Sinuous stem growth in a Douglas-fir (*Pseudotsuga menziesii*) plantation: growth patterns and wood-quality effects

R. Spicer, B.L. Gartner, and R.L. Darbyshire

Abstract: Stem sinuosity is thought to negatively impact wood quality, but no studies have characterized its vertical and radial effects on wood properties. Here we study wood quality along the entire stem in 25-year-old plantation-grown Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) trees (32 trees total) that had been scored for sinuosity at age 12. We also study compression wood formation in the radial direction for one internode that had been scored for sinuosity at age 12 and subsequently produced 13 more annual rings. Trees with highly sinuous leaders at age 12 were more likely to be sinuous in other years, and developed more slope of grain defect (approximately 15% log volume) than less sinuous trees, but did not differ in the size of the pith-containing core. Leaders originally scored as highly sinuous developed more compression wood than control trees but only near the pith. Internode length did not differ among sinuosity classes. The size of the pith deviations (radial distance from centreline) remained constant up the stem despite a decline in internode length. However, the frequency of pith deviations was highest at 10–15 years, when internode length reached a peak. The relationship between temporal patterns of growth rate, sinuosity, and tree biomechanics deserves further attention.

Résumé : On croit que la courbure de la tige a un impact négatif sur la qualité du bois mais aucune étude n'a caractérisé ses effets verticaux ou radiaux sur les propriétés du bois. Cette étude porte sur la qualité du bois le long de toute la tige de douglas (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) âgés de 25 ans en plantation (32 arbres au total) dont la sinuosité a été notée à l'âge de 12 ans. Nous avons aussi étudié la formation de bois de compression en direction radiale pour un entrenoeud dont la sinuosité avait été évaluée à l'âge de 12 ans et qui a depuis produit 13 nouveaux cernes annuels. Les arbres qui avaient des pousses terminales très sinueuses à l'âge de 12 ans avaient plus de chance d'être sinueux les autres années et ont développé plus de défauts liés à l'angle du grain (environ 15% du volume des billes) que les arbres moins sinueux mais ne différaient pas pour la dimension de la partie du cœur formée de la moelle. Les pousses terminales originellement classées comme fortement sinueuses ont développé plus de bois de compression que les arbres témoins mais seulement près de la moelle. La longueur de l'entrenoeud ne variait pas selon la classe de sinuosité. Le degré d'excentricité (distance radiale de la ligne centrale) demeurait constant en montant sur la tige malgré une diminution de la longueur des entrenoeuds. Cependant, il y avait le plus d'excentricité à 10–15 ans alors que la longueur des entrenoeuds atteignait un sommet. La relation entre les patrons temporels du taux de la croissance, la sinuosité et la biomécanique de l'arbre mérite d'être étudiée davantage.

[Traduit par la Rédaction]

Introduction

Sinuous growth in young Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is a conspicuous stem deformity most noticeable in young plantations. Sinuosity is defined as stem crookedness or "waviness" that occurs entirely within an internode or interwhorl (Campbell 1965), rather than spanning several internodes. With the trend toward harvest of trees at younger ages, it is important to be able to predict the effects of sinuosity on current and future wood quality in these trees. The wood-quality effects of sinuous growth, as well as the physiological, genetic, and (or) environmental causes, are still largely unknown. In the current study we evaluated trees in midrotation (25 years old) that had been scored for sinuosity at age 12, to compare basic growth and wood formation characteristics of trees with varying degrees of sinuosity.

Causes of sinuosity and associated growth patterns are poorly understood. Extreme forms of stem deformity (including severe sinuosity) in radiata pine (*Pinus radiata* D. Don) growing in Australia have been linked to nutritional deficiencies (Downes and Turvey 1990*a*, 1990*b*) and previous land use (Bail and Pederick 1989; Carlyle et al. 1989; Birk 1991). In North America, nutritional deficiencies have been shown to cause distorted growth in several species (Carter et al. 1986), but direct evidence is lacking for nutritional status as a cause of sinuous leader growth in Fraser fir (*Abies fraseri* (Pursh) Poir.; Hinesley and Campbell 1992). Forms of sinuosity in radiata pine are heritable (Pederick et al. 1984), but there is contradictory information on the

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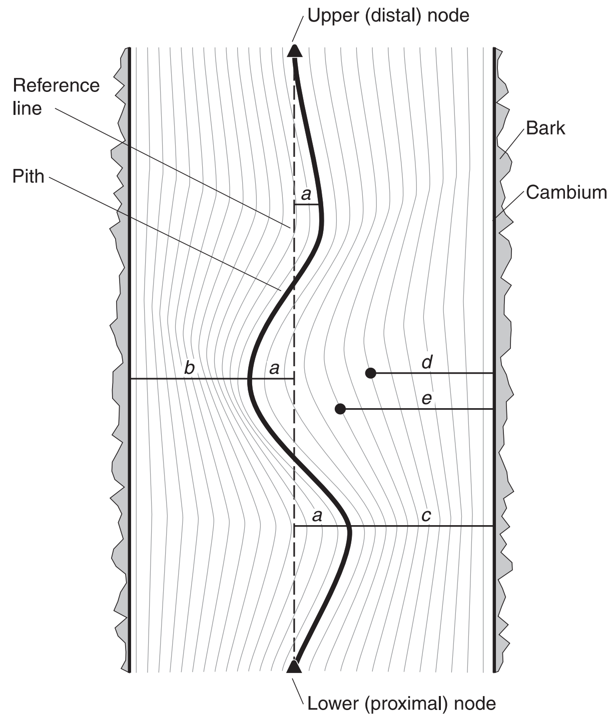
degree of heritability in Douglas-fir (Campbell 1965; Temel 1997). Recent evidence suggests that the cause of sinuosity is biomechanical, with longer, more slender internodes being more susceptible to stem sinuosity than shorter, wider internodes (Downes et al. 1994).

The impact of sinuous growth on wood quality has received little attention relative to other stem deformities. Lumber or veneer degrade could result from increased amounts of compression wood, slope of grain, and the presence of pith in sinuous logs. Studies that attempt to relate sinuosity to compression wood formation (Hans and Williamson 1973; Burdon 1975; Turvey et al. 1993) and drying defects (Middleton et al. 1989) have been inconclusive. The increased longitudinal shrinkage due to compression wood may be a function of both microfibril angle and cell wall thickness (Harris 1977), suggesting that visual grading of compression wood may be a poor predictor of defect due to shrinkage. We know of no studies relating sinuous growth to the amount and location of slope of grain or pith defects, both of which could strongly impact strength properties.

In this study we test the following hypotheses regarding sinuous growth patterns in Douglas-fir: first, that sinuous growth is associated with longer internodes; second, that trees with sinuous leaders in one year are more likely to have sinuous leaders in other years (i.e., genetic or environmental predisposition to sinuous growth); and third, that the incidence of sinuous leader growth decreases with tree age. We also test the following hypotheses regarding wood quality: first, that sinuous growth in a particular internode is associated with compression wood formation; second, that sinuous growth produces grain deviation with respect to vertical near the pith; and third, that trees with sinuous growth have a larger central pith-containing core. Finally, by characterizing trees 12 years (13 growing seasons) after an original sinuosity survey, we are able to link internal wood-quality traits to an on-the-ground scoring approach. This work, combined with investigations of the inheritance patterns of stem form (Temel 1997), represents a first step toward a process by which foresters can predict wood quality at an early age.

Fig. 1. Split stem section showing sinuous pith, central reference line, and measured distances (radial longitudinal view). Only pith deviations where *a* ≥1 cm were counted. See text for further explanation.



Materials and methods

Plant material

Trees for this study were selected from a progeny plantation at Coyote Creek in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program in the central Oregon Coast Range (43°55′N, 123°18′W, 274 m elevation) near Eugene, Oreg. Trees were planted in 1974 as 1-0 container-grown stock at 3.05 × 3.05 m spacing, scored at age 12 (1984) for a variety of stem form characteristics, and thinned to 75% of the original stocking level in 1995 by removal of whole rows. Sinuosity scores were determined in 1984 by ground observers who recorded the frequency (maximum number of sinuosity "crooks" within an internode) and displacement (largest distance the stem is offset from the position it would occupy if the stem had no sinuosity, in 0.5 stem-diameter units) of the second internode from the top of the tree (Adams and Howe 1985). We ignored the frequency data but used the 1984 displacement score to group trees according to the severity of stem deviation, and created four groups: high (displacement scores 7–9), medium (4–6), and low sinuosity (1–3) and control (0). We randomly selected at least 16 trees from each group, discarded trees with recorded forks or ramicorn branches (large, nearly vertical branches), then attempted to locate these trees at the site. From the located trees (i.e., those remaining after thinning) we then randomly selected eight trees per group to be used in the study.

Study trees (32 total) were measured for diameter at breast height (24.6 ± 0.7 cm, mean ± SE, $n = 32$) and felled on September 14, 1997. Trees were labeled, bucked to 40 ft (approximately 12 m) log lengths (6 ft (approximately 2 m) long sections for remaining tops), and transported to the Forest Research Laboratory, Oregon State University, Corvallis, Oreg. Logs were split lengthwise through the pith up to about a 5 cm diameter top (14–18 m up the stem). Placement of the split was random, e.g., there was no attempt to split along the direction of prevailing winds. To split each log, a metal wedge was centered over the pith and forced into the basal end of the log with a maul. The split was continued from the log base to the top by forcing new wedges into the split from the outside near the bark. The split half that had the most pith showing was selected for all of the following determinations except compression wood measurements, for which both halves were used.

Internode length and pith sinuosity

The exact location of nodes (point of terminal bud set from previous year) was visible as a "crown" (darkened constriction) in the pith (Wass and Szabo 1973). We marked each node directly on the stem and measured internode length as the straight-line distance between each pair of adjacent nodes. The region between nodes is referred to here as an internode, which corresponds to an interwhorl, or the region between branch whorls.

For each internode, we measured the radial distances from the upper node to the cambium on both sides of the pith. We then tacked an elastic string between the upper and lower nodes in each internode (Fig. 1, broken line) for use as a reference line in determining pith deviations. The total number of pith deviations ≥1 cm (measured from the reference line to the inner edge of the pith;

Fig. 1, *a*) to either side of the line was then recorded. For the largest pith deviation to each side of the reference line we measured the distance from the cambium to the outer edge of the pith (Fig. 1, *b* and *c*). The pith was noted as offset if it had a distinct J shape, most likely as a result of damage to the bud or leader, but it was still counted as a pith deviation.

Grain angle

For each internode, we marked on the split stem surface the location of grain angles equal to 7 and 14° relative to the cambium, to either side of the reference line, if such grain angles occurred. This was done by viewing the annual rings through a clear sheet of acetate that was printed with both a series of parallel lines (one of which we lined up with the cambium), and two reference angle lines, one at 7° and one at 14° to the parallel lines. Before designating the location of a given grain angle we required that the annual ring follow the reference angle line for a minimum of 5 cm. We then measured the minimum distance from the cambium to the specified grain angle (Fig. 1 *d* and *e*). These grain-angle values were chosen because they are important thresholds in lumber grading of structural softwood timbers in the western United States (Western Lumber Grading Rules 1995), where 7 and 14° represent slope of grain of 1 in 8, and 1 in 4, respectively.

Compression wood

The internode originally scored for sinuosity in 1984 was identified by its age (i.e., 15 annual rings in 1997) and removed from each tree for both of the halves of the split log. Corresponding halves were properly aligned and then sawn into 5 cm thick half disks so that the whole cross-section could be viewed. The upper surface of each half disk was then visually scored for compression wood (CW) in three concentric regions: annual rings 1–5, 6–10, and 11–15 from the pith. For each region, CW was scored as absent (0), mild (1), moderate (2), or severe (3), based on thickness and regularity of the latewood band and extent of CW development within the ring. Normal latewood was about 1–3 mm wide and marked by an abrupt transition from earlywood. In contrast, CW showed a gradual transition to latewood and made up a greater proportion of the annual ring (CW latewood was about 50, 100, and 150% wider than that of normal latewood, for CW classes 1, 2, and 3, respectively). Within each concentric region, we summed scores to produce a cumulative score reflecting CW development throughout the entire internode. Summed scores were normalized for internode length by multiplying by a factor equal to the number of disks contained in a given internode divided by the number of disks contained in the longest internode.

Data summary and analyses

For each internode we calculated the mean inside-bark diameter based on measurements of the upper and lower node locations relative to the cambium. Using the minimum distance from the cambium to each defect (pith, 7°, 14° slope of grain) per internode, we then calculated the diameter of the potentially defective central core. We tested for differences (see below) between sinuosity classes using both the mean and maximum core diameters per tree. Although cumbersome, we feel that both mean and maximum values are needed to fully describe the extent of these defects. We further divided each tree into three approximately 5-m logs. Logs were based on discrete internodes and therefore varied in actual length. Using the actual log length, diameter of upper and lower log ends, and the mean and maximum central core diameter per log, we then calculated the proportion of log volume occupied by the potentially defective cores.

Differences between sinuosity classes were tested with a one-way ANOVA using the Statistical Analysis Systems software (SAS Institute Inc., Cary, N.C.). Differences between logs were tested with a repeated measures analysis using a mixed model with fixed and random effects (Table 1). When model *p* values indicated significance ($p \leq 0.05$), all possible pairwise comparisons were tested with the Tukey–Kramer multiple comparison technique, because it is conservative and allows for unequal sample sizes.

Table 1. Fixed (F) and random (R) effects of mixed model for repeated measures analysis used to test for differences between logs with trees.

Effect	Type	df
Sinuosity class	F	3
Tree(sinuosity class)	R	28
Log	F	2
Log × sinuosity class	F	6
Log × tree(sinuosity class)	R	56
Total		95

Results

Frequency of occurrence

Diameter at breast height (Table 2) and mean internode length (averaged across all internodes per tree) did not differ among sinuosity classes ($p > 0.4$, one-way ANOVA). In contrast, the average number of pith deviations per tree at age 24 was significantly higher for trees with medium and high degrees of sinuosity at age 12, relative to control trees (adjusted *p* values ≤ 0.01, one-way ANOVA, Tukey–Kramer adjustment).

The proportion of internodes per tree with pith deviations (Fig. 2A) and 7° slope-of-grain defects (Fig. 2B) differed among sinuosity classes. Trees classified as nonsinuous at age 12 (control trees) had over 80% of their internodes free of pith deviations and 7° slope-of-grain defects at age 24, which was significantly higher than the proportions for trees in the high and medium sinuosity classes (adjusted $p < 0.05$, one-way ANOVA, Tukey–Kramer adjustment; Fig. 2A and 2B, first set of bars). The occurrence of 14° slope-of-grain was rare (a mean of <3% of the internodes per tree in most cases; data not shown) and did not differ among sinuosity classes.

For all sinuosity classes, most pith deviations occurred to only one side of the reference line within an internode (Fig. 2A). Removal of internodes with offset pith from the analysis (see methods) did not change this result (data not shown). In contrast, 7° slope of grain occurred to one side and to both sides of the reference line (within an internode) with similar frequency in highly sinuous trees (Fig. 2A).

Extent of defects when present

The size of the defect-containing core, and its magnitude with respect to sinuosity class, depended upon the defect in question. The mean diameter of the central core expected to contain pith did not differ among sinuosity classes (Fig. 3A). Core diameters based on the mean diameter per tree were 2–3 cm for all sinuosity classes, whereas means based on maximum core diameters per tree ranged from about 3 cm (control trees) to 5 cm (highly sinuous trees).

The central core containing 7° slope of grain was consistently larger than the core containing pith but differed significantly among sinuosity classes only when based on

Table 2. Overbark diameter at breast height, internode length, and number of pith deviations (that are ≥1 cm from the reference line) per tree of 24-year-old Douglas-fir trees with different extents of leader sinuosity at age 12.

	Age 12 sinuosity				Model
	Control	Low	Medium	High	*p* value
DBH (cm)	24.1±1.4	24.3±1.2	23.9±1.4	26.2±1.4	ns
Internode length (m)	0.86±0.02	0.84±0.02	0.86±0.03	0.90±0.02	ns
No. of pith deviations/tree	3.4±0.9*b*	6.6±1.6*ab*	9.1±1.2*a*	11.5±1.0*a*	≤0.001

Note: Values are means ± SE (n = 8). Treatment means followed by the same letter were not significantly different (adjusted $p > 0.01$, Tukey–Kramer adjustment). ns, not significant at the 0.05 level (one-way ANOVA). DBH, diameter at breast height.

Fig. 2. Proportion of internodes per tree containing (A) pith deviations ≥1 cm and (B) 7° slope of grain (s.o.g.) (mean ± SE, n = 8). The proportion of internodes was determined for each tree, then averaged across all trees per sinuosity class. Within each class (i.e., no deviations, deviations to one side of the reference line within an internode, and deviations to both sides of the reference line within an internode), bars with the same lowercase letter were not significantly different (adjusted $p > 0.05$, one-way ANOVA, Tukey–Kramer adjustment).

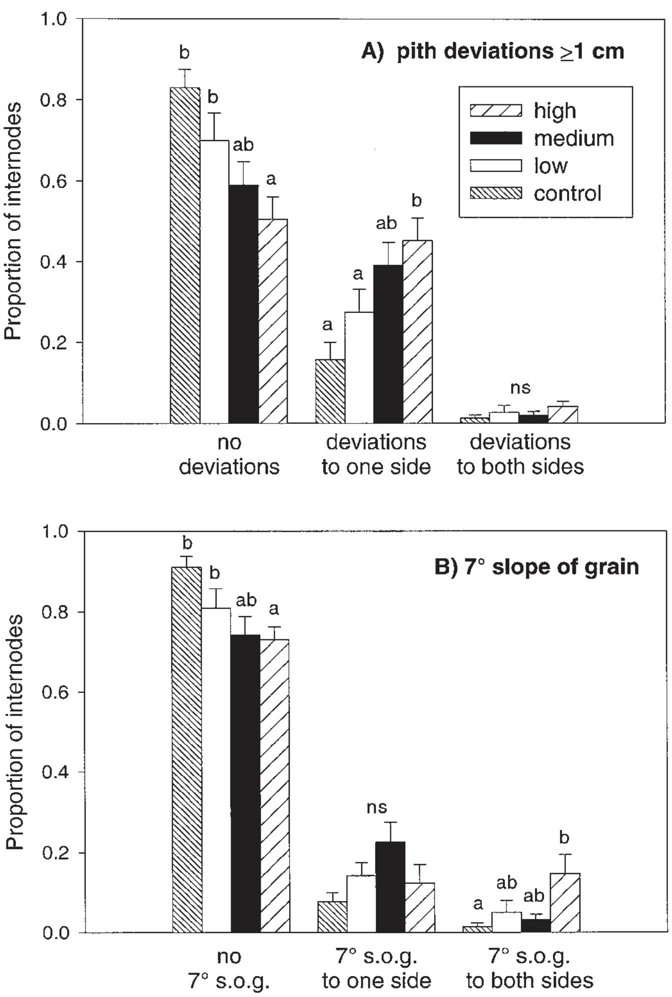
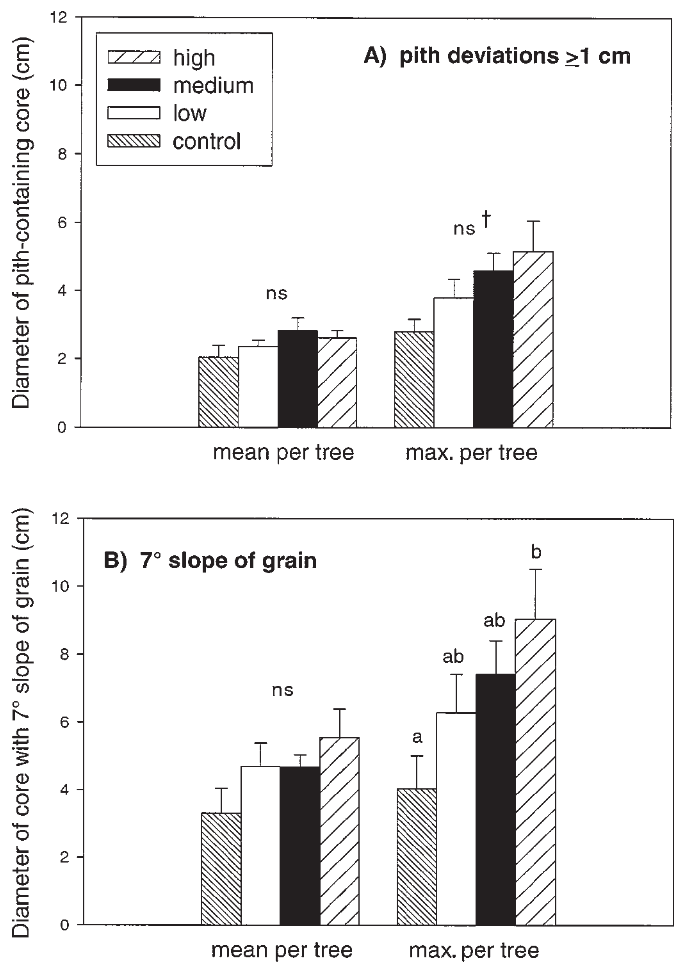


Fig. 3. (A) Mean and (B) maximum diameter of central cores containing pith and 7° slope of grain (±SE, n = 8). Bars with the same lowercase letter were not significantly different (adjusted $p > 0.05$, one-way ANOVA, Tukey–Kramer adjustment; †, p = 0.08).



maximum (rather than mean) diameters per tree (Fig. 3B). Maximum diameters per tree of the 7° slope-of-grain core had a mean of about 9 cm for highly sinuous trees compared with 4 cm for control trees (adjusted $p < 0.05$, one-way ANOVA, Tukey–Kramer adjustment).

Within tree patterns and proportion of log volume

There was no consistent change in the diameter of the core containing pith or 7° slope of grain from the first (basal) log through the third log (Table 3). As a result, the proportion of log volume contained in the defective core

Table 3. Mean and maximum diameter (cm) of the central core expected to contain sinuosity-related defects if the tree has pith deviations ≥1 cm, in 24-year-old Douglas-fir trees with different extents of leader sinuosity at age 12.

		Age 12 sinuosity			
		Control	Low	Medium	High
Mean diameter					
Pith	Log 1	2.2±0.5	2.4±0.2	3.3±0.5	2.6±0.4
	Log 2	1.7±0.4	2.7±0.4	3.0±0.4	2.8±0.3
	Log 3	1.7±0.8	2.0±0.3	2.6±0.4	2.8±0.4
7° slope of grain	Log 1	3.0±0.6	5.1±1.0	6.1±1.2	8.6±3.1
	Log 2	4.5±1.2	4.7±1.0	5.4±0.7	5.5±1.1
	Log 3	3.2±1.8	4.5±0.9	3.9±0.5	5.4±1.1
Maximum diameter					
Pith	Log 1	2.5±0.6	3.2±0.3	3.6±0.5	3.8±0.9
	Log 2	1.8±0.4	3.7±0.6	4.0±0.5	4.8±0.9
	Log 3	2.2±0.9	2.3±0.4	3.3±0.5	3.7±0.4
7° slope of grain	Log 1	3.0±0.6	5.2±1.0	6.5±1.1	9.1±3.2
	Log 2	4.7±1.4	5.9±1.2	7.4±1.0	6.9±1.3
	Log 3	3.3±1.8	4.6±0.9	5.2±1.1	6.1±1.0

Note: Values are means ± SE (*n* ranged from 3 to 8 trees). Logs are about 5 m: log 1, basal; log 2, middle; log 3, top.

Table 4. Percent log volume expected to contain sinuosity-related defects if the tree has pith deviations ≥1 cm, in 24-year-old Douglas-fir trees with different extents of leader sinuosity at age 12.

		Age 12 sinuosity			
		Control	Low	Medium	High
Mean diameter					
Pith	Log 1	1.0±0.5	1.0±0.1	2.8±0.8	1.4±0.4
	Log 2	1.0±0.5	2.2±0.5	2.9±0.6	2.1±0.5
	Log 3	1.8±1.3	2.6±0.6	3.8±0.9	3.4±1.0
7° slope of grain	Log 1	1.6±0.6	5.3±1.8	10.2±3.9	14.6±5.9
	Log 2	6.5±2.5	9.3±4.1	9.8±2.2	11.1±4.9
	Log 3	6.9±5.7	13.8±4.0	7.9±1.4	15.0±6.2
Maximum diameter					
Pith	Log 1	1.3±0.5	1.7±0.2	3.3±0.9	3.2±1.2
	Log 2	1.1±0.5	4.0±1.0	5.1±1.2	8.6±4.8
	Log 3	2.7±1.3	3.6±0.9	6.7±1.9	6.0±1.3
7° slope of grain	Log 1	1.6±0.6	5.5±1.9	11.8±3.9	16.7±6.8
	Log 2	7.2±3.2	13.0±5.4	18.2±3.4	17.0±7.0
	Log 3	7.0±5.7	14.0±4.1	19.9±9.9	18.3±6.1

Note: Values are means ± SE (*n* ranged from 3 to 8 trees). Logs are about 5 m: log 1, basal; log 2, middle; log 3, top.

usually increased toward the top of the stem (Table 4). Pith occupied a smaller proportion of log volume than 7° slope of grain, and although both defects showed a slight increase with sinuosity class, the sample size was unbalanced and too small (n = 3–8) to effectively test these differences. For example, only three control trees had occurrences of 7° slope of grain in the first log.

Total number of pith deviations ≥1 cm was significantly larger for the second 5-m log from the base (Table 5) than the upper and lower logs (adjusted p values = 0.007 and 0.0001, respectively; repeated measures analysis with Tukey–Kramer adjustment). This second log also showed the greatest difference among sinuosity classes. Log 1 had significantly shorter internodes and, as a result, a larger number of internodes than logs 2 and 3 (data not shown). Logs 2 and 3 did not differ in internode length or number (data not shown).

Internode lengths increased up to about age 15 and then declined slightly (Fig. 4). There was no clear evidence of differences in internode length among sinuosity classes.

Compression wood

There were no differences in the amount of compression wood in annual rings 6–10 or 11–15 by sinuosity class as

Fig. 4. Internode length (m) in 24-year old Douglas-fir trees from the base to the tops of trees, shown by sinuosity class at age 12. Internodes were measured as a straight line between nodes in the pith.

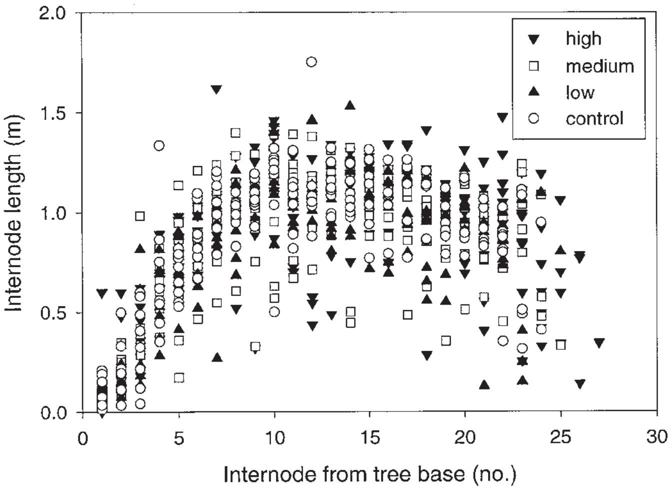


Table 5. Total number of pith deviations ≥1 cm per log in 24-year-old Douglas-fir trees with different extents of leader sinuosity at age 12.

	Age 12 sinuosity				
	Control	Low	Medium	High	Significance*
Log 1	0.8±0.3	1.8±0.6	1.3±0.5	1.8±0.7	*b*
Log 2	1.4±0.4	3.0±0.7	3.9±0.6	5.3±0.6	*a*
Log 3	0.9±0.5	1.5±0.5	3.3±0.7	2.6±0.5	*b*

Note: Values are mean ± SE (n = 8). Logs are about 5 m: log 1, basal; log 2, middle; log 3, top.

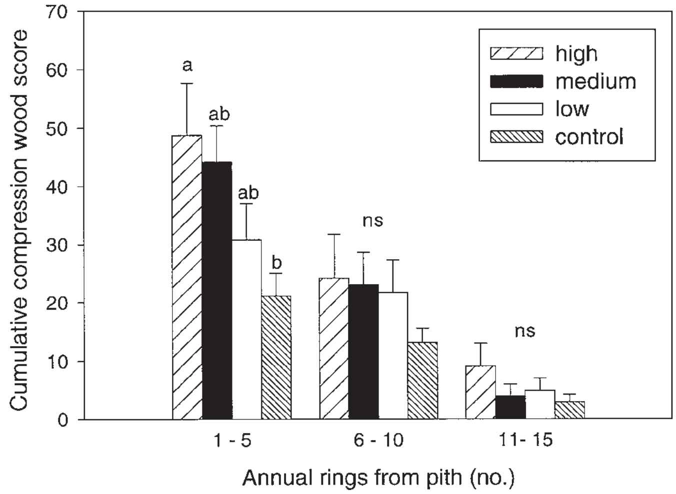
*Logs with the same lowercase letter were not significantly different. Log 2 differed significantly from log 1 and log 3; adjusted p = 0.0001 and 0.007, respectively (univariate repeated measures analysis with Tukey–Kramer adjustment).

judged by the cumulative compression wood scores (Fig. 5). However, for the innermost five annual rings there was more compression wood in highly sinuous trees than control trees (adjusted p = 0.03, one-way ANOVA, Tukey–Kramer adjustment). Compression wood scores decreased from pith to bark for all sinuosity classes (Fig. 5).

Discussion

Sinuous growth has the potential to impact wood quality in several ways. The pith-containing core was so small as to be inconsequential in terms of wood quality. In contrast, the core containing wood with 7° slope of grain or greater made up 11–15% of log volume (17–18% when based on maximum core size, rather than mean) for highly sinuous trees. Grain defects may then represent a less visible form of degrade associated with sinuous growth, causing loss in strength and poor machining characteristics if logs are to be sawn or peeled (Forest Products Laboratory 1987). Compression wood not only causes degrade in sawn and peeled products but also reduces pulp yield due to its high lignin content (Timell 1986*b*). Although highly sinuous trees had

Fig. 5. Mean (±SE, n = 8) cumulative compression wood score for the single internode scored in 1984, when the trees were 12 years old. Scores were determined for three concentric regions about the pith (0, none; 1, mild; 2, moderate; 3, severe compression wood). For each region, scores were summed for the entire internode and normalized for internode length.



more severe CW near the pith, the impact lessened substantially toward the bark, suggesting that the higher quality outer wood remains unaffected. This pattern may explain why Middleton et al. (1989) found no connection between sinuosity and drying degrade.

Sinuous growth may have multiple causes, including intrinsic (e.g., elongation relative to radial growth rates) and extrinsic (e.g., leader damage) factors. Biomechanical hypotheses are based on decreased mechanical stability in the leader of sinuous individuals, suggested in part by the observation of "leader flop" early in the growing season. One hypothesis (Grob and Carlson 1994) is that sinuous growth is the result of a lag between cambium formation and shoot elongation (i.e., a spatial lag between primary and secondary growth). Such a lag could result from either extremely rapid rates of elongation or delayed cambium formation. Recent work (Downes and Turvey 1990*a*; Downes et al. 1994) suggests that seedlings with greater rates of apical elongation are more susceptible to stem deformation following bending, in part because of differences in the timing of reorientation of the tip and lower leader.

Our results showed that the frequency, but not the size of pith deviations, was related to internode length. Severe pith deviations were just as likely to occur in short as in long internodes, and sinuosity classes did not differ in mean internode length nor was there a difference among sinuosity classes in the length of the internode scored in 1984 (data not shown). Similarly, the magnitude of sinuous leader growth did not change with tree age (i.e., pith deviations were just as severe near the top of the tree as they were near the bottom), despite a clear change in internode lengths. In contrast to the size of pith deviations, we found that the frequency of deviations was highest for the second log from the tree base, roughly where internode lengths reached a maximum. It is not known whether this relationship is causal or merely correlative. One drawback of our study is that straight-line internode length is used to represent growth rate, when the length of the curved pith is a more accurate measure of elongation. In addition, accelerated growth rate will not result in longer internodes if elongation occurs over a shorter period of time. Both temporal and spatial patterns of cambial activity are important in studies of wood development (Downes et al. 2000). Clearly further work is needed to study the effect of growth rate on sinuosity, including detailed studies of elongation in the field and the resulting leader form.

One hypothesis regarding an extrinsic cause of sinuosity (reviewed in Timell 1986*a*) suggests that sinuous growth occurs when a branch replaces a damaged leader through the action of compression wood. Compression wood then forms on opposite sides at multiple points along the new leader and an S shape results from this "overcorrection" (Westing 1965; Fielding 1953, 1960, as cited in Timell 1986*a*; Wilson 1973). Our results suggest that leader damage is not a major cause of sinuous growth. Although we recorded multiple (32) cases of sinuosity originating at a point of pith "offset," such instances were distributed equally among sinuosity classes, and their removal did not affect our results. It is still possible, however, that compression wood plays a role in sinuous growth through patterns of overcorrection (Harris 1977; Downes et al. 1994).

By studying the same internode that was scored when trees were 12 years old, we were able to follow the development of wood laid down over a leader of known sinuosity. However, because our splitting technique only gave a view in one plane, there is little reason to compare our measures of sinuosity with those from 1984. Indeed, among these isolated internodes, two control trees showed pith deviations (despite being scored as nonsinuous in 1984), and eight medium- or low-sinuosity trees showed none. In contrast, we viewed compression wood on cross-sectional surfaces, so our cumulative compression wood scores could reflect wood development in the internode that was scored in 1984. In wood formed near the pith, compression wood formation was greatest in the trees that were scored as most sinuous in 1984. It is still unknown whether compression wood is a cause or result of sinuous patterns in secondary growth.

We found that trees noted as highly sinuous in one year were more likely to be sinuous in other years. Given the uniform spacing and topography of the Coyote Creek plantation, it is unlikely that microsite conditions could account for this result, suggesting a genetic predisposition to sinuous growth. This work contradicts previous research indicating that sinuous leader growth repeatability, which estimates an upper limit of heritability, is low (Campbell 1965), but is consistent with research showing stem deformities (Pederick et al. 1984) and sinuosity (Temel 1997) to be heritable. The latter study, conducted in the same stands as the current study but 1 year earlier, found moderate narrrow-sense family heritabilities of 0.41 ± 0.11 (mean ± SE) at age 12 and 0.36 ± 0.11 at age 24. We measured sinuous growth directly by observing the pith for up to 22 internodes along the stem. This gives a more accurate record of past instances of sinuous growth than the external measurements made by Campbell (1965) or Temel (1997).

This research indicates that, except in severe cases, sinuosity has a minor impact on wood quality. Benefits could be gained through early removal of trees that exhibit severe sinuosity at a young age, because they are likely to exhibit it in successive years as well. This research also suggests that the volume containing defects associated with sinuosity does not decrease with tree age, at least within the lower, most valuable region of the bole. Further research is needed to clarify the relationships between growth rate and sinuosity.

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