Primary Cortex Thickness Influences the Location of Ovarian Maturation Feeding and Oviposition of *Pissodes strobi* (Coleoptera: Curculionidae) within a Tree

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ABSTRACT The white pine weevil's [*Pissodes strobi* (Peck)] choice of bark tissue for ovarian maturation feeding was determined. In addition, the thicknesses of primary cortex tissue were determined to ascertain if primary cortex thickness was positively correlated with the selection of oviposition sites. White pine weevils engaged in ovarian-maturation feeding and oviposition, referred to in this article as reproductively active female weevils, preferentially feed on primary cortex tissues of Sitka spruce, *Picea sitchensis* (Bongard) Carriere, and interior spruce (a complex of white spruce [*Picea glauca* (Moench) Voss] and Englemann spruce [*P. englemannii* Parry]) leaders. On these leaders they feed mostly and oviposit almost exclusively in sterigmata ridges where the thickest primary cortex occurs. Branches of open-grown trees have insufficient primary cortex thickness; they are not normally used for oviposition and are used poorly by caged reproductively active female weevils. Reproductively active female weevils do not normally oviposit on the main stem below the leader where the primary cortex is thinner, but will do so when they do not have access to the leader or when caged on lower inter-nodes. This weevil attacked branches and the main stem below the leader in *Picea chihuaiana* (Martinez) and *P. mexicana* [=*P. engelmannii* Parry variety *mexicana* (Martinez)] trees in locations where the thickness of the primary cortex is greater than in other species studied. Only primary cortex thickness increases with tree height in Sitka and interior spruces. The female white pine weevil's preferential feeding upon this tissue in the spring can account for their movement from ground level to tree tops.

KEY WORDS *Pissodes strobi*, white pine weevil, Sitka spruce, interior spruce, Mexican spruce

THE WHITE PINE weevil, *Pissodes strobi* (Peck), also known as the western spruce weevil and the spruce terminal weevil, is the most devastating pest of regenerating spruce forests in British Columbia (Ebata 1991). Feeding on the inner bark (phloem) by the larvae often results in trees with dead tops, this severely reduces the tree's commercial value. At specific sites along the coast of British Columia, the weevil has been responsible for the cessation of planting Sitka spruce, *Picea sitchensis* (Bongard) Carriere. It is currently an economic threat to all of British Columbia's regenerating spruce forests. This same insect causes economic damage to many pine and spruce species in eastern North America.

During the early spring, adult weevils emerge from the duff on the ground in dryer regions of North America (Wallace and Sullivan 1985), or leave the lower stem and branches in warmer and wetter regions (Gara et al. 1971). Toward the end of April, adult female weevils become reproductively active after sufficient feeding and gonadal maturation has taken place (Gara and Wood 1989). Weevils engaged in ovarian maturation and oviposition are referred to herein as reproductively active female weevils. They are commonly observed in nature ovipositing on the terminal leader of susceptible trees (Sullivan 1959a, 1959b; Silver 1968; Gara et al. 1971; Wallace and Sullivan 1985). In the past, it was generally believed that weevils were drawn to treetops by light (positive phototaxis) and gravity (negative geotaxis) (VanderSar and Borden 1977). VanderSar and Borden's research used excised leaders, but no intact trees were examined. Recently, we used whole trees and found that light and gravity were unnecessary factors causing reproductively active female weevils to reach treetops (unpublished data).

Oviposition commences at the tip of the leader and proceeds downward (Johnson 1965). According to Bauce and Hamel (1991; cited in Hamel et al. 1994), reproductively active female weevils are restricted to feeding on leaders. Why reproductively active female weevils feed mostly and oviposit exclusively on the terminal leaders of open-grown native spruces and

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pines has remained an interesting and open question for many decades.

For more than 175 yr, researchers have reported that open-grown trees are more heavily attacked by this weevil than are shade-grown trees (Peck 1817, Graham 1918, MacAloney 1930). Sullivan (1959a, 1959b, 1961) indicated that *P. strobi* is well adjusted to the environment of open stands of white pine (*Pinus strobus* L.), but is unable to adapt readily to the climate of many shaded stands. In addition, Sullivan (1961) observed that reproductively active female weevils exhibit a preference for white pine leaders with diameters of 7–12 mm and a bark thickness of 1.8–2.2 mm. He also reported that reproductively active female weevils were incapable of ovipositing in bark thinner than ≈0.8 mm because the major-axis diameter of the weevil's egg was ≈0.8 mm.

Kriebel (1954) observed that tree vigor appears to be an important factor affecting weevil behavior and success. Vigorous leaders have thick, succulent bark. Vigorous trees were reported to be more susceptible to weevil attack. This would explain why there is more weevil attack among dominant and co-dominant trees than among those in lower crown classes. According to Silver (1968) and Gara et al. (1971), reproductively active female weevils preferred to oviposit on faster growing spruce with terminal leaders longer than 406 mm, and they preferred leaders with diameters >7.6 mm. Terminal leaders with diameters <4.6 mm were not attacked (Silver 1968, Gara et al. 1971).

Plank and Gerhold (1965) measured terminal leader diameter, average bark thickness, average diameter of resin ducts, average depth from the surface to the ducts and the number of resin ducts at one position 25.4 cm below the leader top. They reported that feeding and susceptibility were not linked, and feeding was not linked to any of the morphological features they measured. However, Stroh (1964), Stroh and Gerhold (1965), and Wilkinson (1983) found that bark thickness, depth of inner (closest to the xylem) and outer (closest to the periderm) resin canals, and leader diameter are correlated positively with successful weevil attacks. However, Wilkinson (1983) found no correlation between weevil attack and leader length or between weevil attack and numbers of inner and outer resin ducts.

Beck (1965) concluded that insect behavior and gonadal development are not fully separable and independent; allowance must be made for behavioral manifestations resulting from the insect's physiological state, including nutrition, endocrine functions, and ovarian maturation. Sahota et al. (1998) showed that reproductively active *P. strobi* fed more than nonreproductive females, regardless of host type, demonstrating that physiological state alters feeding behavior.

Conflicting information has been published about the weevil's ability to use branches for oviposition. Gara and Wood (1989) found that weevils with undeveloped ovaries were incapable of developing eggs when caged on branches, but did so readily when caged on leaders. Unsuitability of branches was indicated by 50% mortality of adult weevils caged on branches of *P. strobus* versus 8% on terminal leaders (R. Lavallée, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Center, personal communication). However, weevils have been raised routinely to larval stages by caging reproductively active female weevils from field collections on the severed branches of *P. sitchensis* (McMullen 1976).

Stem diameter, inner and outer resin duct depth, and overall bark thickness have not been linked consistently to this weevil's feeding and oviposition behavior. Nevertheless, bark, the tissue used by weevils for feeding, must hold the key to understanding the behavior of reproductively active *P. strobi* on a single tree.

A recent discovery that light and gravity are not important factors in drawing reproductively active female weevils to treetops (unpublished data) reopens the question as to what mechanism draws this weevil to the leader for ovarian-maturation feeding and oviposition. The current study investigates the relationship between selected weevil anatomical features, bark structure, periderm plus primary cortex thickness, and gonadal-maturation feeding and oviposition behavior. We discuss how these factors may influence female weevils to move to treetops and to locate and oviposit on sterigmata ridges of spruce leaders.

Materials and Methods

Tree Samples. Eleven interior spruce trees, a complex of white spruce [*Picea glauca* (Moench) Voss] and Englemann spruce [*P. englemannii* Parry] from Clearwater, BC, were collected in April 1998. Six Sitka spruce trees from Eve River, BC, were similarly collected in May 1998. Two Mexican spruce trees, one each of *P. chihuaiana* (Martinez) and *P. mexicana* [=*P. engelmannii* Parry variety mexicana (Martinez)], were collected from the British Columbia Ministry of Forests, Kalamalka Research Station, Vernon, BC, in August 1998.

The most recent 4 yr of growth was removed from each of the sampled trees and transported to the laboratory. Each internode was sectioned by hand into slices ≈1–3 mm thick at 2.5 cm below and above each node. The maximum diameter (caliper) of each section, numbered from 1 to 8, starting from the top of the first (youngest) internode, was measured with a digital caliper. Fig. 1 shows the stem and branch labeling system used in this study.

The thicknesses of the brown periderm, with adhering epidermis when present, green primary cortex and primary phloem, and white secondary phloem were obtained from the internode sections using a binocular microscope (Leica Wild M3C, Willowdale, ON) with a Bausch and Lomb (Rochester, NY) ocular micrometer disk (31-16-02) in the eyepiece. Measurements were obtained along several radial lines, which passed through the centers of sterigmata ridges (Jou 1971) whenever these were evident features (see Fig. 2A).

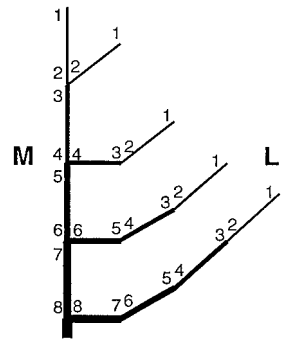

Fig. 1. Tree labeling system used for main stem (M) and branches (L) showing locations of position numbers (1–8).

Needles were removed by hand from each segment and the bark was removed from the wood either intact, or separated according to color into periderm (brown), primary cortex (green), and secondary phloem (white) layers. Bark samples were dried at 70°C for 48 h and ground to a fine powder in a modified coffee grinder. Triplicate nitrogen analyses for the three distinct layers, separate or combined, for both Sitka and interior spruce, were obtained using a Leco Nitrogen Determinator, FP-228 (Leco, St. Joseph, MI, USA). Diffuse reflectance Infrared spectra (DRIFT) of leaf trace fragments were obtained with a Bomem MB-100 FTIR spectrometer. (Bomem, Quebec, PQ, Canada).

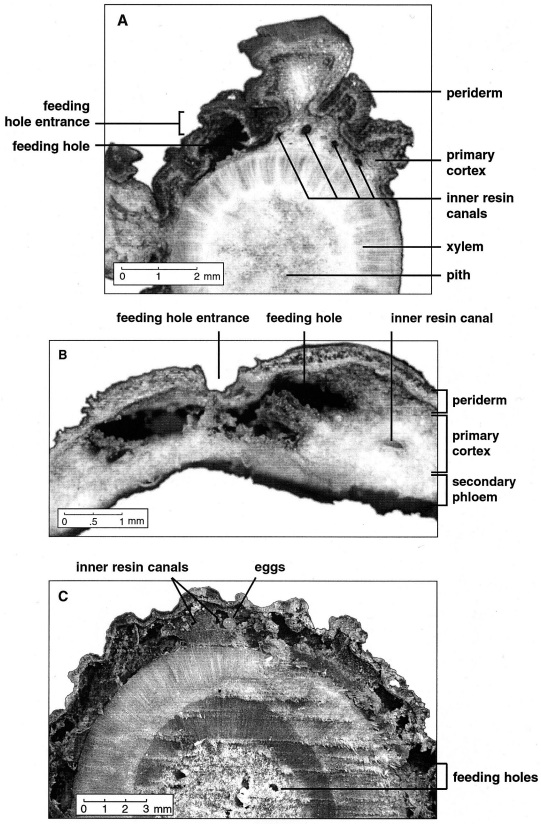

Fig. 2. Typical feeding holes found in, (A) a sterigmata ridge of the leader (M-1), (B) a lower internode of the main stem (M-4), and (c) a cut surface (M-5).

Selected Weevil Dimensions. Weevils were separated by sex according to accepted practice (Lavallée et al. 1993). Twenty adult female and male weevils from coastal (Sitka spruce, Fair Harbor, BC), and 12 each from interior (interior spruce complex, Clearwater, BC) populations were examined; measurements were made on snout length, tip to antennae attachment, and tip to base of eye, and snout-tip width (females). Major and minor egg axes dimensions were also determined for 20 recently deposited eggs using the binocular microscope method given above.

Weevil Feeding and Oviposition. Three reproductively active female weevils were placed in a petri dish, containing several 1–2 cm long sections taken at random from either main stem (M-1–M-8) or branch (L-1–L-8), and allowed to feed and oviposit for 5 d. Additional weevil feeding data on trees in nature, on trees in shade houses, and on severed stems in the laboratory were obtained from hundreds of observations made over several years (Sahota et al. 1994, 1998; unpublished data). Oviposition holes, which are feeding holes into which eggs are deposited, were also noted and diameters were determined. These holes were plugged with a fecal cap made from frass and modified oleoresin.

Weevils Caged on Branches of Sitka Spruce. At Fair Harbor, BC, six reproductively active female weevils and three male weevils were placed in each cage located over positions 3 and 4 on the second segment of a third whorl branch (Fig. 1). Experiments were initiated on 12 May 1993, 17 May 1994, and 25 May 1996. Branches were oriented normally (horizontal) in 1993 and 1996, and both horizontally and vertically in 1994. Weevil success on branches (number of larvae and lengths of galleries, alive or dead branches) was assessed on 21 October 1993, 22 June 1994, and 17 July 1996, respectively.

Means, standard deviations, and standard errors were obtained using Excel spreadsheet statistical routines. Statistica for Windows (StatSoft, 1999) was used for Duncan's multiple means tests of stem and branch diameters after an *F*-test indicated a significant effect. Regressions and one-tailed 95% prediction limits of log-transformed thickness (periderm plus primary cortex minus weevil snout length) versus log-transformed stem or branch position numbers were obtained using PROC GLM (SAS Institute 1988).

Results

Stem and Branch Diameters. Generally, branch segments <3 yr old had diameters below the normal weevil-attacked caliper of 7.6 mm for both Sitka and interior spruces (Table 1) (Silver 1968, Gara et al. 1971) and for white pine (Sullivan 1961). Branch-tip (Lx-1; where Lx = a branch, 1 = position 1, 2 = position 2, and so on) diameters were below the min-

Table 1. Mean maximum diameter (mm) (±SD) of main stem and branches from six Sitka spruce from Eve River, BC, and 11 interior spruce from Clearwater, BC

Position	Sitka		Interior	
	Main	Branch	Main	Branch
1	7.58 (0.58)a	3.84 (0.68)a	7.35 (1.12)a	3.90 (0.70)abc
2	10.75 (1.53)b	4.82 (0.93)a	10.1 (2.27)b	4.22 (1.02)abc
3	13.21 (1.57)c	5.12 (0.68)ab	12.71 (2.39)c	5.01 (0.92)abcd
4	18.15 (1.59)d	6.56 (1.21)bc	16.0 (3.11)d	5.75 (1.33)abcde
5	22.51 (2.75)e	6.52 (0.81)bc	19.92 (4.22)e	6.30 (1.26)bcdef
6	24.83 (2.30)f	7.68 (1.17)bc	23.3 (4.95)f	7.41 (1.68)cdef
7	29.13 (3.07)g	7.71 (0.94)bc	27.16 (5.72)g	7.81 (2.15)defg
8	31.87 (3.80)h	9.20 (1.18)d	31.1 (5.37)h	9.40 (2.49)fg

Means followed by the same letter are not significantly different, Duncan's multiple means test. $P < 0.05$

imum diameter of 4.6 mm acceptable for oviposition (Silver 1968, Gara et al. 1971). At older branch positions (2–8) and all main-stem positions, diameters were at or above this minimum acceptable caliper. Diameters of all examined main stem and branch segments of two Mexican spruce trees were greater than the minimum acceptable level of 4.6 mm (Table 2) (Sullivan 1961, Silver 1968, Gara et al. 1971).

Feeding and Oviposition Behavior. Field and laboratory observations showed that reproductively active female weevils fed and oviposited preferentially on the upper most portion of the leader on sterigmata ridges below the attached needle (position 1). These weevils made a series of feeding punctures, usually three, along a ridge before moving to another ridge. Reproductively active female weevils buried their snouts up to the base of their eyes while feeding there. Entrance holes measured 0.47 mm (SD = 0.06) in diameter, which were just large enough to accommodate the weevil's snout, 0.40 mm (SD = 0.02) in diameter. Examination of feeding holes in tree leaders, see Fig. 2A, branches, severed leaders and branches, and excised bark, indicated that reproductively active female weevils fed on primary cortex tissue in preference to periderm, secondary phloem and xylem. In all oviposition holes examined, evidence of resin canal removal was evident. In addition, leaf trace debris found in these holes was comprised mainly of crystalline cellulose (according to its reflectance infrared spectrum, unpublished). For a typical weevil-feeding hole in a sterigmata ridge on a Sitka spruce leader, see Fig. 2A, and in the lower-main stem (M-4), see Fig. 2B.

A typical petri dish bioassay on stem sections showed feeding occurred on inner bark (56 times), on pith (37 times), but not on periderm or xylem. Within the inner bark, primary cortex was fed upon 48 times versus secondary phloem eight times. Fig. 2C shows feeding and oviposition of reproductively active female weevils on the surface of a typical main-stem segment (M-5).

Bark Nitrogen Content. The percent nitrogen content of primary cortex and secondary phloem was 0.95 (SD = 0.06) and 1.09 (SD = 0.04), respectively. The periderm had the least amount of nitrogen, 0.72 (SD = 0.02) percent.

Selected Weevil Dimensions. In both coastal and interior female weevils the antennae were attached at 0.90 mm (SD = 0.05) from the tip of the snout, a little over half way between the tip and the base of the eye, in agreement with Hopkins (1911). With the antennae folded into the grooves on the sides of the snout, the effective snout length to the base of the eye is 1.60 and 1.48 mm for coastal and interior female weevils, respectively (Table 3). Within each locale, the male mean snout length was ≈0.12 mm shorter. Coastal weevil eggs were equally rounded at each end, with average dimensions of 0.45 by 0.85 mm, which is in general agreement with values reported by Sullivan (1961).

Bark Tissue Thicknesses. Bark (phloem plus primary cortex plus periderm) thickness was essentially uniform for main stem and uniform for branches (Figs. 3 and 4). In Sitka and interior spruces, for segments of equal age, the overall branch bark and primary cortex thicknesses were less than those found in the bark of the main stem. Although the secondary phloem decreased in thickness from position 8 to 1, the primary cortex increased in thickness.

Table 2. Midpoint diameters (mm) of main stem and branch segments from *P. mexicana* and *P. chihuaiana* from Vernon, BC

Segment	*P. mexicana*		*P. chihuaiana*	
	Main	Branch	Main	Branch
1	5.9	5.7	8.6	7.8
2	9.4	8.6	14.0	9.0
3	14.8	11.5	18.1	13.7
4	NS	15.5	NS	15.8

Segment 1, includes positions 1 and 2, segment 2, includes positions 3 and 4, an so on. NS = not sampled.

Table 3. Selected weevil dimensions (mm) for coastal and interior female and male white pine weevils and coastal weevil eggs

	Sex	Dimension, mm	*n*	SD
		Coastal		
Snout length	Female	1.60	20	0.01
	Male	1.48	20	0.02
Snout width	Female	0.40	20	0.02
Egg major (minor)		0.85 (0.45)	20	0.03 (0.03)
		Interior		
Snout length	Female	1.48	12	0.05
	Male	1.35	12	0.09
Snout width	Female	0.39	12	0.03

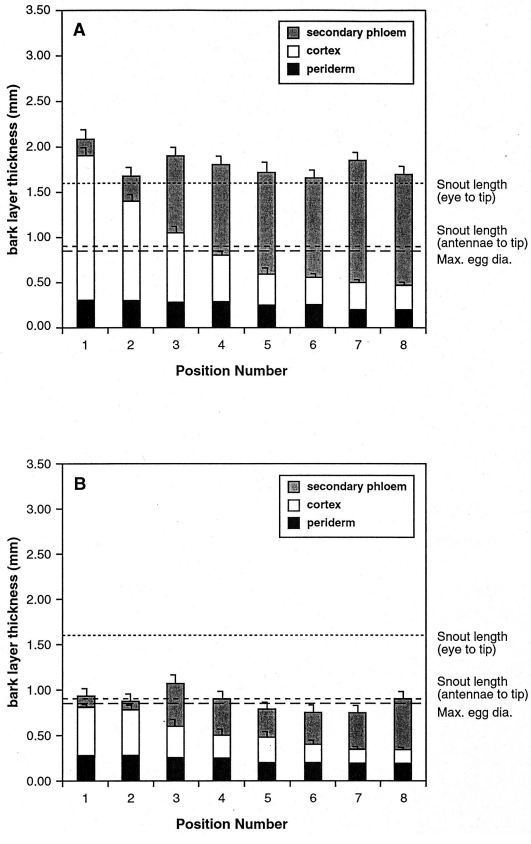

Fig. 3. Mean maximum thicknesses for layers of bark from (A) main stem and (B) branch segments of six Sitka spruce from Eve River, BC, and indicated weevil data. Standard errors (¬) are shown for primary cortex and secondary phloem.

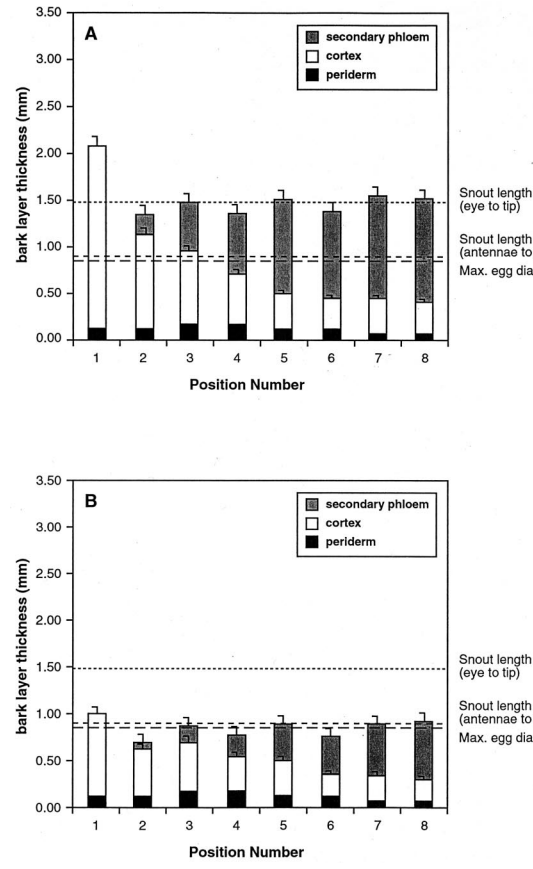

Fig. 4. Mean maximum thicknesses for layers of bark from (A) main stem and (B) branch segments of 11 interior spruce from Clearwater, BC, and indicated weevil data. Standard errors (¬) are shown for primary cortex and secondary phloem.

Superimposed on these figures of bark-tissues thicknesses (Figs. 3 and 4) are two horizontal lines representing snout lengths, from tip to attachment of antennae and to base of the eye. A third line, representing egg length, intersects the columns representing bark thickness at all stem and branch positions, as does the line representing antennae attachment point. In contrast, the line representing snout length to the base of the eye does not intersect the bark thickness of any branch: however, it does intersect bark thickness for all main stem positions. It intersects periderm plus primary cortex thickness at position 1, the location of preferred oviposition on trees in nature (see references). Similar figures are provided for the two Mexican spruces studied (Figs. 5 and 6). Here, the line of total snout length intersects primary cortex at many branch locations as well as the main stem.

Reproductively Active Female Weevils Caged on Branches of Sitka Spruce. Reproductively active female weevils caged on the 2-yr-old segment of 3-yr old branches (L-3–4) did not match weevil performance on the leader (M-1) of the same tree. A few eggs were laid (0–4 oviposition holes) and larval development, assessed by larval gallery length, was poor, from 1 to 6 mm in branches, compared with 100 to 300 mm or more in leaders. Overall, little branch damage was noted. In the 1993 experiment, only two of 30 branches were killed by developing larvae and most branches fully recovered. The 1994 and 1996 experiments resulted in two dead branches out of 46 caged. Vertical branch orientation did not affect the results.

Regression Analysis of Log Transformed Data. The regression of periderm plus primary cortex thickness minus snout length versus position number and its upper 95-confidence-interval lines for interior spruce indicate that oviposition can be expected to occur at and above position 2.86 on the main stem (Fig. 7A; Table 4). Oviposition should not occur on branches of interior spruce, as neither line crosses the x-axis (Fig. 7B). X-axis intercept values (Table 5) indicate the stem position below which attacks will not occur 95 times out of 100.

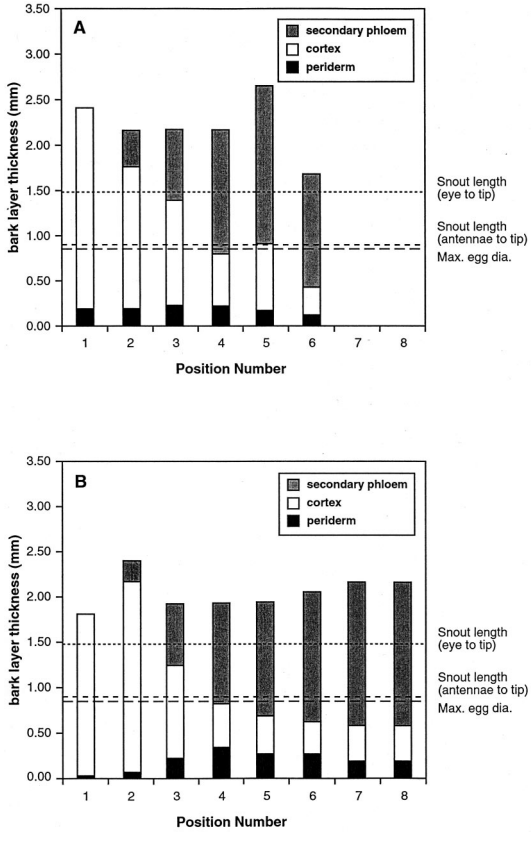

Fig. 5. Mean maximum thicknesses for layers of bark from (A) main stem and (B) branch segments of a *P. mexicana* from Vernon, BC, and indicated weevil data.

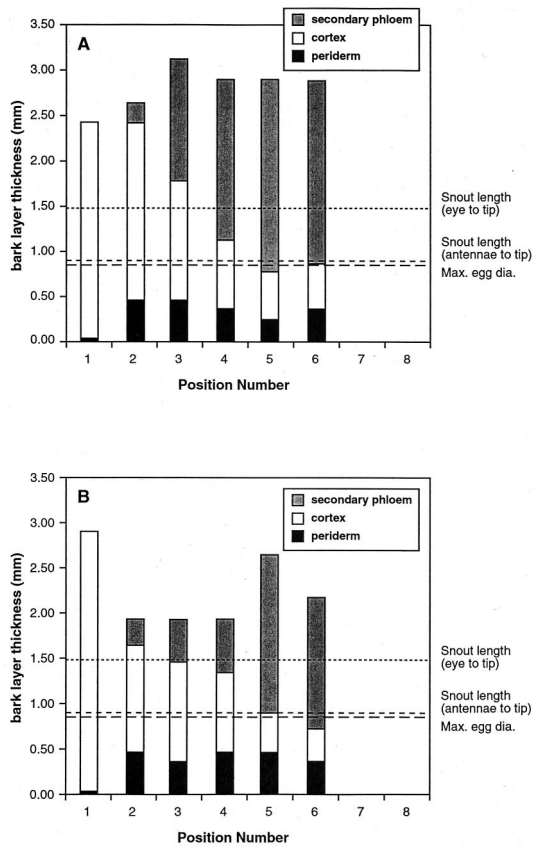

Fig. 6. Mean maximum thicknesses for layers of bark from (A) main stem and (B) branch segments of a *P. chihuaiana* from Vernon, BC, and indicated weevil data.

Discussion

Bark has three main tissue layers: periderm, primary cortex, and secondary phloem. Of these, only primary cortex thickness increases from older to younger growth (positions 8–1). Moreover, in British Columbia, the bark of branches of native spruces is always thinner than the bark of the adjacent main stem (Figs. 3 and 4). Branch bark thickness averages around 0.85 mm, whereas main stem bark is ≈1.75 mm thick.

In the early spring, female weevils leave the lower stem and branches to use tops of leaders (Fig. 1, position M-1) for gonadal-maturation feeding and oviposition (Silver 1968, Overhulser and Gara 1975, Gara and Wood 1989). They make their oviposition holes in sterigmata ridges (Fig. 2A) where the tree's thickest primary cortex is found (see Figs. 3A and 4A). Recently, Sahota et al. (1998) showed that reproductively active female weevils eat more than nonreproductively active female weevils, and we believe that feeding and oviposition activities at treetops are linked to increased metabolic activity of reproductively active female weevils and the need for additional nutrition.

Weevils do not use branches for oviposition. According to Sullivan (1961), bark thickness is an absolute limiting factor; bark thinner than ≈0.9 mm cannot accommodate this weevil's eggs, which average 0.85 mm long (Table 3). Thus, thin bark alone may explain why reproductively active female weevils avoid shade-grown trees and branches of most host trees for oviposition.

Reproductively active female weevils do not normally exploit main stem bark below the leader (positions greater than M-2) for oviposition, although the stem diameter (Table 1) is well above the minimum acceptable to this weevil. The bark below the leader (Figs. 3A and 4A) exceeds the minimum thickness required for oviposition and in comparison with the leader has a lower density of resin canals. In fact, reproductively active female weevils were able to use the bark of the lower stem when access to the leader was blocked, when the leader was killed previously (Cozens 1987), when reproductively active female weevils were caged on lower-stem segments (unpublished data), and in feeding bioassays on stem sections.

We hypothesize that the bark of the lower main stem must lack some feature essential for gonadal maturation feeding. Examination of feeding holes reveals that this weevil makes small entrances. Although a feeding-hole diameter of 2.5 mm was reported by

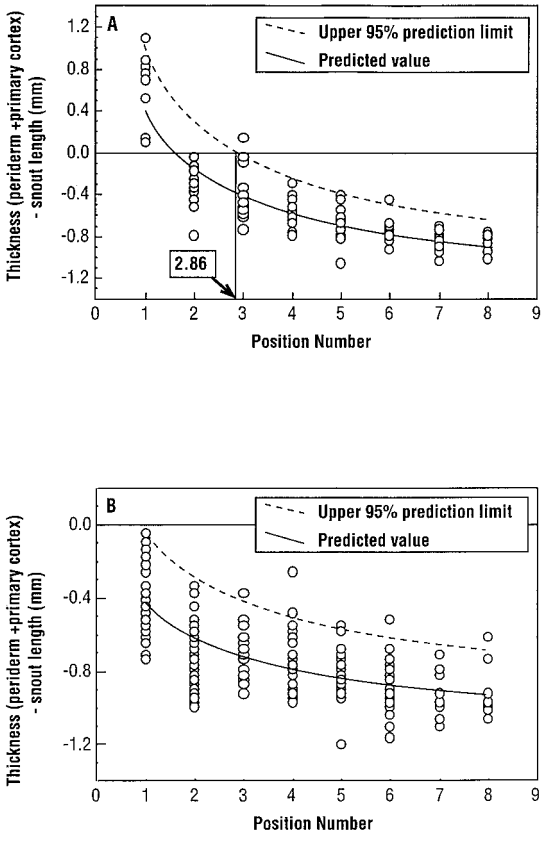

Fig. 7. Regression line and upper 95% prediction limit for thickness of the periderm plus primary cortex minus snout length versus (A) main stem position number, and (B) branch stems position number for interior spruce. See Table 4 for regression equations for this and other species.

Silver (1968), entrance holes in this study averaged only ≈0.5 mm in diameter, slightly wider than the tip of its snout (0.40 mm) (Table 3). A small hole may reflect low nutritive value of the periderm (0.72 ± 0.1% nitrogen). In addition, it appears to be drier than other bark tissues. Weevils feed under the periderm more widely and deeply to a maximum distance of ≈1.5 mm, the length from the tip of the weevil's snout to its eye. At treetops, in bark thinner than ≈1.5 mm, the weevil's snout often reaches the cambium; here the bottom of such feeding holes conforms to the surface of the xylem (Fig. 2A). When feeding weevils encounter leaf traces, they are not consumed and can be found in pieces within such cavities. This avoidance may be due to the refractory nature of Sitka- and interior-spruce leaf traces, which are encased with crystalline cellulose.

Table 5. Stem position (X) intercepts of the upper 95% prediction for the equations in Table 4

Species	Main	Branch
Sitka	2.2	1.1
Interior	2.9	<0
Mexicana	4.0	4.3
Chihuaiana	3.9	6.5

The fate of resin canals is less certain. Often resin canals can be found intact within feeding holes, but not within most oviposition holes. In fact, in the process of constructing oviposition sites, reproductively active female weevils consume resin canals and the resin contained therein. According to Sahota et al. (1998), the volume of feeding/oviposition holes are ≈1.5 mm^3, which translates to a cross section area of 1.76 mm^2. According to Sahota et al. (2000), the density of resin canals in leaders of Sitka spruce is 0.89 (0.25) mm^{-2}, implying that feeding/oviposition holes will envelope one or more resin canals. The fact that reproductively active female weevils eat nearly the entire inner bark tissue of sterigmata ridges when constructing oviposition chambers requires that up to four resin canals be consumed. The photographs presented in Fig. 2 clearly indicate that the resin canals have been removed. Resin appears to be an essential part of fecal plugs used to seal oviposition chambers (unpublished data), and successful artificial diets must contain bark (Trudel et al. 1994). These findings indicate that resin is not a strong deterrent to feeding.

Differential features of bark may account for gonadal-maturation feeding taking place at treetops. In addition, to periderm and primary cortex, the older bark of lower tree internodes contains a preponderance of secondary phloem cells. Examination of feeding holes at positions other than M-1 revealed a marked preference by reproductively active female weevils for primary cortex tissue and surprisingly, an apparent avoidance of secondary phloem tissue (see Fig. 2B). Weevils fed only to a depth of ≈0.75 mm, whereas they fed outward from the entrance hole beneath the periderm for 1.5 mm, a distance that corresponds with the length of its snout. The shape of lower inter-node feeding holes indicates that the wee-

Table 4. Regressions (equation), sample sizes (n) and correlation coefficients (r) for the relationships between PCL and position number (X)

Species	Main			Branch		
	Equation	*n*	*r*	Equation	*n*	*r*
Sitka	Y = 0.39772−0.4857X	48	−0.9599	Y = 0.21857−0.3291X	120	−0.8539
Interior	Y = 0.37815−0.3770X	88	−0.8885	Y = 0.19597−0.1887X	220	−0.7028
Mexicana	Y = 0.50191−0.5885X	6	−0.9459	Y = 0.44132−0.4806X	7	−0.9029
Chihuaiana	Y = 0.53163−0.5074X	6	−0.9014	Y = 0.52415−0.5232X	6	−0.9786

Equations were fitted to log-transformed data PCL, thickness of periderm and primary cortex minus *P. strobi* mean snout length; see methods.

vil, although capable, does not eat all the secondary phloem tissue that is within its reach. This avoidance of secondary phloem cells does not appear to be due to a lack of protein (1.09% ± 0.04) nitrogen for secondary phloem and 0.95% ± 0.06 nitrogen for primary cortex).

Secondary phloem cells have much thicker cell walls and do not appear to contain as much fluid as primary cortex cells. Wilkinson (1975) found that trees treated with an antitranspirant sustained more damage than untreated trees. Cut leaders kept in contact with water produced more and heavier weevils than leaders that were allowed to dry (Lavallée et al. 1993). This avoidance of phloem tissue may be due to lack of moisture or to its relative toughness.

Microscopic examination of primary cortex cells, taken from tree tops and lower on the main-stem, reveals a change in shape from ovoid to thin lenticular structures. This deformation may result from increasing pressure caused by the xylem and secondary phloem continuing to grow while the periderm stretches to accommodate the increased diameter. Deformation implies a weakness in the walls of primary cortex cells. Little or no deformation is apparent in the thicker-walled secondary phloem cells and epithelial cells surrounding resin canals (Chang 1954, Cabrera 1978), implying greater rigidity and toughness. Drier and tougher (less deformed) cells are likely more difficult to chew and ingest, resulting in a lower rate of nutrition uptake by weevils feeding on them. In contrast, primary cortex cells, which have thin walls and are filled with fluid, are preferentially consumed; such cells can provide the weevil with the greatest input of energy, moisture and protein for the least expenditure of energy.

In other feeding choice tests (unpublished data) using cut stems, branches, and pieces of excised bark, weevils were observed to feed from the cut surface on primary cortex more than secondary phloem (Fig. 2C). Weevils also fed on the interior portion of cut needles and on pith when these tissues were made available to them. Our observations indicate clearly the weevil's preference for primary cortex tissue. Primary cortex, needle interiors and pith all have thin-walled moisture-filled cells.

Primary cortex tissue increases in thickness with tree height. Reproductively active female weevils appear to be drawn up the tree by their preferential feeding on this tissue. It seems likely that they follow the increasing thickness of primary cortex tissue to reach the treetop avoiding the more abundant branch tips. These female weevils do not move from stem to branches for oviposition, probably due to the marked decrease in primary cortex thickness of adjacent branches. Branches appear to offer inadequate conditions for successful weevil development. This was shown in our branch caging tests; only 5% of caged branches were killed, whereas 100% of caged leaders of susceptible trees were killed by larvae of this weevil (Sahota et al. 1994).

Examination of primary cortex thickness for various tree segments from Sitka and interior spruce revealed an increasing thickness from lower tree segments to the top of the tree's leader (Figs. 3 and 4). This increase in primary cortex thickness correlates well with within tree movement and normal feeding behavior of reproductively active female weevils. Reproductively active female weevils move progressively up the bole of the tree, starting their oviposition on the upper portion of the leader. They move down the leader as the more suitable oviposition sites become occupied.

Below treetops, many dimensions become larger (e.g., diameter and bark thickness) or remain static (e.g., periderm, and pith); only primary cortex thickness diminishes in size with age. We suggest that reproductively active female weevils stay at the top of the leader for oviposition because they require thick primary cortex as opposed to thick bark. They presumably assess the suitability of the primary cortex thickness by their ability to completely bury their snout in the bark. When they encounter tissues more difficult to consume than primary cortex, at a depth within reach of their snout, they move to adjacent locations where primary cortex may be thicker. We hypothesize that their movement to thicker cortex draws them to the treetop. Their movement to thicker primary cortex even occurs when the tree is upside down (unpublished data).

The above concept is further supported by regression analyses. Bark thickness (periderm plus primary cortex) minus snout length versus position number (X), noting the upper 95% one-tail confidence interval intersection of the x-axis, provides an indication of the tree position number at which oviposition would most likely begin (Fig. 7; Table 4). They indicate that cortex thickness and snout length are important factors in moving reproductively active female weevils to suitable oviposition sites. Oviposition should occur at these predicted locations (Table 5). Indeed such locations are in keeping with field observations and correspond well with the data presented in Figs. 3 and 4. X-axis values estimated from the point where the line for snout length first intersects the primary cortex layer correspond well with those determined by regression analyses (Table 5). Together these data indicate that branches of interior and Sitka spruce would not be attacked. Conversely, if either snout length, to antennae attachment, or egg length were determining features, then all sites should be used for oviposition. This is not the case for native spruces in British Columbia.

However, reproductively active female weevils behave differently on two species of Mexican spruce (Figs. 6 and 7). At the British Columbia Ministry of Forests' Research Station, Kalamalka, BC, these species have been repeatedly attacked on both branches and on several main-stem segments, on and below the leader. The hypothesis that primary cortex thickness determines acceptable oviposition sites is further supported by their behavior on these species, stem and branch diameters (Table 2) and primary cortex of sufficient thickness were not limited to the leader. Rather, these Mexican spruces provided an abun-

dance of sites with thick primary cortex, both on the main stem below the leader and on the branches.

In light of the present findings, the fact that resin canal depth and successful oviposition are positively correlated (Stroh 1964, Stroh and Gerhold 1965, Wilkinson 1983) may be merely an outcome of resin canal placement being further from the outer bark due to thicker primary cortex. Vigorous, dominant and co-dominant, thick-leader and long-leader trees are attacked preferentially (Kriebel 1954, Silver 1968, Gara et al. 1971) probably because they provide thicker primary cortex. Weevils may avoid shade-grown trees because they are less attractive due to spindly tree growth resulting in thin stems with thin bark, and insufficient primary cortex thickness for ovarian maturation feeding and oviposition.

We conclude that *P. strobi* locates its preferred oviposition sites by using its snout to assess primary cortex thickness. This weevil follows the gradient of primary cortex thickness as it undergoes gonadal-maturation feeding and moves up the tree in the spring, eventually reaching the treetop. In Sitka and interior spruce, oviposition occurs in sterigmata ridges located on the upper portion of the previous year's growth, because this is where the thickest primary cortex occurs. On Mexican spruces, oviposition can occur on branches and lower main-stem internodes, wherever primary cortex is of sufficient thickness.

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