UNIVERSITY OF ALBERTA

WOOD STRENGTH AND ANNUAL RING WIDTH CHARACTERISTICS OF VARIOUS ROOT AND TRUNK COMPONENTS OF WHITE SPRUCE FOLLOWING PARTIAL CANOPY REMOVAL

BY ©

SHAWN URBAN

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF FOREST SCIENCE

Edmonton, Alberta
Spring, 1993

ISBN 0-315-82221-X

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TITLE OF THESIS: **Wood Strength and Annual Ring Width Characteristics of Various Root and Trunk Components of White Spruce Following Partial Canopy Removal**

DEGREE: **Master of Science**

YEAR THIS DEGREE IS GRANTED: **Spring, 1993**

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Wood Strength and Annual Ring Width Characteristics of Various Root and Trunk Components of White Spruce Following Partial Canopy Removal** submitted by Shawn Urban in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

Two studies were undertaken to examine the response of white spruce to changes in wind exposure. Dendrochronological methods were used to compare trunk growth with root growth, while mechanical testing methods were used to compare wood strength in the trunk with that in the root.

In the dendrochronology study, ten trees from the edge of a road, cleared 16 years earlier, and ten trees from the interior of a 120 year-old, mixed-wood stand were sampled. Ring widths were compared between the roots and trunks of these trees. Following the road clearing, the rate of trunk diameter growth initially remained unchanged, while root diameter growth increased. These observations suggest that trunk growth may be suppressed for some years following release as a result of increased root growth. The increase in root growth may help stabilize trees after exposure to increased wind stress by increasing the amount of root wood anchoring and supporting them.

In the second study, five trees from the edges of roads, cleared 20 years earlier, and five trees from the interior of a 40 year-old mixed-wood forest were sampled. I compared the strengths of wood produced in response to release and wood produced before release in the roots, stumps and boles of these released and control trees. The response wood and non-response wood were found to be equal in radial bending and parallel compression strength. However, following release, stumps had the highest radial bending strengths and the lowest parallel compression strengths, while the opposite was true in roots. Previous research has shown that wind stress maximizes radial bending strain in the stumps and parallel compression strain in the roots. Wood characteristics that influence strength seem to be correlated with wind-induced strain. This distribution may help stabilize trees by increasing wood resistance to movement.

White spruce appear to stabilize themselves in high winds by changing their pattern of growth and distribution of wood strength after wind stress increases. Movement of the center of gravity may explain these changes as well as the direction of reaction wood formation. Initial partial release may provide transitional conditions for the spruce to safely become windfirm in.

Acknowledgements

I would like to thank the Natural Science and Engineering Research Council (Canada), Forestry Canada, Canadian Forest Products (Grande Prairie), Weldwood Canada (Hinton Division), Weyerhaeuser (Prince Albert), Proctor and Gamble Cellulose Limited (Grande Prairie) and Daishowa Canada Limited (Peace River) who generously funded this thesis through the Forestry Canada / NSERC Research Partnership Grant to Drs. V.J. Lieffers, S.J. Titus and S.E. Macdonald. I would also like to thank Drs. Ellen Macdonald, Victor Lieffers and Lars Bach, who supervised my research, Delinda Ryerson, Heather Kleb, Kathy Skubleny and Mark Conrad, for their technical assistance throughout the project, Drs. Sally John and Terry Taerum, for their statistical advice, and all those graduate students (there are too many to list) of the Forest Science Department (University of Alberta) who helped me through discussions, insights and technical support. I would especially like to thank Ruth-Ann Gal, Jorge Alcazar, Cristina Vega, Ana Salazar and Ron Hall who helped type out the final copy of this thesis so I could print it on a LaserJet printer. Thank you all.

My mother and father also deserve recognition. They have instilled in me not only the value of continued education, but also its enjoyment. I should also mention Mrs. Joyce Anaka of Goodspirit Lake Provincial Park (Saskatchewan) as well as Mr. Frank Switzer, nature photographer, who inspired me to seek the wonders of nature, especially under my feet. One baby chipmunk at Goodspirit knows what I mean.

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Chapter 1

General Discussion

1.1. Mixed-wood Management and Understory Windthrow

In the first 50 to 75 years of stand development, aspen-white spruce mixed-woods consist of a dominant aspen (*Populus tremuloides* Michx.) overstory and a subordinate white spruce (*Picea glauca* (Moench) Voss) understory (Lees, 1966). In these stands, the aspen are fast-growing and shade-tolerant. They usually overtop young white spruce to form the upper canopy. The white spruce are shade-tolerant and, in the juvenile stage, grow slower than the overstory aspen. They typically remain in the understory until the aspen slow in growth and begin to die.

Commercial thinning of these mixed-woods involves harvesting the aspen for immediate use while retaining the understory white spruce for future commercial gain (Brace and Bella, 1988). By retaining the understory, instead of removing it while harvesting the aspen, forest managers 1) take advantage of the growth to date of the existing understory crop, 2) improve the growth potential of this crop and 3) postpone the need to prepare and replant the site (Brace and Bella, 1988).

Once the overstory is removed, the understory white spruce are released from competitive suppression induced by aspen (Yang, 1988). Trunk growth of the understory white spruce usually increases in response to release (Steneker, 1967). When they reach harvestable size, the white spruce can be harvested by a shelterwood regeneration system (Smith, 1986). This harvesting system releases white spruce seed trees from existing intraspecific competitive suppression (Smith, 1986). It also enables the establishment of a new understory crop before the old crop is completely harvested.

The mortality rate of understory white spruce increases following release from overstory aspen (Yang, 1988). Although logging practices also take their toll (Froning, 1980), this increase in mortality is largely due to windthrow (Brace and Bella, 1988). Growth of the white spruce is severely suppressed by overstory competition in unreleased stands (Steneker, 1967), resulting in relatively under-developed trees (Fraser and Gardiner, 1967; Smith, 1986). Since these trees are under-developed, they are vulnerable and susceptible to wind damage and windthrow. Similar problems may be faced by seed trees in a shelterwood system and by trees in an undisturbed forest as they grow into the canopy. These situations expose the trees to an environment more open than the one they were in before (Larson, 1963).

1.2. Wind Forces and Tree Sway

Wind sways the white spruce trunk, starting at the top, and indirectly vibrates the trunk's unswayed portion and the roots (King, 1986). As the wind intensifies, more of the trunk sways and the attached root system rocks in the soil (Fayle, 1978). The soil around the rocking roots is pushed away, losing its fortifying grip on the tree (Anderson *et al*, 1990). This loss undermines the tree's stability.

With increasing wind severity and failing soil hold, the root system lifts. This lifting starts on the windward side of the trunk beneath the stump (Figure 1-1) (Helliwell, 1989). More of the root system tilts as wind severity increases (Coutts, 1983). Meanwhile, the trunk leans leeward.

The outer portions of the root system tilt last since the soil holds them more tightly in place than it holds the inner portion (Coutts, 1983). This tightly held perimeter restricts root movement in the inner portion of the root system, thereby contributing to the buckling of the roots on the leeward side of the trunk (Mergen, 1954). This buckling decreases around the trunk toward the windward side where the root system lifts. Therefore, on the two sides of the trunk which are perpendicular to the wind direction, the root system lifts and buckles simultaneously.

As the root system continues to tilt, the roots eventually break, starting from the windward side and continuing to the leeward side (Coutts, 1983). As more roots break, the tree becomes less stable, since the soil loses its grip on the tree. The leaning tree eventually uproots unless the trunk snaps or the root tears (Mattheck and Bethge, 1990).

1.3. Physical Basis for the Effects of Sway on Spruce

A spruce tree's above ground weight is typically balanced at its center of gravity, which is usually located at the base of the crown (Larson, 1963) and on the trunk's vertical central axis (Johnson, 1987). All parts of the spruce are balanced at this point, which is supported in turn by the trunk. When the center of gravity lies on the central axis, the tree is stable, since its weight is supported by the trunk (Joseph *et al*, 1978). As the center of gravity is displaced from the central axis by a shift caused by wind or leaning, the tree loses balance, since the trunk supports the tree's weight less effectively. The greater the displacement of the center of gravity, the more precarious the tree becomes. Grace (1977) and others argue that this displacement brings about windthrow.

1.4. Root and Trunk Response to Sway

Radial growth of the trunks of understory white spruce usually increases in response to removal of the aspen overstory (Yang, 1988). However, this response growth is often delayed for some years after release (Brace and Bella, 1988). The trunk growth rate may even decline immediately following release, though it eventually improves.

White spruce mortality also increases following release (Yang, 1988), largely due to windthrow (Brace and Bella, 1988) as described above. The delay in trunk response growth may, therefore, be a symptom of wind stress. Neel and Harris (1971) reported a reduction in trunk height and diameter growth in deciduous hazelwood trees (*Liquidambar styraciflua* L.) which they swayed manually. They also reported an increase in stump diameter after manual swaying. Similar stump swell occurs in white spruce after release (Larson, 1963), suggesting that increased diameter growth in the stump and perhaps in the roots occurs at the same time increases in trunk diameter and height growth are delayed. Since there is no initial change in trunk growth after release, one can argue that trunk growth is still suppressed, as it was before release (Steneker, 1967), for some period immediately following the removal of the overstory aspen.

Competition for limited growth resources between the trunk and root (Kienholz, 1934; Coutts, 1987; Deans and Ford, 1985) may explain this hypothetical relationship between high root growth and low trunk growth. Allocation of resources between sinks (regions of the tree which consume growth resources) is affected by the conditions of the tree's environment (Salisbury and Ross, 1985). The mechanism of this environmental influence is not known (Fayle, 1968; Fritts, 1976).

Understory white spruce are likely sensitive to two types of trunk growth suppression (in this context): competitive and wind induced. In unreleased mixed-woods, the spruce are competitively suppressed by aspen (Steneker, 1967). This competition results in relatively under-developed roots and trunks in the spruce (Smith, 1986). After release, white spruce are free from aspen competition; however, they are exposed to relatively stronger winds. To stabilize themselves in severe winds, they might allocate more resources to stump and root growth (Mergen, 1954), resulting in continued or even greater trunk growth suppression.

1.5. Description of Response Growth

Response growth is a change in the growth habit of a tree after it encounters an environment which is relatively more open than the one it grew in previously. The stump and root system are entirely reorganized following release (Figure 1-2) (Wagg, 1967). Stump and root swell increases, especially on the leeward side of the tree, where buckling and bending strains are more pronounced (Coutts, 1983). The stump swells least on the two sides perpendicular to the wind (Mergen, 1954), where bending is least pronounced, while the root swells least on the windward side (Coutts, 1983), where buckling is least pronounced. Swelling results in thicker, and therefore more rigid, stumps and roots (Coutts, 1983). This rigidity reduces the risk and intensity of root plate rocking and tilting.

Increased root branching and adventitious rooting also occur (Figure 1-2), especially on the windward side of the tree (Coutts, 1983; Helliwell, 1989). They both result in more soil being bound to the roots, extending and solidifying the root-soil plate outward and trunkward. The union with the surrounding soil and the increased weight result in greater resistance to root plate lifting. Further, adventitious roots are positioned strategically around the spruce, improving root plate anchorage and tilting resistance (Wagg, 1967). Wagg (1967) also noted that roots which no longer contribute to spruce stability deteriorate following release.

Following release, trunk growth may be delayed or suppressed further by an increase in crown and root growth. Root to shoot biomass does not change following release (Fraser and Gardiner, 1967; Honer, 1971; Johnstone, 1971); however, crown to trunk, root to trunk and crown to root biomass ratios generally increase. This pattern suggests that crown biomass increases most, root biomass increases less and trunk biomass increases least.

The increase in crown biomass might be a response to increases in space and light around the crown following release (Greis and Kellomaki, 1981); however, some response to wind stress may also occur (Milne, 1991; Fayle, 1978). Changes in crown growth (Putz *et al*, 1983; Mergen, 1954; Mitchell, 1969), such as the loss and addition of branches, are beyond the scope of this study.

1.6. Strength and Stiffness of Response Wood

Strength and stiffness are measures of wood resistance to strain[1] (Figure 1-3) (Haygreen and Bowyer, 1989). These properties are determined by: 1) the sizes and shapes of the root and trunk as described in the previous section, 2) the density of wood and 3) the microfibril frame of the wood cell wall[2] (Haygreen and

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[1]Strain is the amount an object is altered (relative to its original state) by stress, which is the amount of force per unit area acting on the object (Haygreen and Bowyer, 1989).

[2]The cell wall is analogous to a cement foundation, which has a metal frame stitched by wires and embedded in a binding matrix, since the wall has a cellulose-

(continued...)

Bowyer, 1989; Commandeur and Pyles, 1991). Generally, as wood density increases, wood strength and stiffness increase, since the molecules comprising wood are packed closer together and there is less free space for the molecules to deform or slip into (Larson, 1963). Therefore, a section of root or trunk of certain form and certain wood density is likely to be stiffer and stronger than a similar section with lower wood density (Haygreen and Bowyer, 1989).

It is possible to have weak, high density tissue and strong, low density tissue (Larson, 1963). Ultimately, wood strength and stiffness are determined by the microfibril frame of the wood cell walls. Like the coils of a spring, microfibrils deform and rupture most easily perpendicular to their lengths, since 1) in this dimension long gaps occur between them and 2) they bend diametrically more easily than they compress longitudinally (Panshin and Zeeuw, 1980).

Response wood is the wood tissue produced during response growth. It may be like reaction wood, which is the wood tissue commonly believed to arise in strained or displaced parts of the tree (Haygreen and Bowyer, 1989). Both wood types occur when and where bending and compression strains increase. Both also have the same eccentric distribution of ring width; in transverse view, narrow rings occur opposite to wide rings. It follows that their stiffness and strength properties might also be similar.

Reaction wood microfibrils are 30 to 50 degrees more perpendicular to the wood cell's long axis than those of non-reaction wood (Figure 1-4a) (Parham and Gray, 1984). Therefore, against a force applied parallel to the cell's long axis, reaction wood is weaker than non-reaction wood, while, against one applied perpendicular to this axis, it is stronger (Figure 1-4b). The advantage of reaction wood is increased perpendicular-strain resistance. However, the price for this advantage is reduced parallel-strain resistance.

Based on the hypothesis that response wood and reaction wood are similar, response wood in the stump probably resists bending caused by sway more than non-response wood. However, the hypothesis also predicts that, in the roots, response wood likely resists parallel compression caused by buckling less than non-response wood. The latter prediction seems unlikely, since, during tree sway, the roots are severely compressed (Coutts, 1983) and resistance to parallel compression is expected since it may be important for avoiding root damage.

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[2](...continued)
microfibril frame flexibly stitched by hemicelluloses and solidly embedded in lignins (Barnett, 1981).

1.7. Physiological Basis for Response Growth and Change in Wood Strength

Different parts and tissues of the spruce probably experience different types and degrees of mechanical stimuli or strains when the center of gravity of the tree moves from the central axis of the trunk (Figure 1-1) (Salisbury and Ross, 1985). These different strains influence the types and proportions of growth regulators in the strained regions (Coutts, 1987; Hale and Orcutt, 1987).

The mechanism by which mechanical stimuli might influence hormone balances is unknown (Fayle, 1968; Fritts, 1976; Salisbury and Ross, 1985). However, Salisbury and Ross (1985) suggest that mechanical stimuli might change cellular electrical resistance and the amount of potassium ion leakage into the apoplast of strained cambial cells. The changed electrical polarity may affect the availability of hormones, and hormone precursors (Fayle, 1968; Salisbury and Ross, 1985).

Auxin and ethylene are believed to induce growth responses to mechanical strains (Larson, 1962; Salisbury *et al*, 1982; Yamamota and Kozlowski, 1987; Wilson and Archer, 1977). These hormones increase diameter increment, decrease height growth, influence xylem differentiation and stimulate reaction wood formation. The resulting response may be a qualitative and quantitative change of wood structure, affecting wood strength, and wood production (Larson, 1963).

1.8. Thesis Objectives

In this thesis, I explore the effects of environmental change on tree growth and wood properties to increase basic understanding about the effects of abiotic factors on trees and the reactions of trees to these effects. I hope to also make practical recommendations which might improve some forest harvesting practices. Specifically, I address the relationship of root and trunk wood production and wood quality in white spruce following release.

I first compare (Chapter 2) diameter growth in the roots and trunks of released and unreleased white spruce before and after a known release event to determine if an increase in diameter growth in the root offsets the observed decrease or lag (Yang, 1988) in diameter growth in the trunk following release. I apply dendrochronological techniques (Fritts, 1976) to roots and trunks to compare their diameter growths.

In Chapter 3, I compared the strength and density of response and non-response tissue in the roots and trunks of released and unreleased white spruce to determine if wood strength increases after release, thereby increasing the windfirmness of the spruce. I measure the radial bending strength, parallel compression strength, green specific gravity and moisture content of these tissues to compare their wood qualities. I also relate outside-bark radius and ring width of these tissues to compare the amount of wood produced.

The delay in white spruce trunk growth and the increase in spruce mortality following release are practical concerns for the forest industry. The delay directly influences the amount of time needed for the white spruce to grow to harvestable size (Brace and Bella, 1988), while the increased mortality influences how many white spruce survive to be harvested (Brace and Bella, 1988). An employable explanation about the underlying cause of the delay in trunk growth and the duration of stand windthrow susceptibility may assist forest managers in developing silvicultural systems which maximize the commercial productivity of stands.

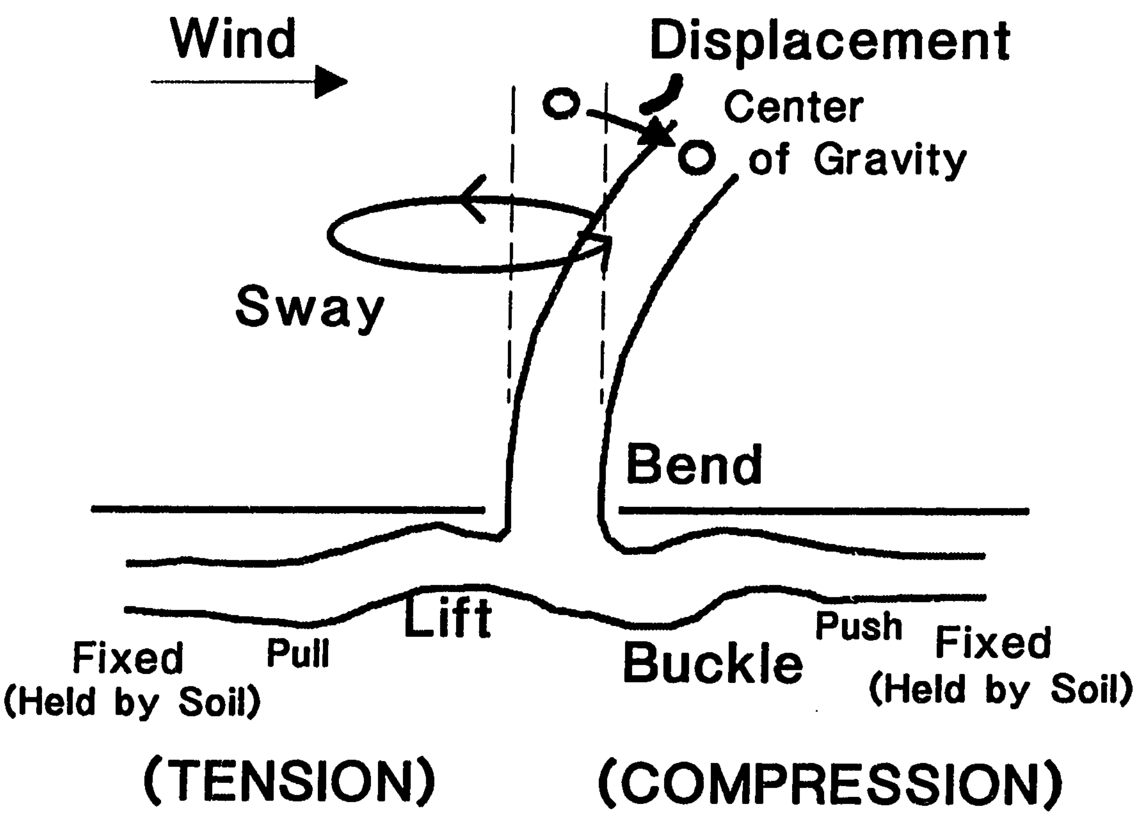

FIGURE 1-1. Trunk bending and root buckling induced by sway. These strains are focussed in the basal portions of the trunk (stump) and root system (structural roots), damping further from the stump (Coutts, 1983). Different strains occur on the leeward, windward and other sides of the trunk (Coutts, 1983), a result perhaps of leeward center of gravity displacement.

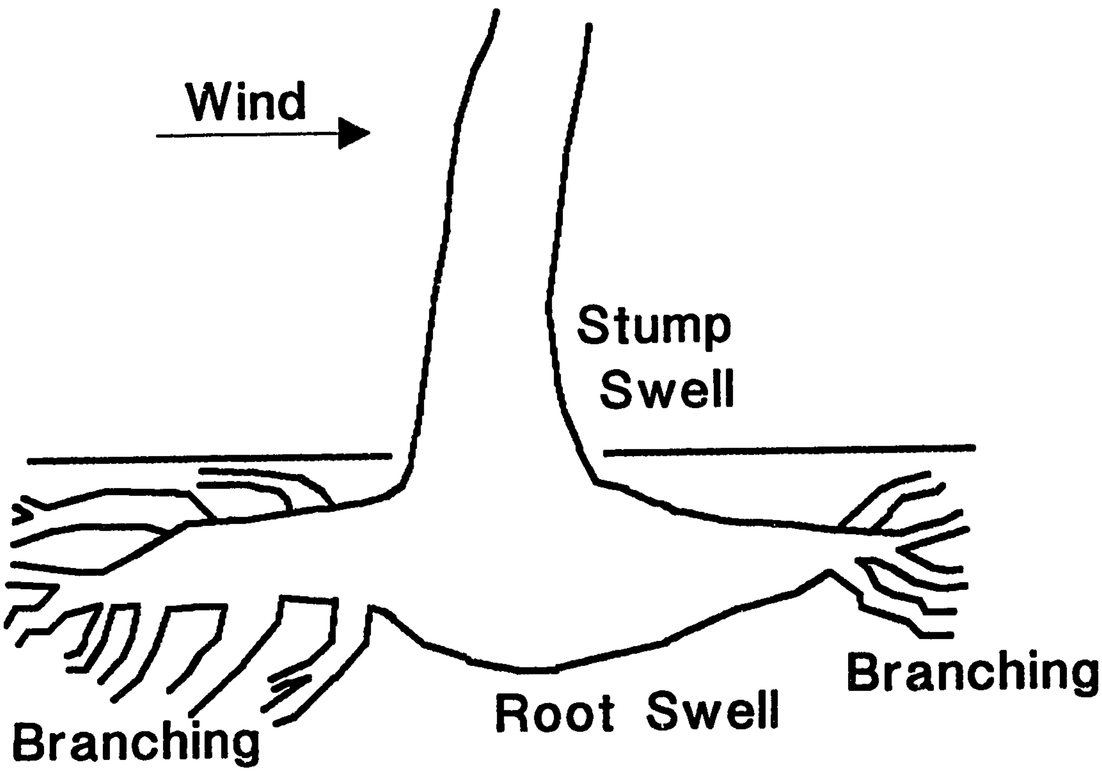

FIGURE 1-2. Response growth in the stump and root plate. Extensive branching occurs on the windward side of the trunk and decreases leeward (Coutts, 1983). Extensive stump and root swell occurs on the leeward side of the trunk, less so on the windward side and least on the other sides (Coutts, 1983). Strategic root degeneration and adventitious rooting also occur (Wagg, 1967).

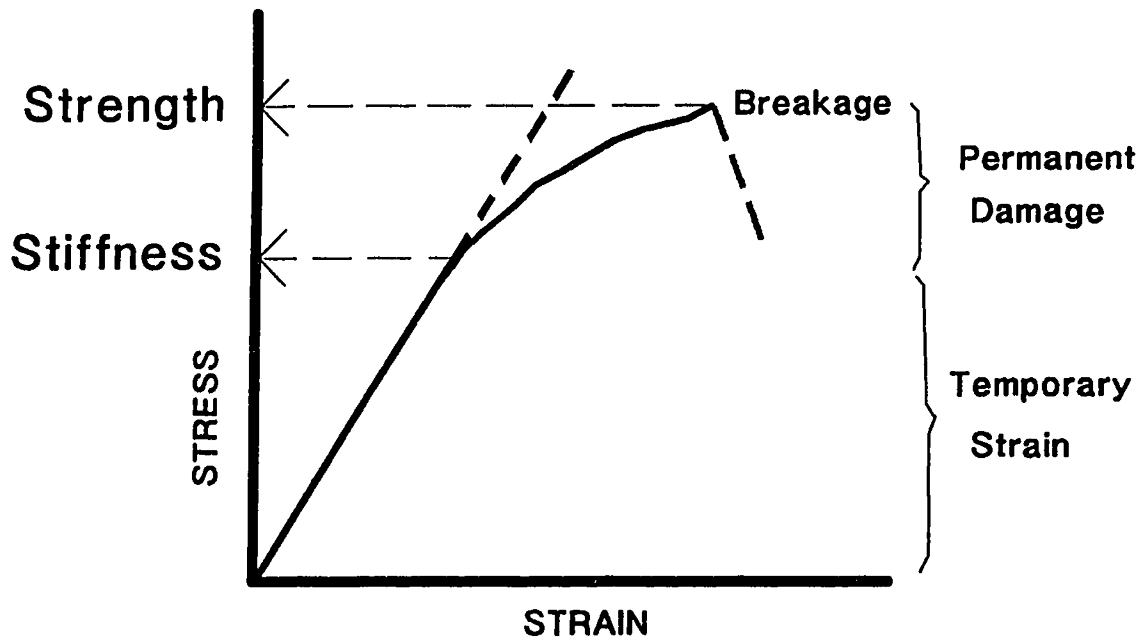

FIGURE 1-3. Stiffness and strength are the stresses at which the object begins to permanently deform and begins to break, respectively. The stress at which the stress - strain curve begins to bend estimates the object's stiffness; that at which the curve begins to drop estimates the object's strength. Modified from Haygreen and Bowyer (1989).

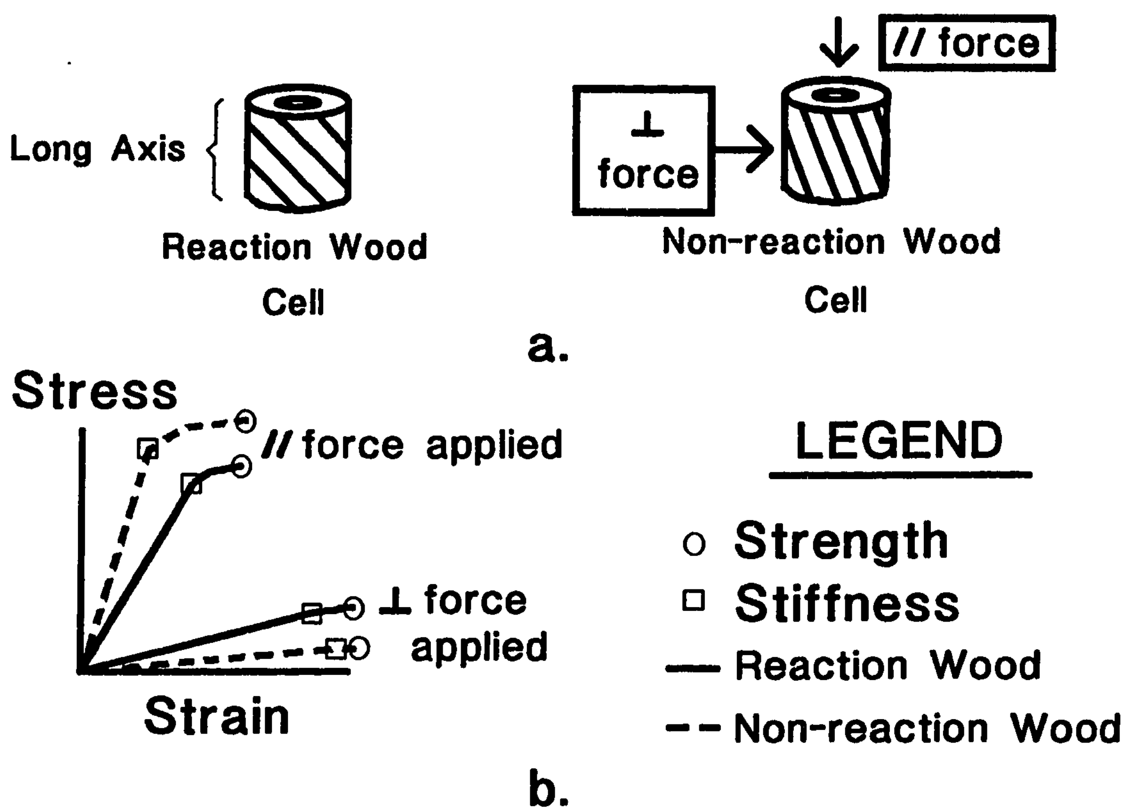

FIGURE 1-4. Wood cell structure and strength. a. Reaction wood microfibrils are orientated more perpendicular to the cell's long axis than non-reaction wood microfibrils (Parham and Gray, 1984). b. Non-reaction wood is stronger against a force applied parallel to the cell's long axis (Panshin and Zeeuw, 1980), while reaction wood is stronger against a force is applied perpendicular to this axis. See Figure 1-3 for a description of stiffness and strength.

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Chapter 2

The Effect of Release on Root and Bole Tree-ring Growth in White Spruce[1]

2.1. Introduction

Release of understory white spruce (*Picea glauca* (Moench) Voss) from overstory aspen (*Populus tremuloides* Michx.) competition ultimately results in a faster growth rate and shorter rotation period for the released spruce (Brace and Bella, 1988). However, trunk response to release, or overstory removal, is often delayed three to six years (Johnstone, 1981; Dang and Lieffers, 1989), while, simultaneously, wind damage and windthrow are intensified (Yang, 1988; Cutler *et al*, 1989). Following this initial period, spruce windthrow hazard decreases (Brace and Bella, 1988) and spruce trunk diameter and height growths increase (Yang, 1988).

Theoretically, following release, the tree should have access to more resources for growth, since competition is reduced and more resources are available (Smith, 1986). If growth does not increase in the trunk, the tree might be allocating resources elsewhere, perhaps to the roots (Johnstone, 1981). Roots normally compete with the trunk for growth resources (Coutts, 1987; Salisbury and Ross, 1985). I hypothesize that the sway associated with relatively open conditions following release causes a shift in biomass allocation to the root, thereby increasing the windfirmness of the spruce.

The objective of this study is to determine whether or not allocation of growth to the root increases following release. Incremental diameter growth, measured by growth-ring width, is compared in released and unreleased spruce trunks and roots before and after a known release event.

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[1]A version of this chapter has been submitted for Publication. Urban, S.T., Lieffers, V.J., Macdonald, S.E. 1993. Can. J. For. Res.

2.2. Methodology

Sampling

The study was conducted in the fall of 1991 in a 120 year-old aspen, white spruce and lodgepole pine (*Pinus contorta* Dougl.) stand located northeast (115°, 45' W by 54°, 30' N) of Whitecourt, Alberta. The understory of this stand was dominated by *Rosa acicularis* Lindl., *Calamagrostis canadensis* (Michx.) Beauv. and moss. The site had flat topography and grey wooded soils (Government of Alberta and University of Alberta, 1969). Wind is a problem at the edges of this stand as evidenced by the high incidence of windthrow along the west and north edges where part of the stand was clearcut two years prior to sampling. Winds blow predominantly from the west at 10 km/hr on average from April to October (Harvey *et al*, 1984-1992).

Ten released white spruce were selected slightly out from the forest edge along an east-west orientated road that was cleared in the early spring of 1976 and ten unreleased spruce were chosen 100 m distance from the road in the forest. Each unreleased tree was surrounded by neighboring trees with crowns no more than 12 m from its own. The trees were unpaired and selected for similar age and size.

In each trunk, single cores were sampled at breast-height from the leeward (east) and windward (west) faces and from a face perpendicular to the wind direction. Three to five large, structural roots were cored in each tree about 30 cm from the stump edge. In 90% of the trees, the vertical diameter of at least one root was too long to include the primary xylem in the increment core. Consequently, only the top portions of the roots were sampled and analyzed. The few root cores from the sampled spruce which included the entire root from bark to bark had top radius to bottom radius ratios greater than 10, implying that growth below the root primary xylem is negligible relative to the top.

Incremental Ring-width Measurement and Analysis

The procedures for cross-dating, ring-width measurement and indexing described by Dang and Lieffers (1989), after Fritts (1976), were implemented in this study, with the following modifications. Increment cores, instead of cross-sections, were used as samples to avoid destructive sampling and to more easily sample roots. In these cores, the widths of the 56 most recent growth rings, counting back from the bark, were measured with a computerized measuring device (Clyde and Titus, 1987). These 56 rings correspond to the 16 growing seasons after release plus 40 growing seasons before release.

Sixty percent of the control and released spruce had basal roots 56 years old or younger that were the same size as 120 year-old roots. Since the age of the roots were not know at the time of sampling, I cored these adventitious roots. However, smaller roots (obviously adventitious) were ignored. Later, those roots less than 56 years of age were removed from the sample to eliminate their growth peculiarities[2]. Adventitious roots older than 56 years seemed to follow the typical growth pattern of trunks and non-adventitious roots (Figure 2-1). Consequently, they were not eliminated from the sample. Annual mean ring widths for the roots and trunks of each tree were calculated by averaging ring widths yearly from those cores that were not eliminated from the sample.

Since ring width generally decreases toward the bark according to a negative exponential growth curve (Fritts, 1976) (Figure 2-1), I attempted to fit negative exponential equations to the averaged, annual ring widths in the pre-release tissue of the roots and trunks for each tree. Where these equations did not fit the data (F-test, pr>0.05), negative linear equations were tried and finally horizontal linear equations, based on the assumption that the measured rings came from flatter parts of the negative exponential curve (Figure 2-1). The correlation coefficients of the significant equations are given in Table 2-1.

The same regression technique was used to fit equations to the averaged, annual ring widths of all pre- and post-release tissue in the roots and trunk of each control tree. Then, the significant pre-release equations for the roots and trunks of the control trees were extrapolated into the post-release period. These extrapolations were compared to the post-release portions of the full-data equations, using paired-sample t-tests, to determine how accurately the extrapolations predicted ring width.

Subsequently, the pre-release equations for the roots and trunks of the released trees were extrapolated into the post-release period. For the released and control trees, the pre-release equations and their extrapolations were then used to predict ring widths in the pre- and post-release tissues of the roots and trunks. The predicted ring widths were divided from the corresponding observed ring widths to produce ring indices.

Eighty-five percent of the unreleased spruce experienced some form of increase in trunk growth after the time of release, suggesting that 1) these unreleased trees also had improved growing conditions following release or 2) this increase in trunk growth is their natural pattern of growth. The increase suggests that part of the response of the released trees in the post-release period might have been related to factors other than the release. The additional response was corrected for by subtracting control spruce ring indices from released spruce

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[2]The cored, adventitious roots generally had wider growth rings than non-adventitious roots and the trunks. Furthermore, these growth rings did not reduce in width over time according to the negative exponential growth curve typical of trunks (Fritts, 1976) and non-adventitious roots (Figure 2-1).

indices (Table 2-2).

The above procedure produced ten root ring indices and ten trunk ring indices for the released trees and for the control trees. Each of these sets of ten indices were averaged yearly to produce mean Released Root, Released Trunk, Unreleased Root and Unreleased Trunk Ring Indices (Figure 2-2). These Indices were then subtracted annually according to Table 2-2 to produce other indices. Subtracting the Unreleased Root Ring Index from the Released Root Ring Index produced a net Root Response (to release) Index (Figure 2-3a). The same subtraction, but for the trunk, produced a net Trunk Response Index (Figure 2-3b). Subtracting the Released Trunk Ring Index from the Released Root Ring Index produced a Released Spruce net-Allocation (to root) Index (Figure 2-4a). This same subtraction with the Unreleased Root Ring Index and the Unreleased Trunk Ring Index produced an Unreleased Spruce Allocation Index (Figure 2-4b). Subsequent subtraction of either the Allocation Indices or the Response Indices, according to Table 2-2, produced an Allocation Response (Real) Index (Figure 2-5) which measured the net effect of release on the allocation of ring-width to the roots.

To determine whether release had any significant effect on the diameter growths of the roots and trunks of released trees, and to compare the effects on the roots and trunks, two-sample t-tests were used to compare the mean values and slopes of 1) the above indices in the pre- and post-release periods and 2) the pre- and post-release periods in the same index. Significant differences in mean value were expressed as percentages of the indices being deducted (as compared to the indices being reduced) or of the pre-release periods (when subtracting from the post-release periods in the same indices). Significant differences in slope were expressed in index units/annum.

2.3. Results

An attempt was made to sample released and control trees of the same height, breast-height age and breast-height diameter. However, the sampled released spruce were generally smaller, in height and diameter, than the unreleased spruce (Table 2-3). They were probably also younger, but the ages of 80% of the sampled trees were underestimated as cores from them did not include the pith.

Ring Indices

All Ring Indices increased following release, except the Ring Index for unreleased roots, which did not change (Figure 2-2). The unreleased Trunk Ring

Index increased by 27% or 0.03 index units/year. Most of this increase occurred eight to two years prior to sampling. Before and after release, the Released Root and Trunk Ring Indices had similar means and slopes (common means and slopes 1) before release: 1.00 and 0 index units/year, and 2) after release: 1.68 and 0.07 index units/year). However, in the first three years following release, the Released Root Ring Index had a steeper rate of increase and a higher peak than the Released Trunk Ring Index (Figure 2-2).

The Root Ring Indices of the released and unreleased spruce frequently peaked a year before the Trunk Ring Indices following release, but generally either lagged a year or matched the Trunk Ring Indices before release.

Response Indices

Before release, the Root and Trunk Response Indices were similar in mean value and slope (Figure 2-3). Their means increased significantly following release, but that of the Trunk Response Index increased to a lesser extent than that of the Root Response Index (31% versus 69% respectively). In fact, the trunk may not have responded to release until after four post-release years passed. Nevertheless, the slope of the Trunk Response Index (0.05 index units/year) was greater than that of the Root Response Index (0.04 index units/year). The higher mean value and gentler slope of the Root Response Index suggests that this Index could have peaked higher or increased sooner than the Trunk Response Index. In fact, it did both (Figure 2-3). Consequently, the root responded to release before the trunk, but the rate of this response decreased with time following release. The opposite was true for the trunk.

Peaks and troughs are hard to match; however, the root seemed to consistently respond before the trunk following release. For example, the Root Response Index peaks at years 48 and 54 and troughs at year 50, while the Trunk Response Index peaks at years 50 and 56 and troughs at year 52.

Allocation Indices

In the 16 years prior to sampling, the Unreleased Spruce Allocation Index decreased 21% or 0.02 index units/year (Figure 2-4b). This decrease was mainly related to the increase in the Unreleased Trunk Ring Index following the time of release, while the Unreleased Root Ring Index remained stable (Figure 2-2). In contrast, the Released Spruce Allocation Index increased 17% in mean value (Figure 2-4a), even though the means of the Released Trunk and Root Ring Indices were statistically equal following release (Figure 2-2). Further, the variation of this Index increased after release. Following release, its slope decreased 0.03

index units/year after initially peaking. Allocation to the root remained positive for the first nine years.

Real Index

The Allocation Response (Real) Index increased 37% in mean value following release (Figure 2-5), implying that ring-width allocation to the root, and therefore root diameter growth, increased following release in the sampled released spruce. The slopes of the Real Index before and after release were equivalent to zero. Consequently, this increase was not a simple rise in ring-width allocation to the root over the years since release. It was an abrupt shift upon release to a new level. Excluding the final peak at year 54, the slope of the post-release Real Index is negative like the slope of the Released Spruce Allocation Index (Figure 2-4a). The final peak in the Real Index (Figure 2-5) corresponds to the peak around year 53 in the Allocation (Figure 2-4) and Ring (Figure 2-3) Indices. Using the final peak as part of the Real Index data, the duration of the high, post-release mean is not estimable from Figure 2-5. However, it appears to last for at least 15 years.

2.4. Discussion

Physiology and Ecology of Response to Release

The Real Index clearly shows an increase in allocation to diameter growth of the root following release. This increase may peak during the reported delay (Yang, 1988) in trunk response to release. The Allocation and Response Indices suggest an initial (three to nine year) delay in trunk diameter growth and a concurrently high root diameter growth in released spruce. Further, the Released Spruce Allocation Index decreases after it initially peaks following release. These growth behaviors suggest that increased root growth may account for the observed delay in trunk response to release.

Different hormone balances in the trunk and root (Hale and Orcutt, 1987) and competition for limited growth resources (Coutts, 1987; Deans and Ford, 1985; Salisbury and Ross, 1985) may explain the relationship between high root growth and low trunk growth. In released spruce, the root may be a stronger sink during the lag period before increased trunk growth (Fritts, 1976). Environmental conditions affect the relative strengths of competing growing regions (sinks) as well as the production and movement of growth regulators (Hale and Orcutt, 1987; Salisbury and Ross, 1985). These hormones, perhaps auxin or ethylene, directly affect the rate of growth by promoting or inhibiting cambial activity (Fritts, 1976) in different regions of the tree. They also may regulate the relative strengths of competing sinks or the transportation or relative distribution of growth resources (Larson, 1963).

The benefits of immediate root response and delayed trunk response to release are: 1) reinforcement of the tree's foundation to withstand the increased wind stress on the tree (Coutts, 1983) and 2) postponement of crown enlargement, which would increase the wind load on the tree (Kounadis and Belbas, 1977; Milne, 1991), until the tree's foundation is reinforced. The foundation is reinforced by increasing resistance to sway-induced movement (Coutts, 1983; Coutts, 1987; Wagg, 1967). Stump and root swell, especially leeward of the trunk, thickens and thereby stiffens and strengthens the stump and roots. Root branching, especially windward of the trunk, binds the root and the soil into a tight, heavy plate. Adventitious rooting along with root deterioration result in a reforming of the tree's foundation, resulting in strategically positioned anchoring roots. In fact, adventitious rooting may be a very common response to release. At least sixty percent of the spruce sampled in this study had adventitious roots, most formed slightly after release. In two similar stands in Saskatchewan (described by Yang, 1980), adventitious roots were found on all fully released spruce (Urban, unpublished). Therefore, the elimination of adventitious roots from the data set underestimated the amount of resources allocated to the roots after release.

Management Recommendations

Although the results of this study are based on trees sampled from one site, I speculate that increased root growth is a general mechanism used by trees to increase their windfirmness as well as a general cause of delayed trunk growth in trees exposed to open conditions. The literature liberally addresses windthrow (Rollerson, 1991; Cutler *et al*, 1989), windfirmness (Mergen, 1954; Larson, 1963), root growth (Coutts, 1983; Coutts, 1987; Helliwell, 1989) and trunk growth delay (Yang, 1988; Johnstone, 1981) in many species in many areas.

Unreleased white spruce are susceptible to wind damage and windthrow upon release (Brace and Bella, 1988) since, being sheltered from severe wind exposure by their neighbors and the overstory, they have not developed a resistance to wind stress (Cutler et al, 1989; Mergen, 1954). The sizes and ages of the trees sampled in this study already place them in the canopy where they are exposed to wind. However, clearing a row of forest for road construction increases the relative exposure of the stand-edge (released) spruce compared to the interior (unreleased) spruce. The fundamental reaction to increased exposure of these trees is probably comparable to that of understory spruce when the overstory is removed.

Releasing understory and interior spruce ultimately increases trunk growth

(Yang, 1988); however, this growth is delayed for some years immediately after release. In addition, windthrow mortality is high during this period (Brace and Bella, 1988). Partial release will still ultimately increase trunk growth relative to that of unreleased spruce (Yang, 1988). However, it may decrease the lag period in trunk response as well as reduce the incidence of windthrow compared to full release.

The spruce in this study are the size and age of harvestable seed trees in a shelterwood regeneration system. The increased allocation of diameter growth to the roots of these trees for 15 years suggests that preparatory cuts may improve the survival of seed trees by allowing them to become more windfirm prior to the seeding cut.

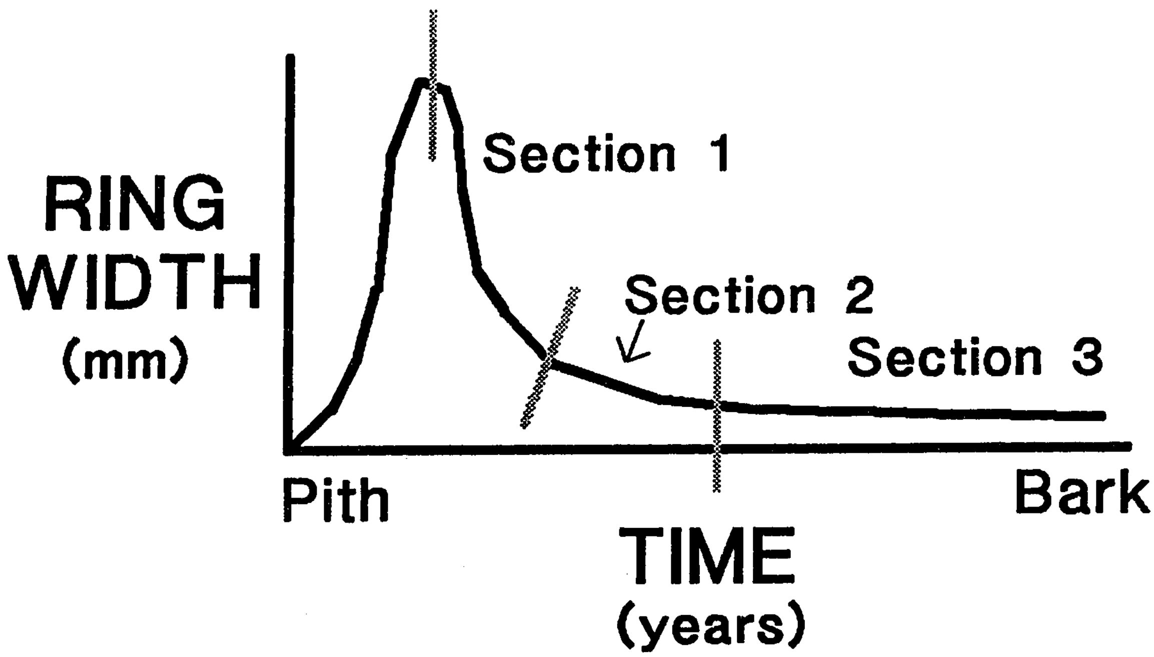

FIGURE 2-1. Typical diameter growth curve of a trunk or root cross-section. Annual ring width data from the trunk or root of each spruce sampled in this study follow either 1) the negative exponential portion (illustrated as section 1 in the figure) of the curve, 2) the negative linear portion (section 2) of the curve or 3) the horizontal portion (section 3).

TABLE 2–1. Correlation Coefficients for Significant (pr<0.05) Negative Exponential, Sloped Linear and Horizontal Linear Equations fit to Averaged Pre–release Root and Trunk Data of Released and Unreleased Spruce.*

		Unreleased Spruce			Released Spruce		
	Nested Tree #	Negative Exponential	Sloped Linear*	Horizontal Linear	Negative Exponential	Sloped Linear	Horizontal Linear
Trunk	1	–	–	0	–	–	0
	2	–0.593			–	–	0
	3	–0.766			–0.757		
	4	–0.777			–0.778		
	5	–0.881			–0.533		
	6	–0.573			–0.950		
	7	–	–	0	–0.831		
	8	–0.576			–0.963		
	9	–0.763			–0.712		
	10	–0.365			–0.800		

Root	1	-	+0.369		-	+0.709	
	2	-0.593			-	-	0
	3	-0.545			-0.635		
	4	-	-	0	-0.855		
	5	-0.667			-0.446		
	6	-	-	0	-0.908		
	7	-	-	0	-0.607		
	8	-	-	0	-0.877		
	9	-	-	0	-0.669		
	10	-	+0.349		-	-	0

* Attempts were made to fit negative exponential equations to the data first, followed by negative linear equations and finally by horizontal linear equations. The significant equations were extrapolated in to the post-release period. Sample size equals 40 in all cases.

** No linear equations with negative slopes fit the data; however, in the root, positively sloped equations fit significantly. This fit implies an increase in ring width of some roots prior to release.

TABLE 2–2. The Derivation of Allocation, Response and Real (see text) Indices by Sequential Subtraction of Released and Unreleased Trunk and Root Ring Indices.

Released Root Ring Index	*minus*	Unreleased Root Ring Index	=	Root Response Index
minus		*minus*		*minus*
Released Trunk Ring Index	*minus*	Unreleased Trunk Ring Index	=	Trunk Response Index
=		=		=
Released Spruce Allocation Index	*minus*	Unreleased Spruce Allocation Index	=	Real Index

TABLE 2–3. Mean (± SEM) Breast–height Ages, Heights and Breast–height Diameters of Released and Unreleased White Spruce.

	n	Age (years)*	Height (m)	Diameter (cm)
Unreleased	10	121.7±3.41	29.46±0.68	48.07±2.16
Released	10	113.2±6.34	26.51±1.15	41.10±2.54
Overall	20	117.5±3.60	27.99±0.67	44.59±1.67

* 80 % of the age data are not true breast–height ages; they represent the maximum number of annual rings without the pith cored from the trunks of the sampled white spruce.

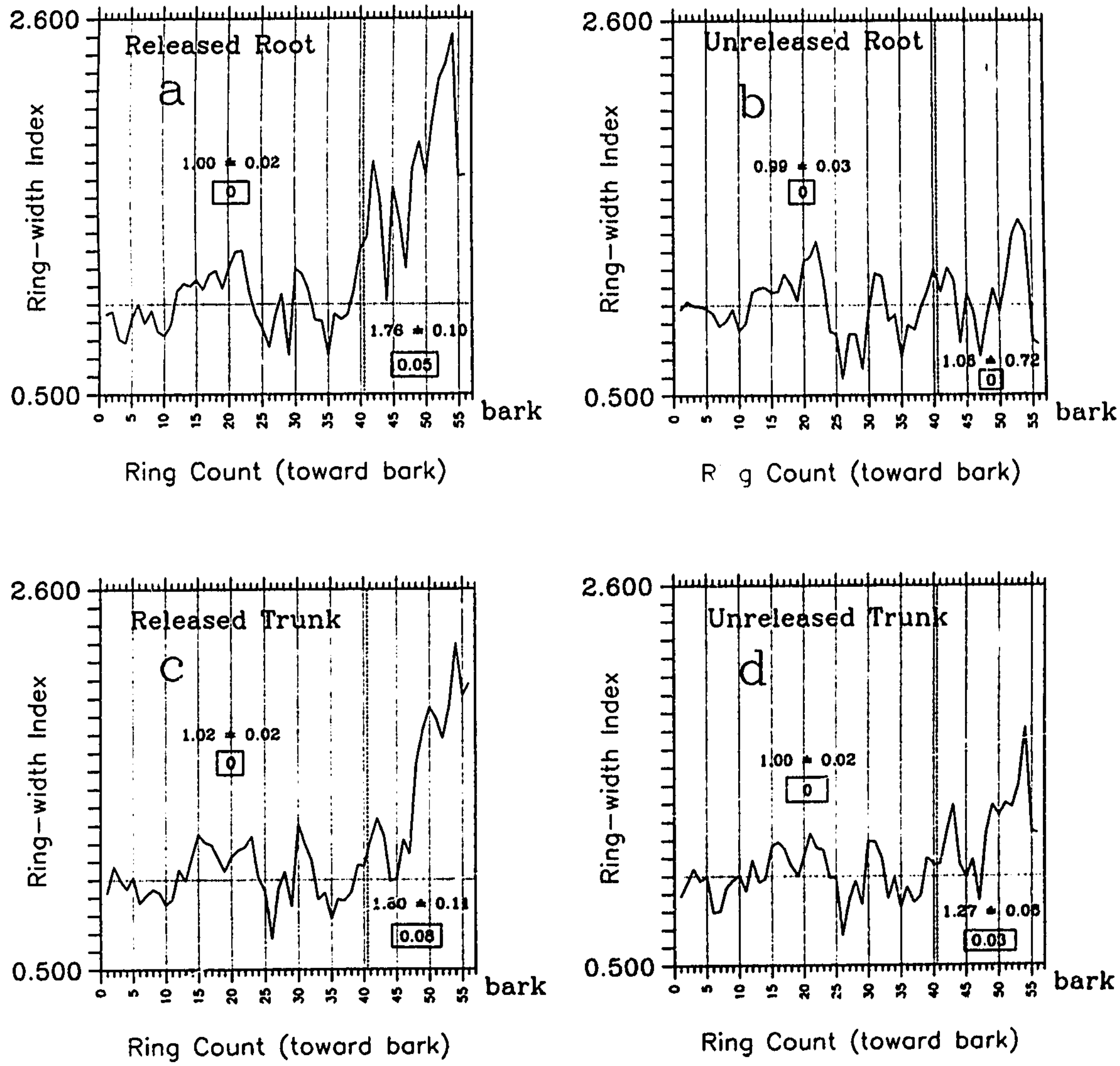

FIGURE 2-2. Mean tree Ring Indices for a) released root, b) unreleased root, c) released trunk and d) unreleased trunk. Release occurred between rings 40 and 41. The values are index mean ± standard error (unboxed) and slope (boxed) for the pre- and post-release periods.

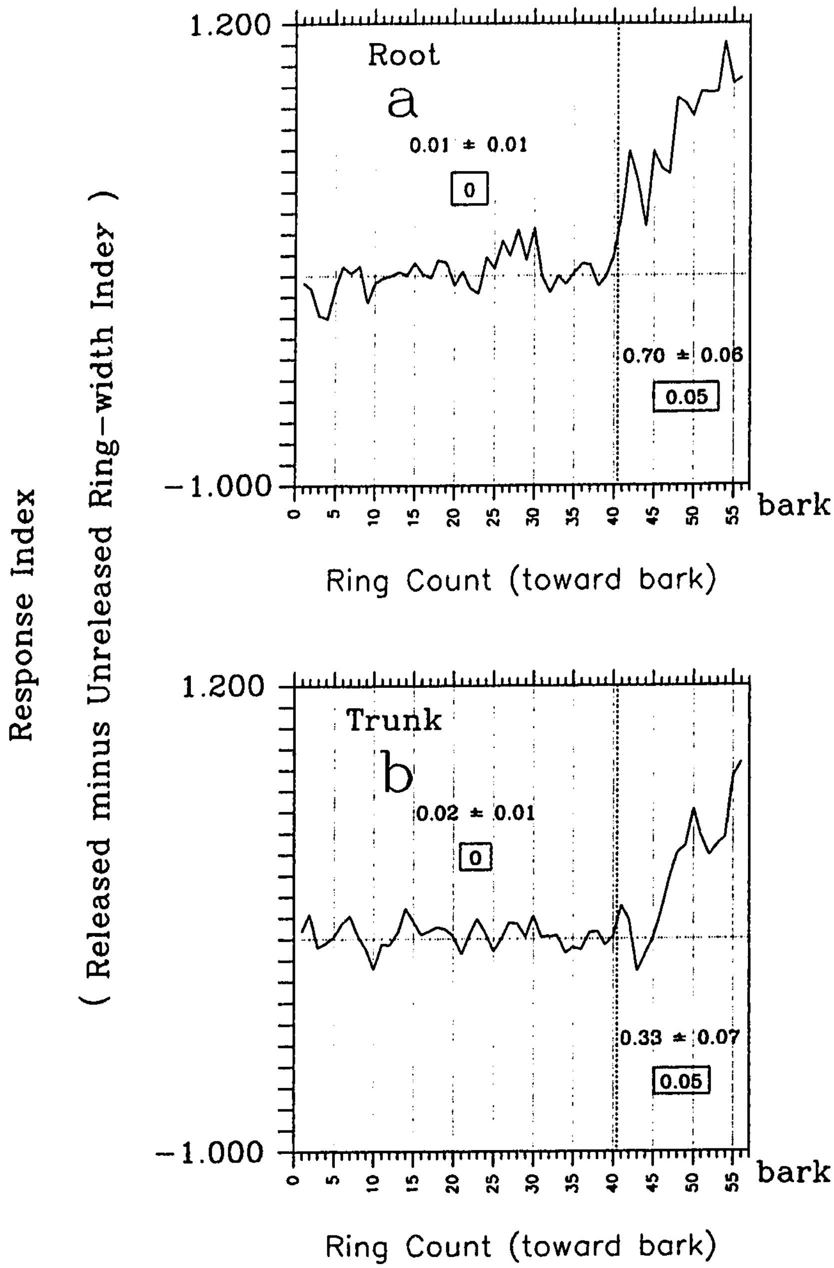

FIGURE 2-3. Response Indices for a) root and b) trunk. Release occurred between rings 40 and 41. The values are index mean ± standard error (unboxed) and slope (boxed) for the pre- and post-release periods.

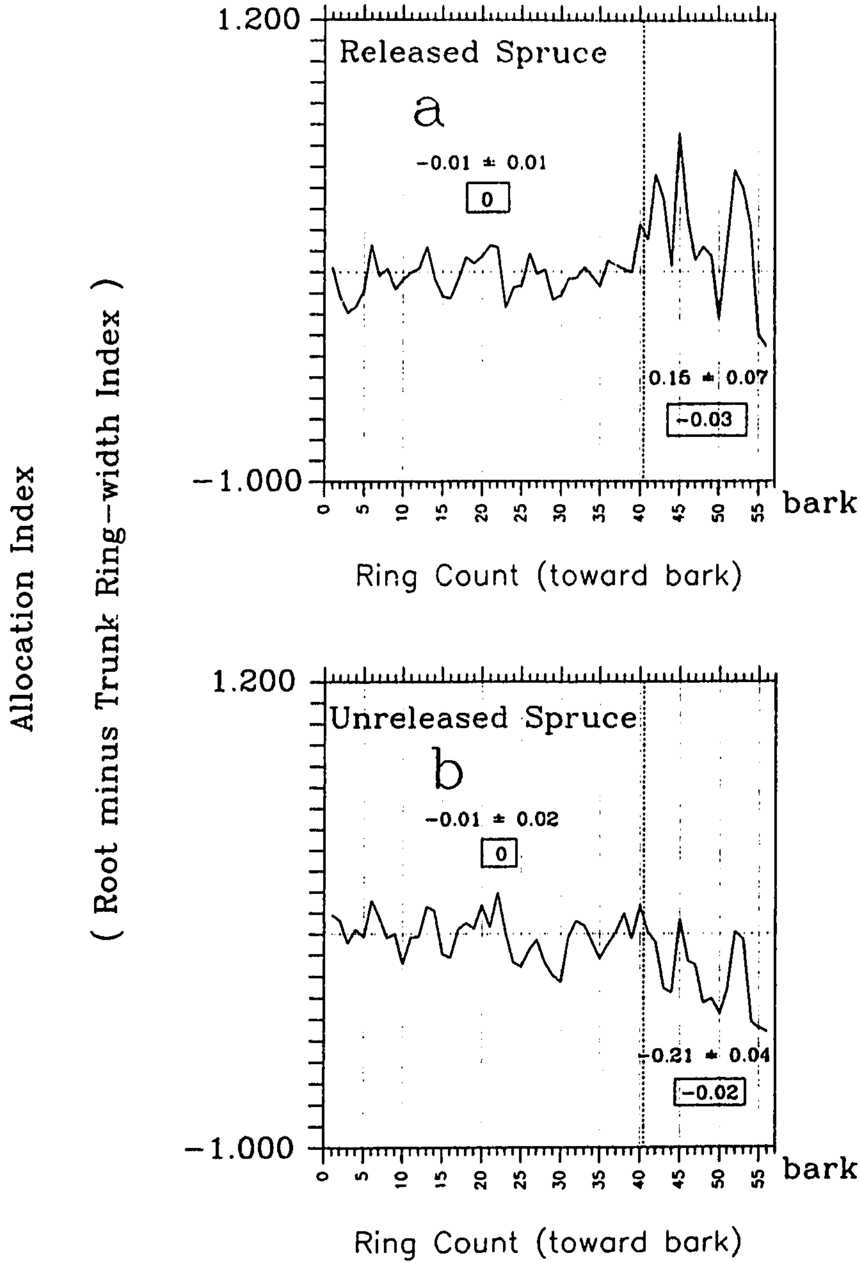

FIGURE 2-4. Allocation Indices for a) released spruce and b) unreleased spruce. Release occurred between rings 40 and 41. The values are index mean ± standard error (unboxed) and slope (boxed) for the. pre- and post-release periods.

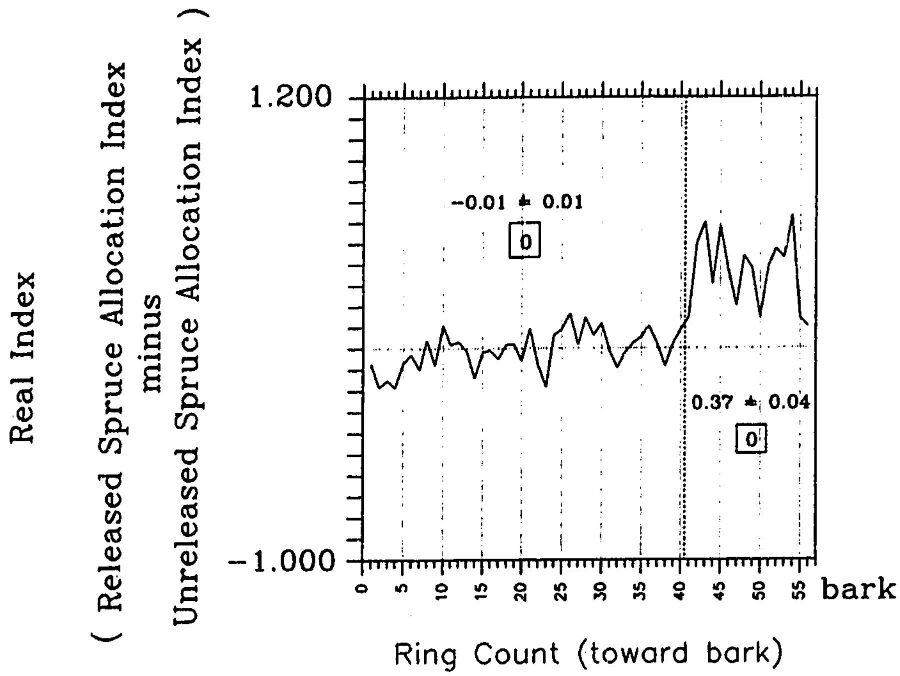

FIGURE 2-5. Allocation Response (Real) Index. Release occurred between rings 40 and 41. The values are index mean ± standard error (unboxed) and slope (boxed) for the pre- and post-release periods.

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Chapter 3

The effect of Release on Root and Trunk Wood Strength in White Spruce[1]

3.1 Introduction

Understory white spruce (*Picea glauca* (Moench) Voss) in boreal white spruce - aspen stands are susceptible to wind stress and windthrow when the overstory aspen (*Populus tremuloides* Michx.) are removed (Brace and Bella, 1988; Yang, 1988). However, white spruce which survive the first years of exposure become more windfirm than their newly exposed counterparts (Cutler *et al*, 1989). This windfirmness results from a change in growth which strengthens the trunks and roots, resulting in better support of the spruce in severe winds (Coutts, 1987).

The increase in trunk and root strength following overstory removal (release) is largely due to a change in trunk and root form (Coutts, 1983), including an increase in the amount of incremental growth (Chapter 2). However, Haygreen and Bowyer (1989) speculate that wood strength is also higher in open grown spruce. Consequently, if the extra wood produced following release is also stronger than the wood produced prior to release, spruce windfirmness would be effectively maximized.

In this study, I tested the hypothesis that white spruce produces more and stronger wood in open environments than in closed stands. Two specific questions were addressed: 1) is more wood produced in released white spruce than in unreleased white spruce? and 2) Is post-release wood stronger than pre-release wood?

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[1]A version of this chapter has been submitted for publication. Urban, S.E., MacDonald, S.E., Lieffers, V.J., Bach, L. 1993. Wood Science.

3.2 Methodology

Experiment

Twelve white spruce wood types were compared in this study. These wood types were determined by three variables: exposure status of the tree (released or unreleased), tree part (root, stump or bole) and wood tissue[2] (response or non-response). Five samples of each wood type were taken from ten hand-selected trees. In total, 60 samples were tested to compare the wood types.

Sampling

All sampling procedures and wood property tests were conducted according to the American Society for Testing and Materials Standard D143-83 as follows.

Study Area and Field Sampling

Five released and five unreleased white spruce of the same approximate age and size (Table 3-1) were selected in the fall of 1991 from several stands in a mixed-wood forest northeast (115°, 45' W by 54°, 30' N) of Whitecourt, Alberta. The study area has rolling topography, grey wooded soils and a forest of fire origin with an aspen overstory and a white spruce understory. The released spruce came from outer protrusions in the edges of east-west orientated roads and cutlines which exposed the spruce to westerly winds. At the time of sampling, these roads were 20 or more years old. The unreleased white spruce, serving as control trees, were selected from within the adjacent mixed-wood stands. Each unreleased tree was covered by an overstory and surrounded by neighbouring trees whose crowns were no more than 4 m away from its own. The released and

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[2]Response wood was identified wherever possible by: 1) relatively wide rings compared to other parts of the cross section, 2) its occurrence on the leeward sides of the stump and bole or the tops of roots and 3) its occurrence in post-release tissue. Non-response wood was identified wherever possible by: 1) narrow rings, 2) its occurrence on the windward sides of the stump and bole or the bottoms of roots and 3) its occurrence in pre-release tissue.

unreleased spruce were not paired.

From each tree, root sections from stump edge (0 cm) to 60 cm distance, stump sections from stump height (30 cm) to 90 cm height and bole sections from breast height (130 cm) to 190 cm were cut. These sections were labelled and stored in plastic bags at room temperature for 3-5 days before processing.

Processing of Samples

A rod 15 mm by 15 mm and up to 60 cm in length was cut from each wood type in each tree. However, due to the sizes and shapes of the roots, most rods sampled from root non-response tissue also included the primary xylem as well as narrow-ringed, response tissue (Figure 3-1). Further, some rods sampled from post-released wood of stumps and boles in unreleased spruce came from sections which did not have wide rings.

The rods described above were further cut into 12.5 by 12.5 by 200 mm sticks for bending strength measurement and 12.5 by 12.5 by 50 mm sticks for compression strength measurement. The sizes and shapes of the roots limited the lengths of the rods that could be cut from them. Therefore, in each tree, two rods were cut from each root wood type and two sticks of each size were cut from the same tree wherever they could be from these rods. This resulted in side matching, an interchange of sticks from similar rods. These root sticks were tested individually. Then, the test results were paired by wood type and tree number and averaged before analysis to even the sample size between roots, stumps and boles.

Tests

1) Outside-bark Radius and Ring Width

Prior to the sawing of the green logs into rods, the radius from the outside-bark to the primary xylem was measured from the stumpward (lower) end of each section. Ring width was measured and averaged from both ends of all compression-test and bending-test sticks before these tests were conducted.

2) Strength Tests

The parallel compression and radial bending tests were conducted only on wet wood. The sticks were stored in plastic bags and frozen prior to and between tests. For two days before each test, the sticks tested were submersed in water. Excess surface water was blotted from each stick immediately before it was tested. Instron Universal Testing Machines (IUTM Models 4204 and 4202) from the Alberta Research Council in Edmonton were used to measure the parallel compression strengths of the compression-test sticks (at a rate of 6.000 mm/min) and the radial bending strengths of the bending-test sticks (at a rate of 2.500 mm/min).

The bending-test sticks were placed across the Testing Machine supports with their growth rings orientated concave (coreward) down when response tissue, from the leeward side of the tree, was being tested and concave up when non-response tissue, from the windward side of the tree, was being tested. This orientation best simulated bending in a standing, wind-exposed tree.

Some bending-test sticks slid inward, off the supports bracing them at each end, toward the applied bending load. The strengths of these sticks were not observed, even when the sticks were allowed to fold about the load bar (radius of curvature of 38 mm). Since the sticks slipped and did not break, their elasticities, and therefore their strengths, must be high. Estimates of the strengths for the sticks that slipped were obtained by plotting, for each wood type, the bending strengths of those sticks that did not slip against normal equivalent deviates (Appendix 3A) (Zar, 1984). By extrapolating the resulting normality lines where needed, the strengths for the slipped sticks of each wood type were estimated.

3) Dry Density, Green Specific Gravity and Moisture Content

After completion of the bending tests, the end of each bending-test stick which was least blemished and most representative, in terms of ring width for that wood type, was cut into a 30 mm long stub. These stubs were submersed in water for two days, then their dimensions were measured with vernier callipers and their weights recorded prior to and following oven-drying at 108°C for 48 hours. From these data, moisture content, green specific gravity and dry density were calculated. These properties were analyzed as indicators of strength, which is generally directly correlated with density and specific gravity and negatively correlated with moisture content. Field moisture content was also measured from disks sampled from the roots and trunks of the sampled spruce to test whether soaking of the stubs changed the relative moisture contents of the different wood types.

Analyses

The data for all wood properties (Appendix 3B) were analyzed using the SAS (SAS Institute, Inc., 1989) general linear model:

$$\text{Wood Property} = \mu + E + T(E) + P + W + PW + EP + EW + EPW + \textit{error},$$

where μ = population mean,
E = exposure status of the tree,
$T(E)$ = tree within exposure status,
P = tree part,
W = wood tissue,
and *error* = PWT(E).

Orthogonal comparisons of the components of each of the terms, except μ, T(E) and *error*, were also conducted. These components were: released versus unreleased (exposure status), root versus stump versus bole (tree part) and response versus non-response (wood tissue) plus interactions of these. Two-sample t-tests were conducted to make further comparisons between the cells of significant interactions ($pr<0.05$) to determine which wood type(s) were responsible for the significance of the significant interactions. The results of these t-tests, and thereby of all the analyses, are summarized in Table 3-2.

3.3. Results

For all wood properties tested, a summary of F-test probabilities, based on the general linear model and orthogonal comparisons, is tabulated in Appendix 3C. The corresponding significant trends, determined by two-sample t-tests of cells in significant interactions and main effects, are listed in Table 3-2. Main effects, whether significant or not, are also listed in Table 3-2. The means of significant interactions and main effects, and their overall averages (averages not necessarily significant), are presented in Tables 3-3 to 3-5 and Table 3-7 with their standard errors. The means of significant interactions were averaged up to the interactions' corresponding main effects. The trends in Table 3-2 are discussed below.

Wood Amount

Released versus Unreleased Spruce

At the time of sampling, the radius of stump response tissue was greater in released spruce than in unreleased spruce (Tables 3-2 and 3-3), resulting in greater overall stump diameter in released spruce. Except in the stump, the mean diameter of released spruce was equal to that of unreleased spruce at breast height (Table 3-1) and in all tree parts (Tables 3-2 and 3-3). However, I assume that the released spruce were not as competitively suppressed as the unreleased spruce following release (Yang, 1988) and that, consequently, they grew faster by the time of sampling. Ring width, which measures diameter increment, indicated that released spruce grew faster than unreleased spruce, except in the root (Tables 3-2 and 3-4). At the time of release, the diameter of released spruce was probably less than that of unreleased spruce. Therefore, released spruce produced more wood than unreleased spruce since release.

Root versus Stump versus Bole

Outside-bark radius was greatest in stump response tissue and least in root non-response tissue (Tables 3-2 and 3-3). These differences resulted in a decrease of tree part diameter from the stump to the bole to the root. Further, ring width was greater in the stumps of released trees (Tables 3-2 and 3-4), though the ring width of non-response tissue decreased from the bole to the root (Tables 3-2 and 3-4). Overall, ring width was similar among tree parts (Tables 3-2 and 3-4).

Response versus Non-response Tissue

Ring width of response tissue was greater in released spruce than in unreleased spruce (Tables 3-2 and 3-4). This suggests that the amount of response tissue produced since release was greater in released spruce. Though response tissue is defined by position, time of formation and ring width, which allows it to be defined in unreleased spruce as well as released spruce, it is fundamentally associated with release and, therefore, essentially restricted to released trees, since unreleased trees should not respond to release. Consequently, the greater ring width in released spruce response tissue implies an overall increase in ring width in released spruce, where response wood is formed, following release. Non-response tissue had simiiar ring widths in both exposure statuses. Released and unreleased spruce had more response than non-response tissue overall (Tables 3-2, 3-3 and 3-4).

Wood Strength

Parallel Compression Strength

Parallel compression strength was least in the roots of unreleased spruce and the stumps of released spruce and greatest in the roots of released spruce and the stumps of unreleased spruce (Tables 3-2 and 3-5). This redistribution of compression strength resulted in equal parallel compression strengths overall among tree parts and exposure statuses (Tables 3-2 and 3-5). Further, parallel compression strength was similar among wood tissues (Tables 3-2 and 3-5), though response tissue in released spruce had the least parallel compression strength, implying that parallel compression strength decreased in released spruce, where response tissue was produced, after release.

Radial Bending Strength

Radial bending strength is greater in stump non-response tissue from unreleased spruce than in other stump wood types (Tables 3-2 and 3-5). This might be an artifact of possible over-estimation of slipped stick (Table 3-6) strengths. Consequently, all stump wood types may have equal bending strengths. Meanwhile, bole wood strength seems to increase after release, since the radial bending strength in bole response tissue from released spruce is greater than that of other bole wood types (Tables 3-2 and 3-5). Further, radial bending strength is greater in root non-response tissue from released spruce than in other root wood types. If one assumes that the bending strength of the root is actually greater in released trees than in unreleased trees ($0.10 > pr > 0.05$, two-sample t-test), then wood strength might decrease in the root following release since root response tissue has weaker wood than root non-response tissue in released spruce (Tables 3-2 and 3-5). Consequently, root radial bending strength may decrease following release, while bole bending strength increases. The overall bending strength in the root of released spruce would still be greater than that of unreleased spruce.

The stump had greater radial bending strength than other tree parts (Tables 3-2 and 3-5). It also had higher radial elasticity than the other parts, especially in released spruce, according to the high incidence of slippage of bent sticks from the stump (Table 3-6). Radial bending strength was similar among wood tissues and exposure statuses.

Indirect Strength-Indicators

The soaked stubs and tree disks had similar relative moisture contents among wood types. Relative trends in green specific gravity and dry density were also similar and generally opposite those of moisture content in the stubs. They are also positively correlated with strength. Consequently, these indicators suggest that the strength of released spruce equalled that of unreleased spruce and that the bole was weaker than the stump and root (Tables 3-2 and 3-7). However, moisture content suggests that the bole was similar in strength to the other tree parts (Tables 3-2 and 3-7). Since neither bending nor compression strength suggested weaker bole wood either, the bole was probably not significantly weaker than the stump and root.

Non-response tissue in the root and stump was denser, and therefore possibly stronger, than non-response tissue in the bole and response tissue in all tree parts (Tables 3-2 and 3-7). Meanwhile, response tissue in released spruce was more moist, and therefore possibly weaker, than other exposure status - by - wood tissue wood types (Tables 3-2 and 3-7). These trends suggest that non-response tissue was stronger than response tissue (Tables 3-2 and 3-7). This suggestion contradicts the parallel compression and radial bending strength results, which suggested no difference in strength between wood tissues.

3.4. Discussion

Strength and Wood Distribution Before and After Release

Since strength is determined by more factors than density (Haygreen and Bowyer, 1989), the compression and bending strength test results are used in the interpretation of strength distribution between wood tissues. Therefore, response tissue and non-response tissue had equal overall strengths, implying that wood strength does not seem to contribute generally to windfirmness. It is possible, however, that windfirmness is increased by changes in tree and tree part structure as speculated by Coutts (1983 and 1987). The generally greater increase in wood biomass in released spruce than in unreleased spruce following release seems to confirm Coutts' speculation. In contrast to my findings, Commandeur and Pyles (1991) found that both root form and wood structure contributed to overall stiffness in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) roots.

Among tree parts in unreleased spruce (Figure 3-2), stump wood had the greatest strength (parallel compression and radial bending) and amount of wood (outside-bark radii), while roots had the least. Bending strength was equal in roots and boles. This distribution of wood amount and strength may benefit the unreleased spruce if the stumps are their primary organ of support. Bending strength may be important in the stumps if unreleased spruce lean or experience sway due to some wind in the understory (Fayle, 1978). Compression strength may be important for supporting the spruces' weight (Larson, 1963). Wide stump radius may supply the stump with more of this strengthened wood and consequently more support. However, before release, ring width was similar in all tree parts, suggesting that stump diameter increased at the same rate as the diameters of the bole and root.

Wind bends the trunks and compresses the roots of released spruce (Mergen, 1954). The amount of strain experienced is probably related to the measure of displacement of the trunks and roots from their resting positions (Grace, 1977). However, since equally displacing larger and smaller masses results in more strain in the larger masses (Joseph *et al*, 1978), strain in the spruce is better measured by moment (the product of mass and displacement) than by displacement alone. Consequently, swaying and buckling strains are focussed in or near the stump (Figure 3-3) (Coutts, 1983; Coutts, 1987).

In released spruce, parallel compression strength was greatest in the roots, where parallel compression moment was highest, and least in the stumps (Figure 3-3). This trend is opposite to that observed in unreleased spruce (Figure 3-2), which suggests that the distribution of parallel compression strength was changed in wood produced following release. Therefore, in released spruce, increasing the resistance to root buckling by having strong (parallel compression strength) wood in the roots superseded the need to carry the spruces' weight by having stronger parallelly compressed wood in the stump.

Meanwhile, stumps had higher bending moments and greater radial bending strengths than roots and boles in released spruce (Figure 3-3). Stumps also swelled more in released spruce than in unreleased spruce (Figure 3-3). Bole bending strength increased following release, while root bending strength decreased. The bole sways more than the root and consequently has a higher bending moment. However, root strength may have been greater overall in the released spruce I sampled than in the unreleased spruce.

Wood production is quantitatively and qualitatively regulated by the balance of hormones in the cambium (Barnett, 1981; Haygreen and Bowyer, 1989). Wind-induced swaying and buckling may change the distributions of auxin and ethylene in white spruce following release (Larson, 1963; Hale and Orcutt, 1987). This change seems to cause increased parallel compression strength in the root (countered by decreased compression strength in the stump) as well as increased ring width in all tree parts. Further, ring width increased more in the stump, where bending strength also was greater, than it did in the root and bole. These changes occurred in tree parts where increases in strength and biomass potentially contribute most to the resistance of bending and buckling strain induced by wind.

Management Recommendation

Unreleased, understory white spruce are sheltered from severe wind exposure by their neighbors and the overstory aspen (Cutler *et al*, 1989). They do not have the windfirmness necessary for survival in severe winds (Mergen, 1954), resulting in high windthrow losses immediately following release (Brace and Bella, 1988; Yang, 1988). An initial partial release, where only some of the aspen are removed, may provide transitional conditions for the understory spruce to develop stronger trunks and roots. These partially released spruce are more likely to withstand the wind stresses associated with full release.

TABLE 3–1. Mean (± SEM) Breast–height Ages, Heights and Breast–height Diameters of Released and Unreleased White Spruce.

	n	Age (years)	Height (m)	Diameter (cm)
Unreleased	5	33.6±2.68	10.2±0.59	18.0±0.76
Released	5	34.2±2.06	9.7±0.39	14.7±1.73
Overall	10	33.4±1.61	9.9±0.34	16.3±1.05

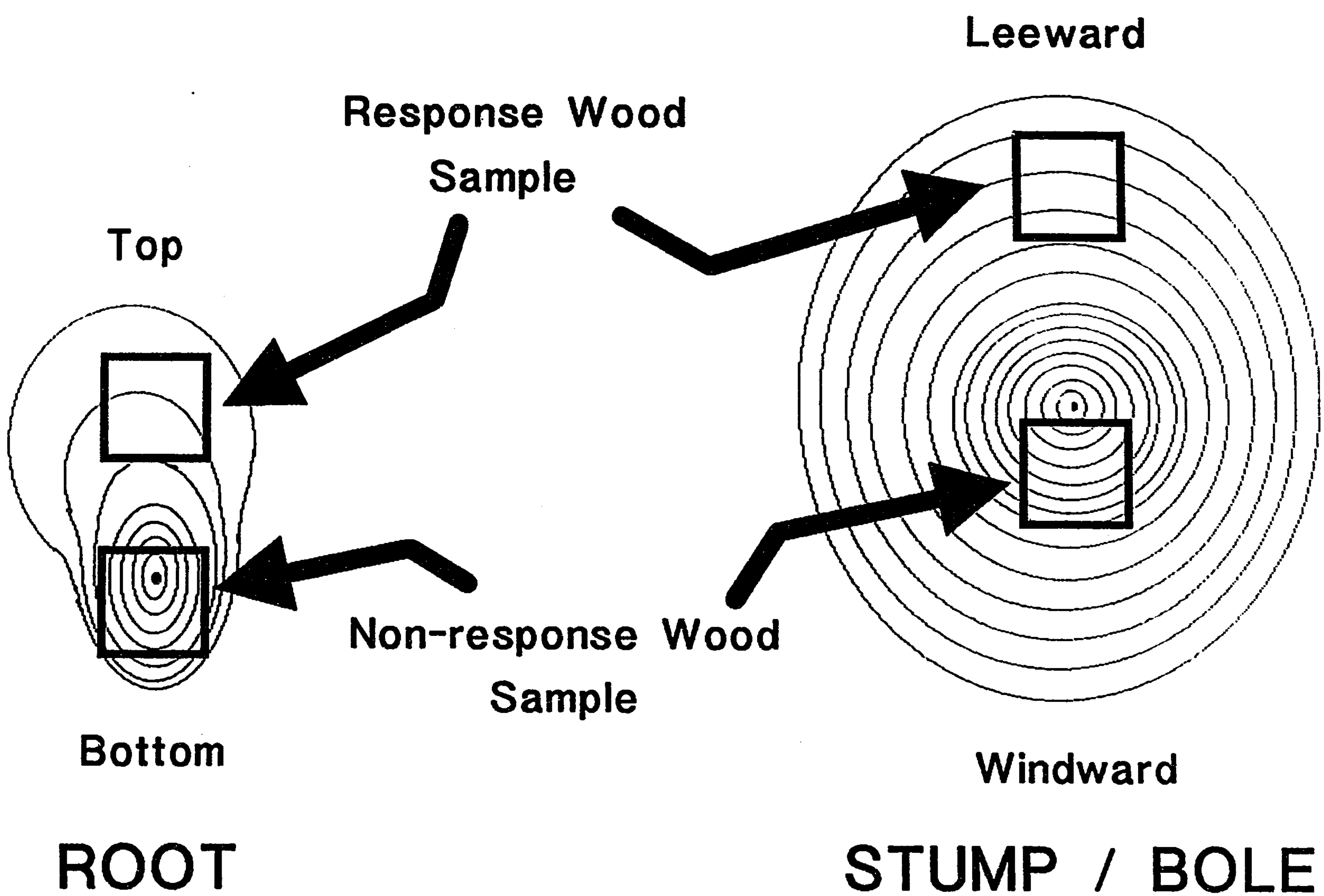

FIGURE 3-1. Sampling from the Root and Trunk Logs.

TABLE 3-2. Significant Trends at Various Levels of Wood Type* for all Properties Tested in Chapter 3. ** ***

Level of Comparison	Outside -bark Radius (cm)	Average Ring Width (mm)	Parallel Compression Strength (N/mm²)	Radial Bending Strength (N/mm²)	Green Specific Gravity	Dry Density (g/cm³)	Moisture Content (%)
Spruce Status (E)	C=O	C<O	C=O	C=O	C=O	C=O	C=O
Tree Part (P)	S>B>R	S=B=R	S=B=R	S>B=R	B<S=R	B<S=R	B=S=R
Wood Tissue (W)	r>n	r>n	r=n	r=n	r<n	r<n	r>n
P by W	ΔP mainly by Δn r/n: R>B=S	(Bn>Sn)		Sn>Br=Sr>rest	Sn=Rn>rest	(Sn=Rn>rest)	(Sn=Rn<rest)
E by P	CS<OS	OS>rest	OS=CR<B<OR=CS				
E by W		Cr<Or	(Or<rest)				Or>rest
E by P by W	(Rn<Rr=CS<OSn<OSr)			CSn>other S=OBr V other B=Orn>othe: R			

* E=spruce status
C=unreleased spruce
O=released spruce

P=tree part
B=bole
R=root
S=stump

W=wood tissue
n=non-response wood
r=response wood.

** Parenthesized trends come from interactions or main effects with probabilities greater than 0.05 and less than 0.10 (Appendix 3C). Other trends come from orthogonal comparisons with probabilities less than 0.05. Main effects which are not different (pr>0.10) are also given.

*** See Tables 3-3 to 3-5 and Table 3-7 for the quantitative data corresponding to these trends.

TABLE 3-3. Mean (± SEM) Outside-bark Radii (cm).*

Tree Part

Bole

Wood	Exposure Status: Unreleased	Exposure Status: Released	Overall
Non-response (n)	6.6±0.9	7.2±0.4	6.9±0.5
Response (r)	7.1±0.9	8.5±0.7	7.8±0.6
Overall	6.8±0.6	7.9±0.4	7.4±0.4
r/n	1.1±0.6	1.2±0.4	1.1±0.4

Stump

Wood	Exposure Status: Unreleased	Exposure Status: Released	Overall
Non-response (n)	7.1±1.0	8.7±0.2	7.9±0.6
Response (r)	8.0±0.9	11.2±0.8	9.6±0.8
Overall	7.5±0.7	10.0±0.6	8.8±0.5
r/n	1.1±0.7	1.3±0.6	1.2±0.5

Root

Wood	Exposure Status: Unreleased	Exposure Status: Released	Overall
Non-response (n)	2.5±0.5	3.3±0.6	2.9±0.4
Response (r)	8.3±1.3	7.4±0.9	7.9±0.8
Overall	5.4±1.2	5.3±0.9	5.4±0.7
r/n	3.3±1.2	2.3±0.9	2.7±0.7

	Exposure Status: Unreleased	Exposure Status: Released	
Overall	6.6±0.5	7.7±0.5	
Wood			
Non-response (n)			5.9±0.5
Response (r)			8.4±0.4

* Interactions and main effects with F-test probabilities less than 0.10 (Appendix 3C) are presented with their overall averages (averages do not necessarily have pr<0.10). See Table 3-2 to determine which components of these interactions and main effects are significant.

TABLE 3–4. Mean (± SEM) Average Ring Widths (mm).*

	Tree Part			Wood		
Exposure Status	Bole	Stump	Root	Non–response	Response	Overall
Unreleased	2.7±0.2	2.4±0.4	2.7±0.4	2.2±0.2	3.0±0.3	2.6±0.2
Released	4.2±0.7	4.7±0.9	3.2±0.6	2.4±0.3	5.8±0.5	4.1±0.4
Wood						
Non–response (n)	2.8±0.3	2.2±0.4	1.8±0.2	2.3±0.2		
Response (r)	4.1±0.7	4.9±0.9	4.1±0.5		4.4±0.4	
Overall	3.5±0.4	3.5±0.6	3.0±0.4			
r/n	1.5±0.4	2.2±0.6	2.3±0.4			

* Interactions and main effects with F–test probabilities less than 0.10 (Appendix 3C) are presented with their overall averages (averages do not necessarily have pr<0.10). See Table 3–2 to determine which components of these interactions and main effects are significant.

TABLE 3-5. Mean (± SEM) Parallel Compression and Radial Bending Strengths (N/mm^2).*

Exposure Status	Tree Part: Bole	Tree Part: Stump	Tree Part: Root	Wood: Non-response	Wood: Response	Overall
Parallel Compression Strength						
Unreleased	12±1	13±1	11±1	12±1	13±1	12±0
Released	12±1	11±1	13±1	12±1	11±1	12±1
Overall	12±1	12±1	12±1	12±0	12±1	
Radial Bending Strength						
Non-response Wood						
Unreleased	33±3	47±4	27±2			36±3
Released	29±4	38±4	33±2			33±2
Overall	31±2	43±3	30±2			35±2
Response Wood						
Unreleased	30±2	36±4	30±4			32±2
Released	39±3	37±4	28±2			35±2
Overall	35±2	36±3	29±2			33±1
Overall	33±2	39±2	29±1			
Unreleased						34±2
Released						34±1

* Interactions and main effects with F-test probabilities less than 0.10 (Appendix 3C) are presented with their overall averages (averages do not necessarily have pr<0.10). See Table 3-2 to determine which components of these interactions and main effects are significant.

TABLE 3–6. Frequency (expressed as a ratio) at which bending strength – test sticks slid inward off supports as bending load was applied.

	Exposure Status							
	Unreleased				Released			
	Tree Part				Tree Part			
Wood	Bole	Stump	Root	Overall	Bole	Stump	Root	Overall
Non–response	0/5	3/5	0/5	3/15	0/5	3/5	0/5	3/15
Response	0/5	1/5	0/5	1/15	1/5	3/5	0/5	4/15
Overall	0/10	4/10	0/10	4/30	1/10	6/10	0/10	7/30

TABLE 3–7. Mean (± SEM) Green Specific Gravities and Percent – Moisture Contents of Soaked Stubs.* **

	Tree Part			Exposure Status		
	Bole	Stump	Root	Unreleased	Released	Overall
Wood	**Green Specific Gravity**					
Non–response	0.33±0.01	0.37±0.02	0.36±0.01			0.35±0.01
Response	0.33±0.01	0.33±0.01	0.34±0.02			0.34±0.01
Overall	0.33±0.01	0.35±0.01	0.35±0.01			
Wood	**Percent Moisture Content**					
Non–response	156±18	122±10	119±16	133±13	131±13	133±9
Response	156±17	158±20	160±19	131±14	185±12	158±10
Overall	156±12	140±12	140±13	132±9	158±10	

* Interactions and main effects with F–test probabilities less than 0.10 (Appendix 3C) are presented with overall averages (averages do not necessarily have pr<0.10). See Table 3–2 to determine which components of these interactions and main effects are significant.

** Dry density (g/cm^3) values are not presented; they have the same relative trends and values as green specific gravity (Appendix 3B).

UNRELEASED SPRUCE

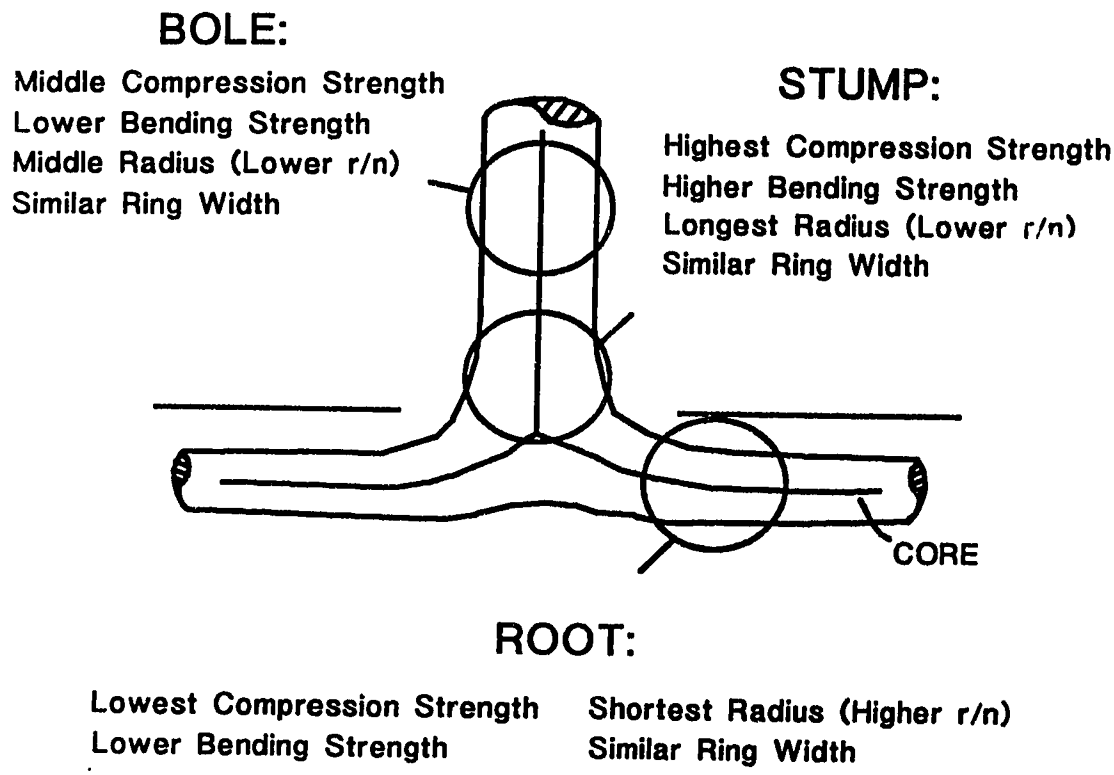

FIGURE 3-2. Summary of relative findings for parallel compression strength, radial bending strength, ring width, outside-bark radius and the ratio of response wood radius to non-response wood radius (r/n) among the bole, stump and root of unreleased spruce.

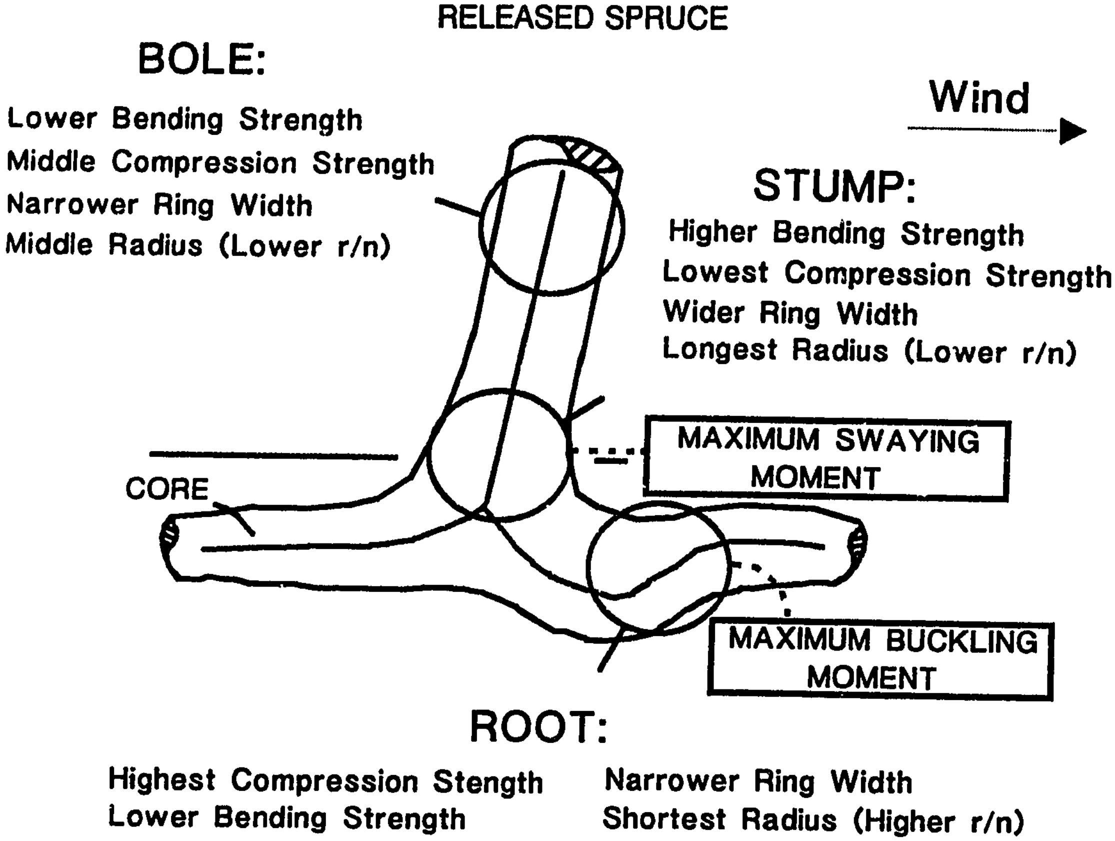

FIGURE 3-3. Theoretical locations of maximum swaying and buckling moments and summary of relative findings for parallel compression strength, radial bending strength, ring width, outside-bark radius and the ratio of response wood radius to non-response wood radius (r/n) among the bole, stump and root of released spruce.

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Chapter Three

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Chapter 4

General Discussion

4.1. Problems Associated with Competitive Release

Understory white spruce (*Picea glauca* (Moench) Voss) live in an enclosed environment where their growth is suppressed by competition, but they are sheltered from abiotic extremes, such as wind (Larson, 1963). These trees have thinner trunks and roots than they would have if they grew in unsuppressed conditions (Smith, 1986). Consequently, they are relatively vulnerable when the stand density is reduced, since their roots and trunks are not strong enough to effectively support them (Cutler *et al*, 1989). When released, they are freed from competition, but exposed to abiotic extremes (Milne, 1991). In these relatively open conditions, they are initially susceptible to wind damage and windthrow and may show a delay in increased trunk growth (Yang, 1988).

4.2. Possible Reasons for Initial Delay of Increased Trunk Growth Following Release

A combination of factors might contribute to the initial delay of increased trunk growth in newly released spruce. Increases in wind and temperature might increase transpiration and soil evaporation around the released tree (Satoo, 1962), leading to water stress and reduced growth. Increases in temperature and light might result in decreases in photosynthesis (Smith, 1986) due to either 1) damage to the light-harvesting complex (Powles, 1984), 2) frequent stomatal closure (Turner, 1991; Farquhar and Sharkey, 1982) or 3) negative feedback inhibition caused by the accumulation of photosynthetic products (Sharkey, 1985). Consequently, trunk growth may not be improved until the tree has had time to develop sun-tolerant foliage (Tucker *et al*, 1987).

Improved trunk growth may also be delayed due to immediate allocation of resources to crown and root growth following release. Since the tree needs more resources to acclimate to its new environment, the crown and root systems, which gathers the tree's resources, may respond to release before the trunk (Smith, 1986; Wagg, 1967). Further, the tree, which might have grown in light-limited conditions before release, might be water- and nutrient-limited after release when light levels increase (Salisbury and Ross, 1985). Consequently, root growth might be favored over trunk growth. Until increases in root and crown growth begin to decelerate, increases in trunk growth may be delayed.

Meanwhile, the crown, stump and roots may entirely reorganize following release (Section 1.5) in order to improve tree stability (Wagg, 1967; Coutts, 1983; Putz *et al.*, 1983; Larson, 1963). Again, trunk growth may be suppressed until increases in root, crown and stump growth begin to drop.

4.3. Tree Response to Sway

The initial delay of increased trunk growth may be part of a pervasive response to wind stress, involving the trunk, crown and root system, which leads to improved tree survival in severe winds. This response seems to involve a change in the growth habit of the tree as well as a change in the distribution of wood strength. It results in improved stability of the tree in persistent winds by increasing resistance to sway and sway-induced movement (Coutts, 1983; Wagg, 1967).

In Chapter 2 of this thesis, I compared bole diameter growth with root diameter growth in released and control trees by examining the ring widths of these trees chronologically for sixteen years following release. In Chapter 3, I compared bole and root diameter growths in another set of released and control trees sampled twenty years after release. Both studies showed equal diameter growths in the bole and root approximately ten to twenty years following release. Therefore, the results regarding strength differences of different wood types from trees sampled in Chapter 3 may also be applicable to the trees studied in Chapter 2. I measured the wood strengths and diameter growths of the bole, stump and root in Chapter 3.

I found that the rate of diameter growth, measured by ring width, eventually increases in all parts of the tree following release (Table 3-4, Figures 2-2 and 2-3, Table 4-1), though the stump swells more that the root and bole (Tables 3-4 and 4-1) and, initially, root diameter growth exceeds bole diameter growth (Figures 2-2, 2-3, 2-4a and 2-5, Table 4-1). Coutts (1983) and Wagg (1967) have speculated that initial stump and root swell, especially on the leeward side of the tree, thickens and thereby stiffens and strengthens the stump and major roots at the expense of immediate improvement in bole growth following release. This swelling occurs in the stump, where bending moment is greatest, and in the basal roots, where compression moment is greatest (Coutts, 1983; Fayle, 1983). I found that parallel compression strength also increases in the root (Tables 3-5 and 4-1), while it decreases in the stump. Prior to release the stump may have had the greatest compression moment due to the weight of the tree on it (Larson, 1963); however, following release the root has the greatest compression moment due to wind stress (Coutts, 1983). Further, radial bending stress is greatest in the stump, where bending moment is greatest (Tables 3-5 and 4-1). It also increases in the bole, while it decreases in the root (Table 3-5).

An additional response to release, reported by Coutts (1983), involves root branching, especially windward of the trunk. This branching binds the root and soil into a tight, heavy plate that resists lifting (Coutts, 1983). Adventitious rooting along with root deterioration also occur, resulting in a re-forming of the tree's foundation and in strategically positioned anchoring roots (Wagg, 1967). I observed extensive adventitious rooting following release.

Those changes in wood strength and biomass that I observed, as well as the reshaping of the root system, probably reinforce the support the root and stump give the tree in severe winds. Changes in crown structure also occur (Milne, 1991; Mitchell, 1969; Tucker *et al*, 1987); however, I did not address these changes.

4.4 Physical Bases for the Characteristics of Tree Response to Sway

The tree responds to wind stress mainly where its response most effectively contributes to wind stress resistance and tree stability (Chapter 3) (Mergen, 1954; Kounadis and Belbas, 1977; Wilson and Archer, 1977). Consequently, it is not surprising that prominent wind-induced strains may determine the locations, types and intensities of response growth and wood strength. The type of strain, and subsequent response, may be determined by the relative association of strained parts of the tree to secure parts (Helliwell, 1989). For instance, the trunk is bent by wind because it is secured only at one end and wind (a lateral force) tends to push it sideways. The leeward root system buckles because its perimeter is secure and wind pushes the leeward side of the root system down and out. Meanwhile, the windward root system tenses since its perimeter is also secure and wind pulls it up and trunkward. Strain intensity is probably related to the displacement of the strained part of the tree weighted by its mass (this product being its moment, which is maximum in and near the stump (Coutts, 1983)) (Chapter 3) (Grace, 1977). Strain location is determined by strain intensity. There is no strain where the intensity is zero.

The direction the strained part is displaced may also determine the direction of response growth and the horizontal distribution of wood strength (Mergen, 1954). Wilson and Archer (1977)generally attribute reaction wood production and eccentric growth to a gravitational stimulus; therefore, reaction wood is produced where strain is greatest, in the direction which would return the strained structure back to its natural orientation relative to gravity. However, there are exceptions and contradictions to this gravitational stimulus hypothesis which Wilson and Archer (1977) explain by a strain stimulation mechanism or fail to explain at all (Section 4.6 presents some). Consequently, I propose a hypothesis (Section 4.6) which explains all observations of reaction wood formation, response growth and wood strength distribution that I am aware of or have studied in this thesis. Differential growth and reaction wood formation may be induced and directed by the displacement of the center of gravity of the tree or tree part. In conifers, compression wood may form on that side of the trunk or branch which faces the direction that the center of gravity is perceived to be displaced in. The opposite would be true for tension wood in deciduous trees.

Response growth may also be directed by movement of the center of gravity. Therefore, stump and root swell occurs mainly on the leeward side of the coniferous tree to lengthen and thicken these roots and to thicken the stump. Further, root branching occurs mainly on the windward side of the tree to weight down the tensed and lifted side of the root plate.

4.5 Possible Physiological Mechanisms Leading to Tree Response to Sway

The mechanism by which differential distribution of strain affects tree growth, wood strength and reaction wood formation is unknown (Fayle, 1968; Fritts, 1976; Salisbury and Ross, 1985). Changes in environmental conditions and mechanical stress may influence the local production and movement of auxin or ethylene (Wilson and Archer, 1977; Salisbury *et al*, 1982; Hale and Orcutt, 1987) which affect their distribution in different parts of the tree (Coutts, 1987; Larson, 1963). Salisbury and Ross (1985) speculate that strain might change the electrical polarity of cambial cells, which might in turn change the accessibility of ethylene and auxin or their precursors to these cells.

Increases in ethylene and auxin concentrations are known to occur after mechanical stimulation (Salisbury *et al*, 1982; Wilson and Archer, 1977). Further, injecting either auxin or ethylene into trees is reported to influence diameter and height growth, xylem cell differentiation and reaction wood formation, as does mechanical stimulation (Larson, 1962); Yamamota and Kozlowski, 1987; Wilson and Archer, 1977). Increasing auxin and ethylene concentrations may affect: 1) cambial activity, which influences the rate of growth and the quality of wood in different regions of the tree (Fritts, 1976), 2) the production and distribution of energy (ATP, sugars) (Berlyn, 1979), 3) the relative strength of competing sinks (Deans and Ford, 1985; Coutts, 1987; Kienholz, 1934) or 4) the transport and relative distribution of limited growth resources (Larson, 1963; Salisbury and Ross, 1985).

4.6. The Induction of Tree Response to Sway by Displacement of the Center of Gravity

Background Information

Figure 4-1 illustrates five examples of reaction wood formation and eccentric growth. In the first example, a conifer branch bends down and compression wood forms on its underside. The concave side of the bend, which is also on the underside of this branch, is compressed. Therefore, either gravity or compression could stimulate this formation[1]. In the second example, compression wood forms on top of a conifer branch that bends up. Consequently, compression seems a more likely stimulus than gravity. However, example three illustrates a vertically looped, conifer leader with compression wood on the lower sides of its horizontal portions and on the flanks of its vertical portions. Since one of these lower sides is tensed, this example contradicts example two; it suggests that gravity stimulates reaction wood formation.

Wilson and Archer (1977) have proposed two models that may account for the examples described so far. In both of these models, gravity induces reaction wood formation and strain determines its location and intensity. However, one of these models allows negative gravity reactions, in which reaction wood is formed on the top of upwardly bent branches, in addition to the normal positive gravity reaction. This model did not explain how a negative reaction could occur in branches such as the one in example two, while a positive reaction occurred in other branches or the trunk, as illustrated by examples one and three. Further, the models fail to explain example four, in which a laterally bent, conifer branch forms compression wood on the concave flank of the branch, even though there is no gravitational stimulus. They also fail to explain how compression wood forms on the compressed flanks of vertical segments of the looped leader in example three even though these vertical segments are not stimulated by gravity. Therefore, a third model was proposed by Wilson and Archer (1977), in addition to the other two, in which strain stimulates reaction wood formation and determines its location and intensity. In example five, however, neither gravity nor compression is a stimulus. A conifer branch is removed from a whorl and compression wood forms at an oblique angle from horizontal on the outer flanks of the adjacent branches.

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[1]In fact, for lack of plausible alternatives, gravity and strain are commonly accepted as the most probable stimuli of reaction wood formation (Salisbury and Ross, 1985), even though neither of these sometimes-contradictory hypotheses wholly explains how reaction wood is induced (Wilson and Archer, 1977).

The adjacent branches shift laterally and close the gap once occupied by the removed branch.

Though the above hypotheses and models do not consistently account for all reported occurrences of reaction wood formation and eccentric growth (Wilson and Archer, 1977), they have significantly advanced basic understanding of tree growth and structure. It is known, for instance, that the trunk and branches of a tree have natural orientations at which they are balanced and therefore resistant to gravitational pull. When a trunk or branch is strained, it is displaced from its natural orientation and forms reaction wood which restores this orientation. Further, the reaction wood is positioned on the trunk or branch where it is most directly able to restore the orientation (Wilson and Archer, 1977). When the tree leans, the branches, as well as the trunk, form reaction wood to restore their natural orientations (Figure 4-2c2), indicating that the branch orientations are not relative to their particular angles to the trunk (Wilson and Archer, 1977), but to some other stimulus. This last point suggests that gravity may play a role in reaction wood induction. However, strain may also influence its induction in addition to its location and intensity.

Displacement of the Center of Gravity

With this background information as a base, I propose a stimulus which, as far as I am aware, accounts for all reported occurrences of reaction wood formation, response growth and possibly the distribution of wood strength in bent or leaning trees or tree parts.

Importance of Tree Balance

All parts of the tree are balanced at the tree's center of gravity, which is supported in turn by the trunk (Joseph *et al*, 1978). The trunk can support the tree's weight most effectively when the weight is balanced somewhere along its central axis, since its cellular grain typically follows this axis and the cells are stronger along their lengths than they are perpendicular to their lengths (Haygreen and Bowyer, 1989). Consequently, when sway displaces the center of gravity off the trunk, or more correctly leans the trunk's central axis from vertical, the downward pull of gravity on the tree's center of gravity exceeds the amount of upward support the trunk is able to provide to the center of gravity (compare Figure 4-2a with Figure 4-2c1). Consequently, the trunk can no longer support the tree's weight effectively. The tree literally loses its balance.

Displacement of the center of gravity affects tree balance only along two dimensions (Figure 4-2). These dimensions fall on the horizontal plane[2]. The third dimension is vertical; displacement of the center of gravity along it does not affect tree balance. The trunk can elongate or shorten, by top-dying, without inducing response growth and reaction wood formation. Further, changes in crown shape, such as the production of epicormic branches, can shift the tree's center of gravity down or up the trunk without inducing response growth, so long as the tree's balance is not upset.

The discussion above applies to tree parts (ie. trunk, individual or grouped branches or roots, leaf petioles) as well as to the whole tree. However, tree parts, other than the trunk and taproot, are not typically vertical. Consequently, displacing their centers of gravity in any direction can affect their balances. For example, large branches can not elongate without inducing response growth and reaction wood formation, since they often droop from their own weights as they grow (Figure 4-2b). The trunk loses some of its ability to effectively counteract the pull of gravity on these branches when the branches are not balanced on straight projections of their central axes[3] (Figure 4-2b).

Function of Response Growth and Reaction Wood

Balance is a problem for a tree since, unlike a motile organism, it is unable to move to shift its weight. However, it may be able to change its pattern of growth, which results in "righting" itself. Reaction wood and response growth probably help 1) to return the tree's center of gravity to its original position and 2) to reinforce support to the tree by building up its foundation and length[4]. Both goals cause the tree to more effectively counter the pull of gravity. Consequently, reaction wood and response growth are likely induced by the displacement of the center of gravity from the vertical central axis of the trunk (cf. Section 4.4). However, gravity and strain are still important contributors to this process. Strain displaces the center of gravity and may influence the location and intensity of reaction wood formation and response growth, while gravity pulls the tree

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[2]However, any horizontal displacement of the center of gravity also displaces the center of gravity downward, since the trunk is attached (fixed in position) at its base.

[3]A straight projection of a branch's central axis begins from the branch's point of anchorage in the wood of the next larger tree part. It runs tangentially to the branch's central axis for as long as possible. Consequently, as the branch's weight increases and the branch droops, the projection dips.

[4]This discussion is applicable to tree parts as well.

downward when the tree is unbalanced.

Support for the Center of Gravity Hypothesis

The displacement of the center of gravity may also explain the induction of compression wood formation and eccentric growth in the examples of Figure 4-1. In conifers, compression wood may form on that side of the trunk or branch which faces the direction that the center of gravity is perceived to be displaced in.

Examples one, two and four illustrate conifer branches that bend down, up or laterally from the branches' natural orientations. The centers of gravity of these branches are displaced down, up or sideways, respectively. Further, compression wood forms respectively on the bottom, top or concave flank of the branches. In example three, the center of gravity of the tree is not displaced, since the looped leader is part of the trunk and the trunk's center of gravity is typically located at the base of the crown. However, the segments of the leader that are looped perceive a displacement of the center of gravity relative to their orientations in the loop (Figure 4-3). They form compression wood toward the center of gravity. Since the leader is also tilted to one side as it is looped, compression woods form on the flanks of the leader in those segments which are otherwise vertical. Example five illustrates the loss of a conifer branch from a whorl. This loss shifts the center of gravity of the whorl away from the resulting gap and may lift it as the weight of the missing branch is lost. Consequently, compression wood forms at an oblique angle (from horizontal) on the outer flanks of branches adjacent to the gap. The outer flanks and the oblique angle face the direction the center of gravity for the whorl is displaced.

Accordingly, when a tree leans or is bent by wind (Figures 4-2c1 and 4-2c2), compression wood forms on the concave side (underside) of its trunk and its leeward (or leanward) branches, on the tops of its windward (raised) branches and on the lower oblique or flank sides of branches which are perpendicular to the direction of the wind or lean.

4.7. Forest Management Recommendations

Release is the practice of removing neighboring trees from potential crop trees (Smith, 1986). It is designed to free stand-enclosed trees from competitive suppression, thereby improving their growth potential (Yang, 1988). While it generally accomplishes this task, it often fails to improve trunk growth immediately upon release (Brace and Bella, 1988). Further, initial survival of newly released trees is relatively low (Cutler *et al*, 1989), probably because they are vulnerable and susceptible to wind stress (Smith, 1986).

Releasing trees from competitive suppression, while minimizing losses due to windthrow and suppression of growth due to wind stress, may be achieved by removing only some of the neighbors of enclosed crop trees (Froning, 1980). This management practice (partial release) may provide transitional conditions during which under-developed, stand-enclose trees can become windfirm. It may also shorten the delay in increased trunk growth compared to full release, since strain, and thereby response, is plausibly less intense than it would be under full release conditions and the time needed to become windfirm in partial release conditions is shorter. A further solution could be to leave an untouched border as a windbreak around a released stand (Cutler *et al*, 1989). Trees can also be released while they are young and more able to tolerate wind stress (Mergen, 1954). The trunks of young trees are more flexible than those of mature trees, which allows them to "spring" in severe winds without being damaged. The probability of windthrow is also low for young trees.

TABLE 4–1. Summary of Relationships of Parallel Compression Strength, Radial Bending Strength and Ring Width among the Bole (B), Stump (S) and Root (R) in Unreleased and Released White Spruce.

Property	Unreleased Spruce	Released Spruce	
		First 3–9 Years After Release (From Chapter 2)	By approximately 20th Year (From Chapter 3)
Parallel Compression Strength	S>B>R		R>B>S
Radial Bending Strength	S>B=R		(=) S>B=R
Ring Width	S=B=R	(↑) R>B (?S)	(↑) S>B=R

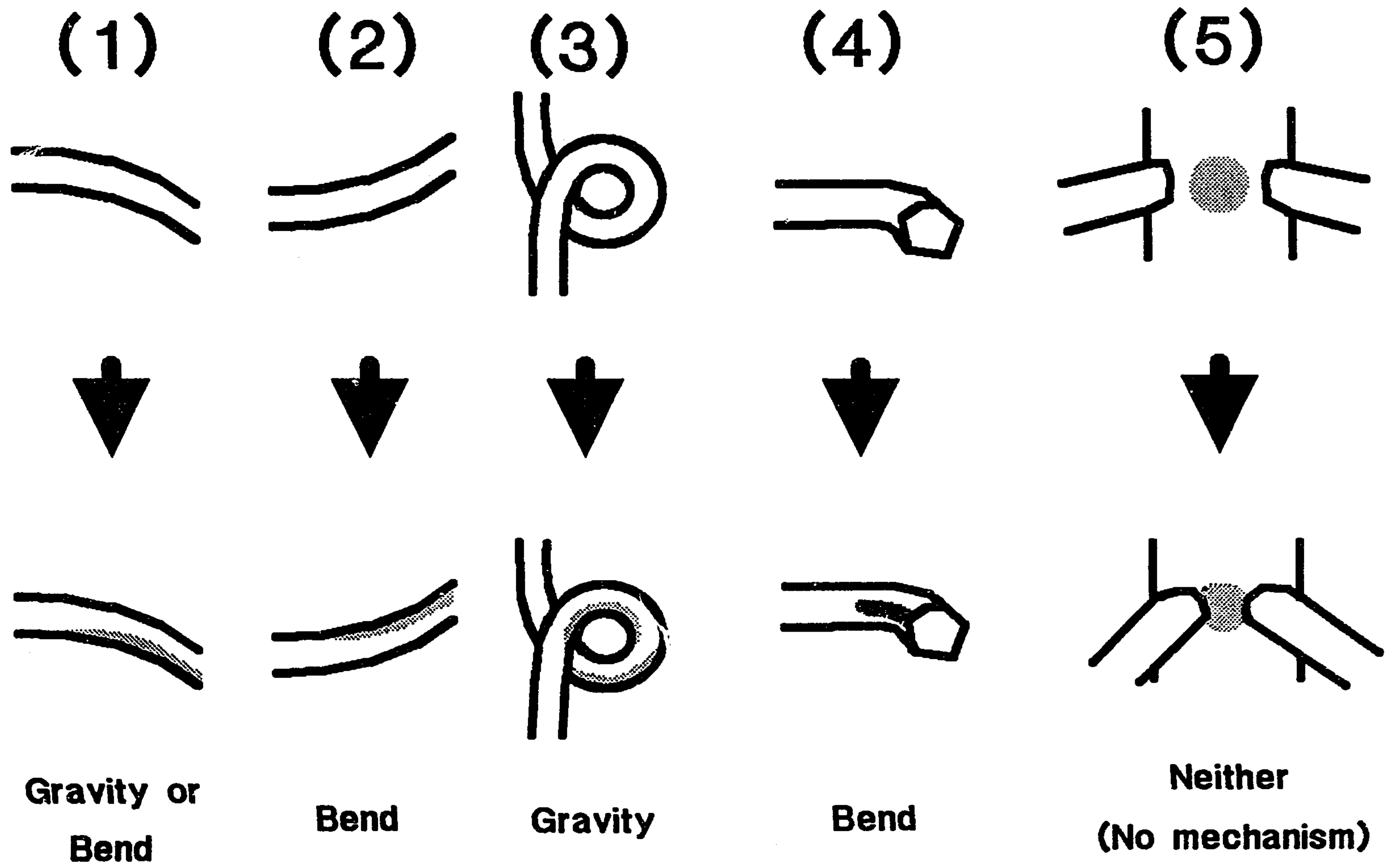

FIGURE 4-1. Examples of reaction wood formation and hypothetical stimuli believed to induce it. Examples (1), (2) and (3) are modified from Salisbury and Ross (1985). All examples are discussed by Wilson and Archer (1977).

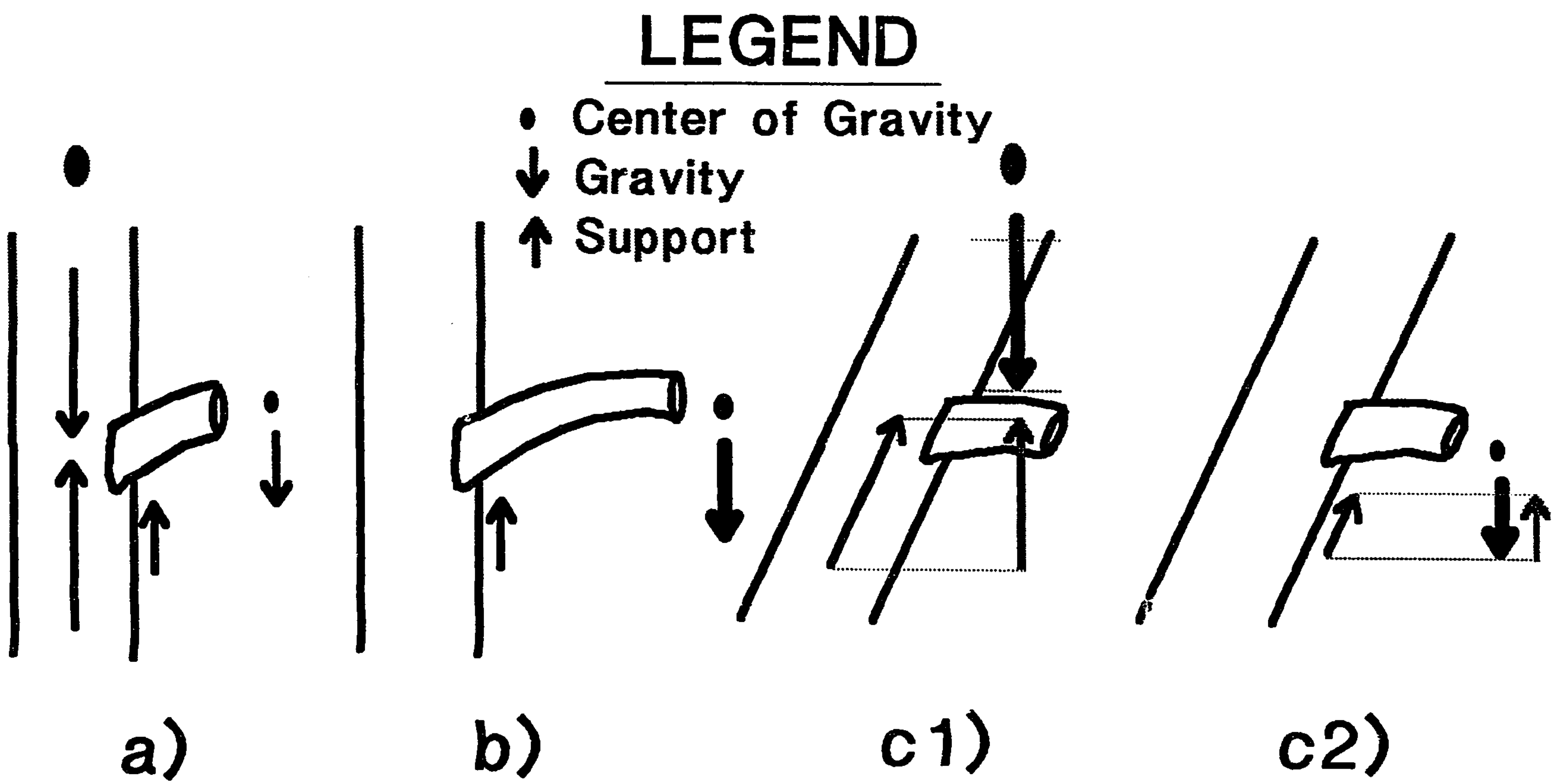

FIGURE 4-2. Forces acting on the centers of gravity of the tree and a branch. Gravity pulls these centers downward, while the trunk holds them up. Trunk support is greatest parallel to the trunk's long axis. a. In an upright tree with a short branch, support is upward and directly opposes gravity. b. As the branch lengthens and increases in weight, the pull of gravity on it increases beyond the upward support the trunk provides it. c. When the tree leans or bends, gravity exceeds the upward support the trunk supplies to the tree (c1) and to the branch (c2). Centers of gravity and forces with greater magnitudes are drawn larger than lighter or weaker ones.

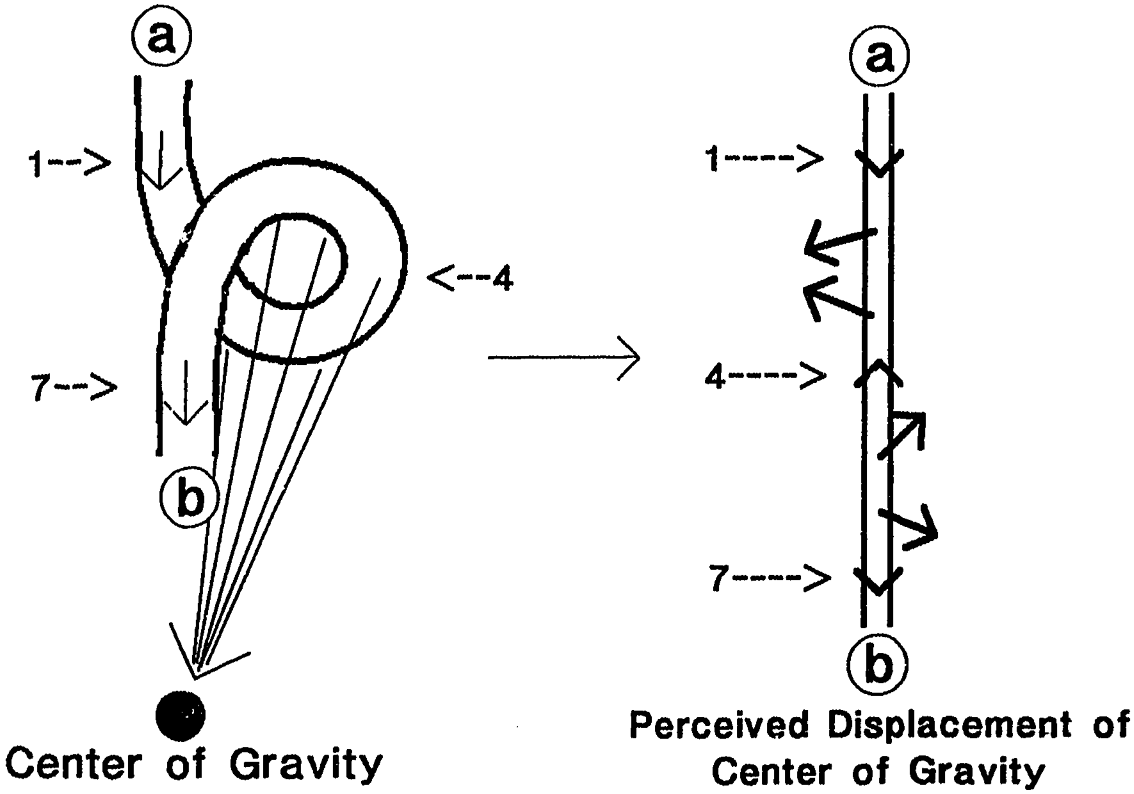

FIGURE 4-3. Perceived displacement of the center of gravity by segments of a looped, conifer leader. To the left is the loop illustrated in example three of Figure 4-1. To the right, this loop is straightened. The arrows pointing from the straightened branch correspond to those pointing toward the center of gravity in the looped branch. They are numbered counterclockwise in the loop from its top (a) toward its bottom (b). Arrows 1, 4 and 7 (labelled) originate from vertical segments of the loop. Compression wood forms to the side of the straightened branch the arrows point out from. It also forms across the branch where the arrows switch to opposite sides (at arrow 4). No compression wood forms at arrows 1 and 7.

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Appendices

Appendix 3A. Estimating the Bending Strengths of Slipped Bending-test Sticks.

One can test whether or not a sample comes from a normal population (Figure 3A-1) by plotting the ranked data of the sample against normal equivalent deviates (Zar, 1984: pp. 93-95). The same procedure can be used to estimate missing values in the sample data, assuming normality of the population.

The first step of the procedure is to rank the sample data in ascending order. For example, the radial bending strengths (N/mm^2) of the response tissue in the stumps of unreleased spruce are: 26.3 (tree 2), 29.4 (tree 3), 35.7 (tree 5) and 41.3 (tree 1). The bending strength for the fourth tree is missing, since its stick slipped rather than broke.

Once the data are ranked, the ranks are converted into percentages with a constant interval between subsequent percentages. For the above example, the range of the known data and the estimate is compressed to one standard deviation from the mean. This range accounts for 68% of the values in a normally distributed population. Therefore, the values, 26.3, 29.4, 35.7 and 41.3, correspond to the percentages, 16%, 33%, 50% and 67%, respectively. The missing datum corresponds to percentage, 84%[1]. By converting the ranks into percentages, the data are assumed to be distributed evenly within the population; in the example, the data seem to be distributed above the population mean (compare Figure 3A-2 with its inset). In essence, the percentages represent cumulative relative frequencies (Figure 3A-2).

The next step is to transform the percentages into normal equivalent deviate units (probits). Therefore, the percentages, 16%, 33%, 50%, 67% and 84%, are transformed into the probits, 4.01, 4.56, 5.00, 5.44 and 5.99, respectively. Normal equivalent deviation assumes that the frequency of values near the population mean (50% in the cumulative relative frequency series) is greater than that elsewhere in the distribution. To transform the percentages into probits, the intervals between the percentages are weighted so they will reflect the normal frequency distribution (Finney, 1971). Consequently, percentages near the mean on a linear scale, corresponding to values with higher frequencies, are separated by narrower intervals on a normal probability scale than are percentages farther from the mean. If the sample is part of a normal population, the resulting curve, when probits are plotted against sample values, will be linear, as it is for the example above (Figure 3A-3).

Missing values can be estimated by extrapolating or interpolating the curve

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[1]For reasons explained in Chapter 3, the value of the missing strength is assumed to be greater than those of the known strengths.

or regression equation to higher, lower or intercalary frequencies and reading the values on the data axis corresponding to the cumulative relative frequencies of the missing data[2]. In the example, the missing radial bending strength is estimated as 47.0 N/mm^2. The probit regression equation for the example is: Probit = 1.76 + 0.09 X Bending Strength.

[2]For all wood types, other than those with missing strength values (Table 3-6), radial bending strengths were used to test this procedure's accuracy and precision at estimating missing values. Data which were already known were estimated by probit regression. The estimates were then compared to the actual values. They were not different (paired t-test, pr>0.05) from the real data.

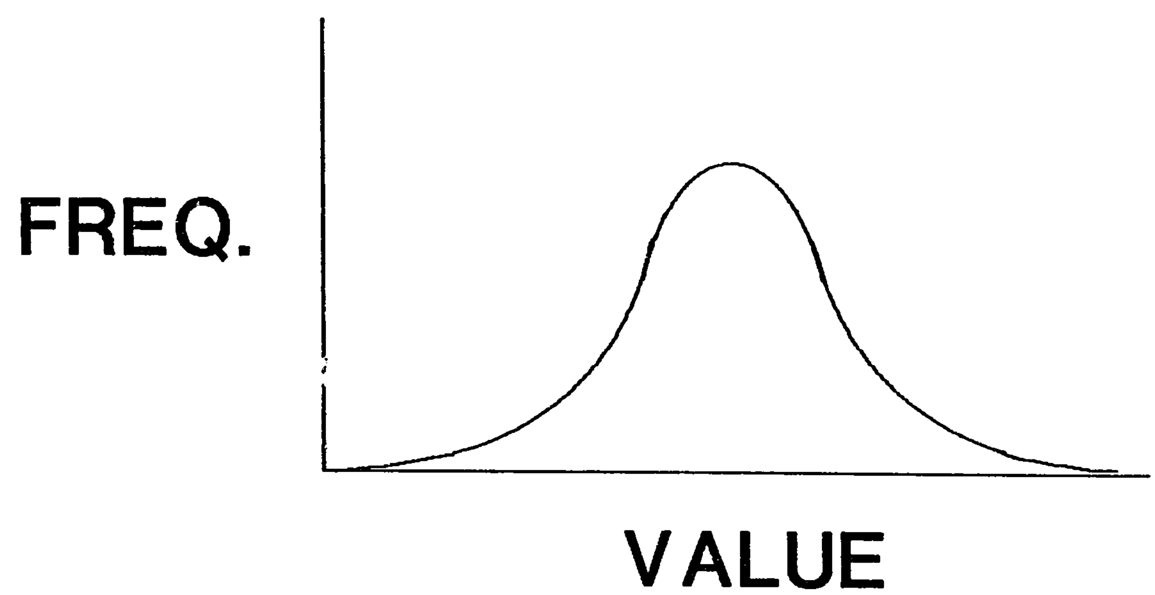

FIGURE 3A-1. Normal distribution of a hypothetical population.

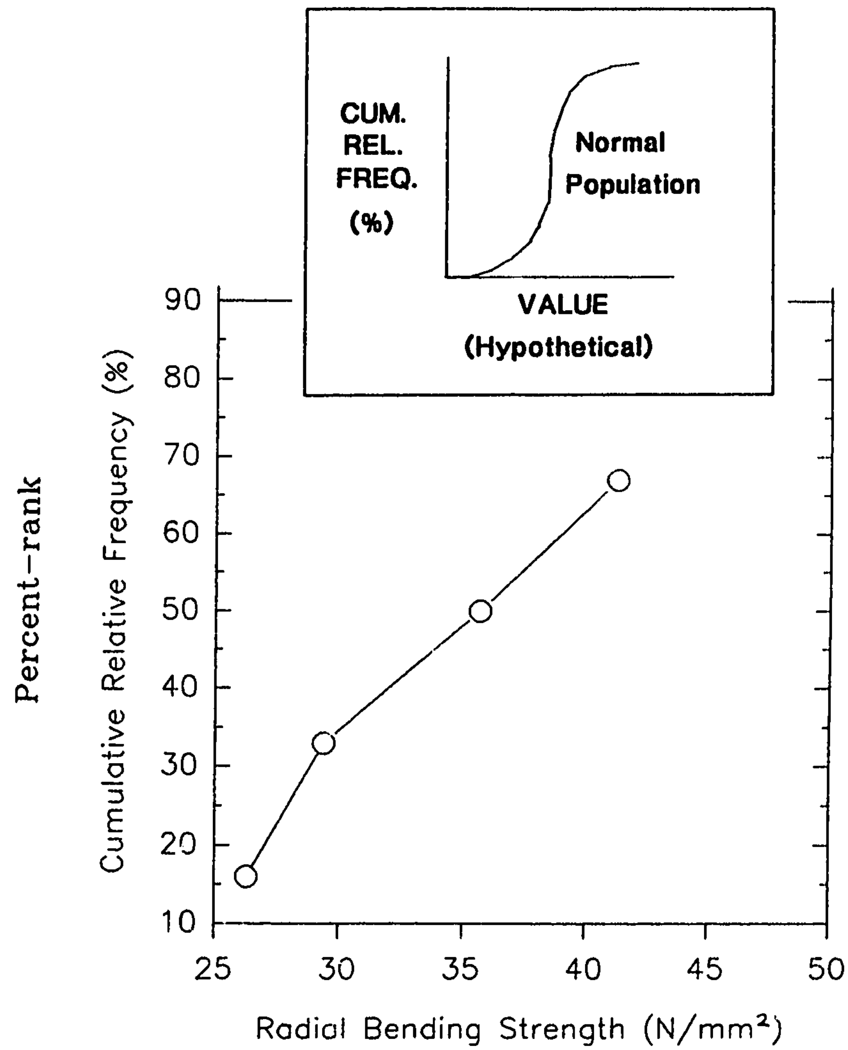

FIGURE 3A−2. Plot of radial bending strength data, for response tissue in the stumps of unreleased spruce, against percent−rank. Inset: Normal distribution plotted against a cumulative relative frequency ordinate axis.

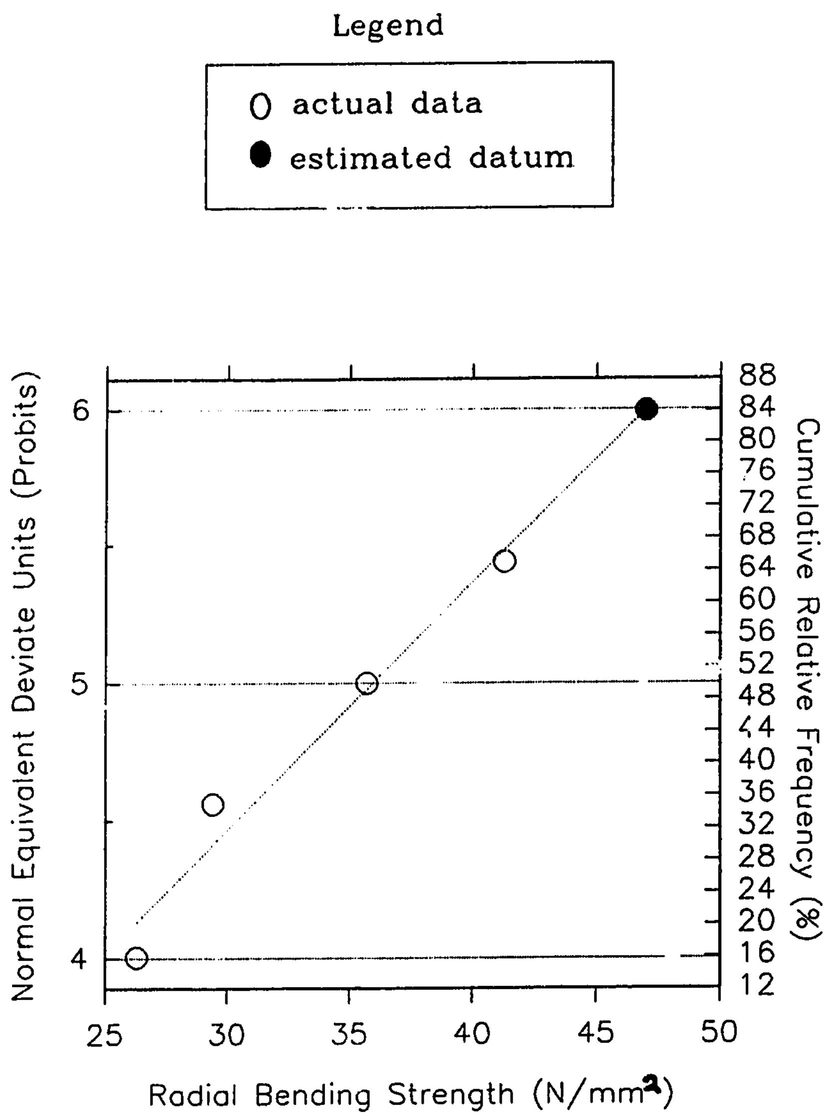

FIGURE 3A–3. Plot of radial bending strength data, for response tissue in the stumps of unreleased spruce, against percent-rank (right axis) transformed into normal equivalent deviate units (probits).

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Appendix 3A

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APPENDIX 3B. Raw Data.

Spruce Status (E)	Tree (#)	Tree Part (P)	Wood Tissue (W)	Outside-bark Radius (cm)	Average Ring Width (mm)	Parallel Compression Strength (N/mm²)	Radial Bending Strength (N/mm²)	Green Specific Gravity	Dry Density (g/cm³)	Moisture Content (%)	Volumetric Shrinkage (%)	Longitudinal Shrinkage (%)
O	1	R	r	8.3	4.1	13	34	0.35	0.38	143	6.8	0.3
O	1	R	n	4.5	1.4	17	31	0.43	0.47	75	9.0	0.0
O	1	S	r	11.5	9.7	6	25	0.35	0.38	147	5.8	0.0
O	1	S	n	8.4	3.1	12	23	0.38	0.41	121	7.3	0.0
O	1	B	r	7.4	9.1	6	49**	0.31	0.33	144	5.4	0.0
O	1	B	n	6.2	3.7	10	23	0.34	0.38	144	9.5	0.0
O	2	R	r	10.1	6.8	13	26	0.34	0.37	174	8.1	0.0
O	2	R	n	2.4	1.1	16	37	0.39	0.44	100	9.7	0.0
O	2	S	r	9.6	5.8	11	37**	0.35	0.37	206	4.7	0.1
O	2	S	n	8.7	2.3	12	38**	0.47	0.52	128	8.7	1.9
O	2	B	r	8.8	4.5	12	41	0.34	0.35	218	4.8	0.0
O	2	B	n	8.0	1.9	15	40	0.37	0.40	194	9.0	0.1
O	3	R	r	7.7	5.4	9	25	0.30	0.32	257	7.7	0.3
O	3	R	n	4.7	1.8	14	35	0.36	0.40	56	8.6	0.2
O	3	S	r	11.3	8.7	9	48**	0.31	0.33	233	7.2	1.5
O	3	S	n	8.2	1.0	8	43**	0.35	0.38	100	8.0	0.0
O	3	B	r	7.2	3.7	13	31	0.34	0.36	206	6.7	0.0
O	3	B	n	6.2	1.4	9	24	0.33	0.36	125	8.9	0.0
O	4	R	r	5.2	3.1	14	28	0.42	0.50	105	13.6	0.4
O	4	R	n	2.9	1.6	14	27	0.34	0.37	156	9.7	0.1
O	4	S	r	14.0	5.6	15	42**	0.36	0.39	106	9.0	0.2
O	4	S	n	9.5	[illegible]	16	37	0.40	0.43	121	7.1	0.0
O	4	B	r	11.0	[illegible]	17	43	0.36	0.39	182	6.6	0.0
O	4	B	n	7.8	2.9	12	36	0.34	0.38	[illegible]	9.9	0.0
O	5	R	r	5.7	4.9	11	27	0.30	0.33	237	7.9	0.1
O	5	R	n	1.8	2.3	13	32	0.34	0.39	213	11.7	0.0
O	5	S	r	9.6	5.1	9	33	0.30	0.32	207	6.2	0.0
O	5	S	n	8.9	4.7	10	49**	0.34	0.36	113	6.2	0.0
O	5	B	r	8.2	5.6	11	33	0.32	0.35	214	8.3	0.1
O	5	B	n	7.7	4.9	10	24	0.27	0.30	231	8.6	0.7
C	1	R	r	6.3	1.6	15	45	0.42	0.46	83	8.7	0.1
C	1	R	n	1.9	1.5	10	33	0.37	0.42	100	10.5	0.0

C	1	S	r	6.1	1.8	16	41	0.42	0.46	57	9.9	0.3
C	1	S	n	5.7	0.9	15	39	0.44	0.49	78	9.7	0.2
C	1	B	r	5.6	2.2	16	33	0.42	0.46	67	9.2	0.1
C	1	B	n	5.5	1.8	13	36	0.41	0.43	61	6.1	0.0
C	2	R	r	5.0	2.0	13	28	0.30	0.32	121	6.2	0.2
C	2	R	n	2.8	1.4	13	25	0.36	0.39	85	7.2	0.1
C	2	S	r	6.9	2.6	12	26	0.28	0.29	133	3.2	0.0
C	2	S	n	6.7	1.7	13	59**	0.34	0.37	77	8.2	0.8
C	2	B	r	5.8	3.1	10	26	0.28	0.30	100	9.0	0.1
C	2	B	n	5.7	3.1	11	24	0.28	0.30	131	7.3	0.1
C	3	R	r	12.3	3.6	12	26	0.37	0.40	98	6.9	0.0
C	3	R	n	2.7	1.7	10	19	0.40	0.43	104	9.1	0.1
C	3	S	r	7.4	2.3	10	30	0.33	0.36	79	7.5	0.1
C	3	S	n	6.9	2.3	12	47**	0.32	0.35	150	8.9	0.1
C	3	B	r	7.3	2.5	13	30	0.34	0.36	156	5.6	0.0
C	3	B	n	6.9	2.8	10	34	0.31	0.33	153	6.8	0.0
C	4	R	r	9.9	5.8	9	23	0.26	0.28	163	6.2	0.0
C	4	R	n	4.2	2.4	8	27	0.30	0.33	107	7.4	0.3
C	4	S	r	11.0	5.1	14	47**	0.31	0.33	214	5.5	0.5
C	4	S	n	11.0	3.1	10	52**	0.29	0.31	154	4.9	0.0
C	4	B	r	10.5	4.3	11	28	0.28	0.30	162	6.6	0.1
C	4	B	n	9.8	3.5	11	30	0.30	0.32	236	6.1	0.0
C	5	R	r	8.1	3.8	10	28	0.35	0.37	220	6.4	0.1
C	5	R	n	1.0	3.0	13	31	0.36	0.40	195	7.7	0.2
C	5	S	r	8.5	2.4	16	36	0.33	0.35	194	7.2	0.0
C	5	S	n	5.1	1.5	17	40	0.36	0.40	181	11.0	0.1
C	5	B	r	6.3	2.4	14	35	0.33	0.36	113	8.9	0.2
C	5	B	n	5.0	1.9	16	41	0.34	0.38	188	9.7	0.0

* Each sample is identified by Spruce Status (O=released, C=unreleased), Tree Number, Tree Part (R=root, S=stump, B=bole) and Wood Tissue (r=response wood, n=non-response wood).
** Estimated using probit regressions (Appendix 3A).

APPENDIX 3C. ANOVA (GLM) and Orthogonal Comparison Probabilities of Significance for all Wood Properties Tested.

Source		Outside -bark Radius (cm)	Average Ring Width** (mm)	Parallel Compression Strength (N/mm²)	Radial Bending Strength (N/mm²)	Green Specific Gravity	Dry Density (g/cm³)	Moisture Content (%)	Volumetric Shrinkage (%)	Longitudinal Shrinkage (%)
GLM		0.000	0.000	0.001	0.021	0.000	0.000	0.000	0.003	0.932
Spruce Status (E)*		0.209	0.027	0.692	0.999	0.669	0.637	0.312	0.520	0.300
Tree Part (P)	Bole vs Root-Stump	0.454	0.531	0.780	0.497	0.010	0.009	0.134	0.589	0.189
	Root vs Bole-Stump	0.000	0.105	0.596	0.001	0.208	0.081	0.432	0.024	0.565
	Stump vs Bole-Root	0.000	0.310	0.801	0.000	0.161	0.349	0.466	0.078	0.063
	Root vs Stump	0.000	0.128	0.651	0.000	0.933	0.630	0.974	0.021	0.157
	Bole vs Stump	0.002	0.820	0.988	0.008	0.022	0.040	0.198	0.470	0.068
	Bole vs Root	0.000	0.193	0.640	0.119	0.027	0.013	0.187	0.102	0.665
Wood Tissue (W)		0.000	0.000	0.609	0.548	0.012	0.007	0.014	0.003	0.944
P by W	Bole vs Root-Stump	0.003	0.082	0.165	0.087	0.038	0.071	0.080	0.782	0.861
	Root vs Bole-Stump	0.000	0.680	0.394	0.905	0.580	0.731	0.279	1.000	0.671
	Stump vs Bole-Root	0.097	0.179	0.585	0.068	0.119	0.140	0.490	0.782	0.802
	Root vs Stump	0.001	0.585	0.858	0.256	0.554	0.507	0.818	0.873	0.696
	Bole vs Stump	0.390	0.076	0.264	0.042	0.037	0.059	0.158	0.749	0.965
	Bole vs Root	0.000	0.211	0.197	0.351	0.126	0.211	0.103	0.873	0.729
E by P	Bole vs Root-Stump	0.826	0.050	0.717	0.324	0.485	0.534	0.386	0.726	0.745
	Root vs Bole-Stump	0.020	0.045	0.001	0.513	0.871	0.771	0.872	0.031	0.745
	Stump vs Bole-Root	0.011	0.039	0.004	0.105	0.390	0.741	0.479	0.068	0.516
	Root vs Stump	0.006	0.020	0.001	0.188	0.554	0.982	0.751	0.023	0.573
	Bole vs Stump	0.105	0.212	0.123	0.133	0.369	0.582	0.364	0.384	0.573
	Bole vs Root	0.210	0.253	0.033	0.846	0.756	0.598	0.552	0.144	1.000
E by W		0.735	0.000	0.084	0.176	0.282	0.323	0.007	0.405	0.944
E by P by W	Bole vs Root-Stump	0.564	0.677	0.232	0.181	0.390	0.822	0.643	0.012	0.383
	Root vs Bole-Stump	0.064	0.447	0.234	0.022	0.820	0.615	0.666	0.271	0.439
	Stump vs Bole-Root	0.193	0.242	0.995	0.309	[illegible]	0.467	0.975	0.135	0.920
	Root vs Stump	0.069	0.265	0.492	0.055	[illegible]	0.478	0.817	0.815	0.696
	Bole vs Stump	0.670	0.359	0.485	[illegible]	[illegible]	0.582	0.775	0.021	0.573
	Bole vs Root	0.158	0.841	0.170	[illegible]	[illegible]	0.872	0.605	0.036	0.342

* Main effects: E= exposure status of spruce, P= tree part, W= wood tissue; interactions: P by W, E by P, E by W, E by P by W.
** Average ring width was measured from compression-test and bending-test sticks; therefore, the sample size was twice that of other wood properties.

Appendix 3D. Is Response Wood Reaction Wood?

The wood properties tested and described in Chapter 3 are used in this appendix to compare reaction wood with response wood. In addition, percent-volumetric and percent-longitudinal shrinkage are used. These two properties are calculated from the oven-dry and wet dimensions of the 30 mm long stubs used in Chapter 3 to determine dry density, green specific gravity and percent-moisture content. Fiber length was also determined from these stubs, but the methods and results associated with this property are not presented in this version of the thesis.

Tables 3D-1 and 3D-2 summarize the results from the analyses (F-test probabilities presented in Appendix 3C) conducted on the percent-volumetric and percent-longitudinal shrinkage data (Appendix 3B). Non-response tissue in all trees and tree parts, except one, and root response tissue in released trees shrunk more volumetrically than bole non-response tissue in unreleased trees and response tissue in all other trees and tree parts. Consequently, non-response tissue shrunk more than response tissue overall. Nevertheless, despite the greater volumetric shrinkage in released tree roots, released trees and unreleased trees did not shrink differently overall. Roots shrunk more than boles which shrunk more than stumps. The opposite was true for longitudinal shrinkage, though the bole and root did not shrink differently.

Table 3D-3 summarizes the comparison of reaction wood properties and response wood properties. Since most properties do not correspond and many oppose each other, I must conclude that response wood does not have the same properties as reaction wood. Consequently, response wood is not reaction wood.

Figure 3D-1. Significant Trends at Various Levels of Wood Type* for Percent-volumetric and Percent-longitudinal Shrinkage.**

Level of Comparison	Volumetric Shrinkage (%)	Longitudinal Shrinkage (%)
Spruce Status (E)	C=O	C=O
Tree Part (P)	S<R	(S>B=R)
Wood Tissue (W)	r<n	r=n
P by W		
E by P	OR>rest	
E by W		
E by P by W	CBn=r<n=ORr	

* E=spruce status P=tree part W=wood tissue
C=unreleased spruc B=bole n=non-response wood
O=released spruce S=stump r=response wood.
R=root

** Parenthesized trends have F-test probabilities greater than 0.05 and less than 0.10. All other trends have probabilities less than 0.05. Main effects with probabilities greater than 0.10 are also presented.

TABLE 3D-2. Mean (± SEM) Percent-volumetric and Percent-longitudinal Shrinkages.

Volumetric Shrinkage — Longitudinal Shrinkage

Tree Part

Bole

Wood	Exposure Status: Unreleased	Released	Overall	Longitudinal Shrinkage
Non-respons	7.2±0.7	9.2±0.2	8.2±0.5	
Response	7.9±0.7	6.4±0.6	7.1±0.5	
Overall	7.5±0.5	7.8±0.6	7.7±0.4	0.1±0.0

Stump

Wood	Exposure Status: Unreleased	Released	Overall	Longitudinal Shrinkage
Non-respons	8.5±1.0	7.5±0.4	8.0±0.6	
Response	6.7±1.1	6.6±0.7	6.6±0.6	
Overall	7.6±0.8	7.0±0.4	7.3±0.4	0.3±0.1

Root

Wood	Exposure Status: Unreleased	Released	Overall	Longitudinal Shrinkage
Non-respons	8.4±0.6	9.7±0.5	9.1±0.5	
Response	6.9±0.5	8.8±1.2	7.8±0.7	
Overall	7.6±0.5	9.3±0.7	8.4±0.4	0.1±0.0

	Unreleased	Released	Overall
Overall	7.6±0.3	8.0±0.4	
Wood			
Non-response			8.4±0.3
Response			7.2±0.4

* Interactions and main effects with F-test Probabilities less than 0.10 (Appendix 3C) are presented with their overall averages (averages do not necessarily have pr<0.10). See Table 3D-1 to determine which components of these interactions and main effects are significant.

TABLE 3D-3. Reaction ' d* versus Response Wood.**

Wood Property	Reaction Wood	Response Wood
Ring Width	reac > n–reac	resp > n–resp
Parallel Compression Strength	reac < n–reac	resp = n–resp
Radial Bending Strength	reac > n–reac	resp = n–resp
Specific Gravity / Density	reac > n–reac	resp < n–resp
Moisture Content	reac < n–reac	resp > n–resp
Vol. Shrinkage	reac > n–reac	resp < n–resp
Long. Shrinkage	reac > n–reac	resp = n–resp

* reac=reaction wood; n–reac=non–reaction wood. Information for reaction wood properties were obtained from Wardrop et al, 1965.
** resp=response wood; n–resp=non–response wood.

List of References

Appendix 3D

Wardrop, A.B., Côté, W.A.,Jr., Day, A.C. 1965. Reaction wood -- its causes, formation and ultrastructure. *In* Cellular Ultrastructure of Woody Plants. *Edited by* W.A. Côté, Jr. Syracuse University Press. pp 369-418.