

Carbohydrate allocation and mountain pine beetle attack in girdled lodgepole pines¹

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Healthy lodgepole pine trees (*Pinus contorta* Dougl. var. *latifolia* Engelm.) were girdled on the lower trunk in patterns designed to selectively eliminate the influence of materials transported from the roots, lateral tissues, and crown. Titres of soluble sugars and starch observed in areas isolated by girdling were significantly lower than those observed in areas open to the upper bole and crown. Corresponding decreases were observed in the numbers of *Dendroctonus ponderosae* Hopkins attacking those areas.

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Des pins de Murray sains (*Pinus contorta* Dougl. var. *latifolia* Engelm.) furent annelés dans la partie inférieure du tronc de manière à bloquer sélectivement le transport des substances en provenance soit des racines, soit de la cime ou des tissus adjacents. La concentration en sucres solubles et en amidon était significativement plus faible dans les zones isolées par l'annélation que dans les zones encore reliées à la partie supérieure du tronc ou à la cime. Une diminution du nombre de *Dendroctonus ponderosae* Hopkins a aussi été observée dans ces zones.

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Introduction

Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) resists attack and colonization by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) by a combination of static and dynamic defensive processes that isolate and intoxify the attacking beetle and its symbiotic blue-stain fungi (Smith 1966; Reid et al. 1967; Shrimpton and Whitney 1968; Berryman 1972; Amman 1975). Attacking beetles may become mired in resin exuding from severed resin ducts (Miller and Keen 1960; Vité and Wood 1961; Smith 1963) or confined within a developing "dynamic wound response" where large amounts of monoterpenes and phenolics are released into the intracellular spaces of a necrotic lesion that develops around the wounded area (Reid et al. 1967; Shrimpton and Whitney 1968; Berryman 1969; Raffa and Berryman 1983a, 1983b). Beetles entrapped within the lesion area may be repelled or killed and their brood intoxicated (Reid and Gates 1970; Berryman and Ashraf 1970; Shrimpton 1973). The growth of pathogenic fungi may likewise be halted by high accumulations of toxic chemicals and a lack of nutrients within the necrotic lesion (Cobb et al. 1968; Shrimpton and Whitney 1968; Whitney and Denyer 1969; Wong and Berryman 1977).

Energy is required to produce defensive compounds associated with the necrotic lesion (Francis 1971; Wright et al. 1979). Photosynthetic energy, in the form of hexoses and starch, is converted to defensive chemicals via the metabolic processes of individual cells activated during the hypersensitive response at a rate of 18 molecules of adenosine triphosphate (ATP) per molecule of monoterpene (Lehninger 1975; Wright et al. 1979). The biosynthesis of defensive compounds may therefore be allied to the availability of carbohydrates to tissues surrounding the necrotic lesion (Christiansen and Ericsson 1986; Croteau et

al. 1972; Clason 1976; Brown et al. 1976; Wright et al. 1979; Miller and Berryman 1985). This availability, along with the numbers of attacking beetles and the virulence of pathogenic fungi (Berryman 1972, 1976; Safranyik et al. 1975; Raffa and Berryman 1983b), determines the outcome of the tree's defensive struggle.

The primary objectives of this study were to determine the carbohydrate content of phloem in trees that had been girdled to inhibit the flow of materials into the girdled area and to establish associations between the aggregation behavior of *D. ponderosae* and carbohydrate titres in selected bole regions.

Methods

Field studies were conducted during the summer of 1983 in a pure stand of *P. contorta* at 1250 m elevation near the Ryan Cabin Trailhead (sec. 30, tp. 38N, rge. 35E), Kettle Falls Ranger District, Colville National Forest, Washington. Daily high temperatures during the period averaged 18°C, while low temperatures averaged near 10°C. Rain fell sporadically as isolated thundershowers.

Twenty trees, averaging 87.6 ± 0.7 years ($\bar{x} \pm SE$) in age and 24.3 ± 0.6 cm in diameter (DBH), were selected for girdling. All trees were located on well-drained Gahee loam on a flat area (50 m × 200 m) north of South Boulder Creek. Moderate *D. ponderosae* infestations had been observed in the stand in 1982.

Four groups of five trees were randomly selected and each tree in each group was engraved with a chainsaw to a depth of approximately 1.5 cm into the sapwood in one of four patterns. (i) A cut made around the circumference of the bole at a height of 1.7 m above ground (full girdle) (Fig. 1a); designed to isolate the lower bole from material translocated from the upper bole and crown. (ii) A cut extending only halfway around the circumference of the bole (1/2 girdle) at 1.7 m above the ground (Fig. 1b); designed to allow materials to move laterally but not vertically into tissues separated by the horizontal cut. (iii) A rectangular cut, open at the base (3/4 box), with width equal to half the circumference of the tree, length 121 cm, and the cut positioned 2 m above the ground (Fig. 1c); intended to permit translocation from the roots and extreme lower bole, while preventing translocation from the upper bole and lateral tissues. (iv) A completely enclosed rectangle (box girdle) with dimensions equal to the 3/4 box (Fig. 1d); intended to isolate the enclosed area from translocated material, except that transported outwardly through the xylem.

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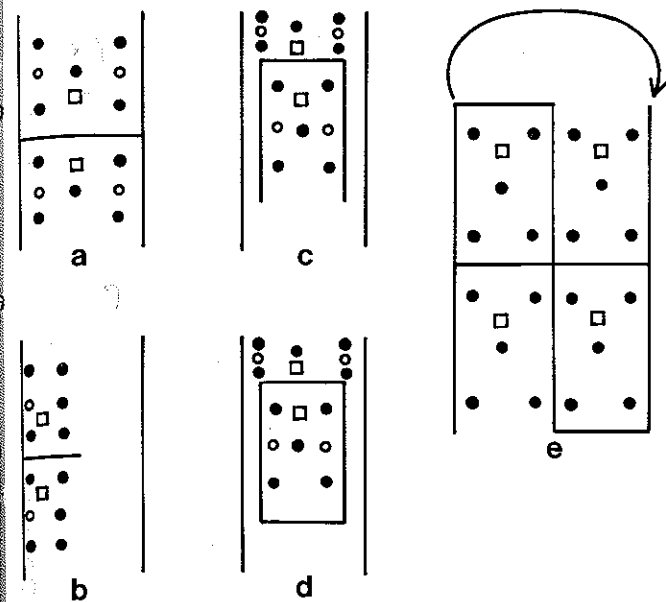


FIG. 1. Girdling patterns employed to study carbohydrate allocation and bark beetle attack on lodgepole pine trees: (a) full girdle extending around the complete circumference; (b) 1/2 girdle extending for half of the circumference; (c) 3/4 box girdle; (d) full box girdle. These patterns were cut into individual trees to a depth of about 1.5 cm into the sapwood with a chainsaw. (e) Girdling pattern was cut to the sapwood surface of six trees with a razorblade knife and was composed of top-open, top-closed, bottom-open, and bottom-closed sections. ●, site of caged beetles; ○, site of resin exudation observations; □, site of phloem removal. Drawings are not to scale.

girdles on each tree were randomly assigned to the cardinal points of the compass.

Resin exudation at the time of girdling (7 July 83) was determined for each tree by screwing a 1.5-dram vial into a 1.1 cm wide hole in the bark (Fig. 1). The volume of resin present was measured after 24 h. Phloem samples were taken 20 days after girdling (27 July 83), frozen in the field over dry ice, and kept frozen below 20°C until laboratory analysis. Phloem thickness was determined by averaging four measurements from each phloem sample removed for chemical analysis. Tree vigor ratings were calculated for each tree from two increment cores using the method of Mitchell et al. (1983), where average vigor is expressed in terms of the mass of newly accumulated sapwood per square metre of leaf area. Age and diameter were also determined at this time.

Bark beetle aggregation was induced on these trees by caging five recently captured female beetles against the bark of girdled and ungirdled regions using translucent medicine vials. A twist of lichen placed in the vial provided footing for the beetle. Caged beetles were positioned at least 10 cm from any girdle (Fig. 1). The positions of subsequent naturally occurring attacks on the bole section were marked daily with thumbtacks to a height of 3 m above ground level. Tree survival and gallery formation were recorded in late October 1983. Five natural beetle attack loci were randomly selected from each girdled and control area, the outer bark was removed from them, and the gallery length, number and average length of larval mines, and extent of necrotic lesion formation were recorded.

Another girdling experiment, designed to eliminate the effects of severing xylem elements of the outer sapwood, was performed on 10 July 1983 on an additional six trees in the same stand. The trees averaged 86.0 ± 1.1 years of age and had an average diameter of 25.2 ± 1.6 cm. The pattern shown in Fig. 1e was engraved through the outer bark and phloem with a razorblade knife, avoiding damage to the underlying tissue. Each of the resulting rectangular box girdles measured 122 cm long extended around 1/2 the trees' circumference and was at least 30 cm above ground. The exposed strip borders

between the boxed areas were approximately 2 cm wide and were covered with duct tape to prevent resin from draining onto the test areas and to reduce dehydration along the edges. This girdling pattern was designed to allow the isolation of two bole sections from substances translocated from the crown, roots, and lateral tissues on each tree. Three girdles were engraved with the upper open box positioned on the east side of the bole and three with it positioned on the west side of the bole. Phloem was sampled after 20 days (30 July 1983). Five female beetles were caged against the bark of each girdled section following phloem sampling on each tree as previously described (see Fig. 1e). The number of naturally occurring beetle attacks, tree survival, and beetle reproduction were recorded in October 1983, as were descriptive data for each tree.

An additional 15 trees lacking girdling treatments were observed concurrently with the girdled trees. These ungirdled trees averaged 89.1 ± 0.7 years of age and had an average DBH of 24.0 ± 0.4 cm. Phloem samples and descriptive data were collected from them in mid-July. Five female beetles were then caged around the circumference of the bole about 1.7 m above ground in the manner previously described.

Each phloem sample was analyzed by the anthrone and Nelson-Somogyi tests for titres of total soluble sugars and reducing sugars, respectively (Nelson 1944; Morris 1948; Hodges and Hofreiter 1962). Tissues used in carbohydrate analyses were dissected from the frozen phloem and placed on dry ice to lower their temperature to -78°C . Samples were then lyophilized, ground to a fine powder, and weighed. Each sample was extracted successively in 25 mL 80% (v/v) ethanol at 65°C . The combined supernatants were then washed in petroleum ether and evaporated to dryness. Hot distilled water was added to the residue and this solution was shaken for 2 h with Dowex 50 \times 8-100+ and Dowex 1 \times 8-100 ion-exchange resin. The solution was filtered, shaken with activated charcoal, and filtered again prior to colorimetric analysis. Results were expressed in milligrams glucose per gram lyophilized phloem.

One-way analyses of variance along with Duncan's multiple-range *a posteriori* tests were used to determine differences among multiple means. Paired means were examined using *t*-tests. Multiple regression was used to rank tree variables associated with bark beetle attack. Results of statistical tests were considered significant if $P \leq 0.05$.

Results

Significant decreases in carbohydrate titres were observed below the girdled section in all but the 1/2-girdled trees (Table 1). Titres of soluble sugars decreased an average of 21% in isolated bole sections, while starch titres decreased by 65%. The greatest decreases occurred in the complete box girdle and in the 3/4 box girdle. Carbohydrate titres in trees girdled around 1/2 their circumference did not follow the same trends as the other trees. Soluble sugars increased slightly below the girdle and starch titres remained about the same (Table 1).

A trend was observed in resin exudation data collected from chainsaw-girdled trees (Table 1). In fully girdled trees, exudation flow rates were generally higher above the girdle than below it. However, exudation rates in 1/2-girdled trees were less above the girdle than below it. Results were also inconsistent in both types of box girdles.

Final bark beetle attack densities varied significantly on chainsaw-girdled sections of trees exposed to natural attack by *D. ponderosae* (Table 1). Bole sections open to the translocation of materials from the crown and upper bole had significantly higher attack densities than those isolated from the upper regions of the tree. Phloem thickness did not vary significantly in the variously girdled sections or between individual trees (Table 1). Vigor also did not differ significantly between trees, averaging 38.11 ± 4.34 g/m².

Results of the second girdling experiment, where bark strips

TABLE 1. Mean values for bark beetle attacks, phloem thickness, soluble sugars, starch, and resin exudation above and below girdles made to a depth of about 1.5 cm into the sapwood of lodgepole pine trees (five trees per replicate)

Variable	Girdling pattern (Figs. 1a-1d)							
	Full girdle		1/2 girdle		3/4 box		Full box	
	Above	Below	Above	Below	Above	Below	Above	Below
Soluble sugars (mg/g)	32.93*	28.70	23.80	31.03	43.35**	31.90	39.74**	31.20
Starch (mg/g)	59.94*	17.29	57.89	56.63	57.40**	11.76	51.01**	30.70
Resin exudation ^a (mg/24 h)	0.21	0.01	0.12	1.28	0.28	0.45	0.67	0.03
Beetle attacks/m ²	47**	22	5**	0.5	20**	12	29**	19
Phloem thickness (mm)	1.75	1.69	2.10	1.89	1.62	1.69	1.57	1.57

NOTE: Levels of significant difference between means: *, $P \leq 0.05$; **, $P \leq 0.01$.
^aSample size insufficient for statistical comparison.

TABLE 2. Mean values for natural beetle attacks, phloem thickness, soluble sugars, and starch within girdled sections carved to the sapwood surface on the boles of six lodgepole pine trees, together with total attack density, gallery lengths (five attacks), and larval mines (five attacks) on one tree that was killed by the beetle attack (killed tree)

Variable	Girdling pattern (Fig. 1e)			
	Top open	Top closed	Bottom open	Bottom closed
Mean of five trees				
Soluble sugars (mg/g)	45.51**	21.67	32.64	28.77
Starch (mg/g)	26.18**	13.31	10.10	9.45
Natural attacks/m ²	10.8*	2.2	3.2	3.2
Phloem thickness (mm)	1.75	1.73	1.51	1.75
Killed tree				
Total attacks/m ²	45	9	8	14
Gallery length (cm)	29.1	29.1	1.1*	27.8
Larvae hatched/cm	3.0*	1.1	0.0	1.6

NOTE: Levels of significant difference between means: *, $P \leq 0.05$; **, $P \leq 0.01$.

were removed from the bole without disturbing the underlying sapwood, are presented in Table 2. A significant decrease (38% average) was observed in titres of soluble sugars in bole sections isolated from the crown and upper bole (Table 2). Starch titres also decreased by an average of 58% in these isolated sections. The number of successful entries by bark beetles naturally attacking the outer bark surface varied significantly among sections, with greater numbers of attacks occurring on the trunk sections open to the crown and upper bole regions of the tree.

Phloem thickness did not vary significantly between girdled sections or among individual trees, averaging 1.69 mm for all sections from all trees. Vigor in these trees averaged 50.46 ± 10.64 g/m².

Of all trees examined in both experiments only one (2S-1) was actually colonized and killed by *D. ponderosae*. Beetle attack densities on this tree (Table 2) were much higher on the trunk section open to the upper bole and crown, whereas attack rates were equal on the other three bole sections.

Beetle reproduction data for tree 2S-1 was collected on October 15, 1983, when larval mines extended an average of 3.8 cm on either side of the parent gallery. At this time mean total gallery length averaged about 28 cm in all but the bottom-open section, where the longest gallery was only 2 cm. Larval production per centimetre of gallery was twice as great in the top-open section as in the others. No larvae were observed in the bottom-open section.

Ungirdled trees had average soluble sugar titres (45.94 ± 4.75 mg/g) slightly higher than those observed in bole areas open to the crown and upper bole of fully girdled, 3/4 box girdled, box girdled (Table 1), and phloem-only girdled (Table 2) trees. Starch titres in ungirdled trees were approximately the same (53.12 ± 7.37 mg/g) as those in the girdled areas just mentioned. Soluble sugar was significantly lower above and below the girdle in 1/2-girdled trees than in ungirdled trees, in which starch titres were about equal. Average vigor for ungirdled trees was 59.63 ± 5.49 g/m² and phloem thickness averaged 1.78 ± 0.12 mm.

Regression of phloem thickness, resin flow, total sugar content, and starch content onto bark beetle attack density was significant only when total sugar and starch content were entered into the equation for trees with full circular or box girdles. These two variables alone accounted for nearly 89% of observed variation in the data for these trees (Table 3).

Discussion

The use of different girdling patterns permits observation of the behavioral responses of attacking bark beetles in patches of the stem possessing different physiological characteristics. Of the two girdling methods employed in this study, girdling with a razor-blade knife is preferable to girdling with a chainsaw as the former technique eliminates possible confounding effects that may result from the destruction of xylem elements in the outer

TABLE 3. Results of regression of phloem thickness, resin flow, total sugar content, and starch content against bark beetle attack density

Step entered	Variable	R ²	df	F
1	Total sugar	0.48	1, 4	3.72
2	Total starch	0.89	2, 3	11.92*
3	Resin flow	0.95	3, 2	13.24
4	Phloem thickness	0.97	4, 1	9.00

NOTE: Data were pooled among all trees with full circular or box girdles. *, $P \leq 0.05$.

sapwood. There appears to be little "edge effect" associated with either girdling technique, possibly because of the occlusion of transport vessels with slime plugs (Zimmerman and Brown 1980). However, transportation of materials into the girdled region probably cannot be restricted completely as water diffuses through the apparent free space from internal sapwood tissue to the sapwood-phloem interface (Briggs and Robertson 1957), prolonging the physical integrity of the bark within the girdled region.

The consistent and significant reduction of sugars and starch in girdled bole regions indicates that when nutrient transport processes are disrupted by girdling, local energy reserves needed to sustain life processes and maintain defensive reactions are depleted. This suggests that sugar and starch reserves utilized in defensive responses in areas open to the upper bole and crown may be continuously replenished by nutrients translocated from elsewhere in the tree. These results are corroborated by studies on *Pinus eliotti* Engelm. in which oleoresin soaking was reduced by cuts made above and below the site of application of paraquat, possibly in response to reduced reserve carbohydrate availability to treated tissue (Brown et al. 1976). These authors and Clason (1976) also reported that decreases in starch reserves in *P. eliottii* were correlated with increases in oleoresin content of paraquat-affected tissues. Clason (1976) suggested that sugars produced via hydrolysis of starch were immediately shunted into metabolic pathways functioning in oleoresin production.

Results from the different girdling experiments consistently indicate that access to the upper bole and crown is the most important factor in maintaining high carbohydrate levels in the face of stress as a result of girdling. Carbohydrates and other substances transported in the phloem may slowly accumulate above a girdle and decrease below it (Meyer et al. 1960). Lateral translocation of nutrients may also play a role in the homeostasis of a local bole section as was perhaps demonstrated by the insignificant differences in carbohydrates above and below the girdles of 1/2-girdled trees.

Although responses observed within a few hours or days of treatment would preclude the metabolism of materials originating far from the affected area, the actual distance that carbohydrates are transported is unclear. Wolter (1977) suggested that oleoresin production results from the use of carbohydrate carbon sources near the site of paraquat application in young *P. eliottii*. Our girdling experiment was conducted over a period of 3 weeks, which was adequate time for nutrients to arrive from the crown. Similar girdling experiments conducted on *Pinus radiata* D. Don in Tasmania indicate that carbohydrate titres in girdled sections of the bole can change approximately 10 days after girdling (J. Madden, University of Tasmania, personal communication).

Mountain pine beetle attack densities were always higher

above the girdled area and, with one exception (1/2-girdled trees), in areas of high carbohydrate concentrations. At least three hypotheses can be proposed for this phenomenon. (1) Phloem parenchyma cells with high carbohydrate levels can synthesize large quantities of terpenes and other compounds in response to beetle attack. Monoterpene constituents are converted by the beetle or its fungal symbionts to *trans*-verbenol and other aggregation pheromones, which attract more beetles into areas of high carbohydrate concentrations. For example, Raffa and Berryman (1983b) have demonstrated greater beetle landing rates on trees that are actively secreting defensive chemicals. (2) After alighting on a tree in response to pheromone attraction, beetles preferentially bore into phloem with high carbohydrate concentrations. For example, a polar compound in the methanol extract of lodgepole pine phloem seems to act as both a feeding incitant and stimulant (Raffa and Berryman 1982). (3) The association between carbohydrates and beetle attack density is coincidental and other variables associated with girdling are involved. These may include the accumulation of feeding deterrents or repellents in tissues isolated from the upper bole regions or the accumulation of water as a result of root pressure in tissue close to the ground below the girdle.

The last hypothesis (3) is supported by at least two observations from our experiments. First, carbohydrate levels were similar below and above the girdle in the 1/2-girdled trees even though attack densities were significantly greater above the girdle (Table 1). Second, in the only tree that was killed by beetles in this experiment, the beetles showed extreme reluctance to bore into tissues isolated from the upper bole but open to the roots. Beetles in this area never bored galleries longer than 2 cm, whereas galleries >30 cm were common in the other 3 areas (Table 2, killed tree). In addition, no larvae hatched in this region (bottom open). These observations suggest that factors associated with the physiological status of the girdled lower bole may inhibit both activity and development and should be examined more fully.

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