Growth responses in individual eastern white pine (*Pinus strobus* L.) trees following partial cutting treatments

by

Eddie Bevilacqua

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for the degree of Doctorate of Philosophy
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Eddie Bevilacqua

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Abstract

White pine (*Pinus strobus* L.) growth following a partial cutting treatment was analyzed to assess the growth response of individual trees from three different crown classes to varying levels of local neighbourhood competitive interference. Trees from all crown classes, with an average age of 69 years, showed increased rates of diameter, basal area and volume growth following release. Only intermediate trees responded with increased height growth.

Specific volume increment (SVI) proved superior to relative growth rate for assessing competition effects on size-dependent volume growth by virtue of its greater sensitivity to and better correlation with indices of competition. Significant differences in SVI among crown classes in both released and control treatments 23 years after release were observed. Released trees had increased levels of SVI for the first 15 years following treatment. The hypothesis of size symmetry in resource competition was rejected by virtue of the stronger relationship between SVI and competition indices that weighted competitors by relative size. However, two-sided competition could not be rejected in view of the significant influence of smaller trees on SVI of larger trees. No difference between intra- and inter-specific competition on white pine growth was detected.

Plasticity in growth form was evident. Intermediate trees exhibited significantly different crown and stem form among crown classes in the control treatment, and different crown form relative to the release treatment. Crown size, which was positively correlated with volume increment, improved as a result of competition release and was inversely correlated with levels of local neighbourhood competition. Vertical distribution of bole area increment in all crown classes was altered in the release treatment. Bole area increment in released trees increased progressively from tree apex to base of the stem for the first 15 years after partial cutting, eventually resulting in significant changes in stem form. Control trees showed relatively constant area increment below the crown with no significant change in stem form.

A cumulative volume growth model based on initial tree size, age, and local neighbourhood competition was developed for use in white pine stands managed under a partial cutting regime, such as the uniform shelterwood system.

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List of Abbreviations

a_h = Bole cross-sectional area at height h above ground

APA = Area potentially available (Voronoi polygon constructed by bisecting distance between each competitor and subject tree at a right angles, and joining right angle lines to form a polygon)

ba = Basal area (bole cross-sectional area at breast-height)

bh = Breast height (1.37 m above ground)

D = Tree diameter-at-breast-height

d_h = Tree diameter at height h above ground

$d(a_h)/dt$ = Rate of growth of bole cross-sectional area at height h

$d(\mathrm{ba})/dt$ = Rate of growth of bole cross-sectional area-at-breast height

$d\mathrm{D}/dt$ = Rate of growth of diameter-at-breast height

$d\mathrm{V}/dt$ = Rate of growth of main bole volume

$d\mathrm{W}/dt$ = Rate of growth of whole plant

FF = Form factor (measure of tree form based on tree volume to volume of standard of revolution)

FC = Form class (measure of tree form based on ratio of diameter at half tree height to diameter-at-breast-height)

GE = Growth efficiency (rate of bole volume growth per unit leaf area)

H = Total tree height

h = Height above ground

LA = Total plant leaf area

LAR = Leaf area ratio (total leaf area to total plant weight)

RGR = Relative growth rate (rate of bole volume growth per unit bole volume)

RPR = Relative production rate (rate of change in growth per unit of growth)

SA = Total bole surface area

SVI = Specific volume increment (rate of bole volume growth per unit bole surface area)

ULR = Unit leaf rate (rate of plant growth per unit leaf area)

V = Total volume of main bole of tree

W = Total plant weight

1. Introduction

Eastern white pine (*Pinus strobus* L.) was the most important commercial tree species that initiated the start of the lumber industry in Canada and the northeastern United States (U.S.) in the 1700s (Horton and Bedell 1960, Aird 1985, Angus 1992). The fine grain, light colour and easily workable wood derived from squared timber and lumber played a significant role in the history and development of Canada and Ontario (McNutt 1985). Early demand for pine by England, in the form of squared timber, helped develop important commercial and political ties. However, the main era of pine harvesting occurred in the latter part of the 1800s, when the commercial trade for white pine lumber with the U.S. was in full bloom (Aird 1985). Harvest levels for pine from crown land in Ontario peaked immediately prior to 1900 at just under 150 M ft^3 (4.25 M m^3).

The importance of the pine harvest to Canada's balance of trade diminished steadily after 1900 due to a number of factors, including overharvesting, lack of adequate reforestation in terms of both quantity and quality, and conversion of forested lands to other uses (Aird 1985). Although white pine is not as significant a commercial commodity as it once was, it is still an important tree species in Ontario and Quebec. The demand for white pine lumber has been relatively constant over the past 50 years (Wray 1986), producing an average annual harvest of approximately 25 M ft^3 (0.7 M m^3) per annum from 1935 to 1984 (Aird 1985).

Despite some regulation of the pine harvest in the 1800s, the resource itself was not managed under any sustainable silvicultural system. It was recognized as early as the 1850s that pine forests had to be managed if the current level of harvest was to be sustained. As early as the 1930s, attempts were made to plant and seed pine on abandoned agricultural land and cutover areas. The use of the clear cutting silvicultural system was not particularly well suited to the silvics of white pine, since the species is unable to compete with broadleaf species on the more fertile sites. In addition, the susceptibility of the species to white pine weevil (*Pissodes strobi* [Peck]) often resulted in almost 100% infestation in plantations, producing poor quality stems that were usually unsuitable for commercial purposes (Gross 1985, Houseweart and Knight 1985, Jones 1992).

The difficulties associated with regenerating and managing white pine under a plantation system proved to be so enormous that, in the 1950s, it appeared that the Ontario government's "acknowledged policy ... was liquidation of white pine" (McNutt 1985). However, this policy changed in the 1960s, and significant research into white and red pine (*Pinus resinosa* Ait.) ecology, silviculture and management by both Canadian and U.S. federal governments, provincial governments, and universities resulted in a number of symposia (Cameron 1978, Anon 1985, Funk 1986, Stine and Baughman 1992, Monty 1994) and detailed reports (Horton and Bedell 1960, Horton and Brown 1960) on the tree species. More recently, public scrutiny of forest management has placed increased pressure on the white pine resource for values other than quality timber, e.g., wildlife, tourism, recreation and old-growth ecosystems.

Given the historically poor success rate with clear cutting and planting, recent emphasis in Ontario has been to manage white pine under the uniform shelterwood system (Pinto 1992, Corbett 1994). Shelterwood harvesting involves removing portions of the mature overstory pine trees over a series of partial cuts that promote the establishment and growth of a new forest stand before the original trees are finally harvested. While this silvicultural system may not meet all the demands on the resource, such as the maintenance of old-growth white pine ecosystems, it promotes successful regeneration of the species (Heckman 1992, Pinto 1992, Rajala 1992) while still providing a supply of wood products. Before forest managers adopt the shelterwood system with any confidence, it is important that they have some knowledge of the growth response of mature residual trees following different degrees of partial cutting (C. Corbett[1], *pers. comm*; M. Woods[2], *pers. comm.*).

Knowledge of the growth response of white pine to partial cutting is also important to forest managers who are attempting to accelerate forest succession in natural mixed species stands by removing the non-pine component in the hop[3]es of converting them to white pine cover-types. In both situations, a better understanding of the competition process within

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[1] Carl Corbett, Chief Forester, Algonquin Forestry Authority, Huntsville, Ontario

[2] Murray Woods, Growth & Yield Specialist, Ont. Min. Nat. Res., Southcentral Sci. Sect., North Bay, Ont.

white pine stands is required. Both management activities create residual stands that are spatially heterogeneous in nature. In such circumstances, it has been suggested that the degree of competitive interference on individual plant growth is best assessed through the use of neighbourhood competition models rather than average density (Weiner 1984, Goldberg 1987, Newton and Jolliffe 1998). However, the appropriate method of measuring growth response, particularly in perennial plants such as trees, has been questioned (Brand *et al.* 1987). The first objective of this study is to demonstrate an alternative size-dependent measure of growth for use in the assessment of tree responses to indices of competitive interference.

Although current tree size is a reflection of historical cumulative competitive interference, larger and (or) older trees may continue to exhibit higher absolute growth rates compared to smaller trees when subjected to similar levels of competitive interference (Ford and Sorrensen 1992, Larocque and Marshall 1988). Therefore, it is more beneficial to assess the influence of spatial competitive interference on different sized trees by using size-dependent growth rather than absolute growth (Ford and Sorrensen 1992, Larocque 1998). One measure of size-dependent growth often used in studies with annual plants is the relative growth rate (RGR) (Weiner and Thomas 1986, 1992). RGR has been equated with the growth efficiency or capacity of a plant (Briggs *et al.* 1920a, 1920b, Fitter and Hay 1987) and with growth performance (Hunt 1982).

In forest growth studies, the growth of the main stem has often been substituted for the total tree biomass in the determination of RGR. Size-dependent measures of stem growth have recently been used in competition studies of forest grown species, and they have included the RGR of the main stem in terms of volume (Larocque and Marshall 1993, Stoll *et al.* 1994, Larocque 1998) and diameter-at-breast-height (Peterson and Squiers 1995). However, a limitation of using RGR when studying older trees is the progressively decreasing contribution of annual increment on the value of size-dependent growth as trees age. This is the result of the proportionally larger amount of nonproductive stem wood at the center of the main bole. Since all increment along the bole originates from the cambial tissue along its surface, another measure of size-dependent growth would be the volume increment per unit cambial area - the specific volume increment (SVI) (Shea and Armson 1972). Very few studies were found which employed individual SVI in the assessment of growth due to local competitive interference (Newton and Jolliffe 1998) or in response to release (Piene 1981).

2. Hypotheses

Four null hypotheses were tested in this dissertation:

I. There is no difference in the utility of the relative growth rate (RGR) of stem volume and specific volume increment (SVI) as a measure of size-dependent growth for assessing the competition effects on tree growth.

II. The uptake of contested resources in white pine is not proportional to tree size (i.e., size-symmetric).

III. White pine does not exhibit plasticity in growth form under competition and in response to release.

IV. There is no difference between intra- and inter-specific competition on size-dependent stem growth in white pine.

The approach used in this thesis to study the process of competition in white pine was to observe growth responses following release in relation to competitive interference. This consisted of analyzing the relationships between size-dependent stem volume growth of subject trees and cumulative competitive interference from neighbouring trees. The alternative hypothesis to the first null hypothesis is that SVI is more sensitive to, and better correlated with, the level of local competitive interference around subject trees. Compared to RGR, SVI is, therefore, a more appropriate index of size-dependent growth.

The second null hypothesis is that there is no size symmetry in the uptake of contested resources in white pine. Peterson and Squiers (1995) suggest that competition is size-symmetric in mixed aspen (*Populus* spp.)-white pine stands, which they attribute to a greater relative importance of belowground competition. However, their conclusions were based on measurements of intra-specific competition only. When the assessment was based on cumulative intra- and inter-specific competition, they could not find any significant correlation between the relative diameter growth of white pine and competitive interference.

From their results, it is not completely clear whether competition in white pine stands is size-symmetric, or the degree to which competition is one-sided (i.e., larger trees influence growth of smaller trees, but not vice-versa) or two-sided (i.e., smaller trees can also influence growth of larger trees). The approach used to study competition symmetry in this dissertation was to stratify competitors into height classes in relation to the subject tree, and assess the relationship between SVI and the accumulation of competitive interference with decreasing relative height.

A third null hypothesis is that white pine does not exhibit plasticity in growth form under competition and in response to release from competition. Plasticity in plant growth form suggests that allometric relationships may be, in part, a result of competitive interactions between plants (Weiner and Thomas 1992). In this dissertation, this was studied in terms of both crown architecture and the vertical distribution of annual bole area increment in relation to canopy dominance and release from competition. Variation in crown architecture reflects alternative strategies between survival under present conditions and height growth for future gain (Takahashi 1996). This was assessed by comparative analysis of crown dimensions among crown classes in control trees and following release, and by the relationship between crown size and the cumulative competitive interference of neighbouring trees.

The effect of crowding on plant shape, e.g., height to diameter ratio, has been shown to occur in both annual plants (Weiner and Thomas 1992) and trees (Larson 1963, Berry 1971). In addition, annual bole area increment in released trees has been observed to be greater in the lower bole relative to the upper bole of tree stems (Thomson and Barclay 1984, Tasissa and Burkhart 1997). The degree and duration in the variation of the vertical distribution in area increment with canopy dominance and release from competition has not been studied in white pine. The approach used to study temporal changes in the vertical profile of growth in this dissertation was to model bole area increment from tree apex to breast height on subject trees through time, and assess parameter estimates in relation to canopy dominance and elapsed time since treatment.

A fourth null hypothesis is that there is no difference between intra- and inter-specific competition on size-dependent stem growth in white pine. In the past, most research on competition modelling in forestry has focused on intra-specific competition. Reasons for this may have been the opportunity to design experiments with more uniform control of competition at the individual tree level in primarily monospecific plantations of commercially important species. Information on inter-specific competition is important for white pine since it is often found growing in association with both conifer and broadleaf species. Peterson and Squiers (1995) indicate that white pine growth on dry sites in enhanced by the local abundance of *Populus* spp. However, their results were based on data containing uneven distributions of intra- and inter-specific competition at varying levels of overall competition. The approach used to assess intra- and inter-specific competition in this study was to stratify neighbourhood competitors based on species group (i.e., white pine and non-white pine), and assess the cumulative competitive interference of the two species groups on size-dependent stem growth.

The research described in this dissertation is aimed at elucidating a greater understanding about the competition process within white pine stands by observing the growth response of individual trees following a partial cutting treatment and analyzing the relationship between the growth response and indices of local neighbourhood competition. This is important information needed before investigating the influence of site and its interaction with level of harvesting following any partial cutting treatment.

3. Literature review

3.1 Eastern white pine ecology, growth and management

3.1(a) Pine species worldwide

The genus *Pinus* contains over 100 species (Mirov 1967) and is arguably the most researched genus of trees worldwide (Gholz *et al.* 1994). There are two main categories of pine trees, the subgenus *Strobus* (Haploxylon, "white" or "soft" pines) and the subgenus *Pinus* (Diploxylon, "yellow" or ""hard" pines). The defining morphological trait of haploxylon pines is their single fibrovascular bundle (Anon 1993) or longitudinal vein (Farrar 1995) per needle, compared to the two fibrovascular bundles per needle found in diploxylon pines.

Other distinguishing characteristics of haploxylon pines include: fascicles contain five needles and have a deciduous sheath; stomata are found only on the adaxial surface of needles; wood is generally whiter and softer with less prominent annual rings than diploxylon pines; and shoots are uninodal (the spring shoots produce only one whorl of branches per year). This contrasts with diploxylon pines, which have fascicles of two to five needles, generally harder and yellower wood with more pronounced annual growth rings, and either uninodal or multinodal growth.

Eastern white pine is the tallest tree in eastern Canada (Farrar 1995) and the only haploxylon pine that grows naturally in northeastern North America. Investigations into the timing of growth initiation and cessation has shown that eastern white pine completes shoot and needle extension in a relatively shorter period of time compared to other pines, while maintaining diameter growth longer into the growing season (Dougherty *et al.* 1994). The duration of diameter growth may be a factor influencing the characteristics of wood formation.

The distinct annual rings in diploxylon pines are a result of the abrupt transition between the formation of early- and latewood xylem cells within a growth year. This contrasts with haploxylon pines, which have a gradual transition between the xylem cell types. Characteristics used to distinguish early- and latewood cells (e.g., relative radial diameter and secondary wall thickness) are attributes controlled by the concentration of plant growth regulators within the cambial region of a tree stem (Little and Savidge 1987). The different wood characteristics between haploxylon and diploxylon pines may be the result of differences in the spatial and temporal distribution of growth regulators. The less prominent annual rings in haploxylon pines, such as *P. strobus*, are possibly related to a gradual, progressive drop in auxin concentration within the cambial region over the growing season (see section 3.4(b) "*Theories on stem form*").

Pinus strobus needles have a relatively low longevity, averaging between two to three years, compared to the wide range of longevity values reported for other pine species (c.f. Schoettle and Fahey 1994) (Table 1). Leaf longevity is influenced by environmental conditions both across and within species (Schoettle and Fahey 1994). The short leaf longevity in eastern white pine implies that the species must allocate a large proportion of its

Table 1: Maximum height of various haploxylon pine species and associated leaf longevity.

Species	Common name	Maximum height[1] (m)	Leaf longevity[2] (years)
Pinus lambertiana	Sugar pine	75	2-3
P. monticola	Western white pine	70	3-4
P. strobus	Eastern white pine	67	2-3
P. strobiformis	Southwestern white pine	30	3-4
P. flexilis	Limber pine	26	5-6
P. balfouriana	Foxtail pine	22	10-12
P. albicaulis	Whitebark pine	21	7-8
P. edulis	Pinyon	21	4-9
P. longaeva	Bristlecone pine	16	10-30
P. aristata	Colorado bristlecone pine	15	8-15

[1] Source: Anon (1993)
[2] Source: Schoettle and Fahey (1994)

resources on an annual basis to replace the high percentage of leaf area it loses each year. There appears to be an inverse relationship between leaf longevity and maximum cumulative height growth for species within the haploxylon subgenus (Table 1). The tallest pines (i.e., *P. lambertina, P. monticola,* and *P. strobus*) have lower leaf longevity compared to shorter haploxylon pines. This is consistent with a conceptual model reported by Schoettle and Fahey (1994) on the inverse correlation between annual shoot growth and leaf longevity.

However, the relative shade tolerance of *P. strobus* (Vose *et al.* 1994, Wetzel and Burgess 1994) compared to other pines does not fit well with the observation that shade tolerant and late successional species retain more leaf cohorts (Schoettle and Fahey 1994). The adaptability of *P. strobus* to vary leaf longevity with changing light intensity within the crown and canopy (Whitney 1982) may be a mechanism of maintaining higher leaf areas under sub-optimal light conditions. Species that have the greatest shade tolerance generally have the greatest maximum leaf area index (i.e., leaf area per unit ground area) (Vose *et al.* 1994).

3.1(b) Ecology

Pinus strobus grows throughout northeastern North America from Newfoundland in the east to Manitoba in the west, and extends south to Georgia in the U.S. Since the natural range of eastern white pine is the result of an interaction between a complex array of site, climatic and ecological factors, it is difficult to assess the main causal factor controlling white pine distribution (Horton and Bedell 1960). However, logging, settlement and fire (Stiell 1978) have modified the original distribution of white pine. Perera and Baldwin (1993) describe the current spatial distribution of white and red pine in Ontario.

The species has a tendency to be most abundant in regions with relatively stable, dry climates (Hills 1952, Horton and Bedell 1960). The northern limit of white pine, however, appears to be controlled by temperature (i.e., frost-free period) (Haddow 1948, Horton and Brown 1960). Spalding and Fernow (1899) found that the distribution of pine in the Lake States was "entirely controlled by the character of the soil, all sandy areas being pinery proper". Although white pine is generally found on warmer than normal sites containing soils with a high sand content (Hills 1952, Stiell 1978, Mader 1986, Kershaw 1993), it grows well on a wide range of soil textures and moisture regimes.

When growing in mixed forests, white pine is often associated with red oak (*Quercus rubra* Du Roi), jack (*Pinus banksiana* Lamb.) and red pine on very dry soils; red pine, white spruce (*Picea glauca* (Moench) Voss.), aspen (*Populus* spp.) and white birch (*Betula papyrifera* Marsh.) on moderately dry to fresh soils; and balsam fir (*Abies balsamea* (L.) Mill.), hemlock (*Tsuga canadensis* (L.) Carr.), red spruce (*Picea rubrens* Sarg.) and tolerant hardwoods on fresh soils (Kershaw 1993). The species grows best on fresh to moist, well-drained, loamy soils, but is often unable to compete with tolerant hardwoods on these sites.

White pine's apparent preference for drier conditions on low to medium productivity sites with sandy soils may be a reflection of its greater ability to tolerate drier conditions and a higher fire frequency relative to hardwoods (Horton and Bedell 1960, Mader 1986). Drier sites are generally more prone to fire, and white pine is considered to be a fire-adapted species. Horton and Bedell (1960) suggest that climate is not directly responsible for natural pine distribution, but it may play an indirect role through fire history.

Fire exposes mineral soil and helps reduce competing vegetation (Maissurow 1935, Methven 1973, Methven and Murray 1974) and is considered to be fundamental for white pine regeneration (Bromley 1935, Maissurow 1935, Henry and Swan 1974, Methven and Murray 1974, Abrams *et al.* 1995). Older white pine trees can survive frequent, light fires by virtue of their thick bark that insulates the cambium. They become the main source of seed for the next forest. Kershaw (1993) indicates that most of the current pine stands in central Ontario were established when a good seed year coincided with a fire. However, when fire frequency and (or) severity increases, large overstory pines and advanced white pine regeneration may be destroyed.

The loss of a seed source in burned stands may have contributed to the decline of white pine in eastern Canada (Maissurow 1935). Often, the original stand is displaced by other pioneer species including aspen or white birch. However, white pine has the ability to establish under aspen and birch canopies through the dispersal of seed by wind, provided a nearby seed source exists. It often takes 20 to 40 years after a fire for white pine to colonize aspen-birch sites (Kershaw 1993), and results in the establishment of multi-species, multi-cohort stands. A significant portion of the current distribution of white pine in central Ontario is found in mixed stands of trembling aspen (*Populus tremuloides* Michx.), white birch, white spruce, jack and red pine, and red oak established following widespread fire in the late 1800s (Kershaw 1993).

White pine is also capable of exploiting any available space and will successfully establish itself in small openings under a tolerant hardwood canopy, usually as individual trees or in small groups (Cline and Lockard 1925, Hibbs 1982). This is partially a result of white pine's moderate shade tolerance. Relative to other pines, white pine is considered more shade tolerant (Spalding and Fernow 1899, Stiell 1978, Schoettle and Fahey 1994, Wetzel and Burgess 1994), and has been noted to maintain maximal height growth at light levels as low as 45% full sunlight (Logan 1966). This may be a competitive advantage for white pine since its shade tolerance allows it to persist longer than red pine on the forest floor (Kershaw 1993) and maintain a presence, albeit as an understory species, for a number of years (Hawley 1936, Stiell 1978, Stearns 1992). This characteristic also probably contributes to its ability to respond to release after extended periods of suppression as an understory species (Berry 1982, Kelty and Entcheva 1993).

Small-scale disturbances in the forest create openings in the canopy. The ability of a suppressed individual to increase growth and fill in a canopy opening in response to small disturbances is a mechanism by which shade-tolerant species eventually reach the upper canopy (Fajvan and Seymour 1993, Kershaw 1993). Since white pine is considered only moderately shade tolerant, the relative importance of this mechanism to white pine is not clear. Fajvan and Seymour (1993) observed normal size distributions, typical of shade-intolerant species, in white pine growing in mixed red spruce-hemlock stands. However, they also found that white pine responded to disturbance with increased growth and, despite being present in all crown classes, showed a clear illustration of dominance and emergence in the stands.

Hibbs (1982) suggests that it is rare for advanced white pine reproduction, which has been suppressed for greater than 10 years, to successfully respond to a release from competition. Fowells (1965) also indicates that response declines rapidly with age and decreasing crown length. However, white pine saplings have been reported to respond with increased height and (or) diameter growth following a partial removal of the overstory after much longer periods of suppression, with smaller trees often showing the greatest response (Downs 1943, Berry 1982, Kelty and Entcheva 1993). Abrams and Orwig (1996) also report that older white pines exhibit the ability to survive prolonged periods of depressed growth with increased radial growth, presumably due to canopy disturbances. Responding to release allows white pine to gradually dominate a stand when growing in association with shorter lived hardwood species (Stearns 1992, Kershaw 1993, Stiell *et al.* 1994, Peterson and Squiers 1995).

Other factors influencing white pine's ability to respond to release include site, the rate of needle retention under different light intensities and root grafts. Wendel (1970) and Yawney (1961) observed greater responses to thinning in white pine on high quality sites compared to low quality sites. Whitney (1982) established that needles of shade-grown trees have double the mean life expectancy of those on open-grown trees. This would permit understory trees to maintain larger quantities of needle biomass, and make use of an extended growing season in the understory of a deciduous forest. Open-grown trees maintain high leaf areas by increased rates of needle formation and lateral branch development per shoot, which produces a relatively denser crown (Whitney 1982). In addition, despite uninodal shoot growth, favourable light conditions may lead to a second flush in shoot elongation in white pine, provided there were sufficient needle primordia in the overwintered terminal buds (Owston 1968).

Root grafts are an almost universal occurrence in white pine stands (Adams 1935, Bormann and Graham 1959, Graham 1959, Bormann 1961, 1966). Most authors suggest that root grafts provide additional absorptive surface and (or) stored food reserves to growing trees. There is evidence that an intact tree supplies photosynthates and growth regulators to the bole and roots of a grafted tree or stump. Stumps with roots grafted to intact trees showed cambial activity after cutting and may survive for up to 10 years after cutting (Bormann 1961). The cambial activity is the result of food and auxin translocation through grafts from intact trees.

Bormann (1966) conducted a series of experiments to assess the non-competitive growth relationships between grafted trees. His results showed that when two trees with functional crowns are grafted together, one tree could not redirect significant amounts of water and minerals from the other tree. However, suppressed trees with poor crown development and little "transpirational pull" may benefit from root graft(s). Supporting this conclusion is the observation that non-grafted suppressed trees often contain missing rings down the main stem to the base of the bole (Bormann 1965). This is in contrast to trees with root grafts which maintain continued xylem development in the roots and up to 3.3 m above the base of the tree (Bormann 1966), despite having no diameter growth further up the stem. This suggests "that food and growth regulators move through root grafts from dominant trees" to suppressed trees (Bormann 1966). It also suggests that root grafts may allow suppressed trees to survive despite being overtopped by larger competitors and delay the death of individuals. This could allow them to respond to later, more favourable conditions.

Death of a tree eliminates the pull of transpiration, causing a cessation of water and nutrient uptake, and there may be some utilization of the dead tree's root system by survivors. This may partially explain why growth rates of residual trees increased following partial cutting. Supporting this hypothesis, Graham (1959) demonstrated that residual, intact trees take up dye injected into nearby cut stumps. Bormann (1966), however, found that non-grafted roots of stumps die within a year, with only grafted roots remaining functional. This suggests that intact trees cannot use entire root systems of stumps for absorption of water and nutrients. He concluded that "such utilization is relatively inefficient" and there is no experimental evidence to suggest that residual trees gain an advantage from cut stumps through root grafts.

Bormann (1966) concluded that non-competitive relationship between grafted trees involved the following:

1. The development of white pine stands is shaped by two ecological forces: competition and non-competitive inter-tree food translocation.
2. If both trees are dominant, there is a balanced exchange of food (i.e., photosynthates and growth regulators) without significant exchange of water and minerals.
3. If one tree is dominant and the other is suppressed, the suppressed tree acts as a hemiparasite in which the dominant tree provides food but is not compensated by additional supplies of water and minerals.
4. If one tree is dominant and the other is dead (stump or snag), there is a neutral relationship in which minor amounts of food are supplied to the stump and the dominant tree gets minor quantities of water and minerals in return.

3.1(c) Growth

Like most other tree species, height growth in white pine is strongly influenced by site conditions. Height is often used to quantify site productivity, e.g., site index curves based on height over age. In reviewing the soil variables which are best correlated with height growth, Mader (1986) found that the best sites for white pine were those with relatively poor drainage (high moisture availability), with finer than average soil texture, high water holding capacity, and high soil pH.

Height growth is generally less in pines than broadleaf trees (Spurr 1956, Hibbs 1982), and white pine grows more slowly than other pines, such as either red or jack pine, when compared on similar sites during the early part of its life (Horton and Bedell 1960). This will result in white pine being overtopped early in stand development, especially on dry sites (Horton and Bedell 1960, Stiell 1978). However, if given enough growing space and in the absence of weevil or blister rust (*Cronartium ribicola* J.C. Fisch.), white pine maintains a relatively constant rate of height growth for over one hundred years and will overtop most other species by age 50 to 70 years. Height growth declines somewhat during the second century, but continues slowly but evenly for another century or two (Spalding and Fernow 1899, Stiell 1978). Some exceptional individuals exceed 75 m in height (Spalding and

Fernow 1899, Anon 1993). Generally, the maximum height for this species is around 45 m on the best sites (Stiell 1978, Botkin 1993), but more commonly ranges from 35 to 40 m.

If severe enough, competition between individual trees will lead to differentiation of individuals into crown classes early in a stand's development (see section 3.2 "*Competition as a spatial process in forest stands*"). White pine differentiates more quickly than other pine species, e.g., red pine (Burns and Irwin 1942). However, white pine can shift from one crown class to the next by responding to an opening in the canopy. Downs (1943) showed how overstory removal of broadleaf species in a mixedwood stand increased the height growth of understory white pine from 17 to 62%. If no distinct overstory develops, whether in pure or mixed stands, density has little effect on height growth (McCormack 1956), and release due to thinning in older stands has been reported to have no effect on height growth in any crown class (Smithers 1954, Fenton and Pfeiffer 1965).

Unlike height growth, which is highly influenced by site, diameter growth at breast height is more directly controlled by crown size, which is indirectly influenced by stand density (i.e., competition). Mature white pine trees have irregular shaped crowns with long, horizontal isolated branches (Stiell 1978). As stands develop, canopy closure occurs and crown size stabilizes. Crown width averages 6.8 m in mature pine and is generally limited by mutual shading and abrasion. In general, white pine responds well to repeated thinning with increased diameter growth. A detailed description of diameter growth responses in white pine to competition is given in "*Partial cutting effects on tree growth*" (section 3.5). Cumulative diameter growth of exceptional old growth individuals has been reported to reach 183 cm at breast height (Anon 1993), while the maximum diameter observed in mature white pine today is in the range of 91 to 101 cm (Stiell 1978, Botkin 1993).

Stem taper results from the vertical variation in cambial activity along the bole. It is also a reflection of crown development and location, and is highly influenced by competition. The vertical variation in tree ring-widths is known as the growth layer profile of a tree (Fayle 1973). Bormann (1965) and Hunt (1968) reported on how the vertical distribution of cambial activity along the main bole of dominant white pine trees resembled that of other species (see section 3.4 "*General growth principles of stem form*"). Bormann (1965), however, could detect no pattern of area growth along the bole in suppressed, 60-year-old white pine trees, when they were sampled at every tenth internode. Year-to-year differences in maximum and minimum ring area occurred anywhere along the bole. He noted, however, that maximum area growth normally occurred in the upper internodes and that, as a proportion of the total, growth shifted to the upper internodes as total growth declined in suppressed trees.

A number of quantitative expressions are used to define stem taper or form, including form factor, form class (Avery and Burkhart 1994), and taper functions (Reed and Byrne 1985, Newberry and Burkhart 1986, Newnham 1988, 1992). Form factor (FF) expresses the deviation of the volume of the main stem from some standard solid, normally a cylinder. FF values vary from 0.40 for older trees to 0.50 for younger trees. An average FF of 0.45 for dominant, 100-year-old white pine is reported (Spalding and Fernow 1899). Form class (FC) measures the ratio of the diameter at half tree height above breast height to diameter-at-breast height, expressed as a percentage. Stiell (1978) gives values of FC between 65 - 75 for white pine under 120 years of age. Lower values of FC were found for more open grown trees, with a rapid increase in FC occurring with crown closure.

Unless the tree environment is drastically altered, the shape of the growth layer profile does not vary significantly from one year to the next, although year-to-year variation in tree ring-widths is still evident. Dendroclimatic analysis of tree ring-width data for white pine suggests that precipitation in the early part of current year's growth is the most significant climatic variable influencing diameter growth, although there are some residual effects of the previous year's rainfall (Goldthwait and Lyon 1937). Changes in the growth layer profile due to alterations in the local environment are discussed in section 3.5 "*Partial cutting effects on tree growth*".

3.1(d) Management

As previously mentioned, original harvesting of white pine in North America paid very little attention to regeneration. Spalding and Fernow (1899), in their detailed description of the commercial importance of this tree species, made some policy recommendations and outlined general principles for the successful management of white pine. They recommended that a "proper policy to grow white pine preferably, if not altogether, in mixture with other species," based on knowledge that "mix growth is in every respect superior to pure growth", and that better development (i.e., less taper) was always observed when pine was grown in mixed stands.

This recommendation was intended for managing existing stands in order to maintain the current area of white pine. They did note, however, that this may not be possible due to "our irrational exploitation [that] has reduced the white pine ... to such an extent that its reestablishment is possible only by artificial means" (Spalding and Fernow 1899). Early efforts at reforesting regions of eastern Canada and northeastern U.S. with white pine in the early 1900s was done using single species plantation forestry practices. While monospecific plantations work well for some species, e.g., red pine and Norway spruce (*Picea abies* L.), white pine had its own unique set of problems (Horton and Bedell 1960, Jones 1992).

When grown on highly fertile, loamy sites, the species is often outcompeted by hardwoods (Hibbs 1982). If tending treatments successfully reduce hardwood competition, vigorous pine growth often results in weevil and/or blister rust attacks. The ultimate result is that white pine plantation management requires considerable planning and effort, making such ventures a high-risk proposition (McNutt 1985, Wray 1986)

A review of the literature since 1950 (Horton and Bedell 1960, Cameron 1978, Funk 1986, Stine and Baughman 1992) reveals that most research on white pine has focused on how to manage even-aged, monospecific stands or plantations. This information was required on account of the abundant pine plantations and natural, even-aged stands that developed in abandoned fields and pastures in the northeastern U.S., which make up the largest proportion of white pine in the northeast (Gould 1986). The use of plantation management techniques to convert less desirable hardwood stands to white pine was recommended (Foster 1986).

While clear cutting with either artificial or natural regeneration was still recommended as late as the 1960s (Horton and Bedell 1960), shelterwood management is preferred for white pine management today (Wray 1986, Heckman 1992, Pinto 1992, Rajala 1992, Kelty and Entcheva 1993, Corbett 1994). Smith (1986) provides an overview of this silvicultural system. Heckman (1992), Pinto (1992), Rajala (1992) and Corbett (1994) provide examples of how shelterwood management has been successfully applied to white pine.

3.2 Competition as a spatial process in forest stands

Although the process of competition between individual trees in a forest stand is still not fully understood, Ford and Sorrensen (1992) have outlined five axioms to explain competition:

I. Plants modify their environment as they grow thereby reducing the resources available for growth of other plants. This defines the occurrence of competition.
II. The primary mechanism of competition is spatial interaction.
III. Plant death due to competition is a delayed reaction to the reduction in growth that follows resource depletion.
IV. Plants respond in plastic ways to environment change, and this affects not only the result of competition, but also its future outcome.
V. There are species differences in the competition process.

It is generally agreed that interplant competition is mainly for light, water, soil nutrients and physical growing space within a given distance around a subject tree. Crowding reduces the average growth rate of individual trees, but it does not necessarily influence all individuals in the same way (Weiner 1988, Schwinning 1996, Schwinning and Weiner 1998). The variability in individual growth response to increased competition within plant populations will increase the size variation among individuals (Weiner 1988) and, possibly, the development of size hierarchies or canopy dominance classes, depending on the shade tolerance of the species (Ford and Sorrensen 1992). A general positive correlation between plant size and relative growth rate is an indication of asymmetry in competition within a population, leading to increasing levels of growth suppression in small plants through time (Schwinning 1996, Schwinning and Weiner 1998). The death of suppressed plants, known as density-dependent mortality, is a time-delayed response to competition.

When density-dependent mortality occurs, there is a prevailing tendency in plant populations to develop a spatial evenness in the distribution of large individuals (Ford 1975, Kendel 1988, Ford and Sorrensen 1992). This is a further indication of the spatial process of competition. Spatial evenness occurs regardless of whether light or soil resources are assumed to be most limiting. Since the direct measurement of resource use is extremely difficult, much of what is hypothesized about the competition process is inferred based on simple observations of disproportionate resource use and mathematical models attempting to quantify spatial competitive interference (Perry 1985, Brand and Magnussen 1988, Weiner *et al.* 1990, Ford and Sorrensen 1992, Schwinning and Weiner 1998).

Ford and Sorrensen (1992) distinguish four general categories of mathematical competition models: (i) competition on regular lattice plantings; (ii) neighbourhood models for irregular spacing; (iii) models describing the distribution of stand structure and increment by plant size; (iv) models of self-thinning, based on the relationship between mean plant-size and mean plant density. All categories of models have axiom I as their central assumption, but only lattice and neighbourhood models explicitly incorporate spatial interaction (axiom II) to quantify competitive interference. Both models assume that the number, size and proximity of neighbouring trees can be used as a surrogate for the degree to which resources needed for growth are being diminished by competition.

In the forestry literature, growth and yield models that attempt to incorporate competitive influences into predictions of total stand increment have generally focused on (a) modelling stand structure distributions and growth symmetry based on distance-independent competition, (b) the use of self-thinning models within stand-density management diagrams, and (c) more recently, adopting neighbourhood, distance-dependent competition models on individual-tree growth. The first two approaches are stand-level methods that generally focused on even-aged, monospecific plantations of relatively uniform size trees. They have had limited applicability to multi-cohort, multi-species stands where the competitive interactions around individual trees are more complex. Neighbourhood models have the potential of detailing the spatial interactions with greater accuracy and precision in forest stands containing greater spatial heterogeneity.

3.2(a) Stand structure and growth symmetry

Variation among individuals is a central aspect in the study of populations of organisms, and growth and size variation among individual plants is one principle of population dynamics of interest to both foresters and ecologists. One of the most frequently observed effects of competition is the dynamic response in stand structure (i.e., size variation) of even-aged plant populations through time. As the total biomass in crowded populations increase, the variability in size of individuals increases (Weiner and Thomas 1986, Hara 1988). Tree populations tend to be normally distributed early in stand development and then become positively skewed (preponderance of smaller trees) through time (Ford 1975). The rate at which size distributions change is species dependent, and is a reflection of the mode of competition between plants and the degree of shade tolerance of the species.

The mode of competition can be described in terms of both one- or two-sidedness (Brand and Magnussen 1988) and size symmetry (Schwinning and Weiner 1998). Perfect size symmetry in competition is said to occur when there is a proportional allocation of a limited supply of resources to all competitors in relation to their relative size (Weiner and Thomas 1986, Schwinning and Weiner 1998). A departure from this in which larger competitors acquire more than their proportional share of limited resources is termed size-asymmetric competition. The increase in size variability in high-density plant populations has been interpreted as strong support for the hypothesis that competition is size-asymmetric (Schwinning 1996). In reality, the competition process within plant populations falls along a continuum from a resource depletion process (symmetrical) to a resource preemption process (asymmetrical) (Weiner and Thomas 1986, Newton and Jolliffe 1998).

The resource preemption process places greater importance on above-ground resources, as large competitors prevent, or pre-empt, light from reaching smaller competitors by overtopping and shading them. Since there has been no observed pre-emptive mechanism in the competition for water and nutrients (Schwinning 1996), asymmetrical competition is often considered one-sided, in that large neighbours influence the growth of smaller trees, but the growth of larger trees are not affected by smaller trees. One-sided competition usually denotes that light is the primary limiting factor (Ford and Diggle 1981). The development of a bimodal size distribution is an indication of one-sided competition resulting from the spatial process of crown interactions (Ford and Newbould 1970, Ford 1975, Perry 1985). The continued existence of a distinct lower canopy of over-topped plants is dependent on the shade tolerance of the species (Ford and Sorrensen 1992).

The resource depletion process is thought to also involve competition for water and nutrient resources in which individuals deplete available soil resources in direct proportion to their relative sizes. This implies that competition is two-sided and that all trees are affected by competition, namely that neighbouring smaller-sized individuals affect the growth of large trees. A resource preemption process does not necessarily preclude two-sided competition for soil resources (Newton and Jolliffe 1998). In a study conducted to separate the competition effect from these other factors influencing stand structure, Brand and Magnussen (1988) found that the competition process was both asymmetric (i.e., small trees lose vigour more rapidly than large trees with increasing density) and two-sided (i.e., growth reduction in larger competitors caused by increased abundance of smaller competitors) within red pine plantations.

Population density, however, is not the only factor affecting stand structure, as size distributions are inherently dynamic through time. It can be shown that size distributions will shift without competition from normal to positively skewed due to the exponential growth of individuals within initially normally distributed populations (Perry 1985). Changes in size distributions are also influenced by differences in initial size, age, vigour (Weiner 1988), microsite (Brand and Magnussen 1988), spatial pattern of local density (Miller and Weiner 1989), and rates of resource uptake and resource use efficiencies (Schwinning and Weiner 1998).

3.2(b) Self-thinning relationship

As even-aged stands develop, competition increases and suppressed trees eventually die. This is termed density-dependent mortality, or self-thinning, and proceeds as a continuous process. The -3/2 power law of self-thinning proposed by Yoda *et al.* (1963) was based on the consistent relationship between average plant size and stand density (equation [1]) in even-aged monocultures.

$$[1] \qquad \log_e(\overline{W}) = \log_e k + \gamma * \log_e(N)$$

where $\log_e(W)$ is the natural logarithm of average plant size, $\log_e(N)$ is the natural logarithm of stand density, k and γ are constants.

Equation [1] has been used to represent the maximum average plant size at a given level of density, with the slope of the equation (i.e., γ) approximately equal to -3/2 for most species. The slope defines the relationship between mortality of suppressed trees and growth of surviving trees, thus defining the self-thinning law. Perry (1985) outlines two unique properties of this relationship: (1) the magnitude of variation in intercept and slope among species is very small; and (2) there is little site-related variation within a given species.

Detailed studies of the self-thinning law provide empirical evidence of the amount of variation within the competition process. Attempts have been made to explain a possible mechanism of the self-thinning relationship based on population mean allometry (i.e., proportional allocation of growth among corresponding components) (Long and Smith 1984, Weller 1987, Weiner and Thomas 1992, Osawa and Allen 1993). Weiner and Thomas (1992) distinguish between the use of allometric relationships from individuals of different sizes at one point in time from those derived from one individual through the course of its development. Osawa and Allen (1993) indicated that individual allometric relationships should not be used to test the allometric theory of self-thinning due to the variability of tree sizes in the population, and that population means are more appropriate. Their results indicate that the size-density relations in self-thinning populations can be explained by the redistribution of a constant level of total foliage among fewer individuals. This implies that the self-thinning model may indirectly account for the plasticity in mean plant response to increasing levels of competition through time (axiom IV). Further, differences in stem form (height to basal area ratio) for different species will give differences in the k parameter of equation [1] (axiom V) (Norberg 1988).

The self-thinning relationship has been the basis for the development of stand density management diagrams (Drew and Flewelling 1979). The self-thinning law is useful for (a) describing the growth trajectory of surviving trees in even-aged monocultures, where size differential between trees is quite small, and (b) quantifying competition based on average tree size and number. However, as with most studies involving even-aged plantations showing little variability in tree size, the results are based on the size or growth of the average tree. Hence, they do not reflect size variability within a plant population, the spatial process of competition at the individual tree level, nor do they provide detailed information on the competition process. As such, they have limited applicability in uneven-aged stands with high variability in tree size or spatially heterogeneous stands.

3.2(c) Neighbourhood competition models

The development of neighbourhood models for quantifying competitive interference in forest tree species has been met with varying success (Perry 1985, Larocque and Marshall 1988). Perry (1985) indicates that "competition indices by themselves explain a disappointingly small proportion of variation in tree growth". The most significant predictor of tree growth is a tree's current size. This is to be expected based on results obtained using biomathematical growth functions to model plant growth (see section 3.3 "*Individual-tree growth models*"), and the fact that a tree's current size is a reflection of its past cumulative competitive interactions.

Perhaps the reason for this poor predictive ability of competition indices is the lack of knowledge of which resources are most limiting as a result of competition. Perry (1985) suggests that two-sided competition indices may not completely reflect the competition process when light is the most limiting factor. However, most indices make the implicit assumption that light rather than moisture is the most limiting factor (Larocque and Marshall 1988). In addition, as the study by Brand and Magnussen (1988) demonstrates, two-sided competition does exist. Furthermore, as Korstian and Coile (1938) and others have shown, the presence and growth of understory plants in dense conifer plantations is limited more by soil moisture, as a result of root competition by overstory trees, than by light resources. For understory white pine growth and survival, Yeaton (1978) indicates that belowground competition is more important than competition for light on poorer sites.

The main application of competition indices appears to be in conjunction with existing empirical or biomathematical growth models (Larocque and Marshall 1988) (c.f. discussion section 3.3 "*Individual-tree growth models*"). All competition indices assume that the number and size of individuals within a defined neighbourhood can quantify the level of competitive interference around an individual tree. The focus of many early studies was on what constitutes a 'competitor'. Initially, the neighbourhood was defined as a circular area of fixed radius around a subject tree and all trees within this area were considered competitors. The approach worked well for young plantations where tree size was relatively uniform. However, in older spatial heterogeneous stands with variable tree size, this approach tended to ignore large individuals located just outside of the circular area, and gave most weight to smaller individuals who contributed little or no competitive influence within the neighbourhood. Consequently, a variable radius plot was used to define the competition neighbourhood, using an angle gauge to select competitors (Spurr 1962, Opie 1968, Martin 1982). With this approach, the probability of a neighbouring tree being selected as a competitor is a function of distance and size. Empirical evidence showed higher correlations between competition indices and periodic annual growth of subject trees with variable radius than fixed radius plots.

Individual-tree growth models used in forest management are often classified by the method in which the competition index is calculated (Avery and Burkhart 1994). *Distance-independent models* are indices in which the aggregate of all competitors is used to derive a stand-level expression of competition, without using the distance between competitors and subject tree. Indices that explicitly incorporate the distance between each competitor and the subject tree are termed *distance-dependent models*. Distance-dependent indices may be better predictors of tree growth due to their more complex nature, more accurate description of the spatial environment around each tree and increased level of detail needed to calculate the index (Avery and Burkhart 1994).

Distance-independent measures of competition include: number of competitors; total basal area of competitors; total basal area of competitors larger than the subject tree; and crown competition factor, which is the sum of the crown projection area of all competitors based on open grown crown width.

The numerous distance-dependent indices that have been developed can be catalogued into one of three categories, based on the original derivation of the index (Avery and Burkhart 1994). Ford and Sorrensen (1992) added a fourth category by classifying Spurr's (1962) Point Density Index (PDI) as a distance-dependent index, although others consider this to be a distance-independent model. Table 2 lists the categories of distance-dependent competition indices while Figure 1 illustrates the basic concepts used in the derivation of each category of index.

In general, models based on Crown Overlap accumulate the influence of competitors by determining the amount of unattainable, or pre-empted, resources normally required for optimal growth (i.e., the amount below the level available under no competition), and assume

Table 2: Categories of distance-dependent competition indices used to quantify competitive stress around individual trees [based on Avery and Burkhart (1994)].

Category of distance-dependent competition index	Principle involved in its derivation
i. Crown Overlap (CO): (Staebler 1951)	Defining a zone of influence around subject tree and each competitor (proportional to open-grown crown width), and accumulating the distance overlap between competitor and subject tree zones
ii. Point Density Index (PDI): (Spurr 1962)	Measure of point density that considers the weighted average basal area per unit area affecting a point or tree
iii. Area Potentially Available (APA): (Brown 1965)	Construction of a Voronoi polygon around subject tree defining potentially available growing space based on the location of competitors
iv. Size-Distance Ratio: (SDR): (Hegyi 1974)	Weighting the competitive effect of a competitor directly by its size relative to the subject tree and inversely by its distance from the subject tree

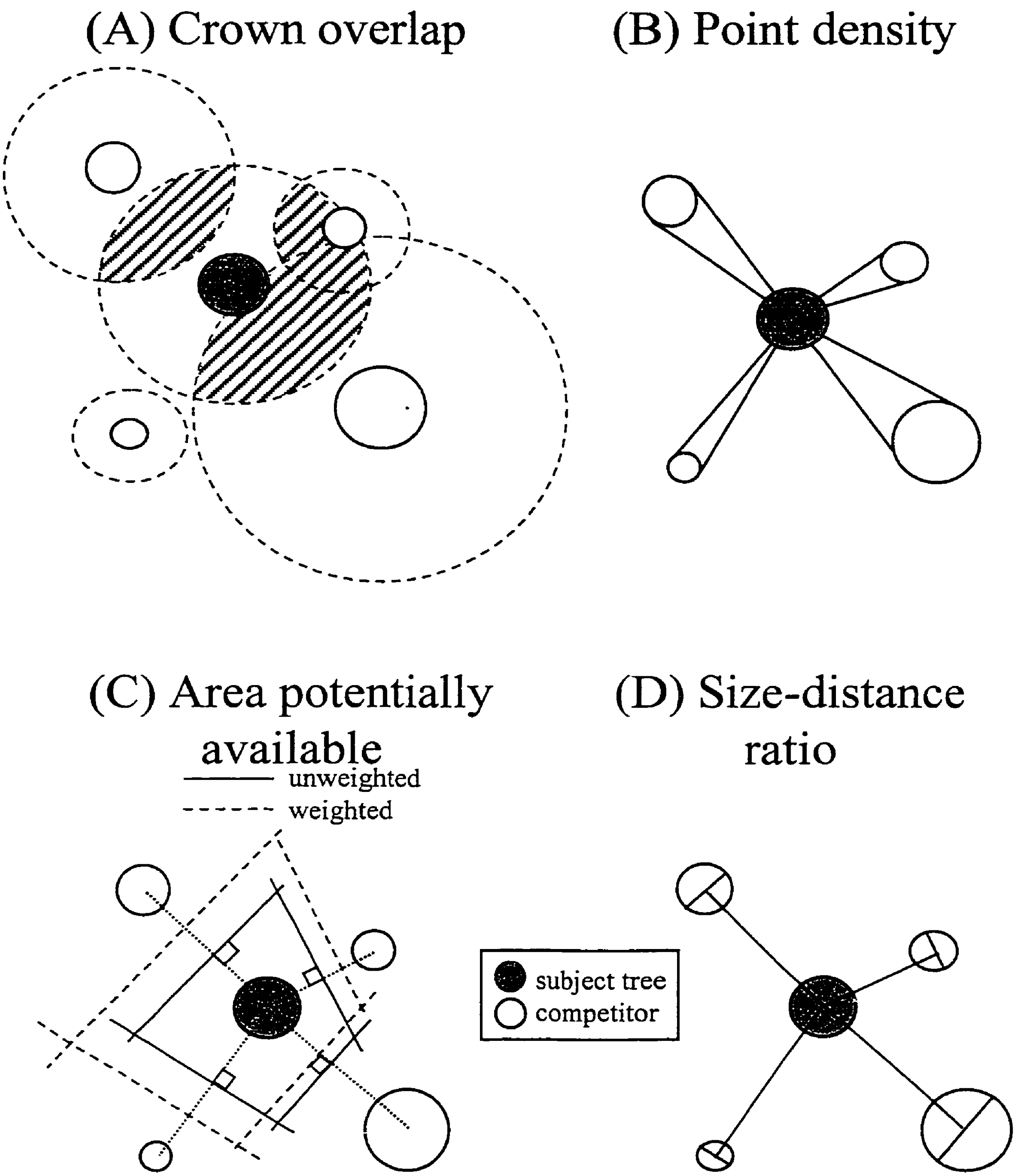
that competition is one-sided. By contrast, indices based on Area Potentially Available (APA) define the net amount of growing space (and resources) which is available for growth to the subject tree and assume that competition is two sided (Weiner 1988). The size-distance ratio has no direct spatial interpretation, except that the greater the number of competitors, the larger the index value. APA is the only index in which the spatial location of competitors is explicitly required in its computation.

Each of the above categories includes a number of variants that expand upon the original concept. For example, Staebler's (1951) crown distance overlap was modified by (i) Newnham (1964), who measured the angle subtended at the intersections of the overlap of the two zones of influence, (ii) Bella (1971) and Arney (1972), who considered the area of overlap, weighted by relative competitor size, and (iii) Opie (1968), Alemdag (1978) and Tome and Burkhart (1989) who modified the definition of area of influence, originally a function of open-grown tree crown radius, to involve linear functions of stem diameter.

Brown's (1965) APA was modified by Moore *et al.* (1973) to weight the distance of a polygon's side from the subject tree by the relative competitor size. Rouvinen and Kuuluvainen (1997) took Spurr's (1962) ratio of competitor diameter to distance from subject tree and accumulated the horizontal angle subtended by this ratio for all competitors, weighted by relative competitor size.

A number of studies have been carried out to compare the efficacy of these competition indices in predicting tree growth (Opie 1968, Daniels 1976, Alemdag 1978, Martin and Ek 1984, Daniels *et al.* 1986, Pukkala and Kolstrom 1987, Tome and Burkhart 1989, Biging 1992, 1995, Schreuder and Williams 1995, Wimberly and Bare 1996, Rouvinen and Kuuluvainen 1997). Ford and Sorrensen (1992) suggest that a weighted APA seems to be the most effective. However, the results from these studies have had varied success, with no index being superior in all instances. Some indices appear species-specific, simple indices may work as well as more complex measures, and performance may vary with the stage of stand development and the management activities (Perry 1985, Larocque and Marshall 1988, Avery and Burkhart 1994). It is unclear whether the lack of generality of any competition index is a result of variation in species responses to competition or a lack of correlation between the level of competitive interference and the index.

Ford and Sorrensen (1992) suggest that the next step in the analysis of the competition process will be the study of competition for specific resources. However, this process-based approach to understanding competition will require a greater understanding of the plasticity in plant morphology under competitive stress, and the development of models of the distribution of resource availability around a plant, both for light and soil resources.



(A) Crown overlap

(B) Point density

(C) Area potentially available

(D) Size-distance ratio

Figure 1: Illustration of four categories of distance-dependent competition indices (A) Crown overlap. (B) Point density. (C) Area potentially available. (D) Size-distance ratio.

3.2(d) Effects of intra- and inter-specific competition on individual tree growth

According to Perry (1985), physiological (i.e., the amount of carbon fixed per unit leaf area) and morphological (i.e., crown architecture) growth responses are directly affected by competition. At the individual tree level, the physiological and morphological responses will vary both the amount of total growth and its distribution among tree components (i.e., allometry). This may include increasing allocation to plant organs involved in the uptake of the most limiting resource (Schwinning 1996) or modifying growth within a particular plant component [e.g., changes in the growth pattern along the main stem (Larson 1963, Bormann 1965)].

As a stand approaches crown closure, branch production is reduced due to abrasion and mutual shading, and crown recession shifts the effective live crown upwards. As the development of a tree hierarchy emerges, dominant trees are generally most efficient in producing stemwood per unit of photosynthetic tissue, while suppressed trees are the least efficient (Satoo *et al.* 1954, Waring *et al.* 1980, Gilmore 1996). However, within any particular crown class, trees with large crowns generally have more and larger branches and thus have less photosynthetic tissue per unit of respiratory tissue. They tend to be less efficient in stemwood production than trees with fewer and smaller branches (Assmann 1970), which may be explained by the higher demand for photosynthate by the larger branches (Ford 1985, Takahashi 1996).

In forest stands, the onset of competition will initially decrease ring widths within individual trees evenly along their whole bole. As competitive interference intensifies, there is a proportionally greater decrease in stem growth below the crown; in some instances, there is no xylem production in the lower bole, resulting in missing rings. Local neighbourhood interference has a greater effect on the growth layer profile relative to average population density. The length of time a tree can survive without any xylem development in the lower bole varies by species. Turberville and Hough (1939) reported older white pine with 28 missing rings (unknown if these were consecutive years) and Harris (1952) reported 11 consecutive years without diameter growth in *Pinus radiata*. Without any release from competition, suppressed trees will eventually die.

Variations in resource acquisition rates and plant growth among species affect the degree to which the level of inter-specific competition by neighbouring plants affect the growth of an individual (Ford and Sorrensen 1992). In predominantly mono-specific stands, all individuals have approximately the same resource demands. In multi-species stands, biological differences in resource requirements (e.g., differences in shade tolerance) may affect the competition process, and possibly the self-thinning relationship (Weller 1987).

Tilman (1982) developed a theory on resource competition and community structure within multispecies communities in which he argues that the species with the lowest minimum requirement for the most limiting resource (i.e., the minimum level of a resource below which population is unable to maintain itself) will be the superior competitor (Grace 1990). The theory is based on the assumption that the best competitor is the one that is able to tolerant resource depletions resulting from the utilization of limited supplies by neighbouring plants. Fajvan and Seymour (1993) conclusions that inter-specific differences in shade tolerance were a cause of canopy stratification in mixed red spruce-hemlock-white pine stands support Tilman's theory. In their work, they found that white pine, a relatively shade intolerant species compared to spruce and hemlock, dominated the upper canopy. The spruce and hemlock showed the ability to persist for extended periods of time with the low light levels found in the lower canopy and display the capability to increase growth rates following partial disturbances. This permits them to eventually reach the upper canopy after many decades of suppression, eventually replacing the pine in the overstory.

Similarly, Peterson and Squiers (1995) observed that the relative diameter growth of white pine exhibits a stronger correlation with competitive interference when aspen competitors are negatively weighted (i.e., better pine growth when in close proximity to aspen than further away). This would support that theory that different degrees of resource requirements (i.e., pine less light demanding than aspen) will affect competitive success. Their results, however, could be the result of the uneven distribution of intra- and inter-specific competition at different levels of overall competition (i.e., mainly intra-specific competition when competition was high, and both intra- and inter-specific competition when competition was low).

Grime (1979) proposed a different theory of plant competition and population structure. His theory is based on the capacity of an individual plant to capture and better exploit the same resources required by neighbouring plants. Under this theory, the superior competitor is the species with the highest maximal growth rate (maximum capacity of resource capture). This theory is supported by the findings of Liu and Burkhart (1994), who observed that hardwood species (i.e., *Quercus* spp., *Carya* spp., and others) were more competitive than loblolly pine when growing together under high levels of overall competition. Eventhough both species groups had ecologically similar resource demands, the hardwoods were better able to capture light resources. Grace (1990) concludes that one of the differences between Tilman's and Grime's theories is their somewhat different objectives and definition of competition. Because of the tradeoff between being tolerant of low resource levels and high relative growth rate, Grime's theory constrains species from being both tolerant to resource shortages and efficient at exploitation (Grace 1990). Tilman (1982) defines competition in terms of tolerance to low resource levels while Grime (1979) interprets competition with respect to the ability to capture resources.

These results suggest that the species mix in the local neighbourhood influences the effect of competitive interference on individual white pine growth and that this may be related to differences in the degree of shade tolerance of the species involved.

3.3 Individual-tree growth models

Earlier work in modeling plant growth mainly consisted of applying biomathematical curves, developed for studies of either chemical reactions or population dynamics, to the growth of individual plants. This approach was used to provide "simple empirical relationships which would ... sum up many individual measurements of attributes of growing plants" (Evans 1972). Some of the most common growth functions tested were the autocatalytic, monomolecular and logistic curves, all which include a variable to describe a constant intrinsic rate of growth.

Although such growth curves illustrate an average growth trajectory that occurs during stand development, individual plants do not follow predetermined growth trajectories but constantly adjust to varying resource levels and neighbourhood densities (Weiner and Thomas 1992, Schwinning and Weiner 1998). For forest trees in particular, such growth curves could not account for the changing dynamics that occur during the life cycle of an individual tree. Growth rate is not an intrinsic constant, and factors such as release from competition, change in the proportion of photosynthetic and non-photosynthetic tissue, and variation in temperature, precipitation and other environmental factors, all influence rate of growth at different times in a tree's development. According to Evans (1972), the failure of curve fitting led to the next phase of development, which involved separating the complex structure of plants into simpler modules which are easier to handle.

3.3(a) Plant growth analysis

Despite these limitations, whole plant growth analysis was not totally abandoned. Some researchers (Evans 1972, Causton and Venus 1981, Hunt 1982) credit Blackman (1919) as having provided the basis for a new method of analyzing whole plant growth. Blackman proposed that the rate of plant growth should be proportional to the size of the plant, and used the analogy that the increase in plant size should follow the compound interest law. This assumed that rates of assimilation and respiration were constant and that the proportion of photosynthetic material to total plant size was constant. He termed the rate of increase the 'efficiency index', which was subsequently renamed 'relative growth rate' (Briggs *et al.* 1920a, b).

According to Briggs *et al.* (1920a), if plant growth is exponential, the intrinsic rate of growth is equivalent to the relative growth rate (RGR). They questioned Blackman's (1919) assumption that the compound interest rate was constant throughout a plant's development. Briggs *et al.* (1920a, b) used the mathematical technique of growth rate decomposition to relate changes in RGR to the difference between the rates of assimilation and respiration per unit of plant biomass. They partitioned RGR into 2 components, (1) the amount of plant growth per unit of leaf material (unit leaf rate, ULR, or sometimes known as the net assimilation rate) and (2) the amount of leaf material per unit of plant biomass (leaf area ratio, LAR) (equation [2]).

[2]
$$RGR = ULR * LAR$$
$$\frac{1}{W}\cdot\frac{dW}{dt} = \frac{1}{LA}\cdot\frac{dW}{dt} * \frac{LA}{W}$$

where W is total plant biomass and LA is total leaf area.

From this, "any factor which alters the relative growth rate does so by causing positive or negative changes in either the net assimilation rate or the leaf area ratio or both" (Blackman 1968). Plant physiologists have applied this method of growth analysis and found them to be useful tools for quantitative analysis of plant growth (Radford 1967).

The '*classical*' approach has been to measure plant weight and leaf area by destructive sampling at two points in time to estimate the variables in equation [2] (Fitter and Hay 1981, Causton and Venus 1981, Hunt 1982). According to Causton and Venus (1981), a sampling problem is created because different plants have to be selected at the two harvest times. Based on the data collected, the three quantities could be estimated by:

[3] $$RGR = \frac{1}{W}\cdot\frac{dW}{dt} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

[4] $$ULR = \frac{1}{LA}\cdot\frac{dW}{dt} = \frac{W_2 - W_1}{LA_2 - LA_1}\cdot\frac{\log_e LA_2 - \log_e LA_1}{t_2 - t_1}$$

[5] $$LAR = \frac{LA}{W} = \frac{LA_2 - LA_1}{W_2 - W_1}\cdot\frac{\log_e W_2 - \log_e W_1}{\log_e LA_2 - \log_e LA_1}$$

where t_1 and t_2 are the time of first and second harvest, respectively, W_1 and W_2 are the total plant weight at times t_1 and t_2, respectively, and LA_1 and LA_2 are the total leaf area at times t_1 and t_2, respectively.

The estimation of RGR, ULR and LAR using equations [3] to [5] has additional problems, including the large number of samples required to maintain a low sampling error (Causton and Venus 1981, Hunt 1982). To overcome this limitation, a dynamic or '*functional*' approach was developed to derive the variables for growth analysis (Hughes and Freeman 1967, Radford 1967). This method involves fitting separate growth curves to describe the development of plant weight and leaf area over time.

[6] $$W = f(t)$$

[7] $$LA = g(t)$$

Causton and Venus (1981) and Hunt (1982) give detailed descriptions of the functional approach and explanations of the advantages of it over the classical approach. Hunt (1982) supports empirical, polynomial growth functions, but also outlines the application of the logistic and Richards growth functions in the curve fitting process. The choice of the fitted curve is dependent on the data collected. From the fitted equations, the quantities for plant growth analysis can be derived using equations [8] to [10].

[8] $$RGR = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{f'(t)}{f(t)}$$

[9] $$ULR = \frac{1}{LA} \cdot \frac{dW}{dt} = \frac{f'(t)}{g(t)}$$

[10] $$LAR = \frac{LA}{W} = \frac{g(t)}{f(t)}$$

This general method of whole plant growth analysis has been extensively used for research in agriculture and horticulture. The technique has been employed to assess the effects of genotype, environment and their interaction on growth (Causton and Venus 1981). While this technique has been applied to the study of tree growth at the seedling stage of development, it has not, however, received much attention for the study of mature trees. This is due to the difficulties associated with estimating the amount of leaf area and total plant material (Causton and Venus 1981). In particular: (i) the greater proportion of nonproductive tissue in larger trees has a greater influence on RGR than annual increment differences (Brand *et al.* 1987); (ii) the variation in the distribution of growth between different tree components (foliage, branches, stem and roots); and (iii) the lack of data on the roots, which are major assimilate sinks.

Due to these limitations, Radford (1967) noted how growth analysis procedures have been modified to enable the measurement of specific components of tree growth, most often the volume of the main stem (V), rather than the weight of the whole tree. Magnussen and Brand (1989) used the ratio of a tree's RGR to the maximum RGR of a tree of the same size to quantify a competition growth modifier, or tree vigour index in red pine. It was based on a tree's size relative to the size distribution of the whole stand, and not on the sizes of its immediate neighbours.

RGR has also been used to assess the impact of competition in young red pine plantations of different initial spacings (Brand and Magnussen 1989, Larocque and Marshall 1993, Larocque 1998). They found that early in a stand's development, before competition becomes severe, RGR decreased with tree size. Over time, when competition increases, RGR increased with tree size. They surmised that small trees were more efficient in biomass production before the commencement of competition, and that the effect of competition, at the stand level, was to increase the efficiency of large trees relative to small trees. Although data were not provided, they suggested that the change in RGR could result from a small crown ratio (i.e., low foliage per unit bole volume).

Burns and Irwin (1942) looked at needle efficiency in 28-year-old white and red pine trees grown at two different spacings. Their measure of efficiency was based on the relationship between annual stem volume increment and the amount of foliage at the end of the growing period, somewhat equivalent to the ULR. While they concluded that needle efficiency increased with increased spacing (i.e., decreased competition), a re-analysis of their data by this author showed that, in fact, there was no significant difference in needle efficiency, only a significant decrease in total amount of foliage with increasing competition. No information was provided regarding the RGR of the trees at the two different spacings.

Other studies suggest that ULR does not vary significantly between trees in the middle to upper canopy at a given stage of development, with only suppressed trees showing lower levels of growth per unit amount of foliage. Satoo *et al.* (1954) found that unit leaf rates in stemwood production in *Chamaecyparis obtusa* were lowest among suppressed trees, increased slightly with tree size, but were not significantly different between average and above-average sized trees. Waring *et al.* (1980) found similar results with Douglas-fir (*Pseudotsuga mensiesii* (Mirb.) Franco). They concluded that the foliage of suppressed trees was less efficient in producing bole wood. Gilmore (1996) applied the term growth efficiency (GE) to the concept of ULR when studying *Abies balsamea* at different canopy positions. He also found suppressed trees to have the lowest GE compared to upper canopy trees. He also attempted to substitute other variables to quantify photosynthetic tissue (e.g., crown length, crown radius, crown ratio, etc) and found similar trends in ULR between crown class, regardless of the variable used. Furthermore, within a crown class, larger crown trees are less efficient in stemwood production than trees with smaller crowns (Assman 1970, Sterba and Amateis 1998).

Waring *et al.* (1980) concluded that the ULR based on stem volume and leaf area could be used as a measure of tree vigour. Mitchell *et al.* (1983) reported that, at the stand level, thinning increases average tree vigour in the residual stand. Such results would tend to support Larocque and Marshall's (1993) findings in red pine plantations undergoing severe competition. In these data, however, it is unclear whether the efficiency of bole wood production decreased due to a decrease in photosynthesis at low light levels within the crowns of suppressed trees, or whether it was due to a redistribution of assimilate away from the bole towards other tree components (i.e., foliage and/or root production).

Kellomaki and Hari (1980), in contrast to the above, found the opposite relationship to occur between dominance class and needle efficiency in Scots pine (*Pinus sylvestris* L.). They found suppressed trees to have the greatest growth efficiency, in terms of diameter, height and total weight per unit needle weight, and concluded that suppressed trees were better adapted to the sub-optimal conditions and were capable of efficiently using the available resources. They also found significant differences in absolute amounts of needle biomass between crown classes, but did not report any information on variability in RGR.

The use of this growth analysis approach to the development of tree growth models has focused on LAR rather than ULR due to the low variability in unit leaf rates compared with the magnitude of leaf area differences for trees of different sizes. It has resulted in the implicit assumption that unit leaf rates are constant and more attention has been given to incorporating leaf area in growth models. A strong, positive, linear relationship has been observed between the amount of foliage and stemwood production.

Schwinning (1996) recently applied the same technique of growth rate decomposition to assess the relative contribution of the mode of competition (relative rate of resource uptake), biomass partitioning, and resource-to-biomass conversion efficiency to differences in the RGR in annual cereal plants grown under different degrees of crowding.

3.3(b) Stand growth simulations using individual-tree models

The use of individual-tree models to simulate forest stand growth started in the 1960s and 1970s (Newnham 1964, Bella 1970, Arney 1972, Botkin *et al.* 1972a, Hegyi 1974). Early research into modeling tree growth tried to develop an index to quantify competitive stress on individual trees and attempted to consolidate these competition indices into a growth function.

One approach taken was to equate the observed volume growth of a tree (dV_{obs}/dt) as the product of the potential growth under optimal conditions using a growth curve (dV/dt) and a correction factor, often expressed as a function of the environment around a tree, that reduces potential growth to actual growth (e.g., Botkin *et al.* 1972b).

[11] $$\frac{dV_{obs}}{dt} = \frac{dV}{dt} * c.f.$$

where V is the volume of the main stem, t is a measure of time, and *c.f.* is a correction factor reducing potential growth to actual growth based on a function related to the environmental parameters.

This correction factor often included variables that described the sub-optimal growing conditions of the subject tree in terms of an index of competitive stress. By incorporating degree-days and precipitation, Botkin *et al.* (1972b) were among the few to also include variables that accounted for year-to-year climatic differences.

The potential growth function was often derived from physiological principles of plant growth. Potential growth was hypothesized to be proportional to the net amount of energy available for growth, which was estimated as the difference between the amount of energy produced by photosynthetic tissue and the energy utilized by non-photosynthetic tissue for respiration and maintenance. Richard's (1959) growth function is an example of such a growth curve. The form of Richard's growth function is:

[12] $$\frac{dW}{dt} = \eta W^{m} - \kappa W$$

where W is current plant biomass, m is slope of the allometric line of metabolism, and n and κ are the assimilation and respiration constants, respectively.

By explicitly using current size (W) as a predictor of future growth, it was reasoned that the stage of development or age was not needed in the growth equation, since current size represents the accumulation of all previous growth. While Von Bertanlanffy (1957, as cited by Richards (1959)) argued that $2/3 < m < 1$ for mammal growth, Richards (1959) showed empirically that for plants the "function will find its chief application with values over 1".

The approach of Botkin *et al.* (1972b) was to incorporate the net available energy as a predictor of tree growth. Their formula, a hybrid between the logistic growth and Richard's (1959) growth function, employed a growth equation for optimum tree volume that was linearly related to leaf area. The function involved a dampening factor to account for the larger respiratory demands by non-photosynthetic tissue (cambial surface area) with increasing tree size (see equation [13]).

$$[13] \qquad \frac{dV}{dt} = r * LA * (1 - \frac{SA}{SA_{\max}})$$

where V is main bole volume, SA is main bole cambial surface area, LA is tree leaf area, r is the growth rate parameter, and SA_{max} is the maximum observed cambial surface area.

Using the above principle, the tree growth function approached zero as trees reached their maximum size. Their growth function thus assumed that as trees age, the net energy available for growth decreases until all the energy produced by photosynthesis was utilized for maintenance and respiration, leaving none available for the main stem growth. The authors simplified their equation by setting foliage area, stem volume and stem surface area to easily measurable variables, namely diameter-at-breast height (D) and height (H). By assuming that tree volume was proportional to D^2H, leaf area was proportional to D^2, and non-photosynthetic tissue respiration was proportional to DH, they derived the following growth function:

$$[14] \qquad \frac{dD^2H}{dt} = r * (c * D^2) * (1 - \frac{DH}{D_{\max} H_{\max}})$$

The assumption that light is the most limiting resource allowed Botkin *et al.* (1972b) to reduce volume growth due to competition by deriving a function relating available light to the canopy depth and leaf area per unit ground area. While their initial work led to the use of simulation models to study gap dynamics and forest succession, it has one limitation in that the model does not account for how trees respond to drastic changes in their immediate environment. A tree may take many years to fully respond to changes induced by thinning, partial cutting treatments and other management activities that create a sudden change in the tree environment. Ford and Sorrensen (1992) argue the need for greater knowledge of plant response to environmental stresses induced by competition. This has led to research on the development of neighbourhood competition models described by Ford and Sorrensen (1992) which quantify competitive interference at the individual tree level (see section 1.2(c) *"Neighbourhood competition models"*).

Although the development of these competition indices used data from thinned, managed stands, not one of them has considered the compensatory growth response of individual trees following thinning. Most of these models assume that the thinning response would be described by the competition index itself (Ford and Sorrensen 1992). Hynynen (1995), however, attempted to explicitly model a thinning response within a distance-independent, individual tree model. His approach was to incorporate a time-dependent thinning response function as a correction factor to a reference growth function,

[15]

$$\frac{dD_5}{dt} = f_1(ref) * [1 + f_2(thin)]$$

where dD_5/dt is the 5-year diameter growth increment, $f_1(ref)$ is the reference growth function and $f_2(thin)$ is the thinning response function.

Hynyen's (1995) thinning response function described the relative diameter growth response of trees in thinned stands compared to unthinned stands based on thinning intensity and time after thinning. This is based on the empirical observation that maximum basal-area growth response occurred 5-10 years after thinning. To incorporate this into his model, he used the Weibull function to describe the temporal distribution of the thinning response, which he found to last 25 years. His reference growth function included a distance-independent competition index (i.e., basal area of trees larger than the subject tree).

3.4 General growth principles of stem form

The study of the distribution of growth along a tree bole and the subsequent taper or form of the stem has been the focus of much research since the nineteenth century. While the analysis of stem form can be approached as either a mensuration study (yield in terms of product) or biological tree growth model (development in terms of a living system), most recent work has concentrated on the latter.

3.4(a) General principles

Pressler (1864, as cited in Larson (1963)) developed three primary growth principles of stem increment which are still generally accepted today (Osawa *et al.* 1991, Chiba and Shinozaki 1994, Rennolls 1994). These are:

1. ring area growth at any height in a tree is proportional to the quantity of foliage above that point;
2. within the crown, ring area will increase from apex downward in relation to the quantity of foliage above the point; and
3. below the crown, within the clear bole portion of the tree, ring area growth is constant.

From these general principles, it is inferred that the point of maximum ring area occurs at or near the base of the live crown. As a tree matures and its crown recedes, or as a tree moves from an open grown condition to a closed canopy situation, the point of maximum ring width shifts upward. This is a result of the upper stem being in closer proximity to source of carbohydrate production (i.e., foliage), and suggests that the lower stem has less priority as a carbohydrate sink than the upper stem (Duff and Nolan 1953). Supporting this hypothesis is the observation that during favourable growth years, the point of maximum ring width may shift downward within a tree, indicating a relative increase in growth in lower sections of the bole, or shift upwards during unfavourable or stressful growing conditions (Duff and Nolan 1953, Smith and Wilsie 1961, Bormann 1965). Larson (1963) concludes from this that year-to-year variation in weather or environment has a greater influence on the growth in the lower portion of the bole than within the active crown.

The resulting cumulative diameter growth at different heights gives a tree its taper. From a forest products perspective, too much taper is undesirable. A straight, more cylindrical bole is preferred in a managed white pine forest, especially if quality lumber is the desired end product. In general, young trees have more taper than older trees and open grown trees have greater taper than trees grown in closed canopy stands (Larson 1963).

Labyak and Schumacher (1954) investigated the contribution of branches from different parts of the crown to the volume growth of the bole in loblolly pine (*Pinus taeda* L.). Their work shows that, although total volume growth increases with crown ratio, the contribution of the foliage in the crown to bole wood production begins to diminish at around 80% of total tree height. Branches located between 80 to 90% of total tree height make the greatest contribution to stemwood volume production. Small branches in the lower half of the crown contribute very little to the main stem, and near the crown base, at about 30% of tree height, branches contribute nothing to bole wood production. Stiell (1969) found evidence in red pine that, within the live crown, stemwood growth within an internode (i.e., stem section between two successive branch whorls) is influenced mainly by the amount of foliage in the whorl immediately above it.

3.4(b) Theories on stem form

Based on the observed relationship between stem form and crown development, four different theories on the control of stem form have been hypothesized: nutritional; water conduction; mechanistic; and hormonal (as cited in Larson 1963).

I. Nutritional

Hartig (1883, as cited in Larson 1963) was the first to propose the nutritional theory of stem form. His theory is based on the hypothesis that stem growth is related to the equilibrium between transpiration and assimilation. In the rationale behind this theory, the annual ring is partitioned into early- and latewood, with the earlywood representing the main conductive tissue and being primarily controlled by transpiration demand. When transpirational requirements are met, demand shifts from transpiration to assimilation, and strength tissue, i.e., latewood, is produced. As Larson (1963) pointed out, Hartig was able to interpret all observed responses in stem form in terms of this hypothesis. Thinning, which increases crown size and, therefore, transpiration demand increases earlywood production and stem taper. Pruning, which reduces crown size and transpiration, decreases earlywood:latewood ratios and stem taper.

II. Water conduction

This theory of stem form is somewhat similar to the nutritional theory, but considers the growth ring as a whole. First proposed by Jaccard (1912, as cited by Larson 1963), the theory looks at the quantitative and mechanistic function of water, rather than the physiological importance of water movement. In this theory, the growth of crown and roots were interrelated and proportional, and the amount of new xylem produced is directly related to the amount of tissue required to conduct water to the quantity of foliage above. The importance of xylem tissue for water conductance was adopted by Shinozaki *et al.* (1964 a, b) in the development of a pipe model theory of tree form (Rennolls 1994). The pipe model theory hypothesizes that a plant can be considered an assemblage of 'unit pipes' each supporting a unit amount of photosynthetic tissue.

III. Mechanical Stress

Originally proposed by Schwendener (1874, as cited in Larson 1963), this theory is based on the observation that forces of wind apply a mechanical stress on tree stems that influence stem form. The theory assumes that the stem can represent a beam of uniform resistance to bending and act as a lever arm anchored at its base. The maximum force exerted on a tree is presumed to be at the centre of gravity, which is the midpoint of the crown. The theory gained support based on the work of Jacobs (1954), which showed that when guy wires were used to prevent swaying due to wind, there was little or no diameter growth at breast height, but a considerable increase in diameter growth above the point of support. A change in plant growth and development due to mechanical stimulation was later termed thigmomorphogenesis (Jaffe 1973).

Larson (1965) experimented with uni- and multi-directional winds to demonstrate a pronounced downward shift of growth towards the stem base, usually at the expense of upper stem parts. Subsequent experimental and observational investigations by Bannan and Bindra (1970), Burton and Smith (1972), Dean and Long (1986), West *et al.* (1989), Valinger (1992) and Osawa (1993) all corroborate the theory that bending stresses stimulate increased radial growth at the stem base relative to the upper stem, resulting in changes in stem form. West *et al.* (1989) and Valinger (1992) suggest that the theory of mechanical stress has received the most support and is the most enduring theory proposed to explain changes in the shape of tree stems. The theory also supports the assumption that the stimulus of sway contributes a positive feedback to the assertion of dominance, i.e., larger trees have increased growth due to greater exposure to wind.

IV. Hormonal

While the nutritional and water conduction theories appear to describe the variation in stem form, they do not appear to serve as the regulatory function of cambial activity. This is based on the observation that cambial activation fails to start, even with nutritional availability, without auxin stimulus originating from the crown (Fraser 1952, Wilcox 1962). The hormonal theory hypothesizes that auxin concentrations regulate cambial activity and the distribution of radial growth along the stem.

Most of the available information on growth hormones and cambial activity is related to indol-3-ylacetic acid (IAA, auxin) (Larson 1962, Little and Wareing 1981, Savidge *et al.* 1982, Little and Savidge 1987, Sundberg *et al* 1987, Savidge 1988), abscisic acid (ABA) (Little 1975, Little and Wareing 1981) and ethylene (Little and Savidge 1987, Savidge 1988, Eklund 1991). Although the resumption of diameter growth in the spring depends on carbohydrate storage in the stem, cambial cell division and differentiation will not commence without the presence of growth hormones, principally IAA (Savidge 1988). However, it is not completely clear if IAA is directly involved in the control of cambial growth, or indirectly through "hormone-directed transport" (Little and Savidge 1987).

The primary source of IAA originates from expanding buds and developing shoots and needles, with small amounts derived from mature needles (Sundberg and Little 1987, Savidge 1988). It has been shown that auxin concentration decreases with increasing distance from the crown (Larson 1962), tracheid diameter is controlled by auxin concentration during the stage of primary wall development (Larson 1964), and IAA has a role in regulating radial expansion of cambial derivatives (Sundberg *et al.* 1987). The temporal variation in IAA production during the growing season has been noted to regulate the distribution of early- and latewood cells within an annual growth ring (Larson 1962).

Experiments with ABA suggest that this hormone inhibits cambial growth, and that the transition from early- to latewood xylem cells and eventually cessation of cambial activity are due to endogenous concentrations of ABA in the cambial region (Little and Savidge 1987). Ethylene is a common compound produced within many plant organs and its endogenous production is often associated with plant stress (Abeles *et al.* 1992). There is mounting evidence to suggest that ethylene has several regulatory roles, including radial growth in conifers (Brown and Leopold 1973, Little and Savidge 1987), cell wall composition (Eklund 1991), lignification (Savidge 1988) and possibly compression-wood formation (Savidge 1988). The concentration of ethylene increases in the cambial region during cambial reactivation and activity, but it is not known if this is a result of or the cause of physiological changes (Eklund 1991). It is known that 1-aminocyclopropane-1-carboxylic acid (ACC) is a precursor to ethylene (Yang and Hoffman 1984) and that IAA promotes ethylene production from ACC (Yang and Hoffman 1984, Savidge 1988).

Larson (1965) hypothesized that stress stimulus, particularly bending stress due to wind, "could induce steeper auxin gradients down the stem", thereby influencing stem form. Mechanical stress also increases endogenous levels of ethylene within the cambial region of trees (Leopold *et al.* 1972, Brown and Leopold 1973, Telewski and Jaffe 1986a,b, Telewski 1990) and exogenous ethylene treatment induces radial growth in conifers (Brown and Leopold 1973, Little and Savidge 1987, Savidge 1988). These results suggest that ethylene plays a role in stem increment when trees are exposed to wind stress.

Forward and Nolan (1961), in determining whether the nutritional or hormonal theory best explained their observation of cambial activity in red pine, state that "it does not seem profitable to set these up as opposing theories since both nutrition and hormone supply must play their roles in growth". Osawa (1993) suggests that plant form based on the pipe model is an over-simplification of actual stem growth. Larson (1965) and Osawa (1993) conclude that the vertical distribution of stem increment is controlled by both 'passive' (morphology of live crown) and 'stimulatory' (swaying of the stem) mechanisms. The two mechanisms must be interlinked, allowing trees to exhibit different stem forms to satisfy any changes in the environment in which they grow.

3.4(c) External factors affecting stem form

Larson (1963) lists over nine factors affecting stem form, including ecological processes such as open-grown versus stand-grown trees, dominance class, inheritance, as well as silvicultural practices such as selection cutting, thinning, and pruning. Most of these, with perhaps the exception of inheritance, deal directly with how local competition controls crown development, which, in turn, influences stem form. Of the main crown variables related to bole growth, crown length plays a decisive role in stem form (Larson 1963).

*3.5 **Partial cutting effects on tree growth***

A review of the literature on partial cutting effects on tree growth indicates that most research has focused on the effects of thinning on young, even-aged plantations. This silvicultural tending treatment is most often applied as a means of spacing control. In general, thinning does not increase overall volume production, but redistributes growth to selected trees (Horton and Bedell 1960) and thereby, improving the health, vigor and growth of the residual trees. This includes controlling the form, clearness and dimensions of the bole. The little research that has been done on older, larger trees suggests that they are less responsive to partial cutting than young trees (Smith 1986).

Since thinning is generally applied to even-aged stands with relatively uniform tree size, the results are often summarized at the stand level or on an average tree basis. At the stand level, volume production is totally dependent on the intensity of the thinning and the age of the stand, with most research supporting the hypothesis that thinning does not increase total volume growth per unit area (Hamilton 1969, Ford 1975, Smith and Seymour 1986). Results based on mean tree size should be interpreted with caution since thinning itself often removes the smaller trees and this will increase average tree size even before any new growth occurs (Spurr *et al.* 1957).

Partial cutting influences the micro-environment surrounding trees by increasing both the amount of light penetrating into the lower canopy and soil moisture availability. Results obtained by Ginn *et al.* (1991), who investigated within-tree variation in photosynthesis following thinning in young loblolly pine, found significant physiological changes in gas exchange in the lower crown due to thinning. In thinned stands, rates of photosynthesis and stomatal conductance in the lower crown approached rates of upper crown needles. Trees in unthinned stands have generally lower gas exchange rates in the lower crown. Despite this adjustment in rates of photosynthesis in the lower crown, Ginn *et al.* (1991) concluded that the increased growth rate of individual trees in thinned stands is largely the result of increased needle area.

Significant increases in soil moisture availability following thinning have been reported in stands of lodgepole pine (*Pinus contorta* var *latifolia* Engelm.) (Dahms 1973, Donner and Running 1986), red pine (Bay and Boelter 1963), ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) (Helvey 1975) and white pine (Hunt 1968). Increased soil moisture following thinning, possibly the result of reduced overall stand transpiration and live root density, has been reported to increase leaf water potentials in red pine (Sucoff and Hong 1974), lodgepole pine (Donner and Running 1986) and loblolly pine (Cregg *et al.* 1990). Donner and Running (1986) concluded that the combination of improved water relations and increased light intensity following thinning resulted in a 21% increase in seasonal photosynthesis in lodgepole pine.

The general growth response of the average tree to thinning has been reported to include increased diameter and volume growth and crown size, with little or no increase in height growth (Smith 1986). The growth response to thinning is often proportional to the amount of cover removed and level of prior suppression (i.e., suppressed trees will benefit the most) (Horton and Bedell 1960). Thinning also influences the distribution of new growth, both within the main stem and between plant components.

Along the bole of a tree, thinning influences stem form by stimulating a relatively greater increase in diameter growth in the lower part of the stem, resulting in increased stem taper (Meyer 1931, Larson 1963, Berry 1971, Tasissa and Burkhart 1997). Forward and Nolan (1961) attributed the relative increase in cambial activity in the lower part of the bole of red pine following release to the proximity of the lower branches which benefited most from the release. However, since the growth response is often observed before any significant increase in crown size is noted, one can conjecture that the trees are partially responding to the increased exposure to wind and the resulting mechanical stresses associated with stem sway, as noted in section 3.4(b) "*Theories on stem form*". Trees having long clear boles show extreme growth increases at the stem base. Trees having a high degree of stem taper prior to release will exhibit no change or a decrease in taper following thinning (Meyer 1931).

The ability of white pine, in particular, to respond following release is strong (Horton and Bedell 1960, Berry 1982, Kelty and Entcheva 1993). Hawley (1936) reported that thinning from below (i.e., removal of the smaller trees in the stand) increased diameter and volume growth but had no effect on height growth of white pine. He noted an increase in crop quality, but no significant increase in the overall quantity. Downs (1943), in an overstory removal, recorded increased height growth in understory white pine. The small trees showed the greatest relative growth response to the partial cutting. McCormack (1956) found that suppressed white pine, when released, maintained increased diameter growth for many years following thinning, and that they exhibited compensatory growth which was greater than the unsuppressed trees.

Spurr *et al.* (1957), in a set of intensively managed white pine plantations repeatedly thinned on a 5 year interval for over 30 years, reported increases of 41% and 15% in the average diameter growth after crown and low thinnings, respectively, compared to unthinned plots. However, they found that no significant stimulation in the growth of the 100 largest trees per acre for the first 20 years and only a 9% cumulative increase in diameter growth after 30 years. Hunt (1968) reported average diameter growth during the first 5 years, following high and low intensity thinning treatments, of 238% and 73% greater, respectively, compared to trees in the unthinned, control plots.

Gillespie and Hocker (1985) quantified the growth response in individual white pine trees to the level of competition. They found, based on a measure of crown overlap (see section 3.2(c) "*Neighbourhood competition models*"), that increasing levels of competition decreased the percent growth in 24- to 45-year-old white pine over an 8 year, post-treatment period. In addition, the growth response increased with superior crown position (intermediate to dominant) but decreased with diameter size class. The change in percent diameter growth from pre- to post-thinning was correlated with the change in competition resulting from thinning. They did not, however, analyze; a) the duration of the growth response, b) the change in competition over the growth period, and c) whether the duration of the growth response was influenced by competition.

Other information on white pine sometimes appears contradictory. Hunt (1968) indicates that individual trees responded with increased diameter growth within five days of thinning in 22-year-old white pine, while Bormann (1965) states that growth responses in 59-year-old pine were not observed until the second growing season following the removal of root-grafted neighbouring trees. It is not clear if this difference in response is due to age, intensity of competitor removal or simply the result of the method of data collection. It becomes apparent, nonetheless, that individual tree growth response will vary with tree size and crown class, and is highly dependent on the intensity of the cut.

Within white pine stands, it is known that thinning induces changes in the physical microenvironment around residual trees, such as increasing soil and crown temperature (Adams 1935) and increasing soil moisture availability (Adams 1935, Hunt 1968). This resulted in earlier growth initiation and overall faster growth rate (Gillespie 1985), longer growth into the season and greater overall cumulative growth (Hunt 1968, Gillespie 1985). Hunt (1968) concluded that the longer growing season was a result of increased soil moisture availability later in the season.

Hunt (1968) detected a change in the longitudinal distribution of cambial activity along the bole in white pine due to the intensity of thinning. Although based on a sample of only one tree in each treatment, Hunt (1968) noted no difference in ring widths in the upper portion of the crown pre- and post-treatment, nor due to thinning intensity. He did, however, find greater ring widths below the crown after thinning, with pre- and post-treatment differences being larger in the higher intensity thinning treatment.

Like diameter growth, taper increases with thinning intensity, and at the extreme level of thinning - i.e., complete release - increased growth at the base can occur at the expense of growth further up the bole (Larson 1963). There may also be an interaction in stem form changes between thinning and site, with greater increases in taper on poorer sites, and little or no change on the best sites (Larson 1963).

4. Model development

Past attempts to relate the level of competitive interference around individual trees with stemwood production have had various levels of success (c.f. Larocque and Marshall 1988, Ford and Sorrenson 1992). One explanation for this lack of general success has been the fact that large trees grow faster than small trees at comparable levels of competitive interference. It is often inferred that stemwood production has less priority than root and primary shoot growth (Gordon and Larson 1968). This is supported by the findings that a shortage in carbohydrate production, brought about either by reduced light, nutrient availability or soil moisture, will increase the proportional allocation to root and foliage growth in pines (Rangnekar and Forward 1973, Grier and Running 1977, Ewel and Gholz 1991, Gower *et al.* 1994, Dewar *et al.* 1994). Thus, a greater proportional allocation of carbon to stemwood production could be used as a measure of tree vigour. Changes in growth allocation may be more important in assessing competitive interactions than physiological mechanisms measured at the individual leaf or root level (Schwinning and Weiner 1998). Therefore, a relationship between vigour and competitive interference should exist.

However, the difficulties of quantifying growth allocation to all tree components (i.e., roots, stem, branches, foliage, cones, etc.) in order to assess tree vigour may not be feasible. Since the current size of the main stem represents a historical record of the accumulated competitive effects on stem growth, any future amount of stemwood production per unit of current stem size can be used as an alternative measure of tree vigour. One can equate this concept of tree vigour back to whole plant growth analysis [section 3.3(a)] by utilizing the relative growth rate (RGR) of the main stem of a tree as a measure of tree vigour. Brand *et al.* (1987), Brand and Magnussen (1988), Larocque (1998) and Newton and Joliffe (1998) have used RGR as a measure of tree vigour in competition studies. However, one shortcoming of using RGR when studying large, mature trees is the large proportion of total bole volume that is made of nonproductive stemwood in the inner core. Hence, bole increment makes a progressively smaller contribution to RGR through time, indicating that tree vigour may decline with age.

Brand *et al.* (1987) suggested that a more appropriate measure of tree vigour would be the relative production rate (RPR), which is a measurement of the rate of change in annual increment per unit of increment (equation [16]). This measure of tree vigour was also used in the assessment of competitive interference in red pine (Brand and Magnussen 1988) and black spruce (Newton and Joliffe 1998).

$$[16] \qquad RPR = \frac{d(^{dW}/_{dt})/dt}{dW/dt} = \frac{f''(t)}{f'(t)}$$

However, since all volume increment along the main bole originates from cambial tissue located along its surface, volume increment per unit of cambial area may be a more appropriate measure of size-dependent growth. Duff and Nolan (1957) were the first to investigate the concept of volume growth per unit cambial area, which they termed the specific increment of volume, and characterized it as a measure of cambial activity. They examined volume growth on an internode basis (defined as the length of stem between two successive branch whorls) and found the specific increment of volume to be equivalent to the average width of an annual ring (Duff and Nolan 1957). In their detailed analysis of the growth of red pine, Duff and Nolan (1953, 1957, 1958) found the specific increment of volume to be a sensitive measure of the balance between the growth and respiration of each internode. It shows a distinct pattern along the bole and is highly influenced by competition and release from competition. Shea and Armson (1972) expanded on the specific increment of volume concept by adopting it to the whole tree and referred to it as specific volume increment (SVI). Taken along the entire length of the bole, SVI is equivalent to the weighted average annual ring width (weighted by internode length or bole section length). Such a measure of size-related growth may better incorporate the longitudinal variation in cambial activity that has been noted to occur due to a change in competition (Larson 1963).

Very few studies were found which employed SVI in the assessment of growth response to competitive interference. Piene (1981) used SVI in the assessment of early growth responses to operational spacing and as a possible indicator of time for spacing. Neither study, however, assessed SVI in individual trees in relation to local neighbourhood competition models in order to study the mode of competition in forest stands. Newton and Jolliffe (1998) recently used SVI to assess symmetry of intra-specific competition in density-stressed black spruce (*Picea mariana* (Mill.) BSP) stands. No studies have used SVI as an index for assessing individual stem growth responses to modifications of the competitive interference around individual trees as a result of partial cutting.

Using the same principles as outlined in Causton and Venus (1981) and Hunt (1982), continuous functions - i.e., polynomial equations - were developed for predicting bole surface area (SA, equation [17]) and volume (V, equation [18]) for each tree over time since treatment. Third order polynomial equations were selected based on their better overall goodness of fit [i.e., higher coefficient of determination (R^2) and lower root mean squared error (RMSE)] with the data.

[17] $$SA = f_{SA}(t) = a_0 + a_1 \cdot t + a_2 \cdot t^2 + a_3 \cdot t^3$$

[18] $$V = f_V(t) = b_0 + b_1 \cdot t + b_2 \cdot t^2 + b_3 \cdot t^3$$

SVI can then be calculated by:

[19] $$SVI = \frac{1}{SA} \cdot \frac{dV}{dt} = \frac{f_V'(t)}{f_{SA}(t)}$$

The relationship between SVI and the cumulative competitive interference of neighbouring trees will be tested, i.e.,

[20] $$SVI = f_c(CI)$$

and if found to be better correlated to indices of competitive interference, then the equation can be reworked and solved for absolute volume increment:

[21] $$\frac{dV}{dt} = SA * f_c(CI)$$

Cumulative volume growth (ΔV) at some time *t* in the future can be estimated by accumulating the predicted current annual volume increments from growth equation [21] using equation [22].

[22] $$\Delta V_t = \sum_{i=1}^{t} \frac{dV_i}{dt} = \sum_{i=1}^{t} SA_i f_c(CI_i)$$

However, this requires predicted values for SA and CI at different times in the future, each with its own error term. Compounding the error associated with estimates of each predictor variable with the error of the underlying model often results in a final estimate with a very large error term.

Another approach to predicting future cumulative growth is to develop a yield equation which expresses the cumulative volume growth at time *t* as a function of three measured variables: initial bole surface area (SA_0), initial level of competition (CI_0), and time.

[23] $$\Delta V_t = f(SA_0, CI_0, t)$$

Equation [23] is the preferred method for predicting cumulative growth during a short time period since the growth response following a partial cutting can be incorporated into the equation.

5. Methodology

5.1 Stand-level treatments

In order to study short- to medium-term growth responses in individual white pine trees to partial cutting treatments, a suitable study area with detailed information of cutting treatments was required. Since data of sufficient detail for individual-tree level growth models are scarce or non-existent, individual-tree growth information had to be collected. A suitable study area for white pine was found in the Cartier Lake Silvicultural Area within the Petawawa Research Forest (PRF), Chalk River, Ontario. Stiell (1984) and Stiell *et al.* (1994) previously used the site to assess stand-level responses to improvement cuts.

The PRF is adjacent to the eastern boundary of Algonquin Provincial Park, Renfrew County, Ontario (45°59'N 77°26'W). This area is part of the Middle Ottawa Forest Section (L.4c) of the Great Lakes-St. Laurence Forest Region (Rowe 1972). Short warm summers and cold winters with an average annual temperature of 4.3°C characterize the climate. The average length of the growing season is 116 frost-free days. Precipitation averages 832.1 mm per year, with 55% falling between April and September. The Cartier Lake Silvicultural Area is at the western edge of the research forest.

The study site, approximately 80 ha in size, consisted of rolling topography with predominately sandy soils and stony till overlaying bedrock. Soil depth was thin with exposed large boulders on the ridge tops, and deeper in the lower lying areas. The selected stands were predominately represented by the Sherborne landtype, based on Hills and Pierpoint (1960) landtype classification (Stiell *et al.* 1994). Site productivity based on height-age relationships of emergent white pine trees (using data obtained from the stem analysis, Table 7) suggests that the study area is average to below-average in productivity for white pine. Productivity was between Site Group II and III using yield tables of Horton and Bedell (1960) (rated on a I to IV scale from best to worst), between Site Class I and II based on Plonski's (1974) yield tables (rated on a I to III scale), and a site index of 17 m (total height at breast-height age 50 years) (Woods and Miller 1996) (rated on an 11 to 24 m scale).

The forest cover consisted of predominantly multi-cohort, mixedwood stands with a wide range of density and species composition (Table 3). The stands contained a predominately hardwood overstory of white birch, trembling and largetooth (*Populus grandidentata* Michx.) aspen averaging 80 years of age in 1971. Lesser amounts of red maple (*Acer rubrum* L.), red oak and scattered white and red pine and white spruce were also in the overstory. The understory was composed of predominately white pine, with some red pine and white spruce, and lesser amounts of jack pine, balsam fir and white cedar (*Thuja occidentalis* L.).

Portions of the mixedwood stands were partially cut in the fall of 1971 to varying levels of residual basal area. The aim was to improve the growth and yield of white pine for sawlog production and "at providing the option of long-term uniform shelterwood management" (Stiell 1984). The cutting treatments consisted of the removal of all species of pulpwood size (9 cm diameter-at-breast height and larger), except for the understory pine and spruce. The residual stands in the treated areas were mainly composed of white pine, with a minor component of red pine and white spruce. The intensity of the cutting treatment varied depending on the pre-treatment pine component density in the stand. Part of the area was left as an uncut control. More detailed descriptions of initial cutting treatments are given by Stiell

Table 3: Average stand values, by species component, before 1971 cut (from Stiell *et al.* 1994).

Component	Number stems (ha^{-1})	Basal area (m^2 ha^{-1})	Total volume (m^3 ha^{-1})
White pine, red pine, white spruce	499	12	95
Other softwoods	17	1	3
All hardwoods	519	14	128
All species	1035	27	226

(1984), Stiell *et al.* (1994) and Williams (1994).

Stiell (1984) laid out a 2x3 factorial design with two levels of cutting treatment (control and treated) and three levels of average pine basal area (6.9, 11.5 and 16.1 m^2 ha^{-1}) within the study area. Permanent sample plots were established and measured within each treatment in the fall of 1971 (Table 4), immediately following cutting treatments, and re-measured in 1981 (Stiell 1984) and 1991 (Stiell *et al.* 1994). The ten-year interval between measurements does not provide enough detailed information to analyze short-term growth responses immediately following cutting. The original study also did not have any information on the form of the individual trees, nor were the trees mapped. For this reason, individual trees from within the study area, but outside of the existing permanent sample plots, were selected for more detailed stem analysis. There were restrictions placed on which trees could be selected for this research due to the on-going study. Specifically, trees were selected from a distance of at least two-tree lengths from the existing permanent sample plots.

5.2 *Individual tree selection*

Trees selected for detailed stem analysis were chosen from within three spatially distinct stands found within the 80 ha study area in order to include spatial replication and account for possible site variation effects. All three stands contained both control and treated areas. Trees were selected in June 1995 from within each of the six treatments outlined in Stiell's (1984) experiment. In addition, trees were further stratified into three dominance classes to analyze variation in tree response due to canopy position: emergent (greater than 3 m above average canopy height); dominant/co-dominant (within +/- 3 m of average canopy height);

Table 4: Average values of pine component for cutting treatment and pine density levels immediately following cutting treatment in 1971 (from Stiell *et al.* 1994).

Cutting Treatment	Pine density class (m^2 ha^{-1})	Number trees (ha^{-1})	Basal area (m^2 ha^{-1})	Total volume (m^3 ha^{-1})	Mean D (cm)
Control	6.9	282.3	7.8	58.3	18.9
	11.5	520.4	12.1	91.6	17.5
	16.1	713.0	16.4	130.3	17.2
Released	6.9	325.8	7.4	52.5	17.1
	11.5	490.3	12.2	93.5	17.9
	16.1	634.9	15.9	128.9	17.9

and intermediate (greater than 3 m below average canopy height).

Tree selection involved randomly selecting representative individuals for each dominance class within each experimental treatment. Selection criteria were based on individuals having a distinct main stem with no forking or broken top and no obvious damage or wounds at the stem base from skidding damage, so as to limit confounding effects. A total of 88 trees were selected, and Table 5 gives the distribution of selected trees based on cutting treatment, pine density and tree dominance class.

5.3 Field measurements

Once the subject trees were identified, the size and location of potential competitors was determined using a BAF=2 m^2 ha^{-1} prism, with each subject tree as the centre point of the prism sweep, following the procedures outlined by Spurr (1962). For each competitor, the following information was recorded: azimuth and distance from the subject tree; species; diameter-at-breast height (D); and height class relative to the subject tree's height (i.e., -1 = more than 3 m shorter than the subject tree, 0 = within +/- 3 m of subject tree, and +1 = more than 3 m taller than the subject tree). Diameter growth since the time of the cutting treatment (i.e., 1971) for the subject trees was measured by stem analysis (see below), while the diameter growth of competitors was estimated based on equations developed using the data from the Cartier Lake Silvicultural Area (Stiell *et al.* 1994).

Following the identification and measurement of competitors, subject trees were felled in

Table 5: Number of sample trees selected based on cutting treatment, pine density class and dominance class.

Cutting Treatment	Pine density class (m^2 ha^{-1})	Dominance class			TOTAL
		Emergent	Dominant	Intermediate	
Control	6.9	2	2	2	6
	11.5	9	11	4	24
	16.1	4	10	1	15
	Sub-total	15	23	7	45
Released	6.9	4	10	2	16
	11.5	5	7	1	13
	16.1	4	8	2	14
	Sub-total	13	25	5	43
TOTAL		28	48	12	88

the summer of 1995. Total height (excluding any elongation originating during the 1995 growing season) and height to the base of the live crown were measured on the fallen tree. The size and number of branches at the lowest live branch whorl containing at least two large branches determined the base of the live crown. The crown was divided into three sections of equal length. At the base of each section, two branches from the nearest whorl and on opposite sides of the main stem were selected and the total length (excluding any elongation during the 1995 growing season), basal diameter and angle from the main stem of each branch were recorded. Average crown radius was estimated using the branch length and angle measurements from the two branches taken at the base of the crown. Total crown volume was estimated by the summation of the sectional volumes, using length and average radius measurements for each section, and assuming that crown shape was parabolic.

The main stem of the tree was then divided into 20 sections, with the base of each section taken at the following heights: 0.15 m (stump), 1.37 m (D), and at 5% intervals from 10-95% of total tree height. A disk was removed from the base of each section to conduct detailed stem analysis on each subject tree back in the laboratory.

5.4 Stem analysis

Stem disks were stored in cold rooms at 5°C for up to 8 months at the Petawawa Research Forest and the Faculty of Forestry, University of Toronto. They were then allowed to air dry for a minimum of two months before being prepared for tree-ring measurements. Disk preparation involved sanding the bottom surface of each disk, first with a 60-80 grit sand paper, followed by a light sanding with a 100 grit sand paper.

On each disk, the width (0.01 mm) of the bark, annual rings and pith were measured along four radii taken at 90° angles from each other (initial radius selected at random) using the Tree Ring Increment Measurement (TRIM) system (Fayle and MacIver 1986). The TRIM system was updated by replacing the Apple™ computer interface with an IBM™ compatible PC and using a LOTUS 1-2-3™ spreadsheet developed by Miller (unpublished 1990). The average of the four ring widths was used to reconstruct diameter, basal area and volume growth using techniques described in Avery and Burkhart (1994). Yearly cumulative height growth was calculated by linear interpolation between the difference in the ring number from successive disk samples and the height from which the disks were taken. Cumulative and annual growth up to and including 1994 was used in subsequent analyses, since the trees had not yet completed their growth when they were felled in 1995.

5.5 Growth profile analysis

Using an approach similar to that of Thomson and Barclay (1984), changes in the vertical profile of bole area increment were analyzed by comparing parameter estimates from regression equations which model periodic annual bole area increment at a given distance from the apex of the tree. Thomson and Barclay (1984) acknowledged some of the limitations of their analyses: (i) the omission of data from within the crown, (ii) the true underlying relationship was not linear and (iii) they did not incorporate the temporal variation of the relationship following treatment. To eliminate these limitations in this dissertation, the vertical distribution of bole area increment was analyzed using a two-stage modeling approach similar to that used by Newberry and Burkhart (1986) for analyzing stem form.

The base model (equation [24]) is a non-linear, variable-shape equation, scaled with respect to height and basal area increment to adequately compare trees from different crown classes. Only data from breast height and above were used in the analysis to avoid the disproportionate influence of butt swell on parameter estimates. The estimated β parameter is used to assess the shape of the vertical profile of bole increment. A value of $\beta=0$ indicates constant area increment along the bole. Values of $0<\beta<1$ indicate non-linear increase in area increment to towards the stem base, and a value of $\beta=1$ indicates a linear increase of area increment per unit length from tree apex to breast height.

During the first stage, parameters of equation [24] are estimated for each tree at different times by non-linear regression analysis using data derived from stem analysis.

$$[24] \qquad \frac{d(a_h)}{dt} = \alpha * \frac{d(ba)}{dt} * \left(\frac{H-h}{H-bh} \right)^{\beta}$$

where H is total tree height, *bh* is breast height (1.37 m), *h* is any height along main stem, $d(a_h)/dt$ is the bole area increment at height *h*, $d(\mathrm{ba})/dt$ is bole area increment at breast height, α and β are the slope and shape parameter estimates, respectively.

The parameter estimates (i.e., α and β) from the first stage are then related to crown class, cutting treatment and time before and after treatment through repeated measures analysis of variance in the second stage.

5.6 Measurement of stem form

Two methods of detecting changes in stem form were conducted. The first involved obtaining measures of both form factor (FF) (Avery and Burkhart 1994) and form class (FC) (Stiell 1978) through time employing data derived from stem analysis. Changes in stem form were analyzed using repeated measures analysis of variance for crown class and cutting treatment effects before and after treatment.

The second procedure involved using a two-stage modeling approach described above (section 3.5) to obtain a stem profile model that accounts for both taper and form changes before and after competition release (Burkhart and Walton 1985, Newberry and Burkhart 1986). During the first stage, parameters of a base model (equation [25]) based on Ormerod (1973) stem profile model, were estimated for each tree at different times based on stem analysis data.

$$[25] \qquad d_h = \alpha * D * \left(\frac{H-h}{H-bh} \right)^{\beta}$$

where D is diameter-at-breast height inside-bark, d_h is the diameter inside-bark at height h, α is the slope parameter, αD is the taper parameter, and β is the form parameter, and H, h and bh are as defined previously. The parameter estimates from the first stage are then related to crown class, cutting treatment and time before and after treatment application through repeated measures analysis of variance in the second stage.

5.7 Competition indices

Three distance-independent and eight distance-dependent competition indices were calculated for each subject tree for each year from 1971 to 1994. The distance-independent (DI) indices included: (1) number of competitors (CI01); (2) cumulative squared relative diameter of competitors (CI02); and (3) cumulative diameter of competitors (CI03).

Distance-dependent indices included Weiner's (1984) neighbourhood interference (CI04), Spurr's (1962) point density index (CI05), cumulative horizontal angle (Rouvinen and Kuuluvainen 1997) (CI06), and Hegyi's (1974) size-distance ratio (CI07). Two of the indices included variations of the crown overlap (CO) index type. Since there is no available information on open growth crown width for white pine of different sizes, the radius of the zone of influence for each tree was directly related to the tree's diameter using the same approach as Tome and Burkhart (1989). The radius of the zone of influence was expressed as a linear function of tree D from 0.1 to 1.0 x D in steps of 0.1. The function that produced the best empirical correlation between size-related growth and competition was selected. One index was based on the cumulative overlap between zones of influences (CI08), while the other weighted the overlap by the relative size of the competitor to the subject tree (CI09).

The final two indices tested were based on area potential available (APA). Since APA increases with decreasing competition, the inverse of APA was employed to be consistent with the other competition indices. One of the APA indices tested was Brown's (1965) original calculation, bisecting the distance between subject and each competitor at right angles, and forming a polygon around the subject tree (CI10). The other applied Moore *et al.*'s (1973) weighted division of distance between trees based on relative tree size (CI11). The formulae for the calculation of each index are given in Table 6.

Table 6: Formulae for calculating competition indices [explanations of index types are given in section 3.2(c)]

Index code	Index type	Reference	Index formula[1]
CI01	DI	---	$\Sigma\ 1$
CI02	DI	---	$\Sigma\ (D_j / D_i)^2$
CI03	DI	---	$\Sigma\ D_j$
CI04	SDR	Weiner (1984)	$\Sigma\ D_j / L_{ij}$
CI05	PDI	Spurr (1962)	$(k / 2) * \Sigma\ [D_j / L_{ij} * (j - ½)]$
CI06	PDI	Rouvinen and Kuuluvainen (1997)	$\Sigma\ (\arctan(D_j / L_{ij}) * (D_j / D_i))$
CI07	SDR	Hegyi (1974)	$\Sigma\ (D_j / D_i)^2 / L_{ij}$
CI08	CO	Arney (1973)	$\Sigma\ (O_{ij} / A_i)$
CI09	CO	Bella (1971)	$\Sigma\ (O_{ij} / A_i)\ (D_j / D_i)^x$
CI10	APA	Brown (1965)	$1/APA,\ l_{ij} = 0.5 * L_{ij}$
CI11	APA	Moore *et al.* (1973)	$1/APA,\ l_{ij} = D_i^2 / (D_i^2 + D_j^2) * L_{ij}$

[1] D_i = diameter-at-breast height of subject 'i' (cm)
D_j = diameter-at-breast height of competitor 'j' (cm)
L_{ij} = distance between competitor 'j' and subject 'i' (m)
A_i = area of zone of influence of subject 'i' (m^2)
O_{ij} = area overlap of zone of influence of competitor 'j' with subject 'i' (m^2)
l_{ij} = distance from subject 'i' of side of polygon between competitor 'j' and subject 'i' (m)
k = constant based on the BAF of the angle gauge used
x = exponent factor
n = number of competitors

5.8 Statistical analysis

All data manipulation and calculation of competition index values was carried out using SAS (SAS Institute Inc. 1988), except for indices based on area potentially available (i.e., CI10 and CI11), which required a separate program written in BASIC. All analyses of variance (ANOVA) and covariance (ANCOVA), ordinary least squares regression (OLS) and non-linear regression (NLN) were carried out using PROC GLM, PROC REG and PROC NLIN, respectively, in SAS.

6. Results

6.1 Pre-treatment characteristics

Table 7 lists the average characteristics of the sampled trees by crown class and treatment group at the time of cutting treatment based on information derived from stem analysis. The trees within the control group were all within 13 years of age of each other at the time of treatment, averaging just less than 70 years. The released group, while not significantly different from the control group in average age, had much greater variation in age, stretching over 40 years. The selection of younger trees within the released group is possibly the result of the increased survival of the smaller individuals following the release treatment. The increased incidence of older individuals within the group of released trees could not be explained.

There are no significant differences ($p>0.05$) between control and released trees within each crown class for diameter, total height and height at age 50 years (H_{50}), but there are significant differences ($p<0.05$) between crown classes for each variable. Analyzing the cumulative height growth for the 12-year period prior to treatment application does show that

Table 7: Characteristics of sample trees in 1971, at the time of cutting treatment application. Information derived from stem analysis.

		Partial cutting treatment							
	Crown	Control				Released			
Characteristic	class[1]	n	Min	Max	Mean	n	Min	Max	Mean
Age at stump height (years)	E	15	65	73	69.9	13	56	87	71.8
	D	23	61	74	69.3	25	42	80	66.4
	I	7	62	71	67.9	5	44	72	63.8
Diameter (inside bark)-at-breast-height (cm)	E	15	22.6	37.6	29.6	13	16.0	38.8	27.8
	D	23	14.7	26.8	20.2	25	8.4	35.2	20.5
	I	7	11.8	17.7	15.6	5	7.5	19.2	11.9
Height (m)	E	15	20.0	26.0	22.5	13	15.4	26.6	21.0
	D	23	13.5	21.3	18.2	25	8.3	25.9	17.1
	I	7	11.2	17.6	15.0	5	7.4	17.0	12.9
Height @ age 50 (m)	E	15	12.8	21.4	16.2	13	10.1	17.3	14.5
	D	23	8.4	15.4	12.2	25	8.0	19.1	12.9
	I	7	8.7	14.2	10.5	5	5.9	13.3	9.7

[1] E = Emergent; D = Dominant; I = Intermediate

the released trees were smaller ($p<0.05$) than the controls (see section 6.2(a) for a further explanation).

An assessment of the variation in site productivity between the three stands from which sample trees were collected was conducted based on H_{50} of emergent trees. There was no significant difference ($p>0.05$) in H_{50} between stands based on a one-way ANOVA, with overall average H_{50} being 15.4 m.

6.2 Cumulative growth responses to partial cutting

Comparisons between crown classes and cutting treatment for the 12 years prior to and 23 years following the cutting treatment were analyzed using repeated measures, analysis-of-variance. Illustrations of the cumulative growth, annual increment and relative growth response of released and control trees for total height, diameter-at-breast height, basal area and bole volume are given in Figure 2 to Figure 5, respectively.

6.2(a) Height

Emergent trees had the greatest cumulative height growth, followed by dominant and intermediate crown classes (Figure 2A). There was no significant difference in annual height increment between crown classes nor between released and control treatments prior to treatment. However, cumulative height growth showed a small difference ($p<0.05$) between released and control trees prior to treatment (Figure 2A). Trees from the treated group were slightly smaller than their respective controls within each crown class. This result was most likely the consequence of selecting trees by crown class after treatment application. Some trees may have shifted from one crown class to the next due to the cutting treatment. Smaller intermediate trees in the control area, which were of similar height at the time of treatment to the released intermediate group, most likely did not survive during the post-treatment period. This conjecture is supported by mortality data presented by Stiell *et al.* (1994) for the study area. The smaller intermediate trees in the treated areas are most likely still alive due to the consequence of the treatment itself.

All three crown classes in the control treatment show a significantly declining height increment during the 1960 to 1994 time period (Figure 2B), with the greatest decline evident in the intermediate crown class. Height increment following the cutting treatment shows no significant difference within and between control and released trees from the emergent and dominant crown classes. There was, however, a significant difference in height growth among intermediate trees from the control and release treatments (Figure 2C). This difference was due to a combined reduced growth in the control trees through time and an increased height growth in the treated trees. The results demonstrate that mature white pine trees whose cumulative height growth has been suppressed due to competitive interference can respond to release.

6.2(b) Diameter

Prior to treatment, emergent trees had the largest cumulative diameters and were growing the fastest, followed by dominant and intermediate crown classes (Figure 3A). There were no significant differences in cumulative and annual diameter growth between released and controls within each crown class prior to release. Intermediate trees from the control treatment had a significantly declining diameter growth from 1960 to 1994 (Figure 3B), while emergent and dominant control trees had no significant temporal variation in diameter growth during the same time period.

Differences in diameter growth due to release treatment were evident two years after treatment. After three years, average diameter increment in all three crown classes from the release treatment exhibited greater growth rates compared to all crown classes in the control group (Figure 3B). The relative response in diameter growth within each crown class (Figure 3C) indicates that intermediate trees had the greatest response to the cutting treatment, with dominant and emergent trees exhibiting a significant, but lower growth response.

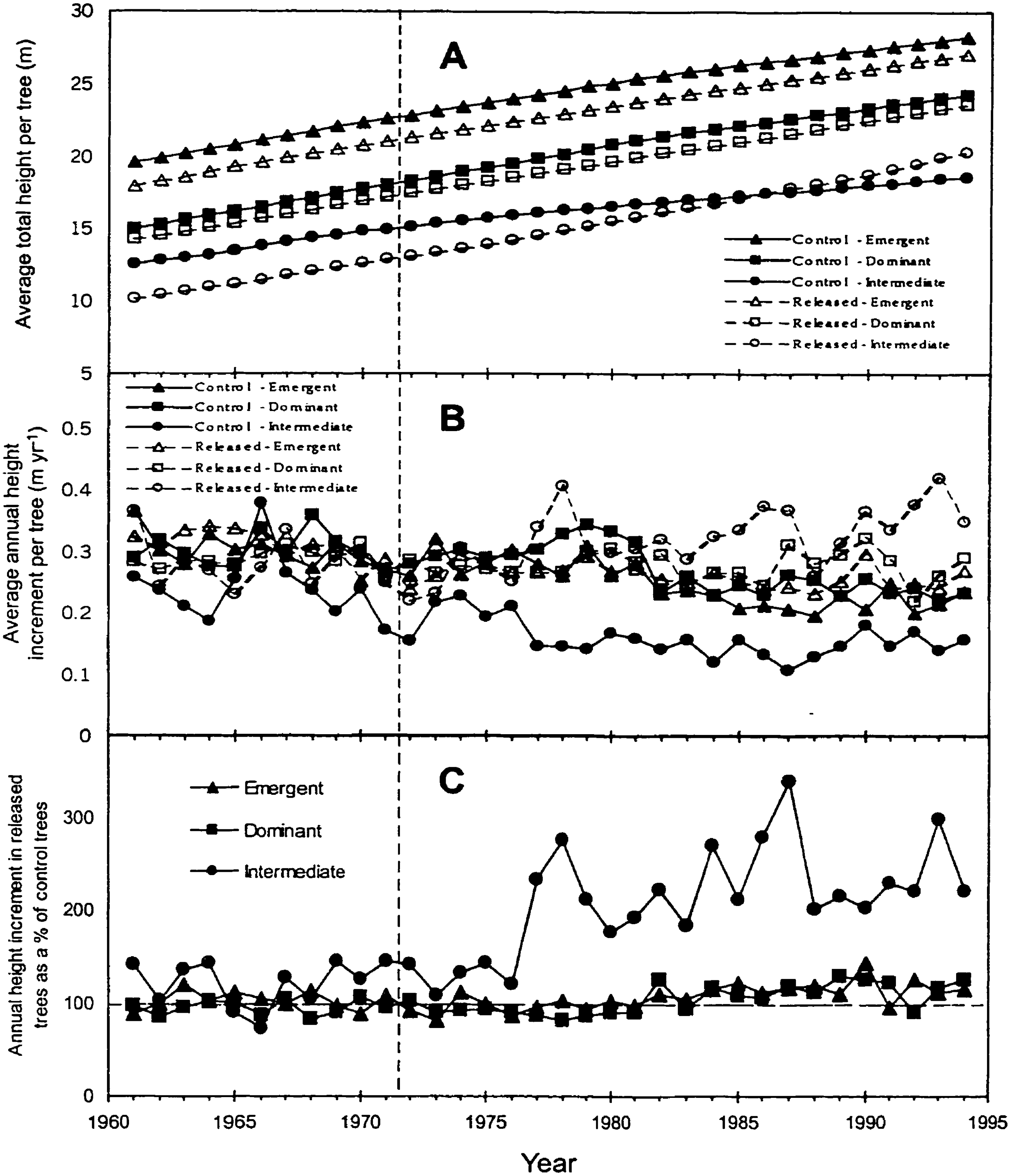


Figure 2: (A) Average cumulative height growth, (B) annual height increment and (C) relative height increment response in released and control white pine trees from three crown classes before and after a partial cutting treatment. Vertical line between 1971 and 1972 indicates time of cutting treatment.

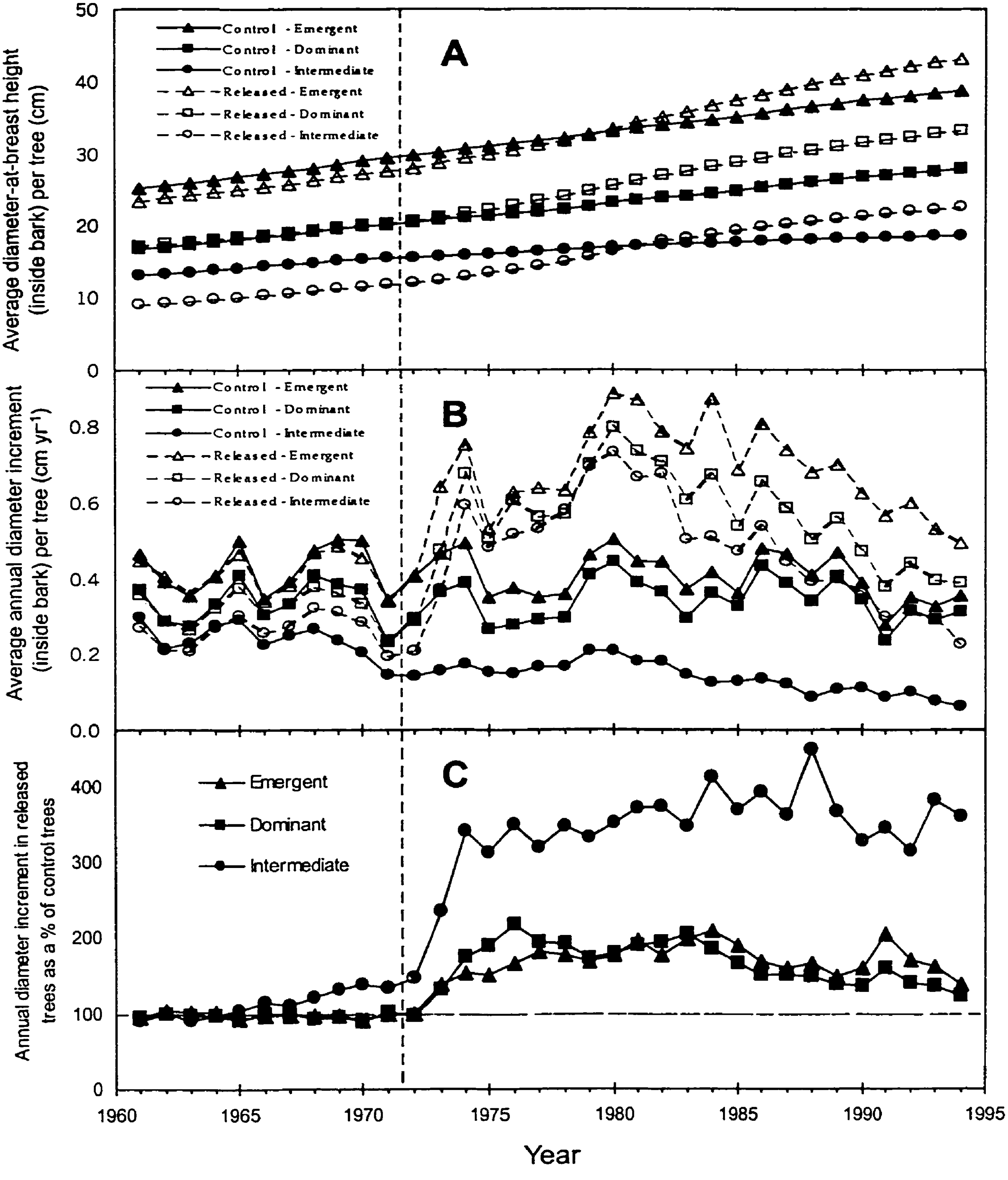


Figure 3: (A) Average cumulative diameter-at-breast height growth, (B) annual diameter increment and (C) relative diameter increment response in released and control white pine trees from three crown classes before and after a partial cutting treatment. Vertical line between 1971 and 1972 indicates time of cutting treatment.

6.2(c) Basal area

Similar to diameter growth, the cumulative and annual basal area growth prior to treatment was greatest in emergent trees, followed by dominant and intermediate trees (Figure 4A). Trees in the treated group show no significant difference from the control group within each crown class prior to the release treatment. Control trees in the emergent and dominant crown classes have significantly increasing annual basal area growth from 1960 to 1994, while intermediate trees in the control growth had declining growth during the same time period.

After the partial cutting treatment, the released trees exhibited increased rates of basal area increment relative to the control group within all crown classes (Figure 4B). Within 5 years of liberation, released intermediate trees had higher rates of basal growth compared to dominant control trees, and released dominant trees had greater rates of basal area growth compared to emergent control trees.

Intermediate trees in the treated group had, on average, up to double the basal area increment of control trees within 3 years of liberation (Figure 4C). The greater rate of basal area growth continued to increase over time, so that 15 years post-treatment, released intermediate trees had 3.5 times the basal area increment of control trees. Released trees from emergent and dominant crown classes exhibited approximately double the rate of basal area growth within 5 years of treatment, and they continued to maintain the increased rate of growth for the remainder of the post-treatment period.

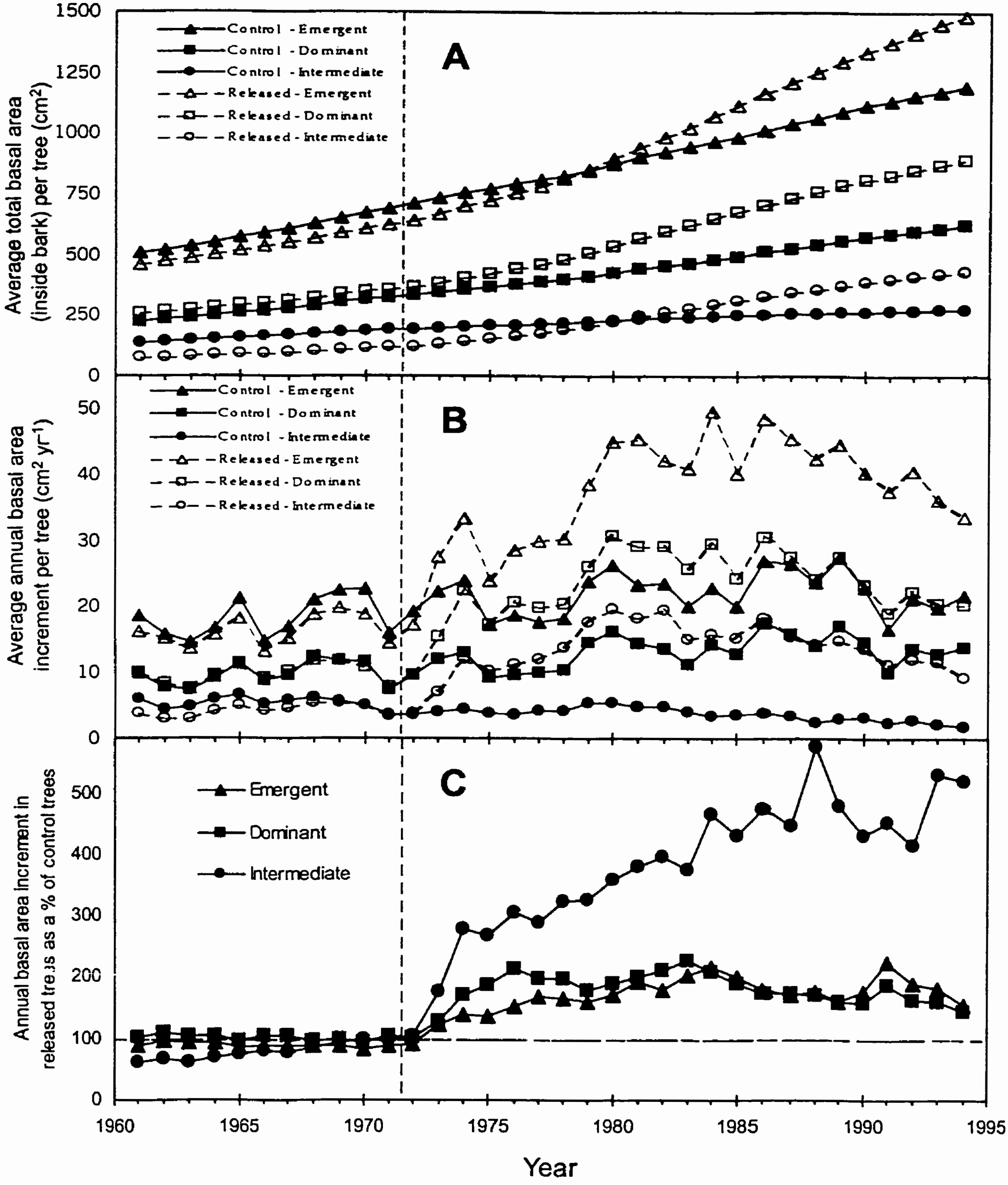


Figure 4: (A) Average cumulative basal area growth, (B) annual basal area increment and (C) relative basal area increment response of control and released white pine trees before and after a partial cutting treatment. Vertical line between 1971 and 1972 indicates time of cutting treatment.

6.2(d) Total volume

Prior to the release treatment, differences in cumulative and annual volume growth between crown classes followed the same pattern as diameter and basal area growth (Figure 5A). Control trees in the emergent and dominant crown classes had significantly increasing annual volume increment from 1960 to 1994, while control intermediate trees showed declining growth during this same period (Figure 5B).

A significant growth response in released trees was evident within each crown class. Unlike diameter and basal area growth response, volume growth response in the lower crown classes from the released group did not exceed the growth of the higher crown classes in the control group (Figure 5B).

Intermediate trees exhibited the greatest growth response (Figure 5C) as a consequence of the combined increased height and basal area growth. Released intermediate trees had, on average, three times the volume growth rate as the intermediate control trees. Released trees from the emergent and dominant crown classes averaged 50% more growth than control trees from 3 to 23 years after the partial cutting treatment.

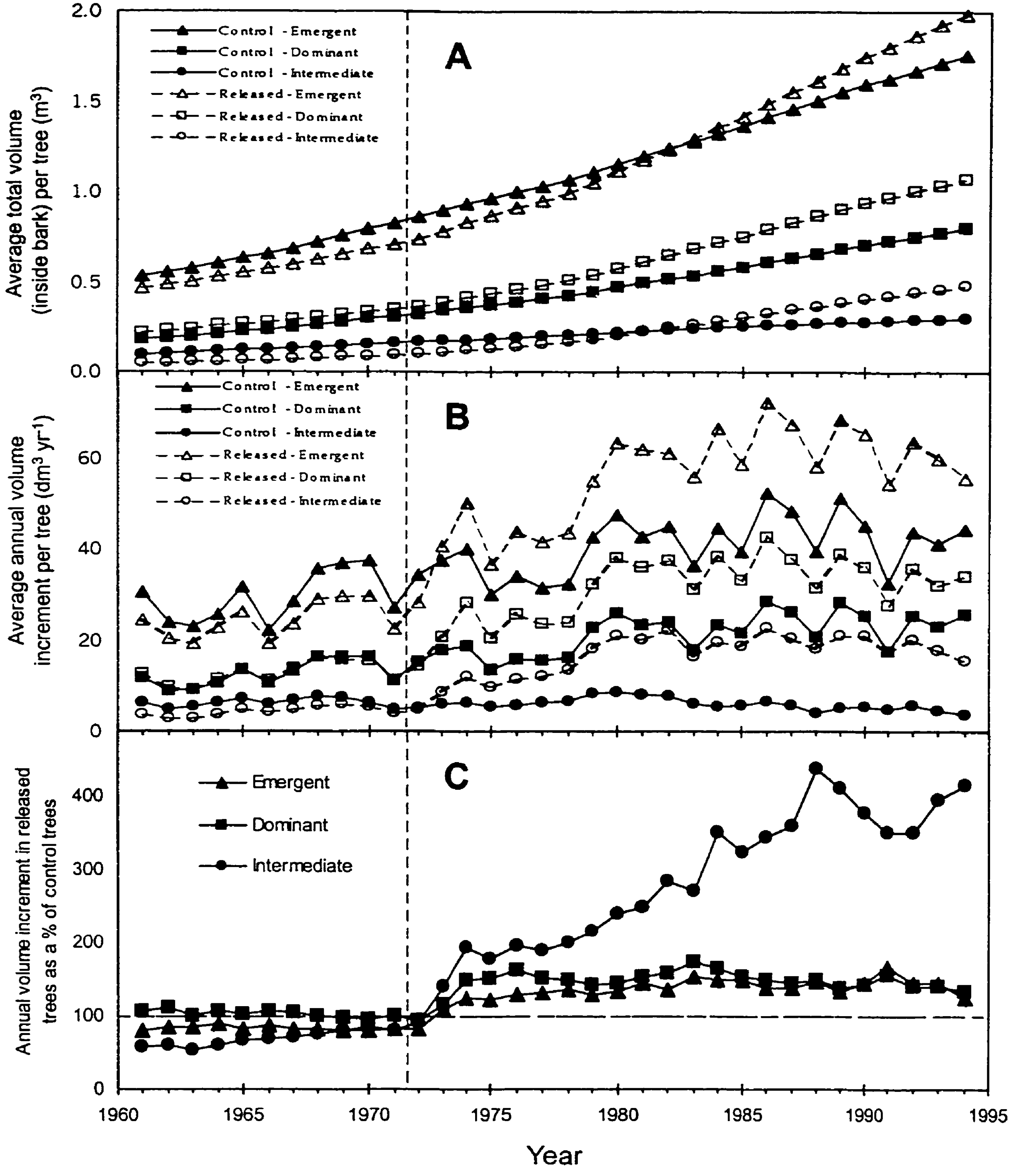


Figure 5: (A) Average cumulative volume growth, (B) annual volume increment and (C) relative volume growth response of control and released white pine trees before and after a partial cutting treatment. Vertical line between 1971 and 1972 indicates time of cutting treatment.

6.3 Size-dependent growth

Figure 6 illustrates that early in a tree's life, the relative growth rate of stem volume (RGR) and specific volume increment (SVI) of the main stem have relatively similar mean values and levels of variation. However, as trees age, there is a rapid decline in both the mean and variance of RGR. In contrast to this, the mean value of SVI displays a much more gradual decline with age, albeit with a large degree of variability between trees. The large variability in SVI would suggest that it might be more sensitive to differences in the genetic variation between individual trees and (or) changes in the growth response of trees to environmental stimuli. As such, SVI may better reflect the relative growth variation among trees that are the result of differences in the neighbourhood immediately surrounding them.

Three measures of size-dependent stem growth, i.e., RGR, RPR, and SVI, were analyzed for their utility in assessing competition effects of partial cutting treatments on growth. Following procedures outlined by Hunt (1982), third order polynomial equations, predicting

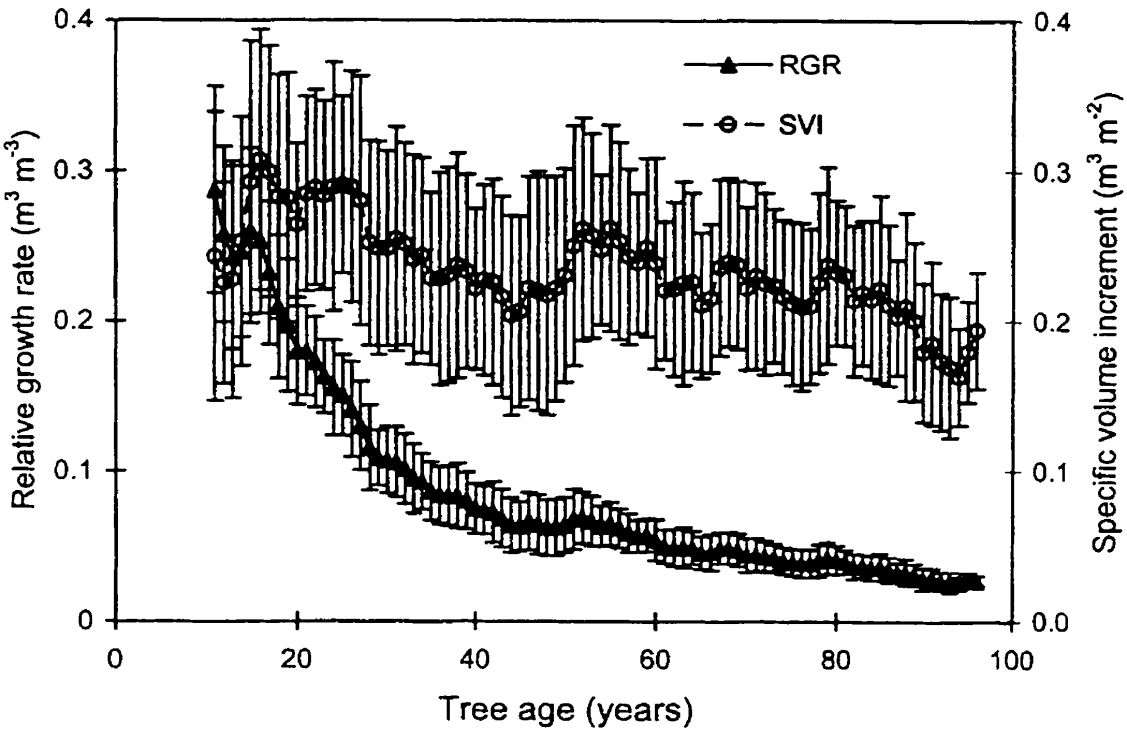


Figure 6: Age related variation in relative growth rate (RGR) and specific volume increment (SVI) of the main stem for 38 emergent and dominant white pine trees calculated on a yearly basis. The data were taken from the control group only, so as to not confound the age-related trend with the release treatment effect. Vertical bars represent one unit of standard deviation about the mean.

under-bark cambial surface area (equation [17]) and bole volume (equation [18]), were developed for each tree for a 24 year period (i.e., 1971-1994). Data on tree size immediately prior to treatment (i.e., 1971) was included in the regression analysis so that a more accurate prediction of growth could be made for the first year following release. Parameter estimates and regression statistics for the equations are given in Appendix 1. Estimates of RGR, RPR and SVI for each year were obtained using equations [8], [16] and [19], respectively.

Analysis of the average growth over that last five years of observations (i.e., 1990 to 1994) shows that there are significant ($p<0.05$) differences in RGR and SVI among crown classes and due to release treatment (Table 8). Released trees had a higher RGR than the control group within each crown class, although there is no significant difference among crown classes in the release treatment. Intermediate trees had the lowest RGR in the control group, but the highest RGR in the released group. In both cutting treatments, dominant trees had a greater RGR compared to emergent trees.

Table 8: Effect of crown class and cutting treatment on size-related growth during the last five years of observation (i.e., 1990 to 1994). Treatment means within a column followed by the same letter are not significantly different (Duncan, $p=0.05$).

Cutting treatment	Crown class	RGR[a]	RPR[b]	SVI[c]
Released	Emergent	0.0326 *ab*	-0.031 *a*	0.274 *a*
	Dominant	0.0351 *ab*	-0.048 *ab*	0.222 *ab*
	Intermediate	0.0382 *a*	-0.076 *b*	0.180 *b*
Control	Emergent	0.0251 *b*	-0.021 *a*	0.191 *b*
	Dominant	0.0313 *ab*	-0.018 *a*	0.176 *b*
	Intermediate	0.0140 *c*	-0.123 *c*	0.054 *c*

[a] RGR is the relative growth rate and calculated using equation [8], page 32
[b] RPR is the relative production rate and calculated using equation [16], page 48
[c] SVI is the specific volume increment and calculated using equation [19], page 49

A slightly different interpretation of the competition process is obtained when analyzing the variation in SVI. The release group had a significantly ($p<0.05$) greater SVI than the control group. However, SVI was highly dependent on crown class, as size-dependent growth increased from intermediate to dominant to emergent trees in both the control and released treatments (Table 8). This suggests that 18 to 23 years after a partial cutting treatment, the size-asymmetric nature of competition in favour of larger, more dominant trees is similar in both released and control treatments.

The change in RGR and SVI in released trees immediately following the cutting treatment (Figure 7A and C, respectively) showed a significant growth response, while RPR displayed a constant decline through time in all crown classes (Figure 7B). The lack of response in RPR following competition release is partially a result of the use of a third order polynomial equation for the volume equation. However, the strength of the correlation and ease of use make the polynomial equation appealing. This result suggests that RPR is unable to properly reflect the change in competition and its effect on growth, and therefore was not used in any further analysis.

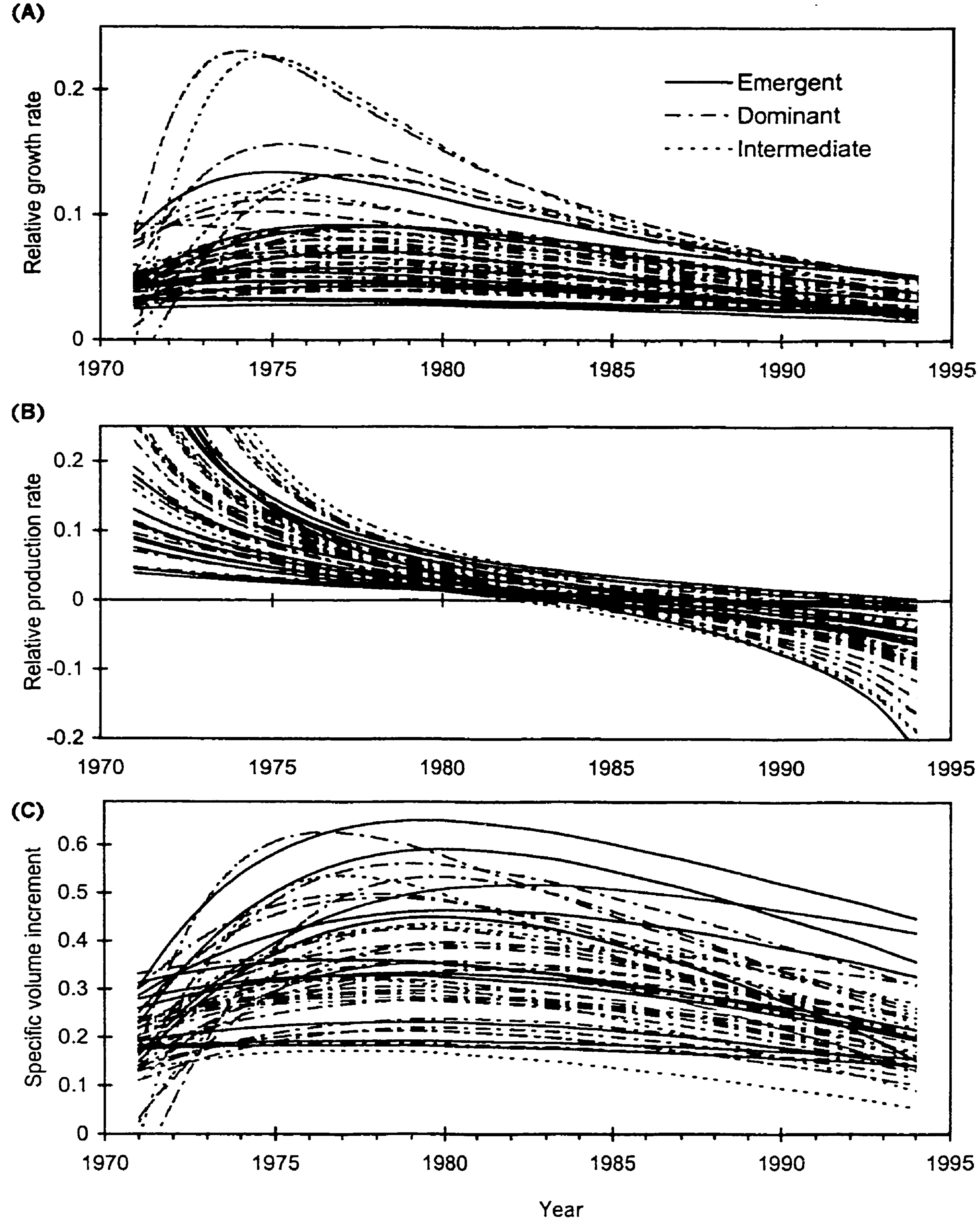


Figure 7: Size-dependent growth response of the main stem of 42 released white pine trees from three crown classes following a partial cutting treatment. (A) Relative growth rate (RGR) (B) Relative production rate (RPR). (C) Specific volume increment (SVI).

6.4 Size-dependent growth and competition indices

Univariate statistics for the distribution of RGR and SVI based on the 88 sample trees for the years 1990-94 are given in Table 9. The data show that the mean and variance of SVI are an order of magnitude greater than RGR, and that the coefficient of variation and skewness for SVI is greater compared to RGR.

Table 9: Univariate statistics of size-related measures of tree growth for white pine trees during the period 1990-1994.

	Variable	
Estimate	RGR	SVI
Mean	0.0306	0.1956
Standard deviation	0.0106	0.0819
Coefficient of variation	34.49	41.87
Skewness	0.7681	0.8437

RGR and SVI were regressed against the 11 competition indices using equation [26] and employing data from the last 5 years of measurement (i.e., 1990-94).

$$ln(Y) = \beta_0 + \beta_1*(CI) \qquad [26]$$

where Y is either RGR or SVI, CI is one of the competition indices, and β_0 and β_1 are parameters to be estimated.

For the crown overlap indices (i.e., CI08 and CI09), the highest correlation was obtained when the definition of the radius of influence zone around each tree was equated to 0.25*D and the exponent factor for CI09 was equal to 1.0. These values agree with the optimum values obtained by Tome and Burkhart (1989) for young *Eucalyptus globulus* plantations. Results of the analyses for all competition indices are given in Table 10.

Table 10: Parameter estimates and regression statistics from regression analysis relating two size-dependent stem growth measurements, (i) relative growth rate (RGR) and (ii) specific volume increment (SVI) of white pine trees to competition indices.

Competition	Y = RGR[a]				Y = SVI			
Index[b]	β_0	β_1	RSME[c]	R^{2d}	β_0	β_1	RMSE	R^2
CI01	-3.111	-0.0287	0.3365	0.1250	-0.973	-0.0494	0.4333	0.2040
CI02	-3.381	-0.0084	0.3337	0.1394	-1.288	-0.0217	0.3376	0.5169
CI03	-3.094	-0.0010	0.3346	0.1349	-1.062	-0.0014	0.4454	0.1590
CI04	-3.138	-0.0054	0.3326	0.1450	-0.973	-0.0098	0.4155	0.2681
CI05	-3.310	-0.0002	0.3282	0.1678	-1.329	-0.0003	0.4189	0.2561
CI06	-3.241	-0.0143	0.3293	0.1619	-0.982	-0.0345	0.3373	0.5178
CI07	-3.380	-0.0054	0.3253	0.1824	-1.320	-0.0129	0.3165	0.5753
CI08	-3.105	-0.1009	0.3216	0.2009	-0.867	-0.1953	0.3722	0.4129
CI09	-3.316	-0.0461	0.3258	0.1800	-1.196	-0.1050	0.3398	0.5104
CI10	-3.494	-0.8585	0.3570	0.0153	-1.562	-2.5281	0.4677	0.0727
CI11	-3.469	-0.8699	0.3365	0.1251	-1.530	-2.1197	0.3738	0.4076

[a] Model: $ln(Y) = \beta_0 + \beta_1 * (CI)$

[b] see section 5.7 on page 56 for definitions of competition indices

[c] RMSE = root mean squared error

[d] R^2 = coefficient of determination.

The results from the regression equations in Table 10 demonstrate that all competition indices explain a larger proportion of the variation in *ln*(SVI) (i.e., higher R^2) as compared to RGR. R^2 values for RGR are comparable to the level of correlation Peterson and Squiers (1995) obtained when they analyzed the relationship between relative diameter growth rate and competitive interference in white pine. This strong correlation between *ln*(SVI) and competitive interference supports the hypothesis that the use of SVI is a more appropriate measure of size-dependent growth compared to RGR when investigating the influence of competitive interference on the growth of older trees.

SVI is negatively correlated with the level of cumulative competitive interference of all species of competitors, and more than half of the variation in SVI could be accounted for by competitive interference alone (Table 10). A comparison of the efficacy of the competition indices shows that the regression models from this study have comparable levels of correlation to that found in the literature.

Distance-dependent indices were generally superior to distance-independent indices, although CI02, based on the summation of the relative size of all competitors, explained a comparable amount of variation in *ln*(SVI). This supports the assumption that competition is a spatial process. However, it could also be a consequence of the method by which competitors were selected. Distance from the subject tree is indirectly used in the selection of competitors, eventhough the distance need not be recorded or used directly in the calculation of the index. Neighbourhood indices which weight each competitor by its relative size to the subject tree significantly improves the performance of the competition index, as seen by the higher correlation for indices CI02, CI06, CI07 and CI09 with *ln*(SVI) compared to the other, non-weighted indices.

The two indices based on the area potentially available (APA) (i.e., CI10 and CI11) had relatively poor correlation with RGR and SVI compared to the other neighbourhood models tested. This contradicts the conclusions of Ford and Sorrensen (1992) who indicated that the modified APA (i.e., CI11) has generally shown the best correlation to growth for a number of species.

6.4(a) One- versus two-sided competition

To assess the influence of small competitors on size-dependent growth (i.e., two-sided competition), two separate, yet comparable approaches were employed. Each approach involved stratifying competitors according to their relative canopy position to the subject tree. Competition indices for each relative canopy position were calculated separately, one representing the competitive pressure by trees of a greater crown class (CI_G), one for competitors of equal crown class (CI_E), and the final one based on competitive influence of competitors from a lower crown class (CI_L). This is similar to the approach used by Newton and Jolliffe (1998). Tome and Burkhart (1989) also stratified competitors according to relative height, except they negatively weighted the inverse ratio of relative size for smaller competitors. Competition indices based on APA (i.e., CI10 and CI11) could not be separated in this fashion due to the principle involved in their calculation, and were not included in this part of the analysis.

By partitioning competition indices based on relative crown classes, it implies that the competition effects are additive and the overall index value is the summation of the individual components.

[27] $$CI = CI_G + CI_E + CI_L$$

The relative influence of small trees on the growth of a larger tree can be assessed based on the strength of the relationship between growth and competition with and without the CI_L term included. The assumption is made that small competitors are primarily competing for belowground resources, although it is acknowledged that there may also be some shading effects on the lower crown of the subject tree. An improved correlation with the CI_L term included in the model implies that competition for moisture and nutrients is important for individual white pine trees and that competition is a two-sided process. Two models were used to test this hypothesis.

The first involved a multiple linear regression equation between *ln*(SVI) and the three components for each competition index (i.e., equation [28]).

[28] $$ln(\mathrm{SVI}) = \beta_0 + \beta_1 {*} \mathrm{CI}_G + \beta_2 {*} \mathrm{CI}_E + \beta_3 {*} \mathrm{CI}_L$$

This model differs from equation [26] by explicitly assuming that the competitive influence of competitors of varying relative heights is unequal. The model assumes the competitive influence of the relative crown classes is additive with no interaction with respect to the *ln*(SVI). The absolute value of the parameter estimates for the coefficients of each term in equation [28] provide a relative measure of the competitive influence exerted by different size competitors. Significance of the CI_L term is based on several measures of multiple linear regression quality: R^2, root mean squared error (RMSE), adjusted-R^2 and partial-F test.

The other approach involved applying equation [26] with and without the CI_L in the calculation of overall competitive interference. Two criteria were used to test for a significant improvement in the equation. One involved a straight comparison of the R^2 and RMSE values between the two models. If R^2 was greater when CI_L was included in the calculation, then a modified partial-F test based on the reduction in the sum-of-squared errors between the two models was used to indicate if the improved R^2 was significant. Results from the regression analyses are given in Table 11 and Table 12.

Table 11 shows that for all competition indices, the coefficients for all terms in the equation are negative, confirming the hypothesis that greater competitive interference reduces growth regardless of crown class. The absolute value of the coefficients usually decreases as the relative crown class of the competitor decreases for all indices tested. The absolute value of the coefficient for the CI_L term was smaller than both the CI_G and CI_E terms for seven of the nine indices tested. This indicates that at a given level of competitive interference, a larger competitor reduces growth more than the same level of competition from a smaller competitor. Considering that competitors are already weighted by their relative D, the generally decreasing trend in the absolute value of the coefficients in equation [28] with declining tree status is further evidence of the asymmetry of competition in white pine. It also suggests that the neighbourhood models might be improved by selecting a more appropriate method of weighting neighbouring competitors beyond just their relative D.

Index CI01, which had a poor correlation with *ln*(SVI) using equation [26], had a

Table 11: Parameter estimates and regression statistics relating *ln*(SVI) of white pine trees to competition indices to determine the competitive interference of relatively smaller-sized trees on subject trees.

Competition Index[1]	Parameter estimates[2] β_0	β_1	β_2	β_3	RMSE	R^2	*p*-value for H_0: $\beta_3=0$
CI01	-0.9145	-0.1162	-0.0494	-0.0246	0.3244	0.5641	0.0205
CI02	-1.3178	-0.0222	-0.0172	-0.0254	0.3401	0.5211	0.0942
CI03	-1.0720	-0.0029	-0.0011	-0.0007	0.3679	0.4395	0.1267
CI04	-1.0407	-0.0184	-0.0091	-0.0027	0.3259	0.5603	0.1817
CI05	-1.4070	-6.53E-4	-2.67E-4	-2.45E-5	0.3401	0.5211	0.7790
CI06	-1.1310	-0.0388	-0.0243	-0.0205	0.3236	0.5665	0.0392
CI07	-1.3039	-0.0127	-0.0146	-0.0113	0.3196	0.5771	0.1507
CI08	-1.0520	-0.2442	-0.1454	-0.0896	0.3401	0.5211	0.0453
CI09	-1.2226	-0.1060	-0.0961	-0.0981	0.3435	0.5115	0.0729

[1] see section 5.7 on page 56 for definitions of competition indices

[2] Model: $ln(SVI) = \beta_0 + \beta_1 * CI_G + \beta_2 * CI_E + \beta_3 * CI_L$

significantly improved correlation based on equation [28]. This index, which is the simplest distance-independent index to calculate (simply count the number of competitors) performed better than a number of the distance-dependent indices. For five of the nine neighbourhood models, the coefficient for CI_L is significantly ($p<0.10$) different from zero. This is particularly true for those indices that explain a larger percentage of variation in *ln*(SVI) (i.e., CI01, CI02, CI06 and CI08). However, the CI that had the highest correlation with *ln*(SVI) (i.e., CI07) did not exhibit any significant improvement with the addition of the CI_L term.

When applying equation [26] to test for two-sided competition, results in Table 12 show that model 1 (i.e., which contains CI_L) had a higher R^2 value compared to model 2 for only three of the nine competition indices tested. For these three indices, the improvement in R^2 was not significant ($p>0.05$) based on a modified partial-F test. This approach assumed that

Table 12: Parameter estimates and regression statistics for determining the competitive influence of smaller competitors on the *ln*(SVI) of white pine trees using different competition indices.

Competition Index[a]	Model[b]	Parameters		R^2	SSE[c]	Partial-F[d]	*p*-value
		β_0	β_1				
CI01	1	-0.973	-0.0494	0.2040	16.150	*	*
	2	-0.988	-0.0720	0.3480	13.228		
CI02	1	-1.288	-0.0217	0.5169	9.953	*	*
	2	-1.349	-0.0216	0.5229	10.085		
CI03	1	-1.062	-0.0014	0.1590	17.061	*	*
	2	-1.088	-0.0018	0.2480	15.256		
CI04	1	-0.973	-0.0098	0.2681	14.849	*	*
	2	-0.986	-0.0138	0.4246	11.673		
CI05	1	-1.329	-3.50E-4	0.2561	15.091	*	*
	2	-1.336	-4.60E-4	0.3849	12.478		
CI06	1	-0.982 -	-0.0345	0.5178	9.783	0.36	0.5501
	2	1.134	-0.0348	0.5157	9.824		
CI07	1	-1.320	-0.0129	0.5753	8.615	2.37	0.1274
	2	-1.378	-0.0133	0.5637	8.852		
CI08	1	-0.867	-0.1953	0.4129	11.911	*	*
	2	-1.045	-0.2074	0.4432	11.297		
CI09	1	-1.196	-0.1050	0.5104	9.933	3.29	0.0732
	2	-1.288	-0.1032	0.4916	10.313		

[a] see section 5.7 on page 56 for definitions of competition indices

[b] Model 1: $ln(SVI) = \beta_0 + \beta_1*(CI_G + CI_E + CI_l)$; Model 2: $ln(SVI) = \beta_0 + \beta_1*(CI_G + CI_E)$

[c] SSE = sum-of-squared errors

[d] $F = (SSE_1 - SSE_2)/[(SSE_1)/(n-2)]$, where n=88

* not applicable (no improvement in model was observed)

competitors from all crown classes exert the same competitive interference per unit of CI. The parameter estimates from Table 11, however, indicate that larger crown classes should be given more weighting than smaller crown classes in quantifying competitive interference. These results suggest that weighting the competitive interference of competitors by relative diameter may not be adequate, and that weighting competitors based on relative height may be more appropriate when calculating competitive inference in stands with variable tree sizes.

6.4(b) Intra- versus inter-specific competition

Using the same approach as Liu and Burkhart (1994), intra- and inter-specific competition was assessed by stratifying competitors into species group (i.e., white pine and non-white pine). Competition indices were then computed separately for each species group (i.e., CIp and CIo for white pine and other species competitors, respectively). The competitive interference around each subject tree attributed to white pine competitors averaged about 66%, ranging from less than 10% to 100% depending on the CI used (Table 13).

The assessment of the impact of intra- and inter-specific competition was conducted using equation [29]:

[29] $$ln(\mathrm{SVI}) = \beta_0 + \beta_1{*}\mathrm{CIp} + \beta_2{*}\mathrm{CIo}$$

where, CIp and CIo are the competitive interference of white pine and none-white pine

Table 13: Summary statistics of competitor interference by white pine competitors as a percentage of total competition.

Competition Index	Percent white pine[a]		
	Mean	Minimum	Maximum
CI01	65.9	21.1	100
CI02	66.3	8.7	100
CI03	66.0	14.3	100
CI04	66.3	8.7	100
CI05	69.5	5.0	100
CI06	66.0	13.9	100
CI07	65.7	10.7	100
CI08	66.8	15.0	100
CI09	66.6	9.2	100

[a] % = CIp/(CIp+CIo)*100,
where CIp = competitive interference of white pine competitors
CIo = competitive interference of non-white pine competitors

neighbours, respectively, and SVI as defined previously

Equation [29] implies additive competition effects and no interaction with respect to *ln*(SVI), and has a similar form to equation [28], used for assessing one- versus two-sided competition. Partial R^2 for each component of competition quantifies the individual impact of intra- and inter-specific competition, respectively. Results from the analysis are given in Table 14.

SVI in white pine was negatively correlated with the presence of both white pine and non-white pine competitors. There does not appear to be any difference between intra- and inter-specific competition on the reduction in white pine growth. Parameter estimates for the coefficients of CIp and CIo were not significantly (p>0.05) different from each other for eight of the nine competition indices tested, implying that both species groups decrease white pine growth by the same amount per unit of competitive interference. These results contradict the findings of Peterson and Squiers (1995), who found that a proportionally higher abundance of aspen competitors (inter-specific competition) increased white pine growth compared to relatively higher levels of intra-specific competition.

The comparison of the behaviour of equations [26] and [29] suggests that the separation of intra- and inter-specific competition does not significantly (p > 0.05) affect the prediction

Table 14: Results from regression analysis relating *ln*(SVI) of white pine trees to intra- and inter-specific competition indices. (Partial R^2 given in brackets)

Competition	Parameter estimates					p-value for
Index	β_0	β_1	β_2	RMSE	R^2	$H_0:\beta_1=\beta_2$
CI01	-0.988	-0.0446 (0.129)	-0.0556 (0.176)	0.4340	0.211	0.3958
CI02	-1.292	-0.0209 (0.232)	-0.0226 (0.258)	0.3393	0.518	0.7381
CI03	-1.096	-0.0012 (0.085)	-0.0017 (0.167)	0.4440	0.174	0.2167
CI04	-0.978	-0.0091 (0.191)	-0.0109 (0.214)	0.4609	0.274	0.3981
CI05	-1.334	-2.30E-4 (0.110)	-4.20E-4 (0.209)	0.4161	0.275	0.0221
CI06	-0.990	-0.0332 (0.286)	-0.0357 (0.228)	0.3389	0.519	0.6723
CI07	-1.321	-0.0113 (0.264)	-0.0156 (0.284)	0.3133	0.589	0.1002
CI08	-0.883	-0.1816 (0.262)	-0.2108 (0.329)	0.3725	0.419	0.3676
CI09	-1.199	-0.1030 (0.273)	-0.1069 (0.300)	0.3418	0.511	0.8453

[1]Model: *ln*(SVI) = $\beta_0 + \beta_1$*CIp + β_2*CIo, (see page 78 for description of variables)

of white pine SVI, which agrees with the previous conclusions. Pooling of the two kinds of competition simplifies the modelling approaches.

6.5 Crown dimensions

Direct measurement of crown dynamics throughout the post-treatment period was not possible. However, measurements of crown dimensions taken 23 years after the partial cutting treatment showed significant differences between crown classes and due to the cutting treatment (Table 15). The progression in canopy dominance from intermediate to dominant to emergent crown classes shows significant (p<0.0001) increases in crown length, radius and volume (Table 16). Although crown ratio (i.e., crown length:total height) shows a marginally significant (p=0.0701) difference between crown classes, mean values appeared to increase only in the control trees. Overall crown shape, expressed as the ratio of crown length to crown radius, showed no significant difference due to canopy position or release treatment. The interaction term is not significant (p>0.05) for any crown dimensions, indicating that all crown classes responded in the same way to the cutting treatment.

At the time of felling, released trees had significantly (p=0.0024) longer crowns than controls within each respective crown class. A comparison of mean values between control and released trees by crown class showed that the dominant and intermediate trees had significantly longer crowns in the release treatment compared to the controls (Table 16). Crown radius was also significantly affected (p=0.0107) by the cutting treatment. Dominant trees were the only crown class that had significantly wider crowns after release (Table 16).

The wider and longer crowns in released, dominant trees resulted in significantly greater

Table 15: P-values from analysis of variance on crown dimensions due to crown class and cutting treatment in white pine 23 years after the application of the partial cutting treatment.

Effect	Crown characteristic				
	Length (m)	Radius (m)	Volume (m^3)	Crown ratio[1]	Crown shape[2]
Crown class (CC)	0.0001	0.0001	0.0001	0.0701	0.1469
Cutting treatment (TRT)	0.0024	0.0107	0.0019	0.0001	0.1873
CC*TRT	0.3408	0.0713	0.1891	0.4345	0.3211

[1] Crown ratio = crown length / total tree height

[2] Crown shape = crown length / crown radius

crown volumes compared to control, dominant trees (Table 16). The emergent crown class showed no significant difference in crown volume between control and released trees. Released, intermediate trees had slightly larger crown volumes relative to the control group, by virtue of their significantly longer crowns, but the difference was not statistically significant. Released trees in both the intermediate and dominant crown classes had significantly greater crown ratios compared to control trees (Table 16), indicating greater amounts of photosynthetic tissue per unit of cambial surface. The mean ratio of crown length to crown radius was slightly greater in released relative to control trees in each crown class, but the large variability among trees resulted in no significant differences, except in the intermediate trees.

Table 16: Mean crown size of sample trees in 1994, 23 years after a partial cutting treatment. Treatment means within a column followed by the same letter are not significantly different (Duncan, p=0.05).

			Crown size				
Crown class	Cutting treatment	Sample size	Length (m)	Radius (m)	Volume (m^3)	Crown ratio[1]	Crown shape[2]
Emergent	Released	13	13.49 *a*	4.93 *a*	551 *a*	0.501 *a*	2.97 *a*
	Control	15	12.96 *a*	4.95 *a*	520 *a*	0.457 *ab*	2.68 *ab*
Dominant	Released	25	11.58 *ab*	4.75 *a*	429 *a*	0.487 *a*	2.50 *ab*
	Control	23	9.44 *b*	3.85 *b*	235 *b*	0.387 *bc*	2.47 *ab*
Intermediate	Released	5	9.43 *b*	3.41 *b*	182 *b*	0.459 *ab*	2.76 *a*
	Control	7	6.69 *c*	3.34 *b*	122 *b*	0.359 *c*	2.04 *b*

[1] Crown ratio = crown length / total tree height
[2] Crown shape = crown length / crown radius

The relationship between crown dimensions and the vertical variation in bole area increment during the final year of measurement (i.e., 1994) is illustrated in Figure 8. Trees from all treatments and crown classes exhibit increasing area increment from tree apex to crown base. Distinct differences in area increment were observed for the three crown classes, with emergent showing the greatest increment, followed by dominant and intermediate trees. In addition, emergent and dominant trees in both control and release treatments exhibit continually increasing area increment below the base of the crown, although the rate of increase with distance down the bole is not as great as observed above the crown base.

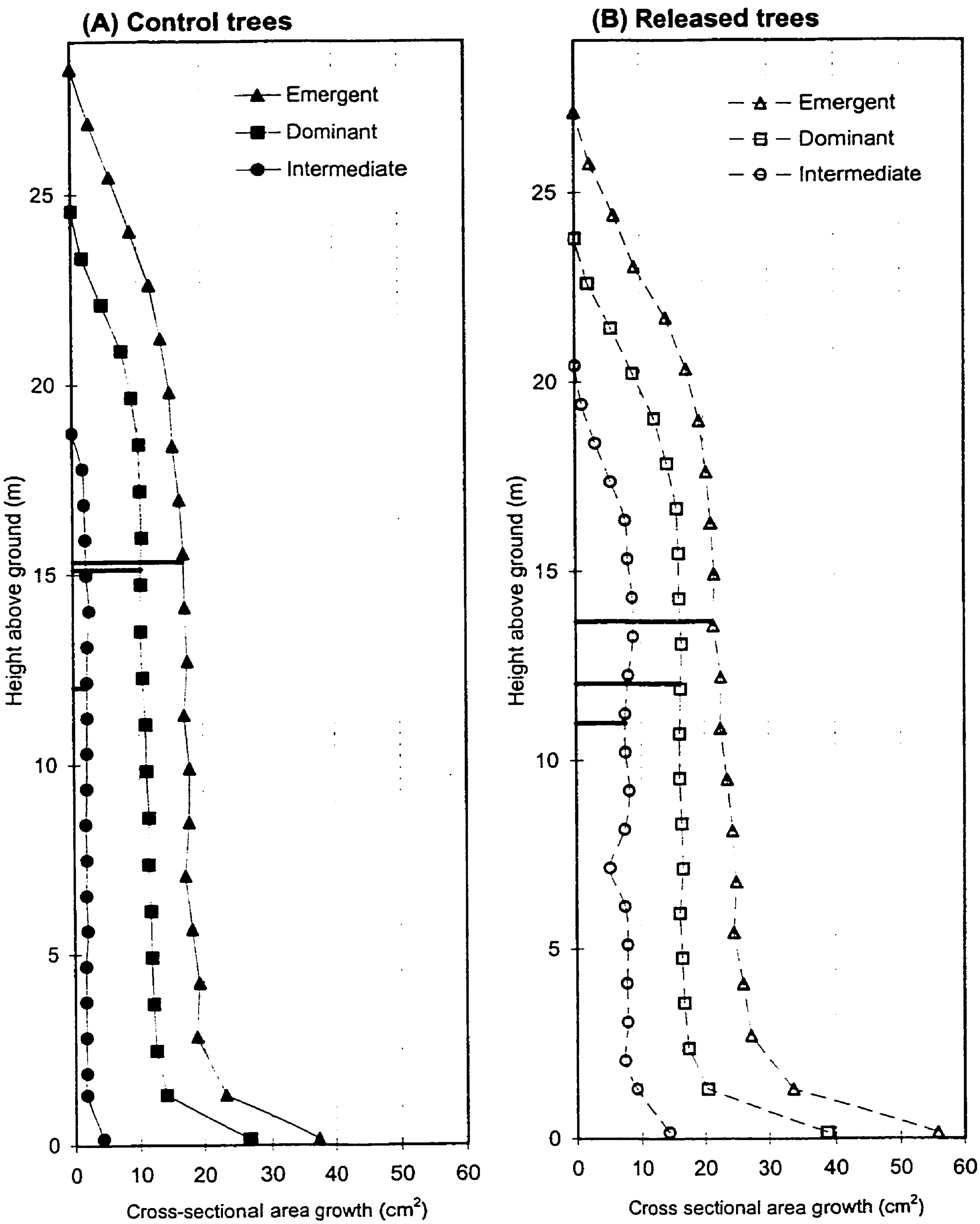


Figure 8: Vertical distribution of bole area increment for (A) control and (B) released average white pine trees from three crown classes in 1994, 23 years after partial cutting treatment. Horizontal lines indicate the base of the live crown.

Correlation coefficients between crown size and bole volume increment for the last year of measurement are given in Table 17. The significant positive correlation between crown volume and annual volume increment (Figure 9) demonstrates how increased crown development in released trees contributed to increased bole growth following the partial cutting treatment. Crown shape was not significantly correlated with either absolute or size-dependent stem growth.

Table 17: Correlation coefficients between crown size variables and bole volume growth for the last year of measurement

	Crown size				
Bole growth[1]	Length	Radius	Volume	Ratio[3]	Shape[4]
dV/dt[1]	0.64277	0.58330	0.68387	0.44947	0.2306
SVI[2]	0.37688	0.45303	0.43505	0.42912	0.0986

[1] $dV/dt = V_2 - V_1$, where V_1, V_2 = bole volume in 1993 and 1994, respectively
[2] $SVI = (V_2 - V_1) / SA_1$, where SA_1 = bole surface area in 1993
[3] Ratio = crown length / total tree height
[4] Shape = crown length / crown radius

To assess the relative influence of crown size and canopy position on bole volume growth, analysis of covariance was used (Table 18). Results show that both absolute and size-dependent volume growth are significantly different between crown classes after accounting for differences in crown volume. This suggests differences in growth allocation, as both emergent and dominant trees had greater amounts of absolute and size-dependent volume growth per unit crown volume relative to intermediate trees.

Table 18: Results from analysis of covariance on absolute (dV/dt) and size-dependent (SVI) volume growth due to crown size and canopy position in 1994.

		dV/dt[1]		SVI[2]	
Effect	df	F	*p*-value	F	*p*-value
Crown volume (CV)	1	95.61	0.0001	21.38	0.0001
Crown class (CC)	2	28.56	0.0001	12.88	0.0001
CV*CC	2	1.95	0.1495	2.47	0.0908

[1] $dV/dt = V_2 - V_1$, where V_1, V_2 = bole volume in 1993 and 1994, respectively
[2] $SVI = (V_2 - V_1) / SA_1$, where SA_1 = bole surface area in 1993

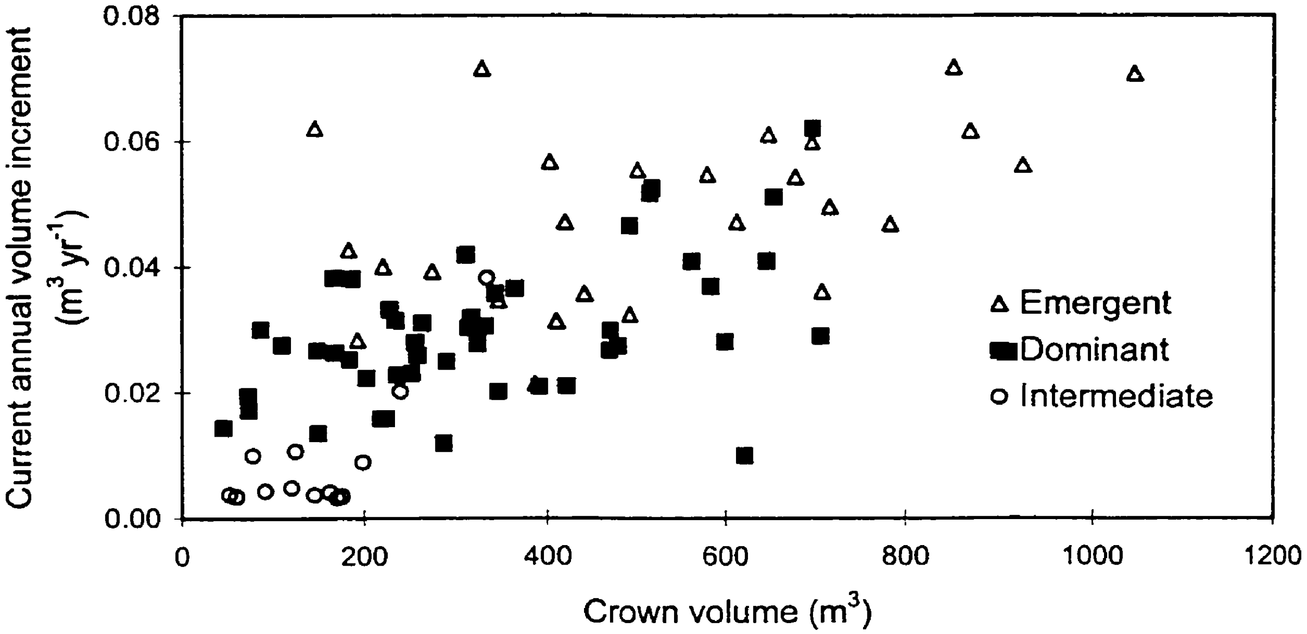


Figure 9: Relationship between volume increment and crown volume of white pine trees from three crown classses

Crown size is strongly correlated with measures of competition around individual trees, illustrating the influence of neighbourhood competition on crown development. Table 19 gives the correlation coefficients between the five measurements of crown architecture and 11 competition indices. Unweighted, distance-independent indices (CI01, CI03, CI04) are generally not well correlated with crown size, although they are significantly correlated with crown ratio. The best correlations between crown size and competition are obtained with those indices that weight each competitor by its relative size to the subject tree (i.e., CI02, CI06, CI07, CI09). Crown shape ratio (i.e., crown length:crown radius) is not significantly related to any measurement of local neighbourhood interference.

Table 19: Absolute value of correlation coefficients for relationship between crown size and 11 different competition indices (based on 88 white pine trees)

Competition	Crown size				
Index[1]	Length (m)	Radius (m)	Volume (m^3)	Crown ratio[2]	Crown shape[3]
CI01	0.3187*	0.2559	0.3040*	0.4606***	0.1319
CI02	0.5995***	0.5517***	0.5906***	0.4723***	0.2084
CI03	0.2033	0.2055	0.2255	0.4255***	0.0806
CI04	0.3681**	0.3555**	0.3868**	0.4656***	0.1239
CI05	0.4006***	0.3536**	0.3908**	0.4882***	0.1519
CI06	0.5976***	0.5466***	0.6043***	0.5390***	0.2107
CI07	0.6025***	0.5683***	0.6075***	0.4914***	0.1866
CI08	0.4718***	0.4749***	0.5068***	0.5160***	0.1493
CI09	0.5528***	0.5417***	0.5668***	0.4752***	0.1841
CI10	0.3742**	0.2765*	0.3504**	0.3498**	0.0423
CI11	0.5145***	0.4414***	0.5806***	0.4142***	0.0903

[1]see section 5.7 for description

[2]Ratio = crown length / total tree height

[3]Shape = crown length / crown radius

*** *p*<0.0001; ** *p*<0.001; * *p*<0.01

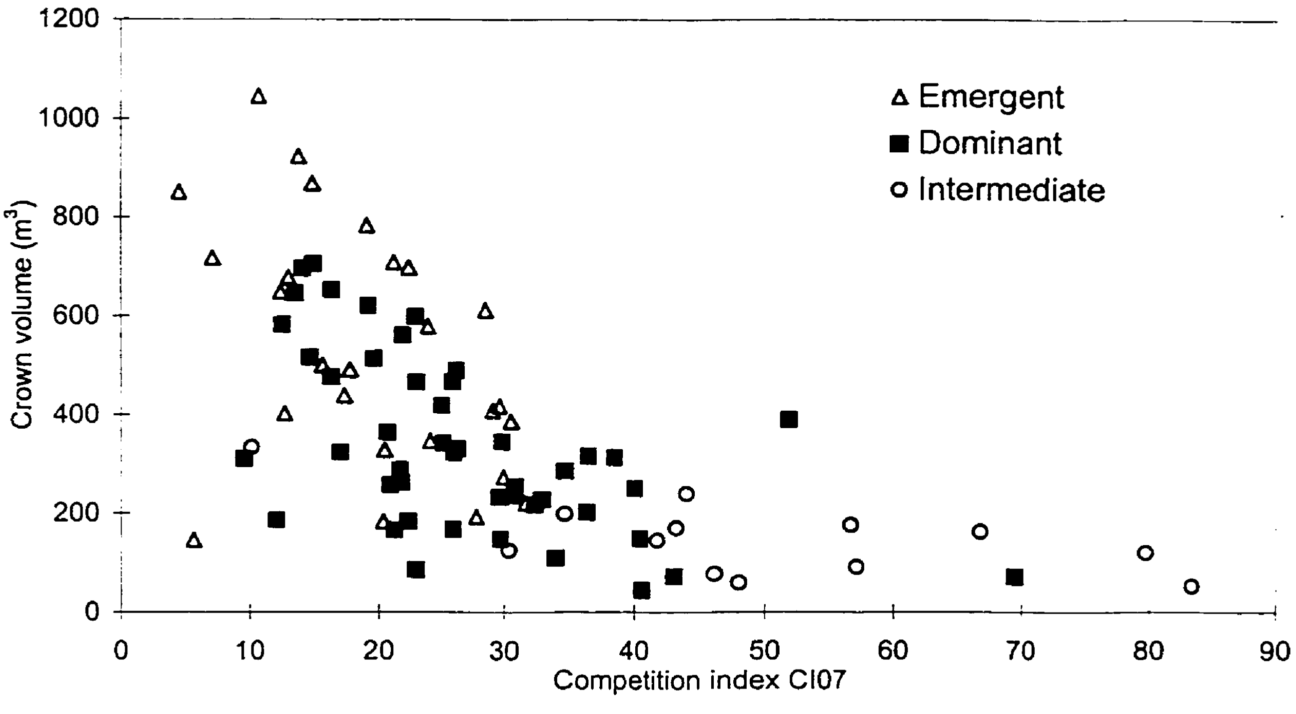


Figure 10: Scatter diagram illustrating the relationship between crown volume and cumulative competitive interference measured using CI07 (see text section 5.7, page 56 for description) by crown class.

Analysis of covariance was used to separate the effects of crown class and competitive interference on crown dimensions. Results for crown shape ratio are not reported since this crown variable was not significantly ($p>0.05$) affected by crown class or competitive interference, separately and in combination. After accounting for differences in mean crown size between crown classes, competition indices still explained a significant portion of the variation in crown size (Table 20). The relationship between crown size and competitive interference varied by crown class [i.e., interaction term was significant ($p<0.05$)]. Over 17% of the variation in crown volume can be explained by Hegyi's size-distance ratio index (CI07), as illustrated in Figure 10. Crown ratio was significantly more affected by competitive interference than by position in the canopy.

Table 20: Percent variation in crown size explained by 11 different competition indices, based on partial R^2, after accounting for variation between crown classes. (Based on 88 white pine trees)

Explanatory variables	Crown length R^2	Crown length Partial R^2	Crown radius R^2	Crown radius Partial R^2	Crown volume R^2	Crown volume Partial R^2	Crown ratio R^2	Crown ratio Partial R^2
CC^a	29.1	--	23.0	--	30.6	--	5.2	--
(CC & CI)^b								
CI01	37.9	8.8	31.1	8.1	38.7	8.1	25.8	20.6 **
CI02	44.6	15.6 **	39.0	15.9**	51.6	21.0 ***	30.5	25.3 ***
CI03	33.0	3.9	28.5	5.5	35.5	4.9	23.4	18.2 **
CI04	29.9	0.8	26.1	3.0	39.8	9.2	17.5	12.4
CI05	39.1	10.0 *	31.4	8.3	40.8	10.2 *	27.1	21.9 ***
CI06	42.7	13.7 **	37.2	14.2**	48.0	17.4 ***	31.3	26.1 ***
CI07	46.5	17.4 ***	41.2	18.1***	53.0	22.4 ***	32.4	27.2 ***
CI08	37.9	8.9	35.1	12.1*	43.2	12.6 *	27.7	22.5 ***
CI09	40.2	11.1 *	38.6	15.6**	48.5	17.9 ***	29.6	24.5 ***
CI10	35.5	6.4	33.2	10.2*	38.6	8.6	10.7	5.5
CI11	40.3	11.2 *	40.0	16.9**	48.1	17.5 ***	18.4	13.2 *

^{a}Model: $Y = \mu + CC_i + \varepsilon$, i = emergent, dominant, intermediate

^{b}Model: $Y = \mu + CC_i + CI + CC_i{*}CI + \varepsilon$, i = emergent, dominant, intermediate

*** $p<0.0001$; ** $p<0.001$; * $p<0.01$

6.6 Vertical bole area increment profiles

Figure 11 illustrates the change in the vertical distribution of 5-year periodic annual area increment (PAAI) for two periods prior to and 4 periods after the partial cutting treatment (final post-treatment PAAI is based on a 3-year period). All trees in the control group (Figure

11A, C, E) show increasing PAAI along the bole from the apex down to approximately 60 to 75% of tree height, followed by relatively constant or marginally increasing PAAI to approximately *bh*, and then a dramatic increase at the stump. Based on Pressler's general laws of stem form, the point of inflection at which PAAI shifts from significantly increasing values to a relatively constant value at progressively greater distances from the top of the tree should approximately represent the crown base.

Based on the same interpretation, emergent and dominant trees show an upward shift of the point of inflection throughout the post-treatment period, combined with a relatively constant (or slightly increasing) PAAI below the inflection point. This would indicate a relatively constant crown size that is gradually shifting upwards as a tree grows. This contrasts with intermediate trees from the control group (Figure 11E) which exhibit diminishing PAAI in the middle portion of the bole throughout the post-treatment period, indicating a decrease in average crown size through time.

The similarity in the shape of the vertical distribution in PAAI prior to the release treatment was analyzed using repeated measures, analysis-of-variance for the shape parameter (i.e., β) of equation [24]. No significant difference in β-values between crown classes and treatment was observed prior to treatment (Figure 12), indicating that the relative variation in area growth along the main bole did not differ with height in the canopy. However, there was a significant difference in the slope parameter (i.e., α) between crown classes, indicating different overall rates of area growth, with intermediate trees having significantly less growth than dominant and emergent trees.

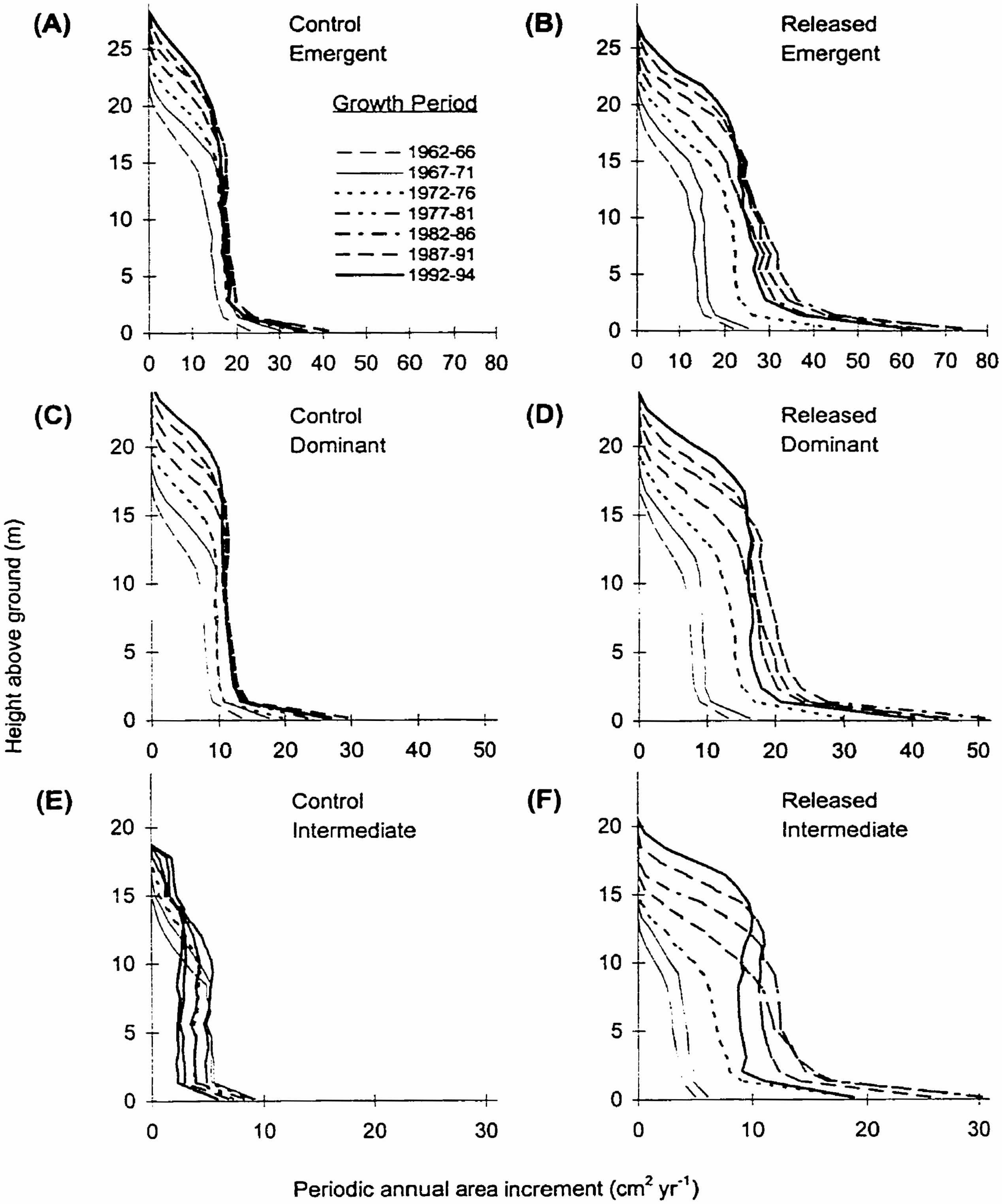


Figure 11: Vertical distribution in periodic annual bole area increment through time in control and released white pine trees from three crown classes. (A) Emergent-Control. (B) Emergent-Released. (C) Dominant-Control. (D) Dominant-Released. (E). Intermediate-Control. (F) Intermediate-Released. (Note scale differences along *x*-axis within columns).

After the cut, emergent trees in the release treatment displayed continually increasing PAAI down the entire length of the bole throughout the post-treatment period. Dominant and intermediate crown classes displayed increasingly PAAI down the bole for only part of the post-treatment, after which, the configuration of the vertical distribution in PAAI reverted back to pre-treatment shape (Figure 11B, D, F).

The difference over time between total tree height and height at which the point of inflection in the vertical distribution in PAAI occurs for released dominant and intermediate trees suggests that these trees had increasing crown size (i.e., length) for the first 10-15 years following release. This was followed by a constant and decreasing crown size for the released dominant and intermediate trees, respectively. In the released treatments, the intermediate trees seemed to initially benefit most in crown length, which is borne out by the fact that the volume response relative to the control was the greatest among the crown classes.

Dominant and emergent trees from the control group had no significant change ($p>0.05$) in β from equation [24] during the post-treatment period. Intermediate trees showed a gradually decreasing β-value through time. Values of β in released trees showed a significant increase ($p<0.05$) from their pre-treatment value during the first 15 years after treatment (Figure 12). Released emergent trees continued to have significantly different ($p<0.05$) β-values compared to their control group at the end of the time period used for analysis. However, β-values for dominant and intermediate released trees were no longer significantly different ($p>0.05$) from their respective control crown classes 23 years after the cutting treatment. The sudden jump in β-values observed in emergent and dominant trees from both control and release treatments in 1988 could not be explained. It is possible that 1988 may have had a number of extreme wind storms or weather conditions, with the wind causing increased stem sway in all trees in the study area. Climatic data for the study area does not provide sufficient information to confirm this speculation.

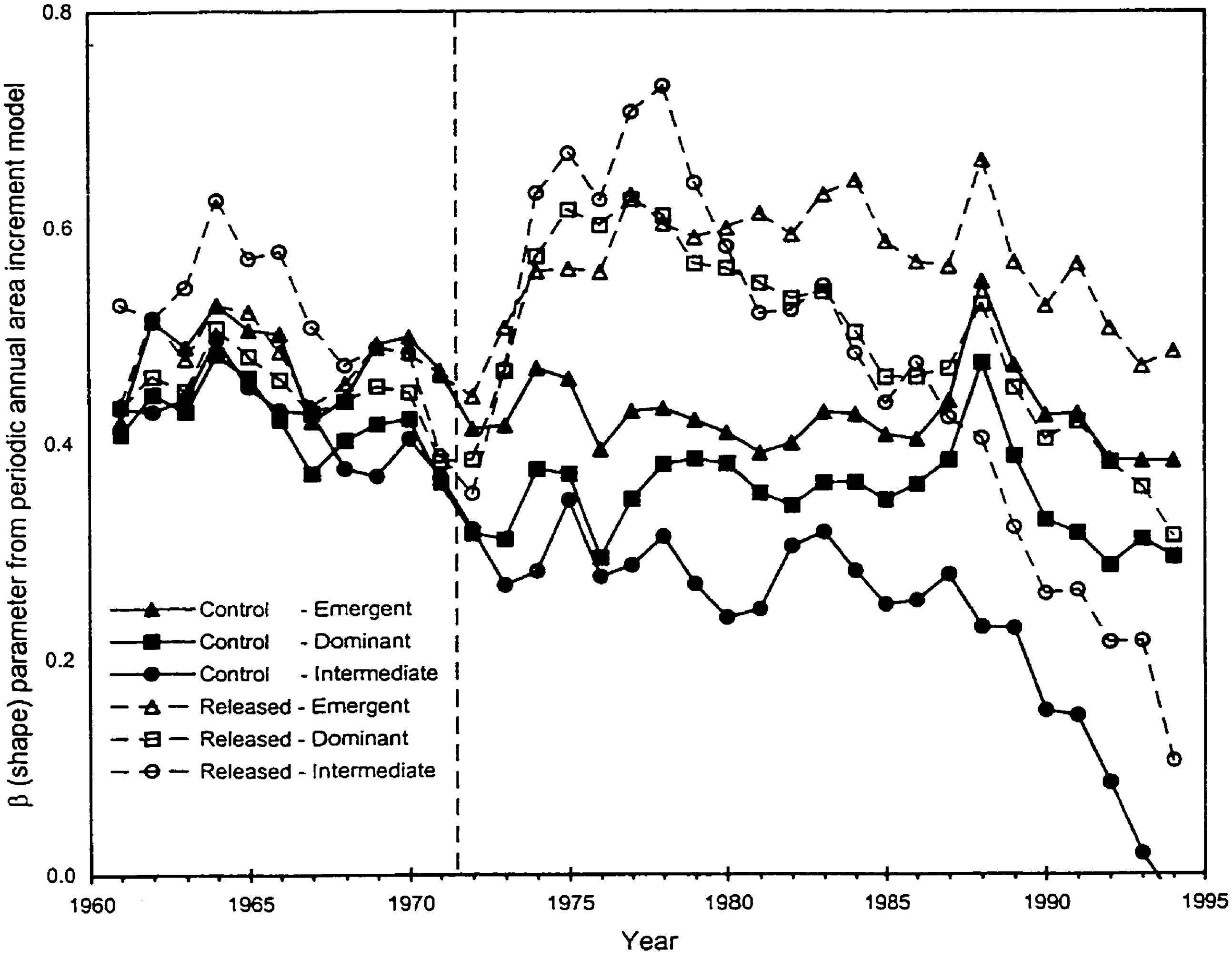


Figure 12: Temporal variation in the average estimate of the shape parameter (β) from equation describing vertical distribution of annual bole area increment for trees of different crown classes and partial cutting treatment.

6.7 *Stem form*

Figure 13 displays the vertical variation in average cumulative diameter through time for released and control trees from the three crown classes. Stem forms measured using FF were slightly greater than what has been reported previously for white pine (Spalding and Fernow 1899), while FC values are consistent with those reported by Stiell (1978) (Table 21). There was a significant (p=0.013) difference in average stem form, as measured by both FF and FC, between crown classes in the control group before and after the cutting treatment (Table 21). In general, the data show that intermediate trees had less taper, followed by dominant and emergent trees, which is consistent with observations reported by Larson (1963).

However, β estimates from a variable-form taper model (i.e., equation [25]) were not significantly (p=0.433) different between the three crown classes. Combining trees from both control and cutting treatments showed no significant difference among crown classes prior to the treatment application. The lack of a significant difference among crown classes is likely the result of released trees changing crown classes as a consequence of the cutting treatment, indicating that some of the released trees classified as being in an emergent or dominant crown class after treatment may have been in a lower crown class during the pre-treatment period.

Table 21: Changes in average stem form before and after a partial cutting treatment in white pine trees from three crown classes. (Values in brackets are stand errors of estimates).

Treatment	Crown class	Form factor[1]		Form class[2]	
		Pre-treatment (1961-71)	Post-treatment (1972-94)	Pre-treatment (1961-71)	Post-treatment (1972-94)
Control	Emergent	0.52 (0.0006)	0.52 (0.0006)	0.73 (0.0009)	0.72 (0.0008)
	Dominant	0.54 (0.0005)	0.54 (0.0005)	0.74 (0.0007)	0.74 (0.0006)
	Intermediate	0.56 (0.0009)	0.57 (0.0009)	0.75 (0.0013)	0.77 (0.0011)
Released	Emergent	0.52 (0.0007)	0.51 (0.0007)	0.73 (0.0010)	0.72 (0.0009)
	Dominant	0.52 (0.0005)	0.52 (0.0005)	0.74 (0.0007)	0.74 (0.0006)
	Intermediate	0.54 (0.0011)	0.54 (0.0011)	0.74 (0.0015)	0.76 (0.0013)

[1] Form Factor measured as ratio of inside-bark volume of main stem to volume of cylinder based on diameter-at-breast height (inside bark) and total height.

[2] Form Class measured as ratio of diameter inside-bark at half tree height above breast height to diameter-at-breast height (inside bark)

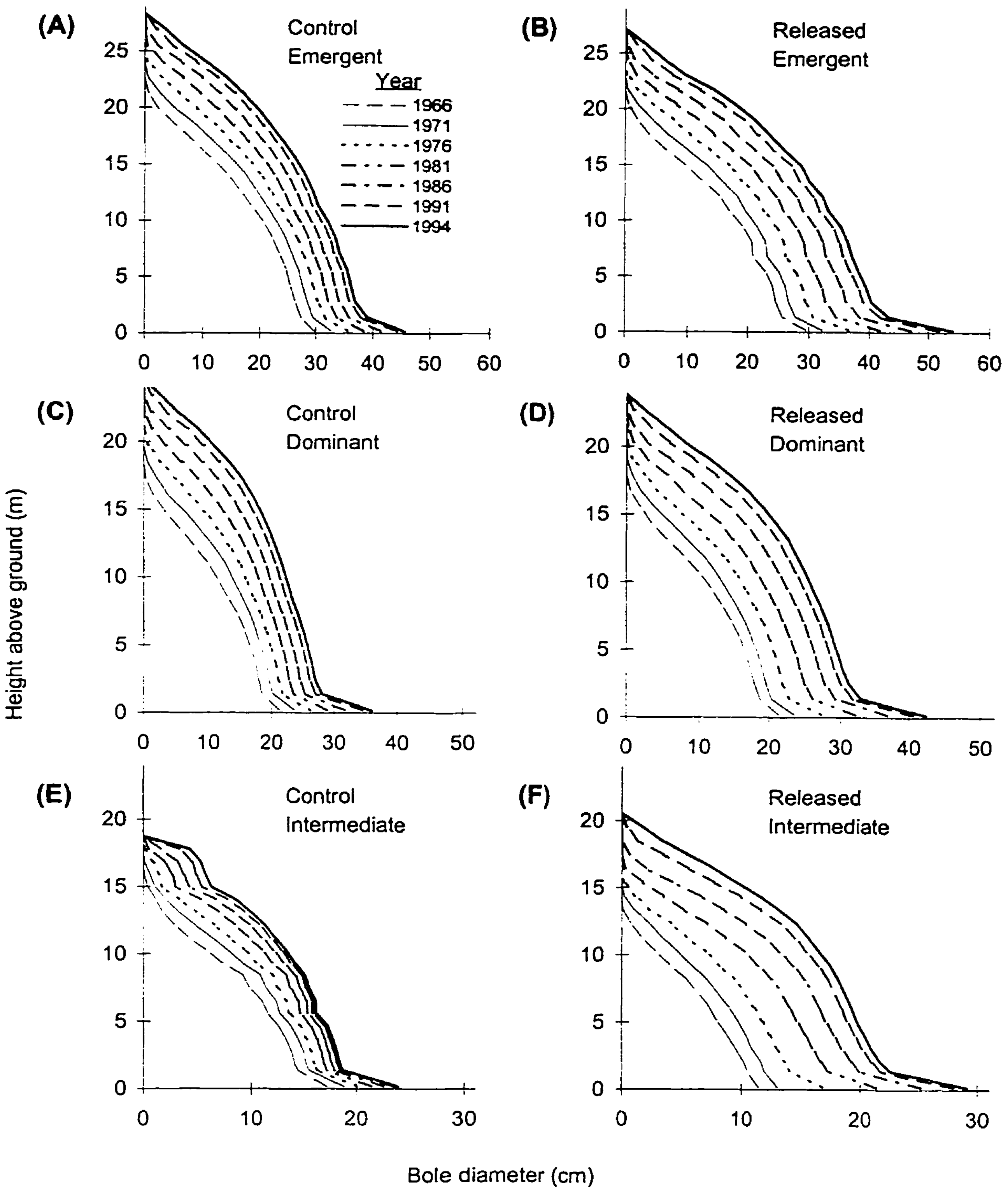


Figure 13: Vertical distribution in cumulative bole diameter growth over time in control and released white pine trees from three crown classes. (A) Emergent-Control. (B) Emergent-Released. (C) Dominant-Control. (D) Dominant-Released. (E). Intermediate-Control. (F) Intermediate-Released. (Note scale differences along x-axis within columns).

Within the control group, there was no significant change in stem form throughout the pre- and post-treatment period within each crown class (Figure 14A and B). However, there appeared to be a constant change in form when using the β parameter estimate from a variable-form taper equation (equation [25]) (Figure 15B). Trees from all crown classes had a significant decrease in β values through time, contrary to the results using FF. This is more consistent with results that showed decreasing stem taper with increasing age and crown closure (Larson 1963).

Following the partial cutting treatment, the greater annual area increment at the base of the bole resulted in a significant change in stem taper and form in released trees relative to the control group. Changes in the vertical distribution of bole area increment were almost immediate, but it took nearly 10 years before any significant changes in stem form were observed. All crown classes had significantly greater taper following release (Figure 15A). Both FF and FC showed a temporary increase followed by a significant reduction in form for all crown classes in the partial cutting treatment (Figure 14A and B). The change in slope for values of β through time during the post-treatment period (Figure 15B) is also indicative of a change in form, though not statistically significant.

There was no evidence that trees with high taper would develop less taper as a result of release, as reported by Meyer (1931). However, employing the Girard form class to quantify tree form, which essentially describes the taper of the first 16 ft. (4.9 m) log, also demonstrates increase in taper in released emergent and dominant trees, with little or no change in form in control trees.

The degree of butt swell, measured as a ratio between bole area at stump height to area at breast height, is significantly greater in dominant and emergent trees in the release treatment compared to their respective crown classes in the control treatment. Intermediate trees in the control group had the least amount of butt swell.

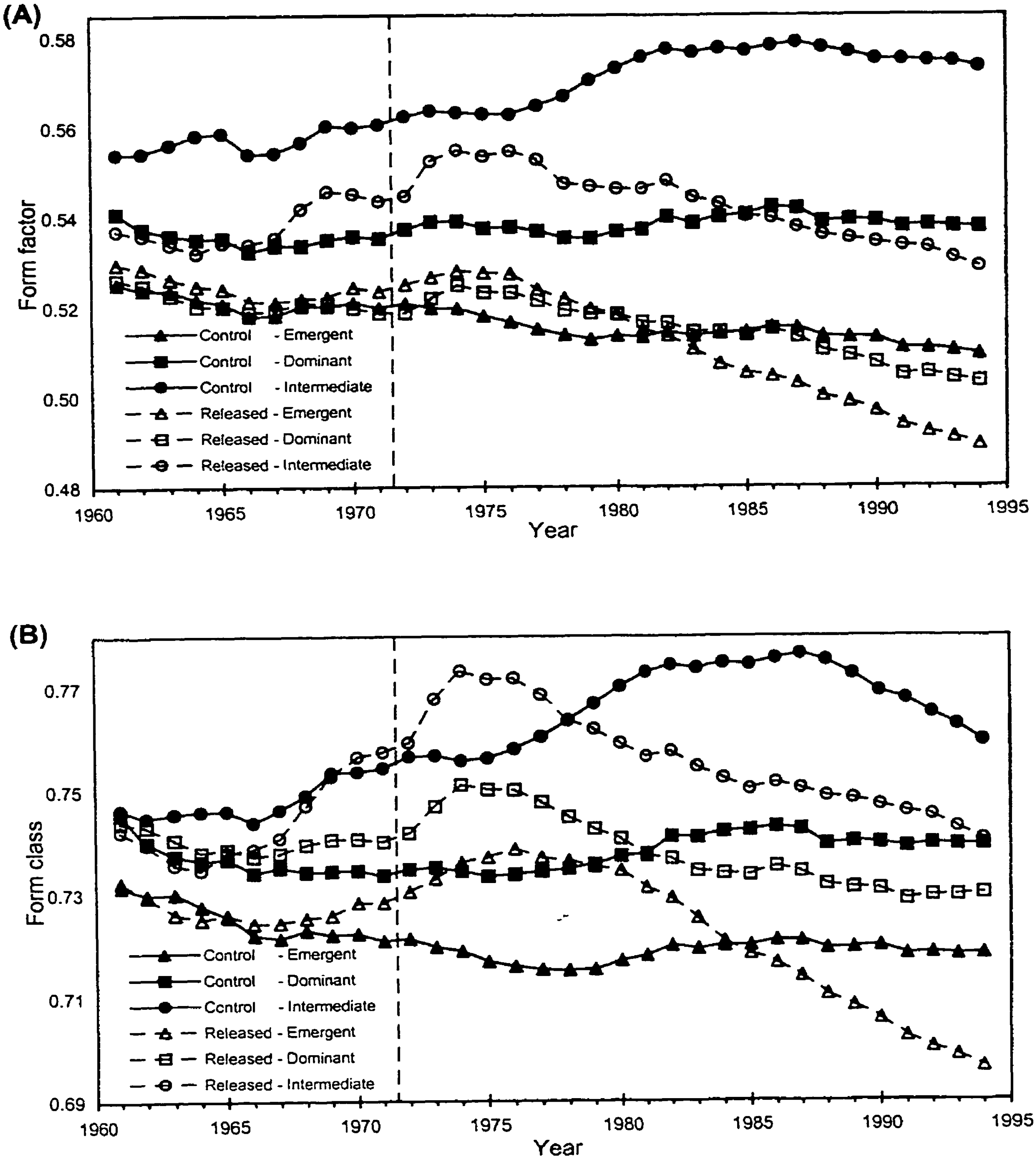


Figure 14: Temporal variation in average stem form for control and released white pine trees from three crown classes. (A) Form factor (ratio tree volume to volume of cylinder based on D and tree height. (B) Form class (ratio of diameter at half total height to D).

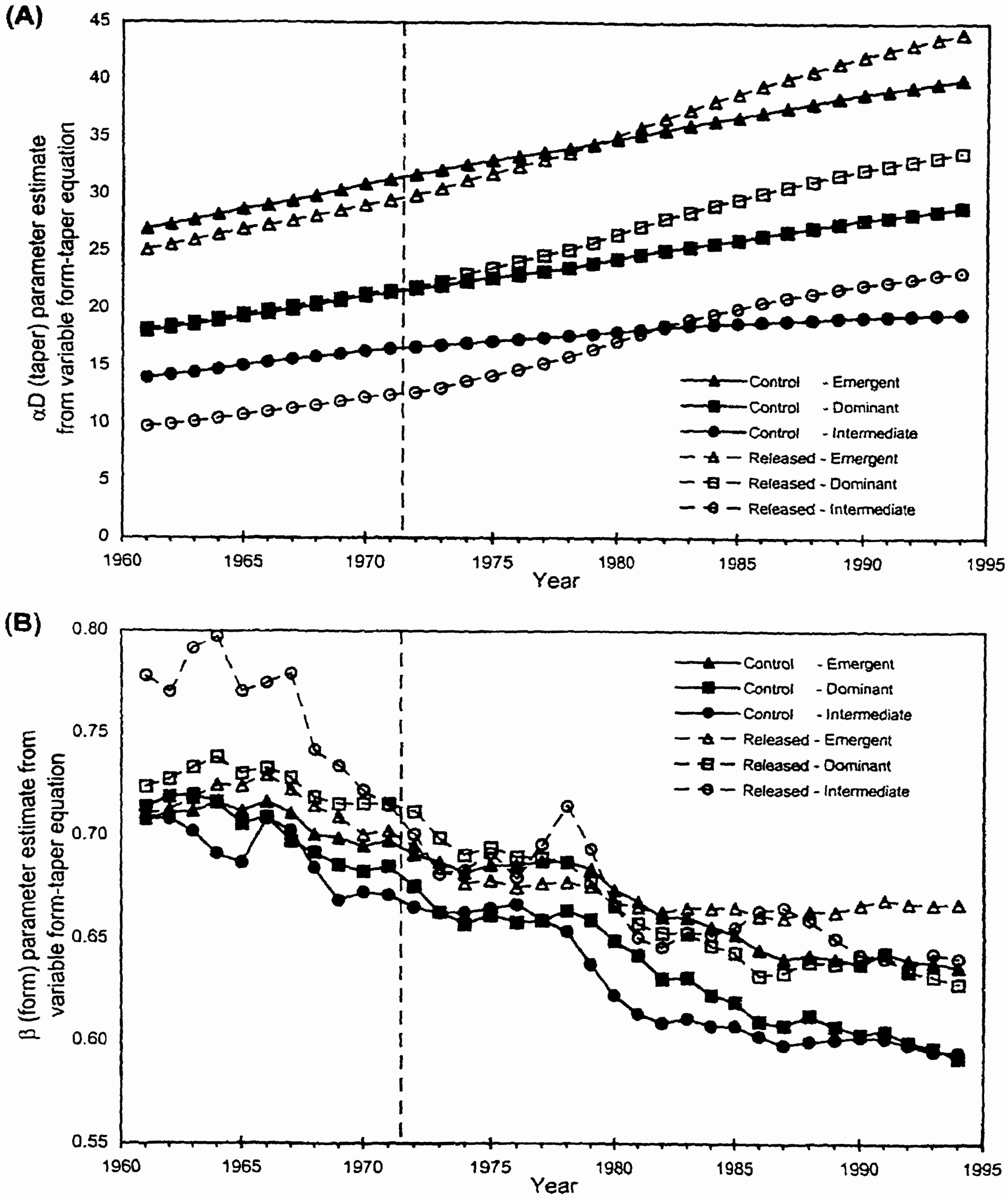


Figure 15: Temporal variation in average parameter estimates of a variable-form taper equation using data from control and released white pine trees from three crown classes. (A) αD parameter (taper). (B) β parameter (form).

6.8 Volume growth model

In order to predict the volume of a tree at a given point in the future, a regression model based on equation [23] was developed. The form of the equation is of the same general structure of Hynynen (1995). For the analysis, initial time (i.e., t=0) was the time of the partial cutting treatment (i.e., 1971), thus, only data from 1971-94 were used. The dependent variable is the cumulative volume increment since 1971, and the independent variables included: (i) total bole surface area and (ii) age in 1971, (iii) height of tree at age 50 years, and (iii) elapsed time since 1971. Bole surface area and age are incorporated to reflect initial tree size and stage of development at the time of cutting, and height at age 50 is added to account for any possible variation in microsite between trees.

The form of the yield equation is:

$$[30]\ \Delta V_t = a_0 * \left\{ S_0^{a_1} * A_0^{a_2} * e^{(a_3 S_0 + a_4 A_0)} \right\} * \left\{ t^{(b_1 + b_2 * TRT)} \right\} * \left\{ e^{(c_0 * TRT + c_1 * CI + c_2 * CI * TRT)} \right\}$$

where ΔV_t = cumulative volume growth over t years;
t = number of years since release treatment;
A_0 = age at t=0;
S_0 = bole surface area at t=0;
TRT = 0 if control, 1 if released;
CI = competition index
$a_0, \ldots, a_4, b_1, b_2, c_0, c_1, c_2$= parameters to be estimated

Equation [30] can be solved using ordinary least squares regression (OLS) using the equation:

$$[31]\quad \begin{aligned} \ln(\Delta V_t) = \ln(a_0) &+ [a_1 \ln(S_0) + a_2 \ln(A_0) + a_3 S_0 + a_4 A_0] \\ &+ [b_1 \ln(t) + b_2 (\ln(t) * TRT)] \\ &+ [c_0 TRT + c_1 CI + c_2 (CI * TRT)] \end{aligned}$$

The model includes a dummy variable TRT that was added to account for differences between control and released trees that cannot be directly accounted for by the competition index. Ideally, a quantitative variable describing the degree of release between pre- and post-cutting competition would be included, as was done by Smith and Bell (1983). However, since no pre-cutting information is available, a qualitative variable is used to explicate the compensatory growth response immediately following release treatment. The interaction term

CI*TRT was included to account for the level of competition is a result of a partial release. Appendix 2 gives the values for the 11 competition indices calculated for control and released trees for the three crown classes in 1971.

Equation [31] was first tested without the TRT or any CI included (model 1), followed by a model with only the TRT variable added (model 2) and then with both the TRT variable and each of the 11 competition indices added individually. Parameter estimates and regression statistics for model 1, 2, and the three best models using competition indices based on R^2 are given in Table 22.

Table 22: Parameter estimates and regression statistics for cumulative volume growth model based initial size, time since treatment, cutting treatment, and competition index (equation [31]). Results given are for best three competition indices.

		Parameter estimates				
Term	Parameter	Model 1 (no TRT/CI)	Model 2 (No CI)	Model 3 CI07	Model 4 CI09	Model 5 CI11
Intercept	a_0	47.1457	42.7143	41.7261	38.5649	39.1125
$ln S_0$	a_1	1.3038	1.4788	1.2882	1.3733	1.2991
$ln A_0$	a_2	-14.4100	-12.8292	-12.6614	-11.5939	-11.8799
S_0	a_3	-1.7071	-3.3793	-3.9530	-3.9492	-3.0282
A_0	a_4	0.1894	0.1654	0.1684	0.1521	0.1553
$ln(t)$	b_1	1.1908	1.0950	1.0950	1.0950	1.0950
$ln(t)$*TRT	b_2	-	0.1961	0.1961	0.1961	0.1961
TRT	c_0	-	-0.0069	-0.3119	-0.3091	-0.2078
CI	c_1	-	-	-0.0089	-0.1047	-1.9833
CI*TRT	c_2	-	-	0.0055	0.0417	1.7621
n		2024	2024	2024	2024	2024
RMSE		0.4139	0.3484	0.3170	0.3154	0.3124
R^2		0.8772	0.9130	0.9281	0.9288	0.9302

For all models, all coefficients were significantly different from zero ($p<0.0001$). Parameter estimates from the regressions indicate that the cumulative growth response is positively related to initial tree size and negatively related to tree age. The RMSE of the model 2 (i.e., including only TRT term) was 15.4% lower than the RMSE of model 1 (i.e., excluding TRT and CI terms). The inclusion of CI terms in models 3-5 decreased the RMSE relative to model 1 by 23.4%, 23.8% and 24.5%, respectively.

The negative coefficient of the CI term for models 3-5 in Table 22 shows that the models reduce tree growth for increasing levels of competitive interference. The positive coefficients for the *ln(t)**TRT interaction term signifies that the growth rate in released trees is always greater than the control group. The interaction term for CI*TRT is positive, but is less than the absolute value of the coefficient of CI term. Hence, the model will predict higher rates of growth in released trees compared to untreated, control trees at a given level of competition. Thus, model behaviour correctly reflects the compensatory growth response in released trees due to a decrease in the level of competition. However, a quantitative expression of the change in competition from pre- to post-release would perhaps have been more appropriate, had one been available.

Figure 16A displays the predicted cumulative volume for both control and released trees of varying initial size, using average values of three crown classes at the time of cutting, for model input. The graph shows that model behaviour correctly predicts released trees to grow at a faster rate than control trees. The model also predicts trees with larger bole surface areas (i.e., the emergent trees) to grow faster than trees with smaller bole surface areas.

The predicted growth response of an average dominant tree under three different levels of competition is presented in Figure 16B. The graph illustrates the effect of a partial cutting treatment on the subsequent growth at each level of competition. Again, model behaviour correctly forecasts increasing growth with lower levels of competition, with the predicted growth in released tree to be greater than growth for uncut areas.

Mean residuals of the growth model for control and released trees are presented with respect to time, predicted cumulate volume growth and initial bole surface area in Figure 17. The analysis shows no systematic distortion in the predicted values.

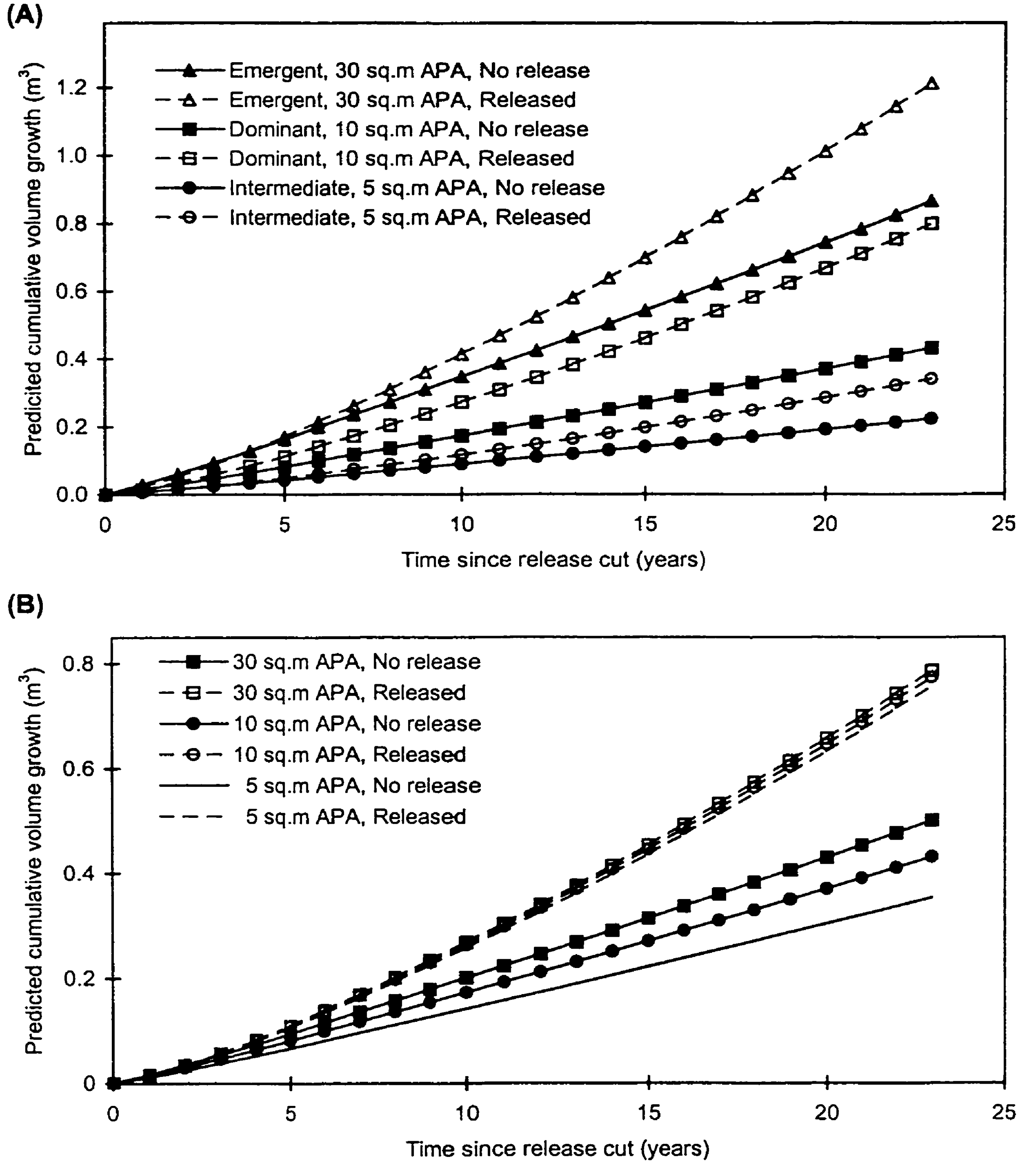


Figure 16: Predicted cumulative volume growth over time using equation [30] and CI11 (see page 58 for explanation) as the measure of competition index. (A) Predicted growth for released and control trees of three crown classes based on average values of initial bole surface area and initial age. (B) Influence of competition interference on cumulative growth over time of average dominant trees in control and released conditions for different levels of competitive interference.

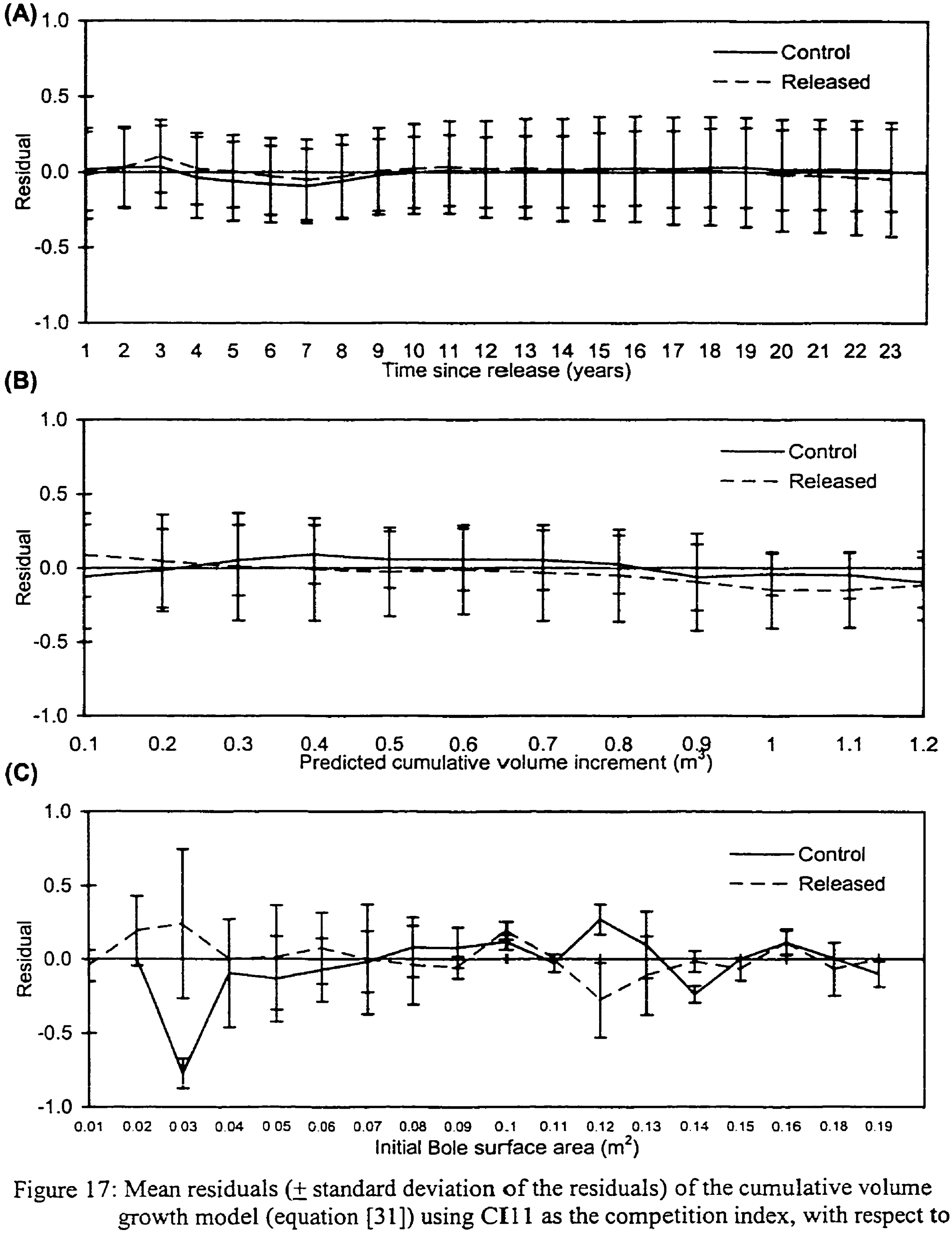


Figure 17: Mean residuals (± standard deviation of the residuals) of the cumulative volume growth model (equation [31]) using CI11 as the competition index, with respect to (A) time, (B) predicted cumulative volume, and (C) initial bole surface area.

7. Discussion

7.1 Size-dependent growth and competitive interference

The general approach used in previous studies to assess the mode of competition in plant populations has been to observe the relationship between size-dependent growth, often assumed to reflect tree vigour, and size among plants. In mature trees, the method of measuring size-dependent stem growth may have great bearing on the conclusions drawn. This is due, in part, to the manner in which trees accumulate secondary growth. The rapid decline in the relative growth rate of the main stem (RGR) with tree age (Figure 6) suggests that all trees rapidly lose vigour with age, regardless of their immediate environment or canopy position. It supports the premise that the increasing size of the non-productive inner bole in large trees has a greater influence on RGR than differences in annual increment. The more gradual decline with age and larger variability in specific volume increment (SVI) compared to RGR would suggest that SVI might be more sensitive to environmental stimuli and better reflect the relative growth variation among trees.

The results obtained in this study are in agreement with those generally associated with size-asymmetric competition (Weiner 1988), in which size-dependent stem production is greater in the larger, more dominant subject trees. Size-asymmetric competition has generally implied a one-sided, resource pre-emptive process in which contested light resources are disproportionately obtained by the larger plants (Schwinning and Weiner 1998). This mode of competition is more often found among shade-tolerant species (Ford and Sorrensen 1992). However, a non-uniform, spatially heterogeneous distribution of competitors may mimic size-asymmetric competition (Miller and Weiner 1989, Bonan 1991), necessitating the need for local, neighbourhood measures of competition and the separation of competitive interference by relative size of neighbours (Newton and Jolliffe 1998).

Results show that the *ln*(SVI) is better correlated with measures of competitive interference than the *ln*(RGR) (Table 10). Recently, Newton and Jolliffe (1998) also found increased sensitivity in SVI to competitive interference relative to RGR in black spruce. If the assumption that relative levels of competitive interference can be accurately assessed based on the number, size and location of neighbouring trees is correct, it suggests that SVI is a more appropriate measure of size-dependent growth in the assessment of competition within older trees. The proportion of unexplained variation in *ln*(SVI) may be due to spatial heterogeneity in site quality, genetic variability among subject trees within the study area, and (or) a lack of correlation between competition indices and competitive interference.

Comparisons of the efficacy of the competition indices used in this study suggest that distance-dependent measures of competition explain a significantly greater proportion of the variation in size-dependent growth than most distance-independent measures. This supports the application of distance-dependent measures of competition within individual-tree, white pine growth models. However, the distance-independent index (i.e., CI02) based on the summation of the squared relative diameter of each competitor, selected using an angle gauge, will provide similar predictive ability as other distance-dependent measures which require distance measurements.

The comparison of index efficacy also indicates that the development of neighbourhood competition models for mature white pine must incorporate size-asymmetry in the competition index. All indices that weighted neighbours by relative size were significantly better correlated with *ln*(SVI) than those which were not weighted, suggesting size-asymmetry in competition. The weighting of competitors by relative diameter, as used in this study, is similar to the modification used by Thomas and Weiner (1989) and Peterson and Squiers (1995) to include asymmetry in the calculation of neighbourhood competition. In those studies, competitive interference of neighbouring plants was discounted based on relative size. However, Peterson and Squiers (1995) used a step function such that only plants smaller than the subject tree were discounted by a constant amount, and all plants of equal or greater size were treated equally, based on their absolute size and distance from the subject tree.

The better correlation between *ln*(SVI) and relative size-weighted competition indices contrasts with the results of Peterson and Squiers (1995), who found a better correlation between relative diameter growth and competition when the competitive influence of smaller neighbours was not discounted (symmetric competition). However, their conclusions were based on the analysis of intra-specific competition only. When intra- and inter-specific competition were combined, no relationship between relative growth rate and competition was observed. Their competition model, however, was based on a linear relationship between relative growth and competitive interference. A number of other studies (e.g., Weiner 1984, Newton and Jolliffe 1998), including this one, found that the relationship is better correlated as a non-linear model, using either a reciprocal or logarithmic transformation of the dependent variable.

Weighting competitors along a continuous scale (i.e., relative diameter) both augments the influence of larger neighbours and discounts that of smaller competitors, which is clearly different from the step function used by Peterson and Squiers (1995). The asymmetry in competition obtained in this study suggests that aboveground competition for light is likely more important than belowground competition for soil resources in increasing size inequalities in mature white pine, even on relatively poor productivity sites were overall stand growth is limited by belowground resources. This agrees with the conclusions of Weiner *et al.* (1997), who indicate that resources that are most limiting for growth are not necessarily the most contested. However, the appropriateness of relative diameter as a comparative measure in assessing size-asymmetric competition for light is somewhat questionable, since it is the overtopping and interference of neighbouring crowns that preempt irradiance levels. A measure of relative height, such as crown class, might be a more appropriate weighting factor to use.

Results obtained from the stratification of cumulative competitive interference based on relative competitor height support the conclusion that larger-sized competitors exert greater influence (i.e., cause greater declines) in stemwood production of subject trees relative to smaller-sized competitors (Table 11). The absolute values of the coefficients for measures of competitive interference become progressively smaller for competition indices $CI_G > CI_E > GI_S$. This infers that the competitive interference of taller competitors is greater than the influence of competitors of relatively the same height, which, in turn, have a greater effect than competitors that are shorter than the subject tree. The results again suggest that the preemption of light resources by the larger competitors has a larger effect of size-dependent growth and that there is a size asymmetry in competition. However, the hypothesis that competition is two-sided and both below- and aboveground resources are contested could not be rejected. Smaller competitors still significantly influence *ln*(SVI) even after accounting for the influence of larger-sized competitors, although their influence on stem growth is significantly less.

Although it is difficult to generalize about the relative importance of above- and belowground competition across resource gradients, belowground competition for moisture and nutrients can be stronger and involve many more neighbours than aboveground competition and often increases with decreasing resource levels (Casper and Jackson 1997). Belowground competition is generally assumed to be size symmetric, i.e., uptake of contested resources is in proportion to competitor size, particularly when soil resources are uniformly distributed. The possibility of size-asymmetric competition for belowground resources may exist if soil resources are spatially heterogeneous. Roots are known to proliferate in regions with greater water and nutrient availability (Grime 1979, Gersani and Sachs 1992). The ability of root systems to "forage" and locate resource-rich patches is dependent on total plant size. This may be due to their overall larger root volumes or the greater amount of energy reserves available and allocated for root development when localized resource levels are insufficient (Eissenstat and Van Rees 1994, Schwinning 1996). Thus, large plants would have a greater probability of success in locating pockets of high water or nutrient availability, indicating possible size asymmetry in belowground competition. However, size-asymmetric competition for spatially heterogeneous or patchy soil resources has largely been unexplored (Schwinning and Weiner 1998).

Schwinning and Weiner (1998) also suggest that even when competition for belowground resources is completely symmetric (i.e., equally shared between all competitors irrespective of size), the smaller individuals lose a greater proportion of their potential resource uptake. They illustrate this hypothesis with the assumption that plants obtain resources from within a zone of influence determined by their size [see section 3.2(c)] and plants contest for resources within the region of overlap of their respective zones. The area of overlap will represent a greater proportion of the zone of influence of smaller competitors relative to that of the larger competitors.

Competition models based on area potential available (APA) (i.e., CI10 and CI11, see Figure 1) had poor correlations with *ln*(SVI). A possible explanation for this poor relationship could be that models in which resources are proportional to area available were conceived based on the assumption that the competition process is two-sided or resource depletion (Mithen *et al.* 1984, Weiner 1988). All other results in this study suggest that competition is predominately one-sided and a resource preemptive process. The computations involved in calculating APA do not adequately permit testing of competition asymmetry. Greater adjustments in the location of the boundaries for the sides of the APA polygons based on relative competitor size might improve the correlation between APA and SVI when size heterogeneity is great.

In white pine, there is an added dimension to the competition process with the existence of root grafts. Bormann (1966) suggests that suppressed trees can act as an additional sink for photosynthates when they are grafted to larger neighbours. Although direct competition for soil or light resources between neighbouring trees may exist, a smaller grafted individual may act parasitically by competing indirectly with the larger competitor for its own photosynthates. Since the occurrence of root grafts in the subject trees used was not investigated, the relative influence of root grafts on subject tree growth is not known.

The fourth hypothesis that there is no relative difference in the influence of intra- and inter-specific competitive effects on size-dependent stem growth in white pine can not be rejected (Table 14). These results conflict with both Peterson and Squiers (1995), who found that white pine benefits from the local abundance of aspen, and the results of Liu and Burkhart (1994), who concluded that hardwood competition had a disproportionately larger effect on loblolly pine growth under high levels of overall competition. Both of these studies dealt with significantly smaller and younger trees. In addition, Peterson and Squiers (1995) had disproportionate amounts of intra- and inter-specific competition at low and high levels of overall competition, potentially biasing their results. However, the results in this study are consistent with the hypothesis that competition is a size-asymmetric process with mature white pine. Both aspen and birch are considered shade-intolerant species, indicating the importance of competition for light in their development (Ford and Sorrensen 1992). Since the majority of the aspen and birch competitors were in the larger size classes, it suggests that they would have a strong competitive interference in the preemptive appropriation of light resources.

While competition for moisture and nutrients can be more severe on less productive sites with increasing density and have a much larger effect on mean plant weight, it is competition for light that will increase size variability and size inequality (Weiner 1988). This suggests that when the density of a plant population is reduced through partial cutting, the relative increase in nutrient and moisture availability and relative growth response in residual plants will be greater on a poor site relative to a more productive site. However, further studies on white pine growth on different sites with different levels of productivity (i.e., soil moisture) may provide additional information on the growth responses following release.

7.2 Stem and crown plasticity and competitive interference

This study demonstrates that mature white pine can respond to the removal of neighbouring individuals. The response of main stem growth and crown architecture to release varied with canopy position. These differences provide insight into the nature of competition within white pine stands.

Diameter and volume growth responses in released trees were observed beginning in the second year after release. A lack of stem growth response in pine during the first year following release has previously been observed (Bormann 1965, Fayle 1976, Kelty and Entcheva 1993) and is likely due to the uninodal nature of pine growth. Needle primordia are formed in the terminal buds during the previous growing season, and thus, shoot growth is predetermined. Although secondary thickening of the main stems occurs within the cambial region along the surface bole, and not the apical meristem, cambial reactivation and development is regulated by auxin produced within expanding buds and shoots (Savidge 1988). In this study, the formation of terminal buds during the last year before the cutting treatment, i.e., 1971, may have been affected by an overall poor growth year, as evidenced by the small diameter growth exhibited by all subject trees (Figure 3B). A limited amount of needle primordia in buds would reduce shoot and branch elongation during the 1972 growing season, despite the improvement in growing conditions following partial cutting. Climate data collected at the Petawawa Research Forest (Environment Canada 1994) show that the 1971 growing season had the second lowest amount of precipitation for the years 1931 to 1992, inclusive. Although this may explain the poor diameter growth in 1971, a more detailed dendroclimatological analysis is required to support this observation.

Intermediate trees had the greatest relative diameter growth response to release, with released intermediate trees surpassing both emergent and dominant control trees in absolute diameter growth. This agrees with previous observations for white pine (Horton and Bedell 1960). However, a smaller average initial size reduced the absolute growth responses in basal area and volume. Since almost all trees that were removed during the cutting treatment were either aspen or birch, root grafts should have little or no direct influence on the growth response of emergent or dominant trees in this study (Bormann 1966). However, root grafts between intermediate and larger white pine neighbours within the release treatment may have had a positive effect on the growth of smaller white pines. Photosynthates can be transferred from emergent and dominant individuals to their smaller grafted neighbours (Bormann 1966).

Resource optimization theory (Bloom *et al.* 1985) and carbon budget models (McMurtrie and Wolf 1983) suggest that plants increase their relative carbon allocation to root growth when belowground resources (e.g., nutrients or water) are more limiting relative to those aboveground (e.g., light or CO_2) (Eissenstat and Van Rees 1994). This would explain why there is a lower proportion of root biomass (a) on more productive sites (Keyes and Grier 1981) and (b) following fertilization (Axelsson and Axelsson 1986). Consistent with this theory is the observation that higher light levels will usually increase root growth more than shoot growth (Field *et al.* 1992). However, responses to competition-induced resource depletion are less well-understood (Schwinning and Weiner 1998), and resources that limit overall population growth are not necessarily the most contested at the individual level (Weiner 1988, Weiner *et al.* 1997).

Plants are constantly adapting to changing levels of competition-induced resource depletion. One adaptive mechanism to avoid competitive suppression by neighbourhood interference is through plasticity in growth form (Schwinning 1996, Schwinning and Weiner 1998). Typically, under increasing competition, plants are taller and thinner with fewer branches than in the absence of competition (Weiner *et al.* 1990, Weiner and Thomas 1992). By reducing average shoot diameter with density, the competitive interactions among plants is less size asymmetric. The more flexible the diameter response, the higher the density threshold before the onset of size asymmetric competition (Schwinning and Weiner 1998).

In this study, significant differences in stem and crown size among crown classes were evident within the control group. Local competition appears to influence the maximum size of a tree crown (Figure 10), although variability in crown size, particularly at low levels of local competition, is also influenced by position in the canopy. However, no relationship between crown shape ratio (i.e., crown length:crown radius) and competitive interference was observed, suggesting there was little or no morphological adjustment in white pine crowns to in response to competition. This is consistent with the theory that less plasticity in morphology will lower the density threshold for size-asymmetric competition (Schwinning and Weiner 1998). Weiner (1988) assumes that the development of size hierarchies is the result of size-asymmetric competition for light. White pine apparently differentiates more rapidly into distinct size hierarchies or size inequalities relative to other pines(Burns and Irwin 1942, Horton and Bedell 1960). The rapid development of size inequality in white pine may result from the inability of the species to adapt its crown structure to increasing competition. This is reflected in white pine's slower branch mortality and crown recession relative to other pines.

It should be noted, however, that mean values in crown shape ratio did decrease with decreasing canopy position in the control trees (Table 16). Intermediate control trees had a significantly lower crown shape ratio compared to dominant and emergent trees, which suggests that a competitive suppression threshold has to be reached before white pine trees modify their crown architecture. This threshold was not directly interpreted by the measures of local competitive interference used in this study. The relatively narrower crown shape in the dominant and emergent trees relative to intermediate trees conforms to Takahashi's (1996) hypothesis of height growth for future gain. Empirical studies have shown that narrow-crowned trees have proportionally greater stem growth per unit needle area (Smith and Long 1989, Jack and Long 1992). A proposed explanation for the increased efficiency in stemwood production in narrow-crowned trees is that allocation to branches is lower when foliage is supported a shorter distance from the stem (Cannell 1985). By maintaining a narrower crown, it reduces the non-foliated portion of the crown, thus providing more photosynthates for stemwood production (Jack and Long 1992). The proportional allocation of carbohydrates to stemwood and height growth is critical for success in competition for light (Stenberg *et al.* 1994). The variation in crown shape among crown classes in control trees is also consistent with the findings that suppressed trees are less efficient in stemwood production, with little or no difference in efficiency in the upper canopy (Satoo *et al.* 1954, Waring *et al.* 1980, Gilmore 1996). No significant relationship between crown shape ratio and SVI using trees from all canopy positions and cutting treatments was found. However, a positive trend between SVI and crown shape ratio was evident within the intermediate crown class. This may be explained by crown size differences in released relative to control trees.

Intermediate trees show the greatest percentage difference in increased height growth (and subsequent crown length) with little or no difference in crown radius between released and controls. This results in significantly longer and relatively narrower crowns (i.e., higher crown shape ratio) in the released trees relative to the controls (Table 16). Narrower crowns permit increased height growth in gaps due to lower biomass increment per unit of height growth (Takahashi 1996). In contrast, dominant released trees, which had the greatest percentage difference in crown radius and length between released and controls, showed no difference in crown shape. Emergent trees, while having the overall largest crowns, do not differ significantly between the control and released treatments with any measure of crown structure. This suggests that morphological plasticity in crown shape in response to the alleviation of competitive stress is only evident in the more suppressed individuals.

The limited morphological plasticity in white pine, relative to other pines, may be offset by greater physiological adaptations to competition. Physiological acclimation to low resource levels are often interpreted as adaptive mechanisms to alleviate competitive suppression (Schwinning 1996) and can delay, but not prevent, density-dependent mortality and self-thinning (Schwinning and Weiner 1998). White pine's moderate shade-tolerance relative to other pines (Wetzel and Burgess 1994) is more likely a reflection of its physiological acclimation to tolerate low light levels under competitive interference than its ability to avoid competition through morphological adaptations. Foliage produced by intermediate trees, and within the lower crown of more dominant trees, will predominately intercept diffuse and reflected light rather than direct radiation. This not only implies lower levels of irradiance, but also different wavelengths of light. Typically, the red:far-red ratio increases in reflected light, influencing the phytochrome ratio in plant leaves, and allows plants to detect the presence and distance of its neighbours via its phytochrome system (Smith *et al.* 1990).

Foliage that develops in predominantly shaded conditions, often characterized as shade leaves, is adapted to the different wavelengths and lower light intensity during its formation and differentiation. Shade leaves generally have lower light compensation and saturation points, high specific leaf areas, fewer but larger chloroplasts per unit area, and a lower chlorophyll a/b ratio relative to sun leaves (Larch 1995). These adaptations tend to optimize net assimilation under the lower irradiance levels. Bourdeau and Laverick (1958) found that white and red pine seedlings had higher photosynthetic rates when grown under shade than under sun, although light saturation in white pine did not vary under various light intensities. In addition, white pine growing in shade conditions tend to have longer mean needle life expectancies (Whitney 1982), an important mechanism when growing under a broadleaf canopy as it provides more photosynthetic tissue capable of utilizing the two major periods of high light intensity (i.e., the spring and fall).

Variability in morphological and physiological plasticity among pines may be an explanation for the observed differences in degree of self-thinning. The relationships between mean tree volume and stand density plotted on logarithmic scales demonstrate that white pine (Smith and Woods 1997) has a different slope relative to red (Smith and Woods 1997) and jack pine (Archibald and Bowling 1995). Although mean size-density relationships can not account for size-inequalities within a population nor the degree of asymmetry in competition, it is known that during self-thinning, mortality occurs predominantly in the smallest individuals, reducing size variability (Weiner and Thomas 1986) and skewness (Mohler *et al.* 1978). However, the theory of self-thinning is inadequate to describe the interaction between individual plant growth, competitive interference and size inequality (Weiner and Thomas 1986).

Physiological acclimation not only promotes improved survival during periods of competitive suppression, but it may provide a mechanism for white pine to respond with increased growth when competitive interference is alleviated. In this study, control and released trees had similar patterns in the vertical distribution of annual bole area increment within each crown class prior to the cutting treatment (Figure 11), indicating little or no difference in the average crown size prior to release. Twenty-three years after the cutting treatment, differences in average crown size were observed between released and control trees, suggesting increased crown development as a result of release, which agrees with the results of Hunt (1968) and Gillespie *et al.* (1994).

A slightly higher crown ratio in released emergent and dominant trees (Table 16), with no difference in height growth (Figure 2), indicates greater branch retention in the lower crown of the released trees (Hunt 1960, Vose *et al.* 1994). Branch retention among trees is influenced by the interaction of environmental factors and the physiological capacity of the leaves to regulate and maintain a positive carbon balance (i.e., photosynthesis exceeds respiration) (Schoettle and Fahey 1994). External factors that have been found to influence leaf retention in pines include light (Whitney 1982, Schoettle and Smith 1991), nutrition (Brix 1981, Vose and Allen 1988) and water availability (Kozlowski 1976, Raison *et al.* 1992). Partial cutting will alter both irradiance levels and wavelengths of light among tree crowns of residual trees, as well as nutrient and moisture availability and physical growing space. This will result in the development of a greater proportion of sun leaves. Under these conditions, high rates of needle formation occur, producing relatively dense crowns. Chlorophyll synthesis and degradation, associated with photo-oxidation under high light intensities (Whitney 1982) may be the cause of the lower mean life expectancy of sun leaves in white pine.

Plants maintain a functional equilibrium between the size and activity of foliage (whose main function is to produce photosynthates for growth and respiration) and the size and activity of fine roots (whose main function is to absorb nutrients and water) (Cannell 1985). Therefore, for a tree to develop and support a larger quantity of foliage, the pipe model theory of plant growth (Shinozaki *et al.* 1964b, Osawa *et al.* 1991, Rennolls 1994) indicates that there must be (a) sufficient capacity within the tree's root system to absorb additional water and (b) a network of conducting pipes to meet the increased transpirational requirements and maintain a positive water balance. Based on this model, the larger crowns observed in the released dominant and intermediate trees relative to their respective controls suggest a similar, positive correction in the size of their root systems.

It is likely that the larger crown sizes in released trees would not have occurred had there not been improved soil moisture availability following release. Given that the study site is considered to be of only below-average to average productivity for white pine, it suggests that the predominately shallow, sandy soils are nutrient poor and that soil moisture may be a limiting resource for growth. It is quite likely that the decrease in evapotranspiration following the removal of a significant portion of the canopy leaf area resulted in an increase in soil moisture availability immediately following release. Improvements in soil moisture availability and water relations following thinning have been reported for a number of pine species (Bay and Boelter 1963, Dahms 1973, Helvey 1975, Donner and Running 1986, Cregg *et al.* 1990), including white pine (Hunt 1968). Without improved moisture conditions, any height growth and resulting crown length extension would have been followed by increased crown recession of the lower crown in order to maintain an equilibrium in the root:foliage ratio. The vertical distribution in bole area increment in control trees through time suggests a constant crown size with the crown shifting upwards as trees age.

Therefore, it is reasonable to assume that the initial response to partial cutting would be an increase in fine root biomass, either through a reduction in fine root turnover, or a greater stimulation of fine root growth relative to foliage production. This is consistent with the temporal differences observed between longitudinal root growth and stem growth (Fayle 1975). This is quite different from the rapid secondary thickening of roots relative to radial stem growth observed following release (Wilson 1975, Fayle 1976, Urban *et al.* 1994), which is more often associated with mechanisms to increase windfirmness than water uptake. Improved moisture availability by itself has been reported to reduce secondary thickening at the base of roots relative to the stem base (Fayle 1983, Fayle and Axelsson 1985). Nevertheless, the assumption of increased carbon allocation to fine roots following release may be partially explained by increased moisture availability. Plants will then follow with increased shoot and crown development until a root:foliage equilibrium has been reestablished. This assumes morphological plasticity and adaptive self-organization within individual trees. Changes in external forces (such as water availability) redefine internal constraints (water balance) resulting in adaptive physiological and morphological responses (increased root and foliage production). If improved moisture availability persists, there will be a greater increase in aboveground growth relative to root production and an overall lower allocation to root biomass at equilibrium (Eissenstat and Van Rees 1994).

On more productive white pine sites, soil moisture is not as limiting for growth (Mader 1976, 1986). Since belowground competition for moisture and nutrients often decreases when soil resources are in greater supply (Casper and Jackson 1997), it suggests a relatively greater role of light competition in stand development with increasing density on more productive sites. The findings that density-dependent mortality and self-thinning proceed more rapidly (Harper 1977) and size variability decreases more quickly (Weiner and Thomas 1986) with increasing site productivity are consistent with the hypothesis that competition asymmetry and self-thinning are due to competition for light (Weiner and Thomas 1986). This would suggest that on sites of relatively low productivity, such as the site used in this study, the process of self-thinning and forest succession would progress more slowly than on a more productivity site. This would imply that the use of partial cutting treatments in mixedwood stands to accelerate forest succession and increase white pine cover should be initially focused on sites of lower productivity, since high productivity sites should self thin more quickly. Relative growth responses in surviving pine on more productive sites, however, may not be as great as observed on relatively poor sites.

The partial removal of a forest canopy on more productive sites would likely lead to a smaller change in water availability following release relative to drier, less productive sites. If the assumption that the primary stimulus for the observed growth response in this study was improved soil moisture availability following release, it would suggest that the relative root growth response, and subsequent foliage development, would be lower on more productive sites. This, in turn, would indicate relative stemwood growth responses in individual trees would most likely not be as large as the results reported in this study. Such generalizations, however, would require additional studies on different sites of variable productivity to confirm these inferences.

The larger crown volumes observed in the released pine not only suggest an increase in fine root production, but would also require an increased sapwood area to meet the greater water requirements of a larger transpiring surface area (Chiba and Shinozaki 1994, Rennolls 1994). This is a possible physiological explanation for the increased basal area increment observed in released trees. However, secondary thickening along the main stem was concentrated along the lower bole (Figure 11B, D, F). Increased secondary thickening in the lower bole, relative to the upper bole, following thinning has been reported for a number of conifer species - e.g., red pine (Berry 1971), Douglas-fir (Thomson and Barclay 1984), and loblolly pine (Tasissa and Burkhart 1997).

The physiological explanation most often suggested for the increased stem thickening in the lower bole is increased ethylene production, enhancing cambial activity and radial stem growth in the cambial region of the lower stem (Telewski and Jaffe 1986a,b, Teleswski 1990). The environmental stimulus for the increased ethylene production is mechanical stress in the lower bole, generally thought to result from an increased exposure to wind (Larson 1963, Thomson and Barclay 1984, West *et al.* 1989, Valinger 1992). Increased radial growth at the stem base is preceded by increased secondary thickening of the structural roots (Fayle 1976, Wilson 1975, Urban *et al.* 1994). Increased secondary thickening of the lower stem and structural roots following release will increase the windfirmness of a tree (Urban *et al.* 1994).

The greatest change in the secondary thickening profile of released trees was observed in intermediate trees, following by dominant and emergent crown classes (Figure 12 and Figure 13). However, the duration of this change in secondary thickening of the lower stem was shortest in intermediate trees, and longest in emergent trees. The persistence of relatively greater lower stem thickening in emergent released trees relative to controls 23 years after release suggests that increased exposure to wind persists long after the opening of the canopy. Since the aspen and birch removed during the cutting treatment were older and larger than most of the pine, they provided some shelter from wind, for even the larger, emergent pines. After the removal, of the aspen and birch, most of the trees surrounding the released emergent pines were not tall enough to reduce the wind effects within the region of emergent crowns. This suggests that the emergent trees may continue to exhibit greater secondary thickening in the lower relative to upper bole for some time after release. It is not immediately clear if the temporal differences in the profile of stem increment among the lower crown classes are the result of reduced exposure to wind following canopy re-closure or the increased mechanical strength which would reduce bending stress in the lower bole and upper roots.

The shift in the vertical distribution in area growth will ultimately increase the taper of the main stem. This was observed in this study among all crown classes of released trees. Intermediate trees showed the greatest change in stem form following release, followed by dominant and emergent crown classes. Changes in stem form and crown architecture following release are also consistent with the hypothesis of Weiner and Thomas (1992). They studied the effects of competitive interactions between plants on the plasticity of plant growth form and found that allometric patterns of growth are not simply a reflection of physiological responses to resource availability, but are also the result of dynamic interactions and morphological responses between individuals. Genotypic allometric patterns can affect competitive relations (Schwinning and Weiner 1998), but plasticity in growth form is a phenotypic response to a variety competitive interactions that are poorly understood at present.

8. Conclusions

The mean and variance in the relative growth rate (RGR) in stem volume rapidly decreases with tree age relative to specific volume increment (SVI), which gradually reduces with age but remains highly variable. Significant differences in SVI were observed among crown classes in both the released and control treatments, and all released trees exhibited increased SVI. Compared to RGR, SVI was better correlated with measures of local competition, demonstrating the greater sensitivity of SVI to competition, permitting the rejection of the null hypothesis that RGR and SVI are equally suitable measures of size-dependent growth in competition studies. The results support the alternative hypothesis that SVI is a more appropriate size-dependent measure of tree vigour to use in the assessment of competition effects on the growth of mature trees. Distance-dependent competition indices were significantly better correlated with *ln*(SVI) than distance-independent indices.

The second null hypothesis, that size symmetry in competition exists in mature white pine, was rejected for the following reasons: (a) larger, more dominant trees had greater size-dependent growth than smaller, less dominant trees; (b) measures of local neighbourhood competition that weighted competitors based on relative diameter were significantly better correlated to *ln*(SVI) than indices that were not weighted; and (c) stratification of competitors into size classes based on relative height to subject tree showed that taller competitors reduced size-dependent growth in subject trees more than competitors of the same or smaller relative height. However, the hypothesis that competition is purely one-sided and that only light resources are contested in mature white pine was rejected in view of the significant influence of shorter competitors on the size-dependent growth of larger subject trees, after accounting for the competitive interference of taller competitors.

The third null hypothesis, that white pine does not exhibit plasticity in growth form under varying levels of local competition, was rejected. Intermediate trees in the control treatment had a significantly lower crown shape ratio (i.e., crown length:radius) and significantly less stem taper than dominant and emergent trees. However, increasing height in the canopy produced very little change in crown shape ratio and stem taper, suggesting that a competitive threshold for change in plant growth form had not been reached in white pine. Intermediate trees were the only crown class to exhibit plasticity in crown form following release, as they developed relatively longer crowns than intermediate trees in the control treatment. Overall crown volume is inversely related to local competition. Intermediate released trees had the greatest relative difference in crown length and crown ratio relative to control trees, but dominant released trees had the greatest increase in crown radius and volume. Emergent trees, which have the largest crowns, do not significantly increase their crown area following release.

Significant changes in the vertical distribution of stem growth resulted in changes in stem form among all crown classes following release. The vertical profile in stem growth showed a continual increase in area increment, from the tree apex towards base of the stem, in released trees. Control trees showed relative constant area increment along most of their lower stems. However, the increased stem thickening in the lower bole following release was not at the expense of upper stem increment as there was no difference in upper stem growth between control and released trees. After 15 years, the shape of the area increment profile returned to the pre-treatment pattern for dominant and intermediate trees. Emergent trees continued to exhibit greater area increment in the lower stem relative to control trees after 23 years, albeit at a diminishing rate.

The fourth null hypothesis, that there is no difference between intra- and inter-specific competition on white pine growth, could not be rejected. The cumulative competitive interference of white pine and non-white pine competitors on *ln*(SVI) showed no significant difference in the parameter estimates for the coefficients for the variables used to define intra- and inter-specific competitive effects. It suggests a similarity in the relative resource demands among the two species groups

The growth response exhibited by residual white pine to the release treatment has certain implications for the management of mixedwood stands. The main recommendation would be to remove the most dominant, non-pine individuals in a stand, as was done at this study site. Since the results in this study suggest that competition is size-asymmetric, the residual trees benefit most from the removal of larger competitors. However, there would also be a recommendation to seed-in or underplant the released areas with white and red pine if no natural regeneration establishes under the partial cut treatment, particularly on sandy soils. This will ensure that the second growth of pine is established by the time the current overstory reaches maturity. The recommendation for this study site would be to apply another partial cutting treatment on part of the treated areas (mainly the higher density areas). This would involve a light cut that would remove the larger emergent and dominant trees. The value of the products derived from the logs should offset the costs of such a light harvest. Again underplanting or seeding with white and red pine would help to establish a second growth.

This dissertation provides an empirical study of the process of competition in mature white pine stands. The main limitation with this approach is that the significant negative correlation between *ln*(SVI) and neighbourhood competition indices does not necessarily imply a causal competition relationship. The effects of release from competition were measured in terms of growth and not the underlying processes. An understanding of the morphological and physiological mechanisms by which plants respond to competition-limited resources would help to determine the basic mechanisms underlying competition.

The use of the relationship between size-dependent growth and indices of competition remains a useful tool in assessing relative size-symmetry and possible modes of competition. The large proportion of variation in *ln*(SVI) not explained by the competition indices suggests the need for further research into quantifying competitive interference. What is needed is a clearer determination of the threshold distance at which an individual tree no longer exerts any competitive influence on a neighbouring tree. If light is the most contested resource, this distance must not only be a function of lateral expansion of crown and roots, and must be a function of relative height. To account for size-asymmetry in competition within this threshold distance, a species-dependent, non-linear weighting is needed that incorporates distance, absolute and relative size of the competitor. The growth model developed in section 6.8 needs to be validated with an independent data set to test the accuracy of the predictions and applicability of the model to white pine covertypes.

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10. Appendices

Appendix 1: Parameter estimates and regression statistics from polynomial equations describing main bole volume (V) and surface area (SA) over time for individual white pine trees in the form: $Y = \beta_0 + \beta_1 * t + \beta_2 * t^2 + \beta_3 * t^3$, where Y = V or SA, and t = time since cutting treatment.

TREE #	Y	β_0	β_1	β_2	β_3*1000	R^2	RMSE
1	V	1.3846	0.052771	-0.0001126	-0.0029104	0.9998	0.004852
	SA	0.1870	0.004769	-0.0000169	-0.0004037	0.9997	0.000535
2	V	0.1467	0.008551	0.0001026	-0.0047212	0.9969	0.003609
	SA	0.0465	0.001935	0.0000241	-0.0012909	0.9959	0.000887
3	V	0.3641	0.011701	0.0011602	-0.0214081	0.9996	0.004168
	SA	0.0853	0.002335	0.0001107	-0.0025945	0.9996	0.000575
4	V	0.0961	0.007478	0.0002668	-0.0099563	0.9989	0.002160
	SA	0.0402	0.001908	0.0000240	-0.0014801	0.9986	0.000482
5	V	0.5674	0.020231	0.0010623	-0.0202687	0.9996	0.005253
	SA	0.1031	0.003409	0.0000503	-0.0011035	0.9997	0.000553
6	V	0.4367	0.014295	0.0005725	-0.0068573	0.9995	0.004016
	SA	0.0935	0.002110	0.0000726	-0.0014633	0.9996	0.000480
7	V	0.3959	0.013174	0.0005648	-0.0003249	0.9998	0.002781
	SA	0.0895	0.002097	0.0001045	-0.0018664	0.9996	0.000543
8	V	1.1238	0.044077	0.0009714	-0.0204539	0.9995	0.009299
	SA	0.1581	0.004263	0.0000646	-0.0018116	0.9996	0.000770
9	V	0.5640	0.022367	0.0011793	-0.0184324	0.9998	0.004017
	SA	0.1158	0.003324	0.0000931	-0.0019393	0.9997	0.000616
10	V	0.3406	0.006528	0.0035139	-0.0474481	0.9998	0.007699
	SA	0.0806	0.001634	0.0003181	-0.0057928	0.9997	0.000825
11	V	0.1688	0.008485	0.0034333	-0.0514690	0.9997	0.008276
	SA	0.0467	0.003050	0.0002181	-0.0041637	0.9999	0.000481
12	V	0.0711	-0.002436	0.0016295	-0.0269552	0.9998	0.002564
	SA	0.0289	0.000228	0.0002384	-0.0046374	0.9998	0.000402
13	V	0.9404	0.033314	0.0038487	-0.0715583	0.9998	0.008526
	SA	0.1387	0.003250	0.0002559	-0.0055278	0.9998	0.000612
14	V	0.0702	-0.000495	0.0021619	-0.0388821	0.9997	0.004119
	SA	0.0267	0.001274	0.0002041	-0.0041953	0.9994	0.000733
15	V	0.1589	-0.002434	0.0020652	-0.0417947	0.9989	0.006575
	SA	0.0473	-0.000650	0.0003277	-0.0073417	0.9988	0.000911
16	V	0.0193	-0.002422	0.0012138	-0.0264055	0.9997	0.001853
	SA	0.0088	0.000518	0.0001817	-0.0041408	0.9994	0.000493
17	V	0.1163	0.005201	0.0006187	-0.0145530	0.9993	0.002527
	SA	0.0447	0.000904	0.0001094	-0.0024536	0.9992	0.000480
18	V	0.4282	0.017339	0.0011811	-0.0274147	0.9996	0.004560
	SA	0.0824	0.002220	0.0001210	-0.0029017	0.9996	0.000546
19	V	0.1163	0.005201	0.0006187	-0.0145530	0.9993	0.002527
	SA	0.0447	0.000904	0.0001094	-0.0024536	0.9992	0.000480
20	V	0.9568	0.035718	0.0023887	-0.0518470	0.9999	0.005734
	SA	0.1508	0.004265	0.0001453	-0.0040793	0.9998	0.000559

21	V	0.8834	0.032225	0.0013088	-0.0278245	0.9997	0.006957
	SA	0.1415	0.003260	0.0001055	-0.0027622	0.9997	0.000612
22	V	0.2461	0.008223	0.0025058	-0.0533989	0.9998	0.004812
	SA	0.0630	0.001777	0.0002321	-0.0053726	0.9997	0.000622
23	V	1.2100	0.036654	0.0024066	-0.0594414	0.9996	0.009147
	SA	0.1738	0.003425	0.0001569	-0.0040495	0.9996	0.000776
24	V	0.8210	0.018620	0.0020493	-0.0456885	0.9996	0.006499
	SA	0.1274	0.002716	0.0001195	-0.0027725	0.9998	0.000493
25	V	0.2265	0.005554	0.0006599	-0.0146736	0.9996	0.002217
	SA	0.0568	0.001125	0.0001084	-0.0025838	0.9993	0.000495
26	V	0.6033	0.011507	0.0011499	-0.0279449	0.9996	0.003927
	SA	0.1102	0.001671	0.0001277	-0.0033910	0.9993	0.000583
27	V	0.2290	0.006516	0.0003697	-0.0119552	0.9994	0.001675
	SA	0.0620	0.001449	0.0000270	-0.0012444	0.9988	0.000376
28	V	0.4571	0.012053	0.0009305	-0.0185441	0.9996	0.003811
	SA	0.0931	0.001991	0.0000866	-0.0020689	0.9996	0.000474
29	V	0.4567	0.014307	0.0008467	-0.0174098	0.9995	0.004497
	SA	0.0929	0.001984	0.0000822	-0.0020847	0.9994	0.000550
30	V	0.1346	0.004001	0.0002094	-0.0070506	0.9993	0.001042
	SA	0.0378	0.000933	0.0000257	-0.0009322	0.9979	0.000372
31	V	0.8064	0.030973	0.0010545	-0.0211085	0.9998	0.005306
	SA	0.1317	0.003226	0.0000974	-0.0025393	0.9997	0.000510
32	V	0.1827	0.005547	0.0001638	-0.0063968	0.9982	0.001942
	SA	0.0499	0.000802	0.0000450	-0.0014894	0.9989	0.000281
33	V	0.3261	0.006639	0.0011543	-0.0215696	0.9997	0.003244
	SA	0.0723	0.001450	0.0001716	-0.0040602	0.9995	0.000597
34	V	0.8439	0.015170	0.0013434	-0.0283746	0.9995	0.005807
	SA	0.1344	0.002276	0.0000959	-0.0022852	0.9994	0.000639
35	V	0.1062	-0.007888	0.0026831	-0.0554245	0.9997	0.003850
	SA	0.0327	-0.000336	0.0003273	-0.0074826	0.9995	0.000611
36	V	0.2068	0.008407	0.0015268	-0.0212747	0.9998	0.003480
	SA	0.0557	0.001594	0.0001554	-0.0028917	0.9998	0.000457
37	V	0.3812	0.013793	0.0025548	-0.0580938	0.9997	0.006056
	SA	0.0836	0.002435	0.0001779	-0.0046240	0.9996	0.000657
38	V	0.1549	0.007420	0.0023664	-0.0478615	0.9998	0.004052
	SA	0.0455	0.001845	0.0002595	-0.0063426	0.9998	0.000515
39	V	0.2168	0.012909	0.0026779	-0.0652105	0.9998	0.004688
	SA	0.0579	0.002003	0.0002552	-0.0069408	0.9997	0.000644
40	V	0.0569	0.002967	0.0003073	-0.0084270	0.9994	0.001127
	SA	0.0265	0.000860	0.0000608	-0.0017057	0.9993	0.000294
41	V	0.3469	0.008180	0.0039510	-0.0748388	0.9998	0.007095
	SA	0.0669	0.002237	0.0002591	-0.0057206	0.9998	0.000549
42	V	0.7189	0.021438	0.0017147	-0.0362995	0.9994	0.008109
	SA	0.1205	0.002675	0.0000998	-0.0022072	0.9995	0.000645
43	V	0.3580	0.006609	0.0020292	-0.0375822	0.9997	0.005153
	SA	0.0781	0.001442	0.0001737	-0.0036501	0.9997	0.000479

44	V	0.0240	-0.000807	0.0015056	-0.0274287	0.9998	0.002251
	SA	0.0111	0.000806	0.0002207	-0.0047157	0.9999	0.000322
45	V	0.1819	0.016569	0.0009160	-0.0132035	0.9998	0.003210
	SA	0.0526	0.002602	0.0001178	-0.0022912	0.9998	0.000428
46	V	0.6937	0.028505	0.0019800	-0.0531285	0.9996	0.007258
	SA	0.1212	0.003183	0.0001799	-0.0055272	0.9996	0.000727
47	V	0.3499	0.015532	0.0012673	-0.0317122	0.9997	0.003897
	SA	0.0793	0.002324	0.0001348	-0.0039121	0.9997	0.000486
48	V	0.8640	0.035142	0.0018108	-0.0430104	0.9995	0.009655
	SA	0.1339	0.003994	0.0000775	-0.0022190	0.9995	0.000769
49	V	1.3681	0.031915	0.0014153	-0.0360976	0.9997	0.006430
	SA	0.1772	0.003009	0.0000846	-0.0023934	0.9994	0.000678
50	V	0.0414	0.002033	0.0007317	-0.0180072	0.9985	0.003038
	SA	0.0196	0.000686	0.0001392	-0.0035501	0.9982	0.000716
51	V	0.2995	0.011532	0.0014863	-0.0354575	0.9996	0.004366
	SA	0.0729	0.001898	0.0001595	-0.0041731	0.9996	0.000530
52	V	0.7224	0.035834	0.0019266	-0.0465878	0.9995	0.009620
	SA	0.1225	0.003981	0.0001160	-0.0033547	0.9996	0.000797
53	V	0.1431	0.003994	0.0014548	-0.0281785	0.9994	0.004645
	SA	0.0473	0.001182	0.0001960	-0.0046030	0.9993	0.000685
54	V	0.8423	0.026697	0.0007002	-0.0134157	0.9989	0.009348
	SA	0.1269	0.002523	0.0000882	-0.0023429	0.9992	0.000734
55	V	0.7509	0.019060	0.0008431	-0.0209625	0.9989	0.007183
	SA	0.1257	0.002562	0.0000611	-0.0018958	0.9989	0.000771
56	V	0.2633	0.011712	0.0004957	-0.0122056	0.9989	0.004346
	SA	0.0674	0.001980	0.0000621	-0.0019435	0.9992	0.000542
57	V	0.3275	0.014710	0.0004695	-0.0067789	0.9993	0.004484
	SA	0.0786	0.002435	0.0000566	-0.0014147	0.9994	0.000591
58	V	0.2827	0.011096	0.0010529	-0.0220391	0.9992	0.005270
	SA	0.0673	0.002042	0.0001121	-0.0029775	0.9993	0.000619
59	V	0.1083	0.001238	0.0000836	-0.0014207	0.9983	0.000792
	SA	0.0349	0.000134	0.0000413	-0.0008143	0.9984	0.000218
60	V	0.3042	0.011870	0.0004779	-0.0106849	0.9996	0.002707
	SA	0.0741	0.001997	0.0000611	-0.0016819	0.9993	0.000518
61	V	0.2487	0.011314	0.0004335	-0.0101284	0.9993	0.003296
	SA	0.0657	0.002219	0.0000417	-0.0014358	0.9993	0.000494
62	V	0.6550	0.021947	0.0014435	-0.0330299	0.9991	0.009054
	SA	0.1166	0.002662	0.0001428	-0.0038654	0.9991	0.000944
63	V	1.1606	0.029049	0.0007722	-0.0156482	0.9991	0.009189
	SA	0.1600	0.003303	0.0000081	-0.0001994	0.9993	0.000668
64	V	0.1817	0.004181	0.0000290	-0.0019488	0.9982	0.001222
	SA	0.0570	0.000730	0.0000186	-0.0008303	0.9893	0.000582
65	V	0.3129	0.010679	0.0007137	-0.0164439	0.9992	0.004118
	SA	0.0751	0.001862	0.0000771	-0.0020028	0.9992	0.000573
66	V	0.2163	0.009910	0.0009127	-0.0099004	0.9997	0.003650
	SA	0.0535	0.001826	0.0001310	-0.0024829	0.9997	0.000490

67	V	0.3923	0.017219	0.0010705	-0.0194948	0.9993	0.006688
	SA	0.0734	0.002501	0.0000835	-0.0018971	0.9994	0.000659
68	V	0.3245	0.017865	0.0006629	-0.0153657	0.9991	0.005939
	SA	0.0763	0.002503	0.0000755	-0.0020585	0.9994	0.000625
69	V	0.4014	0.013107	0.0014400	-0.0347726	0.9991	0.006913
	SA	0.0872	0.002485	0.0001091	-0.0030441	0.9991	0.000790
70	V	0.3054	0.010094	0.0008435	-0.0130097	0.9993	0.004850
	SA	0.0727	0.002251	0.0000650	-0.0012739	0.9995	0.000515
71	V	0.7225	0.022414	0.0014234	-0.0197742	0.9991	0.010992
	SA	0.1278	0.003114	0.0000750	-0.0011951	0.9990	0.001028
72	V	0.1593	0.003401	0.0010579	-0.0181183	0.9997	0.002609
	SA	0.0488	0.001047	0.0001384	-0.0028138	0.9997	0.000412
73	V	0.7588	0.031967	0.0015323	-0.0293472	0.9995	0.008797
	SA	0.1299	0.004163	0.0000636	-0.0018827	0.9996	0.000701
74	V	0.1263	0.002739	0.0006481	-0.0130673	0.9995	0.001998
	SA	0.0411	0.000521	0.0001052	-0.0020248	0.9995	0.000354
75	V	0.7918	0.027496	0.0022717	-0.0417219	0.9994	0.011605
	SA	0.1300	0.003636	0.0001075	-0.0023628	0.9994	0.000895
76	V	0.3263	0.008221	0.0005998	-0.0073994	0.9992	0.004058
	SA	0.0790	0.001550	0.0000678	-0.0010627	0.9994	0.000504
77	V	0.2242	0.009019	0.0004039	-0.0074343	0.9991	0.003438
	SA	0.0624	0.002033	0.0000260	-0.0005869	0.9987	0.000646
78	V	0.1933	0.008175	0.0003708	-0.0074096	0.9994	0.002515
	SA	0.0564	0.001603	0.0000544	-0.0013672	0.9993	0.000443
79	V	0.5413	0.017479	0.0006747	-0.0142635	0.9996	0.003938
	SA	0.1040	0.002230	0.0000863	-0.0023150	0.9994	0.000584
80	V	0.1818	0.004278	0.0008720	-0.0193842	0.9991	0.003438
	SA	0.0535	0.000730	0.0001513	-0.0036440	0.9991	0.000563
81	V	0.6870	0.021868	0.0005408	-0.0095486	0.9994	0.005692
	SA	0.1251	0.002599	0.0000527	-0.0013720	0.9993	0.000642
82	V	0.6491	0.020227	0.0004368	-0.0086327	0.9996	0.004191
	SA	0.1179	0.002329	0.0000505	-0.0013144	0.9994	0.000545
83	V	0.3470	0.007833	0.0012543	-0.0285332	0.9995	0.004055
	SA	0.0780	0.001281	0.0001524	-0.0037701	0.9994	0.000550
84	V	0.2705	0.012633	0.0003258	-0.0052530	0.9995	0.002984
	SA	0.0705	0.001931	0.0000642	-0.0016513	0.9994	0.000495
85	V	0.5479	0.006709	0.0045819	-0.1121483	0.9992	0.012360
	SA	0.1021	0.001679	0.0003332	-0.0086926	0.9996	0.000831
86	V	0.1773	0.001893	0.0018694	-0.0438984	0.9994	0.004356
	SA	0.0496	0.000712	0.0002279	-0.0056917	0.9995	0.000580
87	V	0.2209	0.008510	0.0015340	-0.0279870	0.9994	0.005654
	SA	0.0568	0.001642	0.0001645	-0.0036407	0.9994	0.000679
88	V	0.3774	0.009695	0.0030219	-0.0733819	0.9993	0.009026
	SA	0.0795	0.001374	0.0002700	-0.0068784	0.9994	0.000776

Appendix 2: Mean and range of competition indices in 1972, immediately following the partial cutting treatment for trees from control and release treatment, stratified by crown class.

Competition index[1]	Crown class	Control		Released	
		Mean	Range	Mean	Range
CI01	Emergent	15.9	11.0 - 25.0	13.4	13.0 - 22.0
	Dominant	18.0	12.0 - 28.0	18.6	17.0 - 22.0
	Intermediate	17.9	13.0 - 22.0	13.0	8.0 - 19.0
CI02	Emergent	12.2	6.4 - 24.8	7.2	2.6 - 13.5
	Dominant	27.7	9.1 - 51.0	15.7	5.3 - 60.6
	Intermediate	48.7	19.5 - 92.4	37.5	16.1 - 68.5
CI03	Emergent	382.3	229.1 - 595.1	247.3	94.4 - 417.4
	Dominant	417.6	254.5 - 581.6	252.3	115.6 - 354.8
	Intermediate	419.8	295.2 - 606.4	224.9	174.1 - 305.9
CI04	Emergent	62.2	37.7 - 84.6	40.4	12.8 - 62.9
	Dominant	66.8	40.1 - 123.7	39.6	22.8 - 62.4
	Intermediate	80.4	57.2 - 106.8	48.5	20.8 - 75.1
CI05	Emergent	1258.0	489.2 - 2149.9	572.8	68.5 - 1107.9
	Dominant	1503.4	575.4 - 4230.6	529.0	183.6 - 1198.9
	Intermediate	1950.2	1083.5 - 2937.2	750.1	163.2 - 1395.9
CI06	Emergent	16.8	10.0 - 27.8	10.8	4.9 - 15.2
	Dominant	26.6	12.7 - 41.7	15.8	7.9 - 31.5
	Intermediate	36.1	21.9 - 52.0	24.6	13.3 - 35.0
CI07	Emergent	19.3	9.3 - 41.9	10.6	2.8 - 22.0
	Dominant	40.0	14.4 - 77.5	23.1	6.8 - 81.0
	Intermediate	84.1	46.4 - 134.8	68.2	15.6 - 112.4
CI08	Emergent	2.8	0.9 - 4.4	1.3	0.1 - 2.0
	Dominant	2.9	1.3 - 6.2	1.4	0.1 - 3.0
	Intermediate	4.2	2.3 - 5.8	1.8	0.2 - 3.5
CI09	Emergent	2.5	0.5 - 4.9	0.9	0.1 - 1.6
	Dominant	3.4	1.8 - 6.7	1.3	0.3 - 3.5
	Intermediate	6.9	2.7 - 11.6	2.8	0.3 - 5.4
CI10	Emergent	0.0566	0.0042 - 0.1157	0.0545	0.0044 - 0.2577
	Dominant	0.0537	0.0066 - 0.1964	0.0414	0.0064 - 0.1211
	Intermediate	0.1114	0.0529 - 0.2604	0.0790	0.0079 - 0.1600
CI11	Emergent	0.0425	0.0039 - 0.1008	0.0322	0.0035 - 0.1443
	Dominant	0.0725	0.0122 - 0.1650	0.0541	0.0055 - 0.2801
	Intermediate	0.3181	0.1147 - 0.5051	0.3985	0.0094 - 1.0417

[1] See text section 5.7 for explanation and calculation of indices