University of Alberta

Group tree sway of lodgepole pine, associated crown interactions and their potential role in mediating crown shyness

by

Mark Rudnicki ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta
Spring 2002

0-612-68619-1

University of Alberta

Library Release Form

Name of Author: Mark Rudnicki

Title of Thesis: Group tree sway of lodgepole pine, associated crown interactions and their potential role in mediating crown shyness

Degree: Doctor of Philosophy

Year this Degree Granted: 2002

5373 Clear Lake Rd
North Branch, Michigan
48461 U.S.A.

Submitted to the Faculty of Graduate Studies and Research on Feb 07, 2002

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Group tree sway of lodgepole pine, associated crown interactions and their potential role in mediating crown shyness* submitted by Mark Rudnicki in partial fulfillment of the requirements for the degree of *Doctor of Philosophy* in *Forest Biology and Management*

Victor J. Lieffers

Uldis Silins

John D. Wilson

Yongsheng Feng

James N. Long

Date thesis is approved by committee ____________.

Dedication

To Zbigniew, Maria, Richard, and Connie.

Pingree, Bravo and Dante.

Abstract

In this dissertation, I investigated mechanisms that mediate crown shyness in lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud). To examine how tree bole slenderness mediates crown collisions and crown shyness in closed canopy stands, I developed a technique to measure the simultaneous sway of a group of trees and reconstruct frequency of crown collisions and sway dynamics of individual or groups of trees. I then applied this technique to investigate tree sway and crown collision behaviour of even-aged lodgepole pine stands of different structure in Central Alberta. I hypothesize structural factors regulate crown collision dynamics and therefore the development of crown shyness and loss of leaf area as stands mature. Three stand structures representing differences in bole slenderness coefficient (height/diameter - SC) and stand density were studied. Comparing the sway statistics between stands indicated that crowns of slender trees have greater mean sway displacements, faster mean sway speeds and a greater mean depth of collision; thus indicating a greater likelihood of crown damage and/or growth inhibition. Comparing pre-thinned and thinned stands revealed the thinned stand had increased mean sway displacements, mean sway speeds and mean depth of collisions. Stand structure, specifically slenderness coefficient, is therefore, thought to regulate crown collisions and crown shyness.

Spatial patterns of crown displacement indicate that trees have a generally circular sway pattern that is not aligned with mean wind direction. Tree sway patterns were dramatically affected by thinning with many trees producing an elongated pattern of displacement that in most cases were not aligned with mean wind direction.

My closing investigation into the biomechanical influence on crown shyness involved measuring the percent crown closure (%CC) in groups of three trees (tree triangles) then correlating this to the mean slenderness coefficient (SC) and relative density (RD) of the tree triangle. Tree SC is thought to be inversely related to the collision intensity, while the index of relative density is generally assumed to be an indicator of crown development in closed stands. Tree triangles within each (closed canopy) stand were examined separately to eliminate confounding site-specific influences.

Canopy closure in tree triangles in all stands shorter than 11.4 m were positively correlated to RD, while canopy closure in most stands taller than 15 m were negatively correlated to SC. I believe this indicates a change in the mechanism controlling lateral crown development in even-aged lodgepole pine from light availability to crown collisions. The mean stand %CC (from all triangles within a stand) was negatively correlated with mean stand height; suggesting crown shyness typically increases as stands grow in height.

Acknowledgements

This research was made possible by funding from NSERC and a joint contribution from Canadian forest industries including: Canadian Forest Products Ltd., Millar Western Forest Products Ltd., Sunpine Forest Products Ltd., Weldwood of Canada Ltd. and Weyerhaeuser Canada Ltd. First-rate field assistance was rendered by Sarah Lieffers, Vashti Thompson, Justin Karst, Ben Seaman, Wei Liu, Jim Cuthbertson, Eric Paton, Carolyn Huston and Xiaodong Liu.

Thanks to Tom Flesch in the Dept. of Earth and Atmospheric Sciences at the Univ. of Alberta, for first installing a biaxial clinometer on a tree for displacement measures.

Thanks to my lab mates Ken Stadt, Annie DesRochers, Clark Protz, Brad Pinno, Erin Fraser, Brent Frey and Doug Reid who all helped with morale, and technical assistance in all parts of my work.

A special thanks to my advisors Victor J. Lieffers and Uldis Silins: their enthusiasm, patience, ethics, and determination changed my definition of passion.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

On the earth's surface, wind is ubiquitous and eolian processes shape landscapes via erosion, transportation and deposition. Wind forces have shaped the evolutionary history of terrestrial plants as vertical foraging for light exposed taller plants to wind forces, stimulating development of complex structural adaptations (Niklas 1998). There are many examples of phylogenic convergence in terrestrial plants as structural adaptations to wind forces follow similar design constraints (Niklas 1992). Hence, the general structural patterns of tree bole and crown architecture are inherited; yet remain adaptive to environmental conditions and competition for resources (Assmann 1970; Ford 1985; Oliver and Larson 1990).

Wind induced bending stress of trees results in a plastic feature of adaptation as higher wind loads increase tree radial growth and decrease its slenderness coefficient (height/diameter). This phenomenon is well researched and documented for all tree species examined (Jacobs 1954; Larson 1965; Neel and Harris 1971; Telewski and Jaffe 1986; Hobrook and Putz 1989; Valinger 1992; Osler *et al.* 1996; Peltola 1996) and is a vital link with the stability and survival of trees (Petty and Swain 1985; Mayer 1987; Foster and Boose 1992).

Stability strategies

Since survival of a tree depends on its ability to remain upright, understanding strategies of tree stability and their associated processes are fundamental to understanding stand dynamics. Two strategies of tree stability are self-support and group-support. Self-supporting trees are classically open grown and subject to the full force and variability of wind loading resulting in a structure characterized by a highly tapered bole and full crown. Group-supported trees typically occur in dense stands and have reduced individual wind loads as trees shelter one another. Group supported trees are characterized by slender boles and short, narrow crowns. Open grown trees must be stiff enough to withstand large bending stresses while trees in a group have a reduced wind load from sheltering each other and their bending stresses are controlled by sway inhibiting crown collisions with neighbouring trees.

Studying the sway of trees without neighbours, researchers conclude that when gust frequency matches the natural sway frequency of a tree, resonance effect builds up and stem failure can occur when wind speeds are below the maximum static load (Fraser and Gardiner 1967; Oliver and Mayhead 1974; White *et al.* 1976). The increasing amplitude of resonance vibration is thought to be mitigated by tree crown collisions yet researchers lack the techniques for empirical observation and assessment of this relationship (Kerzenmacher and Gardiner 1998). In contrast to the study of self-supporting trees, the dynamic sway of group-supporting trees has not been studied.

Crown collision effects

Moderate to high winds cause chronic crown collisions that have a stabilizing effect upon tree sway and affect crown structure by the breakage of twigs and branches (Rees and Grace 1980; Robertson 1987; Grier 1988; Peltola *et al.* 1993; Peltola *et al.* 1999). Chronic crown collisions are also thought to affect crown structure by inhibiting shoot extension (Jaffe and Biro 1979; Telewski and Jaffe 1986; Michalsky 1996; Aradóttir *et al.* 1997). Thus, crown interaction has been suggested as a mechanism controlling crown shyness (Putz *et al.* 1984; Grier 1988; Robertson 1987; Long and Smith 1992; Smith and Long 2001; Rudnicki *et al.* submitted). Tree crown interstitial space or "crown shyness" is the unoccupied space in the forest canopy in closed canopy stands not attributable to tree mortality gaps. Crown shyness is found in some forested ecosystems and is usually attributed to poor light conditions between crowns that purportedly inhibit their lateral growth (Koike 1989; Sorrensen-Cothern *et al.* 1993; Umeki 1995; Chen *et al.* 1996; Cescatti 1997; Mäkelä 1997).

Foliage loss via tree collisions (crown abrasion) has also been suggested to be a mechanism responsible for the decline in stand LAI (leaf area index) and productivity during later phases of stand maturation (Long and Smith 1992). Robertson (1987) identified wind induced crown abrasion as the primary mechanism underlying crown asymmetry and shyness in trees during the latter self-thinning stage of stand maturation.

Crown shyness and tree stiffness

Since crown collisions are increasingly thought to have a key role in canopy dynamics, insight into what mediates the intensity of collisions is essential. As the main component of tree stiffness (Petty and Swain 1985; Peltola and Kellomäki 1993), I suspect tree slenderness mediates crown collision intensity. I suggest crown collision intensity can be defined by the average percent overlap during crown collisions. Tree stiffness is determined by bole modulus of elasticity and change in cross sectional area over the bole length (slenderness coefficient – SC: tree height/tree diameter at 1.3m).

Comparing the sway and crown collision characteristics for stands of different mean slenderness coefficients and densities, under similar wind conditions, will reveal the potential role of stand structure in mediating crown shyness. While comparing tree sway and crown collision characteristics of an identical stand structure, experiencing moderate and high winds, will indicate how these measures react to increased loads. To demonstrate tree stiffness is mediating collision intensity and crown shyness, the ability of tree SC to predict %CC will be examined.

The 2-dimensional density distributions of group tree sway patterns should provide insight into any sway pattern changes caused by an altered stand structure or increased wind speed. If sway patterns were unchanged when trees are subject to moderate and high wind loads, this would support the notion that general wind patterns are coherent and organized (rather than random and chaotic) inside forest canopies and that tree boles can be structurally adapted to them to diminish collision intensity (Raupach 1988; Gardiner 1994).

Crown shyness and relative density

The index of relative density (RD) is used to describe the level of stand occupancy by considering the density at a given average tree size. Based on the maximum size-density relationship, RD is an indicator of competition intensity and in closed canopy stands describes the amount of crown development compared to a standard (usually an open grown individual) (Drew and Flewelling 1979; Curtis 1982; Farnden 1996). In describing the amount of crown development, relative density assumes that tree crowns will fill all available space (up to its open grown potential) via lateral growth.

Thus, relative density ignores the proposed biomechanical mechanisms of crown shyness. I suspect the ability of RD to predict %CC will fail as bole SC's increase and crown collisions become more intense.

Productivity decline

The suspected causal role of crown shyness in the decline of leaf area index (LAI) and productivity is of profound importance to ecologists and foresters. It has been hypothesized that even-aged stands of lodgepole pine undergo a change in the canopy structure and the timing of this restructuring is closely associated with productivity decline and the onset of crown shyness (Smith and Long 2001). The nature of this restructuring includes the lifting of tree crowns, the decline in bole SC (Long and Smith 1984; Mohler *et al.* 1978), and the onset of crown shyness. The timing of restructuring is concomitant with the onset of competition mortality and hence is related to stand density (Smith and Long 2001). While the lifting of the canopy is probably a response to low light levels at the bottom of tree crowns, the decline of SC is controlled by stand density and I suggest the declining SC controls crown shyness.

Summary of research opportunities

By investigating crown movement in stands of various structures, I hope to gain insight into the mechanisms controlling lateral crown extension in lodgepole pine. I believe the current paradigm, which suggests resource limitations control lateral crown extent, ignores the relative importance of plant biomechanics and that wind is a pervasive and powerful evolutionary agent acting upon the growth of trees. Understanding the effect of collisions upon the sway damping of trees may mitigate the loss of forests and forest productivity due to windstorms by allowing silvicultural prescription to achieve a structurally wind resistant stand. The following are some important ideas that need further study to advance the understanding of the development of crown shyness:

1. A method to measure and record simultaneous tree sway for a group of trees.
2. A technique to reconstruct and quantify the crown collisions associated with chronic tree sway.

3. Development of 2-dimensional tree sway frequency patterns to compare group dynamic sway response to changes in stand density and wind speed.
4. Determine how stand density, tree SC and wind speeds affect the spatial patterns and metrics of bole displacement.
5. Determine how stand density, tree SC and wind speeds affect the frequency and intensity of tree crown collisions.

Research objectives

I explored the crown collision dynamics and tree sway patterns of *Pinus contorta* var. *latifolia* Dougl. ex Loud. as it typically regenerates in pure even-aged stands that commonly exhibit crown shyness (Jack and Long 1991).

Chapter 2 introduced a new method of simultaneously measuring the bole bending angle (rotation) at the live crown base of ten trees. I derived a stem curvature solution that uses bole rotation to calculate bole displacement. I reconstructed crown collisions using GIS software that combines asymmetrical polygon representation of tree crowns with their respective bole displacements. The output of this approach provides estimation of crown collision frequencies and intensities (area of crown overlap). I hypothesize that tree collisions provide the mechanism for lateral shoot abrasion in even-aged lodgepole pine.

The objectives of Chapter 3 were to examine how stand density, crown width, tree SC and wind speed affected frequency and intensity of crown collisions in *Pinus contorta* var. *latifolia*. To examine the role of tree stiffness and stand density in the crown collisions of lodgepole pine, I studied stands of similar height that experienced similar wind speeds. I hypothesised that trees with higher SC would have a higher frequency and intensity of collisions than trees having low SC, as high SC trees are more flexible. To study the effects of stand density on crown collisions, I compared the crown interactions and sway patterns of a stand with high SC before and after tree thinning. I hypothesize that increased crown wind loads due to partial removal of the overstory would result in higher collision frequencies and intensities and disrupt their sway patterns. I also compared crown interaction and sway patterns in a stand with a low SC at two different wind speeds. I hypothesized that increased crown wind loads would also increase collision frequencies and intensities with a consistent shape in the sway patterns.

In Chapter 4, the objective is to demonstrate the dependence of crown shyness on tree biomechanics in even-aged lodgepole pine. In this study, I use the measured percent crown cover (% CC) as the complement of crown shyness. I hypothesized that in stands where % CC is predicted by RD, lateral crown development is not being affected by crown collisions. In contrast, in stands where % CC is predicted by SC, lateral crown extension is now controlled by crown interaction and tree biomechanics.

References

Aradóttir, A.L., Robertson, A. and Moore, E. 1997. Circular statistical analysis of birch colonization and the directional growth response of birch and black cottenwood in south Iceland. Agriculture and Forest Meteorology, **84**: 179-186.

Assmann, E. 1970. The principles of forest yield study studies in the organic production, structure, increment and yield of forest stands[1st English ed.]. Oxford, Pergamon Press, 506 pp.

Cescatti, A. 1997. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithims. Ecological Modelling, **101**: 263-274.

Chen, H.Y.H., Klinka, K. and Kayahara, G.J. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. Canadian Journal of Forest Research, **26**: 1149-1157.

Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. Forest Science, **28**(1): 92-94.

Drew, J.T. and Flewelling, J.W. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantation. Forest Science, **25**(3): 518-532.

Farnden, C. 1996. Stand density management diagrams for lodgepole pine, white spruce and interior Douglas-fir. Canadian Forest Service. Victoria, British Columbia, Information report BC-X-360.

Ford, E.D. 1985. Competition and stand structure in some even-aged plant monocultures. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of terrestrial ecology.

Foster, D.R. and Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology, **80**: 79-98.

Fraser, A.I. and Gardiner, J.B.H. 1967. Rooting and stability in Sitka spruce. Forestry Commision Bulletin **40**, HMSO, London

Gardiner, B.A. 1994. Wind and wind forces in a plantation spruce forest. Boundary-Layer Meteorology **67**: 161-186.

Grier, C.C. 1988. Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifer forests. Canadian Journal of Forest Research, **18**: 1097-1102.

Holbrook, N.M. and Putz, F.E. 1989. Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *liquidambar styraciflua* (sweet gum). American Journal of Botany, 76(12): 1740-1749.

Jack, S.B. and Long, J.N. 1991. Analysis of stand density effects on canopy structure: a conceptual approach. Trees- Structure and Function, **5**: 44-49.

Jacobs, M.R. 1954. The effect of wind sway on the form and development of *Pinus radiata* D. Don. Australian Journal of Botany, **2**: 35-51.

Jaffe, M. and Biro, R. 1979. Thigmomorphogenesis: the effect of mechanical perturbation on the growth of plants, with special reference to anatomical changes, the role of ethylene, and interaction with other environmental stresses. In: Stress physiology in crop plants (eds. H. Mossel, and R.C. Staples) pp. 26-59. John Wiley and Sons, New York

Kerzenmacher, T. and Gardiner, B.A. 1998. A mathematical model to describe the dynamic response of a spruce tree to the wind. Trees- Structure and Function, **12**: 385-394.

Koike, F. 1989. Foliage-crown development and interaction in *Quercus gilva* and *Q. Acuta*. Journal of Ecology, **77**: 92-111.

Larson, P.R. 1965. Stem form of young *Larix* as influenced by wind and pruning. Forest Science, **11**(4): 413-423.

Long, J.N. and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. Forest Ecology and Management, **53**: 53-62.

Long, J.N. and Smith, F.W. 1984. Relation between size and density in developing stands: a description and possible mechanisms. Forest Ecology and Management, **7**: 191-206.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. Forest Science, 43(1): 7-24

Mayer, H. 1987. Wind-induced tree sways. Trees- Structure and Function, 1: 195-206.

Michalsky, A.J. 1996. An investigation of mechanical abrasion in saplings of sugar maple (*Acer saccharum* . Marsh.), Mont St. Hilaire, Quebec. Masters thesis, York University, Canada

Mohler, C.L., Marks, P.L. and Sprugel D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology, 66: 599-614.

Neel, P.L. and Harris, R.W. 1971. Motion-induced inhibition of elongation and induction of dormancy in *Liquidambar*. Science, 173: 58-59.

Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago.

Niklas, K.J. 1998. The influence of gravity and wind on land plant evolution. Review of Palaeobotany and Palynology, 102: 1-14.

Oliver, H.R. and Mayhead, G.J. 1974. Wind measurements in a pine forest during a destructive gale. Forestry, 47(2):185-194

Oliver, C.D. and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, New York.

Osler, G.H.R., West, P.W. and Downes, G.M. 1996. Effects of bending stress on taper and growth of stems of young Eucalyptus regnans trees. Trees- Structure and Function, 10(4): 239-246.

Peltola, H., Kellomäki, S., Väisänen, H. and Ikonen, V.P. 1999. A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. Canadian Journal of Forest Research, 29:647-661

Peltola, H. 1996. Swaying of trees in response to wind and thinning in a stand of scots pine. Agricultural and Forest Meteorology, 90: 187-194.

Peltola, H. and Kellomäki S. 1993. A mechanistic model for calculating windthrow and stem breakage of Scots pines at stand edge. Silva Fennica, 27(2): 99-111.

Petty, J.A. and Swain, C. 1985. Factors influencing stem breakage of conifers in high winds. Forestry, 58(1): 75-84.

Putz, F.E., Parker, G.G. and Archibald, R.M. 1984. Mechanical abrasion and intercrown spacing. The American Midland Naturalist, **112**(1): 24-28.

Raupach, M. R. 1988. Canopy transport proscess. pp 95-127. In: Flow and Transport in the Natural Environment: Advances and Application. (eds) W. L. Stephan and O. T. Denmead. Springer – Verlag, Berlin.

Rees, D.J. and Grace, J. 1980. The effects of shaking on extension growth of *Pinus contorta* Douglas. Forestry, **53**: 155-166.

Robertson, A. 1987. The centroid of tree crowns as an indicator of abiotic processes in a balsam fir wave forest. Canadian Journal of Forest Research, **17**: 746-755.

Rudnicki, M., Lieffers, V.J. and Silins U. 2001. The crown collisions of lodgepole pine. The Journal of Ecology, submitted.

Smith, F.W. and Long, J.N. 2001. Age-related decline in forest growth: an emergent property. Forest Ecology and Management, **144**: 175-181.

Sorrenson-Cothern, K.A., Ford, E.D. and Sprugel, D.G. 1993. A model of competition incorporating plasticity through modular foliage and crown development. Ecological Monographs, **63**(3): 277-304.

Telewski, F.W. and Jaffe, M.J. 1986. Thigmomorphogenesis: Field and laboratory studies of *Abies fraseri* in response to wind or mechanical perturbation. Plant Physiology, **66**: 211-218.

Umeki, K. 1995. Modeling the relationship between the asymmetry in crown display and local environment. Ecological Modelling, **82**: 11-20.

Valinger, E. 1992. Effect of wind sway on stem form and crown development on Scots pine (*Pinus sylvestris L.*). Australian Forestry, **55**: 15-21.

White, R.G., White, M.F. and Mayhead, G.J. 1976. Measurement of the motion of trees in two dimensions. Tech Report 86. Instutute of Sound and Vibration Research, University of Southhampton, UK.

Chapter 2. Measure of simultaneous tree sways and estimation of crown interactions among a group of trees[1]

Introduction

Interests in the effects of wind on forests usually focus on extreme winds that can cause catastrophic uprooting of trees (windthrow) or stem breakage (windbreak) (Mayer 1987; Foster and Boose 1992; Hedden *et al.* 1995). However, lower wind speeds also affect the growth dynamics of forests (Jacobs 1954; Larson 1965; Holbrook and Putz 1989; Telewski 1995). In fully stocked stands chronic moderate to high winds have effects on stand structure that include stem displacement and crown collisions with neighbouring trees, resulting in branch and foliage loss or inhibition of shoot extension (Robertson 1987; Grier 1988; Peltola *et al.* 1993; Michalsky 1996; Aradóttir *et al.* 1997; Peltola *et al.* 1999). Foliage loss via tree collisions (crown abrasion) has been suggested as one mechanism responsible for the decline in stand LAI (leaf area index) during later phases of stand maturation (Long and Smith 1992). Robertson (1987) identified wind induced crown abrasion as the primary mechanism underlying crown asymmetry and shyness in trees during the latter self-thinning stage of stand maturation. Nevertheless, the current paradigm assumes that low light levels prevent lateral branches from growing into intercrown spaces, thereby maintaining crown shyness. Crown asymmetry is a similar, more widely researched phenomenon that is also explained with the low light hypothesis. Specifically, preferential branch foraging into light rich spaces results in asymmetric crown formation (Koike 1989; Sorrensen-Cothern *et al.* 1993; Umeki 1995; Chen *et al.* 1996; Cascatti 1997; Mäkelä 1997).

While recognizing the importance of collision dynamics, virtually all previous tree displacement studies feature individual and/or pairs of trees that oversimplify or ignore the influence of neighboring trees (White *et al.* 1976; Mayer 1987; Gardiner 1995). Prior investigations into dynamic loading and bending conclude that when gust frequency matches the natural sway frequency of a tree, stem failure can occur below maximum static load due to a buildup of resonance effects (Fraser and Gardiner 1967;

[1] A version of this chapter is published in Trees- Structure and Function (2001) 15:83-90

Oliver and Mayhead 1974). The buildup of resonance effects is thought to be mitigated by tree crown collisions yet researchers lack the techniques for empirical observation and assessment of the relationship (Kerzenmacher and Gardiner 1998). Hence, techniques to quantify the collision dynamics of a group of trees would clearly aid the understanding of wind forest interactions in at least two areas of inquiry; the mechanisms that shape tree crowns, and the effect of dampening stem displacements which mitigates stem failure.

In this paper, I explore techniques to understand wind effects on crown structure of lodgepole pine. To this end I: Introduce a new method of measuring the bole bending angle (rotation) at the live crown base of ten trees simultaneously; derive a stem curvature solution that uses bole rotation to calculate bole displacement; and reconstruct crown collisions using GIS software that combines asymmetrical polygon representation of tree crowns with their respective bole displacements. The output of this approach provides estimation of crown collision frequencies and intensities (area of crown overlap). I hypothesize that tree collisions provide the mechanism for lateral shoot abrasion and resultant crown asymmetry in even-aged lodgepole pine.

Methods

The study area was located 50 km west of Whitecourt, Alberta in a lower foothills stand of naturally regenerated and unmanaged lodgepole pine (*Pinus contorta* var. *latifolia*) burned in 1954. The site was even-aged with a mean density of 2150 trees/ha, mean diameter at breast height (dbh) of 14 cm and mean height of 15 m. The stand had an understory of black spruce (*Picea mariana*) saplings averaging 4 m (mean dbh 7 cm) and ground cover dominated by deep feathermosses, and Labrador tea (*Ledum groenlandicum*). The site had a gentle westerly slope (<5 degrees) and was located 50 m west of the access road. The stand was well into the stem exclusion phase (Oliver and Larson 1990) with dead standing and dying suppressed lodgepole pine trees a common occurrence (approximately 200 trees/ha). A similar stand structure continued for at least 1 kilometer (except for the road itself) in every direction. A cluster of ten lodgepole pine trees, representative of mean stand structural attributes and having a minimum distance of 1 m between stems, was chosen for this study (Table 1).

To determine tree bole rotation θ_h, I used gravity referenced biaxial clinometers (tiltmeter) (Model 900, Applied Geomechanics Inc.) enclosed in lightweight weatherproof housings mounted at the base of each live crown (~10 m). Originally designed for geological applications the low cost sensors have proved accurate and reliable in qualification tests and continuous field use (d'Oreye 1998; O'Reilly *et al.* 1998; Flesch and Wilson 1999). The tiltmeter model used has a resolution of 0.01 degree and a span of 50 degrees (±25 degrees). A liquid filled glass vial houses five internal electrodes whose paired electrical resistances are sensitive to fluid levels and report a DC voltage of ±2.5 volts for each axis. The maximum sway frequency a sensor can dependably record is <10 Hz and since trees sway at a frequency of ~0.2-0.4 Hz, it is well within this range (White *et al.* 1976; Gardiner 1989; Peltola *et al.* 1993).

The sensor housing on each tree bole was mounted facing north to align all tiltmeters to a common azimuth so that sensor outputs from all trees could be compared. Tiltmeter positions on the tree were calibrated in two ways: First, the azimuth alignment was checked using compass bearing off the sensor housing and adjusted accordingly. Second, horizontal resting position of each sensor was recorded during a period with no measurable wind and subtracted from respective sensor outputs. Heights of each sensor housing were measured with a meter tape to the ground. The ten tiltmeters were wired to a high-speed data logger (CR23X, Campbell Scientific) with outputs recorded at a rate of 10Hz (10 times per second). The CR23X recorded data from both axes of all ten sensors (20 voltage readings) within 32 ms allowing calculation of relative tree positions at nearly the same time. To linearize and calibrate individual tiltmeter output, a fifth order polynomial (supplied by the manufacturer) was applied to the raw data before analysis.

The bases of all ten trees were mapped (x,y coordinates) using a laser surveying device and since the boles were remarkably straight, crowns were assumed to be directly overhead. Tree total height, height to the bottom of the live crown, and height of the widest lateral crown extent were measured with a laser range finder (Impulse LR200) from two sides to ensure accuracy. Since crown lengths of these lodgepole pine are relatively short (about ¼ tree height), the center of gravity of each crown was assumed to be at the center of the live crown (Dean and Long 1986). We constructed a Crown Scope™ with a wide 7.6 cm aperture allowing an accurate vertical sighting of the crown edge and precise measurement of lateral crown extent (Rudnicki *et al.* 2001; Vales and Bunnel 1988). The horizontal 2-dimensional shape of each crown was determined by taking 8 radial crown measurements in 45 degree increments.

An 18m meteorological tower was erected adjacent to the tree cluster for monitoring of climatic and wind conditions. The tower was topped with a propeller anemometer (model 05103, R.M. Young) to measure wind speed and direction at the canopy top. A 3-cup anemometer (model 12102, R.M. Young) mounted at ~13 m measured wind speed at the mid-crown level. The top anemometer was sampled every five seconds to generate a five-minute running average of wind speeds. When the wind speed running average was >5 m/s it triggered the high frequency recording of tiltmeters for 15 minutes. Equipment was monitored and data downloaded via a cellular telephone (COM 100, Campbell Scientific) combined with a modem (DC112 modem, Campbell Scientific). Solar panels mounted on the tower powered the entire array with power storage in a 12-volt deep-cycle battery.

Tree bending

Measurement of the tree bending rotation directly allowed an analytical solution of bole displacement from vertical that eliminates the input of the tree diameter, applied load force, and Modulus of elasticity (Young's modulus). I developed a relatively simple equation describing the stem curvature of a tree bending against a point load based on elementary mechanical theory (Leiser and Kemper 1973; Petty and Worrel 1981; Dean and Long 1986; Gardiner 1989) (Figure 2-1). I assume the tree bole shape to be a simple cone with constant taper (tapered cantilever beam) and subjected to a point load at the crown center of gravity (simulating a wind load). The boundary conditions for the derivations are; bole rotation at the ground or bole base equals zero (rigidly fixed to the ground), diameter at tree top equals zero and stem curvature is continuous.

With the above assumptions, the displacement from vertical (v) for any height along the bole (z) can be found:

$$v(z) = K \cdot \left(\frac{1}{2z} - \frac{l_{ct}}{6z^2} + \frac{z}{2L^2} - \frac{l_{ct} \cdot z}{3L^3} + \frac{l_{ct}}{2L^2} - \frac{1}{L} \right) \quad \text{for } z < l_{ct} \tag{2-1}$$

$$v(z) = z \cdot K \cdot \left(\frac{-1}{6l_{ct}^{\ 2}} + \frac{1}{2L^2} - \frac{l_{ct}}{3L^3} \right) + K \cdot \left(\frac{1}{2l_{ct}} + \frac{l_{ct}}{2L^2} - \frac{1}{L} \right) \text{ for } z > l_{ct} \tag{2-2}$$

Where: L is the total height of the tree

v is the bole displacement from vertical at point z

z is the distance along the tree bole measured from tree top

l_{ct} is the distance from tree top to crown center of gravity (and the location of the point load)

The coefficient K depends on the magnitude of the point load and pertains to bole stiffness (being a function of L, the bole base diameter, and Young's modulus of elasticity). However, the measured rotation considers all these factors and by knowing the rotation (given directly by the tiltmeter), θ_h, of the bole at a certain location (h) (tiltmeter mount height) the analytical solution for the response coefficient, K, can be derived:

$$K = \theta_h \cdot \left(\frac{-1}{2h^2} + \frac{l_{ct}}{3h^3} + \frac{1}{2L^2} - \frac{l_{ct}}{3L^3} \right)^{-1} \tag{2-3}$$

Where:

θ_h is the bole rotation reported by the tiltmeter

h is the tiltmeter mount location measured from tree top

The curvilinear formula (2-1) returns displacement for the bole up to the center of gravity, $z < l_{\alpha}$, where the point load is applied. Since I assume there is no load above l_{α}, bending shape of the bole becomes linear above the center of gravity. Displacement for bole locations (heights) above the point load, $z > l_{\alpha}$, requires an alternate formula (2-2), which combines the curvilinear portion of the bending shape below l_{α} with a linear bending shape above l_{α}. While the assumption of linearity above l_{α} may not represent the actual bending shape, I have found it acceptable since all of our displacement queries are below or near the center of gravity. Each tiltmeter outputs the rotation of the bole along both the X and Y-axis requiring separate displacement calculation for each axis. By plotting both X and Y displacement results together, I acquire both direction and distance (location) of bole displacement.

To validate my bending formulas I conducted a field trial to compare predicted and measured displacements. I began by fastening a rope to the crown center in order to apply the point load with a hand winch. To measure displacement I attached five plumb bobs at differing heights along the bole (including one at the point load). Five levels (loads) of increasing force were applied to the sensored tree, and at each I recorded the rotation angles reported by the tiltmeter and measured the displacement of the plumb bobs from the bole. This procedure was applied to two trees in the study plot resulting in identical relationships to the predicted bending curve. It is important to note that the predicted curve is linear above the crown center of gravity and consequently estimates a more conservative displacement above this point. Comparing the predicted versus the measured displacements shows a good agreement- especially at the point load (Figure 2-2). However, the disparity between the curves grows slightly as the rotation angle increases, though rotations above 20° were rarely encountered. This is presumably caused by our simple taper function (cone of constant taper) underestimating the bending curve of an actual taper that is more columnar below the live crown.

Crown interaction

Using the GIS (Geographic Informational System) Arc/Info (Environmental Systems Research Institute inc.), I performed spatial analysis of the crown interactions. I represented the ten tree crowns with eight-sided polygons derived from the crown extent measures (Table 2-2). For each 0.1s time step, the ten polygons were located at their respective calculated bole displacement locations, allowing calculation of any crown area overlap (Figure 2-3). The reconstruction was programmed using Arc Macro Language (AML) which automated the processing of many individual time steps. The AML algorithm read data files of tiltmeter output and tree shape parameter files for each tree. Parameters such as tree heights, crown dimensions and bole resting positions were set to variables in the AML and reused for each timestep. The AML then looped through the algorithm with raw data from each successive time step and output area (m^2) of overlap between tree crowns.

Differentiating between discrete crown collisions and the crown overlap was important for accurate statistics of tree interactions. Since a deep collision between crowns can endure for over a second (during high winds), more than 10 consecutive crown overlaps between tree pairs could be reported (timestep 0.1s). Determining frequency of crown collisions required filtering associated crown overlaps and assigning them to a single collision. The filtering process associated consecutive overlaps while the area of overlap increased to a maximum and then decreased. If area of overlap increased again, regardless if crowns disengaged or not, subsequent overlaps were associated with a new collision. The final collision area is determined by selecting the maximum overlap area from associated overlaps.

The crown interactions at 12 and 14 m above the ground were determined for each tree. This amounts to taking a slice through the stand at 12 m and 14 m from the ground and observing the 2-dimensional interactions. Since crown collisions occur in three dimensions, a second slice at 14 m was used to provide comparative reference of collisions at another elevation in each tree crown. The heights of 12 m and 14 m were chosen because crowns of even-aged lodgepole pines are relatively short (>30% of tree height) and these heights best capture the crown center of gravity. The center of gravity is typically the widest part of the crown and the most probable area of interaction for colliding tree crowns.

Recall that polygons representing the crown dimensions were measured at their height of maximum extent. Since lateral crown extent declines as one deviates from the maximum extent height (with an area of 0 m^2 at tree top), adjustments were made to polygon areas to reflect actual crown extent at 12 and 14 m. At the heights of 12 and 14m, most polygons were reduced from their maximum extent size. A truncated ellipse was assumed to represent the crown shape and dictated the amount of polygon size reduction (Song 1998). Thus, at the queried height the crown extent can be small if the point is near the top or bottom of the crown (e.g. tree #6, Table 2-2).

My reconstruction approach does not take into account the height decline of queried points (12 & 14 m) that would occur in an actual stem with increasing curvature. The effects of a large deflection would also include the reduction of the crown profile during high winds (Hedden *et al.* 1995). The polygon representations of the crowns were not altered to reflect any crown shape changes that may occur during stem deflection.

Results

Understanding crown interactions begins with the basic statistics of collision frequency and intensity. Collision frequency is a rate determined by the number of crown collisions per minute. Intensity or depths of collisions are described using both crown overlap areas (reported in m^2) and percentages of crown area overlap. I assume that interactions for trees interior to the cluster of trees (#2, #4, and #7) were primarily with other sensored trees and therefore should provide the most comprehensive collision statistics (Table 2-3). Averaged for the 12 m level, maximum crown overlap was 0.72 m^2 with a mean of 0.15 m^2. Averaged for the 14 m level, maximum crown overlap was 0.61 m^2 with a mean of 0.10 m^2. The mean percent overlap for both height levels were 24%. The average collision duration for all trees was 0.25 seconds. Relative bole base positions and a sample range of displacements provide a perspective on their magnitudes (Figure 2-4).

The collision summary indicates tree #4 experienced 86 collisions per minute at the 12 m height level and the highest average collision rate at 106 per minute at 14 m (Table 2-3). Its mean overlap percent is lowest for both 12 and 14 m height levels (13% and 14% respectively), while its area of overlap is the highest (0.19 and 0.16 m^2

respectively). Examining the interactions of individual trees with tree #4 shows it collided with all trees at both height levels except with tree #1 at the 12 m level (Table 2-4). Tree #4 collided with trees #3, #5, and #10 for 94% of its collisions at the 12m level and 81% of its collisions at the 14m level (Table 2-4). Tree #4 had the deepest average interactions (% crown overlap > 15%) with tree #5 at the 12 m level, and with trees #2, #3, and #8 at the 14 m level (Table 2-5).

Summary of tree #7 collisions shows it experienced the highest average collision rate of 99 per minute at the 12 m level and 37 per minute at 14 m level (Table 2-3). Tree #7 Examining interactions of individual trees with tree #7 shows it collided with all trees at both height levels (Table 2-4). Tree #7 collided with trees #1, #2, and #9 for 97% of its collisions at the 12 m level and 92% of its collisions at the 14 m level. Tree #7 had its deepest interactions at 12 m (ave % crown overlap >30%) with trees #3 and #9, with its deepest interactions at 14 m (ave % crown overlap >60%) with trees #4 and #8 (Table 2-5).

Lastly, tree #2 collision summary shows its average collision frequency is the lowest of the interior trees having 25 and 36 collisions per minute at the 12 and 14 m height classes respectively. Its mean overlap percents are 35% (highest) and 19% for the 12 and 14 m height levels respectively (Table 2-3). Tree #2 mean area of overlap is 0.10 m^2 for the 12 m level and 0.11 m^2 (highest) for the 14 m level (Table 2-3). Examining tree #2's interaction with individual trees shows collision with nearly every tree and height level (except tree #5, 12 m). Tree #2 collided with trees #1 and #7 for 83% of its collisions at the 12 m level, and with trees #1, #4, #6, #7, #8 and #10 for 91% of collisions at the 14m level (Table 2-4). Tree #2 had its deepest average interactions (% crown overlap >45%) with trees #3 and #10 at the 12 m level, and with tree #8 at the 14 m level (Table 2-5).

Discussion

The technique described above allows simultaneous measurement of tree sway displacements, and for the first time permits measurement of stand level tree bending behaviour, and crown interaction. Collision frequencies and intensities for two canopy height levels offer insight into how bending displacements influence the crown interactions between trees at a moderate 5 m/s windspeed. While collision frequency, and maximum and mean overlap areas are larger for the 12 m level of analysis, this probably reflects the larger crown areas maintained at this level of the canopy. However, the mean percent overlap for the two height levels is identical, suggesting no difference in overall collision intensity. This may reflect the effect of acute or chronic collisions, reducing tree crowns through abrasions, to maintain a constant collision overlap for the entire crown. The resulting crown structure would distribute the collision force throughout the crown and lessen the possibility of branch breakage.

To better understand the role of stand structure upon collision intensities would require comparing data reconstructed from stands possessing different structural attributes such as tree heights, tree tapers or distance between trees. Under the same wind loading a stand with greater crown collision intensities (average % overlap) would be expected to suffer more foliage loss and have a greater risk of stem failure. Comparing stand structures and their collision intensities for a given wind speed can give the relative wind damage resistance for a particular stand structure.

My solution to the tree bending shape and displacement problem is specific to an instrument that measures bole rotation directly. This approach allows simplification of the bending equation that eliminates the need to input the tree diameter, modulus of elasticity, and applied load force. The simplification saves researchers time and expense of recording extraneous tree attributes and reduces the likelihood of introduced error. Another advantage of measuring bole rotation directly, which I have not yet fully explored, is the ability to solve for the applied force if the tree diameter and modulus of elasticity are known. This may have application in research on stand drag coefficients.

Using alternative equations for the bending curve prediction is possible. A quadratic paraboloid bole taper is thought to be representative for dense even-aged stands and its inclusion may predict a more realistic bending shape (Petty and Worrell 1981). The inclusion of an alternate bole taper would make the bending curve derivation more complicated, but the solution would retain the same number of input parameters. The current bole taper assumption may underestimate the bole displacement, in which case the crown contact statistics (depths and frequencies) would result in minimum estimates of the crown interactions.

Another solution of the bending curve that handles extreme deflections and any pattern of stem taper is the transport matrix method (Morgan and Cannell 1987). This method sections the bole into small segments then calculates the bend of each section and the entire bole. Deliberately, the AML used to process the displacement time steps can incorporate any method of bending and displacement calculation. However, even with a modified bending equation the relative differences in collision statistics between trees should be similar.

My results indicate frequent and intense crown collisions, which support the hypothesis that tree collisions provide a mechanism for lateral shoot abrasion, and resultant crown asymmetry in even-aged lodgepole pine. However, more work needs to be done regarding collision characteristics to form firm conclusions. For instance, while all of the trees central to the cluster interact at least once with all nine other trees during the 15-minute data interval, they interact most frequently with trees nearest them. Excepting tree #2 at the 14m level, interior trees interact with 2 or 3 other trees, accounting for most of their collision totals. It is possible that neighbours that dominate the interaction events could cause the most crown damage or growth inhibition. Our reconstruction technique in Arc/Info could also investigate which polygon sides experience the most collisions and compare these frequencies to the presence of crown asymmetry. Polygon sides experiencing the most collision events should represent the shortest lateral extent sides of a crown.

While this chapter has pursued a crown interaction hypothesis, the tiltmeter technique has broad application in wind and tree research including investigation into sway damping effects associated with tree collision (White *et al.* 1976; Mayer 1987; Kerzenmacher and Gardiner 1998). Honami effects are large-amplitude, synchronous bending of trees, and are identified as a crucial problem in forest meteorology because of their important role both in turbulent transport and in causing wind damage (Finnigan 1979; Gardiner 1994). Honami in trees could be studied using my technique, though more trees might be included to observe this larger scale phenomenon.

Using tiltmeters should also allow estimation of collision net force by observing sway velocity before and after collision. By knowing collision forces for all tree pairs, the amount of (wind-induced, tree sway) kinetic energy dissipated from crown collisions could be estimated at the stand level. Sensors may also be place upon the root plate of the tree and simultaneously record the anchorage flexure while the tree is subjected to wind forces. This could improve displacement calculations as movement of the root plate can influence the crown displacement.

Crown abrasion has long been suspected of causing foliage loss. Techniques presented in this paper will aid understanding the mechanisms controlling crown lateral extension, asymmetry and stand canopy maintenance. Understanding the effect of collisions upon the sway damping of trees may mitigate the loss of forests and forest productivity due to windstorms by allowing silvicultural prescription to minimize the loss of leaf area due to crown abrasion.

References

Aradóttir AL, Robertson A, Moore E (1997) Circular statistical analysis of birch colonization and the directional growth response of birch and black cottenwood in south Iceland. Agric For Meteorol 84:179-186

Cescatti A (1997) Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithims. Ecol Modell 101:263-274

Chen HYH, Klinka K, Kayahara GJ (1996) Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. Can J For Res 26:1149-1157

Dean TJ, Long JN (1986) Validity of constant-stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. Ann Bot 58:833-840

d'Oreye N (1998) Qualification test of a dual-axis bubble-type resistive tiltmeter: earth tides recorded and analyzed in the underground laboratory of Walferdange. Bulletin d'Information des Marees Terrestres. 29:9953-9962.

Finnigan JJ (1979) Turbulance in waving wheat. I Mean statistics and honami. Boundary-Layer Meteorol 16:181-211

Flesch TK, Wilson JD (1999) Wind and tree sway in forest cutblocks, II: Relating measured tree strain to wind statistics. Agric For Meteorol 93:243-258

Foster DR, Boose ER (1992) Patterns of forest damage resulting from catastrophic wind in cental New England, USA. J Ecol 80:79-98

Fraser AI, Gardiner JBH (1967) Rooting and stability in Sitka spruce. Forestry Commision Bulletin 40, HMSO, London

Gardiner, BA (1994) Wind and wind forces in a plantation spruce forest. Bound Layer Met 67:161-186

Gardiner BA (1995) The interactions of wind and tree movement in forest canopies. In: Coutts MP, Grace J (eds) Wind and trees. Cambridge University Press, Cambridge, pp 41-59

Gardiner BA (1989) Mechanical characteristics of Sitka Spruce. Forestry Commission Bulletin 40. HMSO, London

Grier CC (1988) Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifer forests. Can J For Res 18:1097-1102

Hassinen A, Lemettinen M, Peltola H, Kellomaki S, Gardiner B (1998) A prism-based system for monitering the swaying of trees under wind loading. Agric For Meteorol 90:187-194

Hedden RL, Fredricksen TS, Williams SA (1995) Modelling the effect of crown shedding and streamlining on the survival of loblolly pine exposed to acute wind. Can J For Res 25:704-712

Holbrook NM, Putz FE (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). Amer J Bot 76:1740-1749

Jacobs MR (1954) The effect of wind sway on the form and development of *Pinus radiata* D. Don. Austral J Bot 2:35-51

Kerzenmacher T, Gardiner BA (1998) A mathematical model to describe the dynamic response of a spruce tree to the wind. Trees 12:385-394

Koike F (1989) Foliage-crown development and interaction in *Quercus gilva* and *Q. Acuta*. J Ecol 77:92-111

Larson PR (1965) Stem form of young *Larix* as influenced by wind and pruning. Forest Science 11(4):413-423

Leiser AT, Kemper JD (1973) Analysis of stress distribution in the sapling tree trunk. J Amer Soc Hort Sci 98:164-170

Long JN, Smith FW (1992) Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. For Ecol Manage 53:53-62

Mäkelä A (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. Forest Science 43(1):7-24

Mayer H (1987) Wind-induced tree sways. Trees 1:195-206

Michalsky AJ (1996) An investigation of mechanical abrasion in saplings of sugar maple (*Acer saccharum* . Marsh.), Mont St. Hilaire, Quebec. Masters thesis, York University, Canada

Morgan J, Cannell MGR (1987) Structural analysis of tree trunks and branches: tapered cantilever beams subject to large deflections under complex loading. Tree Physiol 3:365-374

Oliver CD, Larson BC (1990) Forest stand dynamics. McGraw-Hill, New York, pp 467

Oliver HR, Mayhead GJ (1974) Wind measurements in a pine forest during a destructive gale. Forestry 47(2):185-194

O'Reilley M, Read SAL, Foster PF (1998) Monitoring dam performance using tiltmeters. ANCOLD/NZOLD conference on dams 'The Challenge – Managing Dams in a Competitive Business Environment', Sydney, 31 August – 1 September 1998

Peltola H, Kellomäki S, Hassinen A, Lemettinen M, Aho J (1993) Swaying of trees as caused by wind: analysis of field measurements. Silva Fennica 27(2):113-126

Peltola H, Kellomäki S, Väisänen H, Ikonen VP (1999) A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. Can J For Res 29:647-661

Petty JA, Worrell R (1981) Stability of coniferous tree stems in relation to damage by snow. Forestry 54:115-128

Robertson A (1987) The centroid of tree crowns as an indicator of abiotic processes in a balsam fir wave forest. Can J For Res 17:746-755

Sorrenson-Cothern KA, Ford ED, Sprugel DG (1993) A model of competition incorperating plasticity through modular foliage and crown development. Ecol Monogr 63(3):277-304

Song B, Chen J, Desanker PV, Reed DD, Bradshaw GA, Franklin JF (1997) Modeling canopy structure and heterogeneity across scales: from crowns to canopy. For Ecol Manage 96:217-229

Telewski FW 1995 Wind-induced physiological and developmental responses in trees. In: Coutts MP, Grace J (eds) Wind and trees. Cambridge University Press, Cambridge, pp 237-263

Umeki K (1995) Modeling the relationship between the asymmetry in crown display and local environment. Ecol Modell 82:11-20

Vales DJ, Bunnel FL (1988) Comparison of methods for estimating forest overstory cover. I. Observer effects. Can J For Res 18(5):606-609

White RG, White MF, Mayhead GJ (1976) Measurement of the motion of trees in two dimensions. Tech Report 86. Instutute of Sound and Vibration Research, University of Southhampton, UK

Table 2-1. Structural attributes for all study trees.

Tree #	Top height (m)	Crown center of gravity height (m)	Tiltmeter height (m)	Base diameter (cm)	Diameter at 1.3m- dbh (cm)	Slenderness coefficient (Ht/dbh)
1	14.76	13.11	10.29	12.1	10.9	1.35
2	14.70	12.80	9.45	11.5	10.4	1.41
3	15.90	13.26	10.41	17.0	15.3	1.04
4	17.30	13.95	9.93	16.5	14.6	1.18
5	15.03	12.90	9.88	12.2	10.9	1.38
6	13.26	10.97	8.03	10.6	9.4	1.41
7	14.80	12.50	8.74	12.4	10.2	1.45
8	17.90	14.48	9.60	17.8	15.3	1.17
9	15.40	13.30	9.75	10.3	9.6	1.60
10	15.35	12.50	9.91	12.5	11.3	1.36
Mean	15.44	12.98	9.60	13.3	11.8	1.31

Table 2-2. Polygon areas (m^2) representing each tree crown at the 12 and 14 m.

	Height	
Tree	12m	14m
1	0.73	0.57
2	0.29	0.56
3	0.53	0.95
4	1.46	1.15
5	1.14	0.28
6	0.18	0.0
7	0.73	0.11
8	1.29	2.64
9	0.82	0.12
10	0.68	0.21

Table 2-3. Crown collision summary statistics for trees interior to the cluster with all other trees at both 12 and 14m height levels. Data are from a 15.0 minute time span beginning December 17th, 1998 at 10:13:00 a.m. Stand wind conditions were an average wind speed of 5.2 m/s, maximum wind speed of 14.0 m/s and average wind direction of 278°. Average temperature –2.4° C.

Tree #	Height (m)	Maximum overlap (m^2)	Maximum overlap % of subject tree crown	Mean overlap (m^2)	Mean overlap % of subject tree crown	Number of collisions per minute
2	12	0.29	100	0.10	35	25
	14	0.57	100	0.11	19	36
4	12	1.12	77	0.19	13	86
	14	1.15	100	0.16	14	106
7	12	0.74	100	0.17	23	99
	14	0.12	100	0.05	41	37
	12m mean	0.72	92	0.15	24	70
	14m mean	0.61	100	0.10	24	60

Table 2-4. Number of crown collisions per minute between interior trees and neighbours at 12 and 14m. Data period, wind conditions and temperature as in Table 2-3.

Subject tree	Height (m)	Colliding with tree No.									
		1	2	3	4	5	6	7	8	9	10
2	12	6.5		1.2	0.9		0.9	14.3	< 0.1	1.3	< 0.1
	14	4.5		< 0.1	10.2	0.2	2.8	6.9	5.7	2.7	2.8
4	12		0.9	10.7		31.3	0.1	1.3	2.3	0.3	38.7
	14	0.1	10.2	23.7		41.5	0.2	0.7	8.3	0.3	20.5
7	12	14.3	14.3	0.5	1.3	< 0.1	0.1		0.5	67.6	0.3
	14	9.0	6.9	1.1	0.7	0.1	0.2		0.8	18.0	0.3

Table 2-5. Mean crown collision overlap (%) between all trees at 12 and 14m. Data period, wind conditions and temperature as in Table 2-3.

		Colliding with tree No.									
Subject tree	Height (m)	1	2	3	4	5	6	7	8	9	10
2	12	34		46	43		21	32	2	37	63
	14	33		1	35	8	1	11	50	13	16
4	12		9	12		21	12	14	13	8	13
	14	5	17	29		14	1	7	37	5	10
7	12	29	13	33	28	20	8		28	31	18
	14	54	53	45	74	22	1		62	32	22

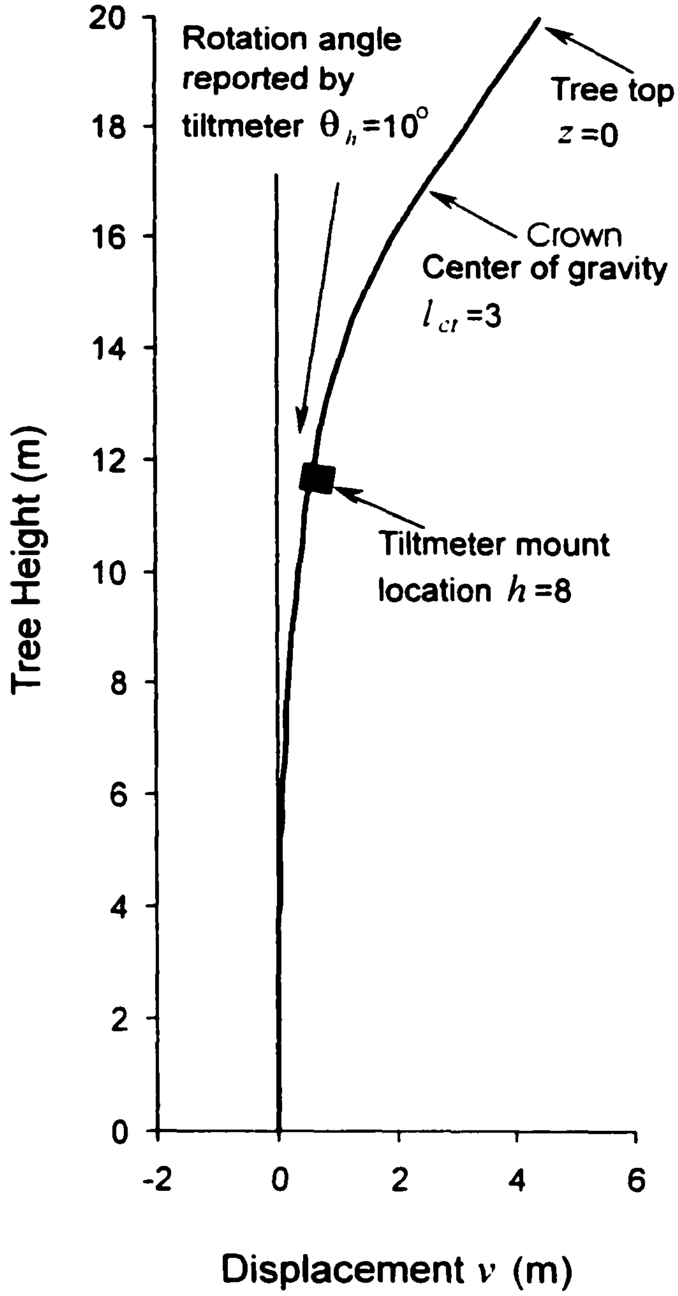

Figure 2-1. Tree bending shape predicted by equations (1) and (2), with a 10^0 tiltmeter rotation angle, for a hypothetical 20 m (L = 20) tree.

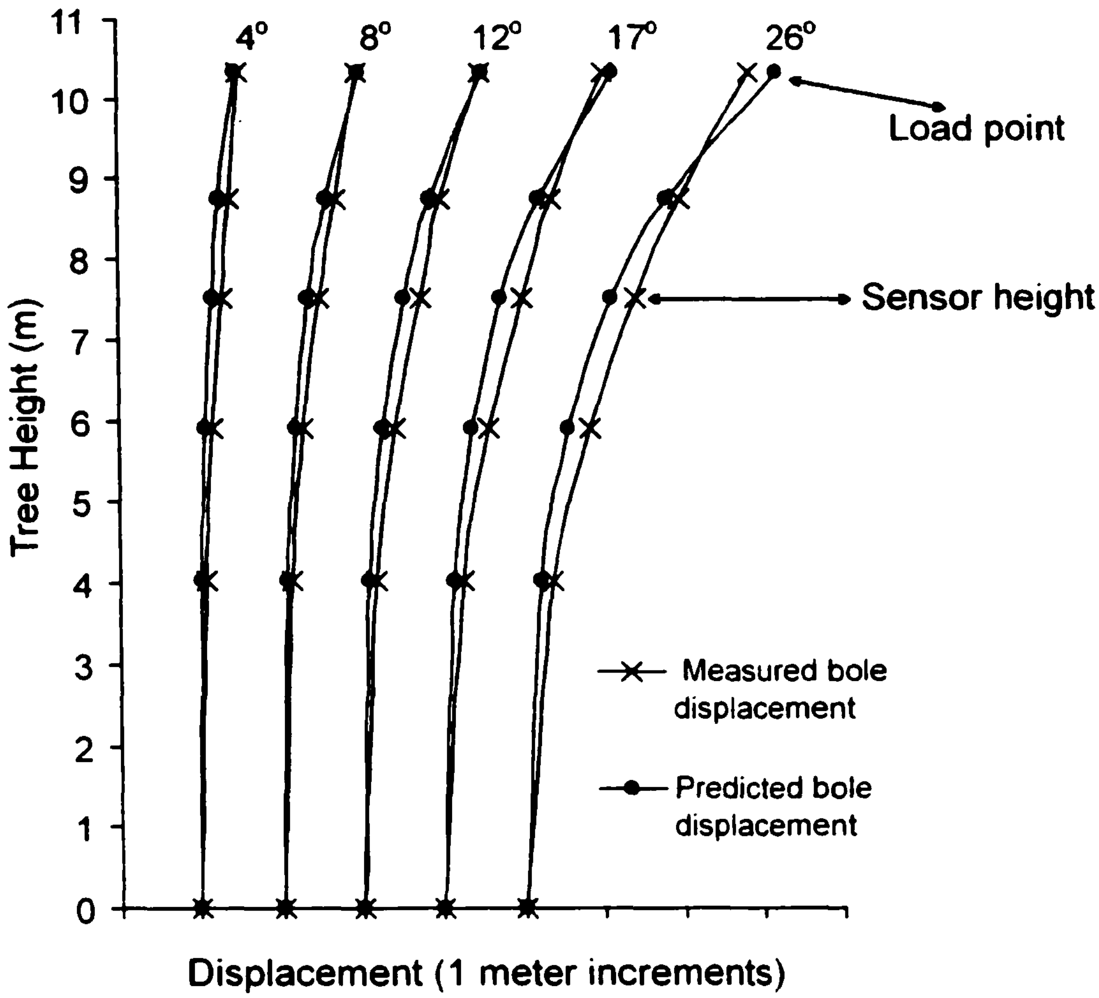

Figure 2-2. Measured and predicted displacements for a sensored tree. Recorded rotation angle θ_h is given above each comparison. To view the bending curves without overlapping them, the bole is displaced one meter for each level of loading. Tree height 13.2 m, dbh 13.5 cm, crown center of gravity 10.35 m, sensor mount height 7.4 m.

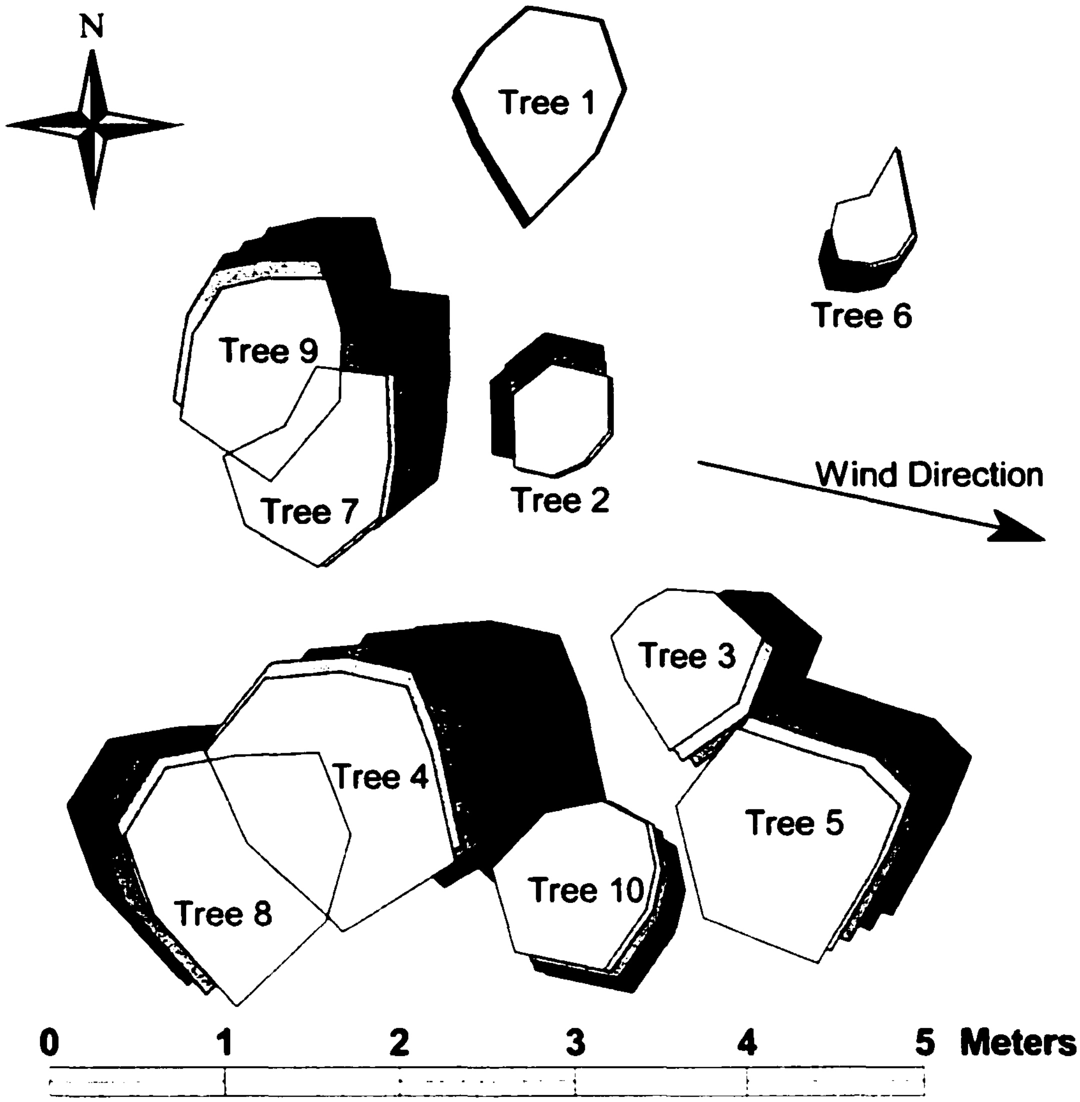

Figure 2-3. Actual polygon shapes used to calculate the crown interaction at the 12m level were rendered from Arc-Info. Five consecutive time intervals (1/10 of a second apart) illustrate crown movement directions, interactions and relative speeds. The first time step polygons are black, becoming lighter in color until the final locations in white. Five minute average windspeed is 4.8 m/s.

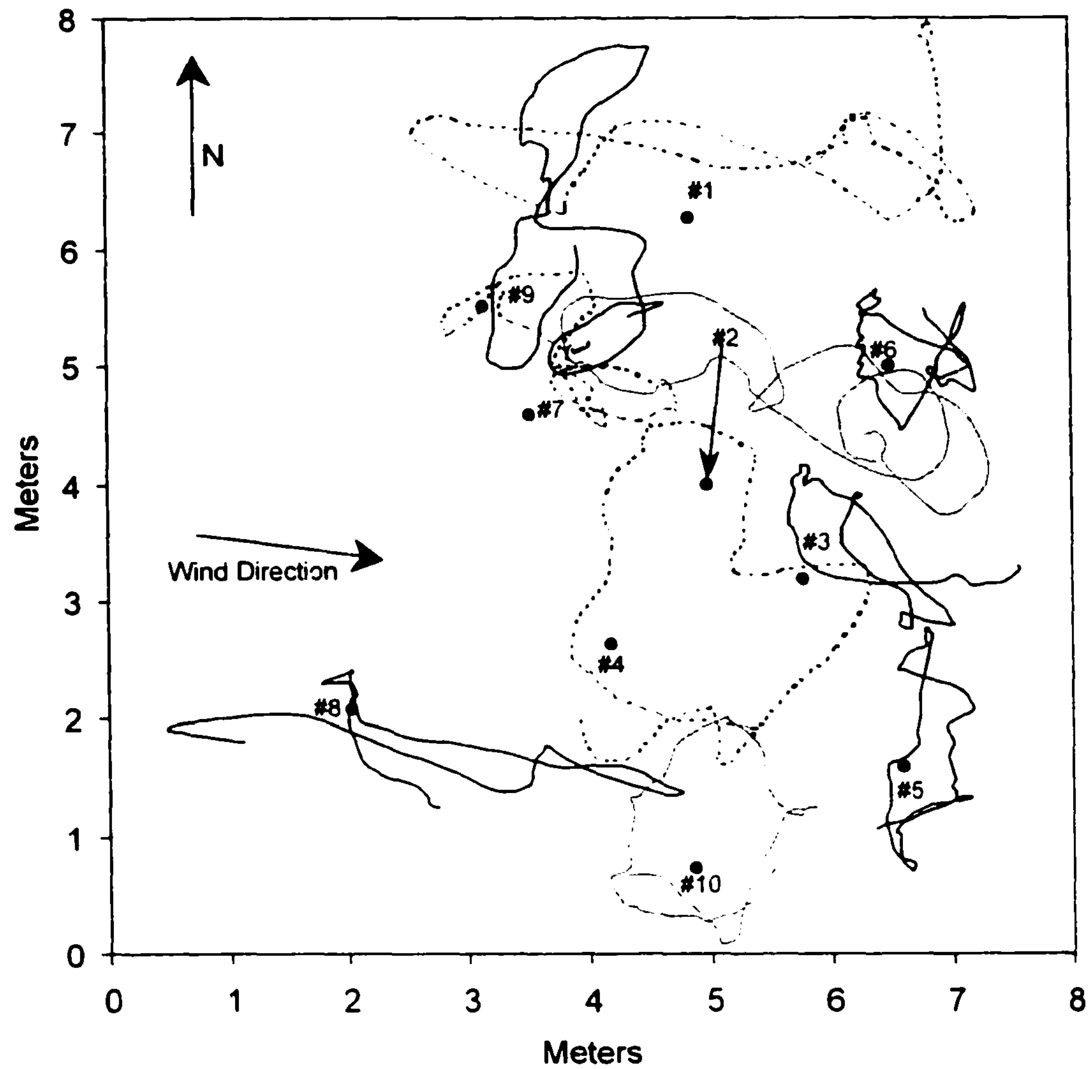

Figure 2-4. Five second bole displacement trace calculated at each tree's crown center of gravity. Numbered points indicate respective bole base position of the tree. Air temperature was 11^{0}C with wind gust speed measured at 11.9 m/s from a 278^0 azimuth. Trace record begins at 10:16:30.0 am on April 25 1999.

Chapter 3. The crown collisions of lodgepole pine

Introduction

Leaf area is one of the major factors controlling forest productivity and stand dynamics (Waring and Schlesinger 1985; Oliver and Larson 1996). Forest stand leaf area is regulated by site water balance (Grier and Running 1977), nutrient status (Binkley *et al.* 1995), stand age (Long and Smith 1992, Kollenberg and O'Hara 1999) and crown dynamics. Canopy gaps play an important role in crown dynamics (Runkle 1982) and affect the leaf area of the stand (Nilson 1999). A poorly explored area of crown dynamics is crown shyness, i.e., the empty space between crowns that is not attributable to tree mortality gaps (Putz *et al.* 1984). It is commonly assumed that low light levels can inhibit lateral shoot growth, thus creating crown shyness (Koike 1989; Sorrensen-Cothern *et al.* 1993; Umeki 1995; Chen *et al.* 1996; Cescatti 1997; Mäkelä 1997). An alternative hypothesis for crown shyness is the loss of leaf area caused by abrasion of tree crowns during wind-induced crown collisions (Putz *et al.* 1984).

Crown abrasion has been suggested to be an important mechanism for loss of leaf area in maturing stands (Jacobs 1954; Putz *et al.* 1984; Grier 1988; Robertson 1987; Smith and Long 2001). Except for a study by Long and Smith (1992), where crown interactions were assessed by examining the breakage of artificial pickets inserted into crowns of lodgepole pine (*Pinus contorta* var. *latifolia*), the effect of crown interactions has been poorly quantified. Crown collisions during wind have been suggested to damage or break off lateral buds and twigs (Jacobs 1954; Nobel 1981; Michalsky 1996; Aradóttir 1997). Violent crown collisions during infrequent high wind events can cause breakage of large branches, resulting in substantial loss of leaf area (Grier 1988; Foster and Boose 1992). In Alberta, I can commonly observe broken conifer twigs and small branches on the forest floor after moderate wind events.

In addition to wind speed, tree biomechanical properties, stand density, crown surface area and crown exposure affect the wind sway of individual trees (Petty and Swain 1985; Peltola and Kellomäki 1993; Kerzenmacher and Gardiner 1998). Tree stiffness is determined by bole modulus of elasticity and change in cross sectional area over the bole length. The bole cross-sectional area at a given point is the second moment of area (I) and if we assume the bole is circular, I can be calculated with:

$$[3\text{-}1] \qquad I = \frac{\pi R^4}{4}$$

where R is the circle radius.

Bole slenderness is described by the slenderness coefficient (tree height/diameter - SC) and is the main determinant of tree stiffness (Petty and Swain 1985; Peltola and Kellomäki 1993). Stand density (trees/hectare) affects crown size (Long and Smith 1984; Muhairwe 1994), crown wind exposure (Peltola 1996) and mediates crown collisions directly by damping tree sway (White *et al.* 1976; Mayer 1987; Gardiner 1989; Gardiner *et al.* 1997). Crown surface areas and exposures determine the amount of intercepted wind and thus affect the magnitude of wind loads.

To gain insight into the potential role of crown abrasion as a crown shaping process I use the techniques developed by Rudnicki *et al.* (2001) to record the simultaneous tree bole sways and reconstruct their crown collisions. I explored the crown collision dynamics and tree sway patterns of *Pinus contorta* var. *latifolia* Dougl. ex Loud. as it typically regenerates in pure even-aged stands that commonly exhibit crown shyness (Jack and Long 1991). Objectives of the study were to examine how characteristics such as stand density, crown width, tree SC and wind speed affected frequency and intensity of crown collisions in *Pinus contorta* var. *latifolia*. To examine the role of tree stiffness and stand density in the crown collisions of lodgepole pine, I studied stands of similar height that experienced similar wind speeds. I hypothesise that trees with greater SC will have a higher frequency and intensity of collisions than trees having low SC. To study the effects of stand density on crown collisions, I compared the crown interactions and sway patterns of a stand with high SC before and after thinning. I hypothesized that increased crown wind loads due to partial removal of the overstory would result in higher collision frequencies and intensities and disrupt their sway patterns when compared to the unthinned condition. I also compared crown interaction and sway patterns in a stand with a low SC at two different wind speeds. I hypothesized that increased crown wind loads would also increase collision frequencies and intensities with a similar shape in the sway patterns.

Methods

Site and species

There were two locations used in the study, which were both even-aged, naturally regenerated and unmanaged stands of pure *P. contorta*, located in the lower foothills of west central Alberta, Canada. The Two Creeks site (TC) (54° 11′ N, 116° 10′ W) regenerated after fire in 1954 and had a mean density of 2150 trees/ha, which includes an understory of *Picea mariana* (black spruce) saplings. The *P.contorta* mean diameter at breast height (dbh) was 12 cm with a mean height of 15 m and a mean SC (height /diameter) of 1.23 (Table 3-1). The *Picea mariana* understory averaged 4 m tall and 7 cm dbh. Dead standing and dying *P. contorta* were common (~200 per Ha) in the lower part of the size distribution and provided evidence of self-thinning mortality. The TC site had a 5° westerly slope with ground cover dominated by feathermosses, and *Ledum groenlandicum* (Labrador tea).

The Windfall rd. site (WF) burned in 1963 (54° 22′ N, 116° 28′ W) and had a mean density of 1500 *P.contorta* trees/ha. Stems had a lower SC of 0.79, with a mean dbh of 18 cm and height of 14 m (Table 1). The WF site had an intermittent understory of *Alnus* spp. ~3m in height with an average 10° westerly slope. The WF site showed no evidence of *Pinus contorta* var. *latifolia* suppression mortality.

Techniques and measurements

I chose 10 adjacent trees at each site that were representative of mean stand structural attributes and had a minimum distance of 1 m between stems (Table 3-1). Lateral crown extent of each tree was measured on eight 45° vectors, from the ground, using a levelled right-angle mirror or "moosehorn" (Rudnicki *et al.* 2001; Vales and Brunnel 1988). Crown extent distances were used to create eight-sided polygons representing crown shape and area. To measure bole rotation on each tree, biaxial clinometers (Applied Geomechanics Inc., California, USA) were installed at the base of the live crown with outputs recorded ten times per second using a CR23X datalogger (Campbell Scientific, Utah, USA) (Rudnicki *et al.* 2001). A meteorological tower with anemometers mounted at mid-canopy and canopy top monitored wind speed in each stand. A three-minute running average of canopy top wind speed >5 m/s was used to trigger the high frequency data collection from clinometers.

After ten months of monitoring wind events, the TC site was thinned to remove the understory *Picea mariana* and smallest diameter *P. contorta* to a density of 1300 stems/hectare, which created the third stand structural type (TCT). The thinned area was about one hectare and since prevailing winds were westerly, the sensored tree cluster was located in the eastern third of the thinned area. After thinning, the remaining trees had a mean dbh of 14 cm and a mean height of 16 m. I replaced three of the original sensored trees removed in the thinning with three adjacent trees and monitored the site for an additional nine months (Table 3-1). The meteorological tower and sway monitoring apparatus were then relocated to the WF site, approximately 27 km southwest, for eight more months.

I used approximately 60 minutes of sway data from each of the three stand structure types. The data set for each stand was combined from 4-5 periods of similar wind speed (5 m/s ± 0.5), wind direction (260° - 310°) and air temperature (>10° C) (Table 3-2). In addition, at the WF site I recorded 20 minutes of sway data with a mean wind speed of 7.9 m/s (Table 3-2).

I estimated bole displacement from resting position by applying the stem flexure formula derived in Rudnicki *et al.* (2001) to the bole rotation data for all 10 trees at each time step (1/10 s). GIS software (Arc/Info) was used to reconstruct collisions by locating polygons on their respective bole displacements for each time step. Polygon overlap sizes and frequencies were quantified for all pairs of interacting tree crowns (Rudnicki *et al.* 2001). I reconstructed crown interactions for the 10 adjacent trees at the mid-crown position of 13 m for the TC site before and after thinning, and at the mid-crown position of 10 m for the WF site. The mid-crown position represents the widest lateral extent of the crowns and the crown centre of gravity (Dean and Long 1986). My approach of reconstruction does not take into account the height decline of crown height that would occur with during bending. Furthermore, polygon representations of the crowns were not altered to reflect any crown shape changes that may occur during stem deflection or collision (Hedden *et al.* 1995).

Data analysis

Mid-crown displacement (m) from bole resting position was calculated at each 0.1 s time step, and tree sway speeds (m/s) were calculated between each successive time step for all trees. Means for tree sway speed and distance were taken from the entire dataset while maxima were calculated for each minute of data with the mean calculated from all minutes. Stand sway statistics were based on the means from all ten trees.

Determining frequency of crown collisions required filtering associated crown overlaps and assigning them to a single collision. I developed two approaches of defining collisions hereafter referred to as 're-advancement' and 'disengagement'. The re-advancement approach associated consecutive overlaps to a single collision while the area of overlap increased to a maximum and then decreased. If area of overlap increased again, regardless of whether crowns disengaged or not, subsequent overlaps were associated with a new collision. In the disengagement approach, a discreet collision was defined only when polygons no longer overlapped (complete crown separation). In both approaches, percent crown overlap was determined by selecting the maximum overlap area from the associated sequence of overlaps.

All crown collision statistics were based on data from the four central trees in each cluster as these trees interacted primarily with other sensored trees. Mean crown overlap is represents the mean of all collisions between the four central trees. Maximum crown overlap represents the averaged maximum overlaps between the four central trees. Mean collision duration represents the average number of time steps or polygon overlaps per collision. Summing collisions for the four central trees then dividing by number of minutes in the dataset and trees determined the collision rate.

Using the same polygons representing tree crowns, I determined percent crown cover for each stand structure. Forming a triangle using three bole base positions I calculated the cumulative area covered by portions of polygons within the triangle and divided this by total triangle area. Percent crown cover was calculated for at least six triangles in each stand to estimate the mean crown cover.

Contour maps of sway patterns for the 10 trees in each stand type were created using the bole displacement position calculated at the mid-crown bole height at every time step. Using the GIS software (ArcView), I mapped the relative density of bole positions for approximately 36,000 time steps for each tree. Occurrences of bole mid-crown position within a search radius of 5 cm were averaged per cm^2 and then assigned to a 1 cm^2 cell to create a spatially smoothed, continuous surface. Density contour maps were calculated for each tree separately. The high wind data at WF was scaled to express relative density of bole positions for an equivalent 60-minute period.

Results

Hourly means of wind speed indicate that wind events > 5 m/s are common and experienced at the study sites ~30% of the time. The hourly means of wind directions indicate prevailing winds are from 290°, and approximate wind direction during data collection. The crown cover for the TC stand was 40% and was reduced to 32% cover following thinning (TCT). The WF stand had 78% crown cover.

Tree sway statistics

Crowns at the Two Creeks site (TC) had a mean sway speed of 1.05 m/s, approximately three times the mean speed of 0.29 m/s found at Windfall Rd (WF) (Table 3-2). Maximum crown speed at TC was 6.18 m/s, nearly four times faster than at WF (1.58 m/s). Similar canopy-top wind speeds after the thinning at Two Creeks (TCT) resulted in greater stand wind penetration into the canopy and nearly tripled the mean mid-crown wind speed as compared to TC. As expected, mean sway speed also increased from 1.01 m/s at TC to 1.31 m/s at TCT and the maximum sway speeds increased from 6.18 at TC to 7.32 m/s at TCT. In the more tapered WF stand, an increase in mean wind speed at canopy-top from 5.1 to 7.9 m/s increased mean sway speed from 0.29 to 0.67 m/s and maximum sway speed from 1.58 to 3.58 m/s. However, during both wind speeds at WF, the mean and maximum crown sway speeds were still well below that of the slender trees at TC (Table 3-2).

Sway distance comparisons between stands and treatment closely paralleled differences in sway speed. Mean crown sway distance was five times greater at TC (0.60 m) than in the more tapered WF stand (0.12 m) with a similar difference for the maximum sway distances (2.6 and 0.47 m respectively) (Table 3-2). Reflecting both greater wind penetration and more space between trees after thinning, the mean sway distance of TC increased from 0.60 to 0.84 m after thinning (TCT). Maximum sway distance increased from 2.60 for TC to 3.04 for TCT. The increase in wind speed from 5.1 to 7.9 m/s at WF resulted in a doubling of mean sway distance from 0.12 to 0.25 m respectively and maximum sway distance from 0.47 to 1.02 m respectively (Table 3-2).

Crown collisions

Differences in sway behaviour among stands and treatment were strongly associated with differences in percent overlap of crown collision, while collision duration and rate also varied with the method of collision definition (Table 3-2, Table 3-3 a,b). Using the re-advancement definition (Table 3-3a) mean and maximum percent crown overlaps, or collision depths, were greater at TC (23.2% and 65.9% respectively) than at WF (12.0% and 50.2% respectively) suggesting that crowns collided with more force at TC. Mean and maximum percent crown overlaps increased between TC and TCT reflecting the increased wind loads and sway speeds after treatment. The increased wind speeds at WF increased both mean and maximum percent overlap using the 're-advancement' collision definition while mean collision depth decreased from 20.1% to 16.0% using the 'disengagement' method (Table 3-3 a,b). Except for percent mean overlap at WF, the relationship between percent crown overlaps was constant regardless of collision definition.

The disengagement method returned increased collision durations and lower collision rates compared to the re-advancement method (Table 3-3 a,b). However, regardless of collision definition, mean collision duration was comparatively shorter in TC than WF, while collision frequency was lower for WF using the disengagement method (Table 3-3 a,b). The thinning treatment decreased mean collision duration and rate of collision when compared to unthinned conditions for both definitions of collision (Table 3-3 a,b). Using the disengagement method, mean collision duration at WF dramatically increased (from 0.45 s to 14.37 s) which indicates an enduring crown engagement. High winds of 7.9 m/s at WF resulted in comparatively brief and more frequent collisions (regardless of collision definition) indicating frequent crown disengagement.

Crown sway patterns

Density contour maps of crown sway clearly illustrate the differences in sway patterns between the stand structures and treatment. The sway patterns for TC are mostly circular or elliptical in shape and posses singular centroids near their respective bole locations (Figure 3-1). After thinning, all remaining trees in TCT show wider sway patterns with six trees displaying dual centroids (Figure 3-2). Tree sway patterns at the WF site had concentrated singular centroids near the bole resting position (Figure 3-3). While sway patterns were larger during high winds at WF (Figure 3-4), it did not appreciably change their shapes with single centroids remaining near their respective bole locations. Sway patterns were clearly more concentrated at WF 7.9 m/s than the slender stand TC at 5 m/s (Figures 3-1,3-4).

Discussion

Tree slenderness coefficient

This study shows how stand structure and wind speed affect tree sway, and the rate and intensity of crown collisions. This empirical evidence supports the idea that crown collisions are an important mechanism in the development of crown shyness and leaf area in *P. contorta*. The intensity and frequency of wind induced crown collisions is governed by stiffness of the stem and the crown loading from the wind. The higher slenderness coefficient - SC for TC (compared to WF) results in a lesser moment of area and a more flexible bole (Niklas 1992). And even though crowns at TC were smaller and less exposed (which presumably results in lower wind loads at the same wind speeds), they experienced 2 to 5 times greater mean sway speeds, sway distances, depth of crown collisions, and had higher frequency of 'disengagement' crown collisions than the stouter trees at WF. Slender trees rely on mutual support for stability and consequently suffer frequent and intense collisions. Hence, bole slenderness regulates bending and collision behaviour. The collision dynamics at TC indicates a greater potential for crown abrasion (loss of lateral branches, foliage, and buds) or inhibition of lateral shoot growth through mechanical perturbation (Rees and Grace 1980; Telewski and Jaffe 1986). Depending on the collision definition, WF had frequent shallow collisions or infrequent but enduring collisions when compared to TC; the collisions at WF could therefore be described as gentle rubbing of crowns compared to the high speed and presumably more abrasive impacts at TC. While both stands were well past crown closure, I suggest chronic and high-speed collisions at TC were the cause of the lower canopy cover (increased crown shyness) at TC compared to the WF site (Table 3-1). Long and Smith (1992) also observed greater canopy cover in stands with low height/diameter ratio.

Increased crown spacing

Thinning the slender Two Creeks stand (TCT) increased the distance between tree crowns, and the wind penetration into the canopy (mid-crown wind speed at TCT increased from 30% to 82% of the canopy-top wind speed). As the slender trees rely on collisions for support, altering these factors also affected crown collisions and tree sway patterns. With the more distant neighbours at TCT, I recorded increased tree mean sway speeds and distances with a concomitant increase in percent mean crown overlap. Thus, more intense collisions were experienced at TCT, which increases the probability of crown damage from collisions.

Sway patterns at TC were mostly circular or slightly elliptical, centred near the bole resting positions (Figure 3-1). Crown sway patterns were not aligned with or perpendicular to wind direction. I suggest that a circular sway pattern centred on the resting position would maximize the use of aerial growing space and minimize bending stresses on the bole. Furthermore, structural adaptation to maintain this pattern, such as growth of support roots or addition of compression wood on the bole in certain directions, are likely to develop gradually with tree and stand development (Telewski

1995). After thinning (TCT), most of the trees had altered (elongated) sway patterns containing two centroids (Figure 3-2). The thinning therefore created a new crown sway regime by increasing wind penetration, changing wind flow behaviour within the canopy and increasing the intensity of sway damping collisions. Hence, the back and forth motion of the trees after thinning probably reflects an obsolete bole structure to withstand the new wind flows and canopy structure.

Crown collisions and patterns of tree sway at the WF site were compared at moderate (5.1 m/s) and high wind (7.9 m/s) speeds. The high wind event resulted in a tripling of sway speeds and sway distances compared to moderate wind speeds (Table 3-2), yet these values remain far lower than at the more slender TC and TCT stands. As the tapered trees at WF are mostly self-supporting, increased wind speeds resulted in a small (2.8%) increase in mean crown overlap. The spatial patterns of tree sway were larger during high wind yet remained remarkably similar, indicating internal canopy wind behaviour remained consistent at both wind speeds (Figures 3-3 and 3-4). Mid-crown wind speed was ~21% of the canopy top wind speed during both wind speeds at WF also indicating a consistent relationship between crown structure and internal wind flows.

Stability strategies

Thigmomorphogenesis is the growth response of plants to mechanical stimuli that typically result in increased diameter and decreased length (Jaffe 1973; Jaffe and Biro 1979). In trees, the thigmomorphogenic response to sway stimuli decreases SC (Larson 1965; Neel and Harris 1971; Holbrook and Putz; Valinger 1992; Pruyn *et al.* 2000). While this response enables more widely spaced trees to develop a self-supporting structure in response to mean wind loads (Jacobs 1954; Niklas 1992; Osler *et al.* 1996) it can also serve to inhibit shoot extension (Michalsky 1996) and thereby restricting lateral crown growth. I suggest the TC stand developed a high SC and crown shyness because a higher establishment density allowed crown collisions to dampen tree sway, thus reducing the stimulus to allocate carbon to radial growth. Further, I suggest that in dense stands, intense collisions (which provides mutual support of trees) promote crown shyness. This damping of wind energy by collisions (Gardiner 1995) may prevent trees from blowing over in most wind storms, but comes at a severe cost to maintenance of leaf area because of branch breakage, twig and foliage loss (Grier 1988; Long and Smith 1992), and loss of buds and future growth (Putz *et al.* 1984). Consequently, collisions limit where trees can forage for light, thereby rendering some areas of canopy space unusable. This may play an important role in the decline in stand leaf area index as stands age (Long and Smith 1992; Sampson and Smith 1993; Smith and Long 2001). In contrast, the lower initial bole density at WF allowed more wind penetration into the canopy and increased bending stress that stimulated radial growth without the possibility of damaging crown collisions. Thus, trees at WF were self-supporting with sway energies absorbed by the bole rather than dispersed through collisions with neighbours. Therefore, stands starting at low-density develop stem biomechanical adaptations that inhibit the development of canopy shyness (Dean and Baldwin 1996).

Cold temperature

I believe the importance of crown collision on crown shyness may be particularly important in forests with cold winters. Because winters are long and there is increased brittleness of branches as air temperature declines below 0 °C (Lieffers *et al.* 2001), increased potential for crown abrasion is likely (Robertson 1993). Crown collisions may be an important factor in the observations that declines in stand productivity with age are most severe in northern forests (Gower *et al.* 1996) and that boreal forests have some of the most clumped canopies in the world (Kucharik *et al.* 1999).

To our knowledge, this is the first study of crown movement and interactions of a group of trees in the wind. Our results demonstrate the high frequency with which crown collisions occur in *P. contorta* stands and how stand structures may mediate it. The close association of stand sway behaviour and crown collisions with stand structural attributes (SC, stem density, and crown cover) support the idea that crown collisions are an important factor in the development of crown shyness and leaf area.

References

Aradóttir, A.L., Robertson, A. and Moore, E. (1997) Circular statistical analysis of birch colonization and the directional growth response of birch and black cottonwood in south Iceland. *Agriculture and Forest Meteorology*, **84**, 179-186.

Binkley, D., Smith, F.W. and Son, Y. (1995) Nutrient supply and declines in leaf area and production in lodgepole pine. *Canadian Journal of Forest Research*, **25**(4), 621-628.

Cescatti, A. (1997) Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithims. *Ecological Modelling*, **101**, 263-274.

Chen, H.Y.H., Klinka, K. and Kayahara, G.J. (1996) Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. *Canadian Journal of Forest Research*, **26**, 1149-1157.

Dean, T.J. and Baldwin Jr., V.C. (1996) The relationship between Reineke's stand-density index and physical stem mechanics. *Forest Ecology and Management*, **81**, 25-34.

Dean, T.J. and Long, J.N. (1986) Validity of constant-stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Annals of Botany*, **58**, 833-840.

Foster, D.R. and Boose, E.R. (1992) Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology*, **80**, 79-98.

Gardiner, B.A. (1989) Mechanical characteristics of Sitka spruce. *Forestry Commission Bulletin*, **40**, HMSO, London.

Gardiner, B.A. (1995) The interactions of wind and tree movement in forest canopies. *Wind and trees* (eds M.P. Coutts and J. Grace), pp 41-59. Cambridge University Press, Cambridge.

Gardiner, B.A., Stacey, G.R., Belcher, R.E. and Wood, C.J. (1997) Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. *Forestry*, **70**(3), 233-252.

Grier, C.C. (1988) Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifer forests. *Canadian Journal of Forest Research,* **18**, 1097-1102.

Grier, C.C. and Running, S.W. (1977) Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology-Durham*, **58**(4), 893-899.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends in ecology and Evolution*, 11:378-382.

Hedden, R.L., Fredricksen, T.S. and Williams, S.A. (1995) Modelling the effect of crown shedding and streamlining on the survival of loblolly pine exposed to acute wind. *Canadian Journal of Forest Research*, **25**, 704-712.

Holbrook, N.M. and Putz, F.E. (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *liquidambar styraciflua* (sweet gum). *American Journal of Botany*, **76**(12), 1740-1749.

Jacobs, M.R. (1954) The effect of wind sway on the form and development of *Pinus radiata* D. Don. *Australian Journal of Botany*, **2**, 35-51.

Jack, S.B. and Long, J.N. (1991) Analysis of stand density effects on canopy structure: a conceptual approach. *Trees- Structure and Function*, **5**, 44-49.

Jaffe, M. (1973) Thigmomorphogenesis: the response of plant growth and development to mechanical stimulation. *Planta*, 114, 143-157.

Jaffe, M. and Biro, R. (1979) Thigmomorphogenesis: the effect of mechanical perturbation on the growth of plants, with special reference to anatomical changes, the role of ethylene, and interaction with other environmental stresses. *Stress physiology in crop plants* (eds. H. Mossel, and R.C. Staples) pp. 26-59. John Wiley and Sons, New York

Kerzenmacher, T. and Gardiner, B.A. (1998) A mathematical model to describe the dynamic response of a spruce tree to the wind. *Trees- Structure and Function,* **12**, 385-394.

Koike, F. (1989) Foliage-crown development and interaction in *Quercus gilva* and *Q. Acuta*. *Journal of Ecology*, **77**, 92-111.

Kollenberg, C.L. and O'Hara, K.L. (1999) Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. *Canadian Journal of Forest Research*, **29**(6), 687-695.

Kucharik, C.J., Norman, J.M. and Gower, S.T. (1999) Characterization of radiation regimes in non-random forest canopies; theory, measurements, and a simplified modeling approach. *Tree Physiology* **19**: 695-706.

Larson, P.R. (1965) Stem form of young *Larix* as influenced by wind and pruning. *Forest Science*, **11**(4), 413-423.

Lieffers, S.M., Lieffers, V.J., Silins, U. and Bach L. (2001) Effects of cold temperatures on breakage of lodgepole pine and white spruce twigs. *Canadian Journal of Forest Research,* In Press.

Long, J.N. and Smith, F.W. (1984) Relation between size and density in developing stands: a description and possible mechanisms. *Forest Ecology and Management*, 7, 191-206.

Long, J.N. and Smith, F.W. (1992) Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *Forest Ecology and Management*, **53**, 53-62.

Mäkelä, A. (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science*, **43**(1), 7-24.

Mayer, H. (1987) Wind-induced tree sways. *Trees- Structure and Function,* **1**, 195-206.

Michalsky, A.J. (1996) *An investigation of mechanical abrasion in saplings of sugar maple* (Acer saccharum *Marsh.*). Masters thesis, York University, Canada

Muhairwe, C.K. (1994) Tree form and taper variation over time for interior lodgepole pine. *Canadian Journal of Forest Research*, **24**(9), 1904-1913.

Neel, P.L. and Harris, R.W. (1971) Motion-induced inhibition of elongation and induction of dormancy in *Liquidambar*. *Science*, **173**, 58-59.

Niklas, K.J. (1992) *Plant biomechanics: an engineering approach to plant form and function.* The University of Chicago Press, Chicago.

Nilson, T. (1999) Inversion of gap frequency data in forest stands. *Agricultural and Forest Meteorology*, **98/99**, 437-448.

Nobel, P.S. (1981) Wind as an ecological factor. *Responses to the Physical Environment* (eds O.L. Lange, P.S. Nobel, C.B. Osmund and H. Ziegler), pp 475-500. Springer-Verlag, Berlin.

Oliver, C.D. and Larson, B.C. (1990) *Forest stand dynamics*. McGraw-Hill, New York.

Osler, G.H.R., West, P.W. and Downes, G.M. (1996) Effects of bending stress on taper and growth of stems of young Eucalyptus regnans trees. *Trees- Structure and Function*. **10**(4), 239-246.

Peltola, H. (1996) Swaying of trees in response to wind and thinning in a stand of scots pine. *Agricultural and Forest Meteorology*, **90**, 187-194.

Peltola, H. and Kellomäki S. (1993) A mechanistic model for calculating windthrow and stem breakage of Scots pines at stand edge. *Silva Fennica*, **27**(2), 99-111.

Petty, J.A. and Swain, C. (1985) Factors influencing stem breakage of conifers in high winds. *Forestry*, **58**(1),75-84.

Pruyn, M.L., Ewers, B.J. and Telewski, F.W. (2000) Thigmomorphogenesis: changes in the morphology and mechanical properties of two *Populus* hybrids in response to mechanical perturbation. *Tree Physiology*, **20**, 535-540.

Putz, F.E., Parker, G.G. and Archibald, R.M. (1984) Mechanical abrasion and intercrown spacing. *The American Midland Naturalist*, **112**(1), 24-28.

Rees, D.J. and Grace, J. (1980) The effects of shaking on extension growth of *Pinus contorta* Douglas. *Forestry*, **53**, 155-166.

Robertson, A. (1987) The centroid of tree crowns as an indicator of abiotic processes in a balsam fir wave forest. *Canadian Journal of Forest Research*, **17**, 746-755.

Robertson, A. (1993) Effects of wind on boreal forests. *Forest development in Cold Climates* (ed J. Alden), pp 203-225. Plenum Press, New York, 1993.

Rudnicki, M., Silins, U. and Lieffers, V.J. (2001) Measure of simultaneous tree sways and estimation of crown interactions among a group of trees. *Trees- Structure and Function*, **15**, 83-90.

Runkle, J.R. (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**(5), 533-546.

Sampson, D.A., and Smith, F.W. 1993. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta var. latifolia*) forests. *Agriculture and Forest Meteorology*, **64**, 63-79.

Smith, F.W. and Long, J.N. (2001) Age-related decline in forest growth: an emergent property. *Forest Ecology and Management*, **144**, 175-181.

Sorrenson-Cothern, K.A., Ford, E.D. and Sprugel, D.G. (1993) A model of competition incorporating plasticity through modular foliage and crown development. *Ecological Monographs*, **63**(3), 277-304.

Telewski, F.W. (1995) Wind-induced physiological and developmental responses in trees. *Wind and Trees* (eds M.P. Coutts and J. Grace), pp 237-263. Cambridge University Press, Cambridge.

Telewski, F.W. and Jaffe, M.J. (1986) Thigmomorphogenesis: Field and laboratory studies of *Abies fraseri* in response to wind or mechanical perturbation. *Plant Physiology*, **66**, 211-218.

Umeki, K. (1995) Modeling the relationship between the asymmetry in crown display and local environment. *Ecological Modelling*, **82**, 11-20.

Valinger, E. (1992) Effect of wind sway on stem form and crown development on Scots pine (*Pinus sylvestris L.*). *Australian Forestry*, **55**, 15-21.

Vales, D.J. and Bunnel, F.L. (1988) Comparison of methods for estimating forest overstory cover. I. Oberver effects. *Canadian Journal of Forest Research*, **18**, 606-609.

Waring, R.H. and Schlesinger, W.H. (1985) *Forest Ecosystems Concepts and Management*. Academic Press, New York.

White, R.G., White, M.F. and Mayhead, G.J. (1976) Measurement of the motion of trees in two dimensions. Tech Report 86. Instutute of Sound and Vibration Research, University of Southhampton, UK.

Table 3-1. Mean dimensions of individual trees representing three stand structures of *Pinus contorta* var. *latifolia*.

	DBH (cm)	Height (m)	Slenderness (ht/dbh)	Height of crown centre (m)	Density (trees/ha)
Two creeks (TCT)	11.8	15.4	1.34	13.0	2150
Two creeks Thinned (TCT)	13.4	16.0	1.23	13.3	1300
Windfall (WF)	18.1	13.9	0.79	10.3	1500

Table 3-2. Wind speeds and tree sway statistics for each structural type and high wind speed at Windfall, with corresponding wind conditions used in collision analyses. Values in brackets indicate standard error.

	Mean top wind speed (m/s)	Mean mid-crown wind speed (m/s)	Mean crown sway speed (m/s)	Maximum crown sway speed (m/s)	Mean crown sway distance (m)	Maximum crown sway distance (m)
Two creeks (TC)	5.0	1.5	1.05 (0.0058)	6.18	0.60 (0.0028)	2.60
Two creeks Thinned (TCT)	5.1	4.2	1.38 (0.0068)	7.32	0.84 (0.0034)	3.04
Windfall (WF)	5.1	1.1	0.29 (0.0015)	1.58	0.12 (0.0005)	0.47
Windfall (WF) (high wind)	7.9	1.6	0.67 (0.0053)	3.58	0.25 (0.0017)	1.02

Minutes in the dataset and mean wind direction respectively are 57.9 min and 278° for TC, 69.4 min and 281° for TCT, 63.6 min and 308° for WF, and 20.2 min and 305° for WF (high wind).

Table 3-3a Crown collision summaries for each dataset using the 're-advancement' method for four trees central to the sensored group of 10. Values in brackets indicate standard error.

	Percent mean crown overlap	Percent maximum crown overlap	Mean collision duration (seconds)	Collision rate collisions/minute/ tree
Two creeks (TC)	23.2 (1.00)	65.9	0.36 (0.125)	73.1
Two creeks Thinned (TCT)	28.8 (0.862)	84.4	0.35 (0.103)	51.0
Windfall (WF)	12.0 (1.27)	50.2	0.45 (0.277)	88.2
Windfall (WF) (high wind)	14.8 (1.87)	65.0	0.37 (0.304)	132.3

Table 3-3b Crown collision summaries for each dataset using the 'disengagement' method for four trees central to the sensored group of 10. Values in brackets indicate standard error.

	Percent mean crown overlap	Percent maximum crown overlap	Mean collision duration (seconds)	Collision rate collisions/minute/ tree
Two creeks (TC)	23.3 (0.9938)	65.9	0.48 (0.2763)	47.4
Two creeks Thinned (TCT)	31.4 (0.9377)	84.4	0.46 (0.2424)	43.3
Windfall (WF)	20.1 (2.227)	50.2	14.37 (46.10)	11.8
Windfall (WF) (high wind)	16.0 (2.204)	65.0	0.68 (1.675)	63.0

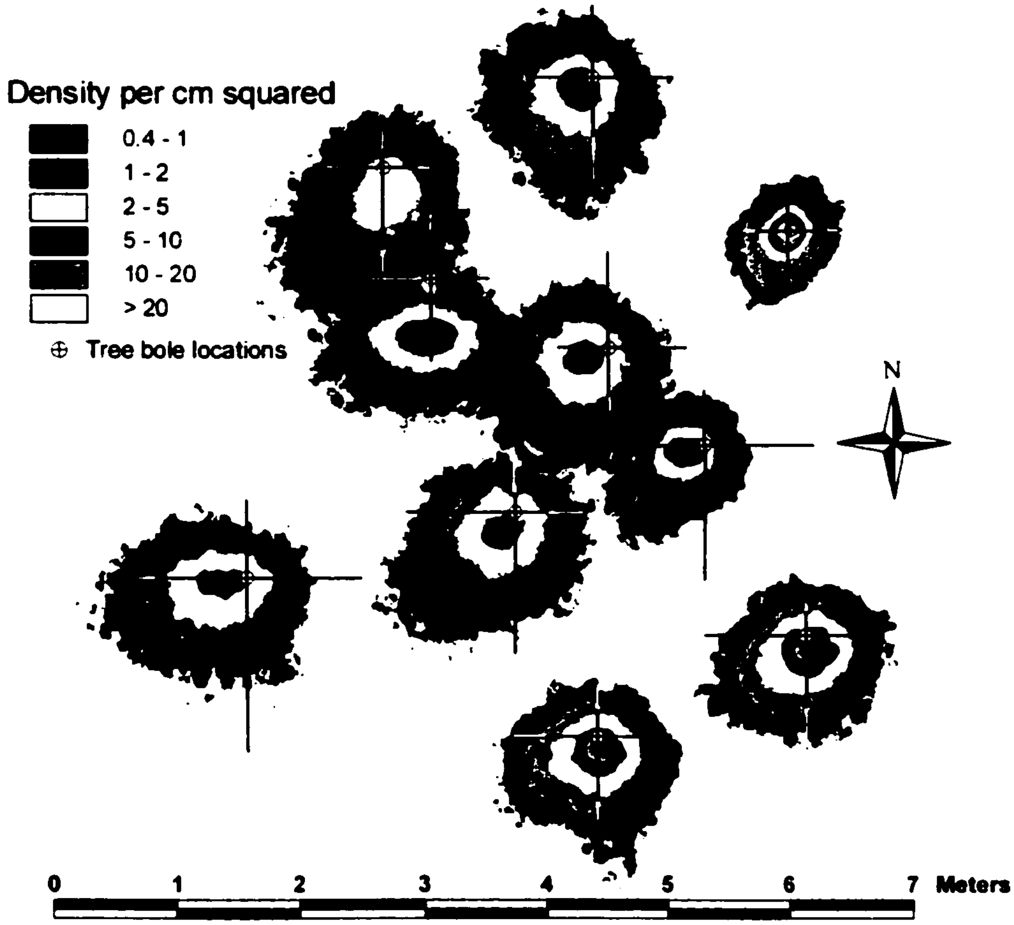

Figure 3-1. Sway patterns of each tree in the TC stand using mid-crown bole positions during a mean wind speed of 5.0 m/s. Contour classes represent bole location frequency in cm^2/hour. Crosshairs are centred on bole base locations and represent lateral crown extent.

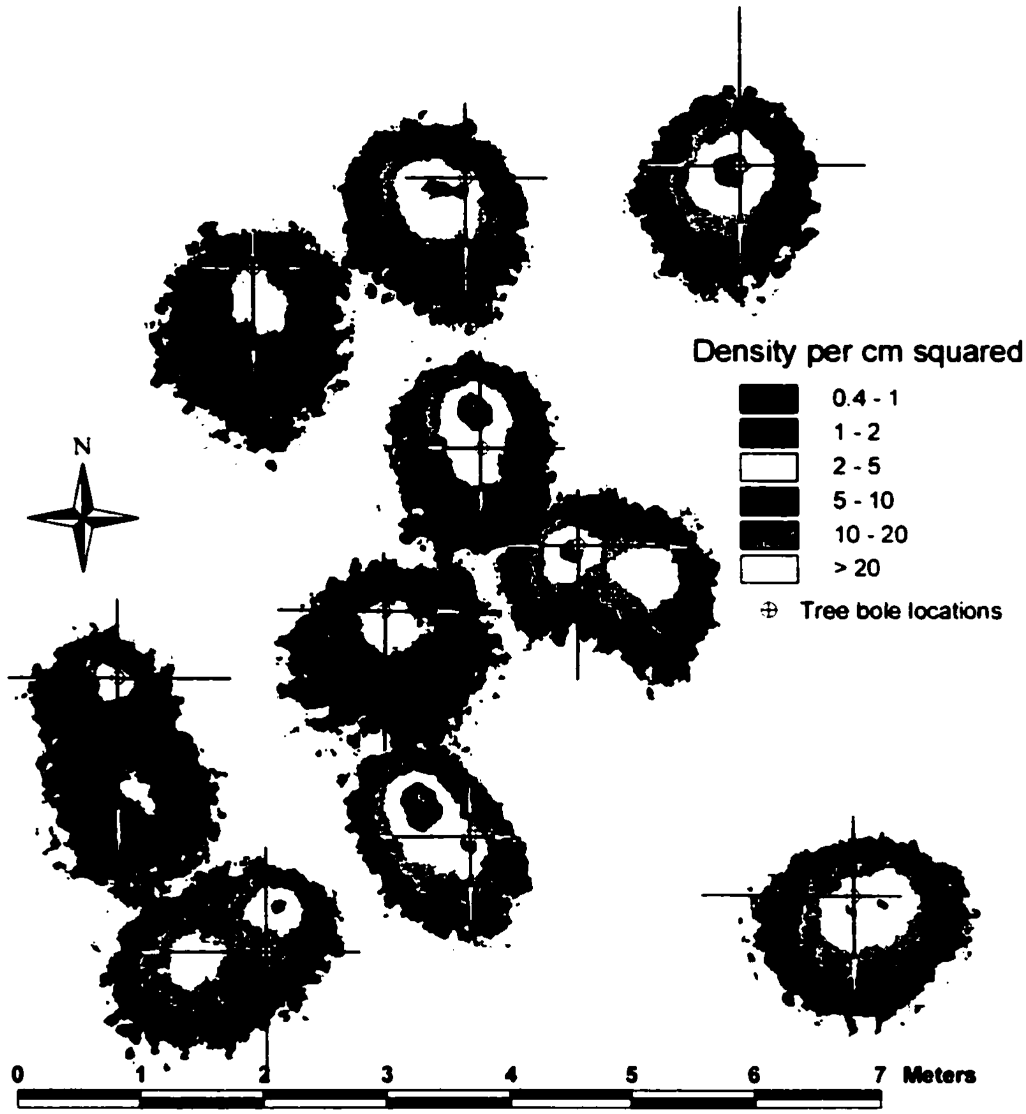

Figure 3-2. Sway patterns of each tree in the TCT stand using mid-crown bole positions during a mean wind speed of 5.1 m/s. Contour classes represent bole location frequency in cm^2/hour. Crosshairs are centred on bole base locations and represent lateral crown extent.

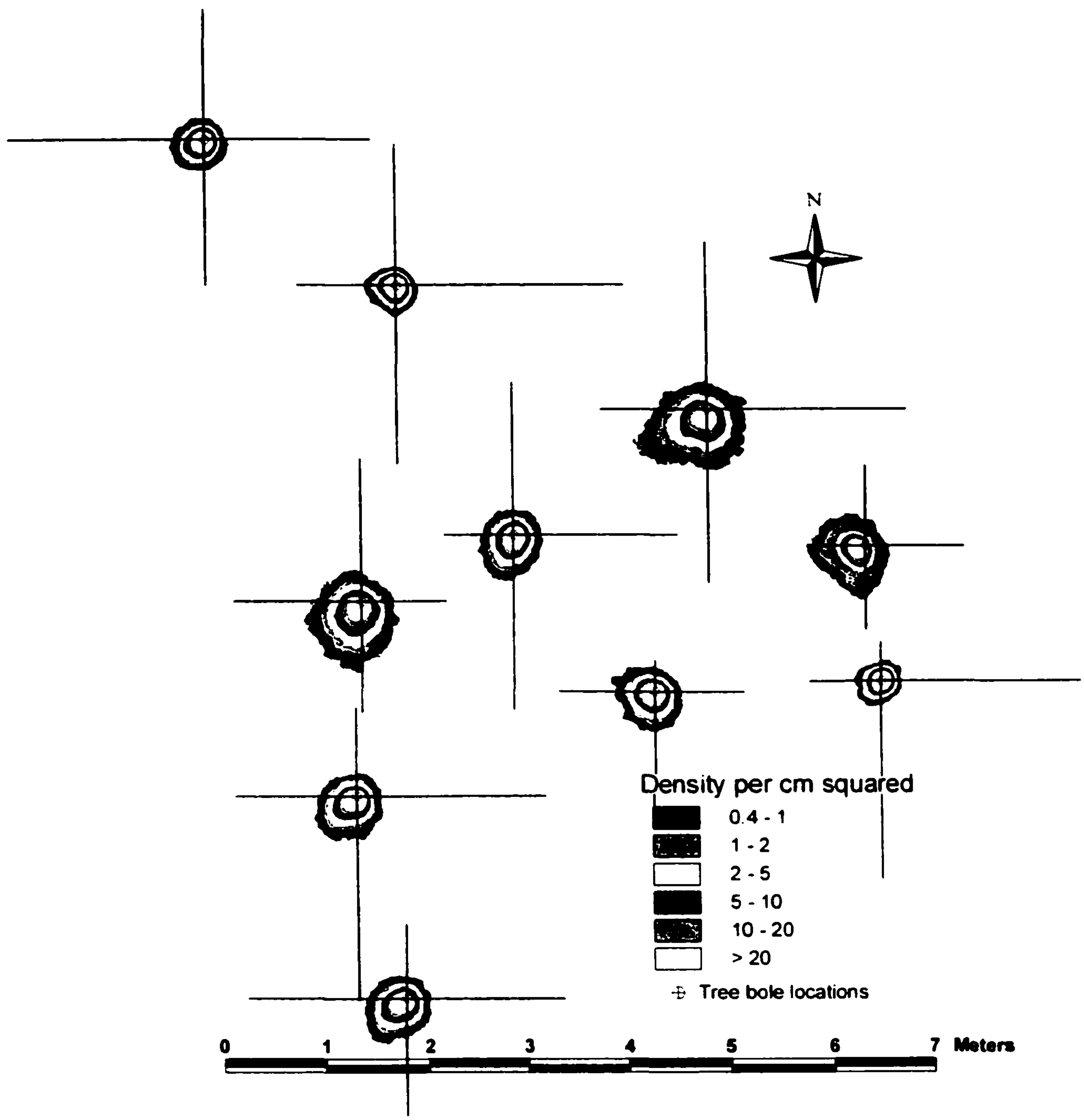

Figure 3-3. Sway patterns of each tree in the WF stand using mid-crown bole positions during a mean wind speed of 5.1 m/s. Contour classes represent bole location frequency in cm^2/hour. Crosshairs are centred on bole base locations and represent lateral crown extent.

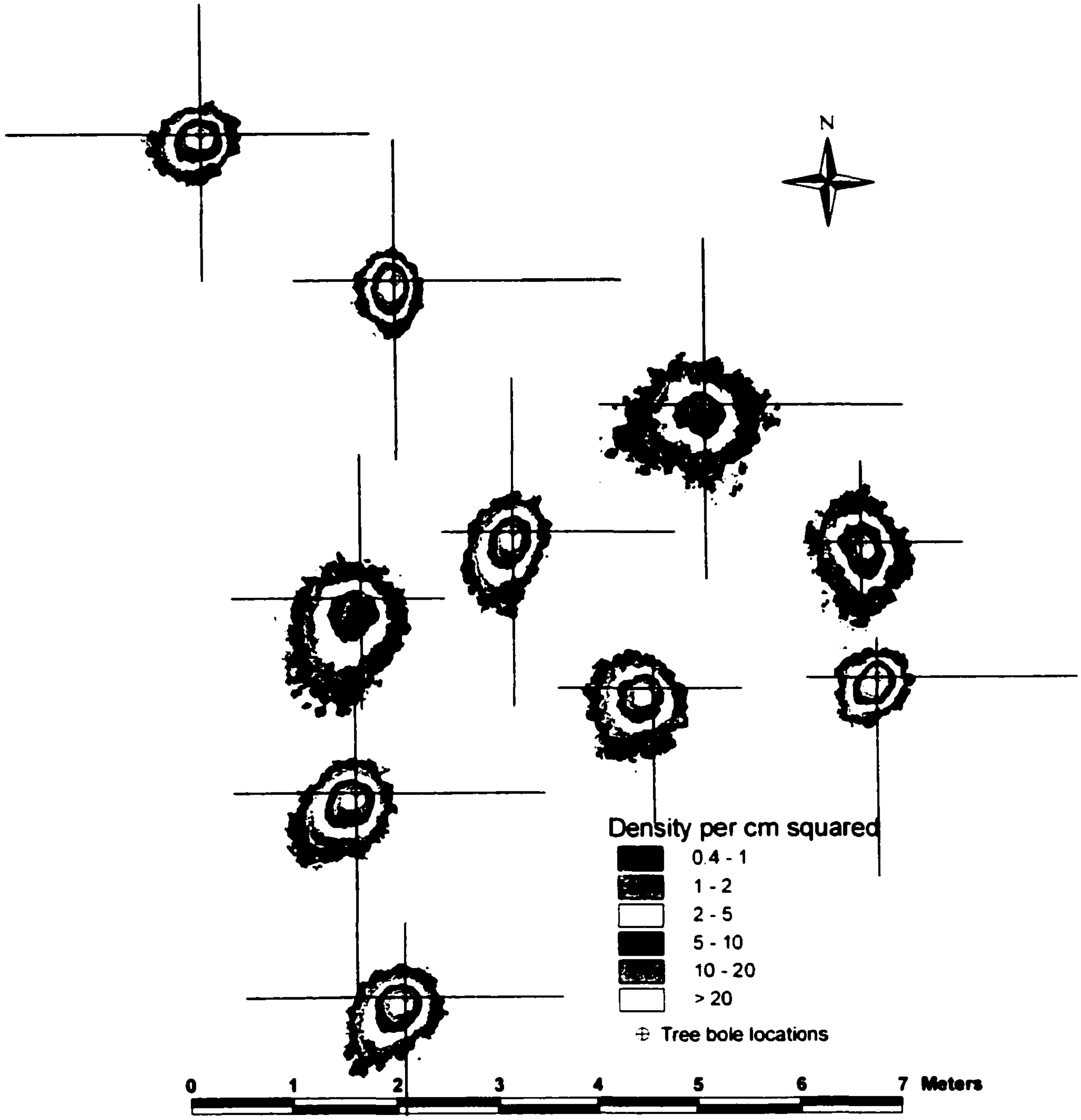

Figure 3-4. Sway patterns of each tree in the WF stand using mid-crown bole positions during a mean wind speed of 7.9 m/s. Contour classes represent bole location frequency in cm^2/hour. Crosshairs are centred on bole base locations and represent lateral crown extent.

Chapter 4: Relative density, tree slenderness and tree height drive the crown closure of lodgepole pine

Introduction

Leaf area is a major component of crown structure, forest productivity and stand dynamics (Waring and Schlesinger 1985; Oliver and Larson 1990). While general structural patterns of tree leaf area are inherited, tree crowns are generally assumed to fill all of the canopy space in a stand (up to their open grown potential) (Assmann 1970; Ford 1985; Oliver and Larson 1990). After crown closure, any unoccupied space in the forest canopy is usually ascribed to tree mortality gaps (Runkle 1982; Oliver and Larson 1990). However, much of the empty space within closed canopy stands can be associated with interstitial space between crowns or crown shyness rather than tree mortality gaps.

Crown shyness is found in many forested ecosystems and has been attributed to inhibition of lateral branch growth due to poor light conditions between crowns (Koike 1989; Sorrensen-Cothern *et al.* 1993; Umeki 1995; Chen *et al.* 1996; Cescatti 1997; Mäkelä 1997). However, there is growing evidence that the mechanism controlling crown shyness is crown abrasion from inter-crown collisions (Putz *et al.* 1984; Grier 1988; Robertson 1987; Long and Smith 1992; Smith and Long 2001, Rudnicki *et al.* 2001). Crown collisions could maintain crown shyness through either lateral branch/bud loss or inhibition of lateral growth due to chronic mechanical contact. Thus, wind and tree biomechanics may be the mechanism controlling crown shyness as collision intensity is regulated by both wind speed and tree stiffness (Rudnicki *et al.* submitted, Rudnicki *et al.* 2001). Tree stiffness is determined by the material properties of the bole (modulus of elasticity) and the bole shape (Niklas 1992). Thus, parameters describing tree stiffness such as slenderness coefficient (SC; height/diameter) of trees (Petty and Swain 1985; Peltola and Kellomäki 1993) may be important stand attributes related to crown shyness and crown occupancy in closed canopy stands.

Relative density index (RD) describes the level of stand occupancy by considering the density of the stand in relation to average tree size. Relative density is an indicator of competition intensity and in closed canopy stands, RD describes crown development compared to open grown individuals (Curtis 1982). It is generally assumed that tree crowns will fill all available space (up to their open grown potential) through lateral growth (Curtis 1982) and thus stands with a high relative density should have high crown cover. RD indices ignore any presence of crown shyness after canopy closure therefore, when crown shyness is observed, and presumably maintained by inter-crown collisions, correlations between RD and canopy cover should be poor.

We suspect the mechanism of crown abrasion may also be dependant on tree height. As stands reach crown closure there is reduction in allocation to tree radial growth, as bending stresses are reduced due to sway damping and mutual sheltering from crown wind loads (Jacobs 1954; Larson 1965; Neel and Harris 1971; Telewski and Jaffe 1986; Hobrook and Putz 1989; Valinger 1992; Osler *et al.* 1996; Peltola 1996; Wang *et al.* 1998). Thus, with the reduction in radial growth and increasing height vital for survival during the stem exclusion phase, tree SC's increase (Mohler *et al.* 1978; Muhairwe 1994). Furthermore, as the stand matures, tree mortality gaps will increase wind loads thereby increasing crown collision intensity (Rudnicki *et al.* submitted). Thus, tree height and associated increases in crown wind loads should play a role in the onset and maintenance of crown shyness (Long and Smith 1984; Jack and Long 1991).

Our objective is to demonstrate the dependence of crown shyness on tree biomechanics in even-aged lodgepole pine. We restricted our sampling to exclude tree mortality gaps so estimates of canopy cover would represent crown shyness. We hypothesized that RD would predict percent canopy cover (% CC) in younger, closed canopy stands, because lateral crown development is controlled by density or environmental conditions. Conversely, we expected poor predictions of % CC by RD in older stands because of the effect of crown collisions. The ability of tree slenderness coefficient (SC) to predict % CC would support the notion that lateral crown growth in these stands is controlled by tree biomechanics and that crown shyness is maintained by crown interactions.

Methods

We selected 10 stands of pure lodgepole pine across west-central Alberta, Canada, from a range of stand densities and tree sizes (Table 4-1.). To ensure that low-density lodgepole pine stands were included in our data set, two thinned stands (Hinton and Huestis) and two stands with both thinned and un-thinned sections (Tri-creek and Nojack) were sampled. These thinned treatments were at least 20 years old, allowing trees sufficient time to potentially fill the space created by tree removal.

Within each stand, we selected groups of three trees whose boles define the corners of a triangle (tree triangle) (Penridge and Walker 1988). Tree triangles satisfied several criteria: 1) A maximum variation of 20% in height or DBH relative to the largest tree in the triangle. 2) Triangles should have relatively equal sides, i.e. the longest side could not be greater than twice the shortest side. 3) Tree triangles achieved theoretical crown closure; a stand density management diagram for naturally regenerated lodgepole pine was used as a guide (Farnden 1996) (Fig. 4-1). 4) Tree triangles were independent, i.e. they did not share trees with other triangles. 5) Tree triangle density and height were representative of adjacent trees. 6) Tree triangles could not be adjacent to tree mortality or edaphic gaps. We assumed that using tree triangles meeting these criteria would allow us to measure and compare crown development where tree stiffness varied as mean triangle DBH was allowed to deviate from the stand average.

Within triangles, we measured tree diameters at 1.4m (DBH), heights, lateral extent of crowns and distance between boles. Distances between boles and DBH were measured with a tape, while tree heights were measured with an Impulse laser range finder (Laser Technology Inc., Colorado, USA). We constructed a Crown Scope™ with a wide 7.6 cm aperture allowing an accurate vertical sighting of the crown edge and precise measurement of lateral crown extent (Rudnicki *et al.* 2001; Vales and Bunnel 1988).

Percent canopy cover (% CC) was determined by dividing the estimated crown cover inside the triangle by the triangle area (Walker *et al.* 1988). Assuming circular crown shapes, the three crown areas inside the triangle form sectors whose area, K_a, was calculated using;

[4-1] $$K_a = \pi r^2 \theta / 360$$

where r is the crown radius and θ is the sector angle (Fig 4-2). Each tree's crown radius is an average of two measures of lateral crown extent (Fig 4-2). As the three side lengths were known, the sector angle (θ) was calculated using the law of cosines. Percent crown cover (% CC) was calculated by dividing the three summed crown sector areas K by the total triangle area T.

In the case of tree crowns overlapping each other, the intersection of two overlapping circles (lens-shaped region) would inflate estimates of crown areas when crown sector areas are summed (Fig 4-3). To correct for the resulting inflation of percent crown cover, we calculated the half-lens area L using;

[4-2] $$L = r_2^2 \arccos\frac{(a^2 + r_2^2 - r_1^2)}{2ar_2} + r_1^2 \arccos\frac{(a^2 + r_1^2 - r_2^2)}{2ar_1} - \frac{1}{2}\sqrt{(-a + r_2 + r_1)\cdot(a + r_2 - r_1)\cdot(a - r_2 + r_1)\cdot(a + r_2 + r_1)}$$

where a is the triangle side length and r_1 and r_2 are the crown radii of trees one and two respectively (Fig 4-3). The half lens area L was subtracted from the total crown area K for a corrected crown area $\acute{K}$. The corrected crown area $\acute{K}$ was divided by T for the corrected % CC. We measured and calculated the percent crown cover for 161 tree triangles from the ten stands.

We calculated relative density (RD) using the Curtis (1982) derivation;

[4-3] $$\mathrm{RD} = G / (Dq^{0.4})$$

where G is basal area (m^2 /ha) and Dq is the quadratic mean diameter of the tree triangle. To determine G, we determined basal area for each tree triangle by summing the basal area sectors formed by the dimensions of the tree triangle (similar to our approach in determining crown areas). The basal area of each tree triangle was scaled to m^2/ha using;

$$[4\text{-}4] \quad G = \frac{10000}{Tg}$$

where g is the tree triangle basal area and T is the triangle area. .

Statistical Analysis

Because of differences in site quality, topography and local wind regimes among stands, we developed the regressions between % CC vs. RD and SC for each stand separately. This minimized the influence of confounding factors and allowed us to isolate the effects of RD and SC on % CC. Given the restricted sampling scheme used in this study, our inferences are restricted to mechanisms associated with crown shyness.

Results

The stands sampled represented a size/height gradient ranging in mean height from 5.6 – 22.1 m and mean DBH from 8.5-25.1 cm. All of the tree triangles achieved closed canopy conditions as they all had a relative density above theoretical crown closure (Table 4-1, Fig 4-1).

A pattern in the strength of relationships between relative density and slenderness coefficient with % crown cover was observed among stands. The tree triangles from the four shortest stands (< 11.4 m height) had positive correlations between % CC and RD (Table 4-2, Fig 4-4). However, relative density was unrelated to crown cover in taller stands (> 12 m height). In contrast, slenderness coefficient was not correlated with % CC in shorter stands. However, significant negative relationships between % CC and SC were observed for 4 out of 6 stands above 15 m in height (Table 4-2, Fig 4-5).

The slope of the negative relationships between % CC and SC were remarkably similar among stands > 15 m in height (Table 4-2) suggesting the mechanism producing these relationships is probably similar. This is supported by a similar negative relationship between mean stand % CC (from all triangles within a stand) with mean stand height (r^2= 0.52, P= 0.018) (Fig 4-6) suggesting mean crown shyness increases as stands grow in height.

Discussion

Our analysis showed the most important predictor of percent crown cover (% CC) shifted from relative density (RD) to slenderness coefficient (SC) between 12-15 m of mean tree height. We believe this indicates a change in the mechanism controlling lateral crown development in even-aged lodgepole pine. In stands shorter than 12 m, results suggest that plant lateral growth is regulated by density or environmental conditions. For stands taller than 15 m, % CC appears related to SC (Fig 4-4) suggesting that in taller stands, crown collisions limit lateral crown extension. The fact that % CC vs. SC regression slopes remained relatively constant but the intercepts differed (Fig 4-5), suggests that the driving mechanisms is also dependent on site conditions such as establishment density, site index, local wind conditions or other factors.

Relative density serves as a good predictor of % CC before the onset of crown shyness. However, contrary to commonly held assumptions regarding density and crown cover (Curtis 1982), RD fails to predict canopy cover in more mature stands. We suggest this failure is because RD does not reflect the potential change in mechanisms controlling lateral growth; specifically the change of bole shape that occurs after crown closure. Furthermore, this may reflect an erroneous assumption the size density relationships (on which the RD is based) that "plants of the same species have a particular shape independent of their size or stage of development" (Yoda 1963; Drew and Flewelling 1977). We support the assertion that in stands undergoing competition mortality, RD indicates competition intensity, but the relationship of RD with crown cover may be limited to younger stands. Additional factors such as the change in slenderness coefficient may be important in size density relationships (Mohler *et al.* 1978). Inclusion of this variable in crown growth models may improve their ability to predict crown development.

We believe the interaction of wind and changing stand structure is an important causal agent in the reduction in crown cover as stands increased in height (Fig 4-6). This is likely related to three factors: 1) Bole slenderness coefficient increases with height and remains high, indicating diminished stiffness throughout the stem exclusion phase of stand development; 2) Taller trees can displace further by virtue of their increased length; 3) Changes in stand structure such as mortality gaps and usual differences in tree height growth are likely to roughen the canopy texture and allow increased wind penetration into the stand. These three factors are thought to combine and cause increased collision intensity and crown damage as stands grow taller. We suggest that the increasing amount of crown shyness with stand height reflects increasing collision intensities, which causes more canopy space to be unusable for lateral crown growth. This supports the contentions of Long and Smith (1992); Sampson and Smith (1993); Smith and Long (2001) who argue that the culmination of current annual increment coincides with the onset of crown abrasion and suggest that it causes the decline.

Kuuluvainen (1992) observed narrow conifer crowns are common in higher latitudes and suggests that low solar angles at high latitudes promotes development of this crown form to maximize light capture. A second possible reason for narrow crowns in these regions may relate to climate. Cold temperatures make branches more brittle and breakable (Robertson 1993; Lieffers *et al.* 2001) during winter, which may exacerbate crown shyness resulting from crown collisions in boreal forests. Short growing seasons and generally slow growth rates would make any abrasion damage difficult to replace in these northern forests.

Mature, open-grown trees that rely on a self-supportive strategy for stability (Jacobs 1954) typically develop low slenderness coefficients. Conversely, in closed canopy stands, slender trees with a high SC rely upon sway damping collisions with neighbours to remain standing (Gardiner *et al.* 1997). Rudnicki *et al.* (submitted) demonstrated that more slender trees experience more intense collisions and conclude the potential for lateral crown abrasion or growth inhibition is higher in such stands. Our results support the suggestion that such stabilizing collisions in slender, closed canopy stands should result in greater crown shyness, and that crown collisions is the probable mechanism involved.

References

Assmann, E. 1970. The principles of forest yield study studies in the organic production, structure, increment and yield of forest stands[1st English ed.]. Oxford, Pergamon Press, 506 pp.

Cescatti, A. 1997. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithims. Ecological Modelling, **101**: 263-274.

Chen, H.Y.H., Klinka, K. and Kayahara, G.J. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. Canadian Journal of Forest Research, **26**: 1149-1157.

Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. Forest Science, **28**(1): 92-94.

Drew, J.T. and Flewelling, J.W. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantation. Forest Science, **25**(3): 518-532.

Dunham, W. 1990. Journey Through Genius: The Great Theorems of Mathematics. New York: Wiley.

Farnden, C. 1996. Stand density management diagrams for lodgepole pine, white spruce and interior Douglas-fir. Canadian Forest Service. Victoria, British Columbia, Information report BC-X-360.

Ford. E.D. 1985. Competition and stand structure in some even-aged plant monocultures. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J.E. Jackson. Institute of terrestrial ecology.

Gardiner, B.A., Stacey, G.R., Belcher, R.E. and Wood, C.J. 1997. Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. Forestry, **70**(3): 233-252.

Grier, C.C. 1988. Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifer forests. Canadian Journal of Forest Research, **18**: 1097-1102.

Holbrook, N.M. and Putz, F.E. 1989. Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *liquidambar styraciflua* (sweet gum). American Journal of Botany, 76(12), 1740-1749.

Jacobs, M.R. 1954. The effect of wind sway on the form and development of *Pinus radiata* D. Don. Australian Journal of Botany, 2, 35-51.

Jack, S.B. and Long, J.N. 1991. Analysis of stand density effects on canopy structure: a conceptual approach. Trees- Structure and Function, 5, 44-49.

Koike, F. 1989. Foliage-crown development and interaction in *Quercus gilva* and *Q. Acuta*. Journal of Ecology, 77, 92-111.

Kuuluvainen, T. 1992. Tree architectures adapted to efficient light utilization – is there a basis for latitudinal gradients. Oikos 65(2): 275-284.

Larson, P.R. 1965. Stem form of young *Larix* as influenced by wind and pruning. Forest Science, 11(4), 413-423.

Lieffers, S.M., Lieffers, V.J., Silins, U. and Bach L. 2001. Effects of cold temperatures on breakage of lodgepole pine and white spruce twigs. Canadian Journal of Forest Research, 31(9): 1650-1653.

Long, J.N. and Smith, F.W. 1984. Relation between size and density in developing stands: a description and possible mechanisms. Forest Ecology and Management, 7: 191-206.

Long, J.N. and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. Forest Ecology and Management, 53: 53-62.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. Forest Science, 43(1): 7-24.

Mohler, C.L., Marks, P.L. and Sprugel D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology, 66: 599-614.

Muhairwe, C.K. (1994) Tree form and taper variation over time for interior lodgepole pine. Canadian Journal of Forest Research, 24(9): 1904-1913.

Neel, P.L. and Harris, R.W. 1971. Motion-induced inhibition of elongation and induction of dormancy in *Liquidambar*. Science, 173: 58-59.

Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago.

Oliver, C.D. and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, New York.

Osler, G.H.R., West, P.W. and Downes, G.M. 1996. Effects of bending stress on taper and growth of stems of young Eucalyptus regnans trees. Trees- Structure and Function. **10**(4): 239-246.

Peltola, H. 1996. Swaying of trees in response to wind and thinning in a stand of scots pine. Agricultural and Forest Meteorology, **90**: 187-194.

Peltola, H. and Kellomäki S. 1993. A mechanistic model for calculating windthrow and stem breakage of Scots pines at stand edge. Silva Fennica, **27**(2): 99-111.

Penridge, L.K. and Walker, J. 1988 The crown-gap ratio (C) and crown cover: Derivation and simulation study. Australian Journal of Ecology, **13**:109-120.

Petty, J.A. and Swain, C. 1985 Factors influencing stem breakage of conifers in high winds. Forestry, **58**(1): 75-84.

Putz, F.E., Parker, G.G. and Archibald, R.M. 1984. Mechanical abrasion and intercrown spacing. The American Midland Naturalist, **112**(1): 24-28.

Robertson, A. 1987. The centroid of tree crowns as an indicator of abiotic processes in a balsam fir wave forest. Canadian Journal of Forest Research, **17**: 746-755.

Robertson, A. 1993. Effects of wind on boreal forests. *In* Forest development in Cold Climates. *Edited by* J. Alden. Plenum Press, New York.

Rudnicki, M. Lieffers, V.J. and Silins U. 2001. The crown collisions of lodgepole pine. The Journal of Ecology, submitted.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, **63**(5): 533-546.

Sampson, D.A. and Smith, F.W. 1993. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta var. latifolia*) forests. Agriculture and Forest Meteorology, **64**: 63-79.

Smith, F.W. and Long, J.N. 2001. Age-related decline in forest growth: an emergent property. Forest Ecology and Management, **144**: 175-181.

Sorrenson-Cothern, K.A., Ford, E.D. and Sprugel, D.G. 1993. A model of competition incorporating plasticity through modular foliage and crown development. Ecological Monographs, **63**(3): 277-304.

Telewski, F.W. and Jaffe, M.J. 1986. Thigmomorphogenesis: Field and laboratory studies of *Abies fraseri* in response to wind or mechanical perturbation. Plant Physiology, **66**: 211-218.

Umeki, K. 1995. Modeling the relationship between the asymmetry in crown display and local environment. Ecological Modelling, **82**: 11-20.

Valinger, E. 1992. Effect of wind sway on stem form and crown development on Scots pine (*Pinus sylvestris L.*). Australian Forestry, **55**: 15-21.

Vales, D.J. and Bunnel, F.L. 1988 Comparison of methods for estimating forest overstory cover. I. Oberver effects. Canadian Journal of Forest Research, **18**: 606-609.

Wang Y., Titus S.J. and LeMay, V.M. 1998. Relationships between tree slenderness coefficients and tree or stand characteristics for major species in boreal mixedwood forests. Canadian Journal of Forest Research, **28**: 1171-1183.

Waring, R.H. and Schlesinger, W.H. 1985. Forest Ecosystems Concepts and Management. Academic Press, New York.

Yoda, K., Kira, T., Ogawa, H. and Hozumi, H. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of the Institute of Polytechnics, Osaka City University, Series D, Biology. **14**: 107-129.

Table 4-1. Mean statistics for all triangles in each stand.

	No. of triangles	Height (m)	DBH (cm)	SC (ht/DBH)	Density (trees/ha)	Relative density	% Crown cover
Hinton	17	5.6	8.7	0.66	2765	7	75
Robb	10	5.6	8.5	0.66	7942	19	97
Swan hills	15	8.0	8.7	0.95	10125	23	94
Tri-creek	30	11.4	12.8	0.96	5806	20	71
Windfall	16	15.1	16.9	0.92	2327	16	79
Huestis	10	15.8	16.1	1.00	2099	13	58
Two Creeks	13	16.6	15.5	1.10	3058	15	60
Gregg	9	17.9	22.1	0.88	1823	16	53
McPherson	14	20.3	19.9	1.03	2223	20	57
Nojack	30	22.1	25.1	0.91	1407	16	71

Table 4-2. Regression coefficients, r^2 and levels of significance (P), for the relationship between triangle % crown cover and the variables relative density (Curtis 1982) or slenderness of the trees comprising the tree triangle for each stand. $Y = b_0 + b_1X$.

	%CC and Relative density			%CC and Slenderness coefficient		
	b_0	b_1	r^2 (P)	b_0	b_1	r^2 (P)
Hinton	.361	.056	.59 (.000)	1.01	-.391	.02 (.536)
Robb	.822	.007	.65 (.015)	1.20	-.354	.10 (.358)
Swan hills	.854	.003	.28 (.034)	1.02	-.086	.02 (.581)
Tri-creek	.560	.007	.38 (.000)	.589	.127	.02 (.435)
Windfall	.915	-.007	.07 (.335)	1.37	-.629	.39 (.009)
Huestis	.566	.001	.00 (.861)	1.12	-.540	.24 (.150)
Two Creeks	.762	-.007	.08 (.444)	1.25	-.549	.32 (.042)
Gregg	.647	-.007	.09 (.433)	1.00	-.541	.69 (.005)
McPherson	.462	.005	.22 (.092)	1.13	-.543	.28 (.053)
Nojack	.642	.004	.04 (.345)	1.21	-.553	.27 (.008)

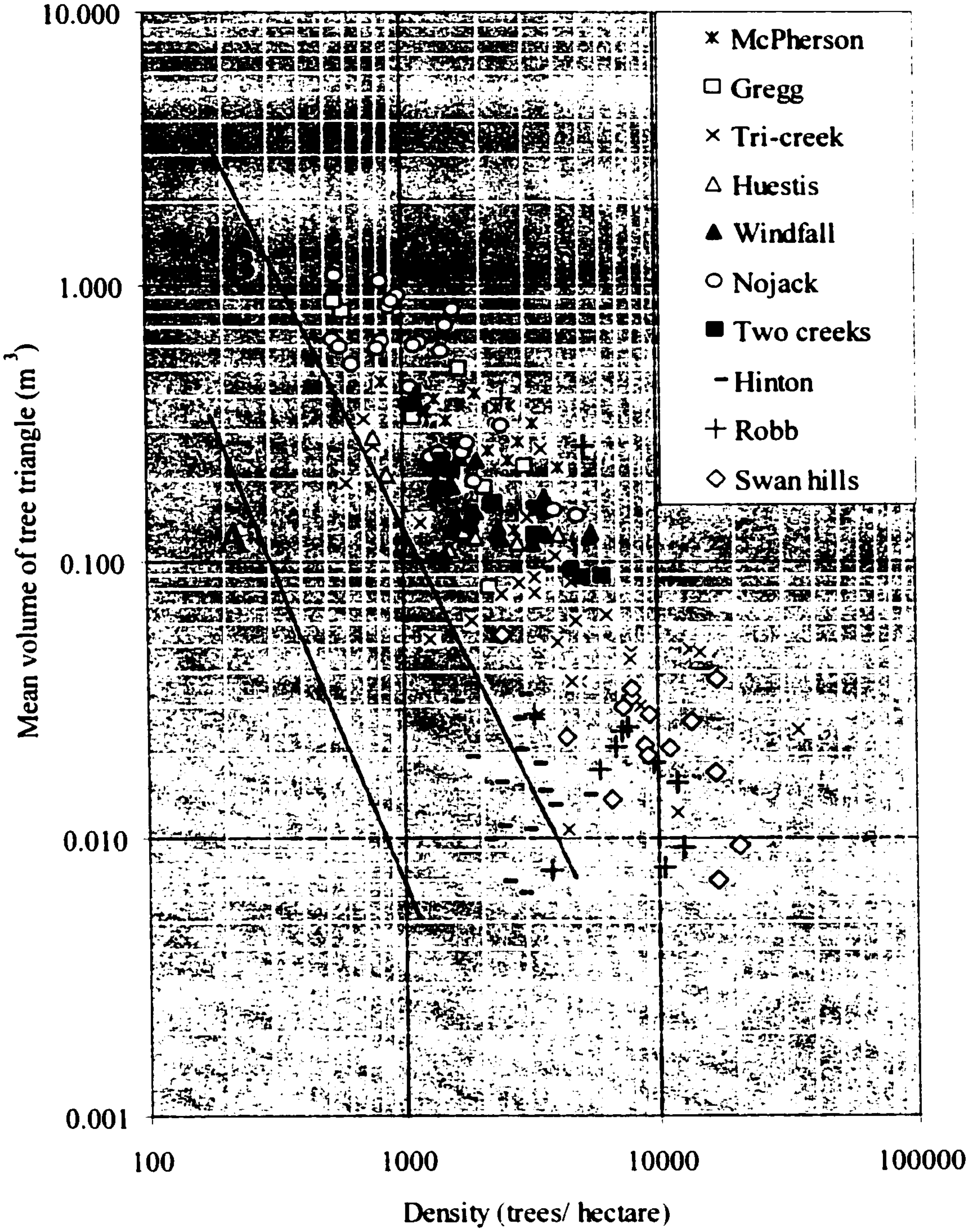

Figure 4-1. Stand density management diagram of all triangles by stand. Line A indicates 'crown closure' and line B indicates the lower limit of the 'zone of imminent competition mortality' for naturally regenerated lodgepole pine (Farnden 1996).

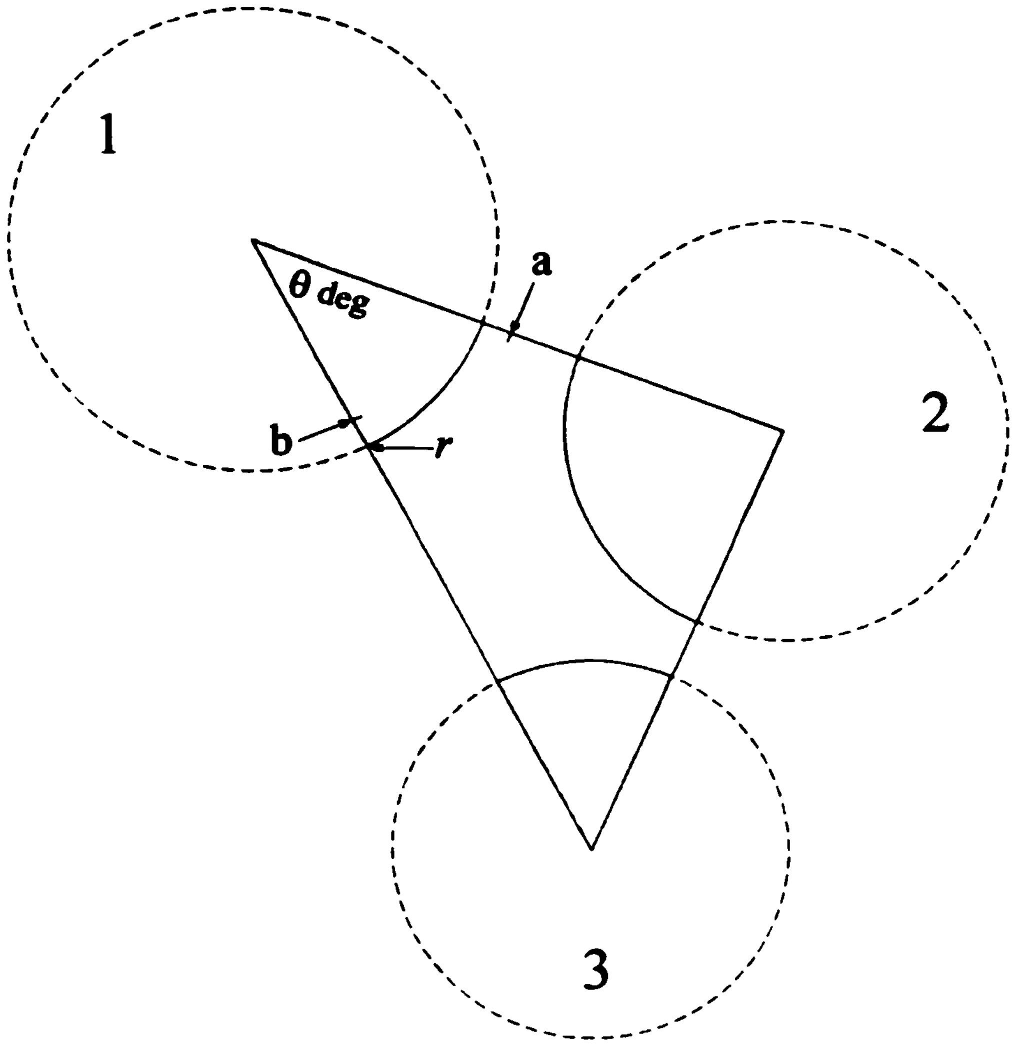

Figure 4-2. Crown positions of three trees in a triangle. Bole locations outline the triangle while simulated tree crowns within the triangle form sectors. Points 'a' and 'b' indicate actual measured lateral crown extents and were used to calculate the mean crown radius *r*.

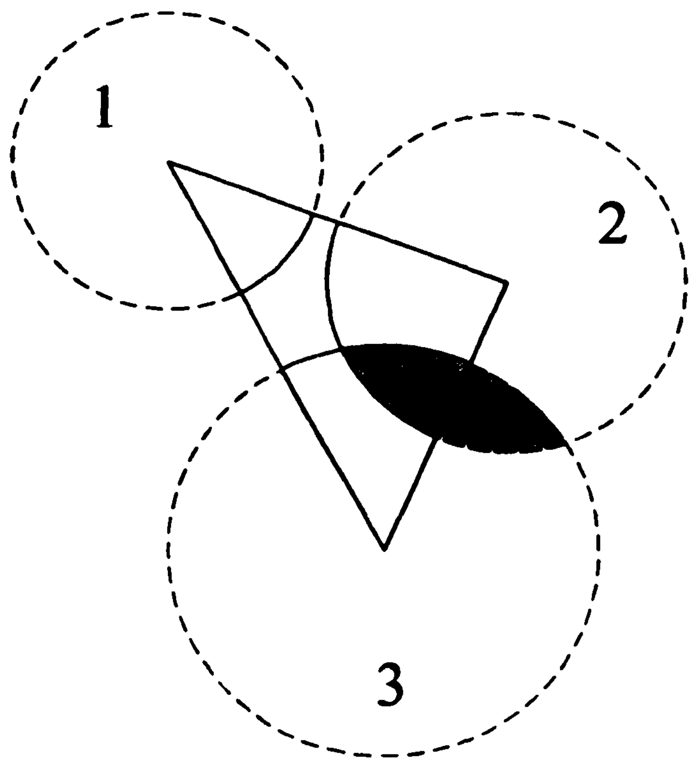

Figure 4-3. The shaded lens shaped region of the tree crowns indicates the occurrence of crown overlap. As part of tree crowns 2 and 3, the half lens area inside the triangle was subtracted from the total crown area inside the triangle.

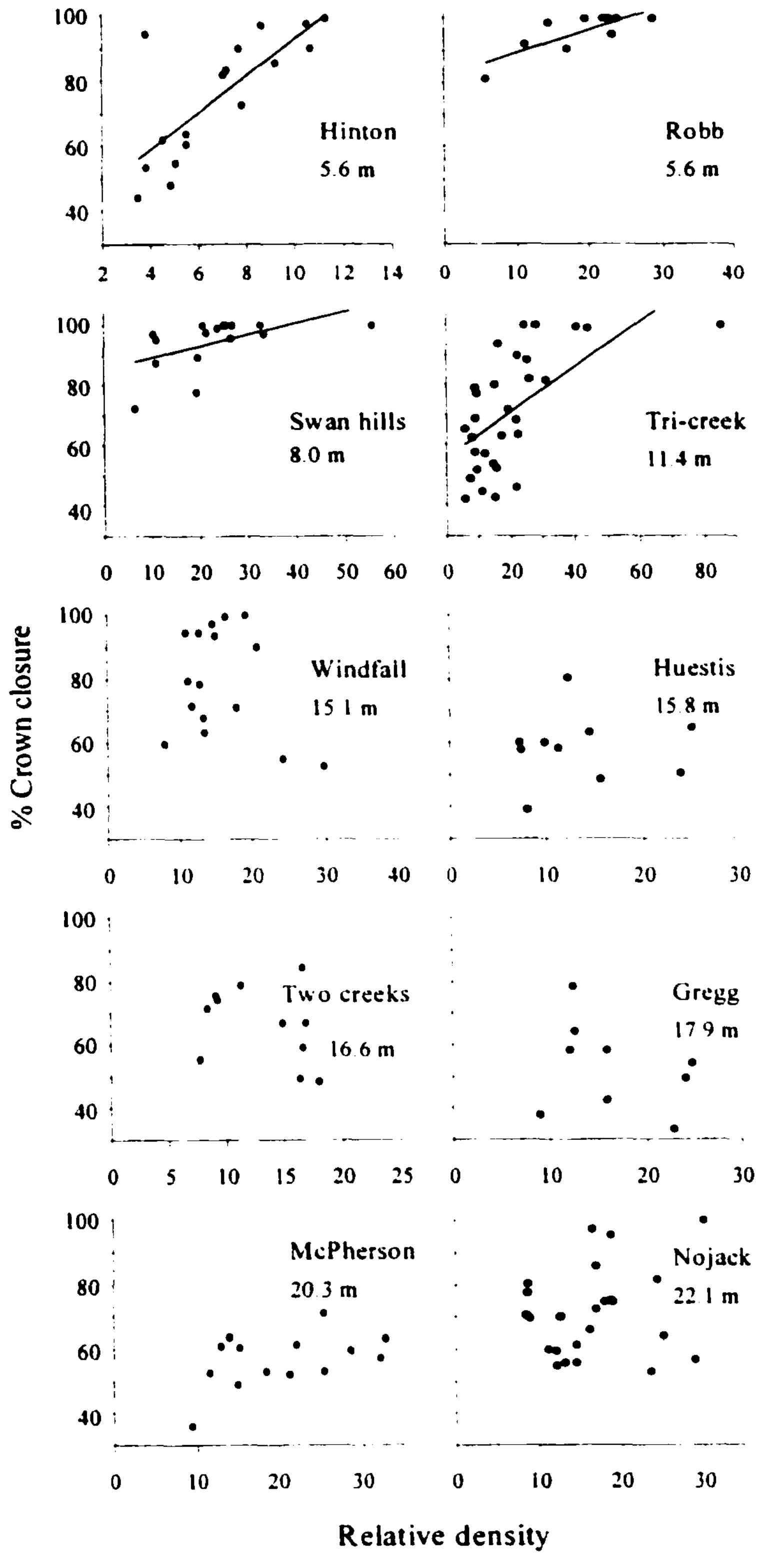

Figure 4-4. Triangle percent crown closure in relation to relative density by stand (with stand names and heights). Regression lines presented for stands with significant relationships ($P < 0.05$).

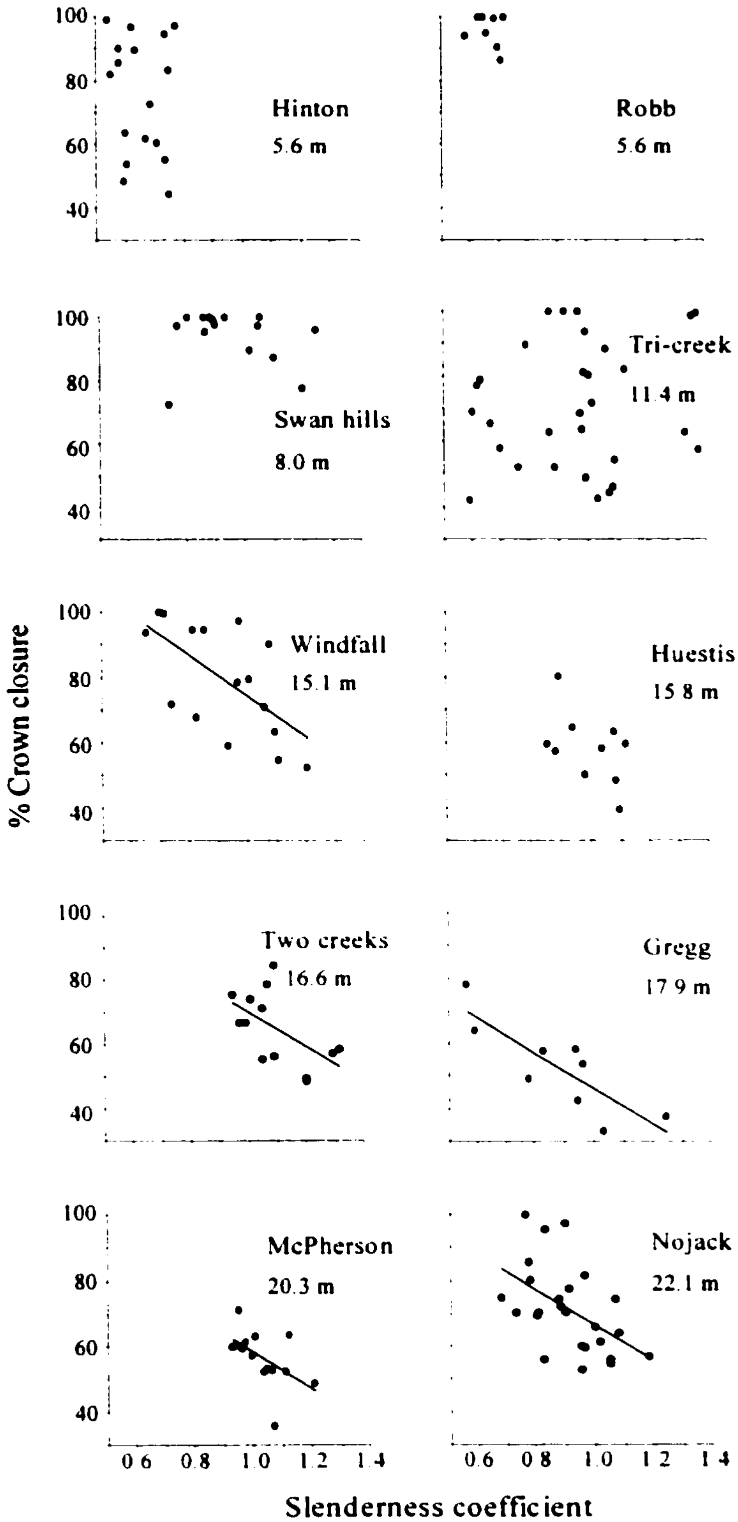

Figure 4-5. Triangle percent crown closure in relation to slenderness coefficient by stand (with stand names and heights). Regression lines presented for stands with significant relationships ($P < 0.05$).

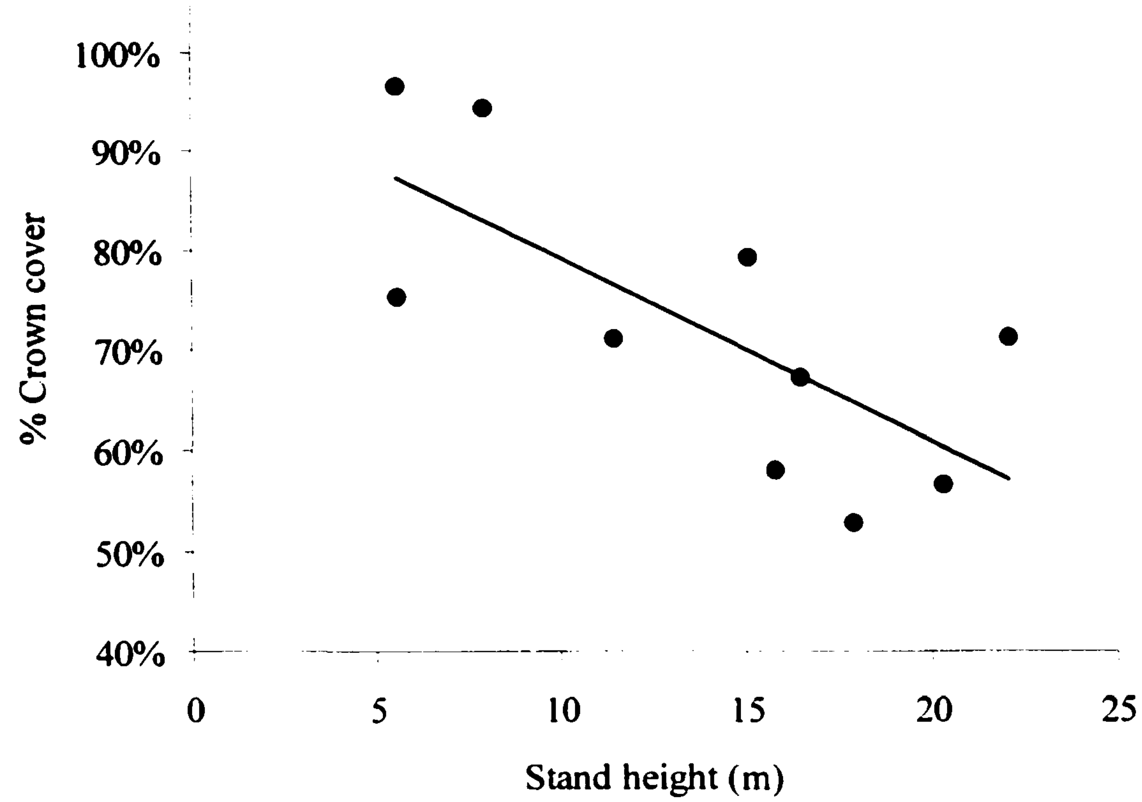

Figure 4-6. Relationship between the overall mean triangle percent crown cover and stand height. $\%CC = b_0 + b_1Ht$. $b_0 = .9744$; $b_1 = -.0182$; $r^2 = .52$; $P = 0.018$.

Chapter 5. Synthesis

The findings of this study revealed that tree slenderness mediates sway displacements and the resulting intensity of crown collision. Increasing tree slenderness is also associated with increasing crown shyness and supports a causal link between tree biomechanics and inhibition or abrasion of lateral crown growth. This work has satisfied these research objectives:

1. A method to measure and record simultaneous tree sway for a group of trees.
2. A technique to reconstruct and quantify the crown collisions associated with chronic tree sway.
3. Development of 2-dimensional tree sway frequency patterns to compare group dynamic sway response to changes in stand density and wind speed.
4. Determine how stand density, tree SC and wind speeds affect the spatial patterns and metrics of bole displacement.
5. Determine how stand density, tree SC and wind speeds affect the frequency and intensity of tree crown collisions.

In satisfying my objectives, I have gained new insight into structural and functional roles of crown collision in lodgepole pine. Opening the door for many questions regarding the dynamic behaviour of tree sway and crown interaction I presented a method of simultaneously measuring bole bending angle (rotation) at the live crown base of ten trees. I (along with another student – Georg Josi) have also developed a stem curvature solution that uses bole rotation to estimate bole displacement (Chapter 2). I reconstructed crown collisions using GIS software that combines asymmetrical polygon representation of tree crowns with their respective bole displacements. The output of this approach provides estimation of crown collision frequencies and intensities (area of crown overlap). My initial reconstructions support the idea that tree collisions provide a mechanism for lateral shoot abrasion and ensuing crown shyness and asymmetry in even-aged lodgepole pine.

Stand density, crown width, tree slenderness coefficient (SC) and wind speed affected frequency and intensity of crown collisions in *Pinus contorta* var. latifolia (Chapter 3). To examine the role of tree stiffness and stand density in the crown collisions of lodgepole pine, I studied stands of similar height, experiencing similar wind speeds. The data supported our hypothesis that trees with greater SC's have a higher frequency and intensity of collisions than trees with low SC's. To study the effects of stand density on crown collisions, I compared the crown interactions and sway patterns of a stand with high SC before and after thinning. My data also support the hypothesis that increased crown wind loads due to partial removal of the overstory will result in higher collision frequencies and intensities. Partial removal of the canopy also disrupted tree sway patterns, indicating trees are structurally adapted to a consistent wind and collision regime. I also compared crown interaction and sway patterns in a stand with a low SC at two different wind speeds. My data indicate that increased crown wind loads will also increase collision frequencies and intensities. The consistent shape in the sway patterns during two wind intensities supports the notion that internal canopy wind flows are organized and coherent (Raupach 1988; Gardiner 1994) and that tree boles are structurally adapted to them.

The hypothesis that crown shyness is dependent on tree biomechanics in even-aged lodgepole pine is supported by the data in Chapter 4. In this study, I use percent canopy cover (% CC), i.e. the complement of crown shyness, to analyse our premise. In stands shorter than 12 m, % CC was predicted by relative density (RD), and presumably lateral crown development is regulated by density or environmental conditions. In contrast, in most stands taller than 15 m % CC was predicted by SC, indicating lateral crown extension was controlled by crown interaction and tree biomechanics.

Stand structural changes

Our research indicates that tree biomechanics plays a critical role in stand development. In order to summarize my findings and elucidate the role and implications of biomechanics and crown interactions I suggest a conceptual illustration of stand development in terms of its structural aspects (Figure 5-1). The critical attributes of stand structure for each phase of development can be defined by tree stem density, height and slenderness (Figure 5-1).

Stand initiation

Before crown closure, trees are self-supporting and exhibit low SC's. Canopy texture is rough due to open space between trees and individual tree experience (relative to crown size) large wind loads. Crown abrasion is not possible as displacement is small due to tree stiffness and small tree proportions - for example, a 2 m tree probably could not displace more than ½ m. Crown closure is dependent on the density of stems as growing space and the availability of light are not limited.

Crown closure

A stand of lodgepole pine with an initial density of 3500 stems/ha will achieve crown closure at approximately 4 m in height (Farnden 1996). After crown closure, tree crowns make contact, though collision intensity is low since slenderness coefficients are still low. Low collision intensities allow the crowns to fill most of the canopy and the canopy texture becomes smoother, thus individual crown wind loads are low. Hence the stage is set for a subsequent decrease in tree SC's; bending stresses are alleviated by wind sheltering neighbours and competition for light begins as neighbours limit lateral growing space.

Competition mortality

When competition for resources is intense enough to cause tree mortality, stands enter into the 'stem exclusion phase' (Oliver and Larson 1990), otherwise known as the 'zone of imminent competition mortality' (Farnden 1996), where suppressed shorter trees can perish in the inadequate understory light regime. Collision intensity is greatest in this phase of development due to three factors. 1. Slender boles: since height growth is paramount to survival and bending stresses are mild as tree sways are dampened via close neighbours, there is little allocation to radial growth. 2. Height: taller trees can displace further by virtue of their increased length. 3. Canopy texture: formation of mortality gaps increase wind penetration and individual crown wind loads. However, even with the increased sway potential with the presence of mortality gaps, self-support is not necessary as remaining adjacent tree crowns assume the role of sway damping.

As the occurrence of stand level decline in productivity is closely timed with the onset of intense crown collisions and the decline of percent crown cover, I strongly suspect they are causally linked. The reduction of canopy cover from crown collisions could easily cause leaf area to decline. Since crown shyness increases with height, it is probable that the mechanism of abrasion is active and affecting tree vigour until the 'old growth' stage of stand development.

Traditional gap theory suggests that individual tree mortality creates gaps in the canopy that are either filled by surrounding trees or provide an improved light regime to other suppressed individuals that then ascend into the canopy (Runkel 1982). In pure even-aged stands of lodgepole pine, recruitment of other pine into the overstory is rare as there is only one canopy layer and little establishment within a few years of stand initiation. Therefore, filling mortality gaps is constrained to lateral growth of surviving individuals. The ability of surviving individuals to fill the canopy and emerging mortality gaps is constrained by the intensity of crown collisions, as the collisions tend to increase areas of crown shyness. Furthermore, the line between crown shyness and mortality gaps becomes blurred, as tree crowns experiencing crown abrasion would have difficulty reclaiming canopy openings, but the effect on percent crown closure is clear - it declines.

I believe the influence of crown collision on crown shyness may be particularly important in forests with cold winters. Because winters are long and there is increased brittleness of branches as air temperature declines below 0° C (Lieffers *et al.* 2001), increased potential for crown abrasion is likely during the northern winter (Robertson 1993). Crown collisions are an important factor in the observations that declines in stand productivity with age are most severe in northern forests (Gower *et al.* 1996) and that boreal forests have some of the most clumped canopies in the world (Kucharik *et al.* 1999).

Scattered canopy dominants retain their low SC as their wind exposure insures a constant bending stress and allocation to radial growth. Thus, their displacement and loss of leaf area due to collisions is relatively low. Their height advantage insures a superior light regime and carbon supply and insures the greatest chance of surviving the competition mortality phase of development.

Old growth

If a given stand of lodgepole pine avoids destruction from its typically frequent fire return interval, it will reach its final phase of development - old growth. I presume that this stage of development typically has low intensity crown collisions due to low slenderness coefficients and increased spacing. Low slenderness coefficients are required for survival at this stage of development as individual crown wind loads are large and sway damping collisions are low in intensity. Provided that stand break-up is not too rapid, self-supporting structure develops as further mortality (via other agents), gradually increases individual crown wind loads and bending stress. Furthermore, individuals that survived the competitive exclusion phase would include many canopy dominants with an already typically low SC.

Thus, with increased wind loads and decreased sway damping the surviving individuals begin to structurally resemble open grown trees. With decreased crown collisions and increased light, the crown lateral growth is increasingly only limited by its biological potential. Thus, the now self-supporting trees resume stem proportions more similar to their juvenile phase. This is perhaps the basis for perpetuating the notion (e.g. assumption in the size/density relationship) that all trees retain the same proportions throughout its development and that any changes (particularly in bole slenderness) are inconsequential for the stand function and structural development.

Application

Productivity prediction

In forestry, the index of relative density (RD) is used to describe the level of stand occupancy by considering the average tree size and density. Based on the maximum size-density relationship, RD is an indicator of competition intensity over a range of stem sizes and densities. In closed canopy stands, RD is thought to describe the amount of crown development compared to a standard (usually an open grown individual) (Curtis 1982). In describing the amount of crown development, RD assumes that tree crowns will fill all available space (up to its open grown potential) via lateral growth. This implicitly assumes that density or environmental conditions control lateral crown extent and therefore RD is insensitive to a biomechanical mechanism of crown shyness. That relative density can accurately predict percent crown cover is built into tree growth models, regardless of stand phase of development. As I believe tree biomechanics and crown wind loads control crown shyness in many stands, incorporating the change of tree proportions into the size density relationship, I can more accurately predict the dynamics of forest crown cover and productivity.

Local wind conditions

Knowledge of local wind conditions can be used to the advantage of the forest manager. As wind intensity profoundly affects the forest stand structure and function, knowledge of its local intensity could provide insight into the stand level development of structure. For instance, the prediction of average bole volume could be improved if, like other stand level variables affecting tree growth (water balance, nutrients, stand age), local wind conditions could be considered. If wind flow patterns and intensities could be mapped at a landscape scale managers could adjust their initial stocking densities and thinning regimes to compensate for high winds or take advantage of milder winds by fewer expensive thinning interventions. To maintain higher amounts of leaf area in high wind areas more frequent thinning would be required to reduce foliage loss due to crown abrasion. The cost of increased thinning might be justified by the increased volume yields due to consistently high bending stresses.

New frontiers

Direct evidence

While fresh branch tips are commonly found on the forest floor following a wind event, I have not directly observed branch breakage from tree crown collisions. Therefore, while our findings strongly support crown collision as the mechanism for crown shyness, our evidence is circumstantial. The need remains to directly evidence the link between the action of crown collisions and the frequency and volume of branch breakage. The direct evidence of crown damage caused by crown collisions would provide a clear explanation as to the mechanism causing crown shyness.

Crown abrasion and lateral growth inhibition

I have identified two possible effects of crown collisions: crown abrasion and lateral growth inhibition. The relative roles of these two factors in the maintenance of crown shyness are unknown, though I suspect their relative roles are dependent upon crown collision intensity and frequency. Crown abrasion is more easily identifiable as branch tips could be traced to their former attachment. I suspect there exists a threshold value of crown collision intensity (mediated by temperature) at which branch breakage begins to occur.

To understand the more subtle effect of growth inhibition would require further research into thigmomorphogenesis (plant morphological response to touch). Recent advances in thigmomorphogenesis indicate touch sensitive genes can begin the signal transduction chain in response to gentle contact (Braam and Davis 2000). Chronic exposure to controlled mechanical perturbation in tree seedlings indicates that growth inhibition responds in a nonlinear fashion to increased stimulus (Telewski and Pruyn 1998). The effect of growth inhibition from inter-crown contact has not been directly studied but is identified as a logical next step (Frank Telewski, personal communication).

Thresholds of bending stress

The amount of bending stress needed to induce increased radial growth is unknown but is also under the scope of thigmomorphogenesis. Knowledge of the thresholds of bending stress above which radial growth is induced would aid forest managers prescribe efficient thinning regimes, without unduly removing leaf area and reducing productivity at the stand level. Understanding bending stress thresholds would guide silvicultural prescription that would produce the desired radial increment without structurally destabilising the stand and making it susceptible to catastrophic wind throw.

Age-related decline

The suggested causes of age-related decline include: increase in respiration cost, increase in hydraulic resistance, decreasing nutrient supply, physiological changes associated with aging, increased reproductive effort, and reduced leaf area from inter-crown abrasion (Ryan *et al.* 1997). While my results support a biomechanical connection to age-related decline in even-aged lodgepole pine (and its affect of reduced leaf area from inter-crown abrasion) (Smith and Long 2001), more research is needed to clarify the relative roles of other proposed causes of age-related decline. For instance, age-related decline that occurs in open grown trees cannot be explained with the mechanism of crown collisions since mechanical interaction is not occurring between widely spaced crowns. In the case of open grown trees, increasing respiration costs related to increasing maintenance tissue due to large branches and bole volumes seems the most plausible driver of decline (Kramer and Kozlowski 1979; Waring and Schlesinger 1985). Hence, it is possible that there are disparate mechanisms operating to produce the decline in productivity, depending upon the structure of the stand.

If trees do have different pathways toward productivity decline which depend on stand level structural attributes, then uneven-aged stands which possess a mixture of structural arrangements, could posses a complex combination of mechanisms causing growth decline that make the approach of finding a single driver incomplete. Clearly, more research is needed on the role of mediators (such as wind) on the feedback between tree structure and function.

References

Braam, J. and Davis, R.W. 1990. Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in Arabidopsis. Cell, 60: 357-364.

Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. Forest Science, 28(1): 92-94.

Farnden, C. 1996. Stand density management diagrams for lodgepole pine, white spruce and interior Douglas-fir. Canadian Forest Service. Victoria, British Columbia, Information report BC-X-360.

Gardiner, B.A. 1994. Wind and wind forces in a plantation spruce forest. Boundary-Layer Meteorology 67: 161-186.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. Trees- Structure and Function, 11:378-382.

Kramer, P.J. and Kozlowski, T.T. 1979. Physiology of woody plants. Academic Press, New York, NY.

Kucharik, C.J., Norman, J.M. and Gower, S.T. 1999. Characterization of radiation regimes in non-random forest canopies; theory, measurements, and a simplified modeling approach. Tree Physiology, 19: 695-706.

Lieffers, S.M., Lieffers, V.J., Silins, U. and Bach L. 2001. Effects of cold temperatures on breakage of lodgepole pine and white spruce twigs. Canadian Journal of Forest Research, 31(9): 1650-1653.

Oliver, C.D. and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, New York.

Robertson, A. 1993. Effects of wind on boreal forests. *In* Forest development in Cold Climates. *Edited by* J. Alden. Plenum Press, New York.

Raupach, M. R. 1988. Canopy transport proscess. pp 95-127. In: Flow and Transport in the Natural Environment: Advances and Application. (eds) W. L. Stephan and O. T. Denmead. Springer – Verlag, Berlin.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, 63(5), 533-546.

Ryan, M.G, Binkley D. and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Advances in ecological research, 27:213-262

Smith, F.W. and Long, J.N. 2001. Age-related decline in forest growth: an emergent property. Forest Ecology and Management, 144: 175-181.

Telewski, F.W. and Pruyn, M.L. 1998. Thigmomorphogenesis: a dose response to flexing in Ulnus americana seedlings. Tree Physiology 18, 65

Waring, R.H. and Schlesinger, W.H. 1985. Forest Ecosystems: Concepts and Management. Academic Press, Orlando, FL.

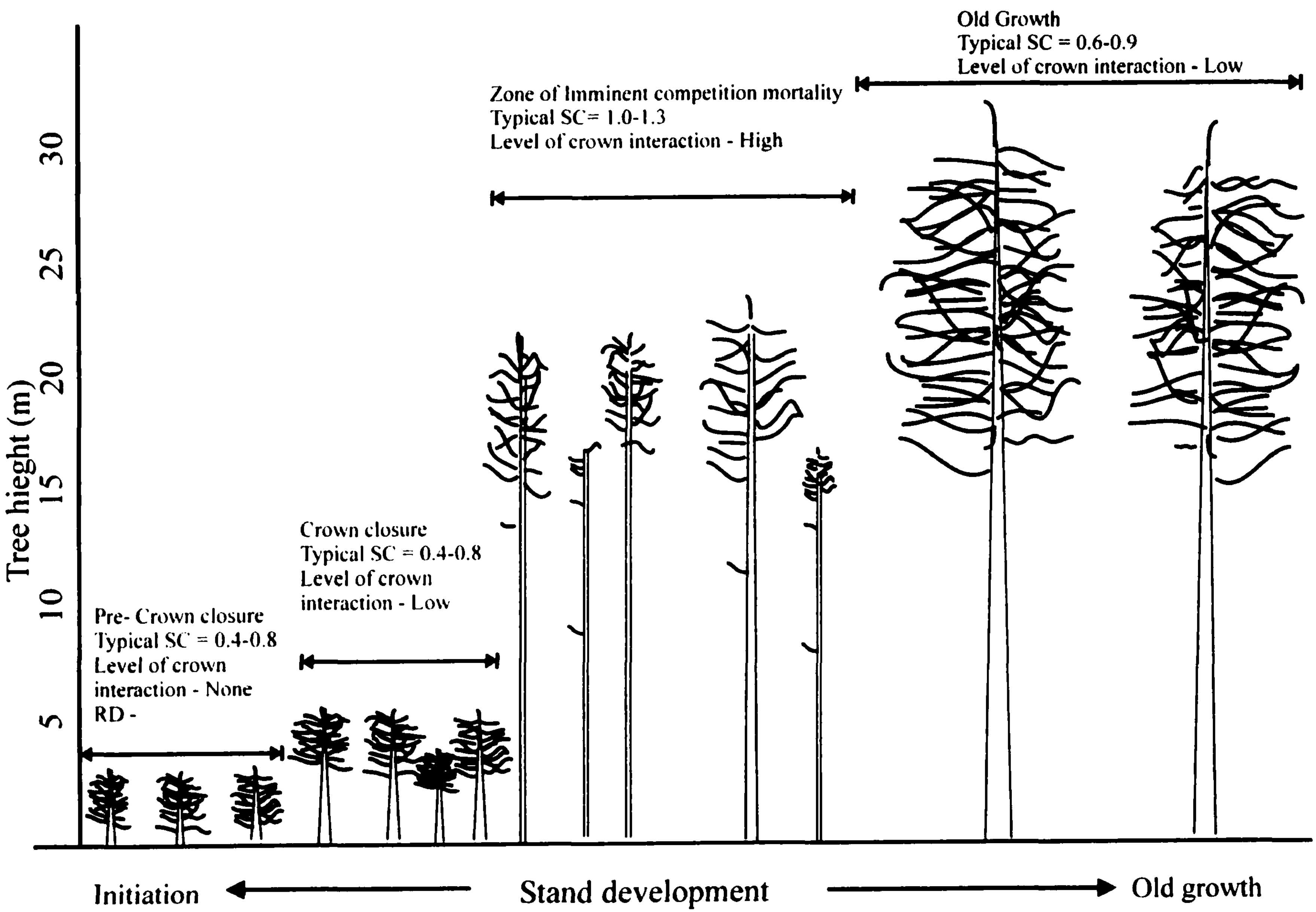

Figure 5-1. Suggested conceptual illustration of stand development in terms of its structural aspects.

Appendix A: Calculating the percent crown cover

Triangle area and angles

With the three sides of the triangle a, b and c (Figure A1) equal to the distance between trees, and typically forming a scalene triangle, I can calculate the area of any triangle T with Heron's formula.

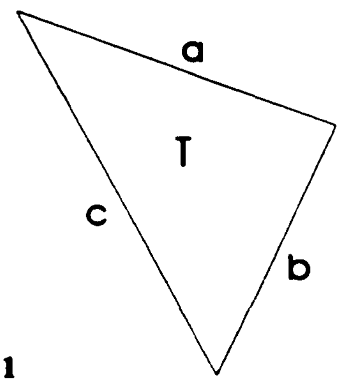

Figure A1

[A1] $T = \sqrt{s(s-a)(s-b)(s-c)}$

where the semi-perimeter s is

[A2] $s = (a+b+c)/2$

The law of cosines enables the calculation of any angle given the three sides.

[A3] $c^2 = a^2 + b^2 - 2ab\cos C$.

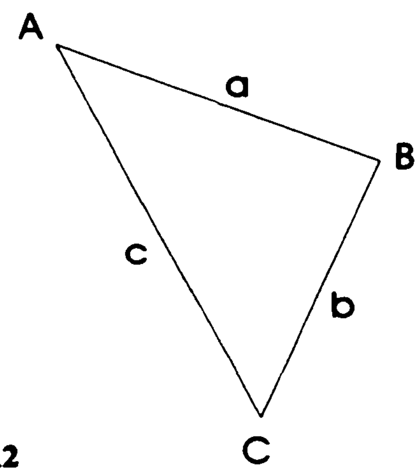

Figure A2

For an output in radians, the angle *C*, opposite of side *a* (Figure A2) I use

[A4] $$C = \theta = \frac{\arccos(a^2 - c^2 - b^2)}{-(2b^2c^2)}$$

and similarly for angles *A* and *B*

[A5] $$A = \theta = \frac{\arccos(b^2 - a^2 - c^2)}{-(2a^2c^2)}$$

[A6] $$B = \theta = \frac{\arccos(c^2 - b^2 - a^2)}{-(2a^2b^2)}$$

I then convert the angles in radians to degrees

[A7] $$\theta \deg = \frac{\theta \text{ rad } 180}{\pi}$$

Crown area

Now that all side lengths and angles are known, I can calculate the area of tree crown that lies in the triangle, which is represented by a sector (Figure A3). The area of a sector is

[A8] $K = \pi r^2 \theta \deg / 360$

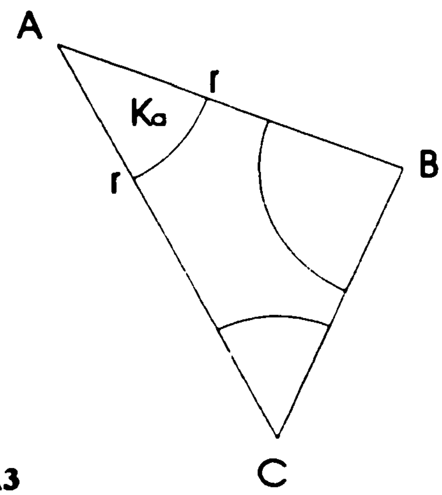

Figure A3

where r is the radius and mean crown extent for each tree. Summing the three sector areas gives the total area of crown cover in the triangle.

[A9] $K = K_a + K_b + K_c$ = crown cover area

Dividing the total crown area by the triangle area gives the percent of triangle area covered by crown.

[A10] K / T = % crown cover

Crown area with overlap

In the case of tree crowns overlapping each other, I have the intersection of two circles, which creates a lens-shaped region (Figure A4). When crown sector areas are summed for the area of crown cover K, any area of overlap is counted twice (as part of each sector) causing an error in the crown cover estimation.

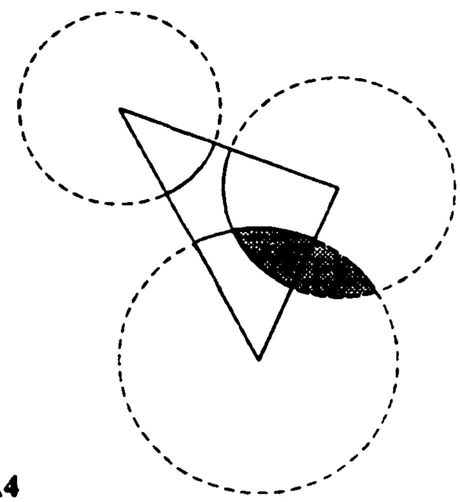

Figure A4

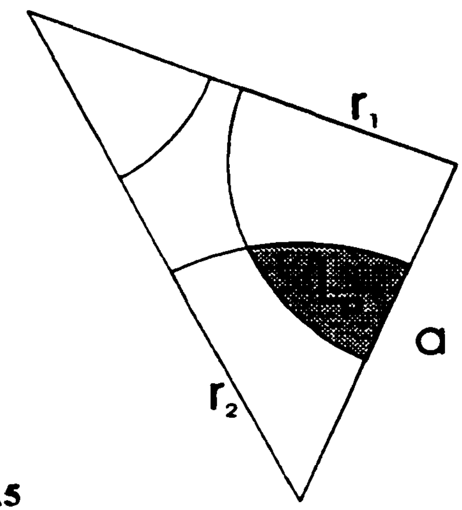

Figure A5

To correct for this error I calculate the area of circle intersection within the triangle (shaded area Figure A5). The lens is typically asymmetrical as crown sizes are unequal requiring a formula to solve all cases.

[A11]
$$L_a = r_2^2 \arccos\frac{(a^2 + r_2^2 - r_1^2)}{2ar_2} + r_1^2 \arccos\frac{(a^2 + r_1^2 - r_2^2)}{2ar_1} - \frac{1}{2}\sqrt{(-a + r_2 + r_1)\cdot(a + r_2 - r_1)\cdot(a - r_2 + r_1)\cdot(a + r_2 + r_1)}$$

Since up to three pairs of crowns can overlap, all crown overlap areas are similarly calculated using formula [11]. The sum of half-lens areas L are subtracted from K, the total crown cover, for a corrected crown cover area, K'.

[A12] $L = L_a + L_b + L_c$

[A13]

$$\acute{K} = K - L$$

Hence, if any crown circles overlap I divide the corrected crown cover area, $\acute{K}$, by the triangle area T for the percent crown cover.

[A14] $\acute{K} / T =$ **% crown cover**