

TREES HAVE HIGHER LONGITUDINAL GROWTH STRAINS IN THEIR STEMS THAN IN THEIR ROOTS

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Longitudinal growth strains develop in woody tissues during cell-wall formation. This study compares stems, which have a mechanical role and experience longitudinal stresses, and nonstructural roots, which have little mechanical role and experience few or no longitudinal stresses, to test the hypothesis that growth strains are produced in stems of straight trees as an adaptive feature for mechanical loads. I measured growth strains in one stem (at breast height) and one nonstructural root (beyond the zone of rapid taper and/or beyond a major change in root direction) for 13–15 individuals of each of four tree species, *Pseudotsuga menziesii*, *Thuja heterophylla*, *Acer macrophyllum*, and *Alnus rubra*. Forty-seven of the 54 individuals had higher strains in their stems than in their roots ($4.3 \pm 0.3 \times 10^{-4}$ and $1.5 \pm 0.3 \times 10^{-4}$, respectively). Growth strain was two to five times higher for stems than roots. The modulus of elasticity (MOE) in bending was also higher in stem tissues (from literature values) than in root tissue (from this study). Calculated growth stresses, the product of growth strain and MOE, averaged 6–11 times higher in stems than roots for the four species. The higher strain and stress in stems than roots indicate that the strains and stresses are adaptive features that are produced in response to, or in “anticipation,” of mechanical loads. The existence of nonzero strain in these roots indicates that production of some level of longitudinal strain is a consequence of wood development, even in situations where it does not appear to be adaptive.

Introduction

In the secondary xylem of trees, each wood cell shortens during development, causing a longitudinal strain (Jacobs 1945). The strains, called longitudinal, or axial, growth strains, vary in magnitude with radial or vertical position along the stem of a tree and with compass direction in leaning trees according to systematic patterns. Strains and stresses follow the same patterns, but, because some studies report strain whereas others report stresses, I will phrase this discussion in terms of strains unless only stresses were reported. The outer third of the stem is generally in longitudinal tensile strain, and the inner two-thirds is in compressive strain (Boyd 1950). The stem region below branches often has higher tensile strains than do other locations (Chanson 1993), and tensile stress can vary by a factor of two with vertical position on the stem (Yao 1979). The underside of leaning stems has lower tensile strains and stresses than does the upper side in both angiosperms and gymnosperms, although the exact mechanisms differ (Nicholson 1973; Nicholson et al. 1975; Boyd 1980). These growth-induced strains and stresses are distinct from gravitationally induced strains and stresses (Nicholson 1973), which result from the distribution and material properties of the structures above them and from external applied forces such as those resulting from wind or snow. The strains and stresses develop during cell-wall maturation when lignin is deposited and/or as the microfibrils shorten (reviewed in Wilson 1981; Archer 1986, 1987; Wilkens 1986; Kubler 1987). If the cells were not fixed into position by their attachment to neighbors, they would change in ratio of length to width in a manner dictated by the orientation of the microfibrils. Because they are fixed into position, strains are generated.

Leaning plants often produce differential growth strains on the lower versus upper sides of the lean that help counter the forces causing the lean (see, e.g., Jacobs 1945; Okuyama et al. 1994; Wilson and Gartner

1996). In one species of buttress-forming tree (*Eperua falcata*), the buttresses of vertical stems had more tensile strain than did the nonbuttressed wood or the wood higher on the trunk, indicating that the buttresses act analogously to guy wires (Chouquet et al. 1995). In these trees, the growth strains have an obvious mechanical role.

In contrast, in vertical, nonbuttressed stems, it is not clear why a plant should produce wood with any growth strain at all. Whereas much research has gone into the mechanisms of generation of growth strains (Watanabe 1965; Boyd 1972; Bamber 1978; Archer 1987; Yamamoto et al. 1993; Okuyama et al. 1994) and their effects on lumber recovery and quality (Jacobs 1945; Dadswell and Wardrop 1949; Boyd 1950; Kubler 1987), little research has assessed their functional significance for living plants.

One hypothesis for growth strains in vertical stems is that they are a neutral consequence of wood development. In this case, the growth strains could result either from other processes in development or from their having adaptive consequences in other canopy situations, such as in branches or leaning stems, and so their presence in vertical stems allows their amplification in situations in which they are needed (Wilson 1981). An alternative hypothesis is that growth strains in vertical stems have a mechanical role for bending situations (Boyd 1950): because wood is weaker in compression than in tension (Forest Products Laboratory 1987, table 4-2), tension pre-stressing of the outer stem should allow the stem to accommodate a higher compressive force (caused by wind) before failing.

The goal of this study was to compare the magnitudes of growth strains in a mechanically active part of the woody plant structure, the stem, and a mechanically inactive part of the structure, the nonstructural zone of woody roots. The stem has a structural role in supporting canopies (Givnish 1995; Waller and Steingraber 1995). Roots close to the stem have this mechanical role as well (Coutts 1983, 1986; Stokes et al.

Table 1

PLANT ATTRIBUTES AT THE LOCATION WHERE SAMPLED: STEMS AND ROOTS FOR THE STRAIN MEASUREMENTS AND ROOTS FOR THE MODULUS OF ELASTICITY (MOE) MEASUREMENTS

Species	n	Strain measurements			MOE measurements	
		Diameter at breast height (mm)	Root diameter (mm)	Root distance (m)	n	Root diameter (mm)
<i>Pseudotsuga menziesii</i>	15	198 ± 12	23 ± 3	1.13 ± 0.09	7	46 ± 4
<i>Tsuga heterophylla</i>	13	227 ± 17	31 ± 4	1.36 ± 0.14	8	46 ± 7
<i>Acer macrophyllum</i>	13	218 ± 10	33 ± 3	1.47 ± 0.27	7	37 ± 4
<i>Alnus rubra</i>	13	210 ± 13	21 ± 4	0.93 ± 0.15	5	25 ± 2

Note. Root distance refers to the distance from the stem along the root (mean ± SE).

1995; Harrington and DeBell 1996; Nicoll and Ray 1996), but roots at some distance from the stem are thought to serve little mechanical role, because the tension and bending forces from the stem are progressively transmitted into the soil (Ennos 1990, 1993). I compared growth strains in four species of trees native to the U.S. Pacific Northwest to test the hypothesis that stems have tensile growth strains and nonstructural roots have no growth strains. I also made crude estimates of the tensile growth stresses in these same trees. Results supporting the hypothesis would corroborate the hypothesis that plants have evolved the ability to develop growth strains and stresses for a mechanical role.

Material and methods

SAMPLE SELECTION

In July 1995, I tested the stem and one root of each of 13–15 individuals (54 total) of four of the most common tree species of western Oregon: the gymnosperms *Pseudotsuga menziesii* var. *menziesii* Mirb. (Franco) (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and the angiosperms *Acer macrophyllum* Pursh (bigleaf maple) and *Alnus rubra* Bong. (red alder). All trees were within stands at the H. J. Andrews Experimental Forest (44°15'N, 122°20'W, 600–850 m elevation) within 30 m of FS road 1506. Many of the strain measurements were done by undergraduate students with my close supervision. The same person always made measurements of strain before and after strain relief on a given tree.

An acceptable stem was within several degrees of vertical, grew on relatively flat and stable soil, and was free of large branches or scars from 0.3–2.3 m above the ground. After choosing a stem, we excavated the spreading roots within 1–5 m of the bole to ascertain that the tree had an acceptable location on a root. Excavation in the vicinity of roots was done with bare fingers, to avoid damaging the roots. An acceptable location on a root was ≥15 mm in diameter, buried for ≥0.3 m in each direction, relatively straight for ≥0.15 m, and nonstructural (see below). The range of root lengths needed to follow these criteria was 0.31–4.54 m. The sampled parts of stems averaged ca. 200 mm in diameter, the sampled parts of roots averaged 20–50 mm in diameter, and the roots were sampled ca. 1–1.5 m from the stem (table 1).

The diameter criterion disqualified roots that would be

hard to remeasure after strain relief. The burial criterion avoided the stemlike structure that can develop when roots form in light (Bannan 1941; Westing 1965; Fayle 1968). My rules for finding nonstructural locations on roots were to follow a root distally from the stem beyond (1) any large change in orientation or (2) the zone of rapid taper. Beyond a large change in orientation, a root is unlikely to experience longitudinal stresses because little of the force is directed in the new direction. The zone of rapid taper may have wood structure more similar to stem than to typical root (Bannan 1941; Wilson 1964, 1975). Second, the wood in the zone of rapid taper appears to have a structural function: in roots (Jacobs 1954; Gartner 1994; Stokes et al. 1995; Nicoll and Ray 1996) as in stems (reviewed in Telewski 1995) the localities experiencing high mechanical forces often have faster diameter growth than do those that experience less force. Wilson (1975) found more root thickening in free than guyed *Pinus strobus* trees only in the first 0.5 m of root. Fayle (1980) measured stress in the horizontal roots of *Pinus resinosa* while he bent the stem. Stresses were encountered only in the basal 0.5 m of the roots.

STRAIN MEASUREMENTS

Once I found an acceptable individual, we measured its longitudinal growth strains. There was no wind during measurement periods. We used the Nicholson (1971) method of strain relief, in which one measures the length of a marked segment, cuts into the wood proximal and distal to the segment, and then remeasures the length of the marked segment. Stem surfaces at breast height (1.37 m) were prepared by removing the bark with a chisel and utility knife from an area ca. 150 mm along the grain by 50 mm across the grain. The bark came off easily because it was the growing season. Most roots had much thinner bark and were in harder-to-reach positions than did the stems, so we left the bark on the roots rather than risk damaging their xylem.

Phillips-head screws (6 mm long, including the head) were inserted into the stem or root ca. 100 mm apart and along the grain, with the cross of the screw's head in an x rather than a + position relative to the grain. The extensometer (Huggenberger tensotast, Zürich, Switzerland) functions much like calipers but with an accuracy of 0.001 mm: one measures distances by placing its fixed point in one location on a sample and a movable point in another location. The x's in the heads of the screws served to channel the extensometer's points. We measured the distance between the screw's x's five times with the extensometer. Then we relieved the strain by cutting the sample 10 mm above and

below the sample along the grain to a depth of 15–20 mm with a 29-mm diameter forstner drill bit. The distance between the screw's x's was then measured again five times. The difference in the average measurements before and after drilling divided by the span distance (100 mm) is the longitudinal growth strain. We measured the diameter of the tree at breast height, the diameter of the root where the sample was tested, and the distance along the root from the tree base to the sample location. The partially cut stems and roots were left attached to the tree, so we were unable to assess samples for presence of reaction wood.

MEASUREMENT OF MODULUS OF ELASTICITY (MOE) IN BENDING AND SPECIFIC GRAVITY IN ROOTS

Values of MOE for roots of these species were unavailable. Therefore, in May 1996, I excavated root systems for eight acceptable roots each from a different individual of each of the four species. I followed the same criteria for roots as above, except that minimum diameter was 20 mm in these samples, to ensure that we could saw beams (see root diameters, table 1). Some accepted roots had some curvature; there was an insufficient number of "ideal roots" at the site. I marked the underside of each root and then removed the root with a saw. Samples were kept at their field moisture condition ("green").

Because strains were measured in one locality (outer growth rings, tops of roots), I needed MOE of that wood, as well, rather than MOE of entire roots. The carpenter cut one beam from the upper side of each root. Beams were 8 mm deep (in the radial direction), 10 mm wide (tangential), and ≥ 160 mm long (with the grain; longitudinal direction). The face was parallel to the growth ring boundaries such that the same growth rings extended the entire length of a sample. Thus, a curved root would result in a curved beam. One sample was too small to saw into a beam, and four others were removed from the data set because results with them differed significantly from the others. Three of these outliers had aberrant form, and one was noted during sampling to be within 10 mm of the surface and covered only with moss, so it probably had a stemlike structure.

We performed three-point bending tests on the tangential surface of the green (moist) samples, using a materials-testing apparatus (Instron model 1130, Canton, Mass.) with a 114-kg load cell. The bottom two pressure points were 112 mm apart, and the top pressure bar was halfway between the bottom two. MOE was calculated from the linear region of the force versus displacement curve. Specific gravity of the samples was determined as dry mass per green volume. We determined volume by displacing water in a beaker on a balance (a modification of mode III of ASTM D 2395-93, ASTM 1995) and determined dry mass after oven drying at 102°C.

CALCULATION OF GROWTH STRESSES

I made a gross estimate of the mean growth stress by species and organ (stem, root) as follows. Growth stress is the product of MOE and growth strain. For MOE of roots, I used the species means from this experiment. For MOE of stems, I used published values for wood of these species at field moisture content. Because the MOEs used were determined in bending, I increased their value by 10% to correct for the effect of shear deflection and to give values more similar to those that derive from tension tests (Forest Products Laboratory 1987).

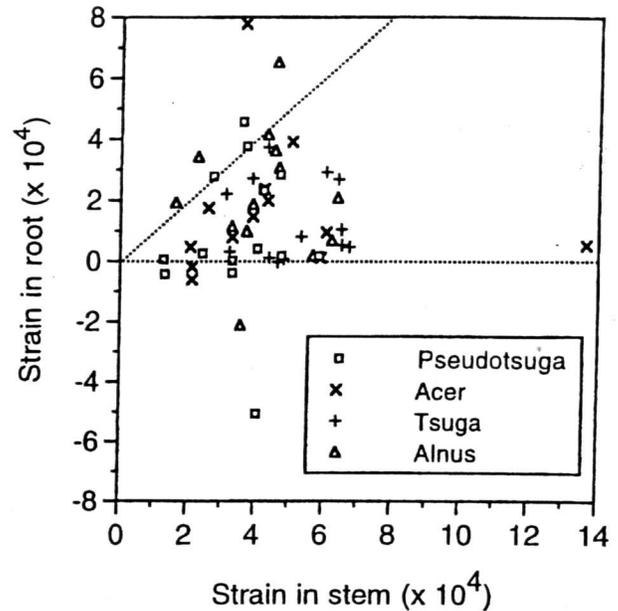


Fig. 1 Growth strain in the stem versus the nonstructural woody root of individuals of four tree species. Points below the diagonal line show individuals for which the growth strain was higher in the stem than in the root. Points below the horizontal line show individuals that had compressive rather than tensile strain in the stems.

Results

Measurements on a single location were very repeatable. The coefficient of variation for the five initial measurements on the stems and roots were 0.24% and 0.22%, respectively ($n = 54$ individuals).

For 47 of 54 individuals, growth strains were higher in stems than in roots (fig. 1). Overall, plant part had a significant effect on growth strain ($4.3 \pm 0.3 \times 10^{-4}$ for stems, $1.5 \pm 0.3 \times 10^{-4}$ for roots; $n = 54$; two-factor ANOVA, $P < 0.0001$), but neither species nor the interaction of species and plant part had a significant effect ($P = 0.20$ and 0.51 , respectively).

Growth strains averaged two to four times higher in stems than in roots for each of the four species studied ($P < 0.05$, ANOVA, fig. 2). The strain patterns were similar in gymnosperms (*Pseudotsuga* and *Tsuga*) and angiosperms (*Acer* and *Alnus*). There were no significant correlations ($P < 0.05$) between growth strain in stems and stem diameter or between growth strains in roots and either root diameter or distance along the root to the sample location (data not shown).

MOE in bending of roots ranged from 2400 ± 240 MPa to 4400 ± 700 (*Pseudotsuga*), and specific gravity ranged from 0.30 ± 0.01 (*Alnus*) to 0.44 ± 0.04 (*Pseudotsuga*) (table 2).

Stress, rather than strain, is the measurement most related to causation of mechanical change. I made a crude estimate of stresses in stems and roots of these trees by multiplying strain (fig. 1) by MOE (tables 2 and 3). Stems had about six to 11 times the longitudinal stress of roots (fig. 3), which is an even larger

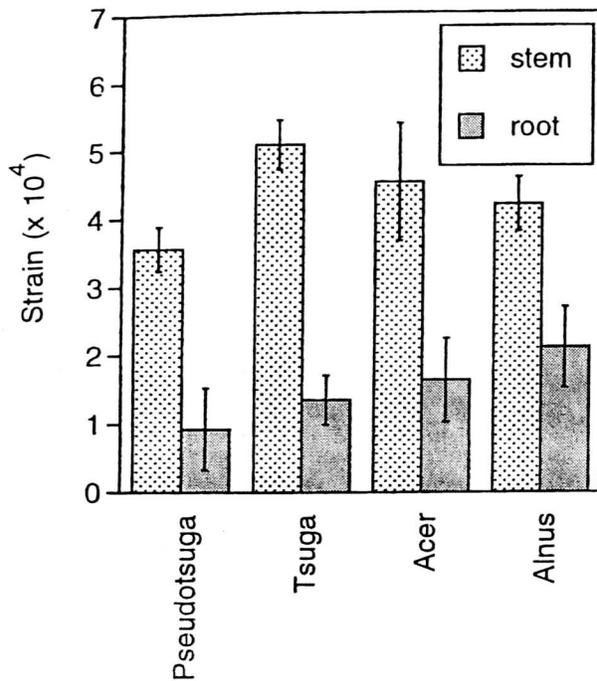


Fig. 2 Growth strain in stems and nonstructural roots, by species. Bars represent standard error. One stem and one nonstructural woody root were measured for each of 15 individuals of *Pseudotsuga* and each of 13 individuals for the other species.

factor than that observed for strain (factor of 2–4, fig. 1).

Discussion

These results corroborate the hypothesis that growth strains develop in vertical stems as an adaptation to the mechanical demands on the stem. Higher growth strains in stems than roots show that different organs (stem, roots) of the same genetic individual can develop wood with different strains, just as previous studies have shown that different stem locations can develop different strains or stresses (e.g., Jacobs 1945; Nicholson 1973; Chanson 1993; Okuyama et al. 1994). When considered in the whole-plant context, both of these observations indicate that growth strains and stresses are produced either in response to mechanical strain or as an adaptive feature to help the plant accommodate its mechanical loads. Because the non-

Table 2

MODULUS OF ELASTICITY IN BENDING (at field moisture content) AND SPECIFIC GRAVITY (dry mass per volume at field moisture content) OF NONSTRUCTURAL TREE ROOTS (mean ± SE)

Species	n	Modulus of elasticity (MPa)	Specific gravity
<i>Pseudotsuga menziesii</i>	7	4400 ± 700	0.44 ± 0.04
<i>Tsuga heterophylla</i>	7	3140 ± 640	0.35 ± 0.03
<i>Acer macrophyllum</i>	8	3210 ± 270	0.40 ± 0.01
<i>Alnus rubra</i>	5	2400 ± 240	0.30 ± 0.01

Table 3

VALUES OF MODULUS OF ELASTICITY IN BENDING (at field moisture content) AND SPECIFIC GRAVITY (dry mass per volume at field moisture content) OF STEM WOOD

	Modulus of elasticity (MPa)	Specific gravity
<i>Pseudotsuga menziesii</i>	10,760	0.45
<i>Tsuga heterophylla</i>	9030	0.42
<i>Acer macrophyllum</i>	7580	0.44
<i>Alnus rubra</i>	8070	0.37

Source. Table 4-2, Forest Products Laboratory 1987.

structural roots in the current study produced nonzero growth strains, some basal level of strain appears to be a consequence of the way cell walls develop, independent of the location's mechanical demands. Alternatively, my assumption may be incorrect that these roots are nonstructural (B. A. Gardiner, personal communication).

There are few reported values of MOE in roots. Vogel (1995) reports MOE in bending for a *Pinus* root of 1127 MPa, lower than the means for the gymnosperms reported here (4400 and 3140 MPa for *Pseudotsuga* and *Tsuga*, respectively). Fegele (1941) reported values of 5990 MPa for nine northeastern conifers pooled and 3810 MPa for 12 northeastern hardwoods pooled, both of which are slightly higher than are the values reported here.

Reported stem MOEs (Forest Products Laboratory 1987) are higher than are root MOEs reported here by

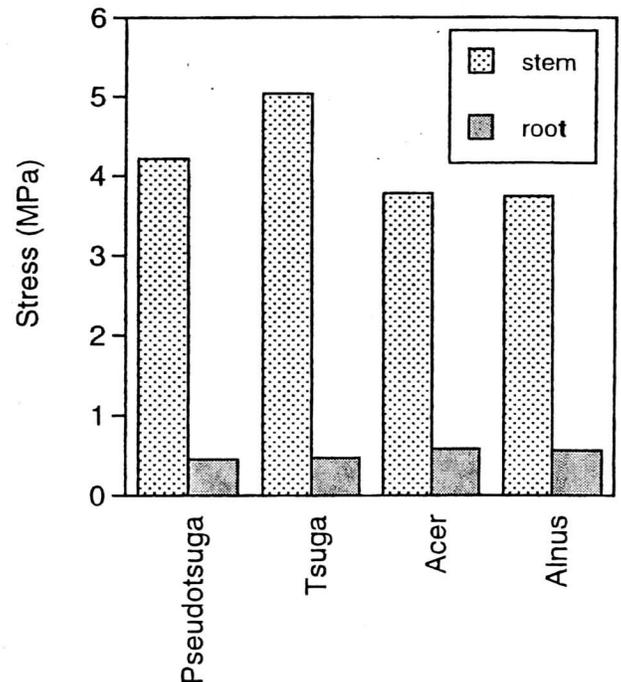


Fig. 3 Calculated growth stresses in stems and nonstructural woody roots, by species.

a factor of 2.4–3.4. Fegel (1941) reported that MOE in bending was higher in stems than in roots by a factor of 1.2 for nine northeastern conifers pooled and 2.3 for 12 northeastern hardwoods pooled. In the current study, as in Fegel's, root wood also had lower specific gravity than did stem wood.

The higher strain variability in root than in stem may have resulted from more measurement error in roots than in stem or from more innate variability. Measurement error could have been introduced by soil knocked into the Phillips-head screws when we drilled the root samples for strain relief, or the drilling may have compacted the soil underlying the samples, thus changing the way the roots sat in the soil. It is possible, however, that roots have a wide range of growth strains. Roots may have had "atypical" tissues that were not screened out by our selection criteria. Bannan (1941), Fayle (1968, 1980), and Wilson (1975) presented a number of conditions and locations in which root wood develops structure similar to stem wood. Wilson (1975) reviewed patterns of secondary growth in roots, including cases in which most growth is on the top of roots, on the bottom of roots, or stimulated locally, such as proximal to branching, or in vertically undulating roots. Some of the roots in the current study were within 20 mm of the substrate surface and therefore may have developed in the light and were only

recently covered with moss, leaves, and/or soil. Yet another explanation for the variability of growth strain values in roots may follow from a recent report on the taprooted tree *Pinus pinaster* (Berthier et al., in press): roots on the leeward side of the stem had compressive rather than tensile growth strains. Further research in this area would benefit from anatomical study of the samples used to determine whether they are typical root wood, to look for reaction wood (although compression wood is very rare in buried roots; Westing 1965), and to assess microfibril angle.

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