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Is long primary growth associated with stem sinuosity in Douglas-fir?

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Abstract: Stem sinuosity is a highly visible stem-form trait in the leaders of fast-growing Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) trees, yet its cause is unknown. We tested the hypotheses that sinuous stems have longer expanses of primary growth than nonsinuous stems (putting the leader at higher risk for curvature, induction of compression wood formation, and possibly overcorrection) and higher leader angle using 4- to 5-year-old saplings in raised beds. As hypothesized, sinuous stems had longer expanses of primary growth than did nonsinuous stems (13.5 vs. 12.3 cm, respectively). However, for the dates for which growth (length/day, primary growth, secondary growth, and total growth) differed significantly among sinuosity class, sinuosity class only explained 15%–21% of the variation in growth rate. There were no significant differences in leader angle for saplings of the three sinuosity classes. Contingency tables indicated some consistency in the category of sinuosity to which we assigned the stems in 2001 and 2002 ($\chi^2 = 11.2$, $p < 0.004$). When we used a more quantitative measure, the ratio of stem length/stem distance, there was a tendency toward a significant relationship between the two years ($r = 0.272$, $p = 0.0893$). These data suggest that, counter to expectation, the rate of stem growth was not a large factor in determining whether leaders become sinuous for this population of trees.

Résumé : La sinuosité de la tige est une caractéristique de la forme de la tige qui est facilement visible chez les pousses terminales des douglas de Menzies (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) à croissance rapide et dont la cause est jusqu'à présent inconnue. Nous avons testé les hypothèses voulant que les tiges sinueuses aient une croissance primaire plus étendue que les tiges non sinueuses (ce qui accentuerait les risques de courbure, d'induction de la formation de bois de compression et possiblement de correction excessive chez les pousses terminales) et un angle de croissance plus élevé en utilisant des gaules de 4 à 5 ans produites en plates-bandes. Comme nous l'avons supposé, les tiges sinueuses avaient une croissance primaire plus étendue que les tiges non sinueuses (respectivement 13,5 vs. 12,3 cm). Cependant, en ne considérant que les dates où la croissance (longueur/jour, croissance primaire, croissance secondaire et croissance totale) différait significativement entre les classes de sinuosité, la classe de sinuosité n'expliquait que 15 % – 21 % de la variation du taux de croissance. Il n'y avait pas de différences significatives dans l'angle de croissance des semis entre les trois classes de sinuosité. Les tableaux de contingence indiquaient qu'il y avait une certaine cohérence dans la catégorie de sinuosité à laquelle nous avions assigné les tiges en 2001 et 2002 ($\chi^2 = 11{,}2$, $p < 0{,}004$). Lorsque nous avons utilisé une mesure plus quantitative, soit le ratio de la longueur de la tige sur la distance de la tige, la relation entre les deux années avait tendance à être significative ($r = 0{,}272$, $p = 0{,}0893$). Contrairement à nos attentes, ces données indiquent que le taux de croissance de la tige n'était pas un facteur important pour déterminer si les pousses terminales allaient devenir sinueuses dans cette population d'arbres.

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Introduction

Sinuosity is defined as crookedness that occurs entirely within an internode or interwhorl (Campbell 1965) as compared to crook or sweep, which spans several internodes. Stem sinuosity is common in the bole and (or) the branches of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), especially in fast-growing individuals, but its causes are unknown. In radiata pine (*Pinus radiata* D. Don), studies have implicated developmental, biomechanical, nutritional, and genetic causes of sinuosity (e.g., Downes and Turvey 1990; Turvey et al. 1992, 1993; Downes et al. 1994). In contrast, there has been very little published research to elucidate the fundamental cause in Douglas-fir (e.g., Grob

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and Carlson 1994). The current study pursues one biomechanical explanation to ask whether there is evidence that sinuosity is more likely to develop in the stems with the longest expanses of primary stem.

Sinuosity is of interest because it is highly visible in fast-growing Douglas-fir trees, and appears to be increasing with increasingly intensive plantation management. In spite of its striking presentation in fast-growing plantations, research suggests that sinuosity can cause either no statistically significant decrease in grade (when examined with small sample numbers) or a significant decrease in grade but only in the extremely sinuous individuals. Middleton et al. (1989) compared value recovery from lumber grade yields in 25- and 35-year-old Douglas-fir trees with moderate sinuosity to those with severe sinuosity and found no significant differences at $p < 0.05$. The 10% decrease in dollar value for the severely sinuous class was only significant at the $p = 0.21$ level suggesting that, with more samples, they may have uncovered a statistically significant difference. They also showed that the wood from this young material had a high incidence of drying defects but that degree of sinuosity had no significant effect on its incidence. Spicer et al. (2000) dissected 25-year-old trees from a genetic trial for which information on stem form was available 13 years before harvest. Looking at slope of grain and incidence of compression wood, they reported that a decrease in grade was unlikely to occur in trees with low or moderate sinuosity, but that it could become important in trees that were highly sinuous when young. The pith-containing core was very small, making up about 3% of the log volume in the most highly sinuous trees. In contrast, the defective core that contained slope of grain (1 in 8, which is 7°), made up 15–17% of the log volume in the highly sinuous trees. Likewise, in radiata pine, Burdon (1975) assessed 18 clones at four sites and found no significant relationship between the rating of the tree's compression wood and sinuosity at any of the sites (r^2 ranging from 0.00 to 0.13).

The leader-flop hypothesis for causation of sinuosity holds that sinuous individuals develop stem curvature in the leader, whose angle is later overcompensated for by compression wood, leaving a permanent crook (Timell 1986; Grob and Carlson 1994; Downes et al. 1994). The vascular cambium has not yet developed in the distal stem portion (defined as the region of primary growth) but is present below the stem's mid-portion. If the distal stem portion flops (leans to one side), then the cambium will produce compression wood and will begin to reorient at the kinked (bent) part of the stem. The midportion will continue to produce compression wood and to reorient the distal stem portion long after the distal stem portion has reached vertical, thus causing overcorrection (reviewed in Timmell 1986). Thus, the tip of the stem will still not be vertical after the process has finished, which can lead to another crook with a lower magnitude, higher up the stem.

We hypothesized that individuals with long expanses of primary growth will be more likely to develop sinuosity than will stems with only short expanses of primary growth. This quantity of primary growth will depend on how quickly the stem elongates at the distal end, relative to how quickly the vascular cambium is produced behind the distal stem portion. Stems with long primary growth would be more apt to develop sinuosity because of their mechanical instability from having a longer lever arm of the same diameter, and they would be more prone to overcorrection because of the longer distance to the vascular cambium where the corrective tissue (compression wood) is being made.

Consistent with this mechanism, in a comparison of several families of radiata pine, the family with most rapid apical elongation was more susceptible to stem deformation (Downes and Turvey 1990; Downes et al. 1994). In a study of 24-year-old Douglas-fir, sinuosity was most common at 10–15 years, where annual height growth peaked (Spicer et al. 2000). Inconsistent with this mechanism, Campbell (1965) reported that shorter, wider leaders of Douglas-fir were more likely to be highly sinuous than were longer, more slender leaders.

The current study compared primary and secondary stem growth over the course of one growing season in the leaders of young Douglas-fir saplings. The hypotheses tested are that (*i*) primary stem length is positively correlated with degree of sinuosity, (*ii*) leader angle (measured from vertical) is greater in more sinuous individuals, and (*iii*) level of sinuosity at age 4 years is a good predictor of level of sinuosity at age 5.

Materials and methods

Plant materials

Douglas-fir saplings of 20 open-pollinated families from the Hebo Ranger District of the Siuslaw National Forest on the Oregon coast were grown in raised beds. When they were 4 years old, we selected 20 saplings of the 240 present that exhibited notable sinuosity in the previous year's leader (2001). These saplings represented the most sinuous individuals of the population that had no other stem deformities (proximal stem damage, forking, or ramicorn branches) and that were neither extremely tall nor extremely short. If morphological differences were to be shown for sinuous trees, we expected them to be found in this extreme population. These 20 saplings represented over one-half of the 20 families represented. Height of these stems was recorded. Next, we marked and measured the heights of 20 nonsinuous saplings of about the same height as each of the 20 sinuous saplings. Saplings were thereafter designated as belonging to one of two groups: either sinuous or nonsinuous in 2001.

These saplings were near the upper limit of the size that could be reached for measurements. We felt that their use was justified because, by this age, there is no reason to expect the apical growth to follow a different set of rules than in older trees, the proximal growth is relatively rigid, and trees were displaying sinuosity.

Phenology of primary and secondary stem development

Length of the secondary and primary stem produced in 2002 was determined for each sapling throughout the 2002 growing season. These were measured 10 times by the same observer during the 14 weeks from 16 May to 23 August. Each stem was manipulated gently between the thumb and next two fingers, from the base to the tip of the 2002 (current year's) growth to detect the location of the notable dis-

Table 1. Comparison of the sinuosity scores (SS) of two observers and the resultant sinuosity designation classes (SDCs).

	Observer 1 SS			
Observer 2 SS	1 (non)	2 (low)	3 (moderate)	4 (high)
1 (non)	6, nonsinuous	4, nonsinuous	1, mixed	0
2 (low)	1, nonsinuous	4, nonsinuous	7, mixed	3, mixed
3 (moderate)	0	0	1, sinuous	6, sinuous
4 (high)	0	0	0	7, sinuous

Note: Values in each cell are the number of samples for which observer 1 and observer 2 gave the listed SS, and the word description of the resultant SDC is given. See text for definitions of SS.

continuity in stiffness. This location process was readily repeatable. Pilot work with stem dissections showed that this discontinuity coincides with the location of the tip of the secondary thickening as evidenced by microscopic and macroscopic examination. The stem above this height was considered to be the primary stem, and the stem below it was considered to be the secondary stem.

Leader angle

On one date (26 June), we recorded the angle of the leader from vertical using a clear protractor with a plumb bob, held parallel to the distal 7 cm of the stem. This measurement is generally repeatable within one or two degrees by the same observer.

Postharvest measurements

On 8 August, the growth produced in 2001 (the fourth year) and 2002 (the fifth year) was harvested. Needles were removed. Stem distance was measured as the shortest span between nodes at the base and top of the 2001 and 2002 stem segments using a metre stick. Stem length, which was longer than stem distance if the stem had any curvature in it, was measured as the actual distance along the stem between the nodes at the base and top of the 2001 and 2002 stem segments using a string that was pressed all along the stem. This string followed all the curves in all dimensions. We calculated the distance/length ratio for 2001 stems and for 2002 stems. We tried other methods to quantify sinuosity, such as measuring the maximum stem deflection from a rod pressed into the nodes; however, because of the needles on the stem and the three-dimensional twisting of the stem, it was both difficult to perform this measure, and it did not necessarily reflect sinuosity as seen by an observer. If the stem had several large deflections on opposite sides of the stem, the stem would have a large slope of grain, but the deflections would not be very far from vertical. Because of these difficulties, we devised this simple, repeatable measure to capture sinuosity.

The 2002 stem was assessed for sinuosity by two observers. A sinuous stem was one that, like the letter S, crossed over the midline between the basal and apical nodes. A simple bow, like the letter C, was considered nonsinuous. The horizontal distance between the midline and the stem was termed the deflection. Initially, the stems were classified in four categories (called the sinuosity scores, SS): (1) nonsinuous, bow allowed; (2) low sinuosity, deflection less than one stem diameter; (3) moderate sinuosity, deflection one to three stem diameters; (4) high sinuosity, deflection more than three stem diameters.

Data analysis

The SS of the two observers were compared by examining a contingency table and examining correlations. One observer designated samples as more sinuous than the other observer, but overall, the scores were very similar (Table 1) with a correlation of $r = 0.795$ ($p < 0.0001$). Thus, SS was considered an objective measure of sinuosity. The two SS were then used to construct sinuosity designation classes (SDCs; Table 1), which were (*i*) nonsinuous (both observers scored as 1 or 2), (*ii*) sinuous (both observers scored as 3 or 4), or (*iii*) mixed (one observer scored as 1 or 2 and the other scored as 3 or 4).

Numerous growth patterns were examined for differences among SDCs: growth rate for each interval, primary growth length, secondary growth length, and total leader length (primary growth length + secondary growth length). Differences among the SDCs were tested for each sampling date with the GLM procedure of SAS (SAS Institute Inc. 1999) using the regression model $Y = SDC_i$, where Y is the dependent variable in question and SDC_i is the effect of the *i*th sinuosity class. The same procedure was used to examine differences in initial sapling height, maximum primary growth length (the largest value, regardless of date), and leader angle.

The consistency of sinuosity class from year to year was examined in two ways. A contingency table presented SDCs from 2002 and the initial designation given in 2001. Statistical significance was evaluated with a χ^2 test. The correlation between the distance/length ratio in 2001 and the distance/length ratio in 2002 for the individual saplings was also calculated.

Results

Differences by sinuosity class

Leader growth rate (cm of length/day) peaked at the beginning of June and then declined (Fig. 1*a*), which resulted in the total growth trend shown in Fig 1*b*. The length of primary growth on the leader peaked about 1 month later at the beginning of July (Fig. 1*c*). The length of secondary growth on the leader followed a linear trend from the beginning to the end of the measurement period (mid-May to late July; Fig. 1*d*).

For all dates at which SDCs differed significantly, the sinuous SDC grew more than the nonsinuous SDC (Fig. 1). Although the differences among SDCs were significant at $p <$

Fig. 1. Seasonal course of stem growth in Douglas-fir with various amounts of sinuosity in their leaders: (*a*) growth rate; (*b*) total growth length; (*c*) primary growth length; and (*d*) secondary growth length. Asterisks show dates at which there were significant differences ($p < 0.05$) in the three sinuosity designation classes.

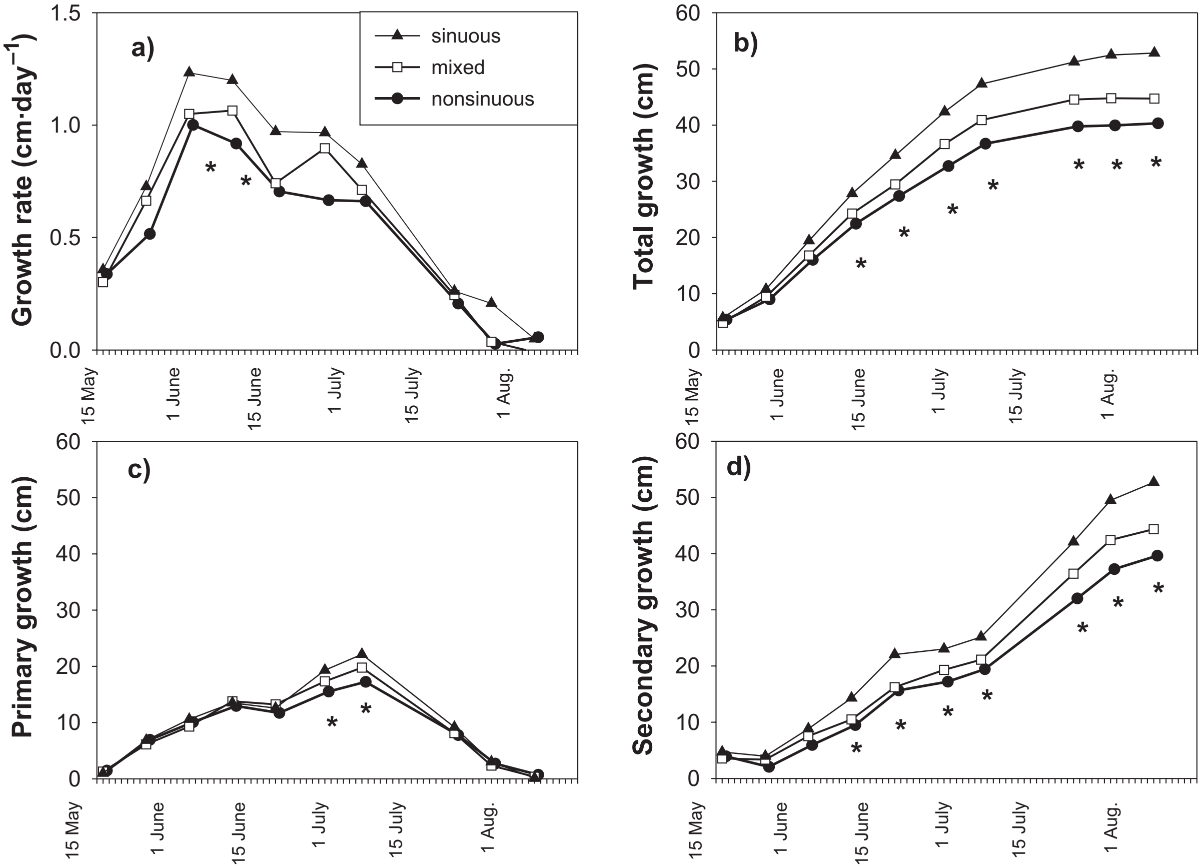

Table 2. Growth parameters of trees in the three sinuosity designation classes (SDCs).

SDC	*n*	Maimum primary growth length (cm)	Length/distance 2001	Length/distance 2002	Leader angle (°)
Nonsinuous	15	12.3 (5)	1.005 (0.0003)	1.009 (0.0004)	7 (2)
Mixed	11	12.8 (4)	1.007 (0.0005)	1.011 (0.0006)	8 (2)
Sinuous	14	13.5 (5)	1.009 (0.0004)	1.016 (0.0006)	9 (2)
p		0.0086	0.1193	0.0164	0.7778

Note: Values are means with SEs given in parentheses. See Table 1 for definitions of SDCs.

0.05, SDC only accounted for a small proportion of the total variation (r^2 ranging from 0.15 to 0.21; data not shown), indicating that growth rate had a statistically significant, but small role in sinuosity. Growth rate was significantly different among SDCs from 30 May through 21 June (Fig. 1*a*). The amount of primary growth differed significantly among the SDCs on 21 and 26 June (Fig. 1*a*). Secondary growth and total growth differed significantly among SDCs starting on 6 June and, being cumulative values, maintained significant differences throughout the season (Figs. 1*c* and 1*d*).

Maximum primary growth was higher in saplings in the sinuous SDC, followed by the mixed SDC, and then the nonsinuous SDC (Table 2). The length/distance of 2001 growth did not vary significantly by SDC; however, the length/distance of 2002 did, with sinuous plants having higher values, as expected (Table 2). There were no significant differences in leader angle among SDCs (Table 2).

Consistency of sinuosity classes from year to year

The contingency table using SDCs from 2002 and initial designations given in 2001 showed that there was some consistency in sinuosity classification between years, and the χ^2 value was significant (Table 3). For example, 11 individuals were designated as nonsinuous in both 2002 and 2001, and 12 individuals were designated as sinuous in both 2002 and 2001. Only six individuals (four sinuous and two nonsinuous, Table 3) were designated as sinuous in one year and nonsinuous in the other year.

Table 3. Sinuosity designation classes (SDCs) determined in 2002 and initial designation given in 2001 ($\chi^2 = 11.2$, $p < 0.004$).

	SDC in 2002		
Designationin 2001	Nonsinuous	Mixed	Sinuous
Nonsinuous	11	7	2
Sinuous	4	4	12

Note: See text for details.

There was a tendency for the length/distance of growth in 2001 to be correlated with length/distance of growth in 2002 ($r = 0.272$, $p = 0.0893$).

Discussion

As hypothesized, primary stem length was positively correlated with the degree of sinuosity. The maximum primary growth of the distal stem portion during the 2002 growing season was 12.3 cm in nonsinuous stems, 12.8 cm in stems designated as sinuous by one observer but nonsinuous by the other, and 13.5 cm in sinuous stems ($p < 0.0086$). However, in spite of significant relationships at many specific dates throughout the season, SDC explained very little of the variation in leader growth rate or length of primary, secondary, or total leader growth ($r^2 = 0.15–0.21$). In other words, sinuosity was only weakly linked to leader growth rate in this study. The study site was relatively sheltered; had it been on a less sheltered, windy site, perhaps we would have seen more of an effect of growth rates. Height growth rates averaged less than 60 cm/year (Fig. 1), and severe sinuosity is typically found on fast-growing sites where annual height growth rates are ≥1 m. Sinuosity class may explain more variation in the growth components on faster growing sites, suggesting that further research needs to be carried out on sites with faster growth rates. We also had hypothesized that leader angle would be positively correlated with degree of sinuosity. There was no significant difference in leader angle in saplings that were later classed as sinuous versus nonsinuous. These results strongly suggest that, in these Douglas-fir saplings, the leader-flop mechanism for production of sinuosity had at most a minor effect.

The study also showed that there was a moderate relationship between sinuosity in one year and sinuosity in the following year for these young saplings. The association was significant between consecutive years, but it was small. Such an association would support the hypothesis that there is a genetic basis for the sinuosity, although it would not go counter to some hypotheses of environmental control. Campbell reported that there was a strong genetic basis for sinuosity (1965), but others have shown low to moderate levels of genetic variation (Christophe and Birot 1979; Birot and Christophe 1983; Temel and Adams 2000). Spicer at al (2000) analyzed the radial-longitudinal surface of split trees and concluded that trees that were highly sinuous at age 12 were still highly sinuous at age 24. They found no consistent changes in the diameter of the defective core comparing among the first, second, and third 5 m logs, when judged by the core containing the pith or containing wood with slope of grain of 7°. They did find more stem deviations per internode in the middle log, but that was also where the internodes were the longest. Temel and Adams (2000) performed a genetic study in the same progeny trial from which Spicer et al. had studied. They found very low consistency between the extent of stem sinuosity at one specific node at age 12, and stem sinuosity of the internode on the lowest log having the greatest sinuosity at age 24. It is unclear whether that result was caused by the different methodology in the two studies or whether it reflects a true lack of correlation of sinuosity from year to year.

Therefore, the major cause of stem sinuosity in Douglas-fir is still unresolved. Environmental conditions are unlikely to have caused the sinuosity, because saplings from all sinuosity designation classes were intermingled in common beds, shared the same access to water and nutrients throughout the growing season, and had similar wind and light environments. It is possible that some individuals produce compression wood that can generate more force than other individuals, as has been studied in radiata pine (Downes et al. 1994). The current study, however, shows very little effect of rapid leader growth on development of sinuosity at the test location. Therefore, the statement that fast-growing trees tend to develop more sinuosity may need to be recast, because it did not appear that the fast growth per se is sinuosity's predominant cause.

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