Stem form and compression wood formation in young *Pinus radiata* trees

Barbara Lachenbruch, Fernando Droppelmann, Claudio Balocchi, Miguel Peredo, and Erika Perez

Abstract: The crooked stems of some individuals of radiata pine (*Pinus radiata* D. Don) can hinder volume recovery and wood quality. To infer causes of crookedness and to learn how lean angle affects compression wood (CW) formation we studied 5-year-old trees in southern Chile. Eight initially straight and eight initially crooked trees were tethered initially to angles of 15° or 30° or were left untethered for 131 days (48 trees total). There were no significant differences between straight and crooked trees in the extent of CW in pretreatment wood or in the relationship between stem angle and CW extent. Crooked trees, however, righted themselves more quickly than did straight trees at angles <15°, a result that supports the overcompensation hypothesis for the development of crooked stems. Stem angle had a complex effect on CW extent. In 2- to 3-year-old wood there was no meaningful effect of angle on CW extent. One-year-old wood produced less CW at stem angles <10° than at stem angles >10°, but above or below that threshold, there was no meaningful effect of angle on CW extent. The intertree differences in CW extent, as well as the correlation of leader CW extent with bole CW in the best individuals, suggests that CW assays could be used for early screening for wood quality.

Résumé : Chez le pin de Monterey (*Pinus radiata* D. Don), certains individus ont une tige tordue, ce qui peut affecter le rendement en volume et la qualité du bois. Afin d'élucider les causes de cette déformation et de comprendre comment l'inclinaison affecte la formation du bois de compression (BC), les auteurs ont étudié des arbres âgés de 5 ans dans le sud du Chili. Huit arbres initialement droits et huit autres initialement tordus ont été inclinés à 15° ou 30° ou ont été laissés libres pendant 131 jours (48 arbres au total). Aucune différence significative n'a été observée avant le traitement entre les arbres droits et les arbres tordus quant à l'ampleur du BC ou à la relation entre l'angle de la tige et l'ampleur du BC. Cependant, les arbres tordus se sont redressés plus rapidement que les arbres droits à des angles <15°, ce qui appuie l'hypothèèse de la surcompensation dans le développement des tiges tordues. L'angle de la tige a eu un effet complexe sur l'ampleur du bois de compression. Dans le bois âgé de deux à trois ans, l'angle n'a pas affecté l'ampleur du BC de manière significative. Le bois d'un an a produit moins de BC lorsque l'angle de la tige était inférieur à 10°, mais au-dessus ou au-dessous de ce seuil, l'angle n'affectait pas significativement l'ampleur du BC. Les différences dans l'ampleur du BC entre les arbres, ainsi que la corrélation entre l'ampleur du BC de la pousse terminale et celle de la tige chez les meilleurs individus, indiquent que la détection du BC pourrait être utilisée pour le dépistage hâtif de la qualité du bois.

[Traduit par la Rédaction]

Introduction

In some cases, radiata pine (*Pinus radiata* D. Don) plantations have individuals with markedly poor stem form, showing kinks and crooks within 1 year's growth as well as sweep spanning several years' growth. Such stem form will hinder volume recovery and lower market value. Recovery is hindered primarily by the log's form. As well, wood quality can be decreased by the elevated incidence of compression wood (CW) in crooked logs and (or) by the embedded CW within straight logs if the crooked saplings eventually improve their stem form. CW decreases log value because of its negative effects on lumber appearance, longitudinal shrinkage, and warp (duToit 1963; Harris 1977; Cown et al. 1996; Donaldson and Turner 2001). CW also makes poor pulp because of the increased lignin content, lower yield, shorter tracheids, and inferior strength properties of the resulting paper (Watson and Dadswell 1957). This study focuses on CW in young straight-stemmed and crooked-stemmed *P. radiata* trees. We investigated whether there is a difference between straight and crooked trees in the incidence of CW and (or) in the angles needed to induce CW production. We also used the data to investigate a biomechanical explanation for stem crookedness and to infer genetic variation in the CW response.

Extent of CW in straight versus crooked trees

Following the assumption that CW will form where stems are inclined beyond their "equilibrium position" of near ver-

Received 17 March 2009. Accepted 29 September 2009. Published on the NRC Research Press Web site at cjfr.nrc.ca on 13 January 2010.

B. Lachenbruch.[1] Department of Wood Science and Engineering, Oregon State University, Corvallis, OR 97331, USA.
F. Droppelmann and E. Perez. Instituto de Silvicultura, Universidad Austral de Chile, Valdivia, Chile.
C. Balocchi and M. Peredo. Bioforest S.A, Concepción, Chile.

[1]Corresponding author (e-mail: barb.lachenbruch@oregonstate.edu).

tical (reviewed in Wilson and Archer 1977, 1979), it is reasonable to assume that vertical trees with straight stems will not have CW, and that vertical trees with crooked stems will probably have CW. Many studies, however, show that straight trees do, indeed, contain some CW (e.g., Zobel and Haught 1962; Barger and Ffolliott 1976; Donaldson et al. 2004) or that there is no positive correlation between the percentage of CW and stem straightness (Shelbourne and Stonecypher 1971). As summarized by Timell (1986, p. 711), "many straight, vertical, stems have attained this favorable growth form because they had been able to counteract earlier displacements by forming compression wood". He continues by stating that "few coniferous trees are completely devoid of compression wood". Donaldson et al. (2004) compared one leaning and one straight tree of *P. radiata*. They reported that 28% of the growth rings examined in the straight tree had CW (1% had severe CW, 27% had mild CW), whereas 38% of the growth rings in the leaning tree had CW (20% had severe CW, 18% had mild CW). In a study of breast height stumps of *Pinus palustris* and *Pinus taeda*, Pillow and Luxford (1937) reported that 10% of the vertical trees had produced CW in their outer growth rings. The amount of CW seen on sequential cross-sections in merchantable logs of vertical 17- to 52-year-old *P. taeda* trees averaged 6% (Zobel and Haught 1962). In vertical *Pinus ponderosa* Dougl. ex P. & C. Laws., CW was present in the outer 2.5 cm of sapwood in 7% of the young trees ($n = 64$) and in 13% of the old-growth trees ($n = 100$) (Barger and Ffolliott 1976). Thus, we would expect to find some level of CW in the boles of both straight trees and crooked trees.

Effect of angle on extent of CW

The extent of inclination necessary to stimulate CW development in *P. radiata* is unknown. Our understanding of where CW will form is surprisingly incomplete in spite of sophisticated research on its formation (e.g., Sinnott 1952; Archer and Wilson 1973) and a century of investigation of its incidence (reviewed in Pillow and Luxford 1937; Westing 1965, 1968; Wilson and Archer 1979; Timell 1986). Timell (1986) stated that CW development in conifers may show any of the following patterns: have very little relationship with inclination angle, increase continuously with increasing inclination, increase to an asymptote, or peak at an intermediate stem angle and then decline. However, some of the variability in reported patterns may result from studying different genotypes (e.g., Zobel and Haught 1962; Burdon 1975), or different ranges of angles, tissue ages (e.g., Barger and Ffolliott 1976; Spicer et al. 2000), or heights (e.g., Low 1964; Burdon 1975). Archer and Wilson's (1973) simulations of where CW would be expected in a growing tree show some of the computational and data-collection difficulties in predicting the location of CW and the duration of its production.

Over some range of angles, there is usually a positive effect of inclination on CW incidence (reviewed in Westing 1965; Timell 1986), although there is often large tree-to-tree variation. Burdon's (1975) study of *P. radiata* clones, however, reported no significant relationship between the average degree of tree lean at four sites and the average CW rating at those four sites. Barger and Ffolliott (1976) showed a weak correlation ($r = 0.22$) between stem angle and CW amount in old-growth *P. ponderosa* at the top of the first merchantable log. Zobel and Haught (1962) conducted a thorough census of CW within the stems of 15 *P. taeda* trees in which they examined cross-sections for CW every 61 cm (2 ft) up the stem. They found broad overlap in the amount of CW in trees in the three inclination classes: straight trees ($n = 5$) had 3%–8% CW, intermediate trees ($n = 5$) had 5%–14% CW, and crooked trees ($n = 4$) had 12%–19% CW. Our prediction for the current study was that there would be a weak positive effect of inclination on CW incidence.

Evidence for overcompensation as a cause of crookedness

There has been much research into the causes of stem deformation (crookedness) in *P. radiata* in old pasture sites and in response to high and low supplies of mineral nutrients (Downes and Turvey 1990, 1993; Turvey et al. 1992, 1993; Downes et al. 1994). The results have shown that nutrition is often related to stem lignification and (or) slenderness relative to foliar mass, both of which could potentially contribute to stem crookedness. On nutritionally good sites stem crookedness in *P. radiata* has been related to previous land use (Carlyle et al. 1989; Birk et al. 1993), wind environment (Burdon 1975; Turvey et al. 1993), understory competition (Peri et al. 2002), and other unidentified site factors (Burdon 1975; Jayawickrama and Balocchi 1993). Stem crookedness in this species has a strong genetic component (Pederick et al. 1984; Downes and Turvey 1993; Jayawickrama and Balocchi 1993; Jayawickrama et al. 1997). However, the knowledge that a cause is genetic does not reveal the actual physiological or structural mechanism by which trees differ in stem crookedness. Compared with crooked trees, for example, straight trees could have a more vertically aligned apical bud, they could have stiffer stems through stoutness (Downes et al. 1994) or material properties, and (or) they could react differently to small changes in the apex's orientation (Sierra-de-Grado et al. 2008).

In this research, we tested only the latter mechanism, related to the reaction to inclination, which is termed "overcompensation". In overcompensation, the apex of a crooked leader may grow toward a vertical orientation relatively quickly, whereas the lower part of the leader adjusts its orientation toward vertical more slowly through the production of CW. The CW is position-appropriate for the lower part of the leader, but if it occurs too quickly or too slowly relative to tip growth, it will push the former apex (no longer at the apex because of continued growth) away from vertical. The former apex then produces CW to adjust toward vertical, and so on (Harris 1977; Timell 1986, pp. 763–771; Downes et al. 1994; Gartner and Johnson 2006).

Tree-to-tree differences in response to inclination

For the purposes of genetic improvement, it would be useful to learn whether some individuals consistently have less CW than others and whether assessment of CW in the leaders can be used to identify the least or most CW-prone clones. Burdon (1975) showed that *P. radiata* genotypes differ in their propensity to form CW. He also showed that genotypes differed in CW amount across different sites, presumably because of differing site conditions.

In the current research, we studied young *P. radiata* trees in a 4-year-old plantation in southern Chile, comparing initially straight and initially crooked trees that we then inclined in several treatments. By following stem angle and then studying the wood formed before and throughout treatments, we were able to test the following hypotheses: (1) trees with straight stems have less CW than trees with crooked stems, (2) the amount of CW in samples from either straight or crooked trees is positively correlated with the sample's stem inclination, and (3) straight trees produce more CW at a given angle of stem inclination than do crooked trees. We also used the results to speculate on whether stem crookedness is caused by overcompensation and to ask whether CW extent can be used as an early screening tool for *P. radiata* wood quality.

Materials and methods

Site and plant material

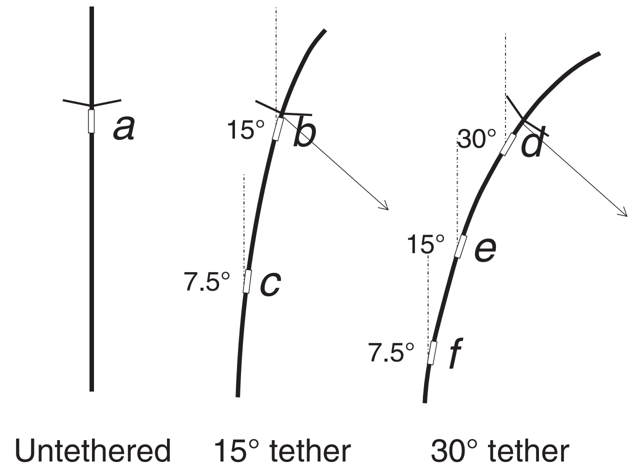
Pinus radiata trees were sampled from the San Alejandro farm (39°45′16″S, 72°54′14″W, 100 m elevation), a 4-year-old operational plantation located 30 km east of Valdivia, Chile. The soil is recent volcanic ash over metamorphic material. Pichoy weather station, 20 km away, receives about 2377 mm of precipitation annually (The Royal Netherlands Meteorological Institute, http://climexp.knmi.nl/getprcpall.cgi?someone@somewhere+85767.4+VALDIVIA/PICHOY+). The plantation had previously supported at least one rotation of *P. radiata* trees. Trees were half-sibs (derived from the same seed trees but with various pollen genotypes) and were planted as 1-year-old seedlings in 2002.

Implementation of treatments

Two observers walked between rows of trees, searching for extremes of stem form that were vertical and either very straight or very crooked. Straight trees had main stems that were within 3° of vertical and that appeared straight, both within interwhorls (the space between major branch whorls) and in the mutual alignment of subsequent interwhorls. Crooked trees had main stems with marked sinuosity and (or) several occurrences of marked sweep. The form of the current year's leader growth was not considered because leaders on straight trees are not always straight.

After 24 straight and 24 crooked trees had been found, we divided them haphazardly into three treatments for each stem form (n = 8 for each treatment and stem form combination): untethered, tethered so that the initial angle was 15° from vertical, and tethered so that the initial angle was 30° from vertical (Fig. 1). Treatments were installed on 11 January 2006 (ordinal date 11, abbreviated here as JD 11), at which time trees were partway through their fifth year of growth. For trees in the 15° and 30° tether treatments, we attached a tether just below the final branch whorl of the previous growing season. The tether was made of heavy-gauge wire that was looped around the stem and attached near ground level to a stake; within the loop the wire was covered with hose. Tethered trees were pulled tightly in the direction of the prevailing wind so that the stem segment in the 20 cm long zone immediately below the tether was either 15° or 30° from vertical. Tethered trees were free to move within the constraints of this one wire. The morphologically identical zone was identified in untethered trees.

Fig. 1. Diagram of the three inclination treatments showing locations of the positions studied along the main stem (white boxes); not to scale. There were eight initially straight and eight initially crooked trees in each treatment.



The center of the 20 cm long zone was marked with white corrector fluid (designed for use on paper), which was durable and very visible on wet bark. The zone was designated as position *a*, *b*, and *d* in each of the trees that were in the untethered, 15°, and 30° treatments, respectively (eight straight trees and eight crooked trees per treatment; Fig. 1). On the 15° trees we also marked the position at which the stem was at 7.5° (position *c*, Fig. 1), and on the 30° trees we marked the positions at which the stem was at 15° and at 7.5° (positions *e* and *f*, respectively, Fig. 1). All stems were also marked at breast height (1.3 m).

Angle measurements

Angles were measured at all positions (*a*, *b*, *c*, *d*, *e*, and *f*) six times throughout the 131 day experiment using a transparent protractor with a weighted string tied to the center. The same observer stood several metres from the tree at 90° from the tether and aligned the protractor visually with the 20 cm zone of each marked stem position. The string on the protractor indicated the stem angle.

Harvest, heights, diameters, and crook index

On 22 May 2006 (JD 142), 131 days after treatments had started, we felled the trees and measured height of each position, total tree height, and over-bark diameter at each marked position and at breast height. Final leader length was the difference between total height and the height of the upper branch whorl. The 20 cm long segments from each position (n = 96) were excised and transported to the laboratory at the Universidad Austral de Chile campus. There they were sawed transversely at their center.

We also brought the leaders from all 48 trees to the laboratory to estimate their crookedness and their CW content. The leader was defined as the main stem distal to the previous year's uppermost branch whorl. The amount of crookedness in the leaders was calculated as the crook index as follows: the stem's length following its curves minus the stem's straight-line length, all divided by the straight-line length, and multiplied by 100. We used a straight coated telephone wire to measure lengths because this product was pliable enough to follow the stem's curves but stretched very little when pulled taut. Next, we excised 10 short stem segments from each leader for observation of CW. The segments were taken at even intervals extending from 5 cm above the leader's base to 15 cm below the tip.

Estimates of number of growth rings

We visually estimated the number of growth rings in the samples from positions *a* through *f*. In some samples this estimate required the use of a razor blade and hand lens to make the annual banding clearer. Some of these trees had several growth periods per year, and so the values we report are our best interpretations and probably contain some error.

Radial growth and eccentricity

For positions *b*, *c*, *d*, *e*, and *f*, we estimated radial growth from the increment of new wood that was detectable on the cross-sections at the location at which the CW was most developed (heavy bar, Fig. 2). For position *a*, which had no new CW to mark the experiment's start, we estimated radial growth from the difference in the over-bark diameter at the beginning and end of the experiment divided by two.

We could not calculate eccentricity of new xylem production because we could only identify the posttreatment increment in the part of a stem circumference that had new CW. Instead, we defined the eccentricity index as the difference between the diameter where the CW was most developed and the diameter perpendicular to that location. Mean xylem diameter was obtained from these two diameters. The same criterion was applied to position *a*, even though the CW present was not induced by tethering. All radial growth and eccentricity measurements were made with digital calipers.

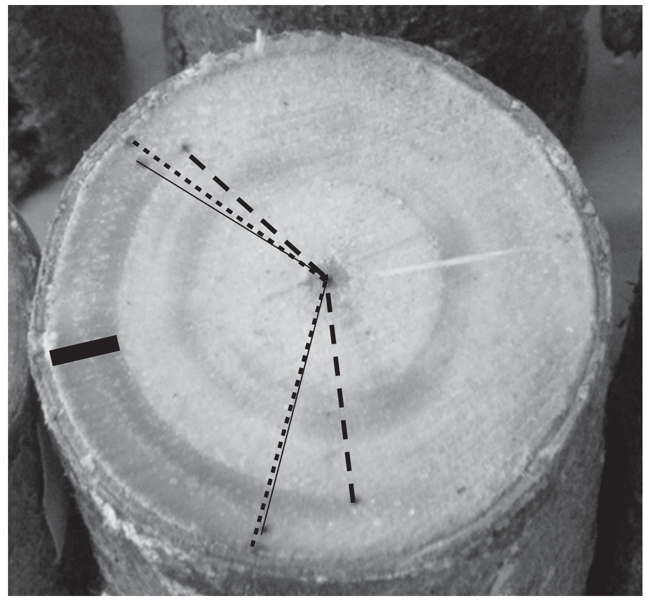
Estimates of CW quantity

We wetted the cross-sections with water to enhance the color contrast between normal wood and CW before undertaking measurements of CW extent. We used the presence of brown coloration as an indicator of CW; microscopy on a subset of samples showed that this method was justified for identification of presence or absence of moderate to severe CW; undoubtedly some mild CW (Donaldson et al. 2004) was undetected. Samples were inspected under a table-mounted magnifying lens.

For pretreatment wood, we identified the zone of the cross-section that was present before the experiment started, evident by the start of the brown crescent in inclined trees (Fig. 2). For untethered trees, we delineated the pretreatment wood with a pencil using pretreatment and postexperiment diameter information. Samples were scored from 1 to 6 on the basis of the proportion of the surface area that was CW: 1, no sign of CW; 2, <5% CW; 3, 6%–15% CW; 4, 16%–25% CW; 5, 26%–40% CW; and 6, 41%–60% CW. Estimates were made visually, with calibration against a paper showing examples of these proportions. All 96 samples were evaluated together with their labels hidden.

Extent of CW in the posttreatment wood was estimated as the proportion of the circumference in which the new wood was brown, at three radial locations within the new growth: at the beginning, middle, and end of the new growth (Fig. 2). We drew radii to delimit the CW zones at each of these radial locations and then measured the angle between the radii. We could then calculate CW extent (%) as 100 × CW angle (°) divided by 360°. We assumed that stems were circular in cross-section (later supported by the eccentricity data, see Table 2).

Fig. 2. Measurement of new radial growth (heavy bar) and compression wood (CW) extent for the CW produced during the experiment. CW extent is reported as the percentage of the stem circumference that has visible CW at the beginning (long-dashed lines, JD 11), middle (solid lines, estimated as JD 77), and end of the new radial growth (short-dashed lines, JD 142). It is calculated as 100 × the angle between pairs of radii/360°. Pretreatment wood is the wood interior to the heavy bar.



We ranked the 48 leaders visually on the basis of the proportion of the cross-section that was CW as follows. All 10 subsamples from one leader were moistened and then placed with their cross-section facing upward in a 15 cm diameter Petri dish. Petri dishes were shifted along the table until two observers agreed with the rankings, where rank 1 was assigned to the leader with the lowest proportion of CW, and rank 48 was assigned to the leader with the highest proportion of CW.

Data analysis

The tree-level variables (initial tree height, final diameter at breast height (DBH), final leader length, crook index, and leader CW rank) were analyzed by two-factor analysis of variance (ANOVA) and type III sum of squares using SAS version 6.11. The factors were stem form (initially straight or initially crooked) and inclination (untethered, 15°, or 30°). Comparisons within a treatment were then conducted using Duncan's *t* tests.

The variables that came from more than one position per tree were analyzed with a two-factor ANOVA using SAS version 6.11. The factors were stem form (initially straight or initially crooked) and position (*a*, *b*, *c*, *d*, *e*, or *f*). These variables were sample height, final number of growth rings in a sample, final sample diameter, radial growth during the experiment, eccentricity index, pretreatment CW score, and CW extent at JD 11, JD 77, and JD 142.

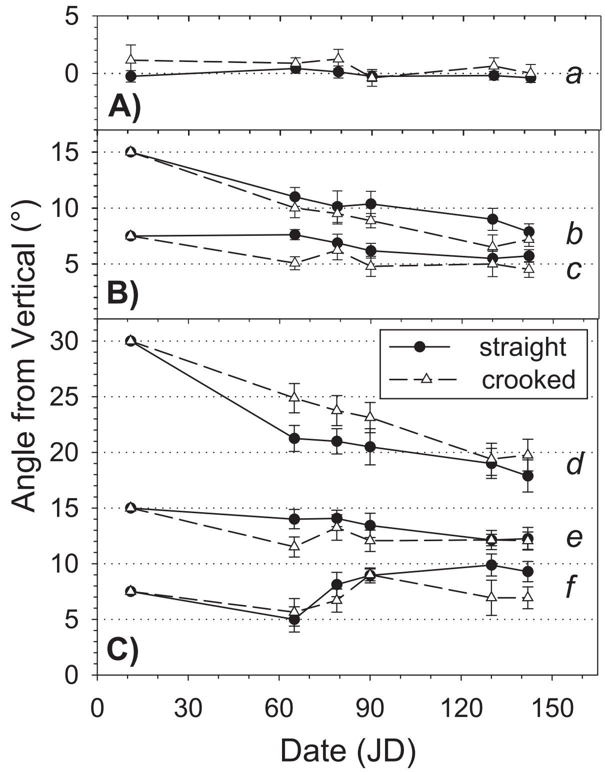
The relationship between crook index and leader CW rank was represented graphically and inspected. The values rose rapidly and then leveled out, suggesting a regression of the form $y = a(1 - e^{-bx})$. Regression analysis was calculated with SigmaPlot 2002 for Windows version 8.

We plotted mean angle of a position against date for both stem forms and all positions (Fig. 3). The plot revealed that straight trees corrected their angle more quickly than crooked trees at angles >15° (position *d*), but that the opposite appeared to occur at positions <15° (*b*, *c*, *e*, and *f*), where straight trees corrected their angles more slowly than did crooked trees. To determine whether these patterns were significant, we conducted a repeated measures one-factor ANOVA for angle, using stem form as the factor (SAS PROC MIXED with repeated measures). We included only the data from positions that were originally at angles <15° (*b*, *c*, *e*, and *f*) for the five dates beginning on JD 65.

As one means of characterizing the within- and among-tree differences in response to inclination, we ranked trees within a treatment by their CW extent. There were two measures of CW extent: the value at JD 11 and the value at JD 142, the beginning and end of the experiment, respectively. First, we plotted CW extent versus position for all trees. There were one, two, or three samples for trees in the untethered, 15°, and 30° inclinations treatments, respectively. Next we calculated the mean CW extent (as the average from both dates and all samples per tree) for each of the 48 trees and then ranked all 16 trees in a treatment from the tree with the least CW to the tree with the most CW. The two best trees in each tether treatment were defined as those with mean CW extent in the lowest five rankings at both dates.

As a second means of characterizing the within- and among-tree differences in response to inclination, we examined the relationship between the CW extent just below the leader (positions *a*, *b*, and *d*) and the leader CW rank. CW extent was calculated in three ways: the mean of the three assessed dates, the maximum value of the three assessed dates, and the value on JD 11. Leader CW rank was tabulated for each of the inclination treatments separately (n = 16 trees per inclination treatment). Low values had the least CW. We plotted CW extent versus the respective leader CW rank and inspected the plots visually.

Fig. 3. Inclination angle versus ordinal date (JD) for straight and crooked trees: (A) untethered trees (position *a*), (B) tethered trees inclined to 15° (positions *b* and *c*), and (C) tethered trees inclined to 30° (positions *d*, *e*, and *f*). Values are means ± SE; n = 8 trees per treatment combination.



Results

Tree and sample description

There was no evidence that the trees differed in height at the beginning of the experiment: the height of the upper position of all trees (mean ± SE) of positions *a*, *b*, and *d*) was similar for straight trees and crooked trees (2.60 ± 0.08 and 2.57 ± 0.08 m, respectively; n = 16). However, at the end of the experiment, on average, the straight trees were significantly taller and had significantly longer leaders than the crooked trees (Table 1). There were no significant differences in tree height or leader length by treatment (Table 1). At the end of the experiment, there were no significant differences in DBH by either stem form or treatment (Table 1). The mean heights from which the samples were taken, the number of growth rings in the samples, the mean sample diameters, and radial growth all varied significantly by position but not by stem form (Table 2). On average, the oldest samples were 2–3 years old and came from position *f*, and the youngest samples were 1–2 years old and came from positions *a*, *b*, and *d*. Stem eccentricity showed no significant difference by stem form or position: the stems were essentially circular in cross-section. For the average sample from straight trees, for example, the xylem diameter was 54.6 mm, and the diameter with the maximum proportion of CW was 0.1 mm smaller than the perpendicular diameter.

Leaders

Both the crook index and the leader CW ranks differed significantly by treatment but not by stem form (Table 1). The lack of difference in crook index by stem form is consistent with our observations that crookedness in the leader is not well-correlated with crookedness farther down the stem. On average, untethered trees had a crook index of 0.36 (their leaders were 0.36% longer than the straight-line length), trees inclined to 15° had a crook index of 0.95%, and trees inclined to 30° had a crook index of 2.25%. An analysis of just the untethered trees also showed no significant difference in crook index between the straight-stemmed trees (0.35 ± 0.08, mean ± SE) and the crooked-stemmed trees (0.38 ± 0.06).

Mean leader CW rank was lowest in untethered stems followed by those inclined to 15° and then by those inclined to 30° (Table 1). There was a significant positive relationship

Table 1. Probabilities (*P* values) and means for the variables associated with individual trees.

	P value			Mean				
				Stem form		Treatment		
	Treatment	Stem form	Treatment × form	Initially straight	Initially crooked	Untethered	15°	30°
Final tree height (m)	ns	<0.004	ns	4.79a	4.35b	4.59	4.66	4.47
Final DBH (mm)	ns	ns	ns	76	73	76	74	73
Final leader length (m)	ns	<0.001	ns	2.15a	1.79b	2.08	1.99	1.85
Crook index (%)	<0.0001	ns	ns	1.15	1.22	0.36a	0.95b	2.25c
Leader CW rank	<0.0001	ns	ns	25.8	23.2	12.5a	24.6b	36.4c

Note: Within rows, means followed by the same letter do not differ significantly according to post-hoc tests.

Table 2. Probabilities (*P* values) and means for variables measured at different positions.

	P value			Mean								
				Stem form		Position						
	Stem form	Position	Stem form × position	Initially straight	Initially crooked	*a*	*b*	*c*	*d*	*e*	*f*
Sample height (m)	ns	<0.001	ns	1.99	2.00	2.49a	2.71a	1.56b	2.55a	1.56b	1.13c
Growth rings in sample (no.)	ns	<0.001	ns	1.9	2.0	1.6a	1.4a	2.0b	1.5a	2.3b	2.8c
Sample xylem diameter (mm)	ns	<0.001	ns	54.6	52.0	45.6	43.1	61.4	42.3	58.2	69.2
Radial growth (mm)	ns	<0.001	ns	10	9	8a	9b	10b	10b	10b	10b
Eccentricity index (mm)	ns	ns	ns	–0.1	0.2	–0.1	0.0	0.2	0.7	–0.2	–0.1
Pretreatment CW score	ns	<0.001	ns	2.8	3.1	2.9ab	2.2b	3.5c	1.9b	3.6c	3.9c
CW extent, JD 11 (%)	ns	<0.001	ns	38	39	5a	44b	43b	45b	46b	47b
CW extent, JD 77 (%)	<0.02	<0.001	ns	33a	30b	6w	29x	36y	39yz	40yz	40z
CW extent, JD 142 (%)	ns	<0.001	ns	29	26	3a	15b	35c	37c	39c	38c

Note: JD, ordinal date. Within rows, means followed by the same letter do not differ significantly according to post-hoc tests. Values for sample height, final growth rings, xylem diameter, radial growth, and eccentricity index are from the end of the experiment.

between a leader's crook index and its CW rank (Fig. 4), showing that the most crooked trees tended to have a higher incidence of CW than less crooked trees. Straight trees tended to have a higher leader CW rank than did crooked trees for the same crook index (Fig. 4).

Angle measurements

As expected, the angle of the samples from the untethered stems (position *a*) did not change substantially over the course of the study (Fig. 3A). There was a gradual decline in mean angle at positions *b*, *c*, *d*, and *e* during the experiment (Figs. 3B and 3C), indicating that there was some degree of angle correction ("righting") for trees in both of the inclination treatments. In contrast to the monodirectional changes in positions *b*, *c*, *d*, and *e*, the angle of position *f* (the lowest position and originally at 7.5° in the trees that were inclined to 30°) decreased in the first 2 months and then increased to angles that were as high as or higher than the initial value (Fig. 3C). These increases may have resulted from the increase in stem length and stem mass (particularly mass near the tip), which would cause the largest overturning moment in stems with the highest inclination.

At the upper position of the 30° trees (position *d*), the straight trees, on average, had lower stem angles than the crooked trees, and this difference was significant at the first date assessed (JD 65). In contrast, the repeated measures ANOVA for positions *b*, *c*, *e*, and *f* showed that straight

Fig. 4. Crook index (the stem's length following its crooks minus the stem's straight-line length, all divided by the straight-line length, and multiplied by 100) versus leader compression wood (CW) rank (low values indicate low CW incidence). Black symbols represent straight trees, and gray symbols represent crooked trees; "u" represents untethered, and 15° and 30° represent tethered trees inclined to 15° and 30°, respectively. The regressions is of the form $y = a(1 - e^{-bx})$. For all trees, adjusted $r^2 = 0.50$; for straight trees, adj. $r^2 = 0.65$; and for crooked trees adj. $r^2 = 0.35$.

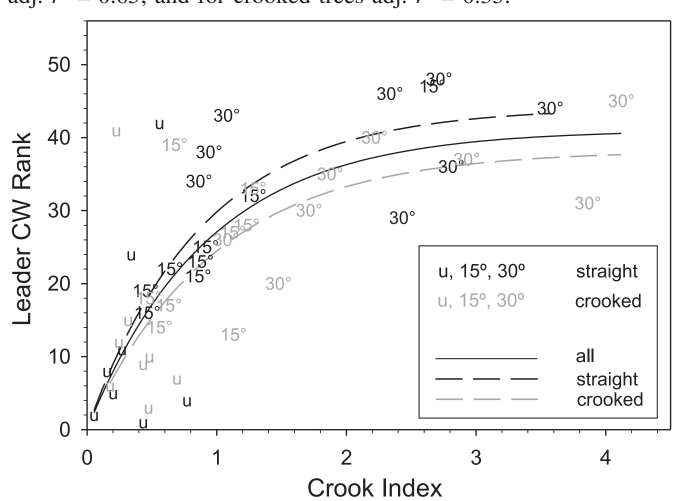
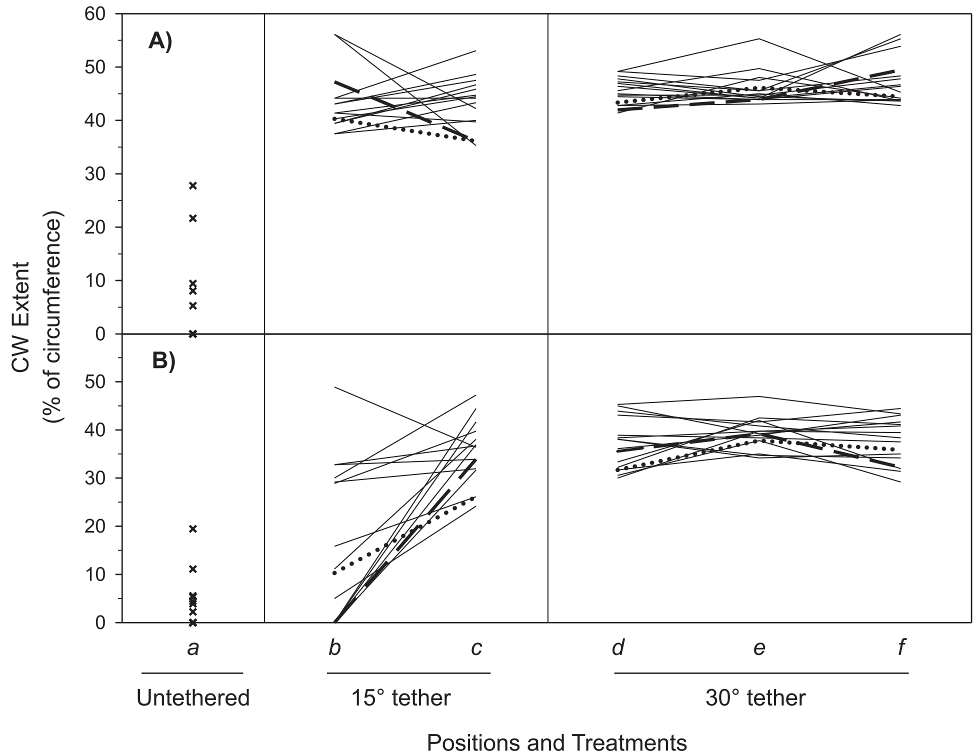


Fig. 5. Compression wood (CW) extent of individual trees by position in wood formed (A) immediately after treatments were imposed (JD 11) and (B) at the end of the experiment (JD 142). Untethered trees had only one position, *a*. Tethered trees inclined to 15° had two positions, *b* near the top and *c* lower on the stem. Tethered trees inclined to 30° had three positions, *d* near the top, *e* in the middle, and *f* lower on the stem. Each line or symbol represents an individual tree (n = 16 trees per treatment). Heavy dashed lines and dotted lines show the best and second best individuals in each tethered treatment, respectively (see Materials and methods).



trees had significantly higher angles (less angular correction) than the crooked trees ($P < 0.001$, data not shown), and as expected, that angles were different at different dates ($P < 0.004$). There was also a significant stem form × individual tree interaction, emphasizing the tree-to-tree variability of responses ($P < 0.001$).

Compression wood in pretreatment wood

The pretreatment CW scores did not differ significantly between straight and crooked trees (Table 2). The overall mean score of about 3 (corresponding to 6%–15% CW on the cross-section) demonstrated the large amount of CW present in wood before the experiment started. There were significant differences with position, with relatively large pretreatment CW scores at the lowest positions (*c*, *e*, and *f*, scores of about 3.7) and smaller pretreatment scores just below the leader (positions *a*, *b*, and *d*; scores of about 2.3).

Compression wood in posttreatment wood

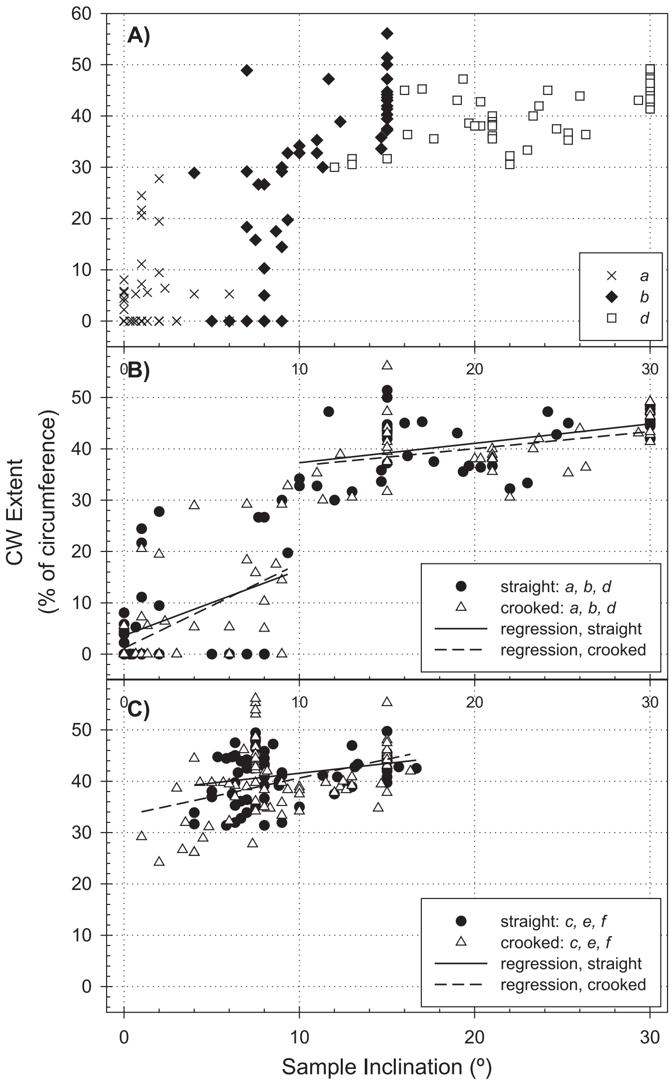
The upper positions (*a*, *b*, and *d*) are the simplest to compare for CW extent because they are in the same position and are thus of the same age but have different inclination treatments. Mean values of CW extent near the beginning of the experiment (JD 11) were 5%, 44%, and 45% for positions *a* (untethered), *b* (15°), and *d* (30°), respectively (Table 2). At the end of the experiment, after the trees had adjusted their angles for 131 days (JD 142), the mean values of CW extent were 3%, 15%, and 37% for positions *a*, *b*, and *d*, respectively (Table 2).

Initially, inclination to any angle induced the production of CW in about 45% of the circumference, on average (Table 2, positions *b*, *c*, *d*, *e*, and *f*; Fig. 5A). Position *a* (untethered) had CW in only about 5% of the circumference at this initial date, and this amount of CW did not change substantially through the experiment (Table 2, Fig. 5A). By the last two dates, differences in CW extent had developed among different positions. At most positions the extent of CW decreased, and position *b* had significantly less CW than did the other positions at both of the later dates (Table 2, Fig. 5B). This decline is consistent with the decline in stem angle for a given position throughout the experiment (Fig. 3).

On the initial and final dates (JD 11 and JD 142, respectively), CW extent did not differ between stem forms. However, at the intermediate date (taken as JD 77), there was a significant difference between stem forms, although the values were not strikingly different (33% vs. 30% CW, Table 2). This significant difference may have resulted from the fact that at the intermediate date, the majority of the positions had higher mean inclination angles in the straight than in the crooked trees (Figs. 3B and 3C).

CW extent versus sample inclination was depicted graphically using three data points per sample, representing values estimated for JD 11, JD 77, and JD 142 (Fig. 6). The upper positions (*a*, *b*, and *d*, averaging 1–2 years old, Table 2) displayed a threshold response: at angles <10°, upper positions produced CW in 0%–30% of the circumference (with two outliers), and at angles of 10°–30°, upper positions produced

Fig. 6. Compression wood (CW) extent versus sample inclination for straight and crooked trees. (A) Upper positions *a* (from untethered trees), *b* (from tethered trees inclined to 15°), and *d* (from tethered trees inclined to 30°). (B) Upper positions (*a*, *b*, and *d* pooled) for samples from trees that were originally straight versus trees that were originally crooked. (C) Lower positions (*c*, *e*, and *f* pooled) for samples from trees that were originally straight versus trees that were originally crooked. There are three data points from each of the 96 samples, representing wood produced on JD 11, JD 77, and JD 142. Regression lines are shown for the straight trees and the crooked trees separately.



CW in 30%–56% of their circumference (Figs. 6A and 6B). The fact that samples from position *b* showed this threshold response (Fig. 6A) demonstrates that the response was not an artifact of the tethering because these samples were initially tethered and inclined to 15° but reoriented to angles as low as 4°, so they spanned both sides of the 10° threshold. In contrast to samples from the upper positions, samples from the lower positions (*c*, *e*, and *f*, averaging 2–3 years old) showed no threshold response (Fig. 6C).

All regression lines for CW extent versus sample inclination were similar for straight and crooked trees (Figs. 6B and 6C), and so data were pooled for further analysis. The slope for samples from the upper positions at <10° was not significantly different from the slope of lower samples over the entire range of angles (Table 3). In all cases the slopes were positive and the coefficients of determination were very low ($r^2 < 0.20$, Table 3).

Within- and among-tree differences in response to inclination

CW extent was highly variable from tree to tree at both dates for untethered trees (position *a*), but for the tethered trees, the tree-to-tree variability increased from the beginning (Fig. 5A) to the end of the experiment (Fig. 5B). The two best trees in each of the inclined treatments (those with means in the lowest five rankings at both dates) are highlighted with bold lines in Figs. 5A and 5B.

CW extent in the upper stem position was associated with leader CW rank in untethered trees but not in tethered trees (Fig. 7) with the exception of a weak positive association for the trees at 15° using mean CW extent (Fig. 7A). The observed pattern (the association in tethered trees and lack of association in untethered trees) was similar for all three measures of CW extent. The straight and crooked trees were distributed throughout the entire leader CW ranks within treatments (Fig. 7) as they had been when all treatments were pooled (Fig. 4).

Discussion

Extent of CW in straight versus crooked trees

The first hypothesis, that trees with straight stems have less compression wood (CW) than trees with crooked stems, was not supported by the data. There was no effect of stem form on either pretreatment CW score or stem eccentricity at the experiment's conclusion (Table 2). The presence of CW in the straight stems is consistent with reports in *P. radiata* (e.g., Burdon 1975), *P. taeda* (e.g., Zobel and Haught 1962), and *P. ponderosa* (Barger and Ffolliott 1976).

Pretreatment wood had less CW in the upper positions of all trees (*a*, *b*, and *d*) than in the older, lower positions (Table 2). This CW distribution is consistent with the results of studies that have reported more CW at the base of trees than higher up along the stem (e.g., Low 1964; Harris 1977).

Effect of angle on extent of CW

The second hypothesis was that the amount of CW is positively correlated with the sample's inclination. The hypothesis was not supported for the lower positions (*c*, *e*, and *f*) and was partially supported for the upper positions (*a, b*, and *d*). Although there were positive relationships between stem inclination and CW extent for the upper positions at inclinations <10°, upper positions at inclinations >10°, and lower positions, the coefficients of determination were extremely low, ranging from 0.12 to 0.20 (Table 3). Variation in stem inclination explains so little of the CW extent that we interpret that there was no meaningful relationship for the lower positions (*c*, *e*, and *f*). We interpret that for the upper positions (*a*, *b*, and *d*) there was a simple threshold effect: below 10°, one range of CW extents was possible; above 10°, a different, higher range of CW extent was possible.

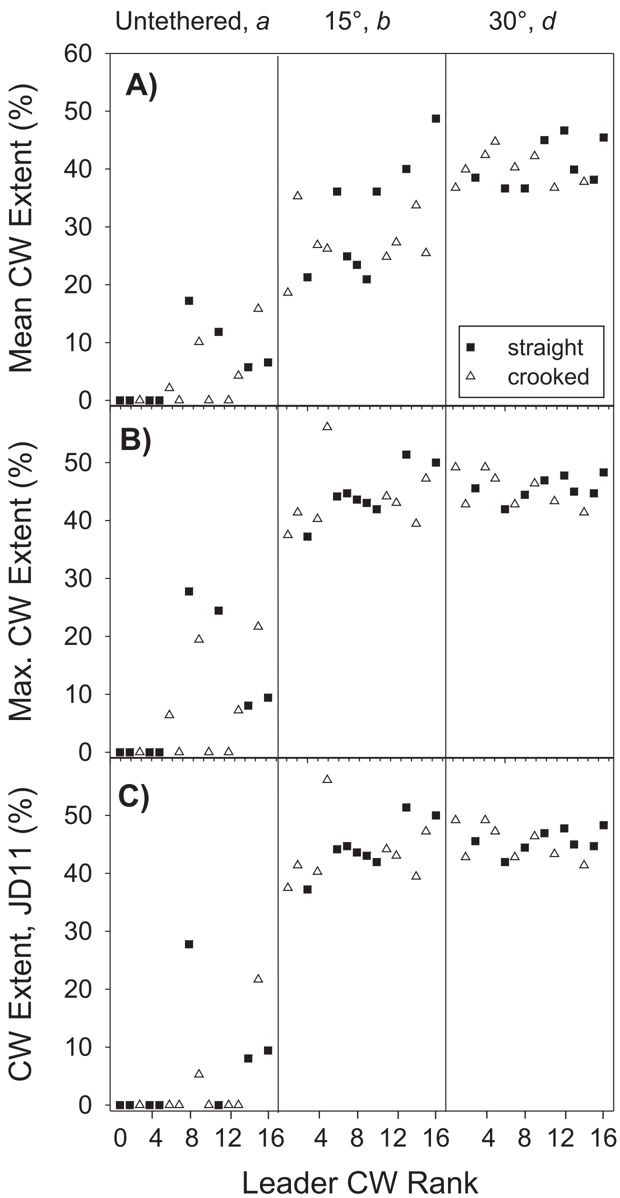
In contrast to the results obtained for lower stem positions, data for the leaders were supportive of the second hy-

Table 3. Regressions of compression wood (CW) extent (*y*) versus sample inclination (*x*) for upper positions at inclinations <10°, upper positions at inclinations >10°, and lower positions at all inclinations.

	Equation	Adj. r^2	*P* value	SE
Upper positions, inclination <10°	$y = 2.63 + 1.43x$	0.197	<0.001	0.34
Upper positions, inclination >10°	$y = 33.66 + 0.35x$	0.146	<0.001	0.10
Lower positions	$y = 32.29 + 0.58x$	0.122	<0.001	0.13

Note: *P* values and standard errors (SE) are for the slope coefficients.

Fig. 7. Compression wood (CW) extent in upper stem positions (*a*, *b*, or *d*) versus the leader's CW rank (low values indicate low incidence) for trees (n = 16) in each inclination treatment. (A) Mean CW extent of the three assessed dates. (B) Maximum CW extent of the three assessed dates. (C) CW extent of the initial date.



pothesis: the mean leader CW rankings were lowest for the untethered trees followed by trees tethered to 15° and then trees tethered to 30° (Table 1).

Moreover, there was a positive correlation between crook index and leader CW rank, showing that the more crooked the leader, the more CW the sample was likely to contain (Fig. 4). This result is consistent with those of a study in *Pseudotsuga menziesii* that investigated CW formation around a target internode that had been categorized as having high, medium, low, or no sinuosity 12 years before the study (Spicer et al. 2000). In rings 1–5 from the pith, the trees that had been highly sinuous had much more CW than did those that had no sinuosity. In rings 6–10 and 11–15, however, there was no longer a significant difference in the amount of CW in the extreme sinuosity classes. In contrast, Burdon (1975) found no effect of stem sinuosity on CW rating within clones of *P. radiata* at any of the four sites surveyed.

The results of the current study as well as those found in the literature (e.g., Zobel and Haught 1962; Barger and Ffolliott 1976) underscore the dangers of modeling the distribution of CW from inclination angle alone. These results also reveal our incomplete understanding of where and when CW will form in stems.

Differences between straight and crooked trees in CW production in response to inclination

The third hypothesis, that straight trees produce more CW than do crooked trees at a given angle of stem inclination, was not supported by the sample inclination versus extent of CW graphs (Fig. 6). Moreover, there were no significant effects of stem form on eccentricity, radial growth, or post-treatment CW extent at the beginning and end of the experiment (Table 2).

Evidence for overcompensation as a cause of crookedness

Crooked and straight trees become upright at different speeds. Crooked trees righted themselves more rapidly than straight trees at angles <15° (Figs. 3B and 3C, positions *b*, *c*, *e*, and *f*), but they righted themselves more slowly than straight trees at angles of 15°–30° (position *d*) (Fig. 3C). Rather than perpetuating their crookedness by being less responsive to angle than straight trees, these crooked trees appeared to respond too quickly to small inclinations with production of CW, tilting the apex that had already reoriented toward vertical, thereby placing it out of vertical. More targeted research would be needed to test this overcompensation hypothesis directly.

Within- and among-tree differences in response to inclination

Trees varied greatly in the amount of CW they produced for a given inclination treatment (Fig. 5). Position *b*, for example, had from 0% to 59% CW in the wood produced at the end of the experiment. There was more tree-to-tree variability at the final date than at the initial date, as would be expected because any CW-caused differences in orientation early in the experiment would cause more differences at later dates. There were individuals in both inclination treatments that consistently produced less CW than other trees (Fig. 5), a finding that is consistent with the literature showing family and individual differences in the tendency of *P. radiata* trees to produce CW in normal (untethered) trees (i.e., Burdon 1975). Bending treatments of clones could therefore be used to screen clones and eliminate those with the highest propensity to produce CW (e.g., Apiolaza et al. 2008) or to eliminate those that were least able to straighten their stems appropriately (Sierra-de-Grado et al. 2008). These assessments could be conducted expeditiously because when radial growth is rapid, the CW can be detected within days (reviewed in Timell 1986, pp. 680–686).

In the untethered trees, the seven individuals with the least CW in their leaders also had very little CW in their upper position (position *a*) (Fig. 7). These data suggest the utility of assessing leader CW content, at least to eliminate the trees with the highest CW content. In trees inclined to 15° or 30°, however, there was no correspondence between the amount of CW in the leaders and the amount of CW in the upper position (positions *b* and *d*, respectively). Therefore, it appears that assaying leader data for CW propensity is a worthwhile strategy only for trees that are not subjected to much bending. It would be valuable to repeat this work on older trees to see whether the same relationships hold. All of the measures of CW extent versus leader CW rank gave similar results, so the simplest assay from an operational viewpoint would be to use either the maximum extent of CW in the stemwood (Fig. 7B) or the initial amount of CW (Fig. 7C).

Overall this study showed that vertical *P. radiata* trees produce a large amount of CW in their young stems (3 years old and younger), and that the amount does not differ significantly between trees that are straight and those that are crooked. When the trees are inclined, most of them immediately produce a large amount of CW, although the amount of CW is related to inclination angle only in the youngest samples. In those young samples there appeared to be a threshold response, with more CW produced at inclinations >10° than at inclinations <10°. Individual trees display a wide range of righting responses, as shown by the large scatter in both CW extent and stem inclination. This variability could be used in clonal selection programs to identify clones that make very little CW in response to an inclination test. The individuals with little CW in the leaders tended to have little CW at the upper position in the stem, suggesting another potential assay for clonal selection programs. The data show that the crooked trees righted themselves from small angular perturbations more quickly than did the straight trees, which is consistent with an overcompensation model to explain stem crookedness in these young trees.

Acknowledgments

We thank Forestal Valdivia S.A. for trees and for site-related data, Eduardo Morales and Alejandra Espina for help with data analyses and fieldwork, and an anonymous reviewer for insightful comments. We appreciate the financial support of the Fulbright Scholars Program, Oregon State University, and the Cooperativa de Mejoramiento Genético Forestal UACh/CONAF/Empresas Forestales.

References

Apiolaza, L.A., Walker, J.C.F., Nair, H., and Butterfield, B. 2008. Very early screening of wood quality for radiata pine: pushing the envelope. *In* Proceedings of the 51st Annual Convention of the Society of Wood Science and Technology, 10–12 November 2008, Concepción, Chile. Society of Wood Science and Technology, Madison, Wis., USA. Available from http://www.swst.org/meetings/AM08/proceedings/WQ-1.pdf [17 December 2009].

Archer, R.R., and Wilson, B.F. 1973. Mechanics of the compression wood response: II. On the location, action, and distribution of compression wood formation. Plant Physiol. **51**(4): 777–782. doi:10.1104/pp.51.4.777. PMID:16658408.

Barger, R.L., and Ffolliott, P.F. 1976. Factors affecting occurrence of compression wood in individual ponderosa pine trees. Wood Sci. **8**: 201–208.

Birk, E.M., Bowman, V.J., Fulton, J.A., and Hides, I. 1993. Merchantability of *Pinus radiata* in relation to previous land use. Aust. For. **56**: 157–164.

Burdon, R.D. 1975. Compression wood in *Pinus radiata* clones on four different sites. N. Z. J. For. Sci. **5**: 152–164.

Carlyle, J.C., Turvey, N.D., Hopmans, P., and Downes, G.M. 1989. Stem deformation in *Pinus radiata* associated with previous land use. Can. J. For. Res. **19**(1): 96–105. doi:10.1139/x89-013.

Cown, D.H., Haslett, A.N., Kimberley, M.M.O., and McConchie, D.L. 1996. The influence of wood quality on lumber drying distortion. Ann. Sci. For. **53**(6): 1177–1188. doi:10.1051/forest:19960611.

Donaldson, L.A., and Turner, J.C.P. 2001. The influence of compression wood and microfibril angle on the occurrence of distortion in window frames made from radiata pine (*Pinus radiata*). Holz Roh- Werkstoff, **59**(3): 163–168. doi:10.1007/s001070100201.

Donaldson, L.A., Grace, J., and Downes, G.M. 2004. Within-tree variation in anatomical properties of compression wood in radiata pine. IAWA J. **25**: 253–272.

Downes, G.M., and Turvey, N.D. 1990. The effect of nitrogen and copper on the characteristics of wood tissue in *Pinus radiata.* Can. J. For. Res. **20**(9): 1369–1377. doi:10.1139/x90-181.

Downes, G.M., and Turvey, N.D. 1993. Relationships between stem structure and bending strength in *Pinus radiata* seedlings. Trees (Berl.), **7**: 86–91.

Downes, G.M., Moore, G.A., and Turvey, N.D. 1994. Variations in response to induced stem bending in seedlings of *Pinus radiata.* Trees (Berl.), **8**: 151–159.

duToit, A. 1963. A study of the influence of compression wood on the warping of *Pinus radiata* D. Don timber. S. Afr. For. J. **44**: 11–15.

Gartner, B.L., and Johnson, G.R. 2006. Is long primary growth associated with stem sinuosity in Douglas-fir? Can. J. For. Res. **36**(9): 2351–2356. doi:10.1139/X06-110.

Harris, J.M. 1977. Shrinkage and density of radiata pine compression wood in relation to its anatomy and mode of formation. N. Z. J. For. Sci. **7**: 91–106.

Jayawickrama, K.J.S., and Balocchi, C. 1993. Growth and form of provenances of *Pinus radiata* in Chile. Aust. For. **56**: 172–178.

Jayawickrama, K.J.S., Shelbourne, C.J.A., and Carson, M.J. 1997. New Zealand's long internode breed of *Pinus radiata.* N. Z. J. For. Sci. **27**: 126–141.

Low, A.J. 1964. Study of compression wood in Scots pine (*Pinus silvestris* L.). Forestry, **37**(2): 179–201. doi:10.1093/forestry/37.2.179.

Pederick, L.A., Hopmans, P., Flinn, D.W., and Abbot, I. 1984. Variation in genotypic response to suspected copper deficiency in *Pinus radiata.* Aust. For. Res. **14**: 75–84.

Peri, P.L., Mason, E.G., Pollock, K.M., Varella, A.C., and Mead, D.J. 2002. Early growth and quality of radiata pine in a silvopastoral system in New Zealand. Agrofor. Syst. **55**(3): 207–219. doi:10.1023/A:1020588702923.

Pillow, M.Y., and Luxford, R.F. 1937. Structure, occurrence, and properties of compression wood. USDA Agric. Tech. Bull. 546.

Shelbourne, C.J.A., and Stonecypher, R.W. 1971. The inheritance of bole straightness in young loblolly pine. Silvae Genet. **20**: 151–156.

Sierra-de-Grado, R., Pando, V., Martinez-Zurimendi, P., Penalvo, A., Bascones, E., and Moulia, B. 2008. Biomechanical differences in the stem straightening process among *Pinus pinaster* provenances. A new approach for early selection of stem straightness. Tree Physiol. **28**: 835–846. doi:10.1093/treephys/28.6.835.

Sinnott, E.W. 1952. Reaction wood and the regulation of tree form. Am. J. Bot. **39**(1): 69–78. doi:10.2307/2438096.

Spicer, R., Gartner, B.L., and Darbyshire, R. 2000. Sinuous stem growth in a Douglas-fir (*Pseudotsuga menziesii*) plantation: growth patterns and wood quality effects. Can. J. For. Res. **30**(5): 761–768. doi:10.1139/cjfr-30-5-761.

Timell, T.E. 1986. Compression wood in gymnosperms. Vol. 1, 2, and 3. Springer-Verlag, Berlin.

Turvey, N.D., Carlyle, C., and Downes, G.M. 1992. Effects of micronutrients on growth form of two families of *Pinus radiata* (D. Don) seedlings. Plant Soil, **139**(1): 59–65. doi:10.1007/BF00012842.

Turvey, N., Downes, G., Hopmans, P., Stark, N., Tomkins, B., and Rogers, H. 1993. Stem deformation in fast grown *Pinus radiata*: an investigation of causes. For. Ecol. Manage. **62**(1–4): 189–209. doi:10.1016/0378-1127(93)90050-W.

Watson, A.J., and Dadswell, H.E. 1957. Paper making properties of compression wood from *Pinus radiata*. Appita J., **11**: 56–70.

Westing, A.H. 1965. Formation and function of compression wood in gymnosperms. Bot. Rev. **31**(3): 381–480. doi:10.1007/BF02859131.

Westing, A.H. 1968. Formation and function of compression wood in gymnosperms. II. Bot. Rev. **34**(1): 51–78. doi:10.1007/BF02858621.

Wilson, B.F., and Archer, R.R. 1977. Reaction wood: induction and mechanical action. Annu. Rev. Plant Physiol. **28**(1): 23–43. doi:10.1146/annurev.pp.28.060177.000323.

Wilson, B.F., and Archer, R.R. 1979. Tree design: some biological solutions to mechanical problems. Bioscience, **29**(5): 293–298. doi:10.2307/1307825.

Zobel, B.J., and Haught, A.E., Jr. 1962. Effect of bole straightness on compression wood of loblolly pine. Tech. Rep. 15, School of Forestry, North Carolina State College, Raleigh, N.C.