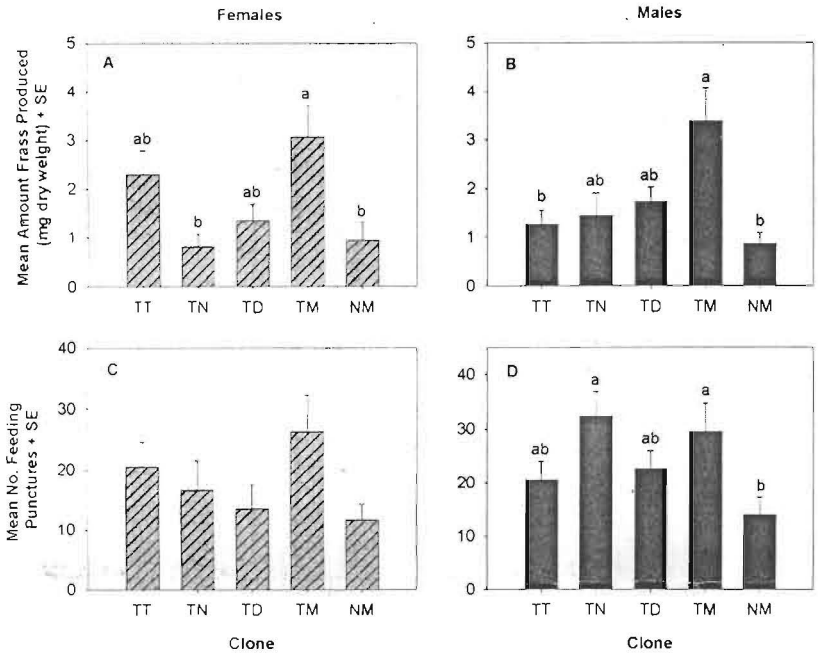

Fig. 2. Results from feeding bioassay experiments in which no choice was given, comparing feeding on four hybrid popla clones and wild *P. trichocarpa*. ANOVA statistics are as follows: (A) $F = 4.61$, df = 4,54, $P = 0.003$; (B) $F = 3.92$, df = 4,5 $P = 0.008$; (C) $F = 1.12$, df = 4,54, $P = 0.36$; (D) $F = 3.61$, df = 4,52, $P = 0.01$. Within each subfigure, bars with the sa letter are not significantly different (REGWQ test, $P < 0.05$).

Female weevils alone fed less on TN or TD than on *P. trichocarpa* in choice situations (Table 3). In no-choice situations, both sexes generally fed the least on NM; however, this feeding was not significantly different from that on TD, *P. trichocarpa*, or TN (Fig. 2). When feeding preferences among NM, TN, and *S. scouleriana* were examined, responses became clear. When presented with a choice, weevils of both sexes avoided NM in favor of the more susceptible hosts TN or *S. scouleriana*. Furthermore, weevils selected TN over its preferred wild host, *S. scouleriana* (Fig. 3). These results were reflected in the no-choice experiment, in which both feeding punctures and frass production on NM were significantly lower for both sexes than on TN or *S. scouleriana* (Fig. 4). The preference for TN over *S. scouleriana* indicates that this hybrid could be very susceptible to attack in the field, especially when first planted. The lack of antixenosis toward TM, which is also highly resistant (Broberg and Borden 2005), and the lack of consistent preference for the susceptible TD and TN in choice and no-choice paired-twig feeding bioassays (Table 3; Fig. 2) suggests that caution should be used in the use of feeding preference screens as indicators of resistance in the field.

Nonpreference for *P. alba* cultivar bolleana remained constant over several choice feeding trials in the work of Dafauce (1976) but not in that of Cadahia (1965). Also, in the only no-choice trial of Dafauce (1976), there was equal feeding on the nonpreferred *P. alba* cultivar bolleana and the (usually) highly preferred clone, *P. deltoides* Marsh cultivar Carolinensis, on which adults also had the greatest longevity. Similarly, we observed that weevils make choices consistent with maximizing fitness by discriminating against NM and for TN, but often fail to do so (Table 3; Fig. 2–4), suggesting that either antixenotic signals or weevil preferences are unreliable. Accordingly, *C. lapathi* showed only weak oviposition preference between TN and NM (Broberg and Borden 2005), yet the fitness costs of making a wrong decision were severe because eggs did not complete development in NM. All four hybrids in this study are from the two closely related *Populus* sections Aigeros (cottonwoods) and Tacamahaca (balsam poplars) (Eckenwalder 1996). Given the similarity in the volatile profiles of the different hybrids, and their evolutionary relatedness, it is possible that their bark chemistry is also quite similar, at least at the time of feeding and oviposition. We intend to investigate bark chemistry in the future. Because we did not examine effects on weevil fitness directly, it is possible that reduced feeding on NM is not a result of antixenosis, but of enhanced nutritive value. This does not seem a likely alternate hypothesis as others have found NM and other clones with *P. maximowiczii* parentage to have antixenotic or antibiotic effects on a number of species including *C. lapathi* larvae (C.B., unpublished data), forest tent caterpillar, *Malacosoma disstria* Hübner, larvae (Robison and Raffa 1994), gypsy moth, *Lymantria dispar* L., larvae (Kruse and Raffa 1996), the aphid, *Chaitophorus leucomelas* Koch (Ramírez et al. 2004), and the meadow mouse, *Microtus pennsylvanicus* (Ord.) (Robison and Raffa 1998). We conclude that *C. lapathi* is

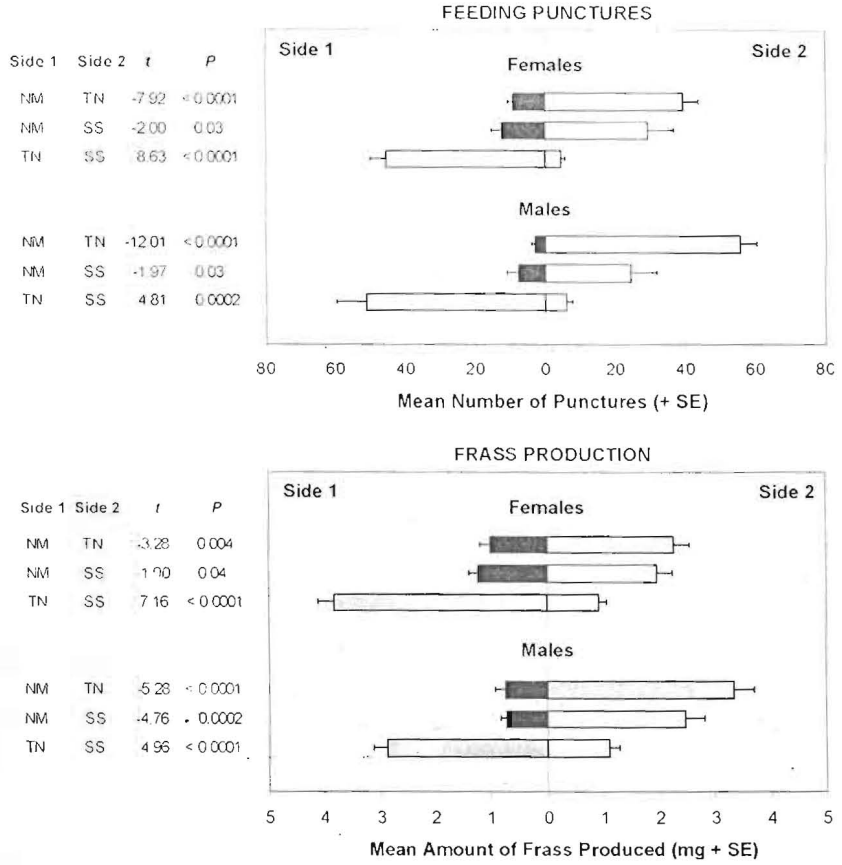

Fig. 3. Number of punctures and amount of frass produced in the second round of feeding bioassays in which a choice is given between the pairwise combinations of NM, TN, and *S. sconleriana* (SS). Results from paired *t*-tests are as given.

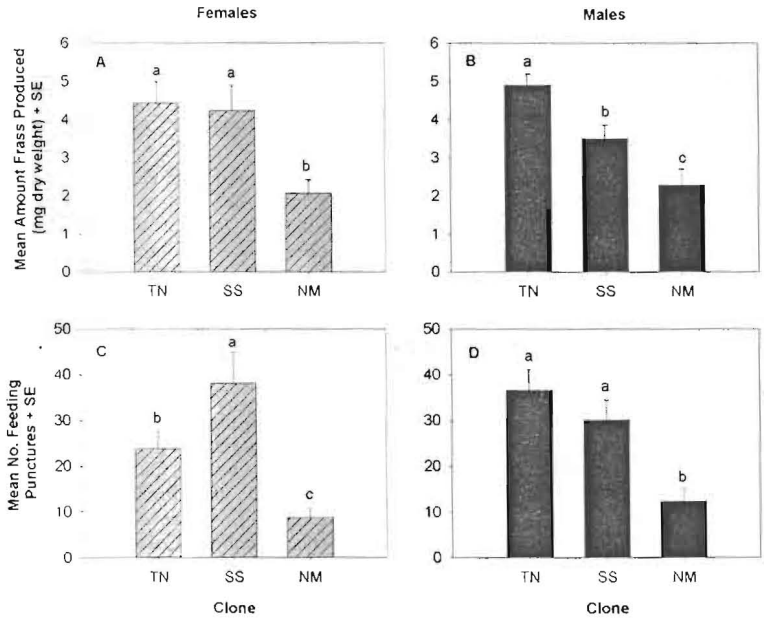

Fig. 4. Results from feeding bioassay experiment in which no choice was given comparing feeding on wild *S. sconleriana* and two hybrid poplar clones: one with and one without *P. maximowiczii* parentage. ANOVA statistics are as follows: (A) $F = 7.43$, df = 2,33, $P = 0.002$; (B) $F = 12.74$, df = 2,33, $P < 0.0001$; (C) $F = 13.93$, df = 2,32, $P < 0.0001$; (D) $F = 7.69$, df = 2,33, $P = 0.002$. Within each subfigure, bars with the same letter are not significantly different (REGWQ test, $P < 0.05$).

capable of discriminating against NM using gustatory cues (Table 3; Figs. 2–4) but not olfactory cues (Table 2; Fig. 1). Thus, resistance is apparently based, at least in part, on antixenosis.

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