1986

Within and between-species competition and individual tree growth in a young jack pine-aspen stand

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LAKEHEAD UNIVERSITY

WITHIN- AND BETWEEN-SPECIES COMPETITION AND INDIVIDUAL TREE GROWTH IN A YOUNG JACK PINE-ASPEN STAND

by

Mugasha Ancelm Godfrey ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Science
IN
FORESTRY

School of Forestry

Thunder Bay, Ontario
May, 1986

ISBN 0-315-34823-2

To my wife MWAJUMA,

my children ARNOLD, WILSON and REHEMA,

and my mother ASTERIA

ABSTRACT

Mugasha, A.G. 1986. Within- and between-species competition and individual tree growth in a young jack pine-aspen stand. 108 pp. Major advisor: Dr. Kenneth M. Brown.

Keywords: mixed stand dynamics, stemwood volume increment, radial increment, diameter increment, height increment, live crown ratio, Daniels' competition index

The competitive relationship between jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) was studied in an 8-year-old mixed stand in North Central Ontario, Canada. During the summer of 1984, a total of 298 subject trees were selected at random within the stand. Half of the study trees were jack pine, the other half aspen. From the trees neighbouring each subject tree, competitor trees were identified by means of a modified horizontal point sample centered on the subject tree. The data include a wide range of conditions with respect to both stand density and composition. Subject trees were measured for initial size (stemwood volume, stem radius at stump height and height) and the 1983 annual increment of the same size attributes. Live crown ratio at the time of sampling was also measured. The current annual increment data were analysed with respect to initial subject tree size and competitive environment by means of multiple linear regression. The objective was to investigate a hierarchy of mutually exclusive hypotheses regarding the nature of the competitive interaction between the 2 study species. The results indicate that jack pine and aspen responded differently to competition, and that the competitive effect of the jack pine component was different than that of the aspen component when both species occurred in a mixture. Specifically, the annual volume increment and annual radial increment of aspen subject trees was affected only by the aspen component of the competing stand. The annual volume increment and annual radial increment of jack pine subject trees, on the other hand, were affected by both the jack pine and aspen components of the competing stand. Although the study is of limited scope, it does provide some interesting insights into the possible dynamics of mixed stands of these important, and commonly associated, boreal species. The work also gives some indication that the competitive effect of aspen on jack pine may be sufficiently strong to warrant the consideration of silvicultural control in situations where jack pine is the crop species.

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LIST OF SYMBOLS AND ABBREVIATIONS

Symbol	Page first used	Meaning
ΔR	65	the 1983 radial increment at stump height of all subject trees
ΔRp	48	the 1983 radial increment at stump height of jack pine subject trees
ΔRa	49	the 1983 radial increment at stump height of aspen subject trees
ΔHp	48	the 1983 height increment of jack pine subject trees
ΔHa	49	the 1983 height increment of aspen subject trees
ΔV	58	the 1983 volume increment of all subject trees
ΔVp	48	the 1983 volume increment of jack pine subject trees
ΔVa	49	the 1983 volume increment of aspen subject trees
R	65	initial radius at stump height of all subject trees
Rp	48	initial radius at stump height of jack pine subject trees
Ra	49	initial radius at stump height of aspen subject trees
V	58	initial volume of all subject trees
Vp	48	initial volume of jack pine subject trees
Va	49	initial volume of aspen subject trees
Hp	48	total height of jack pine subject trees
Ha	49	total height of aspen subject trees
Dp	48	diameter over bark at stump height of jack pine subject trees
Da	49	diameter over bark at stump height of aspen subject trees
CRp	48	live crown ratio of jack pine subject trees
CRa	49	live crown ratio of aspen subject trees
DC1	38	Daniels' total competition index due to all selected competitors
DC2	38	Daniels' total competition index based on competitors whose crown class is equal or greater than the crown class of the subject tree
DC'	38	DC1 - DC2

DClp	43	Daniels' competition index due to jack pine competitors
DCla	43	Daniels' competition index due to aspen competitors
DClo	43	Daniels' competition index due to competitors other than jack pine and aspen
LCl	39	Lorimers' total competition index due to all selected competitors
LC2	39	Lorimers' total competition index based on the competitors whose crown class is equal or greater than the crown class of subject tree
LC'	39	LCl - LC2
SC	37	Spurr's modified point density
SP	58	dummy variable subject tree species
Std err	59	Standard error
N	59	number of observation
F	59	F-ratio
df	59	degrees of freedom
Res ss	59	residual sum of squares

AKNOWLEDGEMENT

I am indebted to the following: My employer, the Principal Secretary, Ministry of Natural Resources and Tourism, Tanzania, for granting me a two and a half year Forestry study leave; the Ontario Ministry of Natural Resources for allowing me to use their plantation as a study area; the Canadian Forestry Service for funding this study; and the School of Forestry, Lakehead University for offering me a two year fellowship.

I wish to express my appreciation to Dr. K.M. Brown for his valuable guidance throughout, and to Dr. W.H. Carmean and Dr. R.E. Farmer for their helpful advice. I am grateful to Mr. D. Nix and J. Knight for their assistance, respectively, with field data collection and stem analysis. The assistance of Dr. G. Hazenberg, Dr. T.A. Dickinson and Mr. Graeme Spiers is sincerely acknowledged. Mr. George Marek a retired forester of the OMNR in the Nipigon District, deserves a special mention for suggesting the problem and helping me locate the study area.

I also wish to thank my wife Mwajuma, my sons Arnold and Wilson and my daughter Rehema for their understanding and for enduring my two and a half year absence from the family. Finally, I should like to thank all those who contributed in one way or another to make this thesis a success.

INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) are commonly associated species of the boreal mixed forest (Rowe 1972). In today's market in Ontario, aspen is generally considered a weed species. It invades cutover and burned land where it often competes for growing space with jack pine, a commercially important tree species. Of course, potentially, both species are of commercial value. Furthermore, aspen may play an important ecological role during secondary succession by redistributing nitrogen to the soil surface layers (Daubenmire 1953).

Previous work on mixed stand dynamics has dealt both with annual crops and forest trees. Much of the work with annual crops has focused on the effects of species mixture and stand density on yield. Forestry research in this area has been of several types. There have been many forestry yield studies, but these have dealt almost exclusively with pure stands. There have been studies on the effects of spacing, thinning and intercropping. These kind of studies give some insight into mixed forest growth. As well, there have been numerous studies of the effects of intertree competition on the increment of individual trees. In spite of the prevalence of the type, I have been unable to find any previous work on the quantitative effects of competition in mixed aspen - jack pine stands. Furthermore, there seem to have been no studies on the differential competitive effects of the member species in mixed forest stands.

Both forest ecologists and silviculturists need more information about the mutual competitive relationship between jack pine and aspen in order to understand and control the dynamics of mixed stands of these species. My goal was to study these relationships with the following specific objectives: 1) to determine whether individual trees of both species respond to competition in the same way, and 2) to determine whether both species are equally effective competitors.

Field work was carried out during the summer, 1984, in an 8-year old mixed stand of jack pine and aspen located near the village of Jellicoe in North Central Ontario, Canada. A random sample of 298 subject trees was selected within the stand. Half of the study trees were jack pine; half were aspen. Each subject tree was measured for initial size and current annual increment for the 1983 growing season. Daniels' competition index (Daniels 1976) was used to characterize the competitive situation impacting on each subject tree. The level of competition due to both jack pine and aspen components of the neighbouring stand were measured separately. The data were analysed by means of multiple linear regression to investigate the competitive interaction between the 2 study species.

The results suggest that aspen and jack pine responded differently to competition. Furthermore, subject trees of both species responded differently depending on whether the species composition of the competitor population was jack pine, aspen or some mixture of the two.

My study is of limited scope, and, therefore, inferences must be drawn with caution. It appears, however, that when jack pine and aspen compete on an initially equal footing, aspen will eventually dominate the stand. My results do not indicate how long this transition might take, nor how factors such as stand age and site quality might affect the outcome. But, the implication is that, in stands like the one I studied, the competitive advantage shifts to aspen in only a few years. The competitive effect of aspen on jack pine seems to be strong enough to warrant silvicultural control in situations where jack pine is the crop species.

LITERATURE REVIEW

THE ECOLOGICAL AND SILVICULTURAL RELATIONS OF JACK PINE AND ASPEN

The silvicultural characteristics of jack pine have been compiled and reviewed by Fowells (1965) and the species' history and ecological characteristics have been reviewed briefly by Cayford (1957a) and more recently by Marshall (1980). The silvical characteristics of aspen have been compiled by Strothman and Zasada (1957) and Fowells (1965). The autecology and silvics of aspen was recently reviewed by Harvey (1982). My review is focused only on those characteristics of aspen and jack pine that influence their regeneration and early growth.

Jack Pine

Jack pine most commonly occurs on ground and terminal moraines, and on outwash plains. It grows on dry to fresh, shallow to deep sand and sandy loams soils (Day and Harvey 1981). Due to its intolerance, jack pine is often excluded from better sites by competition from other species. It is this competition, rather than limiting soil or moisture conditions, that usually restricts jack pine to poorer sites (Baker 1949, Rudolf 1950, 1951, Benzie 1977).

Many attempts have been made to regenerate jack pine. Early attempts at natural regeneration of jack pine often failed (Hacker *et al.* 1983). These poor results were due mainly to failure to meet seed germination and seedling establishment requirements, e.g. moisture relations, soil temperature and light. Hacker *et al.* (1983) observed that the shelterwood system has some promise where non-serotinous coned jack pine stands exist. This is because shade during seedling establishment can reduce the high mortality that results from excessive heat and desiccation. These are also common problems on clear cut sites. However, Cayford (1957a) cautioned that a residual overstory may also present a threat, since it favours damage from jack pine budworms.

Attempts have been made to regenerate jack pine in clear cuts. For successful establishment without prescribed fire on clear cuts, mineral soil should be exposed by scarification and seed should be released from slash by scattering. Predation by squirrels, chipmunks, mice and birds can seriously deplete seed supplies (Hacker *et al.* 1983).

Fire has been used to induce natural regeneration of jack pine. Hacker *et al.* (1983) observed that fire helps to open and disperse serotinous cones. Fires create suitable seed beds and also help to break down the thick logging slash that otherwise would shade seed beds excessively. The use of fire sometimes cause some problems. Prescribed fire sometimes destroys the cones and seed. Thus, unburned slash may need to be reserved for scattering over areas with prescribed burns. It has also been observed that in some cases, especially on mesophytic sites, fire will stimulate considerable growth of shrubs, grasses and sedges (Ahlgren 1979). Moreover, burning on sandy soils has resulted in large losses of essential nutrients as a result of surface runoff and leaching (Farrel *et al.* 1981, Grier and Cole 1971, Schantz-Hansen and Jensen (1952). Burning on soils shallow to bedrock might result in destruction of an organic mat and subsequent oxidation after the fire.

Jack pine is an intolerant tree species (Baker 1949, Horton and Bendell 1960). Jack pine may be relatively more tolerant in the seedling stage (Bates and Roeser 1928). It becomes more intolerant with increasingly warmer environments (Bakuzis and Hansen 1960). Young jack pine seedlings can exist in light as low as 2.4 per cent of full sunlight; however, more light is required for maximum growth.

Jack pine is sensitive to competition. Schantz-Hansen (1931) observed that overstocking depresses both height and diameter growth. He observed that thinning in seedling, large sapling and small pole stands with 3,707 to 12,355 stems per hectare has resulted in good growth. Jack pine dominance is not well expressed in dense young stands. The per cent of dominant and codominant trees increases with a decrease in stand density.

The spacing factors of the stand between 10 and 80 years decrease from 21 to 18 on good sites, and 27 to 20 on medium sites, and 30 to 20 per cent on poor sites (Gevorkiantz 1947).

In Upper Michigan on moist, sandy soils with a water table about 76 cm below the surface, roots penetrated to 55 cm in 2 years and went to only 61 cm in 7 years; the lateral spread, however, increased from 91 to 124 cm at 2 years, to between 4.3 and 4.9 m at 7 years (Day 1958). Direct seeded jack pine growth is very slow during the first three years but increases rapidly during the fourth and fifth years. Average height of wild seedlings is about 5 cm at 1 year, 16 cm at 2 years, and 30 to 90 cm at 4 years (Sterrett 1920). Initial height growth in plantations is more rapid on medium sites (Gevorkiantz 1947).

During the first 20 years, jack pine in its native range is the second fastest growing conifer; tamarack (*Larix laricina* (Du Roi) K. Koch) is the fastest growing conifer. Jack pine seedlings reach breast height in 5 to 8 years (Kabzems and Kirby 1956, Rudolf 1950). Jack pine reaches its maximum size in 50 to 60 years when it averages between 18 to 20 cm breast height diameter (Dbh) and 17 m height. On better sites the physical rotation age can be extended up to about 80 years without substantial reduction in growth rate. On poor sites, growth slows down when a stand is between 40 and 50 years old, depending on the site conditions (Benzie 1977). Recent studies in the Thunder Bay area show that the height of jack pine ranges between 10 to 22 m at age 50 (Lenthall 1986).

Aspen

Day and Harvey (1981) observed that aspen grows on medium to deep loamy till, and on well aerated silts and clays that originated from ground moraine and lacustrine. According to Stoeckeler (1948) and Zehngraff (1947) aspen grows best on soils that have developed from a gray glacial till. These soils are rich in lime that are usually porous, loamy and humic. The growth of aspen on sandy soils is often poor because of low moisture and low nutrient levels.

Aspen regenerates naturally from seed and root suckers. Regeneration from seed is often inadequate. This is because, for adequate aspen reproduction from seed to occur, a favourable seed bed, a good seed crop, and abundant soil moisture are required. This often happens when a fire exposes bare soil during the spring of a good seed year (Zehngraff 1947). Maini (1960) found that the shortage of natural trembling aspen stands of seedling origin is due to i) short seed viability, ii) presence of a water soluble germination and growth inhibitor in the seed hair, iii) occurrence of unfavourable moisture conditions during seed dispersal, iv) susceptibility of seedlings to high temperatures that occur on soil surfaces blackened by fire, v) susceptibility of seedlings to fungal attack, vi) the adverse influence of diurnal temperature fluctuations on initial seedling growth and vii) the unfavourable chemical nature of some substrates on which seeds are likely to fall.

The major means of aspen natural regeneration is by root suckers. Maini and Horton (1966) observed that warm soil temperatures, around 23°C, stimulate aspen sucker production. Suckering takes place in surface soil ranging from 5.0 to 9.5 cm depth (Maini 1960). This is because surface horizons have relatively higher temperature than do deep horizons.

The intensity of sucker production appears to be related to the degree of stand disturbance (Jarvis 1965). Harvesting and site preparation expose mineral soils. The temperature of exposed soil is usually higher than that of unexposed soils. Felling of aspen causes loss of apical dominance. The net effect of these practices is aspen root sucker production (Jarvis 1965). It has, however, been observed that excessive forest disturbances might reduce the intensity of aspen sucker production (Zasada and Tappeiner 1969). This may be due to the fact that most roots are severed.

Baker (1949) observed that aspen is a shade intolerant species. Shirley (1944) reports that aspen is characterized by a pronounced ability to express dominance. Day and Harvey (1981) observed that root suckers grow from 1 to 2 m per year for the first 5 years; this enables them to dominate the stand early and mechanically whip most competitors. Aspen trees growing under good conditions will reach 27 to 30 m in height and to 60 cm in diameter at 80 years of age. In eastern Canada and the Prairie Provinces, the rotation age for trembling aspen varies from 65 to 80 years (Jarvis 1965). In Ontario, the optimum biological rotation age for trembling aspen is 53 years (Plonski 1974). Deschamps (pers. comm., Nov. 1985) observed that the mean height of aspen in the Thunder Bay area varies between 14 and 26 m at age 50.

STAND DENSITY AND STOCKING AS EXPRESSIONS OF COMPETITION

The growth of trees is influenced by two types of competition, i.e: competition below ground level and aerial competition. In the soil trees compete for moisture and nutrients; above ground trees compete for light and space. Root competition is difficult to measure. On the other hand, some progress has been made in the evaluation of the influence of aerial competition on tree growth.

The degree of crowding present in a stand and the level of site utilization are evaluated through expressions of stand density and stocking. Stocking is an indication of the number of trees in a stand as compared to the desirable number of trees required for best growth and management. Stand density refers to the density of stocking in terms of numbers of trees, basal area, volume or other criteria expressed on a unit area basis (Society of American Foresters 1950, Bickford *et al.* 1957). The number of stems per unit area is not a good indicator of density because the number of trees per hectare needed to achieve full stocking decreases markedly as a stand ages (Czarnowski 1961, Curtis 1970). Bickford *et al.* (1957) suggested that a good measure of stand density should be independent of age.

Smith and Bailey (1964) defined stand density as the degree of crowding of individual trees within the portion of the area actually stocked with trees. Stocking measures on the other hand involve a comparison of existing stand with a norm. Gingrich (1967) observed that stand density reflects the degree of crowding of stems within the area. He also observed that stocking is a relative term used to describe the adequacy of a given stand density to meet management objectives.

Most of the relative measures of stand density commonly used in forestry can be interpreted as ratios of some average crown area or land area occupied by, or available to, trees of a given stand. Area occupied may be assumed equivalent or proportional to crown projection area, and average crown projection area of "open grown" trees (i.e. subject tree not suffering form lateral competition) of a given diameter can be estimated from measurement of crown width (Krajicek *et al.* 1961). Similarly, the areas of average trees in normal stands may be estimated by the area technique of Chisman and Schumacher (1940) or by direct measurement of tree crown (Curtin 1964).

Curtis (1970) observed that any appropriate measure of density should express average area available per tree, compared to either the "open grown" conditions or the normal stand. He also observed that in closed stands or in conjunction with some measure of stand closure, they should be viewed as expressions of average crown development relative to a standard condition, and hence, expressions of cumulative competition effects on tree development.

All measures of stand density and stocking are dynamic rather than static. That is, direct measures of stand density such as the number of trees or the basal area per hectare, change with time. It is also possible for stocking levels to be drastically reduced at one or more points in the life of the stand as a result of catastrophic mortality (Clutter *et al.* 1983).

MEASUREMENT OF STAND DENSITY IN RELATION TO TREE GROWTH

Measures of stand density to express the level of intertree competition are important in the analysis of tree and stand growth relationships (Smith and Bell 1983). The stand density and prediction of stand growth by integrating the growth of individual trees has been studied for many tree species by several research workers for the past three decades. During this period a number of indices have been developed to quantify the relative competitive stress of individual trees in the stand (Ganzlin and Lorimer 1983). Competition indices have been used in tree growth simulation models to describe variability in the tree growth and mortality attributable to competition. Some of the research done in this field will be briefly reviewed under the following sub-headings:

- crown competition factor

- crown ratio
- competition indices based on the concept of crown overlap
- a competition index based on rooting zone overlap
- single tree density in terms of basal area around the subject tree
- available growing space around the subject tree
- crown surface area and height of the subject tree
- diameter and/or distance of the neighbouring trees

Crown Competition Factor

Krajicek *et al.* (1961) investigated crown competition as a measure of density in white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), shagbark hickory (*Carya ovata* (Mill) K. Koch) and Norway spruce (*Picea abies* (L.) Karst). They developed the theory of maximum crown area (MCA) which they expressed in terms of percentage of the maximum area that could be occupied by the crown of a tree of specified breast height diameter (Dbh). The Crown Competition Factor "CCF" is defined as the sum of MCA values for all trees in a stand, divided by unit of an area. The CCF was used as an expression of stand density. They observed that the CCF varies with species because of variation in crown area development when there is no competition, variation in basic shape of the crowns and species tolerance.

Vezina (1962) observed that CCF for jack pine could be estimated from stand tables by accumulating MCA values of the trees comprising the stand. He confirmed reports by Krajicek *et al.* (1961) that CCF as a measure of stand density varied somewhat with stand age and site quality, but no consistent relationship was evident.

Alexander *et al.* (1967) employed the procedure by Krajicek *et al.* (1961) to developed a CCF equation for lodgepole pine (*Pinus contorta* Dougl). They observed that there was no correlation between CCF per unit area and age. The CCF per unit area decreased slightly with increase in site quality. The regression accounted for only about 6 per cent of the total variation in CCF between plots. They concluded that CCF as a measure of density for lodgepole pine was independent of stand age and site index.

Crown Ratio

There are two crown ratios, namely the crown width to Dbh ratio and the live crown length to total tree height ratio.

Crown Width to Dhb Ratio

The ratio of the crown width to Dbh was first introduced into the literature by Duchaufour in 1903 as reported by Lane-Poole (1936). He established that there was a significant relationship between crown width and Dbh of *Eucalyptus* species.

Smith (1958), Smith and Ker (1960) and Smith *et al.* (1961) investigated the influence of crown closure and stand density on the variation of crown width in relation to Dbh for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). They showed that average width of the widest part of the crown and Dbh are strongly correlated. At the same time, fully "open grown" trees of the species studied were shown to have crowns roughly twice as wide as stand grown trees.

More studies on crown ratio have been done on other tree species e.g. van Laar (1963) on radiata pine (*Pinus radiata* D. Don), Ayhan (n.d.) on Scots pine (*P. sylvestris* L.), and Vezina (1963) on jack pine.

Although crown width to Dbh ratio has been used in various ways to express stand density, it has some limitations. One of the major assumptions is that in a forest stand trees grow in one strata (story) and that there is 100 per cent utilization of space. Such conditions are rarely met in nature. Another assumption in computing the crown width to Dbh ratio is that the crown and roots occupy about the same horizontal area. This might be a reasonable assumption in rain forests. However, the situation might be different in semi-arid areas where moisture availability is a problem and tree roots extend beyond the crown. Under such circumstances competition for soil moisture and nutrients may occur between trees even if their crowns do not overlap.

Live Crown Ratio

Live crown ratio is defined as the ratio of the length of the live crown to the total tree height. The ratio approaches one when there are live crowns down near the stump. However, with shorter live crowns the ratio decreases. Czarnowski (1961) proposed that the live crown ratio might be a useful measure of stand density.

The live crown ratio is influenced by the tolerance of the tree species. The live crown ratio of tolerant trees is usually higher than that of intolerant trees growing under similar stand density conditions. The technique of expressing density in terms of the live crown ratio was recently tested by Smith (1980). He observed that there were no consistent differences among live crown ratios of Douglas-fir and western cedar (*Juniperus scopulorum* Sarg.) in their relation to stand basal area. For a given basal area, young trees had a greater percentage of live crown.

Competition Indices Based on the Concept of Crown Overlap

According to Alemdag (1978), Staebler was one of the first researchers to study individual tree competition. Staebler (1951) assumed that the growing space occupied by an individual Douglas-fir tree was a circular area whose radius, denoted cr, was related to the breast height diameter by the linear function: cr = a + b(Dbh). Zones of competition occurred whenever circular areas of adjacent trees overlap. He hypothesized that the competition exerted upon an individual tree was directly proportional to the relative competitive status of neighbouring trees.

Newnham (1964) developed a stand growth model for Douglas-fir by assuming that a tree is selected as a competitor when its "open-grown crown" has an overlap with the "open grown crown" of the subject tree. Newnham's (1964) competition index for the ith subject tree is:

$$CI_i = \sum_{j \neq i}^{n}((\theta/2\pi).(CR_j/CR_i)) \qquad [2.1]$$

where:

θ - an angle (in radians) subtended at the point of the subject tree by the intersection of the "open-grown crown" of the subject tree and the "open-grown crown" of the competitor.

CR_j - crown radius of the competitor

CR_i - crown radius of the subject tree

Newnham (1966) further developed Staebler's idea. He studied stand structure and diameter growth of young red pine (*Pinus resinosa* Ait.) trees as well as the relationship between total height to the base of the live crown, crown width and breast height diameter. He computed two competition indices: one was a measure of linear overlap of competition circles; the other was a measure of the proportion of circumference of the competition circle occupied by the competitors.

Gerrard (1969) also expanded upon Staebler's (1951) original hypothesis. He developed a new competition index that accommodates differences in the degree of dominance associated with variation in tree size. He hypothesized that the competitive stress sustained by a tree is directly proportional to the overlap of its competition with those of its neighbours and inversely proportional to the area of its own competition circle. Gerrard (1969) tested his new competition index along with other competition indices. The results show that none of the measures of competition tested by Gerrard contributed significantly to the growth prediction equation when combined with diameter and other tree attributes.

Bella (1969) extended the influence-zone concept by hypothesizing that the effect of competition on a subject tree is proportional to the amount of influence-zone overlap of the competitors and that of the subject tree. He assumed that the actual contribution of a competitor is dependent on the relative size of the competitor and the subject tree. The hypothesis was tested with permanent sample plot data from pure, even-aged, fully stocked, untreated stands of aspen (14 years old) and jack pine (11 years old). The regressions of two independent variables, diameter increment and basal area, with the competitive influence zone overlap (CIO) for competing trees were highly significant. The calculated CIO values in the growth-competition regression equation, accounted for as much as 70 per cent of the variation in individual tree basal area increment. Bella's (1969) results are of limited application, however, due to the small size of his sample.

Keister (1971) further developed Newnham's (1966) and Gerrard's (1969) approaches. He defined the circle of influence as an area approximating a circle occupied by both tree roots and crowns. He theorized the following: i) each tree in the stand interacts within a circular area surrounding the tree; ii) the size of this circular area is proportional to the size of the tree; and iii) intraspecific competition occurs in proportion to the area within the zone where two or more of these circles overlap. The competition index for a particular tree was expressed as the ratio of the sum of the areas of overlap within the particular tree's influence circle to the total area of the tree's influence circle. Keister tested his hypothesis by studying a two year diameter increment of subject trees from several 15-year-old slash pine (*Pinus elliottii* Engelm. var. elliottii) plantations. He found that initial tree diameter was the best single variable for predicting growth in most plantations. Fifty per cent of the variation in diameter growth could be accounted for by this variable alone. The addition of a competition index accounted for a slight, but statistically significant, improvement in the equations for all but one of the seven plantations studied.

Arney (1973) developed a competition index based on the selection of competing trees when their "open-grown crown" had an overlap with the "open-grown crown" of the subject tree. He developed a uniform method of quantifying competition stress on individual Douglas-fir trees, regardless of the stand age, site index or geographical location. Arney's Competition Stress Index for any given subject tree is a function of the number of neighbouring competitors with crown overlap with the subject tree's crown and area of overlap between "open grown crown" area of the subject tree.

Ker (1975) described the calibration of Arney's (1973) competition stress index for use with balsam fir (*Abies balsamea* (L.) Mill.) in Newfoundland. The data used for the computation of the competition index were obtained from only semi-mature and mature trees. The index, therefore, lacks the necessary data base to allow its use with young trees and stands. Consequently, Schooley (1976) adopted Arney's (1973) "Competition Stress Index" to quantify competition stress on individual, juvenile balsam fir trees. He speculated that the competition stress index should be useful in future studies to isolate competition factors in tree growth from other factors such as age, site quality, insect or disease attack.

Smith and Bell (1983) evaluated Arney's (1973) "Competition Stress Index" CSI model. They used CSI as an independent variable to improve significantly the prediction of periodic diameter growth after thinning of a young Douglas-fir stand. They used the CSI levels before and after thinning as a dynamic measure of expressing the effect of changes in stand density on the growth response of individual trees. They also assessed the relative contribution of CSI levels to the prediction of periodic diameter increment following thinning.

Smith and Bell (1983) observed that a simple linear function of initial CSI and the change in CSI contributed significantly to the prediction of periodic diameter growth for young growth Douglas-fir. These independent variables provided a quantitative measure of relative tree density and the degree of release from competition after treatment. Although initial size (Dbh) alone account for the largest single proportion of the variation in diameter growth, adding a function of CSI variables significantly reduces the error mean square term for the model and increases the predictive power of the model over a function of Dbh alone.

One major limitation of competition models involving an influence-zone overlap index is that they assume that for competition between trees to occur, there should be crown overlap. In fact trees may experience root competition even though there is no crown overlap.

A Competition Index Based on Rooting Zone Overlap

Most of the competition studies reviewed in this thesis assume that competition is confined within the area directly under the subject tree crown. As already noted, this assumption may not be true in areas where moisture availability is a problem. Thus, a competition indeces that takes into account root overlap might be of interest.

Smith and Scott (1983) derived a competition index for lodgepole pine trees from seasonal growth patterns in central Oregon. The level of competitive interaction was examined on "open grown", paired, and grouped trees (i.e. subject tree centred between four competitors). Competition was hypothesized to occur when the rooting zones of two trees overlapped, and a grouped tree's rooting zone overlapped that of four other trees. A number of root systems of "open grown" trees were excavated to establish the linear relationship between Dbh and the lateral extent of the root system. A regression between basal area growth and sapwood basal area (an estimator of leaf area) was used as a predictor of maximum potential basal area growth for trees growing free of competition. The competition index was determined as the ratio of actual to potential basal area growth for individual trees. Smith and Scott (1983) observed that this index standardizes growth against differences in tree size and site conditions. Their competition index indicated a correspondence between the index and relative density of grouped trees. However, the weekly diameter growth rates appeared related to changing climatic conditions during the growing season, but were not strongly related to measured plant and soil status.

Single Tree Density in Terms of Basal Area Around the Subject Tree

Lemmon and Schumacher (1962) studied volume and diameter growth of ponderosa pine (*Pinus ponderosa* Laws.) trees as influenced by site index, density, age and size. The basal area as an expression of density surrounding the subject tree was measured by the angle gauge. They observed that basal area contributed strongly to the prediction of the model. They also observed that only the basal area of the dominant portion of the stand surrounding competitors contributed significantly to the periodic growth of subject trees. This is because dominant trees contributed about 71 per cent of the surrounding basal area irrespective of the site or age.

Spurr (1962) proposed the angle summation technique where the size and relative position of each tree within the sample contributes to the basal area estimate. The method takes into account the angle subtended from the point by each selected tree. It is useful in evaluating stand density at a given point rather than over a given area. Spurr studied the relationship between point density and a three year periodic annual increment in basal area of Douglas-fir plantations. He found that the correlation coefficient (r) was 0.68 - highly significant.

Opie (1968) critisized Spurr's (1962) angle summation technique. He pointed out that it is an arduous method, and the procedure of weighting the various competitors is arbitrary. Gerrard (1969) observed that an unsatisfactory feature of Spurr's method is its failure to specify precisely which of the neighbouring trees qualify as competitors. He observed that in each new situation a decision is necessary as to the size of the angle a tree must subtend to be included.

Steneker and Jarvis (1963) made a preliminary study to assess competition in a white spruce and aspen stand. They determined Dbh, a 10-year diameter increment of subject trees, the Dbh of competitors, and the distance between the subject tree and competitors within a 7.6 m radius. They observed that the index based on basal area summation gave the best correlation. They also observed that the increase in distance from a point centre to 4.57 m was accompanied by an increase in accountability in diameter increment by the surrounding basal area. Steneker and Jarvis' method has limitations because more information is needed on the size and shape of the plot. The spatial distribution of the trees was not considered.

Opie (1968) studied competition in red river gum (*Eucalyptus camaldulensis* Dehnh). He expressed the relative area of overlapping circles in terms of basal area per unit area. He noted that a circle zone of influence existed around each tree. The radius of the circle varied both with site and tree size. Opie developed a method for measuring the basal area density of a given tree by determining the area of overlap of a given subject tree's zone of influence by adjacent trees, combined with the number of trees involved in the overlap. An angle gauge was used to sample for overlap throughout the zone of influence of the subject trees.

Opie's results should be treated with caution, since he only used one basal area factor (i.e. 21.04, 16.60 and 14.57 $m^2.ha^{-1}$) on best, medium and poor site classes respectively to identify competitors. Moreover, the choice of the basal area factor was subjective. The use of various basal area factors on each study site would have helped in identifying the best basal area factor in order to obtain the highest correlation coefficient for each site class.

Adlard (1974) developed a competition model for individual trees within a stand. He developed a computer program for the calculation of three competition indices i.e. an influence zone overlap index , an index based on the angle count method, and growing space calculated on different assumptions of overlap of individual tree growth zones.

Adlard used a basal area factor that resulted in a count corresponding to the number of competing neighbours defined by the geometric growing space model. The model assumes that growth of the subject tree is not influenced by trees beyond those whose crowns contact it. He observed that using the angle count index, the coefficient of determination varied between 17 and 99 per cent for Mexican weeping pine (*Pinus patula* Schiede & Deppe) and 83 and 98 per cent for cypress (*Cupressus lusitanica* Mill.). On the other hand, the growing space resulted in a coefficient of determination of 43 to 100 per cent for the pine and 78 to 98 per cent for the cypress.

Available Growing-space Area Around the Subject Tree

Brown (1965) introduced the concept of "Area Potentially Available"(APA). He defined APA as the growing space area in a polygonal shape around a subject tree defined by the bisectors of the lines connecting the subject tree and its immediate neighbours. Assuming that competition is inversely related to growing space, the reciprocal of APA is in some sense a measure of the level of competition experienced by the subject tree. However, the concept has not been used as a measure of intertree competition.

Brown's technique of finding the APA to a given subject tree fails to account for variation in the competitive ability of different trees. Subsequently, Gerrard (1969) proposed that Brown's model could be remedied by dividing the distance between neighbouring trees in relation to their relative sizes or their characteristics believed to reflect their ability to compete. Gerrard noted that Brown's method automatically determines which trees qualify as neighbours, thereby eliminating the necessity of guess work.

Moore *et al.* (1973) proposed another modification of Brown's method for use as a competition index. Their index was intended to express aerial and root competition by describing the following: i) a zone of primary influence, and ii) growing space of an individual tree as limited by the competition exerted by the surrounding trees. They observed that APA may be regarded as a growing space or competitive status index while competition circle methods are indices of crowding. The method was tested in a complex, uneven-aged stand composed of 19 different hardwood species. It was found that a modified APA exhibited a strong correlation with individual tree basal area growth.

The APA and the other competition indices already reviewed do not directly use number of competitors in the expression of competition indices. Subsequently, Alemdag (1978) suggested a new concept based on the following assumption: for a given growing space of a subject tree, the intensity of the competition received by this tree varies with the number of competitors. The larger the number of competitors around a given space, the greater is the competition and vice versa. Alemdag's first approach is as described by Brown (1965). The second approach assumes that a large tree distant from the subject tree or a small tree close to the subject tree may be equally competitive with the subject tree irrespective of the size of the subject tree. Competitors were identified by the angle-count method. The two approaches were tested on white spruce (*Picea glauca* (Moench) Voss).

Alemdag (1978) observed that the prediction was weak if diameter increment was estimated by initial diameter alone. When the diameter increment was estimated by the competition index, the best correlation coefficient was produced by Bella's (1969) model followed by Hegyi's (1974) model. Alemdag also observed that, in most cases the correlation coefficient increased with increase in influence-zone areas or with more trees selected as competitors.

Crown-Surface Area and Height of the Subject Tree

Hatch *et al.* (1975) studied indirectly the individual tree's relative growth potential represented by exposed crown surface area as a mathematical index. They proposed an index that takes into account the spatial arrangement, size and number of neighbours. This index was to resolve some of the limitations associated with some indices employed by Bella (1971), Gerrard (1969), Keister (1971), Moore *et al.* (1973) and Opie (1968). The two major limitations of their indices are:

- the spatial pattern of trees surrounding the subject tree was often not considered,
- the vertical development of the subject tree in relation to surrounding trees is only indirectly considered.

Hatch *et al.* (1975) proposed a new competition index that was a function of the following: (i) directly exposed surface area of the crowns of the subject tree when light is restricted by neighbouring trees, ii) basal area of the subject tree, iii) the inverse of subject tree height, and iv) competitive effect of the subject tree in relation to competitor trees.

Diameters and/or Distances of the Neighbouring Trees

Hamilton (1969) studied the dependence of the volume increment of individual trees on dominance, crown dimensions and competition in a 23-year-old stand of Sitka spruce (*Picea sitchensis* (Bong.) Carr). Measurements of crown diameter, breast height diameter and distance from the selected tree were taken for all trees less than 3.1 m from the selected subject tree. He observed that the regression of volume increment on breast height diameter, crown volume, crown projection and crown surface area were all significant at the 1 per cent level. The coefficient of determination was 92.2 per cent.

Bella (1971) developed a model that expresses the competition between individual trees. This model consists of the following components: i) the distance between subject tree and competitors, ii) relative size of the subject tree and its competitors and iii) the influence zone of each tree as represented by a function of the tree's size.

Bella (1971) developed competition models for both jack pine and aspen. The data were collected from fully stocked, even-aged stands. Both models described the effect of competition and accounted for a greater proportion in variation in the tree growth than some of the earlier competition indices.

Hegyi (1974) proposed and tested a model for managing jack pine stands. He modified Arney's (1970) competition stress index and Bella's (1969) competitive influence-zone overlap index. Growth rates of 77 trees from 12 stands were obtained by stem analysis. He also measured width and length of crowns and distance between subject trees and their competitors. Although some of the correlations were found to be fairly good, a detailed investigation on an individual tree basis indicated that the general relationship between either Arney's CSI or Bella's CIO and growth rate was often affected by irregularities of jack pine crowns. As a result Hegyi proposed a new diameter-distance competition index (DCI) for jack pine.

$$DCI_i = \sum_{j=1}^{N} (D_j / D_i) / Dist_{ij} \qquad [2.2]$$

where:

DCI_i - competition index of the i subject tree

D_j, D_i - Dbh of the jth and the ith subject tree respectively

$Dist_{ij}$ - distance between subject tree i and competitor j

N - number of competitors within 3.1 m radius of the subject tree

The rational of the DCI lies in the assumption that a tree may be subjected to competition in the absence of crown overlap.

Daniels (1976) observed that Hegyi's DCI is unsatisfactory since it does not allow inclusion of new competitors as neighbours grow. He observed that Hegyi's index will, in general, decrease over time due to mortality of neighbours within the fixed circles. Daniels also observed that Hegyi's index will tend to underestimate competition of older stands.

Daniels (1976) modified Hegyi's index by defining N so that competitors are chosen based on their size and distance from the subject tree. Point sampling was used in the selection of competitors. A further modification is that Hegyi's index was calculated by expressing the competitive effect as a ratio of basal area (D^2_j/D^2_i) of competing trees. Correlations with growth were greater when competitors were chosen by angle gauge technique than by a fixed radius. Some of the tested indices were as highly correlated with tree growth as the area overlap and weighted area overlap competition indices.

Lorimer (1983) studied age-dependent competition indices for individual trees in natural hardwood stands. He concurred in Daniels' observation that a major limitation of diameter-distance indices is that their numerical values decrease in a given stand over time even when the stocking level remains constant. Lorimer observed that the highest correlations were obtained when competitors were defined to be only those trees of equal or higher crown class than the subject tree. He recommended therefore, the general use of the index (D_j/D_i), where D_j is the diameter of competitor j and D_i is the diameter of subject tree i.

Lorimer's method of including only those competitors whose crown class is equal or higher than that of the subject tree can only be used in some stands. The method might not be appropriate for assessing competition subjected to aspen trees in jack pine aspen mixed stands. This is because aspen subject trees will be high above jack pine competitors. Under such circumstances it might appear as if there is no competition for aspen although the competition below ground might be severe.

Conclusions

Most of the work done in this field, for the past three decades, has focused on the competition between trees of the same species in even-aged stands. Even where stands of mixed species were evaluated, no effort was made to evaluate the competitive effects of individual species components of the competitor population on the growth of subject trees.

As oberved by Smith and Bell (1983) the growth models can be placed into two groups:

i) the group of whole stand models and other aggregate measures of stand density such as basal area per hectare tend to conceal the causal relationships between stand density and tree groups by averaging the competitive effect on individual trees (Bella 1971, Bickford *et al.* 1957, Curtis 1970, Husch *et al.* 1972, Krajicek *et al.* 1961, Vezina 1963).

(ii) models that directly measure competition by quantifying the relative stand density as a function of size, proximity, number and spatial arrangement of the trees in the stand around a specific point (Adlard 1974, Arney 1974, Daniels 1976, Ek and Monserud 1974, Keister 1971, Lorimer 1983, Spurr 1962).

Lorimer (1983) observed that the coefficients of determination between growth rate and competition indices are often fair to good (r^2 0.40 to 0.80). Ganzlin and Lorimer (1983) observed that competition indices generally show a reasonable relationship with observed growth in midtolerant and intolerant species (r^2 0.8 to 0.9), but growth-competition index relationship in tolerant species are typically not as strong (r^2 0.3 to 0.5). Most investigators have found little difference in predictive ability of various indices despite the substantial differences in index design. It has also been found in row plantations that the use of a distance-dependent competition index may be inferior to a simple non-spatial variable such as plot basal area (Meldahl 1979).

Lorimer (1983) observed that the essentially equal predictive ability of the different indices suggests that it may be desirable to focus more attention on the simpler diameter distance indices. Lower computational cost was the major reason that Hegyi (1974) developed his diameter-distance index in preference to the influence-zone overlap models available at that time. Lorimer (1983) pointed out that a further advantage of the diameter-distance index is that it is the only one of the competition models reviewed above that can be measured easily in the field. Furthermore, use of a computer, while advantageous, is not essential for this index. Like growing space polygons, diameter-distance indices allow for asymmetrical development of crowns and root systems. In addition to their use in forest growth projection and simulation, diameter-distance indices are potentially useful for experimental purposes in biological field studies.

Some studies have indicated that distance independent competition indices were superior to distance-dependent competition indices (Opie 1968, Alemdag 1978, Moore *et al.* 1973, Martin and Ek 1984). This perceived superiority of distance independent competition indices may be due to the fact that these researchers were working with row plantations with little variation in spatial arrangement of the trees.

The models reviewed above do not take into account the growth vigour and size of the crown that is responsible for the tree growth. This could be an area of interest in future research.

LIVE-CROWN RATIO: ITS INFLUENCE ON GROWTH AND STEM FORM

The live crown ratio varies with species and stand density. For young open-grown trees, it may approach one. However, in stand grown trees, as competition increases live crown ratio decreases.

Stem taper and radial growth are governed by the size and vertical distribution of the live crown. The development of stem taper and radial growth in relation to live crown is discussed by Duff and Nolan (1953, 1957), Farrar (1961), and Larson (1963a,b, 1966).

Stem radial growth is due to cambial activity, and cambial growth is largely regulated by crown (Kozlowski 1971, Larson 1963b). Larson (1963a) observed that the stem within the crown is strongly tapered because of the progressive increase in branch numbers downward from the apex and the cumulative contribution of these branches to stem growth. In open-grown trees with long, vigorous crowns, the high stem taper either continues or diminishes slowly down the branch-free bole. As the crown base recedes and the clear bole elongates with increasing tree age or stand closure, the stem becomes cylindrical. Larson observed that this tendency towards cylindrical stems results from a concentration of stemwood growth in the general vicinity of the live crown base.

The review above shows that stem form is governed by the same conditions of growth that dictate the size of the crown and its distribution on the stem. Thus, in young stands, it might be appropriate to evaluate the live crown ratio instead of stem form.

INTERACTION BETWEEN DIFFERENT TREE SPECIES

Little information is available on the effects of the competitive interaction of different tree species on mixed stand growth. On the other hand, a lot of information is available on such interactions among agricultural and range crops.

Harper (1977) observed that in nature, the distance between individuals and the times at which they become established produce growth effects that are confounded. As a result, the analysis of the growth of such plants communities is difficult or impossible. He observed that in forestry, it is possible to determine spatial relationships between individuals, but it is only when trees are of the same age that the effect of distance from neighbours will account for much of the variation in the size of individuals.

Harper observed that in a competitive struggle for limited resources there is a great premium on early germination and growth. Success depends on the capture and use of resources that are then denied to a competitor. Capture of resources deprives neighbours and brings competitive advantages. Successful capture depends on i) distance from neighbours and ii) relative size. Size advantage can result from earlier establishment, a faster growth rate, a large starting capital (large food reserve), or a longer period of growth.

As already noted, most of the research on the growth of mixed plant populations has been on annual or short lived plants. The general conclusion made from most of the species mixture experiments (van de Bergh 1968, Donald 1963, England 1968) is that the yield of mixtures usually slightly exceeds the mean yield of pure stands.

Several researchers have investigated the effects of aspen on the growth of white spruce. They observed that white spruce growth was improved by its release from aspen competitors (Cayford 1957b, Lees 1966, Steneker 1963, 1974, Steneker and Jarvis 1963).

Recently, Harvey (1982) investigated the effects of white spruce-aspen interaction on 5 and 13 year old stands. She observed that, in a 13-year-old stand, fast growing white spruce are usually found with slow growing aspen trees; slow growing white spruce are usually found with fast growing aspen trees; and intermediate growing white spruce trees are usually found with intermediate growing aspen trees. She also observed that in a 5-year-old stand there were no problems of competition.

Shirley (1944) investigated the reproduction of upland conifers in the Lake States as affected by root competition and light. He observed that forest competition of the under-vegetation was far more important in determining the success of coniferous seedlings, including jack pine, than the shade or root competition of the aspen in the overstory. He also observed that root competition tends to reduce growth irrespective of light intensity. Seedling weight was more sensitive to treatments than height.

Species mixtures also have beneficial effects on the growth of trees. Such benefits of species mixtures might include shading effects for shade tolerant species in the process of succession. Increased species diversity might reduce the spread of disease or insect outbreaks. An indirect beneficial effect of species mixtures is that of growing desirable species with nitrogen fixing legumes.

Tarrant (1961) investigated stand development and soil fertility in a Douglas-fir plantation that had been invaded by red alder (*Alnus rubra* Bong.). He observed that 20 to 27 year old dominant Douglas-fir in the mixed stand showed significantly greater average diameter than those growing free of alder competition. The form class of Douglas-fir grown with alder was higher than that of Douglas-fir grown alone. Also, limb measurements indicated a generally broader, more vigorous upper crown in the Douglas-fir grown with alder. The nitrogen content, both of the soil and of Douglas-fir foliage, was significantly greater in the plantation that contained alder. This attests to the reputed soil improving quality of alder through symbiotic fixation of nitrogen by actinomycetes infected root nodules.

Haines *et. al.* (1978) investigated the effect of underplanting crimson clover (*Trifolium incarnatum* L.), Mississippi subterranean clover (*T. subterraneum* L.), Yuchi clover (*T. vesiculosum* L.), hairy vetch (*Vicia villosa* L.), and Nova vetch (*Vicia* spp) on the growth of 2-year-old sycamore (*Platanus occidentalis* L.). They observed that after 4 years of growth Mississippi subterranean and crimson clover both gave good ground coverage, maintained a low profile, reseeded themselves well. Sycamore grown in association with these species had increased nitrogen content of foliage, and improved height and volume growth.

Funk *et. al.* (1979) studied the effect of autumn-olive (*Elaeagnus umbellata* Thumb) as a nurse plant for black walnut (*Juglans nigra* L.). They observed that interplanting with autumn-olive stimulated a 34 per cent increase in walnut height compared with walnut grown alone. They also observed that increased height of the walnut in mixed plantations was first apparent about 4 years after planting, and the best group of four plots averaged more than 6.8 m tall at age 9.

Schabas (1983) observed that growing alternate rows of alder with commercially more interesting species is beneficial. He noted that the alder will eventually die, leaving nitrogen for the crop species. He also observed that pines growing near alder under a harsh environment do better, probably because they take advantage of the alder's nitrogen fixing capabilities.

Binkley (1983) studied the interaction of alder with Douglas-fir and site fertility. He observed that the presence of alder on an infertile site increased the diameter and basal area growth rate of Douglas-fir. He concluded that alder seems to have great potential for increasing Douglas-fir growth and ecosystem production on infertile, N-deficient sites, but probably has limited value on fertile, N-rich sites.

Binkley (1984) studied the importance of size-density relationship in mixed stands of Douglas-fir and alder. He observed that on fertile sites, the mixed stands experienced higher mortality than the pure conifer stands. On infertile sites, the pure conifer stands were well below the maximum tree size and density relationship compared to fertile sites or mixed stands, suggesting under-utilized site resources were available for nitrogen-fixing alder.

STAND DENSITY AND TREE GROWTH

Jack pine

Research into the effects of density on the growth of jack pine began early in the 1900's. The first study was reported by Hansen and Brown (1929). They observed that 37-year-old jack pine did not respond to thinning because the thinning was carried out too late in the life of the stand. Since then several spacing and thinning studies have investigated effects of stand density on the growth of jack pine in both natural forests and plantations (Schantz-Hansen 1931, Rudolf 1951, Buckman, 1964, Bella 1974, Bella and De Franceschi 1974a,b, 1980, Wilson 1952, Cayford 1961,1964, Roe and Stoeckeler 1950, Ralston 1953, Chrosciewicz 1971).

The major observations from some of these studies can be summarized as follows: planting jack pine at wide spacing reduces height growth and encourages the development of heavy branches with a consequent deterioration in tree form. At the widest spacings, there is a considerable loss in stem wood production, but the reduction is expected to be reduced or even eliminated with continued rapid growth over time. It has also been observed that jack pine stand productivity whether in basal area, volume or biomass is highest at the closest spacing. However, the rate of mortality is also highest at close spacings. Finally, the live crown ratio is reduced at close spacing.

It has been observed that the current annual increment per tree in diameter and volume of jack pine increases with intensity of thinning. However, there might be loss in volume production as a result of heavy thinning. Most studies show that thinning has no significant influence on the height growth of dominants and codominants. Also thinning has been shown to have no significant effect on the growth of jack pine on poor sites.

Aspen

Studies to control aspen stand densities by intermediate cutting operations began in the early 1930's (Bickerstaff 1946). Since then, many studies have been made on the control of density in aspen stands (Day 1958, Pike 1953, Steneker 1964, Steneker and Jarvis 1966, Zehngraff 1947, Zasada 1952).

The following conclusions can be drawn from some of these studies: for the thinning treatment to be effective, it should be done when aspen stands are young, 10 to 20 years old, because young trees respond faster than old trees. It has been observed that diameter increment of individual trees increases as competition is reduced. Larger trees maintain a higher increment than smaller ones, although the latter show a greater percentage response. Crowding may reduce by half the diameter increment of dominant and codominant trees at an age as early as 5 years. Thinning studies also show the following: i) the gross total volume increment per hectare drops markedly at very wide spacings, ii) height increment of the dominants is not affected by thinning, and iii) mortality rates are higher on unthinned plots than on thinned plots.

MATERIALS AND METHODS

STUDY AREA

The present study was conducted during the summer of 1984 in an 8-year-old jack pine plantation of approximately 300 ha. The plantation is located 275 km northeast of Thunder Bay on Trans-Canada Highway 11-17. It is in the Domtar Management Unit, Nipigon District of the Ministry of Natural Resources. Its coordinates are 49° 51' 30''N latitude and 87° 37' W longitude (Figure 3.1).

The topography of the study area varies from flat to gently rolling. The soil is a shallow to deep till over bedrock with pockets of deep sand. Ground vegetation includes *Vaccinium myrtilloides* L., *Cornus canadensis* L., *Epilobium anguistifolium* L., *Lonicera involucrata* (Richards.) Banks. *Ledum groenlandicum* Oeder, *Rosa acicularis* Lindl, *Rubus odoratus* L., *Amelanchier sangunea* (Purch) DC, *Dicranum* spp, and *Salix* spp. The working group species of the previous stand was jack pine of site class 2 (Plonski 1974).

The study area was harvested in 1973, scarified in June 1974, and direct seeded to jack pine in May 1975. It has been widely invaded by aspen and a scattering of other species including alder, white birch (*Betula papyrifera* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), balsam fir and black spruce (*Picea mariana* (Mill.) B.S.P.)

The plantation had not been tended prior to my work in it. A stocking assessment carried out in November 1982 revealed that the average stocking of jack pine was between 40 and 50 per cent. However, small areas were found where the stocking of jack pine was as high as 70 to 80 per cent. These better stocked spots were located in areas having few aspen or balsam fir residuals and/or regeneration.

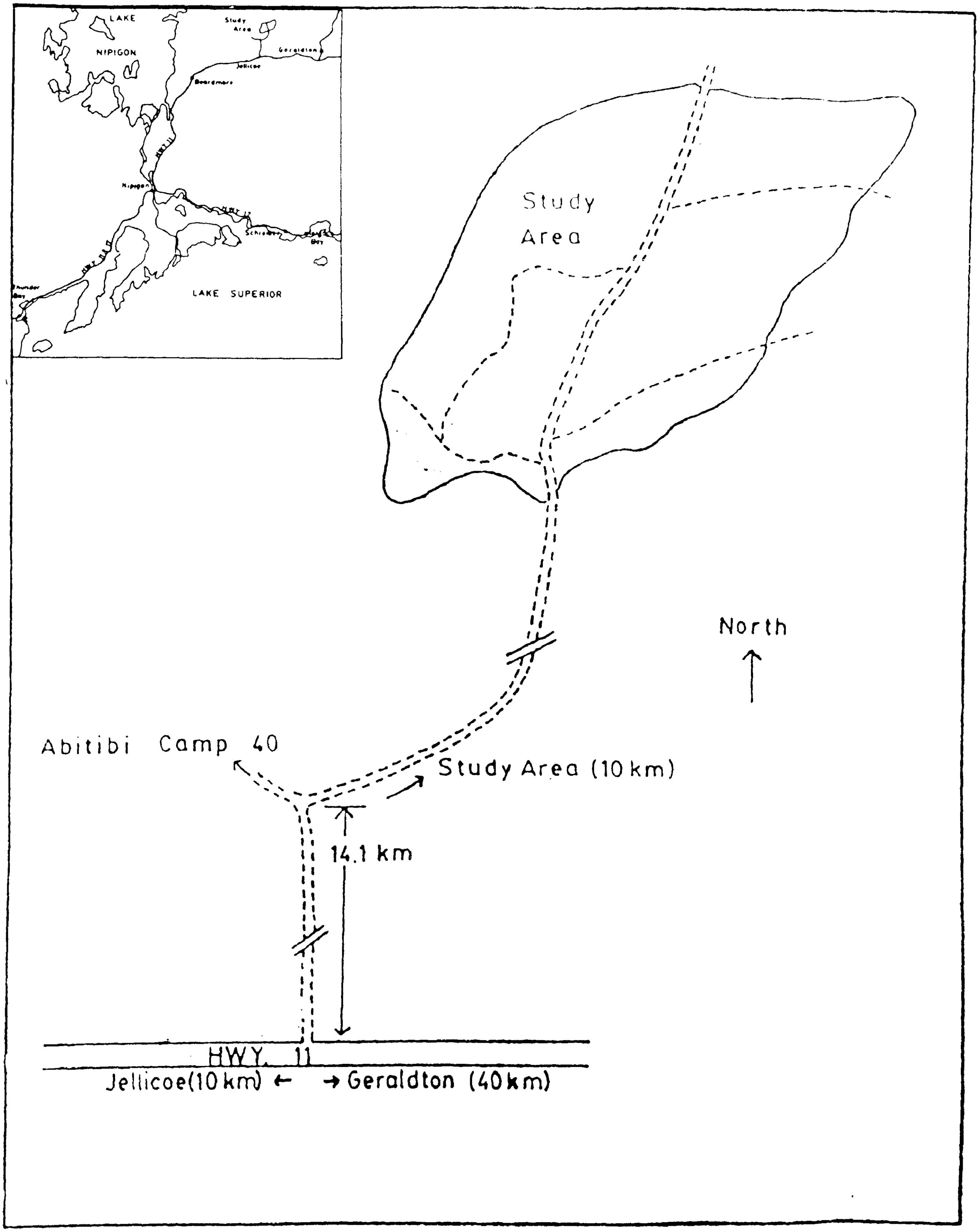

Figure 3.1: Location of the study area

SAMPLE TREE SELECTION AND MEASUREMENT

Subject Tree Selection

A random sample of 298 subject trees was drawn from the study area under the following restrictions: (1) half of the subject trees were jack pine and half were aspen; (2) the surrounding stand had to be either pure jack pine or pure aspen or a mixture of these two species; (3) the subject tree was free of damage, disease, and, except as noted below, either dominant or codominant. In the case of jack pine growing under dense aspen, jack pine subject trees overtopped by aspen competitors were allowed in the sample. This exception was necessary because it was difficult to find jack pine trees in the dominant or codominant crown classes when dense aspen competition was present. In spite of these sampling restrictions, stand conditions around the subject trees spanned a wide range of both density levels and species composition.

Preliminary Selection of Competitors

The trees neighbouring each subject tree were screened to identify potential competitors. Vertical point sampling was used as the selection criterion (Husch *et al.* 1982). In order to qualify as a potential competitor a neighbouring tree had to be located not more than 1/2 its total height from the subject tree (the vertical gauge angle was 63.4°). The choice of this criterion, and the conversion to a horizontal point sampling criterion, are explained below under selection of competitors.

Field Measurement

The following measurements were taken on all potential competitors and subject trees: (a) species, (b) total height, and (c) stump diameter. Total height was measured to the nearest 10 cm with a height measuring rod. Because the stand was only 8 years old, I decided to measure stem diameter at 10 cm above the root collar (stump diameter) instead of at breast height. This procedure ensured that all competitors, even those less than 1.3 m tall were measured. Stump diameter was measured in both the shortest and longest dimension to the nearest millimetre using a small calliper. The arithmetic mean diameter was then calculated from these two extremes.

The distance of each competitor from its subject tree was measured to the nearest centimetre. Live crown length and the most recent (1983) height increment were measured on all subject trees. In order to measure crown length, the first step was to identify the base of the live crown. The base of the live crown was defined as the point where more than 50 per cent of the foliage was alive. Then the height to the base of the live crown was measured to the nearest 10 cm using the height measuring rod. Live crown length was obtained by subtraction.

The 1983 height increment was measured to the nearest centimetre on all subject trees. The limits of the 1983 height increment were determined for aspen trees by means of the 1983 and 1984 terminal bud scale scars. In the case of jack pine trees, these limits were determined by means of the primary 1983 and 1984 false whorls of branches.

STEM ANALYSIS

Stem analysis sections from subject trees were taken at stump height (10 cm) and, thereafter, at 50 cm intervals up the stem. Thus, sections were taken at 10 cm, 60 cm, 110 cm, ... The length of the stem tip section was also recorded. Stem analysis sections were transported to Lakehead University, and held in cold storage for measurement.

A Holman Digimicrometer was used to measure the length along a geometric mean radius from pith to the beginning of the 1983 growth ring. The width of the 1983 growth ring was measured along the same radius. From these data, stemwood core volume and the 1983 sheath volume were computed for each subject tree using Smalian's summation formula (Husch *et al.* 1982).

FINAL SELECTION OF COMPETITORS

As explained above, potential competitors were identified in the field by means of a vertical point sampling criterion even though some of the conventional measures of intertree competition are based on a horizontal point sampling selection criterion.

I chose to use vertical point sampling in the field as a matter of convenience. Trees neighbouring the subject trees were small and, in some instances, large numbers were present. The use of a limiting horizontal angle to identify competitors directly in the field would have been difficult. The criterion would be further complicated by the use of stump height rather than breast height as the point of reference. A vertical limiting angle, on the other hand, was easy to apply in the field. I chose a height to limiting distance ratio of 2. This choice was based on my impression that competitors whose height to limiting distance ratio was less than 2 were not significantly interfering with the growth of the subject trees.

In the office, the potential competitors of each subject tree were further screened by means of a limiting horizontal angle criterion to make the final selection of competitor trees. In selecting a limiting horizontal angle, my goal was to select an angle that was at least as restrictive as the vertical angle used in the field to minimize the possibility that qualifying trees in the field would go undetected. This was accomplished in the following manner. A scatter diagram was produced of the stump diameter (over bark) vs the total height of 5,971 competitors. These were randomly selected from a total of 6,658 competitors in the vertical point sample. The number 5,971 was chosen simply because this was a limit of the workspace on the SPSS subprogram used to produce the scatter plot. A line was drawn by hand through the origin of the scatter diagram such that most of the points were below the line (Figure 3.2). The line has a the following equation:

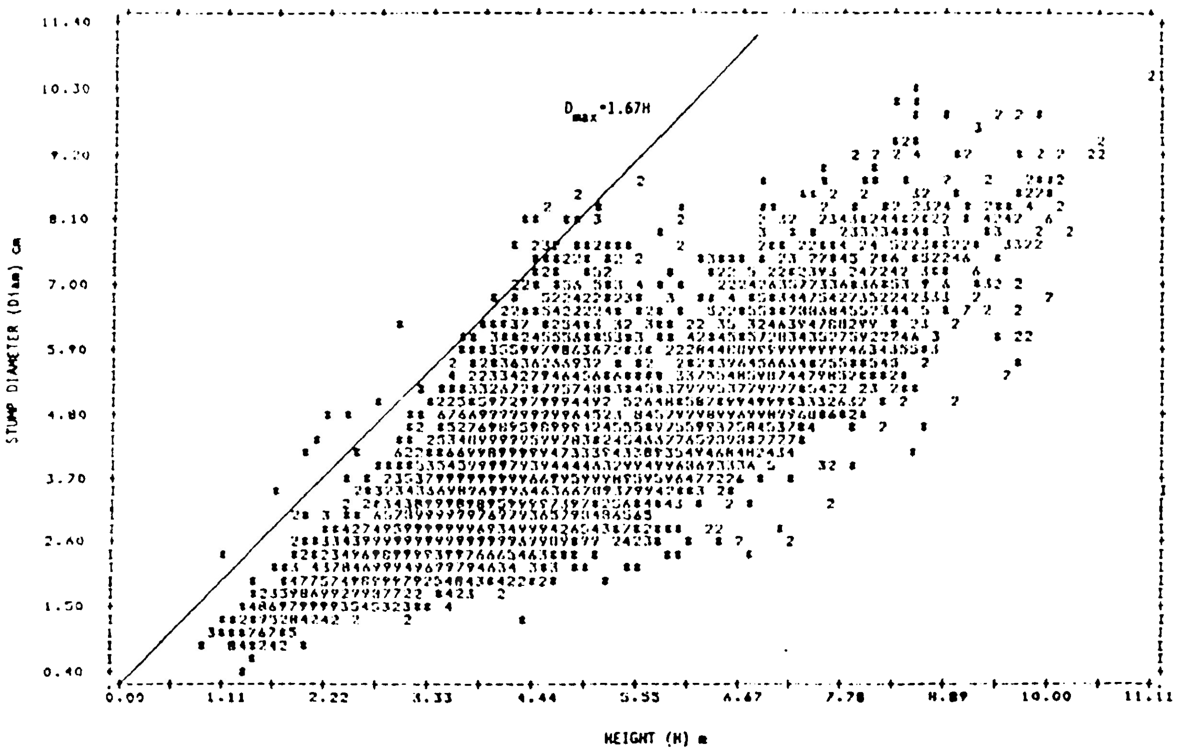

Figure 3.2. Scatter diagram of height and stump diameter of a randomly selected sample of 5,971 competitors.

$$D_{max} = 1.67\ H \qquad [3.1]$$

where:

D_{max} - "maximum" stump diameter in cm of a competitor of height (H) in metres. Here "maximum" is used in the practical rather than the literal sense.

As already pointed out, the vertical point sampling procedure used in the field assumed that potential competitors were located at a distance from the subject tree no more than half the height of the competitor. That is:

$$L_{max} = H/2 \qquad [3.2]$$

where:

L_{max} - maximum distance between subject tree and a competitor

H - height of the competitor

Figure 3.3 illustrates the relationship between D_{max}, H and L_{max}.

With these points in mind, the size of the required limiting horizontal point sampling angle can be derived as follows:

Let α_{min} denote the smallest angle that is at least as restrictive as the vertical point sampling angle of 63.4° used in the field sampling. Then from Figure 3.3 and horizontal point sampling theory (Husch *et al.* 1982) it can be seen that

$$\alpha_{min} = 2 \arcsin ((D_{max}/2)/(100\ L_{max})).$$

Since $D_{max} \cong 1.67\ H$ and $L_{max} = H/2$, it follows that:

$$\begin{aligned}\alpha_{min} &\cong 2 \arcsin ((1.67\ H/2)/(100H/2))\\ &\cong 2 \arcsin (0.0167)\\ &\cong 1.91^\circ.\end{aligned}$$

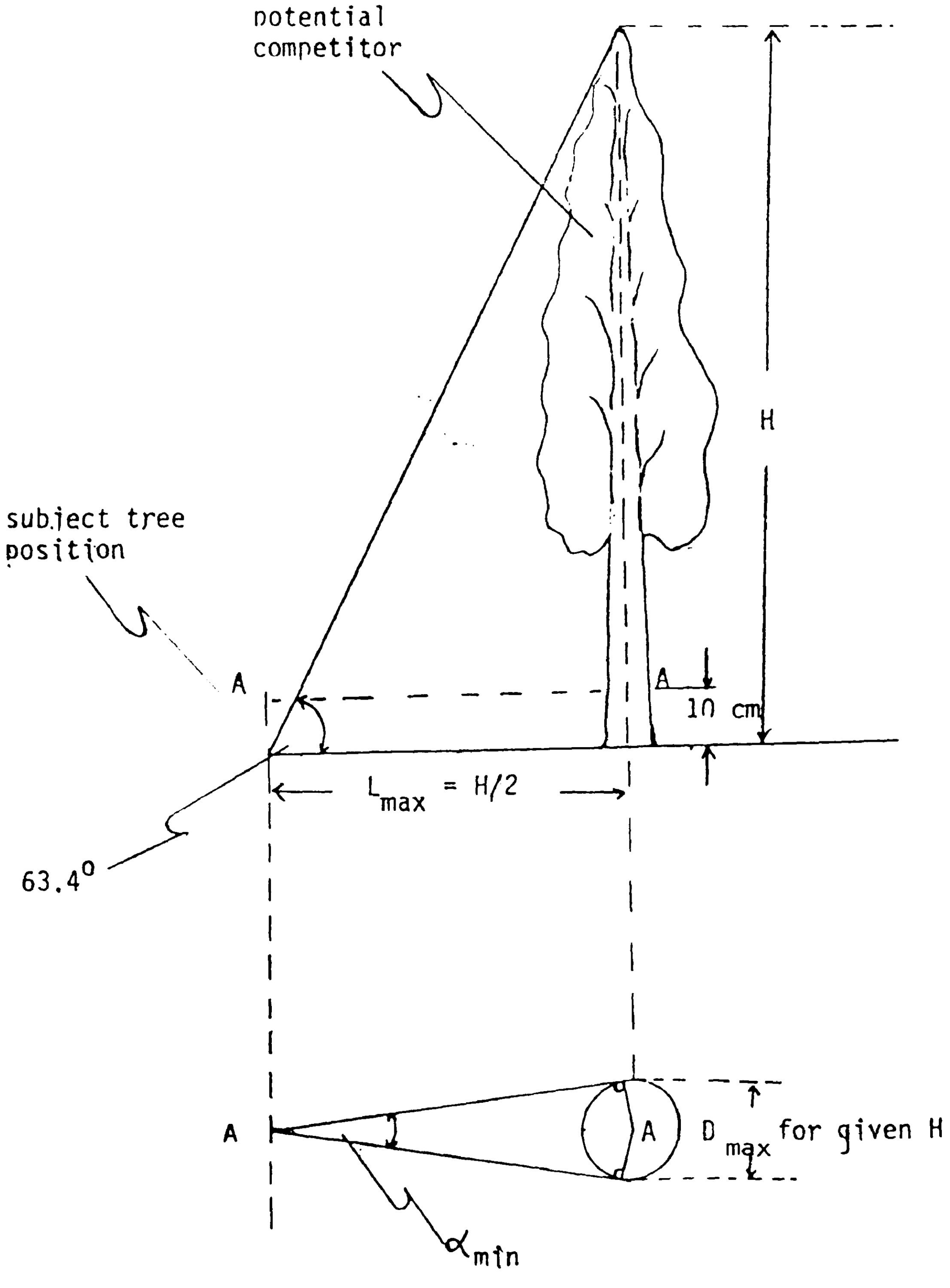

Figure 3.3. A borderline tree in a vertical sampling situation based on a height:limiting distance ratio of 2.

This result is approximate only in the sense that there were a few trees in the field sample that exceeded the assumed diameter to height ratio of 1.67 cm m^{-1} (Figure 3.2). Therefore, it is conceivable that a few trees exist in the field that would have been sampled had the field sample been based on a horizontal point sample of 1.91° that were not sampled in the vertical point sample. I believe, however, that the number of such cases is negligible.

The basal area factor associated with a limiting horizontal point sampling angle of 1.91° is 2.778 $m^2.ha^{-1}$.

MEASURES OF COMPETITION

The field measurements were used to compute several measures of competition. These were of two types: distance-dependent competition indices and distance-independent competition indices.

Distance Dependent Competition Indices

Spurr's point density

Spurr's point density (Spurr 1962) can be computed with or without the inclusion of the subject tree. I elected to exclude the subject tree since it is the competition of the surrounding stand that was of interest. Spurr's point density, excluding the subject tree, and modified to use stump diameter instead of breast height diameter, was computed using competitors selected by the limiting horizontal angle of 1.91°. The competitors were ranked in descending order and Spurr's point density was calculated as follows:

$$SC = \sum_{k=1}^{n}[0.25(k-0.5)(D_k/L_k)^2]/k \qquad [3.3]$$

where:

SC - Modified Spurr's point density ($m^2.ha^{-1}$)

k - the rank of the kth competitor

D_k - stump diameter (over bark) of the kth competitor in cm

L_k - distance from subject tree to the kth competitor in m

0.25 - the quotient of 10,000 the number of square metres of basal area ($m^2.ha^{-1}$) divided by 40,000, the product 10,000 necessary to convert square centimetres and the 4 representing the square of the 2 to convert radius to diameter.

Daniels' Competition Index

The second distance dependent competition index tested was Daniels' (1976) modification of Hegyi's (1974) diameter-distance competition index. Competitors were selected by the point sampling technique using a limiting horizontal angle of 1.91°. Daniels' competition index was computed according to equation [3.4]:

$$DC_i = \sum_{k=1}^{n}(D_k/D_i)/L_k \qquad [3.4]$$

where:

DC_i - Daniels' competition index for the ith subject tree

D_k - stump diameter over bark of the kth competitor

D_i - stump diameter over bark of the ith subject tree

L_k - distance between kth competitor and the subject tree.

Two variations of Daniels' competition index were computed. Under one variant all qualifying competitors were included. This variation of the index was denoted DC1. Under the other variant only competitors whose height was equal or greater than the height of the subject tree were included. This variation was denoted DC2. The competition due to competitors whose height was less than the height of the subject tree, denoted DC', was found by subtraction.

Distance-independent Competition Index

Lorimers' Competition Index

Lorimer's (1983) non-spatial competition index was also tested in this study. Competitors were selected by the horizontal limiting angle of 1.91°. Lorimer's competition index was then computed as follows:

$$LC_i = \sum_{k \neq i}^{n} (D_k / D_i) \qquad [3.5]$$

where:

LC_i - Lorimers' competition index for the ith subject tree

D_k - stump diameter over bark of the kth competitor associated with the subject tree

D_i - stump diameter over bark of the ith subject tree.

As in the previous section, two variants of Lorimer's competition index were computed. LCl is based on all selected competitors; LC2 is based on competitors whose height was equal or greater than the height of the subject tree. Lorimer's competition index for competitors whose crown class was less than the crown class of subject trees i.e: LC' was computed in the same way as DC'.

ANALYSIS

Descriptive Statistics, Frequency Distributions and Correlation Matrix

The response variables were: (a) the 1983 height increment; (b) the 1983 ring width at stump height, and (c) the 1983 volume increment. Descriptive statistics (mean, minimum, maximum, standard deviation and coefficient of skewness) were obtained for all three response variables, for other attributes of subject trees, and for the various measures of competition. The frequency distributions of stump diameter and the 1983 increments of height, ring width at stump height, and volume were also determined.

Simple correlation was used to determine the degree of linear relationship between subject tree attributes and the various indices of competition. Since some of the response variables were not normally distributed, Spearman rank correlation analysis was used.

Evaluation of Competition Indices

The objective of the analysis was to evaluate the usefulness of various competition indices (SC, DCl, DC2, DC', LCl, LC2 and LC') as measures of stand competition. The evaluation criterion used was the ability of the alternative competition indices to predict the 1983 volume increment of the subject tree. The 1983 volume increment of the subject tree was chosen for this analysis because it integrates the increments of both diameter and height.

Figure 3.4 outlines the evaluation strategy. The following is an outline of what was done. Since the above correlation analysis showed that jack pine and aspen subject trees respond differently to density and individual species components of the competitor population, the data were grouped into two subsets according to the species of the subject tree (each subset was made up of 149 subject trees).

Several workers have observed that there is no consistency in the performance of various competition indices in predicting the growth of subject trees (Chapter 2). In order to judge the ability of each competition index to predict the 1983 volume increment, it was

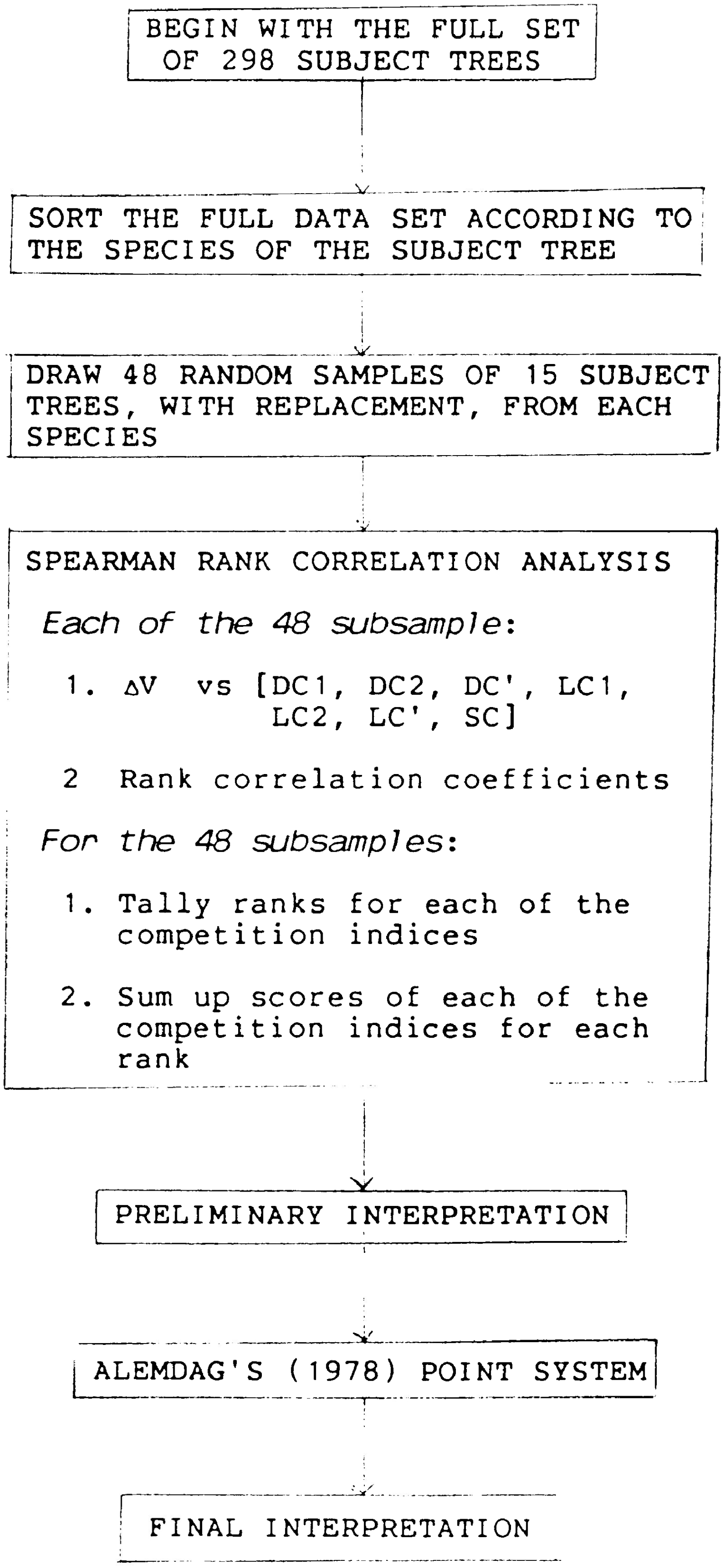

Figure 3.4. A flow chart showing the steps in the procedure used to evaluate the competition indices.

necessary to repeat the test as many times as possible. Since the data set was limited, such tests were done with the help of random subsampling many times. Thus, each subset was randomly sampled 48 times with replacement. The size of each sample was 15, about 10 percent.

Each of the 48 random sub-samples was subjected to a separate analysis of the Spearman rank correlation between the 1983 volume increment of the subject tree and each of the seven competition indices. For each analysis, the correlation coefficients associated with each competition index were ranked, and on completion of 48 analyses the score per rank were totalled. Since there was no obvious consistency in the performance of any of the competition indices, Alemdag's (1978) point system was used to identify the best overall competition index.

Subject Tree Growth Analysis

Multiple regression analyses were employed to test two null hypotheses: Hypothesis 1: Jack pine and aspen subject trees respond in the same way to competition. Hypothesis 2: Aspen and jack pine competitors have the same effect on subject trees of both species.

These hypotheses were tested with respect to each of three response variables: the 1983 increments of height, stemwood volume and stem radius. The predictor variables investigated were as follows:

a) species of the subject tree - a dummy variable equal to 0 whenever the subject tree was aspen and 1 whenever the subject tree was jack pine;
b) initial stump radius - the radius (inside bark) at stump height prior to the formation of the 1983 growth ring;
c) initial volume - the stemwood volume (inside bark) prior to the formation of of the 1983 stemwood volume increment;
d) individual species components of the competitor population as explained below;
e) cross products of the predictor variables.

According to Alemdag's (1978) point system criterion, Daniels' total competition index, DCl, was more often correlated with the 1983 volume increment than other competition indices tested. Therefore, DCl was used in the subsequent analysis of the effects of the total density and species composition of the competitor population on the growth of subject trees. DCl was partitioned into components due to each species as follows:

$$DCl = DClp + DCla + DClo \qquad [3.6]$$

where:

DCl - Daniels' total competition index

DClp - Daniels' competition index due to jack pine competitors

DCla - Daniels' competition index due to aspen competitors

DClo - Daniels' competition index due to competitors other than jack pine and aspen

The procedure for the hierarchy of hypothesis testing outlined by Chartterjee and Price (1977:pp 56-68, 85-94) was employed in testing hypotheses 1 and 2. Figure 3.5 outlines the test strategy.

All models were fitted by stepwise least-square regression. In each of the analyses the assumptions underlying linear regression analysis were tested. These assumptions are: a) dependent and independent observations are random variables, b) residuals are normally distributed, c) residuals are from a single, normally distributed, population with mean zero and common variance.

Sensitivity Analysis of Growth of Subject Tree

It is possible for the effects of a biological relationship to be statistically significant, and yet to be too weak to be of practical significance. For this study, I wondered whether the effect of various factors including competition on the 1983 volume increment of the subject trees was of sufficient magnitude to be of practical importance in the management of jack pine and aspen. The 1983 volume increment was evaluated because it integrates both

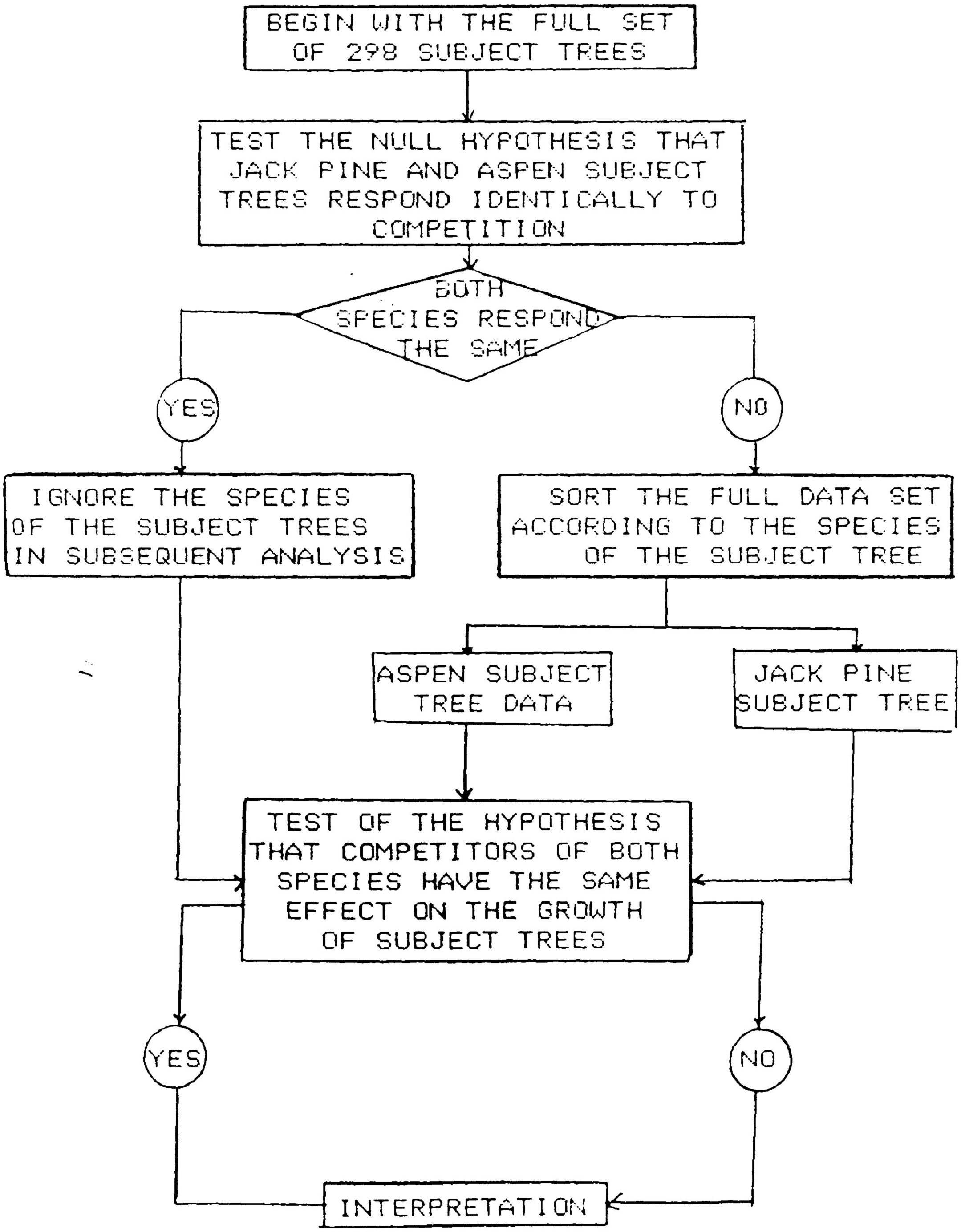

Figure 3.5. A flow chart showing the hierarchy of hypothesis testing.

diameter and height increments.

The 1983 volume increment depends to varying degrees on all factors that have influenced the growth of subject trees from the time of plantation establishment. The effects of these factors were indirectly assessed by evaluating the simultaneous effects of the present competition, initial volume of the subject tree and the live crown ratio of the subject tree. This is because the present tree attributes and stand conditions are consequent effects of the past tree attributes and stand conditions. Figure 3.6 outlines the analysis strategy followed. Details of the analysis strategy are given in Appendix III.

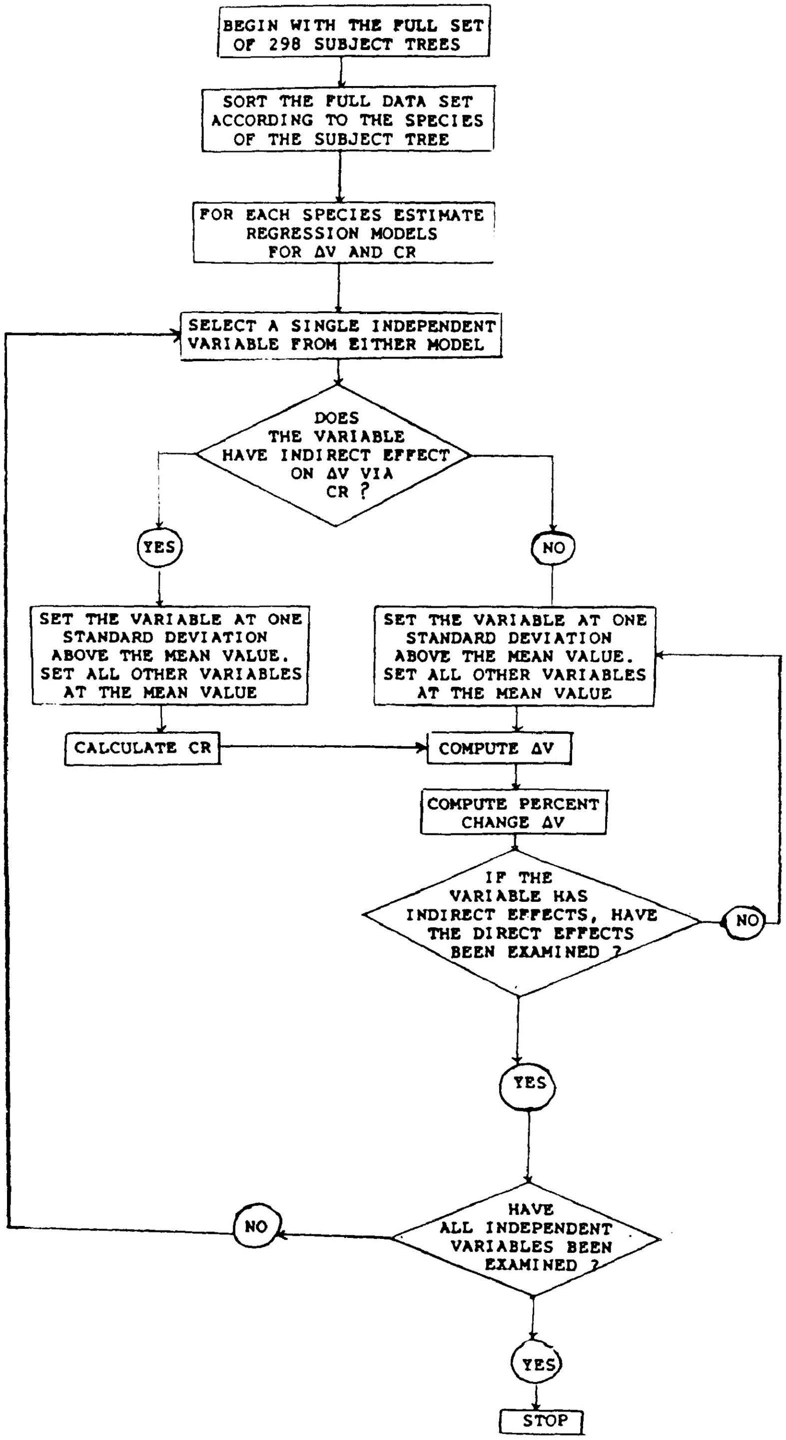

Figure 3.6. A flow chart showing the steps in the procedure used in sensitivity analysis of the 1983 volume increment of the subject tree

RESULTS

DESCRIPTIVE STATISTICS AND FREQUENCY DISTRIBUTIONS

Descriptive statistics for jack pine and aspen subject tree attributes and their associated competitors are summarized in Tables 4.1 and 4.2 respectively. Frequency distributions of diameter (over bark) at stump height, and the 1983 increments of ring width at stump height, hereafter referred to as radial increment, height and volume of subject trees are shown in Figures 4.1 and 4.2.

EVALUATION OF THE COMPETITION INDICES

Tables 4.3 and 4.4 summarize the rank scores of the competition indices for the aspen and jack pine subject tree data sets, respectively. Lorimer's total competition index (LCl) most often had the highest correlation with the 1983 volume increment of aspen subject trees (Table 4.3). On the other hand, Lorimer's competition index (LC2), most often had the highest correlation with the 1983 volume increment of jack pine subject trees (Table 4.4). Comparison of Tables 4.3 and 4.4 show that there is no regular pattern of the order of performance of the other competition indices.

One way to compare the overall superiority of competition indices is by means of a point system (Alemdag 1978). Therefore, the results in Tables 4.3 and 4.4 were considered together. This was done as follows: the competition index that ranked first was assigned seven points and the competition index that ranked seventh one point. The other competition indices were assigned points in an analogous manner. The points obtained by each competition index were then totalled (Table 4.5). Daniels' total competition index based on all potential competitors, DCl, had the highest total score.

This result agrees in general with the findings of Daniels (1976), Hamilton (1969), Ker (1980), Lorimer (1983) and Martin and Ek (1984). All of them observed that

TABLE 4.1: Summary of statistics for attributes of jack pine subject tree and their associated competitors.

Variable	Units	Mean	Min.	Max.	SD.	Coefficient of Skewness
ΔVp	dm^3	0.545	0.110	1.780	0.731	0.029
ΔRp	mm	2.371	0.730	4.530	0.772	0.444
ΔHp	m	0.257	0.150	0.370	0.043	0.148
Vp	dm^3	0.828	0.120	2.940	0.516	1.270
Rp	mm	14.464	7.450	26.320	3.878	0.708
Dp	cm	4.215	2.000	7.300	1.140	0.666
Hp	m	4.026	3.540	5.950	0.638	-0.940
CRp		0.867	0.650	0.990	0.072	-1.032
DC1		11.781	0.660	52.200	8.784	1.813
DC1p		7.650	0.000	52.200	9.042	2.124
DC1a		3.981	0.000	36.540	5.382	2.341
DC1o		0.143	0.000	3.750	0.585	4.657

Legend:
ΔVp - 1983 volume increment of jack pine subject tree
ΔRp - 1983 radial increment of jack pine subject tree
ΔHp - 1983 height increment of jack pine subject tree
Vp - initial volume of jack pine subject tree
Rp - initial radius at stump height of jack pine subject tree
Hp - total height of jack pine subject tree
Dp - stump diameter (over bark) of jack pine subject tree
CRp - live crown ratio of jack pine subject tree
DC1, DC1p, Dc1a, Dc1o - components of Daniels' competition index as defined on pages 38 and 43.

TABLE 4.2: Summary of statistics for attributes of aspen subject tree and their associated competitors.

Variable	Units	Mean	Min.	Max	SD.	Coefficient of skewness
ΔVa	dm^3	1.098	0.300	3.480	0.513	1.168
ΔRa	mm	1.910	0.470	3.920	0.667	0.451
ΔHa	m	0.802	0.400	1.120	0.135	-0.206
Va	dm^3	3.158	0.500	11.920	1.836	1.452
Ra	mm	21.367	11.060	43.410	5.398	0.535
Da	cm	5.774	2.900	9.100	1.248	0.186
Ha	m	6.768	5.260	9.510	1.104	-0.357
CRa		0.786	0.510	0.970	0.103	-0.554
DC1		8.961	0.640	42.810	7.131	1.837
DC1p		4.566	0.000	42.810	6.342	2.436
DC1a		4.323	0.000	32.030	5.521	2.593
DC1o		0.072	0.000	2.420	0.299	5.055

Legend:
ΔVa - 1983 volume increment of aspen subject tree
ΔRa - 1983 radial increment of aspen subject tree
ΔHa - 1983 height increment of aspen subject tree
Va - initial volume of aspen subject tree
Ra - initial radius at stump height of aspen subject tree
Ha - total height of aspen subject tree
Da - stump diameter (over bark) of aspen subject tree
CRa - live crown ratio of aspen subject tree
DC1p, DC1a, DC1o - Components of Daniels' competition index as defined on pages 38 and 43.

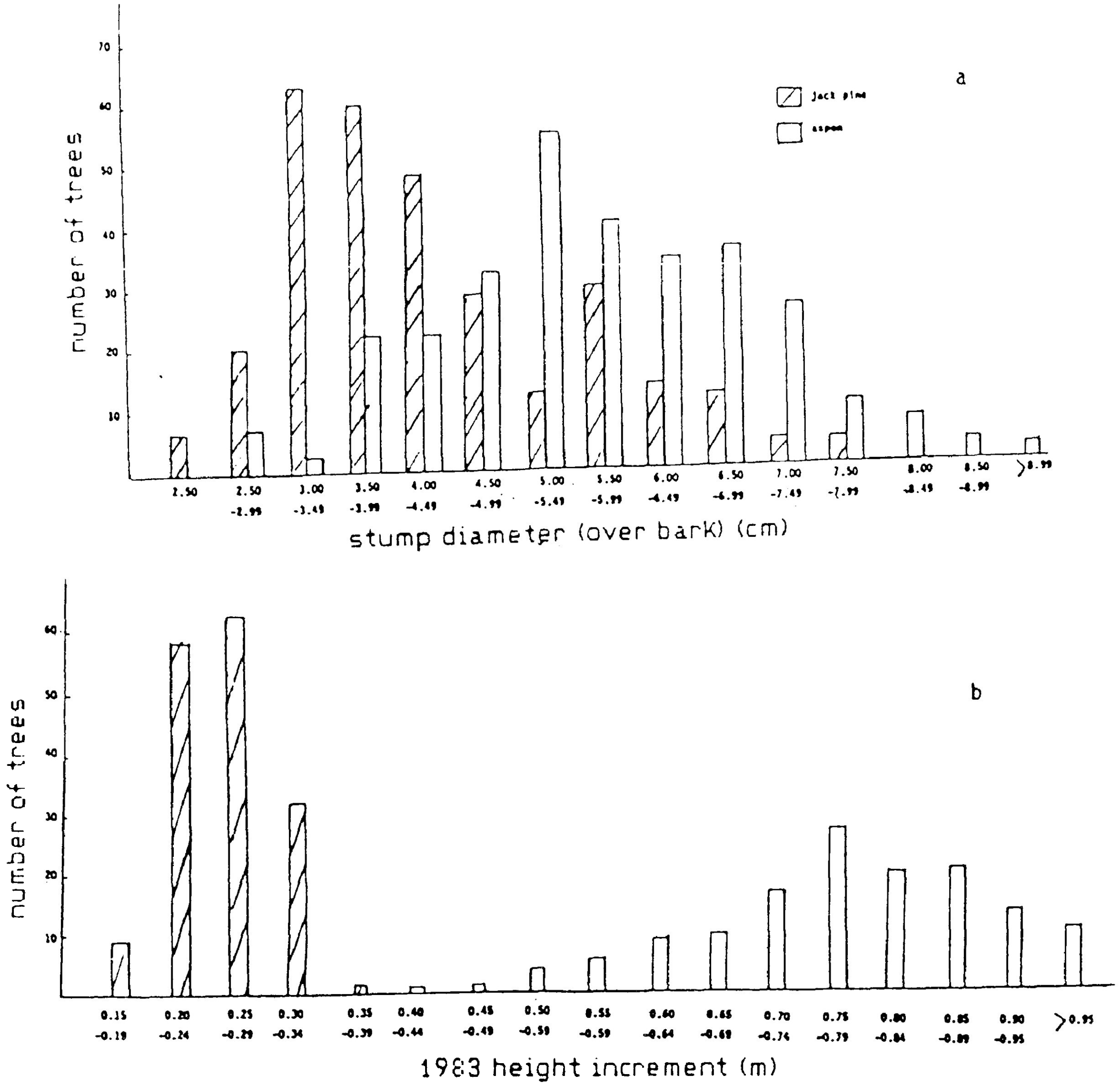

Figure 4.1. a) The distribution of the stump diameter (over bark) of jack pine and aspen subject trees.
b) The distribution of the 1983 height increment of jack pine and aspen subject trees.

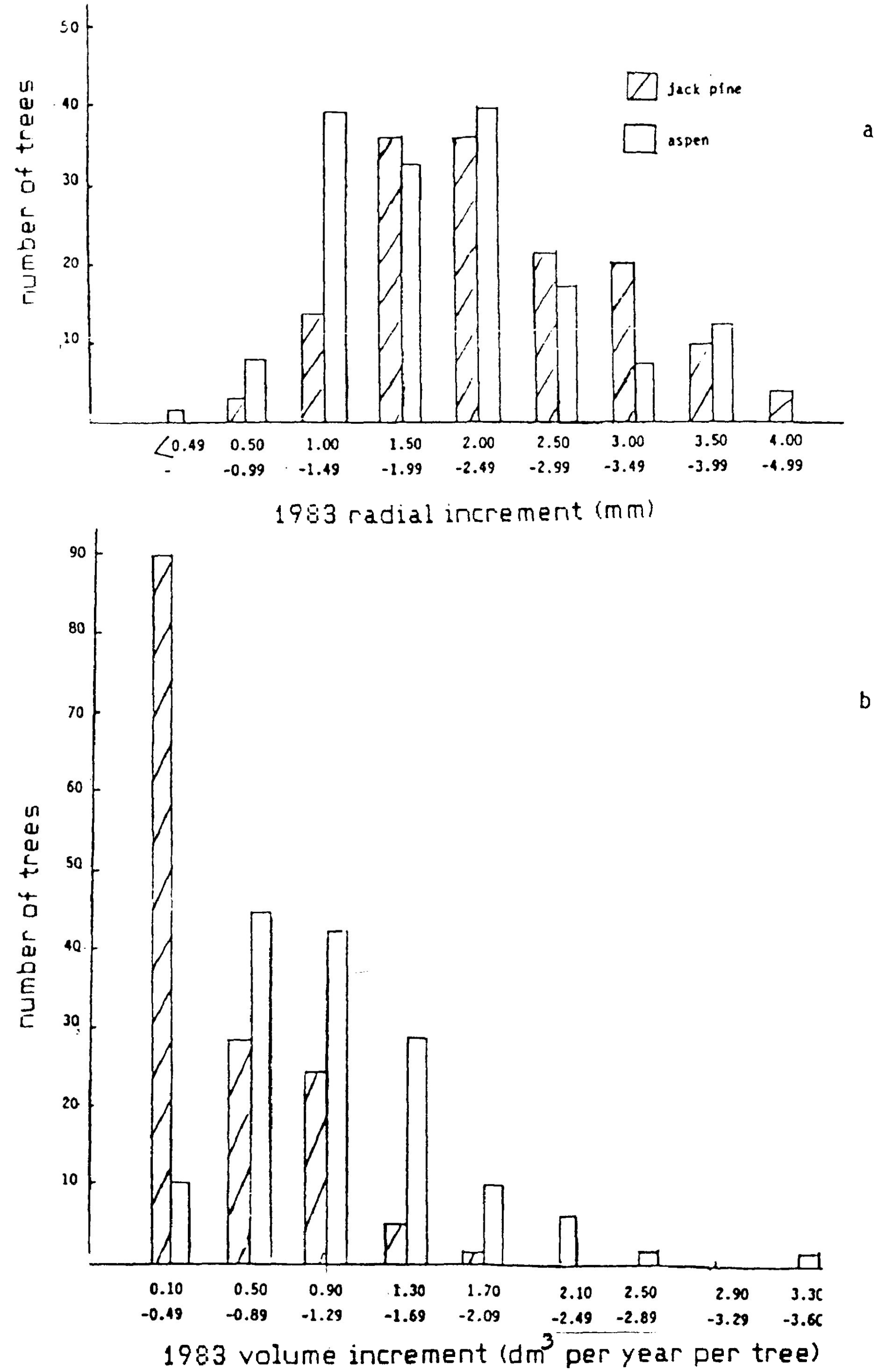

Figure 4.2. a) The distribution of the 1983 radial increment at stump height of jack pine and aspen subject trees.
b) The distribution of the 1983 volume increment of jack pine and aspen.

TABLE 4.3: The number of times out of 48 that each competition index ranked 1st, 2nd, ..., and 7th according to the degree to which the competition index was correlated with the 1983 volume increment of aspen subject trees[1].

Competition index	Rank 1st	2nd	3rd	4th	5th	6th	7th	Total
DC1	2	11	11	14	7	3	1	48
DC2	8	3	6	16	5	8	3	48
DC'	3	19	14	4	4	3	1	48
LC1	30	8	3	3	1	3	0	48
LC2	0	4	5	4	14	8	13	48
LC'	7	0	6	9	9	16	17	48
SC	3	1	4	3	5	8	24	48

Legend:

[1] The correlation analyses were performed on 48 random samples of the size of 15 subject trees from the total aspen subject tree data base.

DC1 - Daniels' total competition index due to all selected competitors

DC2 - Daniels' total competition index due to competitors whose height is equal or greater than the height of subject tree

LC1 - Lorimers' total competition index due to all selected competitors

LC2 - Lorimers' total competition index due to competitors whose height is equal or greater than the height of subject tree

SC - Spurr's modified competition index

TABLE 4.4: The number of time out of 48 that each competition index ranked 1st, 2nd, ..., and 7th according to the degree to which the competition index was correlated with the 1983 volume increment of jack subject trees[1].

Competition index[2]	Rank 1st	2nd	3rd	4th	5th	6th	7th	Total
DC1	11	14	16	4	2	1	0	48
DC2	8	10	4	7	8	6	5	48
DC'	2	4	5	4	9	13	11	48
LC1	2	3	5	17	3	6	12	48
LC2	15	14	8	9	2	0	0	48
LC'	3	2	5	8	14	9	7	48
SC	6	2	7	2	13	11	7	48

[1] The correlation analyses were performed on 48 random samples of the size of 15 trees from the total jack pine subject tree data base.

[2] Indices are as defined on Table 4.3.

TABLE 4.5: Point scores associated with 7 competition indices by subject tree species. Individual scores were calculated according to the method of Alemdag.

Competition index'	Species of subject tree		Total
	Jack pine	aspen	
DC1	265	219	484
LC1	154	294	448
LC2	271	136	407
DC2	205	201	406
LC'	143	240	380
DC'	157	139	296
SC	165	114	278

'Indices are defined on Table 4.3.

distance-dependent competition indices are superior to distance-independent competition indices.

The results of this study differ from the result obtained by Alemdag (1978), Ganzlin and Lorimer (1983), Moore *et al.* (1973) and Opie (1968) who observed that distance-independent competition indices were superior to distance-dependent ones. These studies, however, all involved row plantations in which there was little variation in the spatial arrangement of the trees.

SPEARMAN RANK CORRELATION ANALYSES

Tables 4.6 and 4.7 show Spearman rank correlation matrices of subject tree attributes and associated measures of competition for jack pine and aspen subject trees, respectively.

ANALYSIS OF SUBJECT TREE GROWTH

This section presents the results of the regression analyses used to test a hierachy of hypotheses about the effects of the competitors on the subject trees. The flow chart summarizing these tests is shown in Figure 3.5.

The results of the regression analysis of the 1983 volume increment are presented in some detail to illustrate the procedures used. Results for the other dependent variables are presented in less complete detail.

Analysis of the 1983 Volume Increment

The Response of Jack Pine and Aspen Subject Trees to Competition

The first null hypothesis tested was that subject trees of both species respond identically to the individual species components of Daniels' total competition index. To test this hypothesis two regression models were fitted. The "full model" assumed that subject

TABLE 4.6: Spearman rank correlation matrix for jack pine subject tree attributes, and the total and individual species components of Daniels' competition index.

	Measures of 1983 increment			Measures of initial size				Measures of competition		
	Δ Rp	ΔHp	ΔVp	Rp	Vp	Hp	CRp	DC1p	DC1a	Total DC1
Δ Rp	1.000	0.1396	0.7631c	0.7362c	0.6204c	0.4674c	0.4012c	-0.3442b	-0.3286c	-0.7689c
Δ Hp		1.0000	0.0937	0.0545	0.0421	0.0449	0.0146	-0.0207	-0.0200	-0.1149a
Δ Vp			1.0000	0.8715c	0.9386c	0.7397c	0.2366c	-0.1643a	-0.4583c	-0.7009c
Rp				1.0000	0.9167c	0.6728c	0.1761b	-0.1030	-0.6331c	-0.6112c
Vp					1.0000	0.8015c	0.2123b	-0.1818a	-0.6432c	-0.5220c
Hp						1.0000	0.1305b	0.0806	-0.3858c	-0.3910c
CRp							1.0000	-0.4037c	-0.0346	-0.4667c
DC1p								1.0000	0.5722c	0.6198c
DC1a									1.0000	0.2111b
Total DC1										1.0000

a - denotes Pr (r = 0) < 0.05
b - denotes Pr (r = 0) < 0.01
c - denotes Pr (r = 0) < 0.001

TABLE 4.7: Spearman rank correlation matrix for the aspen subject tree attributes, and the total and individual components of Daniels' competition index.

	Measures of 1983 increment			Measures of initial size				Measures of competition		
	ΔRa	ΔHa	ΔVa	Ra	Va	Ha	CRa	DC1p	DC1a	Total DC1
ΔRa	1.0000	0.1614a	0.4480c	0.2702b	0.1690a	0.1843a	0.2950c	0.0735a	-0.3795c	-0.3352b
ΔHa		1.0000	0.3371c	0.2223c	0.2298b	0.3257c	0.1498a	0.0150	-0.0594	-0.0573
ΔVa			1.0000	0.8683c	0.8783c	0.8052c	0.3435c	-0.0237	-0.0733	-0.5919c
Ra				1.0000	0.9168c	0.7305c	0.3924c	-0.3777c	-0.1789b	-0.6156c
Va					1.0000	0.8616c	0.2330b	-0.3003c	0.1060	-0.5430c
Ha						1.0000	0.2160b	-0.4844c	0.2200b	-0.4139c
CRa							1.0000	-0.0279	-0.3753c	-0.5556c
DC1p								1.0000	-0.5482c	0.4836c
DC1a									1.0000	0.3469c
Total DC1										1.0000

trees of both species respond differently. The "reduced model" assumed that the two species respond in the same way.

The full model was fitted by regressing the 1983 volume increment of 287 subject trees on initial volume of the subject trees, subject tree species (represented by a dummy variable), the individual species components of Daniels' total competition index and all possible cross products of these independent variables. Eleven subject trees were dropped from the analysis because they were judged to be outliers. The best full model was selected by the stepwise elimination procedure. The result is presented as Eq. 4.1:

$$\begin{aligned}\Delta V = {} & 0.2723 + 0.2984V - 0.1413SP \\ & + 0.3922(V \times SP) - 0.0032(V \times DCla) \\ & + 0.0218(V \times DClo) \\ & - 0.0095(V \times DClp \times SP) \\ & - 0.0126(V \times DCla \times SP) \qquad [4.1]\end{aligned}$$

where:

ΔV - 1983 volume increment of the subject tree regardless of the species of the subject tree

V - initial volume of the subject tree regardless of the species of the subject tree

SP - dummy variable equal to 0 whenever the subject tree was aspen and 1 whenever the subject tree was jack pine

DClp, DCla, DClo - the individual species components of Daniels' total competition index as defined on pages xi and 43.

The statistics associated with Eq. 4.1 are shown in Table 4.8 and Appendix I (Table I-1).

The reduced model was fitted by recomputing the regression without dummy variable for the subject tree species. The result is presented as Eq. 4.2:

TABLE 4.8: A comparison of regression statistics associated with full (Eq. 4.1) and reduced (Eq. 4.2) 1983 volume increment models.

	Model	
Statistics[1]	full (Eq. 4.1)	reduced(Eq. 4.2)
N	287	287
R^2	0.90	0.83
Std err	0.17	0.22
Res ss	7.96	13.28
F^2	344.79	451.21
df	7,279	3,283
$P(F > F^2)$	0.01	0.01

[1] Abbreviations are defined on page xi

[2] F-ratio to test the general linear hypothesis that regression coeffients associated with models are equal to zero.

$$\Delta V = 2.761 + 0.3174V - 0.0046(V \times DCla) - 0.0269(V \times DClo) \quad [4.2]$$

The dependent and independent variables are as defined in Eq 4.1. The statistics associated with Eq. 4.2 are shown in Table 4.8 and Appendix I (Table I-2).

The F-ratio to test the general linear hypothesis that the regression coefficients associated with the dummy variable for the subject tree species are equal to zero is

$$F = [(13.28 - 7.96)/5]/(7.96/279)$$
$$= 37.32 \text{ with 5 and 279 degrees of freedom.}$$

The F-ratio is highly significant and so the null hypothesis was rejected and the alternative hypothesis accepted. The alternative hypothesis may be stated thus: jack pine and aspen subject trees responded differently to initial volume and competition. Jack pine and aspen subject tree data sets, therefore, are treated separately in subsequent analyses.

The Competitive Effect of Jack Pine and Aspen on the Growth of Subject Trees

The second null hypothesis to be tested was that the jack pine and aspen neighbour trees have the same competition effect on the 1983 volume increment of subject trees. The hypothesis was tested separately for jack pine and aspen subject trees.

Jack Pine Subject Trees

In order to test the second hypothesis with respect to the jack pine subject trees two models were fitted to the jack pine subject tree data. The full model assumed that the individual species components of Daniels' total competition index had different effects on the 1983 volume increment of jack pine subject trees. The reduced model assumed that individual species components of Daniels' total competition index had the same effect on the 1983 volume increment of jack pine subject trees.

The full model was fitted as follows: the 1983 volume increment was regressed on the initial volume of the subject tree, the individual species components of Daniels' total competition index and all possible cross products. The best model was selected by the stepwise elimination procedure. The result is presented as Eq. 4.3:

$$\begin{aligned}\Delta Vp = {} & 0.1312 + 0.6946Vp - 0.0096(Vp \times DCIp) \\ & - 0.0157(Vp \times DCIa) \qquad [4.3]\end{aligned}$$

The dependent and independent variables are defined on pages 43 and 48. The statistics associated with Eq. 4.3 are as shown in Table 4.9 and Appendix I (Table I-3).

The reduced model was fitted by regressing the 1983 volume increment on the initial volume of the subject tree, Daniels' competition indices due to jack pine plus aspen, and their cross products. The best model was selected by stepwise elimination. The result is presented in Eq. 4.4.

$$\begin{aligned}\Delta Vp = {} & 0.0466 + 0.7161Vp \\ & - 0.0103 \times Vp \times (DCIp + DCIa) \qquad [4.4]\end{aligned}$$

The statistics associated with Eq. 4.4 are shown in Table 4.9 and Appendix I (Table I-4). Table 4.9 also contrasts the overall statistics associated with equations 4.3 and 4.4.

The F-ratio to test the general linear hypothesis that regression coefficients associated with individual species components of Daniels' total competition index are equal is

$$\begin{aligned}F & = [(0.93 - 0.92)/1]/[(1 - 0.93)/141] \\ & = 33.5470 \text{ with 1 and 141 degrees of freedom.}\end{aligned}$$

The F-ratio is highly significant (P(F 33.5) 0.000). The null hypothesis was, therefore, rejected.

TABLE 4.9: A comparison of regression statistics associated with full (Eq. 4.3) and reduced (Eq. 4.4) volume increment models for jack pine subject trees.

	Model	
Statistics[1]	full (Eq. 4.3)	reduced (Eq. 4.4)
N	145	145
R^2	0.93	0.92
Std err	0.09	0.10
F[2]	684.67	779.31
df	3,142	2,142
P(F > F[2])	0.01	0.01

[1] Abbreviations are defined on page xi

[2] F-ratio to test the general linear hypothesis that regression coefficients associated with models are equal to zero.

Aspen Subject Trees

A procedure analogous to the one used in the previous section was used here to test the following null hypothesis: individual species components of Daniels' total competition index had the same effect on the 1983 volume increment of aspen subject trees. The full model is presented as Eq. 4.5.

$$\Delta Va = 0.2714 + 0.2976Va - 0.0313(Va \times DClo) - 0.0032(Va \times DCla) \qquad [4.5]$$

The dependent and independent variables are defined on pages 43 and 49. The statistics associated with Eq. 4.5 are shown in Table 4.10 and Appendix I (Table I-5).

The reduced model is presented as Eq. 4.6.

$$\Delta Va = 0.2140 + 0.3163Va - 0.0037 \times Va \times (DCla + DClo) \qquad [4.6]$$

The statistics associated with Eq. 4.6 are shown in Table 4.10 and Appendix I (Table I-6). Table 4.10 also contrasts general statistics associated with model [4.5] and [4.6].

The F-ratio to test the general linear hypothesis that the regression coefficients associated with individual species components of Daniels' total competition index are equal to zero is highly significant (P(F 11.18) 0.0000). The null hypotheses was, therefore, rejected.

Analysis of the 1983 Radial Increment

Response of Jack Pine and Aspen Subject Trees to Competition

The full model assumes that jack pine and aspen subject trees respond differently to individual species components of Daniels' total competition index. The result is presented as Eq. 4.7:

TABLE 4.10: A comparison of regression statistics associated with full (Eq. 4.5) and (Eq. 4.6) volume increment models for aspen subject trees.

	Model	
Statistics[1]	full (Eq. 4.5)	reduced (Eq. 4.6)
N	141	141
R^2	0.81	0.80
Std err	0.24	0.24
F[2]	205.13	344.76
df	3,137	2,139
P(F> F[2])	0.01	0.01

[1] Abbreviations are defined on page xi

[2] F-ratio to test the general linear hypothesis that regression coefficients associated with models are equal to zero.

$$\Delta R = 1.2357 + 0.0442R - 0.0693(SP \times R) - 0.0278(SP \times DC1p) - 0.0017(R \times DC1a) \qquad [4.7]$$

where:

ΔR - 1983 radial increment of subject tree regardless of the species of the subject tree

R - initial radius at stump height of subject tree regardless of the species of subject tree

- other independent variables are defined on pages 43 and 58.

The statistics associated with Eq. 4.7 are shown in Table 4.11 and Appendix I (Table 1-7).

The reduced model assumes that jack pine and aspen subject trees respond in the same way to individual species components of Daniels' total competition index. The result is presented as Eq 4.8:

$$\Delta R = 1.9589 + 0.0255R - 0.0021(R \times DC1a) \qquad [4.8]$$

The statistics associated with Eq. 4.8 are shown in Table 4.11 and Appendix I (Table I-8).

The F-ratio to test the general linear hypothesis that the regression coefficients associated with the dummy variable for subject tree species are equal to zero is highly significant (P(F 77.77) 0.000). Consequently, the null hypothesis was rejected. The conclusion is that jack pine and aspen subject trees respond differently to the initial stem radius of the subject tree and the individual species components of Daniels' total competition index. Jack pine and aspen subject data sets, therefore, were considered as two independent populations and treated separately in subsequent analyses.

TABLE 4.11: A comparison of regression statistics associated with full (Eq. 4.7) and reduced (Eq. 4.8) 1983 radial increment models.

	Model	
Statistics[1]	full (Eq. 4.7)	reduced (Eq. 4.8)
N	288	288
R^2	0.55	0.18
Std err	0.51	0.69
Res ss	74.21	135.39
F[2]	85.67	30.22
df	4,284	2,285
$P(F > F^2)$	0.01	0.01

[1] Abbreviations are defined on page xi

[2] F-ratio to test the general linear hypothesis that regression coefficients associated with models are equal to zero.

The Competitive Effect of Jack Pine and Aspen on the Growth of Subject Trees

Jack Pine Subject Trees

The full model assumes that the individual species components of Daniels' total competition index have different effects on the 1983 radial increment of a jack pine subject tree. The result is presented as Eq. 4.9:

$$\begin{aligned}\Delta Rp &= 1.1874 + 0.1270Rp - 0.0025(Rp \times DClp)\\ &\quad - 0.0024(Rp \times DCla) \qquad [4.9]\end{aligned}$$

The dependent and independent variables are defined on pages 43 and 48. The overall statistics associated with Eq. 4.9 are shown in Table 4.12 and Appendix I (Table I-9).

The reduced model assumes that individual species components of Daniels' total competition index have the same effect on the 1983 radial increment of jack pine subject trees. The result is presented as Eq. 4.10:

$$\begin{aligned}\Delta Rp &= 0.7130 + 0.1483Rp\\ &\quad - 0.0029Rp \times (DClp + DCla) \qquad [4.10]\end{aligned}$$

The overall statistics associated with Eq. 4.10 are shown in Table 4.12 and Appendix I (Table I-10).

The F-ratio to test the general linear hypothesis that the regression coeffients associated with individual species components of Daniels' competition index are equal is highly significant (P(F 10.95) 0.000). Thus, the null hypothesis was rejected.

TABLE 4.12: A comparison of regression statistics associated with full (Eq. 4.90) and reduced (Eq. 4.10) radial increment models for jack pine subject trees.

	Model	
Statistics[1]	full (Eq. 4.9)	reduced (Eq. 4.10)
N	144	144
R^2	0.73	0.70
Std err	0.41	0.45
F[2]	124.32	164.21
df	3,140	2,141
P(F> F[2])	0.01	0.01

[1] Abbreviations are defined on page xi

[2] F-ratio to test the general linear hypothesis that regression coefficients associated with models are equal to zero.

Aspen Subject Trees

The full model assumes that individual species components of Daniels competition index have the same effect on the 1983 radial increment of aspen subject trees. The result is presented as Eq. 4.11:

$$\Delta Ra = 0.9627 + 0.0561Ra - 0.0519DC1a - 0.0041(Ra \times DC1a) \qquad [4.11]$$

The dependent and independent variables are defined on pages 43 and 49. The statistics associated with Eq. 4.11 are shown in Table 4.13 and Appendix I (Table I-11).

The aspen component of Daniels' competition index initial radius at stump height of aspen subject trees and their cross product are variables selected for Eq. 4.11. The null hypothesis was, therefore, rejected.

Analysis of the 1983 Height Increment

It is clear from Tables 4.6 and 4.7 that the 1983 height increment of both jack pine and aspen subject trees was almost independent of other attributes of the subject trees themselves. Height increment of both species also was almost independent of the attributes of the competitive environment as measured by Daniels' competition index. Therefore, 1983 height increment was dropped from further analysis.

Sensitivity Analysis of the 1983 Volume Increment of Subject Trees

The aim of the analysis presented in this section is to estimate the degree to which change in the 1983 stemwood volume increment of the subject trees was due to: a) the initial volume of the subject tree, b) the live crown ratio of the subject tree, and competition from c) jack pine and d) aspen neighbouring trees.

TABLE 4.13: Regression statistics associated with the full model (Eq. 4.11) volume increment for aspen subject tree[1].

Statistics[2]	
N	144
R^2	0.23
Std Err	0.59
F[3]	13.97
df	3, 140
P(F > F[3])	0.01

[1] The reduced model was not fitted since only aspen component of Daniels' competition index was selected for fitting full model;

[2] Abbreviations are defined on page xi

[3] F-ratio to test the general linear hypothesis that regression coefficients associated with the model are equal to zero.

The analysis is summarized in Figure 3.6. It proceeded as follows: the data were grouped into two sets according to the subject tree species. Then two different models were estimated from each data set. The first model was fitted by regressing the live crown ratio of the subject tree on the initial volume of the subject tree, the jack pine and aspen components of Daniels' competition index and all cross products. The second model was fitted by regressing the 1983 volume increment of the subject tree, on the live crown ratio of the subject tree, the jack pine and aspen components of Daniels' competition index and all two way interactions. The best models were selected by the stepwise elimination procedure. The results are presented as equations 4.12 through 4.15.

$$CRa = 0.761 + 0.019Va - 0.008DC1a \qquad [4.12]$$

$$\Delta Va = 0.256 + 0.305Va - 0.019(CRa \times DC1a) \qquad [4.13]$$

$$CRp = 0.901 + 020Vp - 0.003DC1p - 0.005DC1a \qquad [4.14]$$

$$\Delta Vp = 0.128 + 678(Vp \times CRp) - 0.005DC1p$$
$$- 0.017(Vp \times DC1a) \qquad [4.15]$$

The dependent and independent variables associated with Eqs. 4.12 through 4.15 are defined on pages 43, 48 and 49. The statistics associated with Eqs. 4.12 through 4.15 are shown in Table 4.14 and Appendix II.

The sensitivity of estimated 1983 volume increment (ΔV) to individual independent variables was determined by increasing each independent variable by one standard deviation (Tables 4.1 and 4.2) while holding all other independent variables at their mean value. The change in ΔV was also expressed as a percentage of the observed mean 1983 volume increment as reported in Tables 4.1 and 4.2. The procedure followed in the analysis of the change in the 1983 volume increment is summarized in Appendix III. The changes in the 1983 volume increment due to the predictor variables are as shown in Tables 4.15 and 4.16.

TABLE 4.14: A summary of statistics associated with Equations 4.12 through 4.15.

	Response variable[1]			
Statistics	CRa (Eq. 4.12)	ΔVa (Eq. 4.13)	CRp (Eq. 4.14)	ΔVp (Eq. 4.15)
N	147	142	145	146
R^2	0.30	0.83	0.41	0.93
Std err	0.09	0.24	0.05	0.09
F[2]	31.30	347.52	32.22	597.55
df	2,144	2,139	3,141	3,142
P(F > F[2]	0.01	0.01	0.01	0.01

[2] Abbreviations are defined on pages xi.

TABLE 4.15: Partial change in the 1983 predicted volume increment of jack pine, $\Delta\hat{V}p$, in response to one standard deviation increase in individual predictor variables. Direct effects are via Eq. 4.15; indirect effects are via Eq. 4.14.

Predictor variable	Average value[1] dm^3	Std dev.[1] dm^3	Partial change in $\Delta\hat{V}p$	
			dm^3	% of $\Delta\hat{V}p$
Vp	0.828	0.516		
direct[2]			0.268	49.2
indirect			0.006	1.1
CRp	0.867	0.072	0.040	7.4
DC1p	7.650	9.042		
direct			-0.045	-8.3
indirect			-0.025	-4.7
DC1a	3.981	5.382		
direct			-0.076	-13.9
indirect			-0.009	-1.7

[1] obtained from Table 4.1;

[2] direct effect refers to the effect of competition or initial size of the subject tree on the volume increment of subject tree;

- indirect effect refers to the effect of competition or initial size of the subject tree on the volume increment of the subject tree via its effect on the live crown ratio.

TABLE 4.16: Partial change in the 1983 predicted volume increment of aspen subject tree, $\Delta\hat{V}a$, in response to one standard deviation increase in individual predictor variables. Direct effects are via Eq. 4.12, indirect effects are via Eq. 4.13.

Predictor variable	Average value[1] dm^3	Std dev.[1] dm^3	Partial change in $\Delta\hat{V}a$ dm^3	% of $\Delta\hat{V}p$
Va	3.158	1.836		
direct			0.560	51.0
indirect			-0.003	-0.3
CRa	0.786	0.103	-0.008	-0.8
DC1a	4.323	5.521		
direct			-0.082	-7.5
indirect			0.004	0.3

[1] obtained from Table 4.2.

DISCUSSION

The goal of this study was to describe the competitive relationship between jack pine and aspen in a young plantation. To accomplish this goal two hypotheses were tested: (1) that the growth response of jack pine and aspen subject trees to competition is the same, and (2) that jack pine and aspen competitors have the same effect on both subject trees species.

RESPONSE OF JACK PINE AND ASPEN SUBJECT TREES TO COMPETITION

Jack pine and aspen subject trees responded differently, in terms of both the 1983 volume increment and radial increment, to competition (Tables 4.8 and 4.11). These differences may be due to differences in the shade tolerance of the two subject tree species. Baker (1949) classified aspen as very intolerant of shade, and jack pine as intolerant of shade especially when it is young.

The 1983 height increment of both jack pine and aspen subject trees was independent of the competitive environment of the tree (Tables 4.6 and 4.7). This is not surprising since the annual height increment of jack pine and aspen is not normally influenced by stand density (Bella 1974, Bella and De Franceschi 1974a,b, 1980, Bickerstaff 1946, Krinard 1971, Marshall 1980, Martin and Ek 1984, Steneker 1964, Steneker and Jarvis 1966, Zehngraff 1947, Wilson 1952).

THE COMPETITIVE EFFECT OF JACK PINE AND ASPEN ON THE GROWTH OF SUBJECT TREES

Aspen and jack pine competitors had significantly different effects on the 1983 volume increment and radial increment of jack pine and aspen subject trees (Tables 4.9, 4.10, 4.12 and 4.13). In the case of jack pine subject trees the 1983 volume increment and radial increment were significantly influenced by both jack pine and aspen competitors. This may have been because jack pine subject trees were often in the same or lower crown class than jack pine competitors, and were often overtopped by aspen competitors.

In the case of aspen subject trees, the 1983 volume increment and radial increment were significantly influenced only by aspen competitors. This is not suprising, however, since most of the aspen subject trees were dominants and/or codominants. My results concur with those of Day and Harvey (1981) and Hosie (1979). Both studies showed that the early growth of aspen is fast. Aspen overtops associated tree species and, therefore, does not suffer from competition to the same degree as associated tree species.

SENSITIVITY ANALYSIS OF THE 1983 VOLUME INCREMENT OF THE SUBJECT TREE

Equations 4.12, 4.13, 4.14 and 4.15 together summarize some of the main elements of the competitive interaction between jack pine and aspen in the young plantation that I studied. I undertook the sensitivity analysis of these equations in an attempt to gain additional information about the probable nature of the competitive relationship between the study species. The results are presented in Tables 4.15 and 4.16. For the purpose of this discussion, the same information is illustrated graphically in Figure 5.1.

Figure 5.1 contains several kinds of information. The focus of the figure, and of the analysis, is the sensitivity of a single, annual, stemwood volume increment to variation in the levels of tree and stand variables. For purposes of the sensitivity analysis, I assumed that both jack pine and aspen subject trees were of average initial volume, that they had an average live crown ratio, and that they were growing in an average competitive environment. An example will demonstrate how to read the figure. In the paragraphs below, terms in capital letters refer to similarly labeled blocks in Fig. 5.1.

From the structure of Figure 5.1 it is clear that the 1983 annual stemwood increment of jack pine was affected by, among other things, a) the LIVE CROWN RATIO of the subject tree itself and b) the level of ASPEN COMPETITION in the surrounding stand. The

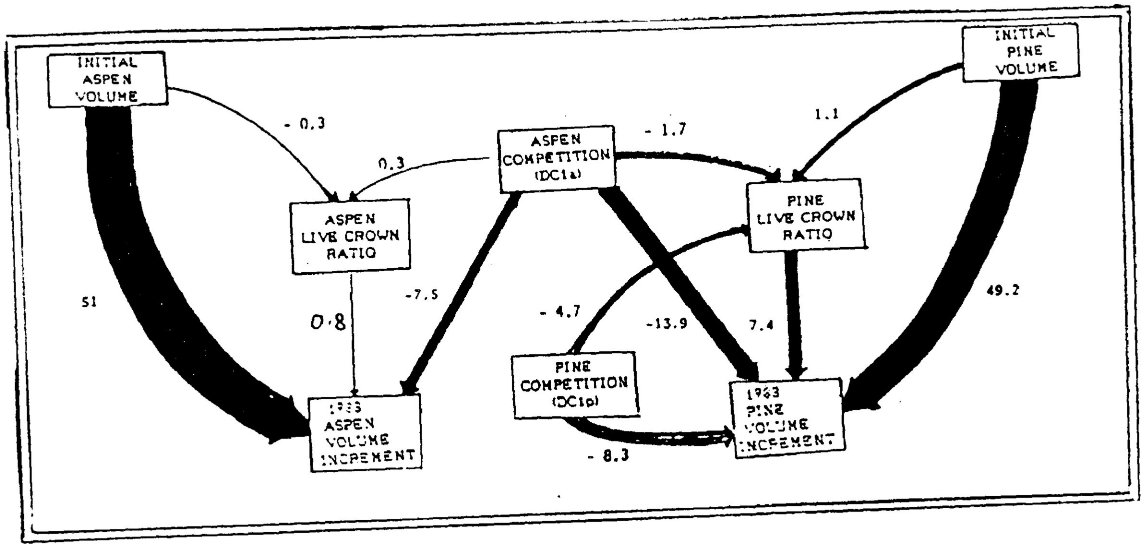

Figure 5.1. The apparent nature of the mutual competitive relationship between jack pine and aspen in young mixed stands of these species. The direct and indirect effects of initial size of the subject tree, live crown ratio of the subject tree and current competitive environment on the 1983 volume increment of the subject tree are shown. The effect of each variable on the 1983 volume increment of the subject tree is indicated by the relative thickness of the line joining the two variables. The numbers are per cent changes in the 1983 volume increment. Source: Tables 4.12 and 4.13.

number beside the arrow that connects LIVE CROWN RATIO and 1983 PINE VOLUME INCREMENT is 7.4. This means that if all components of the system are held at their mean value, and LIVE CROWN RATIO is increased from its mean value (0.867) to one standard deviation above the mean value (0.867 and 0.072) the effect is to increase the estimated, annual stemwood volume increment of the jack pine subject tree by 7.4 per cent. Increasing the level of ASPEN COMPETITION in the same way decreases (-) the estimated, annual stemwood volume increment by 13.9 per cent.

It is clear from the structure of the figure that ASPEN COMPETITION affects the LIVE CROWN RATIO of the jack pine subject tree. Thus, ASPEN COMPETITION has an indirect effect on the 1983 jack pine stemwood volume increment as well. The number above the arrow that connects ASPEN COMPETITION with PINE LIVE CROWN RATIO is - 1.7. This means that the indirect effect of ASPEN COMPETITION on the 1983 PINE VOLUME INCREMENT (not PINE LIVE CROWN RATIO) is to diminish that increment by 1.7 per cent.

Throughout the figure, the width of each arrow is roughly proportional to the magnitude of the direct or indirect effect of the source component on the 1983 annual stemwood volume increment of the subject tree. Thus, it is possible to get a feeling for the relative contribution of various components of the system just by casual inspection of Figure 5.1. When this is done, the most striking thing about the network is the profound effect that the INITIAL VOLUME had on annual volume increment. In short, the bigger the tree of either species was initially, the greater its annual stemwood volume increment. This is consistent with general experience with the early growth pattern of individual trees.

The second most striking thing about Figure 5.1 is the substantial negative effect that ASPEN COMPETITION had on the volume increment of subject trees of both species. Jack pine was affected more heavily than aspen by aspen competition, and the relationship involves both direct and indirect effects via the negative effect on LIVE CROWN RATIO.

PINE COMPETITION had a negligible effect on aspen subject trees, although it had a negative effect on jack pine subject trees. These latter effects include both direct and indirect effects via the effect on the live crown ratio.

Finally, there is, in this system, a feedback of great practical significance that is not shown in Figure 5.1. The feedback occurs because when a tree produces an annual volume increment it simultaneously increases both the initial volume of that tree and the local level of competition due to that species in the next growing season. With reference to Figure 5.1, consider the following hypothetical sequence of events that illustrate the effects of this feedback relationship.

The scenario begins with a young mixed stand of jack pine and aspen. For simplicity, suppose that at the beginning of the first growing season of the simulation the two species occur in a 50:50 mixture, and that all trees of both species begin with the same initial volume. In short, both species start off on an equal footing in terms of the physical state of the system. Under the initial conditions just mentioned, Figure 5.1 suggests that aspen will have a slight competitive advantage for two reasons. First, aspen suppresses jack pine more than it suppresses itself. Secondly, jack pine suppresses itself, but does not suppress aspen. Thus, aspen will experience slightly more growth than jack pine in the first growing season, and, as a result of the feedback, aspen will begin the second growing season with slightly more initial volume and a slightly greater proportion of the total competitive pressure within the stand. These effects will result in an even greater advantage to aspen in the second growing season.

If these inferences are correct, and if they apply beyond the limits of the plantation studied, it appears that when jack pine and aspen compete on initially equal footing, aspen will eventually dominate the stand. These results are supported by my field observations. It was difficult to find jack pine trees in the dominant or codominant classes when dense aspen competition was present (Figure 5.2). A similar situation has been reported between aspen and white spruce (Cayford 1957b, Harvey 1982, Lees 1966, Steneker 1963, 1974, Steneker and Jarvis 1963).

My results do not indicate directly how long this transition might take, nor how factors such as stand age and site quality might affect the outcome. But, the implication of

Figure 5.2. A dense 8 year old mixed stand of aspen. Aspen is overtopping the jack pine.

Figure 5.1 is that the competitive advantage probably shifts to aspen in only a few years in stands like the one I studied.

In addition to the passive competition effect of aspen on jack pine, my field observations revealed that aspen also has mechanical effects on jack pine. Through abrasion between jack pine and aspen stems, jack pine trees may be debarked (Figure 5.3); jack pine needles might be removed by aspen branches (Figure 5.4); and sometimes there is stem deformation (Figure 5.5).

CONCLUDING REMARKS

The results of this study are restricted because only one stand was studied. Thus, inferences must be drawn with caution.

This study, however, provides some insight into the possible dynamics of young mixed stands of jack pine and aspen. The results of this study suggest that the growth of jack pine is inhibited by aspen competition. The observed competitive effect of aspen on jack pine may be sufficiently strong to warrant silvicultural control in situations where jack pine is a crop species.

Although the study was limited in scope, the procedures used show promise and may provide a lead for the use of competition indices to study the dynamics of mixed stands.

Figure 5.3. Debarking effect of aspen on jack pine tree.

Figure 5.4. Jack pine tree partly defoliated by aspen.

Figure 5.5. Jack pine stem deformation by aspen.

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APPENDIX I

SUMMARY OF STATISTICS ASSOCIATED WITH EQUATIONS 4.1 THROUGH 4.11

TABLE I-1: Summary of statistics associated with Eq. 4.1.

	Associated statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	0.27	0.03	0.21 - 0.33	82.45	0.01
V	0.30	0.01	0.28 - 0.32	973.44	0.01
SP	-0.14	0.05	0.04 - -0.24	8.53	0.01
V x SP	0.39	0.03	0.33 - 0.45	155.75	0.01
DCIo x V	-0.02	0.01	0.40E-2 - -0.04	4.33	0.05
DCIa x V	0.32E-2	0.51E-3	0.21E-2 - 0.43E-2	30.25	0.01
DC1p x SP x V	0.01	0.18E-2	0.64E-2 - 1.35E-2	27.04	0.01
DC1a x SP x V	0.01	0.37E-2	0.27E-2 - -1.72E-2	11.09	0.01

TABLE I-2: Summary of statistics associated with Eq. 4.2.

	Associated statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	0.23	0.02	0.19 - 0.27	196.84	0.01
V	0.32	0.95E	0.30 - 0.34	1113.56	0.01
DC1a x V	-0.46E-2	0.70E-3	0.32E-2 - -0.60E-2	43.30	0.01
DC1o x V	0.03	0.01	0.01 - 0.05	4.04	0.05

TABLE I-3: Summary of statistics associated with Eq. 4.3.

Independent variable	Associated statistics				
	b	SE b	95% conf. interval for b	F	Pr>F
Constant	0.13	0.02	0.09 - 0.17	41.34	0.01
Vp	0.69	0.02	0.65 - 0.73	1870.56	0.01
CIDp x Vp	-0.95E-02	0.98E-03	0.76E-02 - -1.14E-02	93.32	0.01
CIDa x Vp	-0.02	0.20E-02	1.61E-02 - -2.39E-02	60.84	0.01

TABLE I-4: Summary of statistics associated with Eq. 4.4.

Independent variable	Associated statistics				
	b	SE b	95% conf. interval for b	F	Pr>F
CONSTANT	0.17	0.03	0.11 - 0.23	35.84	0.01
Vp	0.72	0.02	0.68 - 0.76	1541.90	0.01
V x (DCIp + DCIa)	-0.01	0.10E-02	0.77E-02 - 1.3E-02	58.02	0.01

TABLE I-5: Summary of statistics associated with Eq. 4.5.

	Associated statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	0.27	0.04	0.19 - 0.35	47.75	0.01
Va	0.30	0.01	0.28 - 0.32	563.59	0.01
DCIa x Va	-0.30E-02	0.75E-03	0.15E-02 - -0.45E-02	18.23	0.01
DCIo x Va	0.03	0.02	0.01 - 0.07	4.23	0.01

Table I-6: Summary of statistics associated with Eq. 4.6.

	Associated Statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	0.21	0.04	0.13 - 0.29	27.46	0.01
Va	0.32	0.01	0.20 - 0.34	636.05	0.01
Va x DC1a + DCIo	-0.37E-02	0.11E-02	-0.15E-02 - -0.59E-02	10.58	0.01

TABLE I-7: Summary of statistics associated with Eq. 4.7.

	Associated Statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	1.23	0.14	0.97 - 1.51	79.21	0.01
R	0.04	0.60E-02	0.03 - 0.05	54.91	0.01
R x SP	0.07	0.47E-02	0.06 - 0.08	108.63	0.01
DCIp x SP	-0.03	0.33E-02	0.02 - -0.04	69.22	0.01
DCIa x R	-0.17E-02	0.24E-03	0.12E-02 - -0.22E-02	51.84	0.01

TABLE I-8: Summary of statistics associated with Eq. 4.8.

	Associated statistics				
Independent variable	b	SE b	95% conf. interval for b	F	Pr>F
Constant	1.96	0.14	1.69 - 2.23	204.78	0.01
R	0.03	0.71E-02	1.64E-02 - 4.39E-02	12.96	0.01
DC1a	-0.21E-02	0.30E-03	0.15E-02 - 0.27E-02	49.28	0.01

TABLE I-9: Summary of statistics associated with Eq. 4.9.

Independent variables	Associated statistics					
	b	SE b	95% conf. interval for b		F	Pr>F
Contant	0.19	0.21	0.78	- 1.60	31.81	0.01
Rp	0.13	0.01	0.11	- 0.15	136.42	0.01
DC1p x Rp	-0.25E-2	0.29E-3	0.19E-2	- 0.31E-2	85.56	0.01
DC1a x Rp	-0.24E-2	0.49E-2	0.14E-2	- -0.34E-2	26.63	0.01

TABLE 1-10: Summary of statistics associated with Eq. 4.10.

Independent variable	Associated statistics					
	b	SE b	95% conf. interval for b		F	Pr>F
Constant	0.71	0.16	0.39	- 1.03	17.88	0.01
Rp	0.14	0.01	0.12	- 0.16	75.69	0.01
Rp x DC1p + DC1a	-0.30E-02	0.37E-03	0.22E-02	- -0.37E-02	70.56	0.01

TABLE I-11: Summary of statistics associated with Eq. 4.11.

Independent variables	Associated statistics						
	b	SE b	95% conf. interval for b			F	Pr>F
Contant	0.96	0.30	0.37	-	1.55	10.05	0.01
Ra	0.06	0.01	0.04	-	0.08	15.92	0.01
DC1a	0.05	0.03	0.01	-	0.09	2.25	0.14
DC1a x Ra	-0.41E-2	0.17E-02	0.77E-03	-	-0.71E-02	5.57	0.05

APPENDIX II

A. SUMMARY OF STATISTICS ASSOCIATED WITH EQUATIONS 4.12 THROUGH 4.15

TABLE II-1: Summary of statistics associated with Equation 4.12.

Independent variable	Associated statistics				
	b0	SEb	95 % Conf. Interval for b	F	Pr>F
Constant	0.761	0.015	0.732 - 0.790	2461.85	0.01
Va	0.019	0.004	0.011 - 0.027	23.78	0.01
DC1a	-0.008	0.001	-0.006 --0.010	41.01	0.01

TABLE II-2: Summary of statistics associated with Equation 4.13.

Independent variable	Associated statistics				
	b0	SEb	95 % Conf. Interval for b	F	Pr>F
Constant	0.256	0.043	0.172 - 0.340	35.75	0.01
Va	0.305	0.012	0.281 - 0.329	695.85	0.01
CRa x DC1a	-0.019	0.005	-0.009 --0.029	11.58	0.01

TABLE II-3: Summary of statistics associated with Equation 4.14.

	Associated statistics				
Independent variable	b0	SEb	95 % Conf. Interval for b	F	Pr>F
Constant	0.901	0.014	0.874 - 0.928	4360.09	0.01
Vp	0.020	0.010	0.000 - 0.040	3.93	0.05
DC1a	-0.003	-0.001	-0.001 - -0.005	9.08	0.01
DC1p	-0.005	0.536E-02	-0.004 - -0.006	75.69	0.01

TABLE II-4: Summary of statistics associated with Equation 4.15.

	Associated statistics				
Independent variable	b0	SEb	95 % Conf. interval for b	F	Pr>F
Constan	0.128	0.022	0.085 - 0.171	34.54	0.01
DC1p	0.005	0.935E-03	0.003 - 0.007	23.36	0.01
Vp x CRp	0.678	0.018	0.643 - 0.696	1387.1	0.01
Vp x DC1a	-0.017	0.004	0.009 - 0.025	20.20	0.01

APPENDIX III

SENSITIVITY ANALYSIS OF THE 1983 VOLUME INCREMENT OF THE SUBJECT TREES

SENSITIVITY ANALYSIS: DETERMINATION OF THE CHANGE IN THE 1983 VOLUME INCREMENT OF THE SUBJECT TREE DUE TO CHANGE IN PREDICTOR VARIABLES

The change in the 1983 volume increment of aspen subject trees is used as an example. An analogous procedure was used to determine the change in the 1983 volume increment of jack pine subject trees.

The change in the 1983 volume increment of aspen subject trees due to direct and indirect effects of predictor variable in question was determined after deriving equations 4.12 and 4.13.

$$\Delta Va = 0.256 + 0.305Va - 0.019(CRa \times DC1a) \qquad [4.12]$$

$$CRa = 0.761 + 0.019Va - 0.008DC1a \qquad [4.13]$$

The dependent and independent variables are defined on pages 43 and 48.

The change in the 1983 volume increment of aspen subject tree due to direct effect of initial volume of aspen subject tree was determined by increasing the initial volume of aspen subject tree (Eq. 4.12) by one standard deviation, S.D., (obtained from Table 4.2 on page 48) while all other predictor variables are held at their mean value. The computations were done as follows:

Change in the 1983 volume increment due to direct effect of Va

$\Delta\widehat{Va}$ (before change) = 0.305Va

$\Delta\widehat{Va}$ (after change) = 0.305Va + 0.305(1 x $S.D._{Va}$)

Change in $\Delta\widehat{Va}$ = $\Delta\widehat{Va}$ (after change - before change)

= 0.305Va + 0.305(1 x $S.D._{Va}$) - 0.305Va

= 0.305(1 x $S.D._{Va}$)

= 0.305 x 1.836

= 0.55998

% change in mean $\Delta\widehat{Va}$ = (0.55998 x 100)/1.098

= 51 %

where:

1.098 and 1.836 are respectively 1983 mean volume increment of aspen subject trees and its standard deviation (Table 4.2)

Change in the 1983 volume increment due to indirect effect of aspen competition via the live crown ratio

Change in $\Delta\widehat{Va}$ = -0.019(-0.008 x 5.521)4.323

= 0.00363

% change in mean $\Delta\widehat{Va}$ = (0.00363 x 100)/1.098

= 0.3 %

where:

4.323 and 1.098 are respectively mean aspen components of Daniels' competition index and its standard deviation; while 1.098 is the 1983 mean volume increment of aspen subject tree

An analogous procedure was repeated for all the predictor variables where applicable.