

Coarse root elongation rate estimates for interior Douglas-fir

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Summary Accurate estimates of root growth rates are important for root system modeling, and the spread of root systems may be an important determinant of belowground site occupancy. Estimating root system growth rates is complicated because missing, discontinuous, and false annual growth rings make root cross sections difficult to age. These irregularities can occur even in roots of dominant conifers with rare or absent stem growth ring abnormalities. Incomplete rings were noted in the root growth rings of nine co-dominant interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) trees. Coarse root (> 1.0-cm diameter) elongation rates were estimated by fitting a geometric mean regression line to ring count and lateral distance data. In all nine roots examined, the geometric mean regression slope was well within the range of the 95% confidence interval for the ordinary least squares regression of lateral distance versus age, suggesting that measurement error may have been negligible. Coarse root elongation rates (which ranged from 2.8 to 15.3 cm year⁻¹ and averaged 7.4 cm year⁻¹) in the interior Douglas-fir trees studied were much lower than those reported by others. This discrepancy may be a result of limited soil water availability, soil heterogeneity (both soil water content and soil texture were highly variable across short distances) and fragmentation of belowground growing space.

Keywords: annual growth rings, geometric mean regression, incomplete rings, measurement error, *Pseudotsuga menziesii*, root growth.

Introduction

Root growth rings are not as well studied as stem growth rings for three main reasons. First, root growth rings are difficult to access compared with stem growth rings. Second, until recently, the importance of root growth (both radial and longitudinal) was deemed of minor importance compared with stem growth. However, changes in root elongation rate may be important for assessing the effects of certain silvicultural prescriptions, such as spacing and thinning on dry sites, where belowground site occupancy may be as important as aboveground growing space. Additionally, complex models of root growth are now being developed (e.g., Jourdan and Rey 1997), and these models generally require parameterization of root elongation rate.

Third, root growth rings can be discontinuous and are often hard to measure or count compared with shoot growth rings. Schulman (1945) studied root growth rings of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growing on dry sites in the American southwest, and occasionally found false rings, missing rings and discontinuous rings. Fayle (1975a, 1975b) made several studies of red pine (*Pinus resinosa* Ait.) root system growth and found incomplete or discontinuous rings along the entire length of the root. Close to the bole, growth irregularities were more common in the outer rings of older roots. In younger roots farther from the bole, growth irregularities increased in occurrence and extent with increasing distance from the trunk. This corresponded to a decrease in mean ring width with increasing distance from the trunk. On the other hand, Fayle (1975b) noted that false rings were common in the first 15 years of root growth, but were generally absent beyond 1 m from the stem. Reynolds (1983) found both false and incomplete rings in root cross sections and concluded that growth irregularities, in conjunction with tapering radial growth and small radial growth in young roots, make accurate ring counts difficult.

An additional source of error comes from using ring counts as a proxy for root age, because counts are by definition discrete. Thus, although there may be 10 rings in a root cross section, we do not know, without more detailed sectioning and stem analysis, whether that point was reached near the beginning or end of the season's elongation 10 years ago. This could be especially important in fast-growing roots, or when cross sections are taken at close intervals.

The effects of measurement error in root age on estimates of root growth rate can be assessed. If we assume that the lateral distance (y) of a root tip from the tree is a function of the age of the root (x), then the slope β_1 represents the elongation rate in m year⁻¹:

$$y = \beta_0 + \beta_1 x + \epsilon. \quad (1)$$

The mean elongation of the tip is $\beta_0 + \beta_1 x$, and variation around this mean is the same as the variation in ϵ . Because both missing and false rings may cause measurement error (δ) in x , we actually observe $x + \delta$. Ordinary least squares regression (y versus x) can result in downward-biased and inconsistent (Pindyck and Rubinfeld 1981, Neter et al. 1996) estimates of β_1 , even when the measurement error (δ) is not correlated

with the true x values. In this simplified case ($\text{cov}(x, \delta) = 0$), the bias of the least squares estimate of β_1 (as a percentage of β_1) is $1 - \lambda$, where (Draper 1992):

$$\lambda = \frac{\text{var}(x)}{\text{var}(x) + \text{var}(\delta)}. \quad (2)$$

As an example, consider five root sections, with true ages 100, 80, 60, 40, and 20 years. If the age of each disk is measured with $\delta \sim N(\mu = 0, \sigma = 5)$, and if $\text{cov}(x, \delta) = 0$, then the ordinary least squares regression estimate of β_1 will be biased downward by about 2.4% ($\text{var}(x) = 1000$, $\text{var}(\delta) = 25$, $\lambda = 0.976$). On the other hand if $\delta \sim N(\mu = 0, \sigma = 10)$, then the downward bias increases to 9.1%. However, the variance of δ is usually unknown and so λ cannot be calculated.

Therefore, λ cannot normally be used to correct for the bias in the estimated value of β_1 . Draper (1992) suggested that the geometric mean method was an appropriate procedure when measurements of variables x and y are associated with some error. The geometric mean estimate for β_1 is the geometric mean of the slope of the least squares fit of y versus x and the reciprocal of the slope of the least squares fit of x versus y :

$$\hat{\beta}_1 = \sqrt{\frac{\text{var}(y)}{\text{var}(x)}}. \quad (3)$$

The geometric mean slope estimate is intermediate between the x versus y and y versus x slope estimates. However, as Draper (1992) points out, the main problem with the geometric mean approach is that there is no straightforward method for estimating the confidence intervals for the geometric mean slope estimate.

The purpose of this research was to estimate elongation rates of coarse roots (i.e., > 1.0-cm diameter) of interior Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, and to compare ordinary least squares regression estimates of elongation rates with those obtained by the geometric mean approach.

Materials and methods

Research was conducted in the north-east corner of the British Columbia Ministry of Forests' Pothole Creek research site (49°54' N, 120°36' W, elevation 1210 m), near Merritt, British Columbia. The site is classified as a dry, cool variant of the interior Douglas-fir (IDFdk1) biogeoclimatic zone (Lloyd et al. 1990). The site is dominated by Douglas-fir, with occasional lodgepole pine (*Pinus contorta* Dougl.) and hybrid spruce (*Picea engelmannii* × *glauca*). The soils at Pothole are coarse-textured (sandy loams with 5–10% gravels and 10–30% cobbles) and poorly developed, and are classified as predominantly Orthic melanic brunisols or Eluviated eutric brunisols (C. Braybrook, Ministry of Forests, Victoria, British Columbia, unpublished data). Soils are generally mildly acidic to neutral, with pH values ranging from 5.7 to 6.8. The soils exhibit considerable spatial heterogeneity, with texture and

coarse fragment percentage varying widely over short distances.

Soil water potential was measured in both 1998 and 1999 from late spring to midsummer along a 45-m transect (David Simpson, British Columbia Ministry of Forests, personal communication). This transect may have been more mesic than the nearby root excavation site, but the data illustrate the spatial and temporal variability in soil water potential at Pothole Creek. Gypsum block probes (Delmhorst Instrument Co., Towaco, NJ), spaced at 3-m intervals, and a Soilmoisture Equipment Corp. (Goleta, CA) meter were used. From late May to early July, soil water potential was higher in 1999 than in 1998 (−0.073 versus −0.833 MPa). From early July to late August, soil water potential was similarly low in both study years (−1.61 MPa in 1998 and −1.63 MPa in 1999). The data indicated high temporal and spatial variability in soil water potential. For example, the coefficient of variation (CV) in mean soil water potential across all sampling dates (both years) was 121%. Soil water potential at individual sampling positions was not highly correlated over time in either 1998 ($r = 0.40$) or 1999 ($r = 0.35$). Measurements from adjacent sampling positions were better correlated in 1999 ($r = 0.12$) than in 1998 ($r = -0.03$), but in both cases the low correlation indicates tremendous spatial heterogeneity.

Root systems of four mature Douglas-fir trees were hydraulically excavated with a fire pump (Wajax Industries Ltd., Edmonton, Alberta, Canada) powered by an 18 hp engine (Briggs and Stratton Corp., Milwaukee, WI). These trees averaged 136 years old and 34 cm at breast height, and grew in a clump approximately 8 m × 5 m. Most excavation was done at relatively high water pressure, approximately 1100 kPa, in order to break apart the hard, cemented soil peds. Although this damaged many roots of less than 0.5-cm diameter, larger diameter roots, which were the focus of this study, were unharmed. Two or three roots (generally one larger diameter root and one smaller diameter root) from each tree were arbitrarily selected for study before complete excavation. The longest root excavated was about 13 m in length. Roots were followed to a diameter of approximately 1.0 cm.

Root cross sections, or disks, were cut every 50 cm along each root and were brought to the laboratory and aged in order to determine approximate rates of woody root elongation. Disks were oven-dried and sanded on a belt sander before ring counting with the aid of a dissection microscope. Every second disk was aged, except when rings were especially difficult to count, in which case all disks were aged. Because radial growth was frequently eccentric, rings were counted along the longest axis, where they were widest and easiest to read. Disks with very small rings were sanded by hand with fine sandpaper. If the rings could still not be read, disks were polished with levigated alumina and stained with a phloroglucinol solution (Graeme Berlyn, Yale Univ., personal communication, Fayle 1975a). Despite this preparation, some disks still could not be read, either because the rings were too fine, or because the center of the section was filled with hardened resin that completely obscured the rings.

Mean ring width was 0.64 mm in root sections taken close

to the bole, and decreased by approximately 0.03 mm for every meter of distance from the bole. Cross sections were thus more difficult to age the further they were from the bole. Many of the youngest disks could not be aged. In contrast, Reynolds (1983) suggested that, in some species, root ring analysis might only be suitable for the youngest roots.

Incomplete and irregular rings were observed; however, certain wide or narrow 'indicator years' of radial growth matched up well between sections from different roots, indicating that there were few, if any, missing rings. Based on the data obtained, it is concluded that the age counts were accurate to ± 5 years.

Results

The ring count data are illustrated in Figure 1. Root extension rates varied both between trees, and between roots on the same tree, as indicated by the regression slope estimates presented in Table 1. On average, roots grew at about 7.4 cm year^{-1} (geometric mean). The fastest- and slowest-growing roots both came from Tree 3: Root 3-B grew at a rate more than five times greater than Root 3-A. In general, root growth was more or less linear. The fit of all ordinary least squares regressions

(y versus x) was good, ranging from $R^2 = 0.93$ to 0.99 , with a mean $R^2 = 0.96$.

The difference between the geometric mean and ordinary least squares y versus x regression estimates of elongation rate averaged 1.9%, with a maximum of 3.4% (Root 2-B). The geometric mean elongation rate was always within one standard error of the ordinary least squares estimate. The difference between the two methods of estimating elongation rate was sufficiently small that, when plotted, the two regression lines were virtually identical. The ordinary least squares y versus x regression line is plotted in Figure 1.

Discussion

Measurement error was probably not a significant factor in the roots studied. In all cases, the geometric mean and ordinary least squares estimates of elongation rate were not significantly different. In other species where false rings or missing rings may be more common (e.g., paper birch, *Betula papyrifera* Marsh.), the geometric mean technique may be useful for reducing the downward bias of measurement error.

Fayle (1975a) observed that lateral extension more or less stopped by the end of the second decade of root growth in red

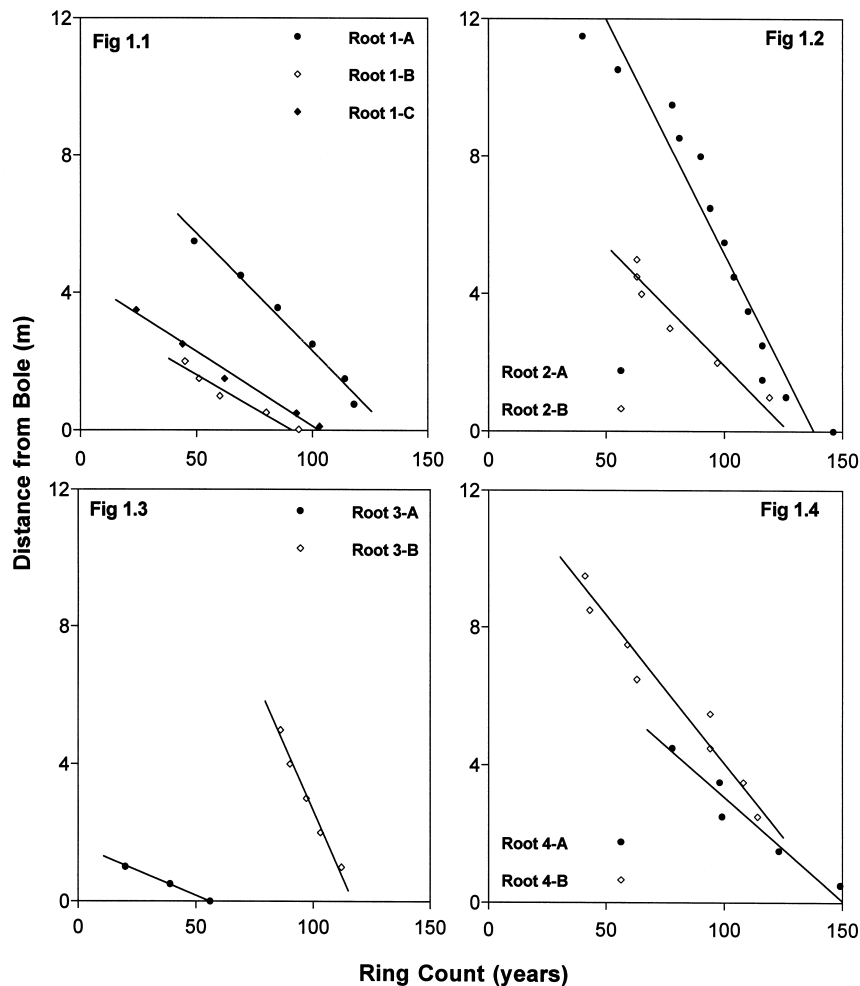


Figure 1. Root ring count (x) and lateral distance from trunk (y) data for four interior Douglas-fir trees. Best-fit lines are ordinary least squares regression lines of y versus x .

Table 1. Root elongation rates estimated by standard, reciprocal and geometric mean regression analyses.¹

Tree	Root	No. of disks measured	Root elongation rate (cm year ⁻¹ ± SE)			
			Standard	R ²	Reciprocal	Geometric mean
1	A	6	6.67 ± 0.45	0.98	6.79	6.73
	B	5	3.71 ± 0.46	0.96	3.88	3.79
	C	5	4.21 ± 0.27	0.99	4.26	4.24
2	A	13	12.79 ± 1.07	0.93	13.77	13.27
	B	6	6.50 ± 0.86	0.93	6.96	6.73
3	A	3	2.77 ± 0.09	0.99	2.78	2.78
	B	5	15.14 ± 1.10	0.98	15.38	15.26
4	A	8	5.61 ± 0.84	0.96	5.99	5.80
	B	5	8.27 ± 0.72	0.94	8.64	8.45
Mean		56	7.30 ± 1.39	0.96	7.61	7.45

¹ Standard estimate is the ordinary least squares regression slope with ring count as the independent variable (y versus x). Reciprocal estimate is the reciprocal of the regression slope with distance from bole as the independent variable (x versus y). Geometric mean estimate is the mean of these two elongation rate estimates. No standard errors were calculated for the reciprocal or geometric mean estimates. See text for further details.

pine plantations, and concluded that as roots get longer, their rate of elongation slows or even ceases. Based on the good fit of the geometric mean and ordinary least squares regression lines, there is no indication that this occurred in the Douglas-fir roots in this study. This finding is of interest because carbon translocation to longer roots should be reduced: partitioning should favor shorter roots with a lower pathway resistance (see Thornley 1998 for a discussion of the transport-resistance model). However, because the rings of the smallest diameter roots could not be counted, it is not possible to demonstrate unequivocally that a reduction in growth rate did not occur in the most distal coarse roots of Douglas-fir.

The mean rate of extension of 7.4 cm year⁻¹ is considerably lower than has been reported previously for this species. For example, Douglas-fir planted in the Netherlands grew at a mean extension rate of 18 cm year⁻¹ (Kuiper and Coutts 1992). Extension rates of up to 63 cm year⁻¹ were measured in young plantation-grown Douglas-fir in England (Reynolds 1983). However, both of these studies were probably conducted in more mesic environments than the xeric environment at the Pothole Creek site. Furthermore, root growth patterns may differ between subspecies of Douglas-fir. It is known that Kuiper and Coutts (1992) studied the coastal (var. *menziesii*) variety of Douglas-fir rather than the interior variety used in this study. Rapid growth of roots has also been demonstrated in other conifer species. For example, Fayle (1975a) reported a maximum lateral root elongation in red pine of 130 cm year⁻¹, and a mean extension rate of 68 cm year⁻¹ for the first 10 years of growth. Drexhage and Gruber (1998) estimated a growth rate of 11.5 cm year⁻¹ for lateral roots of *Picea abies* (L.) Karst., although bends and curvature were not taken into account when measuring root length. Of the seven conifers studied by Reynolds (1983), hemlock (*Tsuga heterophylla* (Raf.) Sarg.) roots grew most slowly, at about 20 cm year⁻¹. The root extension rates measured at Pothole Creek are therefore ex-

tremely low compared with rates reported in the literature. The exact cause for this is unknown, but limiting water and the dense, stony soils may be contributing factors.

Under poor soil conditions, the proportion of carbon allocated to the root system generally increases (Fitter 1997), although it has long been known (Büsgen and Münch 1929) that this is not always the case. Root growth is thought to be compensatory, with increased growth where competition is low or soil resources are abundant (Brisson and Reynolds 1994). However, Triboulot et al. (1995) found that minor water stress stimulated maritime pine (*Pinus pinaster* Ait.) seedling root growth despite reduced turgor pressure, whereas higher stresses resulted in reductions in both turgor pressure and root growth rates. Root growth rates of some conifer seedlings exposed to drought may be reduced to 25% of the rate when soil water is at field capacity (Kaufmann 1968). Fayle (1975a) reported that root elongation in red pine was correlated with soil water availability in June and July. Therefore, seasonally limited water availability may account for the low root elongation rates in this study. In general, roots are the last part of a tree to exhibit water stress, and several studies have shown that root growth of some herbaceous plants is maintained for much longer than shoot growth under drying conditions (reviewed in Kozłowski et al. 1991). The Pothole Creek site is classified as dry and the site is characterized by significant spatial and temporal variability in soil water. Such variability could have a strong negative effect on root growth. For example, in Root 2-A, there was evidence of serial correlation among the residuals (Figure 1). This root may have grown in discrete steps, corresponding to soil heterogeneity and some degree of compensatory root growth.

In another study, artificial, nonfunctional root systems were used to provide physical obstructions and fragment belowground space (McConaughay and Bazzaz 1992). Increasing fragmentation was correlated with reduced plant

growth, and the authors concluded that physical space was a resource. Thus, the high coarse fragment percentage at Pothole Creek could cause spatial fragmentation and reduce root elongation rates. This effect could be enhanced by low resource (water and nutrient) availability. The effects of below-ground fragmentation may also carry over to aboveground growth.

There was more than a fivefold difference in elongation rates between the fastest- and slowest-growing roots. Based on these findings, I conclude that the wide range of root elongation rates was the result of soil heterogeneity or carbon allocation, rather than measurement error. Furthermore, it is unlikely that measurement error accounts for the large difference between the elongation rate estimates in this study and those reported for Douglas-fir by other researchers. The geometric mean regression results were indistinguishable from those obtained by ordinary least squares, indicating that the downward bias of measurement error did not have a significant effect on the elongation rate estimates. Additional research is needed to determine the causes of the slow root growth of Douglas-fir at Pothole Creek.

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