Relationship between phloem thickness and lodgepole pine growth characteristics

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Received February 20, 1985[1]

Accepted May 17, 1985

SHRIMPTON, D. M., and A. J. THOMSON. 1985. Relationship between phloem thickness and lodgepole pine growth characteristics. Can. J. For. Res. **15**: 1004–1008.

Depth of the phloem (inner bark) layers in lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) is a factor in the development of outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.). Five lodgepole pine stands in the interior of British Columbia spanning the ages affected by this beetle (47–147 years) were studied. Relationships were determined between thickness of the phloem layer and radial and area increments over various periods of time, as well as DBH. The thickness of the phloem layer declined over the age spanned in this study. The best predictor of phloem thickness was the basal area increment in the 6–10 years before sampling. Diameter was a poor predictor of phloem thickness.

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L'épaisseur du liber du pin tordu (*Pinus contorta* Dougl. var. *latifolia* Engelm.) influe sur les proliférations du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopk.). Cinq peuplements de pin tordu de l'intérieur de la Colombie-Britannique, dans la gamme des âges (47–147 ans) attaqués par ce dendroctone ont été étudiés. On a déterminé les relations entre l'épaisseur du liber et un certain nombre de caractéristiques des arbres. L'épaisseur du liber diminuait selon l'âge. La meilleure façon de prédire cette épaisseur était l'accroissement de la surface terrière au cours des 6–10 années avant l'échantillonnage. Le diamètre était un mauvais indicateur.

[Traduit par le journal]

[1]Revised manuscript received May 13, 1985.

Introduction

The phloem layer of conifers is produced by the vascular cambium and the greater the number of fusiform cells in the cambial zone the greater the radial production of both xylem and phloem. In lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), only the current year's sieve elements are functional. As additional phloem layers are formed annually, the older layers are forced outward; they gradually become compressed and finally are lost through the formation of phellogen (cork cambium) (Srivastava 1963). In lodgepole pine, the average period of phloem retention was 21.7 years with three elements contributing to the phloem thickness: period of retention, increment, and compression, in decreasing order of importance (Cabrera 1978).

Mountain pine beetle is one of the major causes of death for lodgepole pine in western North America (Wellner 1978). Thickness of the phloem layer has been identified as having an influence upon the development of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) outbreaks because the phloem layer is the major source of nutrition for these insects (Amman 1978). The most frequently used parameters in exploring the tree – mountain pine beetle relationship are DBH and phloem thickness. Age is used to establish a threshold (Amman 1978). Two previous studies of phloem thickness in lodgepole pine suggest that other things being equal, larger diameter trees have a thicker phloem layer (Cole 1973; Hawksworth *et al.* 1983).

Shrimpton (1978) found that phloem thickness reached a maximum and then declined with advancing tree age. Cole (1973) presented five equations for estimating phloem thickness using different combinations of variables. Depending on the equation used, age had either a positive or negative coefficient; thus, the role of age in determining phloem thickness is not clear. Since these relationships were obtained by grouping trees sampled from a large area, a bias may exist where some trees are suppressed trees from plots of a large average diameter and others are dominant trees of plots with small average diameters. In addition, similar-sized trees within plots may have different growth rates (Shrimpton and Thomson 1983). In the present study, we clarified the role of age by examining the relationship of phloem thickness to tree characteristics using a method of analysis that avoided the above bias, i.e., by analyzing each stand separately.

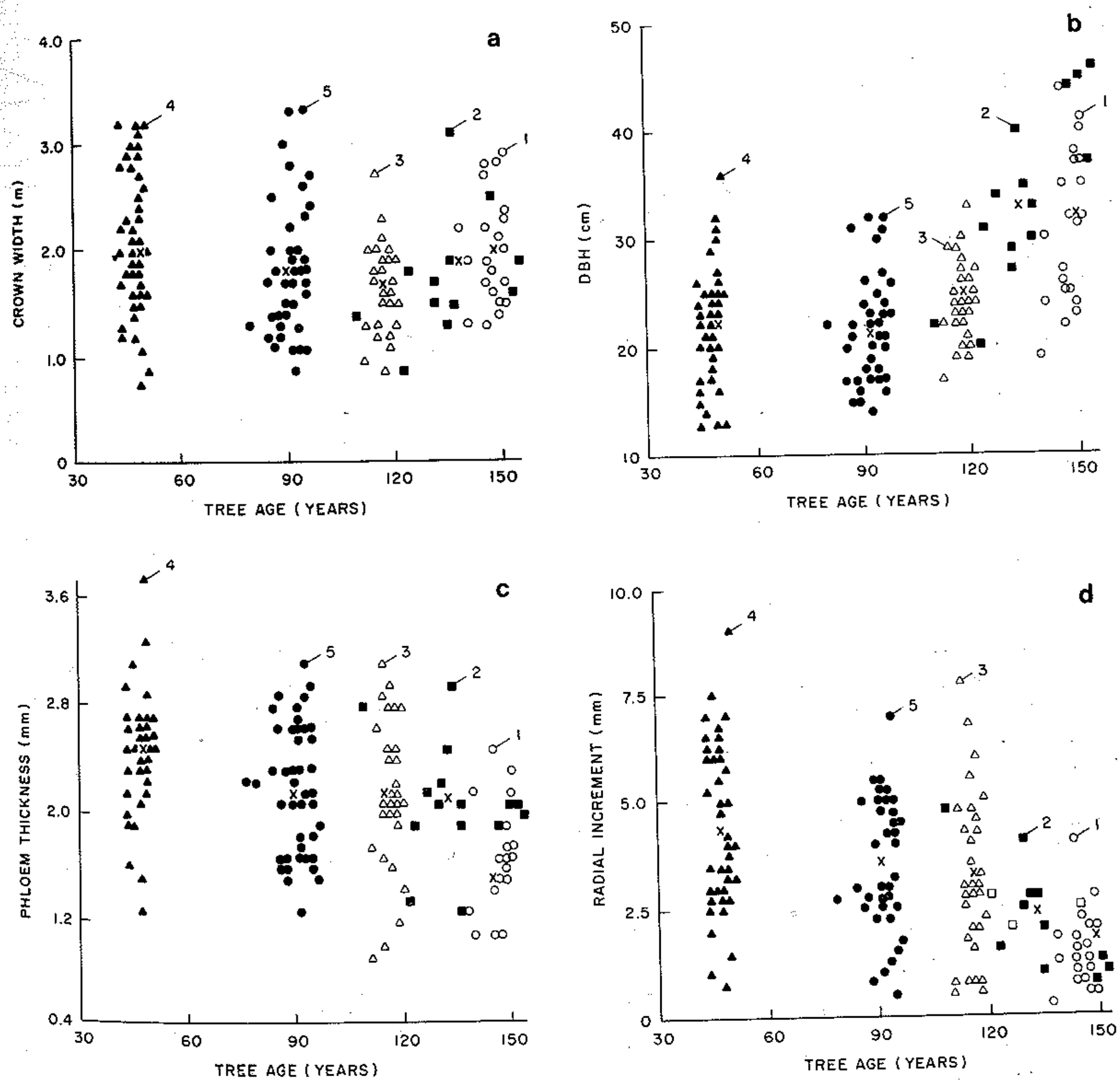

FIG. 1. The relationship for each plot (1–5) between tree age and (*a*) crown width, (*b*) DBH, (*c*) phloem thickness, and (*d*) growth rate. The average value for each plot is indicated by an X.

TABLE 1. Physical descriptions and stand parameters for the five plots

Plot No.	Site index*	% lodgepole	Stems/ha	Average age (years)	Average height (m)	Diameter (cm)
1	27.3	65	1060	147	27.9	30.8
2	26.9	70	900	135	27.4	33.7
3	26.0	95	1000	117	26.3	24.3
4	27.5	97	1140	47	21.1	22.7
5	24.5	80	1280	90	24.1	21.5

*Metres at 100 years.

Methods

The study area was about 30 km south of Merritt, B.C. Plot locations were selected on the basis of uniform ground cover and similar density of stems. Increment cores were removed from a few trees to estimate stand age before each plot was established. A plot 20 × 25 m was established in each of five locations. All plots were on gentle slopes with southern aspect at elevations between 1000 and 1100 m and in the pine grass type, pachystima group. In general, as the stands increased in age the proportion of coniferous species other than pine increased. Percentage of lodgepole pine, stand density, site index, age, and height are given in Table 1. The diameter at 1.3 m and crown width were measured for all trees greater than 12.5 cm diameter. A numeric code was assigned to record crown length and fullness, bark type, one-sided or forked crowns, and the presence of top or stem damage. Two increment cores, one in the direction of the slope and the other at 90° to the slope, were collected from each tree. Two 1-cm^2 phloem samples were cut from each tree about 2 cm above each increment core. Thickness of the phloem layer, defined for this study as the live tissue external to the cambium, which was active at the time of sampling, was measured immediately with calipers.

The height of five dominant and codominant trees was measured on each plot. An additional two increment cores were removed from these trees at one half of the tree height from the same aspects as the lower samples; phloem thickness was also measured at these positions. In the laboratory, age at breast height was measured from the cores. The 10 most recent annual growth increments were measured on each core. For the purposes of the analysis, increments were totalled by 5-year periods and the measurements on the two cores were averaged.

Site indices were calculated using published coefficients for lodgepole pine (Anonymous 1983). Regression analysis was used to determine if the slopes of the relationships differed significantly among plots. Residuals were related to the numeric codes describing tree crown and bark characteristics.

Results

Analysis of variance was used to determine that the average phloem thickness at breast height (1.3 m) was not significantly different from the average phloem thickness at half the tree height on all plots. For these plots, half of the tree height was just below the base of the live crown. All relationships were therefore calculated for phloem thickness at breast height.

Figure 1 illustrates a high within-plot variability in tree characteristics with age. While the plot averages indicated certain trends, such as a decline in radial increment and an increase in DBH with age, these trends were not significant because of the high variability of the data. Within plot 2, there is evidence of a relationship of DBH to age, but there is no relationship of phloem thickness to DBH or age.

The average radial growth in the last 5 years was compared with that of the preceding 5 years to detect if the growth rate was increasing or decreasing on each plot. Radial growth rates on plots 1, 2, and 4 had declined by 12.2, 9.0, and 13.6%, respectively. Growth had not changed significantly on plot 3

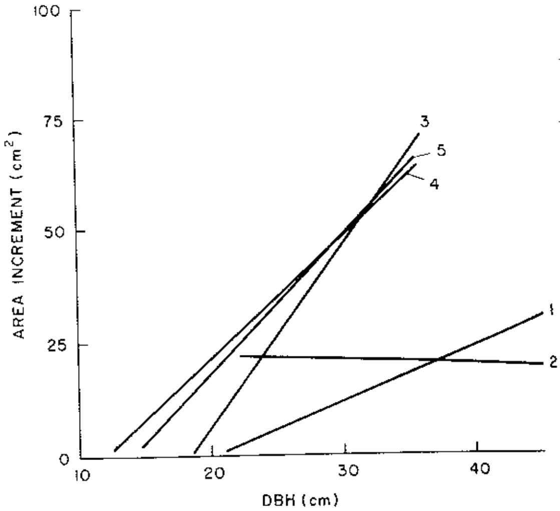

FIG. 2. Relationship of basal area increment in the last 5 years of growth (BAI1−5) to DBH for each plot (1−5).

and on plot 5 the growth rate had increased by 17.6%. Growth rates measured on increments parallel to the direction of the slope were not significantly different from those measured at 90° to the slope except for the oldest plot where the growth rate was greater in the direction of the slope. On all plots, phloem thickness was similar along and across the slopes.

As potential predictors of phloem thickness at 1.3 m, five variables were studied: DBH, the last 5 year's radial increment (RI1−5) and basal area increment (BAI1−5), basal area increment in the past 10 years (BAI1−10), and basal area increment in years 6−10 (BAI6−10). These values are intercorrelated, but relationships between growth rates and diameter are different in younger plots than older plots (e.g., Fig. 2). The relationships of phloem thickness to these growth characteristics were linear as indicated in Fig. 3; thus, linear regression was used to characterize relationships. Plots 1 and 2, which were the oldest with the greatest basal area and average diameter, had lower x-intercepts than the three younger plots (Fig. 4). On plots 2, 4, and 5 the best predictor of phloem thickness was BAI6−10 (Table 2). RI1−5 and DBH were the best predictors in plots 3 and 1, respectively. In plot 1 BAI6−10 was a better predictor than RI1−5. Using diameter or age in addition to any period of radial or area increment in a multiple regression did not significantly improve the prediction of phloem thickness. Combining data from all plots RI1−5 had the highest correlation coefficient, but all other predictors except DBH performed almost as well.

Given the linear relationship between phloem thickness and growth rates (e.g., Figs. 3 and 4), the relationship of residuals to other measures was examined. A number of interesti

TABLE 2. Correlation coefficient (r) of relationships of diameter (D) radial increment (RI1−5) and basal area increments (BAI1−5, BAI6−10, and BAI1−10) to phloem thickness (P)

Plot No.	n	P vs. RI1−5	P vs. BAI1−5	P vs. BAI6−10	P vs. D	P vs. BAI1−10
1	21	0.3871	0.5217	0.5500	0.6603*	0.5442
2	15	0.4384	0.6903	0.7672*	0.0533	0.7415
3	34	0.8128*	0.7808	0.6688	0.6953	0.7372
4	56	0.4076	0.5027	0.5623*	0.4233	0.5384
5	49	0.6186	0.6636	0.6971*	0.5204	0.6829
All	175	0.6688*	0.6544	0.6592	0.1085	0.6670

*Highest correlation coefficient for the plot.

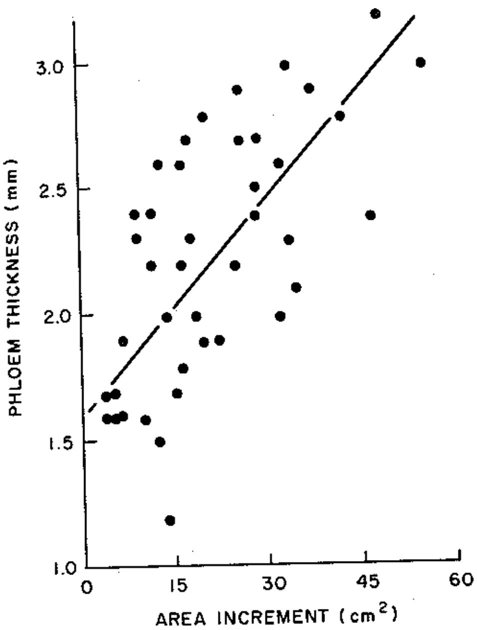

FIG. 3. Average phloem thickness for all trees in plot 5 in relation to their basal area increment in the 6−10 years preceding sampling (BAI6−10).

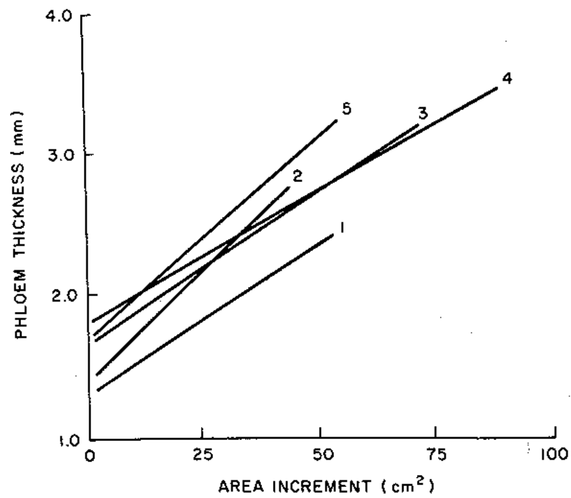

FIG. 4. Relationship between phloem thickness and basal area increment in the 6−10 years preceding sampling (BAI6−10) for each plot (1−5).

trends were observed even though there were insufficient data to evaluate the relationships statistically. Trees with exceptionally full crowns had thicker phloem than expected and trees with sparse crowns had thinner phloem than expected. Trees whose crowns were exceptionally large in circumference had thinner phloem than expected. Trees whose outer bark layer consisted of large scales tended to have thick phloem whereas trees with outer bark consisting of coarse plates had a thin phloem layer. Forked-topped trees had thinner phloem than expected on the basis of crown fullness. Phloem thickness was greater than the thickness predicted for a given growth increment when that increment was on a small-diameter tree. This effect was especially marked when radial growth was used as the predictor. The use of area increment reduced this effect. For the largest diameter stems, the measured phloem thickness was notably less than that predicted by their incremental growth. A few trees had a thick phloem layer and no relationship to measured tree characteristics could be detected. No relationship existed between site index and the increment − phloem thickness relationship.

Discussion

As a predictor of phloem thickness, the basal area increment in the 6−10 years prior to sampling was most reliable in individual plots. The basal area increment and radial increment in the last 5 years of growth also provided good predictive power, as did the basal area increment in the last 10 years of growth. However, diameter was a poor predictor of growth or phloem thickness in most situations. When the data from the different plots was combined, all independent variables except DBH provided similar predictive capability.

Age appears to exert an effect through its relationship with the effects of physiological maturity. As trees get to be very old, their growth rates and hence their phloem thickness will decline, although thick phloem may persist for many years after tree growth rates have culminated. It is therefore possible to have trees of large diameter which have phloem too thin to support a mountain pine beetle brood. Also, because phloem is long lived and its thickness is most related to the growth increment 6−10 years previously, situations can arise where tree growth and resistance to mountain pine beetle can be lowered by factors acting in the most recent years of growth (Shrimpton and Thomson 1983; Thomson and Shrimpton 1984) and yet the thickness of the phloem layer remain adequate for a mountain pine beetle brood.

Within each plot, all measured characteristics exhibited high variability in relation to tree age, which therefore has little predictive value. Also within each plot, there was often a high degree of correlation among the various growth characteristics measured, i.e., diameter, radial growth, and basal area increment in various periods. However, the actual relationships varied widely from plot to plot.

Cole (1973) used logarithmic transformations of phloem thickness and growth rate in developing a relationship between diameter and phloem thickness. However, in our study, no transformations were required to develop linear relationships on either a within-stand basis or for all stands combined. The failure of diameter alone to predict phloem thickness in specific situations may be as follows. Xylem and phloem have a common origin in the vascular cambium and the formation of these two tissues is related (Srivastava 1963). Xylem production in lodgepole pine, as measured by stem volume increment, increases with age, reaches a peak at a particular tree age, and then declines (Shrimpton and Thomson 1983). Therefore, similar phloem thickness at different diameters can occur if smaller trees in an increasing growth phase are compared with larger trees in the declining phase of growth.

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