Biological performance of the white pine weevil in relation to the anatomy of the resin canal system of four different host species

Dominique Boucher, Robert Lavallée, and Yves Mauffette

Abstract: The anatomy of the resin canal system was observed on lateral branches of four host species of the white pine weevil (*Pissodes strobi* Peck) in relation to weevil performance. The host species studied were Norway spruce (*Picea abies* (L.) Karst.), white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), and white pine (*Pinus strobus* L.). Survival, number, and mass of adult weevils were measured on attacked terminal leaders collected before adult emergence. One uppermost lateral branch was collected at the base of each attacked leader. Cross sections of these lateral branches were observed to measure the number, diameter, depth, and density of inner and outer resin canals. Nearly all resin canal measurements differed significantly among species, with white pine differing greatly from the other species with larger canals and lower canal density. Correlation analysis demonstrated that the anatomy of the resin canal system was principally related to adult mass, with the most important variable being the density of inner canals ($r = -0.54$). Trees characterized by low density of large inner resin canals, like white pine, seemed to favour mass gain in adult weevils. The present study suggests that a high density of inner resin canals constrains the insect to feed on canals early in larval development, which subsequently reduces weevil mass.

Résumé : L'anatomie du système résinifère a été observée sur les branches latérales de quatre espèces-hôtes du charançon du pin blanc (*Pissodes strobi* Peck) en relation avec la performance de celui-ci. Les espèces-hôtes étudiées sont l'épinette de Norvège (*Picea abies* (L.) Karst.), l'épinette blanche (*Picea glauca* (Moench) Voss), l'épinette rouge (*Picea rubens* Sarg.) et le pin blanc (*Pinus strobus* L.). La survie, le nombre et le poids des adultes du charançon ont été mesurés à partir de flèches terminales attaquées et récoltées juste avant l'émergence des adultes. Une branche latérale a été récoltée à la base de chaque flèche terminale attaquée. Des coupes transversales de ces branches ont été observées afin de mesurer le nombre, le diamètre, la profondeur et la densité des canaux résinifères internes et externes. Presque toutes les mesures des canaux résinifères différaient significativement entre les espèces. Le pin blanc, qui présentait une faible densité de larges canaux résinifères, se démarquait davantage des autres espèces. Des analyses de corrélation ont démontré que l'anatomie du système résinifère est principalement reliée au poids des adultes, la variable la plus importante étant la densité des canaux internes ($r = -0,54$). Les arbres possédant une faible densité de larges canaux résinifères internes, tel le pin blanc, semblent favoriser le gain de poids chez les adultes du charançon. Cette étude suggère que les arbres ayant une forte densité de canaux internes contraignent les insectes à consommer ces canaux tôt au cours de leur développement larvaire, ce qui provoquerait une réduction du poids des insectes.

Introduction

The white pine weevil (*Pissodes strobi* Peck) is an important pest of spruce (*Picea* spp.) and pine (*Pinus* spp.) in

D. Boucher[1,2] and Y. Mauffette. Groupe de recherche en écologie forestière interuniversitaire, Département des sciences biologiques, Université du Québec à Montréal, C. P. 8888, succursale A, Montréal, QC H3C 3P8, Canada (e-mails: dboucher@cfl.forestry.ca and mauffette.yves@uqam.ca).
R. Lavallée. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 3800, Sainte-Foy, QC G1V 4C7, Canada (e-mail: rlavallee@cfl.forestry.ca).

[1]Corresponding author.
[2]Present address: Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 3800, Sainte-Foy, QC G1V 4C7, Canada.

North America (Belyea and Sullivan 1956; Wallace and Sullivan 1985). In its immature stages, this weevil destroys terminal leaders of trees when feeding on the inner bark; this results in growth losses and deformations of the stem, thereby severely reducing the value of lumber (Brace 1971). In the province of Quebec, Norway spruce (*Picea abies* (L.) Karst.) and white pine (*Pinus strobus* L.) are the most affected: 90 and 85% of Norway spruce and white pine plantations, respectively, were affected in some regions in 1999 (G. Gagnon, personal communication). This situation has led to a strong reduction in the number of seedlings of susceptible species planted annually in Quebec, particularly for Norway spruce, a species that was intensively planted during the 1980s (MRNQ 1994). The white pine weevil also attacks other hosts to a lesser degree, including white spruce (*Picea glauca* (Moench) Voss) and red spruce (*Picea rubens* Sarg.) (Paradis 1995).

Different host species can lead to differences in oviposition, larval development rate, and number or mass of adults of the white pine weevil (Dirks 1964; McMullen 1976; VanderSar et al. 1977; Phillips and Lanier 1983;

Alfaro 1988). In Quebec, we recently found that adults emerging from white pine had a greater body mass, but survival and number of emerged adults tended to be greater on Norway spruce (Boucher et al. 2001). Many factors could explain this variation in biological performance: nutritive quality of the bark (Scriber and Slansky 1981; Haack and Slansky 1987), size of the leader (Graham and Satterlund 1956; Dirks 1964), bark thickness (Amman 1972; Haack et al. 1987), host defenses (Hanover 1975a; Berryman 1988), or host phenology (Hulme 1995). However, the resin canal system in conifers is considered as the first line of defense against insects and pathogens (Berryman 1972). Resin has been reported to cause considerable mortality of eggs and larvae for the white pine weevil (Silver 1968; Overhulser and Gara 1981; Dixon and Houseweart 1982). In response to insect attack, the tree can develop traumatic resin canals in the xylem, in addition to the preformed resin canals of the cortex (Berryman 1972; Alfaro 1995; Alfaro et al. 1996).

The anatomy of the preformed resin canal system has often been studied in relation to host resistance to the white pine weevil. Shallow resin canals seem to be related to tree resistance (Stroh 1964; Stroh and Gerhold 1965; Wilkinson 1983). Plank and Gerhold (1965) found that western white pine, a species resistant to weevil attacks, has larger and more numerous resin canals than eastern white pine. High density of resin canals has been reported to be correlated to resistance in Sitka spruce (Tomlin and Borden 1994, 1997; Alfaro 1996a) and in white spruce (Alfaro et al. 1997). However, Stroh and Gerhold (1965) did not find any correlation between resin canal structure and adult emergence.

The study of Stroh and Gerhold (1965) was the only one in eastern North America to investigate the anatomy of the resin canal system in relation to white pine weevil development. To evaluate the role of resin canals in weevil performance, the present study was initiated with the following objectives: (i) to compare the structure of the vertical resin canal system between four different host species and (ii) to examine the relationship between these anatomical characteristics and the biological performance of the white pine weevil.

Materials and methods

Study area and host species

The study was conducted in two different regions of southern Quebec: the Chaudière–Appalaches region (east of Québec; 46–47°N) and the Outaouais region (north of Ottawa; latitude 45.5–46.5°N). Both of these regions have been extensively planted with spruce and pine, and numerous infestations of the white pine weevil were recorded (MRNQ 1996). We selected four different tree species: Norway spruce, white pine, white spruce, and red spruce. Red spruce was only studied in the Appalaches region, because plantations were lacking in the Outaouais region. Within each region, we selected five plantations for each species for a total of 35 plantations. Criteria used for plantation selection were based on the presence of the white pine weevil and tree age, which had to be less than 20 years old. Trees are usually less susceptible after this age. Tree density was approximately the same for all plantations with an average of 2 m between trees. Plantations in the Outaouais region generally had a better drainage and a more sandy soil texture, compared with the Appalaches plantations. The Outaouais region is characterized by linden (*Tilia americana* L.) – sugar maple (*Acer saccharum* Marsh.) stands as dominant vegetation, mean annual temperature is 4.0–5.0°C, and total precipitation is 800–

1000 mm annually; the Appalaches region is characterized by yellow birch (*Betula alleghaniensis* Britt.) – sugar maple stands, mean annual temperature is 2.5–4.0°C, and total precipitation is 900–1200 mm (Bérard 1996).

Biological performance of the weevil

In each plantation, three trees were selected and their attacked terminal leaders were harvested in June 1996 (June 3–6 in Outaouais; June 11–19 in Appalaches) to estimate the number of eggs per cavity. Leaders were kept in a dark cold room at 4°C until they were dissected for egg counting in October.

In July 1996 (July 8–12 in Outaouais; July 16–19 in Appalaches), five newly selected attacked leaders were collected in each plantation, by then larval development was completed, but adults were still present inside the leader (Lavallée et al. 1990). Each leader was immediately caged in a cardboard tube (5.5 × 92.5 cm) closed at one end with nylon-mesh tissue and at the other end with a plastic bottle (Pharma No. 16, MHAC, Pointe-Claire, Quebec). These caged leaders were then kept at room temperature. Leaders were observed on a daily basis during a period of 45 days (July 28 to September 10, 1996) to record adult emergence. The emerging adults were counted for each leader, weighed, and sexed according to Lavallée et al. (1993). Once the adults completed their emergence, the number of oviposition cavities per leader was recorded. To estimate the number of eggs per leader, the number of oviposition cavities was multiplied by the number of eggs per cavity. Weevil survival on each leader was estimated as follows: (no. of emerged insects from the leader/no. of eggs laid on the leader) × 100.

Measurements of the resin canal system

Since leaders were damaged by larvae, characterization of the resin canal system was made on upper lateral branches. Alfaro et al. (1997) found that white spruce resin canal measurements in lateral branches were correlated with measurements in leaders. Tomlin and Borden (1994) found similar patterns of variation in resin duct measurements between resistant and susceptible Sitka spruces in lateral branches and leaders. In July 1996, at the same time that we collected the five terminal leaders (July 8–12 in Outaouais; July 16–19 in Appalaches), we also collected one uppermost lateral branch at the base of each leader. Lateral branches were kept at 4°C until they were used for histological observations from November 16, 1996, to January 17, 1997. Cross sections were obtained at about 5 cm from the base of the branch using a cryostat microtome (Reichert Histostat). One section of each lateral branch was observed with a microscope at 100× magnification. Measurements were made with an ocular micrometer.

For each tree species, we measured the following characteristics on cross sections (Fig. 1): the inner resin canals were the large canals occurring in the cortex, in a ring closest to the cambium; the outer resin canals were the small canals located on the periphery of inner resin canals. For the two types of canals, we measured the number, diameter, and depth. The depth of the canals was measured from the inner side of parenchyma cells surrounding the canal to the outer surface of the bark. Measurements of diameter were taken from the inner side of parenchyma cells surrounding the canal. We measured the diameter of lateral branches at two different locations in a cross section and the bark thickness at four different locations. Bark thickness was assessed as the distance between the cambium and the outer surface of the bark. The density of resin canals was expressed as the number of canals per square millimetre of bark area.

Statistical analysis

The number and diameter of inner and outer resin canals were log transformed, whereas the number of emergences per leader and survival were square-root transformed to achieve homogeneity and normality of the residuals.

Fig. 1. Schematic representation of a cross section of a white pine lateral branch showing the cortical resin canal system (adapted from Stroh and Gerhold 1965).
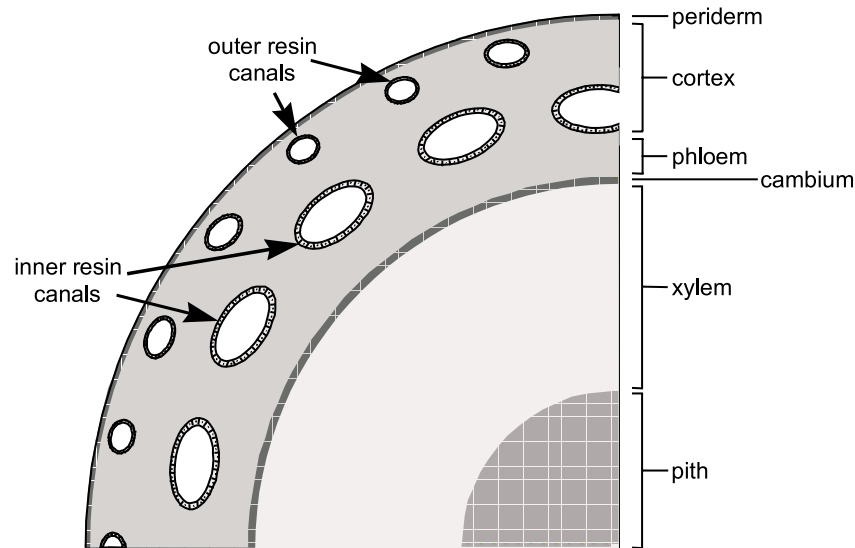
To compare number, diameter, depth, and density of inner and outer resin canals among host species, analyses of variance on a nested experimental design were made using PROC GLM type IV sums of squares (SAS Institute Inc. 1990). Analyses included the following effect: species and species nested within plantation as an error term. Plantation (species region) was considered as a random effect. Means were compared between species using Tukey's honest significant difference test.

We used Pearson's simple linear correlation to determine the relationship between resin canal measurements on lateral branches and survival, number, and mass of adults of *P. strobi* emerging from the corresponding leaders.

Results

Resin canal anatomy of the hosts

Analysis of variance for each variable related to the anatomy of the resin canal system is presented in Table 1. Values of these measurements for each species are presented in Table 2. There were significant differences between species for all variables, except the number of outer resin canals ($P = 0.3637$). White spruce had the greatest mean number of inner resin canals per cross section (27.0 canals), whereas white pine had the lowest number of inner canals with only 11.4 canals ($P = 0.0001$). Diameter of inner resin canals in white pine was 0.350 mm, which was wider than those of all other species ($P = 0.0001$). White pine also had the largest outer canals with 0.137 mm, and Norway spruce and white spruce had the smallest outer canals with 0.066 mm and 0.065 mm, respectively, ($P = 0.0001$) (Tables 1 and 2).

Both inner and outer resin canals were deepest in Norway spruce and shallowest in white pine (both $P = 0.0001$). Red spruce had the highest mean density of inner resin canals with 1.096 canals/mm^2 of bark area, and white pine had the lowest mean density of inner canals with 0.452 canals/mm^2 ($P = 0.0001$). Red spruce also had the highest density of outer resin canals with 0.956 canals/mm^2 of bark area and the density was lowest in Norway spruce with 0.554 canals/mm^2 ($P = 0.0006$) (Tables 1 and 2).

There was also a significant plantation effect for all resin canal measurements except for the number and the diameter

Table 1. Analysis of variance of number, diameter, depth, and density of inner and outer resin canals in the bark of uppermost lateral branches of four species.

Source of variation	df	MS	F	P
No. of inner canals				
Species	3	0.9729	93.32	0.0001
Plantation (species)	30	0.0149	1.43	0.1003
Error	93	0.0104		
No. of outer canals				
Species	3	0.0435	1.07	0.3637
Plantation (species)	29	0.1093	2.71	0.0002
Error	92	0.0403		
Diameter of inner canals				
Species	3	0.6081	68.25	0.0001
Plantation (species)	30	0.0110	1.24	0.2165
Error	93	0.0089		
Diameter of outer canals				
Species	3	0.8500	101.26	0.0001
Plantation (species)	29	0.0301	3.59	0.0001
Error	92	0.0084		
Depth of inner canals				
Species	3	1.1895	67.23	0.0001
Plantation (species)	29	0.0449	2.54	0.0004
Error	92	0.0177		
Depth of outer canals				
Species	3	1.5801	100.80	0.0001
Plantation (species)	28	0.0310	1.98	0.0083
Error	91	0.0157		
Density of inner canals				
Species	3	1.9411	48.58	0.0001
Plantation (species)	29	0.1214	3.04	0.0001
Error	91	0.0400		
Density of outer canals				
Species	3	0.5254	6.37	0.0006
Plantation (species)	29	0.1962	2.38	0.0010
Error	91	0.0825		

Table 2. Mean (±SD) number, diameter, depth, and density of inner and outer resin canals in the bark of uppermost lateral branches of four species.

	Norway spruce	White pine	White spruce	Red spruce
No. of inner canals	24.6±6.2*ab* (35)	11.4±2.8*c* (41)	27.0±5.7*a* (33)	21.7±4.6*b* (18)
No. of outer canals	18.9±9.8*a* (35)	19.4±6.3*a* (41)	17.5±12.3*a* (33)	18.6±5.3*a* (18)
Diameter of inner canals (mm)	0.190±0.054*b* (35)	0.350±0.076*a* (41)	0.183±0.036*b* (33)	0.185±0.030*b* (18)
Diameter of outer canals (mm)	0.066±0.017*c* (35)	0.137±0.023*a* (41)	0.065±0.021*c* (31)	0.081±0.024*b* (18)
Depth of inner canals (mm)	0.866±0.216*a* (35)	0.458±0.104*c* (41)	0.748±0.140*b* (32)	0.703±0.139*b* (17)
Depth of outer canals (mm)	0.696±0.168*a* (35)	0.209±0.147*d* (41)	0.546±0.085*b* (30)	0.452±0.127*c* (17)
Density of inner canals (no./mm² bark area)	0.788±0.238*c* (35)	0.452±0.198*d* (41)	0.932±0.227*b* (35)	1.096±0.358*a* (18)
Density of outer canals (no./mm² bark area)	0.554±0.240*c* (35)	0.769±0.337*ab* (41)	0.629±0.358*bc* (35)	0.956±0.418*a* (18)

Note: Host species values followed by the same letter are not significantly different (Tukey's honest significant difference test). Number of replicates is given in parentheses.

Table 3. Pearson's correlation coefficients (*r*) between survival, mass, and number of adults emerged per leader of *Pissodes strobi* and measurements of resin canals of uppermost lateral branches of four host species.

| Resin canal measurements	No. of adults emerged per leader	Survival	Adult mass
No. of inner canals	–0.06	0.18	–0.38***
No. of outer canals	0.17	0.07	0.25*
Diameter of inner canals	0.15	–0.15	0.47***
Diameter of outer canals	0.10	–0.12	0.43***
Depth of inner canals	0.07	0.11	–0.25*
Depth of outer canals	0.08	0.15	–0.32*
Density of inner canals	–0.19*	0.12	–0.54***
Density of outer canals	–0.02	0.00	0.04

Note: *, $P < 0.05$; ***, $P < 0.0001$.

of inner canals (Table 1), showing probably that plantations differed in site conditions. However, we used an analysis of variance with nested design acknowledging that the variation among species was more important than between plantations.

Relationship to weevil development

Correlation analyses between weevil performance and resin canal characteristics are presented in Table 3. The number of emerged adults per leader was negatively related to the density of inner resin canal, whereas weevil survival was not related to any of the resin canal measurements.

Adult mass was significantly correlated with all resin canal variables, except the density of outer resin canals. Correlations between the number of outer canals and the diameter of inner and outer canals were positive, whereas all other correlations were negative. The highest relationship observed was the negative correlation between adult mass and inner resin canal density ($r = -0.54$) (Fig. 2*a*). White pine strongly differed from other host species, as it had the lowest density of inner resin canals and the highest mass of adult weevils (Fig. 2*a*). The second highest relationship observed was between adult mass and diameter of inner canals ($r = 0.47$). Figure 2*b* shows this relationship, where white pine again differentiates itself from other species by having the largest inner canals. Figure 3 shows that diameter and density of inner resin canals were inversely and significantly

Fig. 2. Relationships between (A) the mass of white pine adult weevils and the density of inner resin canals in lateral branches and (B) the adult mass and the diameter of inner resin canals in lateral branches on four host species of the white pine weevil.

△ Norway spruce + White pine ○ White spruce ✳ Red spruce
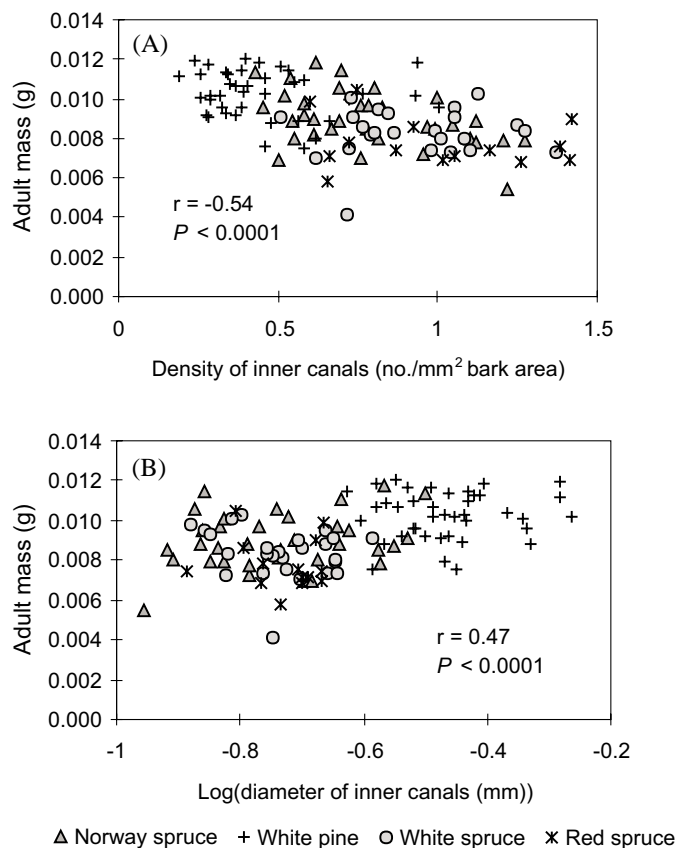
correlated ($r = -0.67$); trees with large inner canals also had a low density of inner canals.

Discussion

The resin canal system differs significantly among host species, with the exception of the number of outer resin canals. Although there are differences among the three species of the genus *Picea*, the resin canal system of the *Pinus* species is very different from that of the other species. White pine had very large canals, located shallow in the bark, and

inner canals were less numerous. Our measurements of resin canal diameter and depth of white pine lateral branches are comparable with those taken on white pine leaders in other studies (Stroh 1964; Stroh and Gerhold 1965; Harman and Brown 1974; Wilkinson 1983). However, our results on the density of resin canals in white spruce are lower than those obtained by Alfaro et al. (1997) on white spruce laterals in British Columbia. These differences could be due to the geographical variation of this genotype, as white spruce is known for its great genetic diversity (Farrar 1996). It is interesting to note that eastern white spruces, which appear to be resistant in British Columbia (Kiss et al. 1994), have lower density of resin canals than western white spruces.

Adult mass was correlated with the structure of the resin canal system and, therefore, could explain, in part, the differences in weevil mass among host species reported by Boucher et al. (2001).

The highest correlation was a negative relationship between density of inner resin canals and adult weight ($r = -0.54$). Thus, weevils emerging from trees with a low density of inner resin canals had a higher body mass (Fig. 2a). Red spruce had the highest density of inner canals, followed by white spruce, Norway spruce, and white pine (Table 2). Likewise, we found previously that adults emerging from red spruce were the smallest and those emerging from white pine were the biggest (Boucher et al. 2001). However, the diameter of inner resin canals was also positively correlated with adult mass ($r = 0.47$; Fig. 2b). This relationship can be explained by the fact that the diameter and density of inner resin canals are strongly interrelated ($r = -0.67$; Fig. 3). Trees with large inner canals have a lower density of inner canals, whereas trees with small inner canals have a high density of inner canals. Even if the proportion of resin canal area compared with bark area can be similar in both cases, it is possible that in trees having a low density of large inner resin canals, such as white pine, the spaces between these canals would be wider, whereby larvae could more easily avoid resin canals. It is known that the white pine weevil can avoid resin canals during adult feeding (Stroh and Gerhold 1965) and initial larval feeding (Alfaro 1995, 1996b). Conversely, in trees having a high density of small inner resin canals, the insects could be constrained to feed on canals earlier in their larval development. This could affect the insect mass, since resin is low in nutrients and may be toxic (Shrimpton and Whitney 1968; Raffa and Berryman 1982; Everaerts et al. 1988; Raffa and Smalley 1995).

Boucher et al. (2001) observed that adult mass was correlated with basal leader diameter ($r = 0.38$). However, the relationships observed in the present study between adult mass and inner canal density and diameter had higher r values than the previous results (with density: $r = -0.54$; with diameter: $r = 0.47$). We can assume that these two resin canal variables, particularly the density of inner canals, are more closely related to adult mass than leader diameter and, thus, could probably explain a greater part of the differences in adult mass among host species. In fact, thick leaders with large but few inner resin canals would certainly be the most favourable for mass gain of the white pine weevil.

The density of inner resin canals seems an important variable affecting weevil biological performance, since it can also explain weevil mass differences within a host species.

Fig. 3. Relationship between the density of inner resin canals and the diameter of inner resin canals in lateral branches on four host species of the white pine weevil.
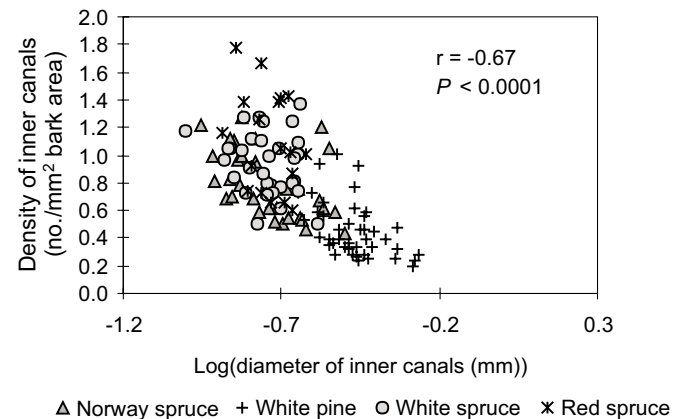
When we completed correlation analyses using residuals that excluded the species effect, the relationship between inner canal density and weevil mass was still significant ($r = -0.24$), whereas the relationship between inner canal diameter and weevil mass was not significant (Boucher 1998). This means that for some host species trees having an inner canal density lower than the average for their species also support insects with higher mass than the average for this host species.

No significant correlation was found between resin canal measurements and survival, nor for the number of emerged adults per leader, with the exception of a weak negative correlation between inner canal density and number of adults emerged per leader (Table 3). Similarly, Stroh and Gerhold (1965) found no correlation between resin canal anatomy and adult emergence. The absence of negative relationships between the number of emergences and the resin canal system is surprising, since the latter is considered an important factor of mortality in the white pine weevil (Silver 1968; Overhulser and Gara 1981; Dixon and Houseweart 1982) and other insects (Berryman and Ashraf 1970; Reid and Gates 1970). It is possible that the characteristics of the resin, like its chemical composition (Hanover 1975a; Wilkinson 1980, 1985; Tomlin et al. 1996), flow (Blanche et al. 1992; Nebeker et al. 1992), viscosity (Hanover 1975b; Bridgen et al. 1979), or rate of crystallization (Santamour 1965; van Buijtenen and Santamour 1972; Overhulser and Gara 1981), which were often investigated in relation to host resistance, influence the survival of the weevil much more than the anatomy of the resin canal system. It is also possible that weevil survival could be more influenced by the capacity of the host to produce traumatic resin canals when attacked (Berryman 1972; Alfaro 1995; Alfaro et al. 1996), resulting in the production of more toxic resin (Berryman 1972; Raffa and Smalley 1995). Furthermore, weevil survival might be much more related to factors other than host defense mechanism, such as predation (Dixon and Houseweart 1982; Therrien 1995) or larval competition (Sullivan 1961; Dixon and Houseweart 1982).

Thus, the density of inner resin canals seems to be the most important variable related to weevil performance. However, host resistance has been more often related to outer resin canals than inner ones (Plank and Gerhold 1965;

Tomlin and Borden 1994, 1997; Alfaro et al. 1997). As outer resin canals are the first encountered by the weevil, it is plausible that the size and location of these canals have more influence on the acceptance or rejection of the weevil before eggs are laid. However, it is conceivable that the inner resin canals have more of an impact on the performance of larvae and eggs, because these canals are much larger, and often more numerous, than outer resin canals.

In addition to variation between species, it has been established that the resin canal system can vary within species, whereby different anatomies have been attributed to resistant and susceptible trees (Tomlin and Borden 1994, 1997; Alfaro 1996a; Alfaro et al. 1997). Therefore, our results have to be used with caution, since all trees sampled in this study showed signs of weevil attack and, thus, were probably susceptible. If we had sampled the populations of attacked or unattacked trees of each species, the mean anatomical measurements might have been different from our results.

In summary, our results suggest that the structure of the resin canal system is related to weevil biological performance as measured by adult mass. The density of inner resin canals appears to be the most important variable related to adult mass. White pine was very different from spruce species, having a low density of very large inner resin canals. This structure seems to be favourable for weevil body mass gain, probably because larvae can more easily avoid the canals and minimize resin consumption. However, the structure of the resin canal system certainly does not explain all the variation in adult mass between host species, and other factors might also be involved. The structure of the resin canal system did not seem to affect the survival and number of weevils produced.

Acknowledgements

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