

Lean in red alder (*Alnus rubra*): growth stress, tension wood, and righting response

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Abstract: Natural stands and a 3-year-old plantation of red alder (*Alnus rubra* Bong.) trees were used to study the incidence of leaning stems, the level of growth stresses and tension wood formation, and the ability of the stems to right themselves to vertical. Overall, 10% of the 512 trees in 10 natural stands leaned $>22^\circ$. The largest diameter trees on the steepest slopes leaned most. Most (61%) of the trees curved upward, showing a righting response. For samples without tension wood, growth stress levels on the upper side of leaning stems, but not on the lateral or lower sides, were positively correlated with lean angles above 6° . These leaning stems had a significant righting response without tension wood. Tension wood formation was variable at leans from 9° to 26° both within and among trees, but was correlated with eccentric growth rings. We measured stem recovery in the year-old stem of 3-year-old trees bent to angles of 0 – 37.5° . During the 5-month experiment all stems righted to near vertical. Tension wood formed on the upper side in stems bent $>6^\circ$, but reversed to the lower side before reaching vertical in 22 of 30 trees.

Résumé : Des peuplements naturels et une plantation âgée de 3 ans d'aune rouge (*Alnus rubra* Bong.) ont servi à étudier l'incidence de l'inclinaison des tiges, le niveau de stress dû à la croissance et la formation du bois de tension, ainsi que la capacité des tiges de se redresser. Dans l'ensemble, 10% des 512 arbres dans 10 peuplements naturels avaient un angle d'inclinaison de plus de 22° . Les arbres qui avaient le plus fort diamètre sur les pentes les plus abruptes étaient les plus inclinés. La plupart (61%) des arbres étaient inclinés vers le haut, indiquant une réaction de redressement. Dans le cas des échantillons qui ne présentaient pas de bois de tension, le niveau de stress dû à la croissance du côté supérieur des tiges inclinées, mais non dans la partie latérale ou du côté inférieur, était positivement corrélé avec l'angle d'inclinaison au-dessus de 6° . Ces tiges inclinées avaient une réaction de redressement significative sans former de bois de tension. La formation de bois de tension était variable à des angles d'inclinaison de 9° à 26° tant dans qu'entre les arbres mais était reliée à des anneaux de croissance excentriques. Nous avons mesuré le redressement dans la portion de la tige âgée de 1 an chez des arbres de 3 ans inclinés à des angles de 0° à 37.5° . Pendant l'expérience qui a duré 5 mois, toutes les tiges se sont redressées presque à la verticale. Le bois de tension se formait du côté supérieur dans les tiges inclinées de plus de 6° mais passait du côté inférieur avant qu'elle atteigne la verticale chez 22 des 30 arbres.

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Introduction

Red alder (*Alnus rubra* Bong.) is the most common and most commercially important hardwood in the Pacific Northwest. Stem lean and sweep is common in natural stands (DeBell and Giordano 1994). Photographs illustrate leaning trees (Bormann 1985; Willits et al. 1990), but lean within stands has not been measured systematically. Sweep is gradual. In one 14-year-old natural stand the mean central deflection was 8.3 cm over a 4.9-m span for 312 crop trees (W.H. Emmingham and D.E. Hibbs, unpublished data). Trees in plantations can be kept nearly vertical by thinning equally on all sides, but stems may lean toward openings (Bormann 1985). Willits et al. (1990) summarized

the general impression that "trees appear to respond to competition by leaning towards open areas." There are few significant effects of lean on wood quality in red alder, and tension wood is uncommon (Leney et al. 1978; Willits et al. 1990; Lowell and Kraemer 1993), although cut stems may split, presumably from high growth stresses (Leney et al. 1978).

Most angiosperm trees respond to lean by producing wood with higher tensile stress on the upper side than on the lower side of the lean. The higher stresses may develop in "normal" wood or in tension-wood fibers identified by their special cell wall layers (Wilson and Archer 1979; Fournier et al. 1994; Okuyama et al. 1994). This stress differential generates an internal bending moment that tends to bend the stem back toward vertical in a righting response. In alder the righting response apparently is inadequate in many cases and stems do not return to vertical.

The percentage of tension-wood fibers may increase with lean under experimental conditions (Robards 1966; Ohta 1979), but there is high variability among trees in natural stands (Berlyn 1966; Arganbright and Bensed 1968). Tension wood is usually associated with increased cambial activity

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and eccentric annual rings in experimentally bent trees (Robards 1966; Ohta 1979), but may not be related in naturally leaning trees (Sorensen and Wilson 1964).

Our objectives were to determine how much red alders really do lean and how red alder responds to natural and experimentally induced lean by developing differential growth stresses in normal wood or tension wood. Our study had three parts: (1) we measured the lean and curvature of trees in natural stands; (2) we measured growth stresses and tension wood in naturally leaning stems; (3) we bent young trees to determine their righting response under experimental conditions.

Methods

Lean in natural stands

We measured stem lean in 10 natural stands selected to cover a wide variation in site and tree diameter. In each stand we measured all trees (excluding dead or fallen trees) in a plot that was varied in area to include 50 trees. We miscounted in one stand and measured 62 trees. For each tree we measured at breast height the diameter and the angle from vertical (the lean) on the lower side. We also recorded curvature along the entire stem (curved up, straight, or curved down). For roadside stands we measured only edge trees adjacent to the opening created by the road. All the stands were in the Oregon Coast Range. Five stands were at Soap Creek (44°29'N, 123°20'W), two stands were near Woods Creek Road (44°32'N, 125°53'W), two stands were at Cascade Head (45°4'N, 123°57'W), and one stand was along Route 20 near Toledo (44°41'N, 123°53'W).

Statistical analyses used SAS (SAS Institute Inc. 1990). Analysis of variance showed significant differences in mean lean among natural stands for data in Table 1 ($df = 9$, mean squares = 111 702, $F = 40.9$, $p = 0.0001$), so we used Fisher's protected LSD to test for differences among stands.

Strain, tension wood, and eccentricity in naturally leaning trees

To investigate the relationships among growth stress, stem angle, and wood structure, we took 30 sets of samples from 29 trees at Soap Creek with a range of lean angles (5–57°) and diameters (8.5–39.9 cm). We did not determine tree ages. Three samples were taken from each of 28 trees on the upper, lateral, and lower sides of the lean around a circumference at about breast height. The tree with the greatest lean had two distinct angles, so we sampled at both angles on two separate circumferences.

Samples were taken in February and March before bud break. First we measured growth strains using strain release methods (Nicholson 1971; Archer 1986). At each sample point we removed the bark in an area 5 cm tangentially by 20 cm longitudinally parallel to the lean axis. Within the bark-free area two 5 mm long nails with tapered holes in the heads were hammered into the wood 10 cm apart along a line parallel to the lean axis. Distance between the nails was measured with a Huggenberger Tensotast. Growth strain was released by drilling 2.5 cm diameter holes 2 cm into the wood 1 cm above the upper nail and 1 cm below the lower nail. Then the distance between the nails was remeasured. The reduction in distance after strain release divided by the 10-cm span length was the growth strain. This method of strain release underestimates total strain by about 15%, but is suitable for field comparisons among trees (Archer 1986).

The wood between the holes was removed with a hammer and chisel to a depth of >1.5 cm. One end was cut from each sample for sectioning. Transverse 30- μ m microtome sections

Table 1. Lean at breast height in 10 red alder stands.

Site*	Mean DBH (cm)	Lean (degrees)			
		Mean [†]	Min.	Max.	SD
CH, 37° slope	17.5	22.4a	12	37	5.8
CH, 45° slope	22.6	17.4b	2	43	8.7
T, roadside	25.0	14.9c	0	32	7.0
SC, stream flat	33.2	12.6d	3	30	6.6
SC, upland	23.4	11.5de	3	26	5.2
SC, stream flat	18.3	10.8de	3	29	4.5
WC, roadside	4.9	10.7de	2	23	4.8
SC, stream flat	6.8	9.4e	0	21	5.0
SC, stream flat	4.8	6.1f	0	14	3.7
WC, upland	4.6	6.0f	0	14	3.3

*CH, Cascade Head; T, Toledo; SC, Soap Creek; WC, Woods Creek Road.

[†]Means followed by the same letter are not significantly different at $p = 0.05$.

were cut and stained with toluidine blue. Tension wood stained darker than normal wood. Gelatinous cell walls were used as definitive identification of tension wood. Annual ring width (average of the three outer rings) and the radial percentage of tension wood in the outer 5 mm were measured from the sections. Eccentricity was expressed as the ring width on the upper side divided by the ring width on the lower side. Trees with tension wood were resampled on the upper side with an 8-mm increment core to a depth of >5 cm for determination of variability in tension wood among rings. We did not take increment cores from trees without tension wood, so we do not know if they formed tension wood deeper in the tree than the sample depths. Transverse 30- μ m sections were made from the cores and stained with toluidine blue.

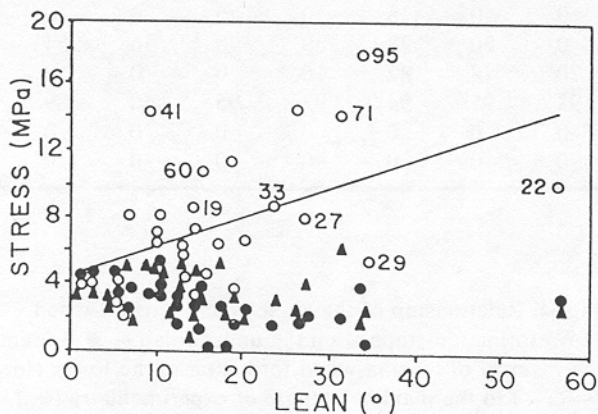
Beams 6.35 by 6.35 mm in cross section and 10 cm long were cut from each sample. The modulus of elasticity in bending was determined for each beam with three-point loading in the radial direction using an Instron Universal Testing Instrument, model 1130 (Canton, Mass., U.S.A.). Growth stresses were calculated for each sample as the product of growth strain and the modulus of elasticity.

Bending experiments

We selected 36 trees from a 3-year-old plantation near Toledo, Oregon (44°38'N, 123°38'W). Trees were straight, single stemmed and 3–4 m tall. Eighteen trees were from a relatively open stand (1556 trees/ha, mean DBH = 2.0 cm), and another 18 were from a denser stand (3260 trees/ha, mean DBH = 2.9 cm) that achieved crown closure during the experiment. We randomly assigned six bending treatments, with three trees in each treatment, to each stand.

On February 8–11, 1995, controls were left untreated and bent trees were secured by a wire attached to rubber tubing around the stem just below the base of the 1994 terminal shoot leading to a metal stake in the ground. The initial angles of the terminal shoots were 7.5°, 15°, 22.5°, 30° or 37.5° to vertical. In the open stand one of the 37.5° trees loosened to 30° and so was considered as an initial 30° treatment. On each stem we marked a reference point proximal to the bending point on the 2-year-old stem and three points at 50-cm intervals on the year-old, distal stem. On March 6, April 4, May 8, June 7, and July 6–7, 1995, we measured stem angle to vertical at each of the four points and stem diameters at the proximal and

Fig. 1. Relationship of growth stress on the top side (○), lateral side (▲), and lower side (●) to lean angle in naturally leaning trees. The numbers indicate the percentage of tension wood in specimens with tension wood. For the upper side, stress = $4.53 + 0.180(\text{lean})$, $p = 0.0025$, $r^2 = 0.26$. Regression coefficients for the lateral and lower sides were not significant ($p = 0.19$ and 0.074 , respectively). Mean stress and SD for lateral sides = 3.43 ± 1.23 MPa and for lower sides = 2.78 ± 1.30 MPa.



nearest distal point. After the usual measurements on July 6–7 all 1995 shoots were clipped off the distal shoot segment to remove new bending moments from self weight (except for diameter increments on the 1994 shoot), and the angles were remeasured. There was usually $<2^\circ$ change in stem angles after cutting off all 1995 shoots, indicating little effect of bending moments from self-weight, so we did not include the measurements in our analysis.

The stem segments with the three distal measuring points were taken to the laboratory. Transverse 30- μm sections were cut at each of the 108 measuring points and stained with toluidine blue. From the sections we measured 1995 ring widths and the radial distance from the 1994 ring to points where tension-wood formation started or stopped on the upper or lower side of the stem.

The stem angle at the reference point below the wire attachment decreased gradually in most trees over the 5 months of the experiment. This decrease was partly due to stretching of the rubber tubing and movement of the iron rod in soil, but could also have been from curvatures of the stem below the attached wire. This simple rotation would increase all the angles in the distal segment equally, so we calculated curvature as the difference between the proximal angle and the furthest distal angle.

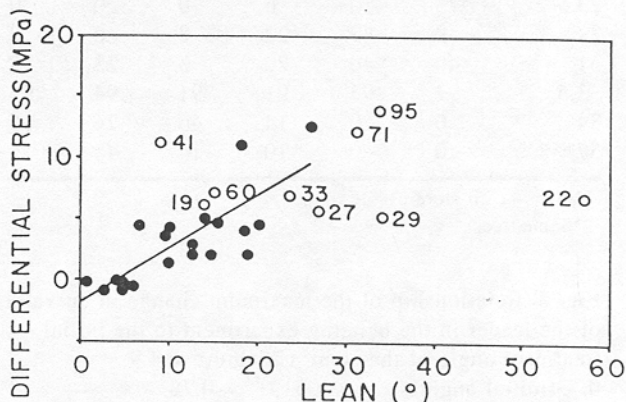
We estimated the angle of the stem when tension-wood formation started or stopped on the upper and lower side. This was done by first estimating the date using diameter growth data and then estimating the angle on that date using the angle data.

Results

Lean in natural stands

Lean of individual trees ranged from 0° to 43° (Table 1). The largest mean lean within stands was in the two larger diameter stands on steep slopes and the least mean lean was in the two small-diameter stands growing on flats (Table 1). All but the stand on the steepest slope had a few trees near vertical. Of the 94 trees leaning $<6^\circ$, 51 (61%) were in the two small-diameter stands on flats. Overall,

Fig. 2. Relationship of differential growth stress (stress on the upper side minus stress on the lower side) in specimens with only normal wood (●) and in specimens with tension wood (○) to lean angle in naturally leaning trees. The numbers indicate the percentage of tension wood in specimens with tension wood. For specimens without tension wood, differential stress = $-1.82 + 0.43(\text{lean})$, $p = 0.0001$, $r^2 = 0.60$. Differential stress was not related to lean in specimens with tension wood ($p = 0.95$, mean and SD = 8.34 ± 3.01 MPa).



only 51 (10%) of the trees leaned $>22^\circ$, and 35 (69%) of these were in the two stands on steep slopes.

Overall, 315 (62%) of the trees curved upward, 169 (33%) were straight, and 28 (5%) curved down. Of the 28 trees that curved down, 16 were on the two sites with steep slopes. Of the 103 trees with $<6^\circ$ lean, 76 were classified as straight, presumably because nearly vertical trees do not have curvature. The other 93 straight trees were distributed through all diameters and leans $<42^\circ$.

Strain and tension wood in naturally leaning trees

Growth stresses were low (1.8–4.9 MPa) on all sides of trees leaning less than 6.5° . In trees with higher leans, growth stresses increased on the upper side, but did not change significantly on the lateral or lower sides (Fig. 1). Mean stresses on the lateral side were slightly higher than those on the lower side (3.5 vs. 2.8 MPa, Student's t -test, $p = 0.045$). The differential stress between the upper and lower sides is the righting response (Fig. 2). Lean angle was positively correlated with differential stress in trees without tension wood, but not in trees with tension wood.

All but two upper samples without tension wood had growth stresses <8 MPa, but one had 11.4 MPa and another 14.6 MPa. These two samples without tension wood had higher stresses than six of the nine samples with tension wood (Fig. 1). We checked both ends of these samples for tension wood, and there was none present in the outer 10 mm. Tension wood farther in the stem should not have affected strain release measurements.

Nine of the 30 upper samples had tension wood. All 5 samples from trees with leans $>26^\circ$ had tension wood, and none of the 7 samples from trees leaning $<9^\circ$ had tension wood. Only 4 of the 18 upper samples from trees leaning 9 – 26° had tension wood. Samples with tension wood had stresses ranging from 5.6 to 17.9 MPa. Growth stress increased

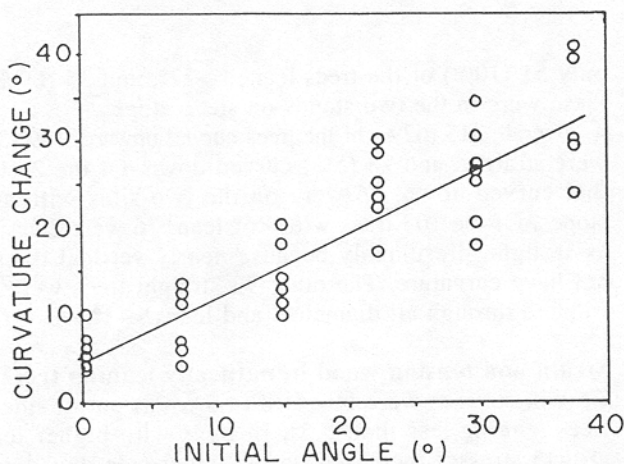
Table 2. Percentage of tension wood in the outer 15 rings on the upper side of the nine naturally leaning trees that contained tension wood.

Stem angle (degrees)	Year of ring formation														
	1994	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980
9	36	37	0	0	0	60	40	38	0	45	0	0	0	0	0
14	0	58	0	0	30	14	0	6	23	29	0	18	24	0	0
15	69	0	87	91	87	92	29	39	—	—	—	—	—	—	—
23.5	25	0	6	0	0	0	0	0	0	18	0	45	0	0	22
27	9	33	22	8	0	0	0	0	50	28	89	75	36	54	35
31	40	40	20	3	23	79	79	70	78	82	16	0	0	0	31
33.5	92	95	91	91	94	95	94	93	95	94	93	95	40	89	63
34*	0	0	14	40	26	15	0	0	0	0	0	0	0	0	0
57*	0	0	10	14	48	33	0	0	0	0	0	0	0	0	0

Note: —, no more usable rings.

*Same tree.

Fig. 3. Relationship of the maximum change in curvature of the leader in the bending experiment to the initial treatment angle of the stem. Curvature = $4.9 + 0.73(\text{initial angle})$, $p = 0.0001$, $r^2 = 0.78$.



as the percentage of tension wood (TW) increased (stress = $5.47 + 0.12(\%TW)$, $p = 0.006$, $r^2 = 0.64$). Regression analysis showed that the amount of tension wood in the nine samples with tension wood was not significantly related to lean ($p = 0.93$), ring width ($p = 0.17$), or DBH ($p = 0.13$).

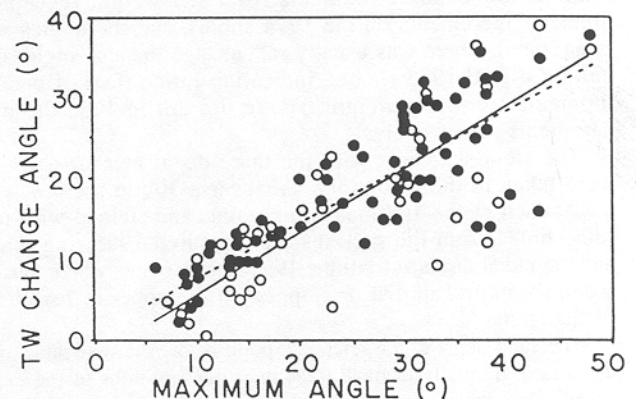
Only one of nine cores from trees with tension wood had tension wood in all 15 rings (Table 2). The others had some rings without tension wood. In six trees tension wood was present in one ring, missing in the next one or more rings, and then present again.

Samples without tension wood had nearly equal ring widths on the upper and lower sides, but samples with tension wood had rings on the upper side twice as wide as those on the lower side (mean ratios of 1.13 and 2.11, respectively, Student's *t*-test, $p = 0.0019$).

Bending experiment

Bud break occurred by March 6, but shoot elongation and cambial activity was slow until April. Some stems sagged

Fig. 4. Relationship of the angle where tension-wood (TW) formation stopped on the upper side (---●---) and the reversal of tension-wood formation to the lower side (—○—) to the maximum angle of experimentally bent stems. For cessation of tension-wood formation, angle = $1.3 + 0.68(\text{maximum lean})$, $p = 0.0001$, $r^2 = 0.68$. For the reversal of tension-wood formation, angle = $-1.7 + 0.76(\text{maximum lean})$, $p = 0.0001$, $r^2 = 0.64$.



initially from self weight. By May upward curvature was visible in many bent trees. By July most trees had reached near vertical at the top measuring point and 17 of the 30 treated trees had bent beyond vertical. At the last measuring periods some trees near vertical bent back down so the stem curvature decreased. The maximum change in curvature (the maximum righting response) was linearly related to the initial angle of the bent trees (Fig. 3).

Tension-wood arcs formed in the first earlywood of the 1995 ring in at least one measuring point for all 30 bent trees, but none of the 6 controls. We observed no differences between the two stands, so we combined the results. Tension wood formed at estimated stem angles from 6° to 48° (Fig. 4). Tension wood occurred throughout the entire upper side for only one measuring point. In the other 71 measuring points on the upper side of bent stems, there was an inner arc of tension wood followed by an outer

layer of normal wood. The angle at which tension-wood formation stopped ranged from estimated angles of 2.5° to 38°. That angle was positively correlated with the maximum angle measured for the measuring point (Fig. 4).

In 21 of the 24 bent trees, tension-wood formation reversed to the lower side of the measuring point so that there was a band of normal wood on the inner portion of the ring on the lower side followed by a crescent of tension wood. Reversal occurred at estimated angles of 0° to 38°, always before the segment had bent backwards. The angle at reversal was positively related to the maximum angle measured for the stem segment (Fig. 4). Thus, the greater was the maximum angle of the segment, the greater was the angle of both cessation of tension-wood formation on the upper side and reversal of tension-wood formation to the lower side.

Discussion

The mean leans of 6–22° that we measured in red alder stands appear to be greater than for most commercial species, but there are few comparative data available. Berlyn (1966) had trouble finding leaning *Populus deltoides* Bartr. in natural stands. His selected leaning trees had a maximum lean of 26°, and 90% were <16°. Cano-Capri and Burkart (1974) measured lean in *Quercus falcata* Michx. stands, and for 215 trees, found 53% at 0–2.5°, 37% at 3–6°, 7% at 7–10°, and 3% at >11°.

Leaning alder stems do have a righting response, but it may not be great enough to return the stem to vertical in natural stands. At leans >6°, alder stems produce wood with growth stress differentials tending to bend them up. In a 3-year-old plantation, this response bent the stems to vertical in a few months. In natural stands most trees are not vertical, but the predominance of upwardly curved stems indicates a response that keeps the lean of most stems at <20°.

Our results emphasize the potential importance of normal wood in the righting response for red alder, as already shown for other species (Okuyama et al. 1994). Tension wood may or may not form at angles >7°, and the proportion of tension wood in a ring is not determined by the lean angle. Even when tension wood does form, the tree may not develop as high a stress differential as other trees at the same lean with only normal wood.

Tension-wood formation may be unpredictable in trees (Berlyn 1966; Arganbright and Bensed 1968), and red alder is no exception. Tension-wood formation is variable in natural stands of large trees at leans from 9° to 30°. In natural stands leaning trees may stop forming tension wood for 1 year or more and then start again. We do not know the history of stem angle changes in these trees. Plantation trees bent experimentally to angles >6° produced tension wood briefly, but subsequently stopped and even reversed to the lower side, even though there was little change in the stem angle. A similar effect occurred in *Pinus strobus* L., where a bent stem reversed compression-wood formation while the stem was still 7–12° from vertical (Archer and Wilson 1973). In both naturally leaning and experimentally bent red alder trees, an angle sufficient to induce tension-wood formation may not be adequate to maintain continued tension-wood formation without some other, presently unknown, factor.

Three mechanisms for the righting response are the development of higher growth stresses in normal wood on the upper side, the production of tension wood on the upper side, and the development of eccentric rings (wider on the upper side) that amplify the effect of higher growth stresses by increasing the total stress differential in a ring. The primary stimuli hypothesized for the righting response are gravity, tensile stress at the surface of the tree, and the position of the most productive part of the crown. Fisher (1985) combined experimental reorientation with mechanical bending in *Terminalia* and concluded that both gravity and tensile stress can stimulate tension-wood formation, but gravity dominates in most situations. In *Quercus rubra* L., tension wood was always on the upper side of the lean, but eccentric rings formed below the most productive part of the crown whether on the upper, lower, or lateral side (Sorensen and Wilson 1964). Our results from red alder suggest that the stimulus for high growth stresses in normal wood is different from the stimulus for tension wood and eccentric rings. Growth stress levels in normal wood appear to be consistently correlated with lean and, we assume, to the gravitational stimulus. Tension wood and eccentric rings appear to be correlated with each other and may be responses to the same stimulus, but they are not consistently related to lean. We did not measure crown characteristics, but eccentricity and tension wood were always on the upper side of the lean in natural stands. Perhaps the sporadic formation of tension wood in naturally leaning trees and the reversal of tension wood to the lower side in experimentally bent trees reflect the relatively weak effect of gravity on tension-wood formation in red alder. The gravity stimulus may be overcome by changes in bending stress so tension wood does not form even though the stem is leaning.

Splitting of leaning red alder trees when they are cut presumably results from the accumulation of high growth stresses on the upper side of leaning trees. Growth stresses stay low on the lateral and lower sides of leaning trees and are low in vertical trees, so this problem should be avoidable with thinning that keeps trees vertical.

An inadequate righting response in red alder often leads to leaning stems. This type of response may have adaptive value for the growth of a shade-intolerant species in dense natural stands. Site conditions and tree size appear to affect the extent of lean in stands. Further research would be necessary to answer the ecological questions raised by our study.

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