

PARTIAL CAMBIAL MORTALITY IN HIGH-ELEVATION *PINUS ARISTATA* (PINACEAE)¹

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Partial cambial mortality is a growth form that is characteristic of *Pinus aristata* trees. To better elucidate their cambial death pattern, tree size and aspect of cambial death data were gathered from three *Pinus aristata* forests in central Colorado, USA. Stripping frequency tended to be higher for larger diameter classes. Partial cambial mortality exhibits significant directionality within each stand. Furthermore, cambial death was measured to be most frequent on the wind-exposed side of stripped trees in two of the three study sites and appeared to be at the third. Data presented here support the hypothesis that wind plays a role in the occurrence of partial cambial mortality in *Pinus aristata*. The mechanisms by which wind causes cambial mortality remain unclear.

Key words: bark stripping; bristlecone pine; Colorado; partial cambial mortality; *Pinus aristata*; Rocky Mountains; wind.

Partial cambial mortality of woody plants has been documented in Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) (Brunstein and Yamaguchi, 1992; Schauer, 1999), Great Basin bristlecone pine (*Pinus longaeva* Bailey) (Schulman, 1954; Westing, 1964; Currey, 1965; Wright and Mooney, 1965; Fritts, 1969; LaMarche, 1969; Beasley and Klemmedson, 1973, 1980), eastern white cedar (*Thuja occidentalis* L.) (Kelly, Cook, and Larson, 1992; Larson, Matthes-Sears, and Kelly, 1993), common juniper (*Juniperus communis* L.) (Ward, 1982), other juniper species (*Juniperus* spp.) (Larson et al., 1999), California chaparral shrubs (*Ceanothus* spp.) (Keeley, 1975), and manzanitas (*Arctostaphylos* spp.) (Davis, 1973). This phenomenon is characterized by either a strip of exposed wood and thus dead cambium or a strip of bark and thus live cambium extending up and down the stem of a woody plant. Individuals with constrained growth growing in harsh environments tend to exhibit partial cambial mortality more often than vigorous individuals in the central portion of the species' distribution (Schulman, 1954; Westing, 1964; Currey, 1965; Wright and Mooney, 1965; LaMarche, 1969; Beasley and Klemmedson, 1973, 1980; Ward, 1982; Briand et al., 1991; Brunstein and Yamaguchi, 1992; Kelly, Cook, and Larson, 1992; Larson et al., 1999).

Bark stripping is thought to be a consequence of an initial injury that is propagated between the crown and the roots via a radially sectoried architecture. Larson, Matthes-Sears, and Kelly (1993) submit that the presence of partial cambial mortality is evidence for sectoried radial architecture. Plants exhibiting sectoried radial architecture are divided into relatively discrete units among which very little fluid exchange occurs

(Waisel, Liphscitz, and Kuller, 1972; Watson, 1986; Vuorisalo and Hutchings, 1996). Under this stem design, if a unit of the plant loses vigor, other units of the plant cannot compensate with their resources because exchange is inhibited. Sectoriality has been documented in herbaceous plants (Moss and Gorham, 1953; as reviewed by Watson, 1986; Marshall, 1996; Murphy and Watson, 1996; Preston, 1998) and in woody plants (Moss and Gorham, 1953; Waisel, Liphscitz, and Kuller, 1972; Larson and Dickson, 1973; Barlow, 1979; Larson, Matthes-Sears, and Kelly, 1993; Larson, Doubt, and Matthes-Sears, 1994). Larson, Doubt, and Matthes-Sears (1994) demonstrated radially sectoried hydraulic pathways in *T. occidentalis* through the use of dyes but were unsure of any anatomical or physical barriers that might lead to such a phenomenon. Inter- and intraxylary cork formation or orientation of xylem elements may play a role in dividing woody plants into several independent physiological units (Moss and Gorham, 1953; Waisel, Liphscitz, and Kuller, 1972). The internal architecture seems important to the propagation of bark stripping, and external forces appear necessary for the initiation.

While there is no unifying theory for the cause of cambial dieback, there are several proposed hypotheses. Davis (1973) suggested that shade, fire, soil moisture stress, and extremes of temperature might contribute to the occurrence of partial cambial mortality in *Arctostaphylos* shrubs. LaMarche (1963, 1969) suggested, as possible mechanisms for the initiation of partial cambial mortality, abrasion of root tissue by soil particles, abrasion of shoot tissue by wind-borne particles, or repeated loss of tissue on the windward side of the shoot. Beasley and Klemmedson (1973) also suggested that cambial death might be initiated by damage to shoot tissues by wind. The most thorough investigation of partial cambial dieback has been conducted with *T. occidentalis*. *Thuja occidentalis* exhibits the strip-bark growth form only on cliff-face habitats on the Niagara Escarpment in southern Ontario (Kelly, Cook, and Larson, 1992). Kelly, Cook, and Larson (1992) documented directionality of cambial death on the trunk in *T. occidentalis*. For this species, the exposed wood and thus dead cambium was commonly found on the underside of cliff-face trees. Cambial death was attributed to exfoliation of rocks away from the root system, consequently exposing and killing a por-

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tion of the root system (Kelly, Cook, and Larson, 1992; Larson, Matthes-Sears, and Kelly, 1993). Here, as a consequence of the species' sectorial radial architecture, initial root death is thought to have led to the death of a portion of the stem and the crown tissue (Larson, Matthes-Sears, and Kelly, 1993; Larson, Doubt, and Matthes-Sears, 1994).

Partial cambial mortality also appears to be more common in older trees (Currey, 1965; LaMarche, 1969; Brunstein and Yamaguchi, 1992). Kelly, Cook, and Larson (1992) found a decrease in the percentage of the stem circumference covered by cambium with increasing tree age. Davis (1973) noted that large *Arctostaphylos* shrubs are covered by proportionally less live cambium than small shrubs. In *P. longaeva*, diameter and age were significantly correlated (Hiebert and Hamrick, 1984). While *P. aristata* seems to experience increased frequency of cambial death with age, it is unknown whether larger individuals exhibit the same trend as in *Arctostaphylos* shrubs.

What specific environmental factors are contributing to the occurrence of partial cambial mortality in *P. aristata*? This question may be addressed by looking at directionality of cambial death. If the cambium consistently dies on a specific side of trees within a forest, it is likely that a directional external factor is operating to yield that sidedness. This approach was successful for understanding the bark-stripping patterns of *T. occidentalis* (see above) and has been used in the past to illustrate other relationships between plant mortality and/or die-back and a specific environmental factor. Balsam fir (*Abies balsamea* (L.) Carr.) (Sprugel, 1976; Marchand, Goulet, and Harrington, 1986; Robertson, 1987; Boyce, 1988; Foster, 1988), southern beech (*Nothofagus betuloides* (Mirb.) Blume) (Puigdefábregas et al., 1999), and maritime pine (*Pinus pinaster* Ait.) (Campbell, 1998) have been shown to exhibit wave mortality and regeneration associated with wind. Krummholz and/or flagging of trees is directional and is generally associated with wind (Holroyd, 1970; Thomas, 1973; Hadley and Smith, 1983, 1986, 1989; Benedict, 1984; Wooldridge et al., 1996). Root damage has been shown to be directionally influenced by slope (LaMarche, 1963; Larson, Matthes-Sears, and Kelly, 1993) and wind (Rizzo and Harrington, 1988; Stokes, Fitter, and Coutts, 1995).

Patterns in the distribution of partial cambial mortality may provide insights into the important environmental factors that yield the growth form in *P. aristata*. In this study, we test the hypothesis that tree size affects the frequency of bark stripping in *P. aristata* and test for a directionality of stripping.

MATERIALS AND METHODS

Study sites—Three separate *P. aristata* stands were chosen for this study and were identified by the closest major landscape features. Each of these sites is on the Mount Evans massif, ~50 km west of Denver, Colorado, USA. Mount Evans is located in the Front Range of the Rocky Mountains (39°35' N, 105°38' W) and has an elevation of 4346 m. *Pinus aristata* at Goliath Peak and Lincoln Lake dominate the relatively high elevation forests extending up to treeline from 3300 to 3600 m and from 3530 to 3660 m, respectively. These two stands are classic bristlecone pine forests in that most individuals exhibit stunted and distorted growth forms. The Echo Lake site is a relatively low-elevation forest, extending from 3200 to 3350 m. The bristlecone pines of this stand are taller, thinner, and have a pole-forming growth habit relative to those individuals located at the two high-elevation sites. All three stands are on south-facing slopes and are dominated by *P. aristata*. Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), limber pine (*Pinus flexilis* James), lodgepole pine (*Pinus contorta* Dougl.), common juniper (*Juniperus communis* L.), and quaking aspen (*Pop-*

ulus tremuloides Michx.) are also present. A willow (*Salix* spp.) understory is prominent only at the Lincoln Lake site.

Partial cambial mortality—Cambial mortality was evaluated in terms of tree size and direction on a tree. During the 1997 and 1998 growing seasons, a total of 195 rectangular 100-m² plots were placed in the three stands. Each plot was 14.14 × 7.07 m with the long side oriented parallel to the slope, as recommended by Bormann (1953) and Brower, Zar, and von Ende (1989). While the first plot of each site was arbitrarily placed, all plots thereafter were systematically located 10 m from each other. Aspect and slope of the plot itself were measured at each plot. Within each plot, diameter at 1.37 m above the ground (dbh) was measured for all *P. aristata* trees. Each individual was classified as either nonstripped or stripped. Nonstripped indicates a tree that was totally covered in bark. Stripped trees were those exhibiting exposed wood that extended from at least one major dead branch in the canopy all the way down the trunk and presumably into the roots. The presence of spiral grain was also noted for each stripped individual. Other tree species were tallied only by number of individuals present.

The partial circumference of exposed wood and the median aspect of exposed wood were measured on stripped *P. aristata* individuals at 1.37 m above the ground. For each individual tree, the range of exposed wood in degrees could then be calculated. Trees exhibiting exposed wood in 72, five-degree-range categories were summed and plotted as polar histograms to illustrate the distribution of cambial death around the circumference of the trees. Individuals with a spiral grain were not included in any of the directional analyses as the direction of exposed wood depended on both the height of measurement and the degree of spiraling.

Meteorological towers—A 10-m meteorological tower that was erected near the Echo Lake study site as well as a second, 3-m, tower that was erected on the Goliath Peak site were used to monitor within stand climatic variables. Anemometer/wind direction sets (Wind Sentry, R. M. Young, Traverse City, Michigan, USA) were used to measure wind speed and direction every minute. Mean wind speed and unit mean vector wind direction were calculated every hour and stored on dataloggers (CR10, Campbell Scientific, Logan, Utah, USA). Data for July 1998 through February 1999 are reported here.

Statistical analyses—Chi-square tests were conducted on the distribution of exposed wood around the trunk of a tree within each site (Batschelet, 1981), with null hypotheses that all aspect categories are equal in terms of number of trees exhibiting cambial death. Rejection of a null hypothesis would indicate that cambial death favors a certain direction on the trunk. Rayleigh tests for randomness were also conducted on the distribution of exposed wood around the trunk of a tree within each site (Batschelet, 1981), with null hypotheses that data are distributed randomly among aspect categories. Both the chi-square and Rayleigh test give a good indication as to whether there is statistical evidence of directionality (Batschelet, 1981).

Descriptive circular statistics were conducted on the direction of exposed wood to determine the unit mean vector direction (Batschelet, 1981). The length of this vector (*r*) is a measure of dispersion. It is calculated for a unit circle and thus ranges from 0 to 1. The farther it extends from the origin, the more concentrated the data are in that direction. This vector was scaled up from the unit circle vector by multiplying it by the maximum number of individuals in a five-degree category for each site's data set. The vector length for the mean direction of exposed wood must be corrected because those data are categorical (72 5° classes) (Batschelet, 1981). When data are concentrated in more than one direction a mean angle of the entire data set may not be biologically informative and thus can be arbitrarily divided into multiple data sets (Batschelet, 1981). Division of the distribution can evoke an increase in the vector magnitude because the calculation assumes a 360° distribution, and the now divided data set contains a fraction of the possible 360°. Inflated vector lengths can be multiplied by the proportion of individuals in their respective distribution. With this correction, the length of the vectors is not likely to be an artifact of dividing the data set into two distributions and can be compared to the vector lengths at other sites. Angular deviations were also calculated to further characterize the variation of those data.

TABLE 1. Attributes of the three sites used in this study. Forest density is the average number of trees per plot at each site. Mean density, number sampled, number stripped, and number spiraled all refer to *P. aristata*. All measures include individuals above 1.37 m tall. Number spiraled indicates the number of stripped trees possessing the spiral grain growth form.

Study site	Elevation range (m)	Number of plots	Mean slope (°)	Forest density (trees/100 m ²)	Mean density (trees/100 m ²)	Number sampled	Number stripped	Number spiraled
Echo Lake	3200–3350	23	26	29	18	404	31	5
Goliath Peak	3300–3600	111	21	7	4	420	126	44
Lincoln Lake	3530–3660	61	22	3	2	129	43	9

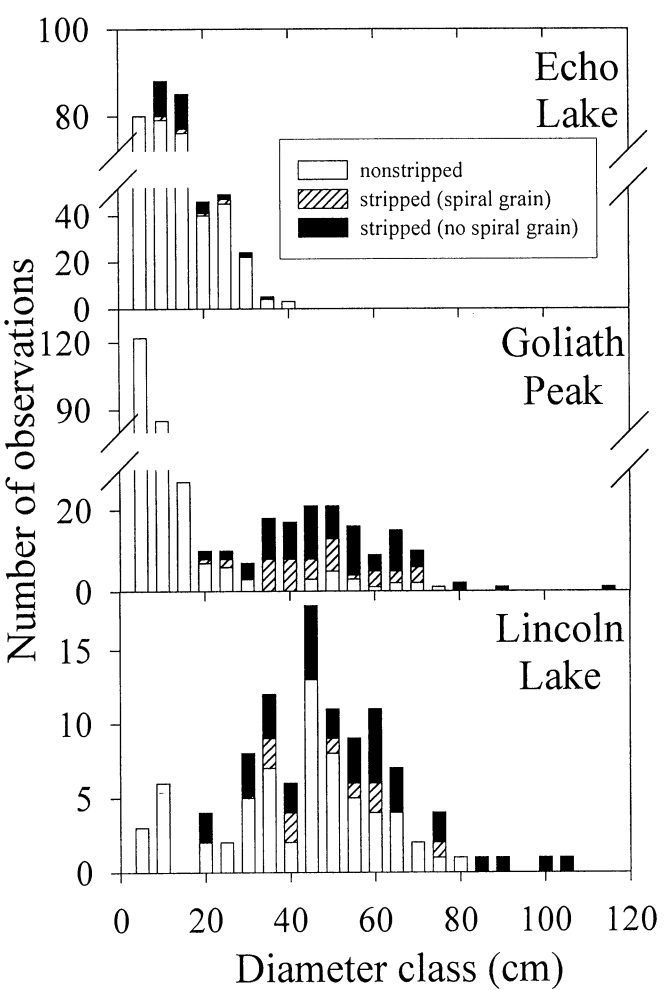


Fig. 1. Stacked histograms for the three study sites showing the number of nonstripped and stripped *P. aristata* present in 5-cm dbh categories. The stripped population is divided into two groups, those individuals with spiral grain and those individuals without.

RESULTS

Partial cambial mortality—Table 1 summarizes site level tree variables. Relative to Echo Lake, the density of trees is sparse at Goliath Peak and Lincoln Lake (Table 1). The percentage of stripped trees is markedly higher at these two low-density, upper-elevation sites (30 and 33%, respectively) relative to the lower elevation Echo Lake site (8%). All three sites possessed trees with no stripping in the smallest diameter classes (Fig. 1). The occurrence of exposed wood increases with tree size. No individuals over 80 cm dbh were totally covered in bark. Goliath Peak had a large number of individuals under 20 cm dbh that were nonstripped relative to the number of individuals in these size classes at the Lincoln Lake site. Stripped individuals dominated all of the middle size classes in the Goliath Peak stand. While the number of stripped trees increased with size at Lincoln Lake, nonstripped individuals were present until just above 75 cm dbh.

Significant directionality of the partial cambial dieback was evident at each site (Echo Lake $\chi^2 = 119.2$, $df = 71$, $P < 0.001$; Goliath Peak $\chi^2 = 349.1$, $df = 71$, $P \ll 0.001$; Lincoln Lake $\chi^2 = 136.1$, $df = 71$, $P < 0.001$). The mean directions, $\pm$ one angular deviation, of exposed wood for Goliath Peak

and Lincoln Lake are southwest ($227^\circ \pm 71^\circ$) and west southwest ($268^\circ \pm 71^\circ$), respectively (Fig. 2). The Rayleigh test for Goliath Peak and Lincoln Lake also indicated significant directionality ($r_{\text{stat}} = 0.242$, $N = 72$, $P = 0.032$; $r_{\text{stat}} = 0.243$, $N = 72$, $P = 0.032$, respectively). At the Echo Lake site, initial inspection of the data showed a bimodal distribution, thus two mean angles were calculated (Fig. 2). The mean angles were calculated by separating the individual distribution into two separate distributions and the division boundaries were arbitrarily selected (Batschelet, 1981) as 1 to 180° and 181 to 360° . The mean directions, $\pm$ one angular deviation, for the Echo Lake data set are southeast ($105^\circ \pm 42^\circ$) and west southwest ($253^\circ \pm 41^\circ$) (Fig. 2). The Rayleigh test for each of these distributions indicates significant directionality ($r_{\text{stat}} = 0.436$, $N = 36$, $P < 0.001$; $r_{\text{stat}} = 0.300$, $N = 36$, $P = 0.042$, respectively).

Arrows extending from the origin of each polar plot (Fig. 2) represent mean vectors. The length of each vector is inversely related to the dispersion of the data in that the longer the vector, the more nonuniformly distributed (directional) the data are (Batschelet, 1981). Both distributions of Echo Lake exhibited longer vectors relative to Goliath Peak and Lincoln Lake.

Environmental factors—Each of the sites exhibited a southern aspect; mean aspects were Echo Lake— 201° , Goliath Peak— 142° , and Lincoln Lake— 196° (Figs. 3c, 4c, 5b). Linear regression analyses conducted with average median-exposed-wood-direction within a 100-m² plot vs. plot aspect indicated no relationship in Echo Lake ($P = 0.2$, $R^2 = 0.15$), Goliath Peak ($P = 0.4$, $R^2 = 0.02$), or Lincoln Lake ($P = 0.3$, $R^2 = 0.05$).

Wind direction exhibited a bimodal distribution at both the Echo Lake and Goliath Peak towers (Figs. 3b, 4b). Wind direction was most commonly out of the west and to a lesser extent out of the east at the Echo Lake site (Fig. 3b). At the Goliath Peak tower, wind direction was commonly out of both the west and southeast (Fig. 4b). Westerly winds exhibited the fastest wind speed at both towers (Figs. 3b, 4b). High-speed westerly winds were most common in the winter months, whereas the easterly and southeasterly winds were most common in the summer months (data not differentiated in figs.). Partial cambial dieback was more frequent on wind-exposed sides of the trees at each of our sites (Figs. 3–5).

DISCUSSION

Data presented here suggest that *P. aristata*, at all sites, is more likely to experience cambial death with increases in tree diameter (Fig. 1). This trend is similar to that found in *Arc-tostaphylos* shrubs (Davis, 1973). Beasley and Klemmedson (1980) hypothesized that the strip-bark growth form was related to tree vigor. Among trees of similar size but increasing age, growth parameters remained constant for *P. longaeva* (Connor and Lanner, 1989), but we know that growth decreases with increasing tree size in *P. aristata* (Schoettle, 1994). Therefore, tree size may contribute to a decline in vigor for *P. aristata* trees (Schoettle, 1994). As a result, our observed relationship between stripping and tree size is consistent with the hypothesis of Beasley and Klemmedson (1980).

Partial cambial mortality of *P. aristata* exhibits significant directionality in the three sites studied (Fig. 2). The directionality of partial cambial mortality of *P. aristata* was very con-

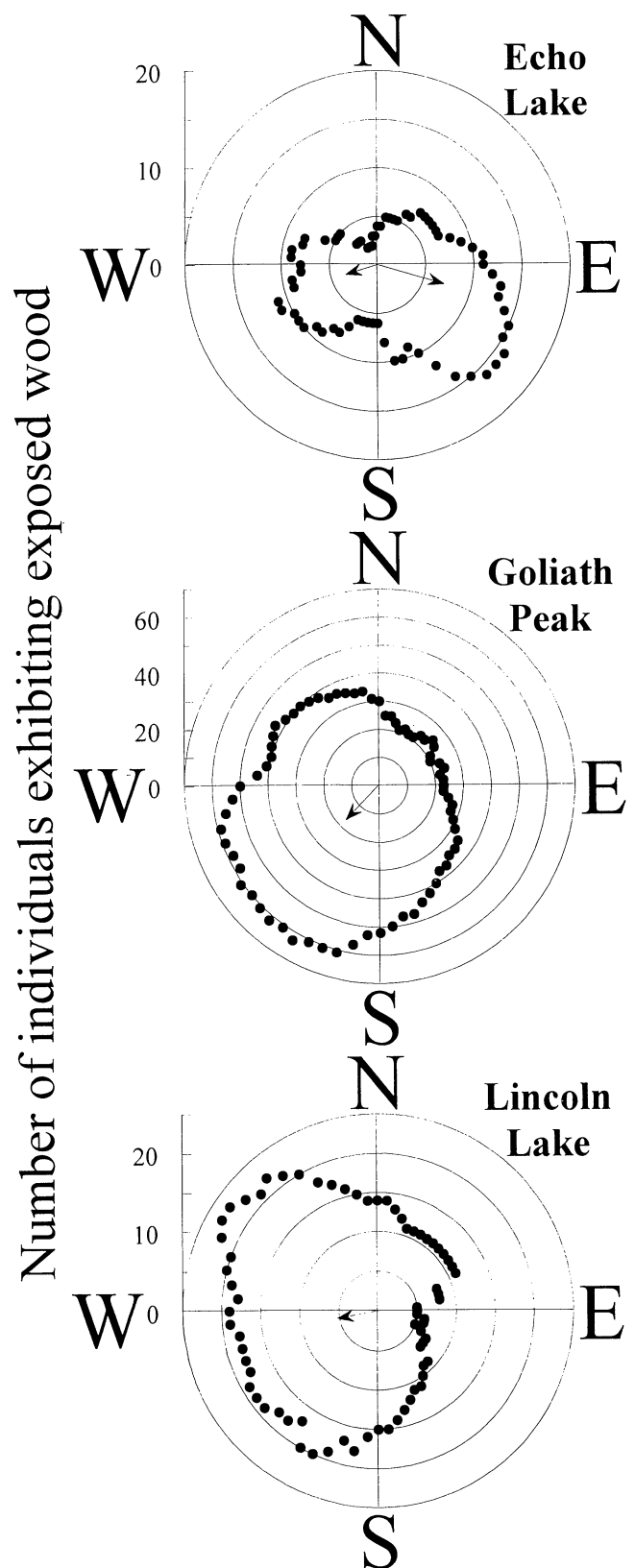


Fig. 2. Polar histograms for all three study sites with number of individuals exhibiting exposed wood on the radial axis and compass direction on the angular axis. Individual data points are five-degree-range categories. Arrows indicate scaled-up unit mean vector directions. Echo Lake, $N = 26$; Goliath Peak, $N = 82$; Lincoln Lake, $N = 34$.

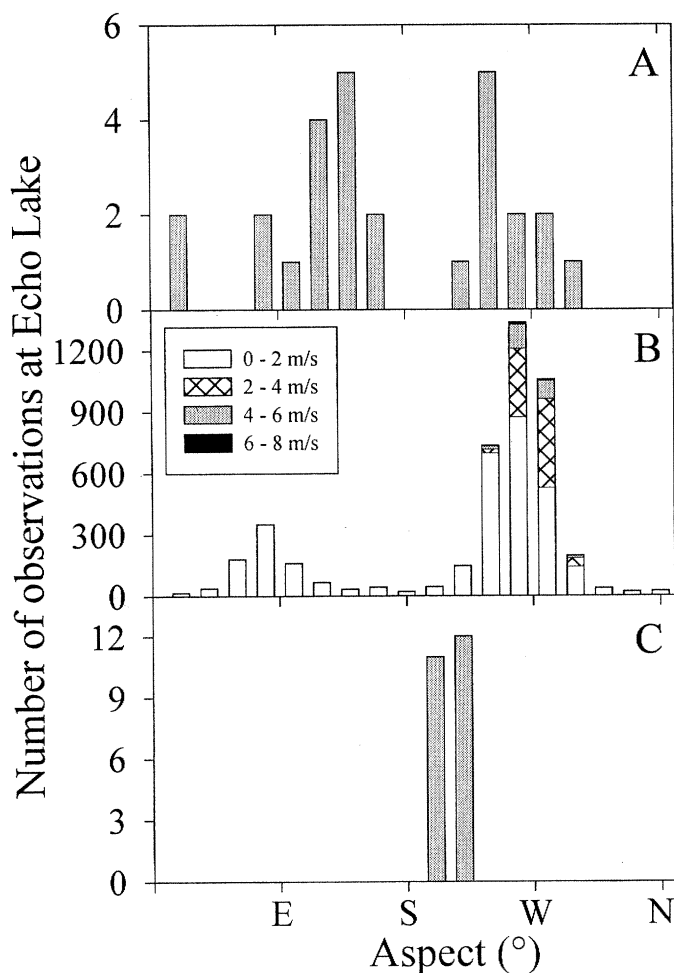


Fig. 3. Histograms for Echo Lake with compass direction divided into 20° range categories on the x-axes and (A) number of trees exhibiting exposed wood, (B) number of hours that wind direction and speed were in that category, and (C) number of 100-m² plots on the y-axes.

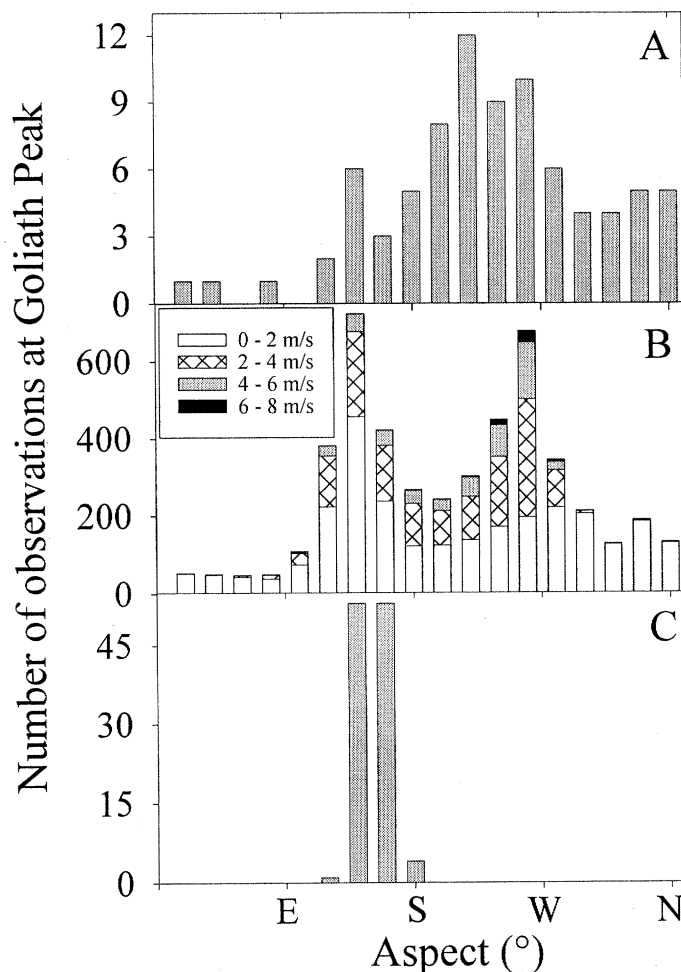


Fig. 4. Histograms for Goliath Peak with compass direction divided into 20° range categories on the x-axes and (A) number of trees exhibiting exposed wood, (B) number of hours that wind direction and speed were in that category, and (C) number of 100 m² plots on the y-axes.

sistent among trees within a site yet differed among sites. These data sets excluded spiral-grained trees as the direction of cambial death on those individuals varied with height of direction measurement and degree of spiraling. Perhaps these spiral-grained individuals could be used to resolve where on the tree damage is occurring by measuring direction of cambial death at different heights. The height where cambial death directionality converges is likely to be the location of tissue damage. The presence of directionality (on nonspiral-grained trees) suggests an external factor that also has directionality is operating to yield cambial death. Environmental factors that have a direction across these sites include solar radiation, aspect and slope of the terrain, and wind.

Sun scald and repeated freeze-thaw cycles have been shown to cause cambial death in other species (Kozlowski, Kramer, and Pallardy, 1991). Afternoon sun could be causing sun scalding as evident from the southwest or west cambial death directionality data collected from all three study sites (Fig. 2). The easterly stripping direction at Echo Lake is inconsistent with afternoon sun influence (Fig. 2). If sun scalding were the primary factor yielding partial cambial mortality, it seems that all sites of *P. aristata* would have the same stripping direction.

Partial cambial mortality was shown to be associated with slope for *T. occidentalis* by Kelly, Cook, and Larson (1992), who documented increased frequency of cambial death on the underside of the trunk. LaMarche (1968) also provided evidence that cambial death in *P. longaeva* could be related to slope through a consistent abrasion of root bark by mobile angular soil particles. The substrates studied by LaMarche (1968) were mobile enough to effectively exclude herbaceous plants and shrubs by burying and overturning them. While the moderate slope angles observed here (Table 1) are in the range that LaMarche (1968) observed (albeit at the lower extremity), the mobility of substrate appears to be reduced relative to those studied by LaMarche (1968) as indicated by the presence of an herbaceous and shrub understory. If partial cambial mortality was the result of substrate movement in a downslope direction, one might expect aspect of the slope to be related to the direction of exposed wood. LaMarche (1968) did not test for any relationship between the directionality of root abrasion and bark stripping. The lack of coincidence between slope aspect and stripping for *P. aristata* at our sites (Figs. 3–5) and the moderate slope angles at our sites suggest that root

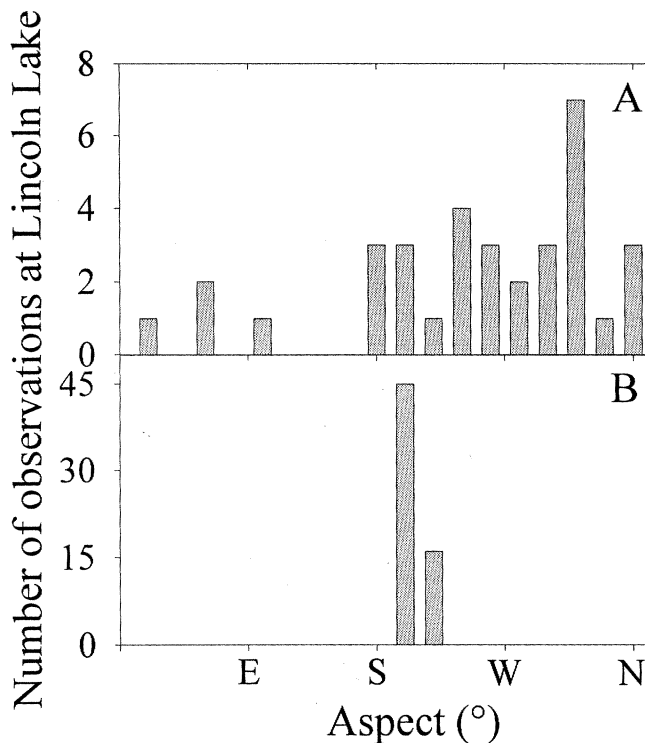


Fig. 5. Stacked histograms for Lincoln Lake with compass direction divided into 20° range categories on the x-axes and (A) number of trees exhibiting exposed wood and (B) number of 100-m² plots on the y-axes.

exposure is unlikely to be the primary injury causing cambial dieback for this species at these sites.

Our data are consistent with LaMarche's (1969) hypothesis in that cambial death is most frequent on the windward side of trees. It is interesting that both the direction of exposed wood and wind direction exhibited bimodal distributions at the Echo Lake site. The west-southwest directions of cambial death and wind direction exhibited match each other closely, but the easterly distribution of stripping and wind do not match up as well (Figs. 2, 3). This discrepancy may be explained by the location of the Echo Lake meteorological tower in relation to the *P. aristata* stand. That is, topography may be changing the east-northeast wind direction at the tower site to a southeast wind direction at the bristlecone pine stand. Wind direction would then correspond to the east-southeast bole direction that exhibits high frequency of exposed wood at the Echo Lake site (Figs. 2, 3). In mountainous or hilly terrain, wind direction can be drastically different between sites as little as 30 m apart (Allstott, Bashkin, and Baron, 1999). Trees at the Goliath Peak site also appear to exhibit the greatest frequency of cambial death on the windward side (Figs. 2, 4). While wind direction was not directly measured at the Lincoln Lake site, the shape of krummholz mats and flagging of upright trees suggest a westerly wind direction. Tree deformation (krummholz or flagging) has been shown to be a useful tool for indicating prevailing wind direction (Holroyd, 1970; Thomas, 1973; Boyce, 1988; Wooldridge et al., 1996). The side of the trunk that most commonly exhibited exposed wood at Lincoln Lake was the west (Figs. 2, 5).

The similarity between the directionality of stripping for *P. aristata* and wind could be coincidental, but it does prompt

questions concerning mechanisms through which wind is potentially acting to yield partial cambial mortality. Wind is an environmental factor that can sculpt vegetation from the leaf to the stand level (Grace, 1977; Coutts and Grace, 1995; Ennos, 1997), especially at high-elevation locations such as those studied here. Wind can act as either an acute or a chronic stress (Telewski, 1995), and, furthermore, chronic wind may have a greater effect on the ecology of forests than the more acute winds of severe storms (Ennos, 1997). Wind can cause stem damage as a result of wind-blown particulate abrasion (as hypothesized by LaMarche, 1969), suggesting the origin of the partial cambial dieback may be injury to the stem.

Root damage on the windward side of trees can result from severe tree swaying (Rizzo and Harrington, 1988), suggesting the origin of the partial cambial dieback in *P. aristata* may be injury to the roots. Root death, whether caused by wind as suggested here or exposure as suggested for *T. occidentalis* (Kelly, Cook, and Larson, 1992; Larson, Matthes-Sears, and Kelly, 1993) or *P. longaeva* (LaMarche, 1963, 1968), could restrict water flow and result in partial stem and crown death for a tree with a hydraulically sectorial radial architecture. Alternatively, winter wind can cause crown damage as a result of leaf and shoot abrasion by wind-blown ice crystals (Hadley and Smith, 1983, 1986, 1989), suggesting the origin of partial cambial dieback may be injury to the crown. Summertime winds can reduce the photosynthetic performance (Cordero, 1999) or damage the leaf surface and cause increased water use in conifer leaves (van Gardingen, Grace, and Jeffree, 1991), which could lead to premature leaf senescence. For the injury or death of a portion of the crown to lead to partial cambial dieback down the stem to the roots requires an assumption of the sectoriality of carbon flow. Past research on stem sectoriality has focused on it as a characteristic of water flow in the xylem, and it is unclear whether sectoriality also applies to carbon flow in the phloem.

It appears unlikely that there is one mechanism that leads to the strip-barked growth form among species or habitats. Directionality of cambial dieback is essential when attempting to assign a causal directional external factor. While any number of external factors could play a role in cambial death of a single tree, wind is likely to be an external environmental factor contributing to partial cambial mortality in *P. aristata* forests. How wind acts on *P. aristata* to yield partial cambial mortality is not clear. Experiments to elucidate cambial stripping mechanisms may also yield a better understanding of radial limitations of water and carbon transport in woody species.

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