# STAND AND TREE DYNAMICS IN UNEVEN-AGED INTERIOR DOUGLAS-FIR STANDS

by

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### **Abstract**

The Interior Douglas-fir Biogeoclimatic Zone covers 4 million hectares in the southern interior of British Columbia. This zone is dominated by interior Douglas-fir forests which are valued for their timber, wildlife, range and recreational values. Interior Douglas-fir can be found growing naturally in unevenaged structured stands; a structure that forest managers often want to maintain for its ability to sustain multiple values. However, the growth dynamics in these stands are complex and little is known about the interactions that occur among the individual trees of varying ages and sizes. The objectives of this study are to address this lack of understanding at both the individual tree and stand levels.

Data were collected at an installation of permanent sample plots established in uneven-aged stands of interior Douglas-fir at the Knife Creek Block of the Alex Fraser Research Forest, near William's Lake, B.C. These data were used to explore growth trends that may be attributed to the differences in stand structures among the plots. These data were also used to assess several competition indices representing a range of complexity in order to investigate the growth dynamics within the study stands. The competition indices were evaluated by testing non-linear regressions that used the indices and dbh to predicting dbh growth. The performance of the regressions were then compared to the performance of a base regression that used dbh alone.

It was found that the growth of the various stand level attributes measured was similar among the plots despite the differences in stand structures. The assessment of the competition indices revealed that the least complicated of the individual tree level indices tended to produce the best performance. The distance dependent indices consistently performed better than the distance independent indices. From the analysis results it was inferred that a relationship of relative symmetry, also termed resource depletion, exists among the study trees. This implies that competition occurs mainly for below ground resources. The relationship between the trees was found to be two-sided due to the influence that small trees had on larger trees.

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### 1 Introduction

One of the most important goals in forest management is to ensure the sustainability of forest resources. Forest policy often requires that the sustainability of any planned treatment or harvesting operation must be proven before the plan can be implemented. This is difficult to prove because it involves predicting the long-term effects of the management actions on the growth and development of the treated stands. A key tool to making these predictions is a reliable model. A stand growth model can be used to estimate the future structure and composition of a stand after various management actions have been applied and thereby can give a certain level of confidence that the selected actions will not jeopardize the sustained production of forest resources. However, the level of confidence will vary according to the reliability of the model. The credibility of the predictions made by a model depends on the quantity and quality of the recorded growth data that were used in its calibration and it also depends on how well the model reflects the growth dynamics of the species being modelled on a given site.

These requirements of a reliable model have been problematic when creating management plans for interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) stands in British Columbia (B.C.). Little is known about the growth dynamics of these trees and limited growth data have been collected (Bonner 1990). This is mainly due to the fact that interior Douglas-fir grows in highly variable stands that can be found in a wide diversity of structures ranging from dense even-aged structures to widely spaced uneven-aged structures. A large amount of growth data representing all of these structures is required to calibrate a model that would be able to reliably predict the development of the range of structures found across the landscape.

The growth dynamics of even-aged interior Douglas-fir stands are already fairly well understood because they follow similar growth patterns to the coastal variant of the species, which has a long history of management and modelling in B.C. The growth dynamics of uneven-aged stands of interior Douglas-fir are more complicated than in even-aged stands because each stand can be composed of trees from a wide range of ages and sizes. Little is known about the interactions among trees of various ages and sizes, which makes it difficult to predict how a stand will respond to management actions. The importance of gaining an understanding of these growth dynamics in order to develop sustainable management plans for uneven-aged stands has been increasing recently because of a growing public pressure towards managing stands in uneven-aged structures that are able maintain particular values (Schmidt 1990).

With the intent to fill some of these gaps in the current understanding of interior Douglas-fir growth, an installation of six permanent sample plots was established in 1988. The plots were placed in the Interior Douglas-fir biogeoclimatic zone in the vicinity of William's Lake, B.C. Marshall and Wang (1996) described the original purpose of the installation as follows:

The intent was to provide long-term information on individual tree and stand dynamics that could be used to explore relationships between various characteristics of stand structure and several measures of tree and stand growth. Stands representing three visibly different stand structures were selected and two plots were established in each stand condition. Specific plot locations were selected to reflect as wide a diversity of stand density and structure as possible, while still maintaining a mixture of different height and diameter classes within each plot.

As part of the process of selecting appropriate plot locations that represented the different stand structures, the plots were subjectively placed in relatively uniform stands. Since the plots avoided the many openings in the stands that are common in the study area, the average value of the attributes measured in the plots will be higher than what would be expected across the landscape. The study was not designed to contribute data that could be used to calibrate growth models; it was designed with the exploratory objective to increase the current understanding of the growth dynamics in uneven-aged interior Douglas-fir stands.

After the 1992 growing season, a second measurement of the plots was conducted and the data collected were compiled together with the data recorded during the establishment. Marshall and Wang (1996) calculated the growth of the various measured attributes that occurred over the period between the two measurements and looked for trends between the growth values and the different stand structures represented in the plots. Due to the relatively short growth period, distinct growth patterns and relationships were difficult to find. Overall, they concluded that the growth of the various stand attributes appeared to be independent of differences in stand structures, within the densities studied. Before the 1997 growing season, a third measurement of the plots was completed for use in this study. Marshall and Wang (1996) hypothesized in their report that clearer indications of the trends in growth would be found when growth data covering two growth periods would be combined and analyzed.

The first objective of this study is to continue the investigations of Marshall and Wang (1996) to "explore relationships between various characteristics of stand structure and several measures of tree and stand

growth". Data from the 1997 measurement was used to calculate the growth of the measured attributes over the second growth period. The results were then analyzed in an attempt to check the validity of Marshall and Wang's hypothesis.

In the original purpose statement for the installation of the permanent sample plots, it was stated that the plots were established so that both individual tree and stand dynamics could be explored. Thus far, the plot data have mainly been used to look at the relationships between stand-level attributes and stand structure. In order to make investigations at the individual tree level possible, detailed measurements of the diameter, height, crown width and the spatial location of each tree were recorded in the plots. These data offer the opportunity to investigate the relationship between tree growth and stand structure at the more detailed individual tree level. The spatial data also make it possible to investigate the potentially more interesting relationships between an individual tree's growth and its immediate growing environment.

The relationship between an individual tree and its immediate environment is of particular interest in uneven-aged stands because almost every tree in an uneven-aged stand structure has a unique position within the stand canopy and a unique combination of neighbouring trees of varying sizes. This results in a wide range of both growing environments and individual tree growth rates within a stand. When individual tree growth rates are averaged out to a stand level value, this wide range of variation is masked. The influence of neighbouring trees on an individual tree is often measured in terms of competition. This is because most interactions between neighbouring trees occur as each tree attempts to maximize its access to the available resources. This results in interactions such as shading and root competition which have a large impact on individual tree growth rates. Therefore, a greater understanding of the growth dynamics within uneven-aged stands can be found through investigations into the processes of competition.

The second objective of this study is to use the individual tree measurements and spatial data to investigate the competitive relationships that exist in the study stands. The competitive relationships were quantified and analyzed using competition indices. A diversity of competition indices covering a range of computational complexities can be found in the literature. This diversity has developed because each index is based on a different hypotheses about the nature of the competitive relationships that exist in the stands being studied. Considering this, several competition indices representing the range of complexity were selected from the literature. The ability of each index to represent the competitive stress experienced by individual trees was tested using the data from the study plots. From the relative

performance of each index, inferences were made as to how well the underlying hypothesis used for each index applied to the study stands. Through this evaluation process, insights were gained into the nature of the competitive relationships influencing growth in the study stands.

The overall objectives to be met by this study were:

- 1) to describe and discuss stand growth trends that may be attributed to the differences in stand structures among the plots; and
- 2) to assess several competition indices representing a range of complexity in order to investigate growth within the study stands.

The study begins with a literature review containing a brief synopsis of the silvics of interior Douglas-fir and a description of the region of B.C. in which the study was conducted. A review of the literature concerning studies of competition and the development and testing of competition indices is also provided as a background for this study. The literature review is followed by a detailed description of the methods. Chapter 4 presents the results of the various analyses that were conducted. This is followed by a general discussion and conclusions in the fifth and sixth chapters, respectively.

### 2 Literature Review

#### 2.1 The Interior Douglas-fir Zone

The Interior Douglas-fir (IDF) Biogeoclimatic Zone covers 4 million hectares in the southern interior of British Columbia. The zone extends approximately from William's Lake in the north to the southern end of the Okanagan Valley. It follows the main valleys in the south central part of the province and expands onto the adjacent Fraser and Thompson plateaus in the north (Bonner 1990, Newsome *et al.* 1990). The main portion of the IDF Zone is located on these plateaus, where it spreads over the rolling terrain and skirts the lower slopes of the mountain ranges (Vyse *et al.* 1990). Here the zone is typically bounded by the Montane Spruce (MS) Zone at higher elevations and the Ponderosa Pine (PP) Zone at lower elevations (Hope *et al.* 1991).

The IDF Zone ranges in elevation from 350 to 600 m in valley bottoms to a maximum height of 900 to 1450 m (Hope *et al.* 1991). It is the warmest and driest of the forested Biogeoclimatic Zones (Vyse *et al.* 1990). The climate within the zone is continental and is characterized by warm, dry summers, a fairly long growing season, and cool winters. The mean annual temperature ranges from 1.6 to 9.5° C with 2 to 5 months of the year below 0° C (Hope *et al.* 1991). Frost can be experienced in any month of the year, especially in low lying areas with poor air drainage (Steen 1987). Precipitation is low due to the influence of the rainshadow cast by the Coast and Columbia Mountains (Vyse *et al.* 1990). Substantial growing season moisture deficits are common within the zone. Mean annual precipitation ranges from 300 to 750 mm, with 20 to 50% falling as snow (Hope *et al.* 1991). Peaks in precipitation come in early winter (December to January) and early summer (June to July). However, year to year variation in the amount and distribution of precipitation is considerable (Steen 1987).

Forests of varying species composition and structure cover much of the IDF Zone landscape. Pure interior Douglas-fir climax stands are common, as well as mixed stands with lodgepole pine (*Pinus contorta* Dougl.). Ponderosa pine (*Pinus ponderosa* Dougl.) occurs as a climax species in low elevation, drier sites in the southern portion of the zone. It also can be found as an early seral species that is eventually replace by interior Douglas-fir. Trembling aspen (*Populous tremuloides* Michx.) is a widely distributed seral species throughout the zone. Interior white spruce (*Picea engelmannii* x *glauca*) can be found at higher elevations. Western redcedar (*Thuja plicata* Donn.), grand fir (*Abies grandis* (Dougl.) Lindley) and paper birch (*Betula papyrifera* L.) are limited to wetter areas. Western Larch (*Larix occidentalis* Nutt.) is restricted to the southeastern part of the zone (Hope *et al.* 1991). Grassland communities are also found across much of the IDF landscape.

#### 2.1.1 Silvics of Interior Douglas-fir

#### 2.1.1.1 Individual Tree Characteristics

Interior Douglas-fir has the broadest ecological amplitude of any western tree (Monserud and Rehfeldt 1990 in Arno 1990). It can be found growing in a range than covers the length of North America from British Columbia to northern Mexico. The range appears to be limited from higher elevations by insufficient growing season warmth and repeated frost damage (Arno and Hammerly 1984 in Arno 1990).

Interior Douglas-fir can be found growing on all slope aspects and almost all geological parent materials (Arno 1990). The dry regions of the IDF Zone contain relatively young and infertile soils with shallow organic horizons and compact soil parent materials (Mitchell and Green 1981 in Vyse *et al.* 1990). Interior Douglas-fir is sensitive to varying levels of organic materials because the organic horizons and organic deposits are high in moisture and rich in nutrients. Natural regeneration is often found on large deposits of soil humus or buried decayed wood (Graham *et al.* 1990). The nutritional requirements of interior Douglas-fir have been categorized as moderate to high. Growth has been found to be best on sites rich in calcium and magnesium (Steen 1987).

Interior Douglas-fir reproduces profusely following small scale disturbances to the overstory (Vyse *et al.* 1990). Seed production is generally prolific and abundant crops usually occur every two to seven years. Interior Douglas-fir is moderately shade tolerant. Shade is not required except perhaps at the time of germination (Vyse *et al.* 1990). During the period of early growth, interior Douglas-fir can survive in moderate to deep shade and has been found to release well after growing in shaded conditions (Steen 1987).

The growth of interior Douglas-fir is likely to be reduced more often by water availability than by any other factor (Lopushinsky 1990). Interior Douglas-fir has been categorized as more drought resistant than Englemann spruce (*Picea engelmannii* Parry), but is less resistant than ponderosa and lodgepole pine (Minore 1979 in Lopushinsky 1990). Severe water deficits can cause growth reductions, dysfunction of many processes occurring within the tree, and can increase the susceptibility of the tree to attacks by pathogens and insects (Lopushinsky 1990).

The productivity and growth of interior Douglas-fir is highly variable due to the wide range of growing conditions and factors affecting growth that occur in the IDF zone. In a growth and yield study of the IDF zone, Bonner (1990) observed growth rates from 2 m<sup>3</sup>/ha/yr to more than 9 m<sup>3</sup>/ha/yr. This was

higher than other studies referred to by Bonner such as Clark (1952 in Bonner 1990) who found growth rates of 2.8 to 3.9 m³/ha/yr, Johnstone (1985 in Bonner 1990) who reported 1.8 m³/ha/yr, and the British Columbia Ministry of Forests timber supply analysis which estimates 3.7 to 4.4 m³/ha/yr for good sites and 2.0 to 2.7 m³/ha/yr for medium sites. Arno (1990) referred to studies that reported growth rates of 0.7 to 1.4 m³/ha/yr to well over 7 m³/ha/yr in very wet areas (Pfister *et al.* 1977 in Arno 1990; Steele *et al.* 1981, 1983 in Arno 1990).

Genetic variability is wide in interior Douglas-fir. The necessity to adapt to the wide ecological gradient that occurs in the IDF zone is the most likely cause of the development of this trait (Rehfeldt 1990). The maintenance of a healthy forest depends on the presence of high levels of genetic variability. Therefore, a large proportion of the genetic variability exists within stands and extensive variability in susceptibility to pest damage can be found among trees in a stand. Individual trees that are resistant to the attacks of one pest are often susceptible to attacks from another pest (Linhart and Davis 1990). A diversity of other genetic differences relating to traits such as growth potential and cold hardiness are also readily detectable. Strong genetic correlations between adaptive traits have resulted in tree breeders accepting less than maximum growth characteristics to ensure that the adaptiveness of the tree is not reduced (Rehfeldt 1990).

#### 2.1.1.2 Stand-level Characteristics

The structure of interior Douglas-fir stands is highly variable due to the wide range of climatic conditions in the IDF zone (Steen 1987) and other factors such as pathogens, insects, and fire (Vyse *et al.* 1990). Interior Douglas-fir can be found growing in mixed stands with a wide range of species (Arno 1990). It can occupy all positions within the canopy and can act in different successional roles (Schmidt 1990).

On the driest and warmest sites, interior Douglas-fir acts as a climax species. It grows in relatively open stands replacing ponderosa pine which grows as the seral species (Steen 1987). These stands are characterized by an overstory composed of over-mature trees, covering a range of ages with full or ragged crowns. The trees are widely spaced and have heavy limbs. The older trees range in age up to 350 years and can reach up to 35 m in height and 100 cm in dbh. There is typically an intermediate story of mid-sized dbh trees or a regeneration layer; sometimes there are both (Vyse *et al.* 1990). On moister sites, interior Douglas-fir grows in even-aged stands with other species such as lodgepole pine (Vyse *et al.* 1990). As the amount of moisture increases and the temperature decreases, the stands become more closed and multi-storied and the density of the regeneration increases (Steen 1987).

The IDF zone is characterized by fire regimes that range from frequent low intensity ground fires to severe stand replacing fires (Arno 1990). The warm dry sites often experience frequent low intensity fires that favour the growth of the more seral and fire resistant ponderosa pine and larch, forming stands that are more open (Schmidt 1990). Less frequent and more intense fires occur on moister sites, where interior Douglas-fir often acts as a seral species after the fire (Arno 1980 in Harrington 1990).

Historically, fire frequency in the IDF zone has been estimated to range from 20 to 40 years (Arno and Gruell 1983 in Jay and Hutton 1990). However, the current practice of fire suppression is altering the characteristics of many stands within the IDF zone. On dry sites, where the seral species were favoured by frequent fires, fire suppression has allowed interior Douglas-fir to continue to grow towards climax and it can often begin to invade surrounding grasslands. Both logging and fire suppression encourage interior Douglas-fir regeneration (Vyse *et al.* 1990). Stands often begin to form multiple layers as regeneration, that would have typically been killed by fire, continues to grow in the understory. These multi-layered stands have been found to have an increased susceptibility to many insects and diseases (Schmidt 1990).

By altering the stand conditions through harvesting or fire suppression, humans have created more hospitable environments for many species of forest pests. Outbreaks of these pests were common before these human interventions; however, now the outbreaks frequently are increased in duration and intensity (Byler and Zimmer-Gore 1990). Damaged trees can be salvaged to reduce economic losses, but the unplanned harvest may conflict with other management goals.

Interior Douglas-fir acts as a host to bark beetles (*Dendroctonus pseudotsugae* and *Scolytus* spp.), western spruce budworm (*Christoneura occidentalis*), and Douglas-fir tussock moth (*Orgyia pseudotsugata*) which can be found in stands alone or in combinations (Byler and Zimmer-Gore 1990). High density stands with multiple layers provide sheltered habitat for Douglas-fir tussock moth and western spruce budworm (Vyse *et al.* 1990, Byler and Zimmer-Gore 1990). The damage caused by western spruce budworm is mostly restricted to growth losses and mortality in lower canopy classes or mature stems on poor sites. However, Douglas-fir tussock moth can cause extensive mortality in low elevation stands (Vyse *et al.* 1990). Failures of natural regeneration have also been attributed to cone damage caused by western spruce budworm (Jay and Hutton 1990).

Pathogens such as shoe string rot (*Armillaria ostoyae*), laminated root rot (*Phellinus weirii*) and Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) can be found in stands of interior Douglas-fir (Hepting 1971 in Graham 1990). *Armillaria* and *Phellinus* contribute to the gaps commonly found in stands of interior

Douglas-fir. The occurrence of *Armillaria* is often associated with sites on which surface fires have historically maintained primarily seral species. Douglas-fir dwarf mistletoe is passed from upper canopies to the understory and is therefore easily spread in multi-layered stands (Byler and Zimmer-Gore 1990).

#### 2.1.2 Forest Uses

Interior Douglas-fir forests are valued for many potential uses. However, it is difficult to identify any one value as outstanding above the rest (Schmidt 1990). This makes it hard to justify the management of these forests for one value over another and often it is necessary to try to manage these forests for many values simultaneously.

#### 2.1.2.1 Timber

Interior Douglas-fir stands are valued for the high quality timber they produce. The low elevation of the stands and their proximity to highways and manufacturing plants make these stands highly desirable for harvesting (Day 1996). Interior Douglas-fir contributes to a large portion of the timber processed by many of the interior sawmills (Vyse *et al.* 1990). The history of timber harvesting in interior Douglas-fir stands has been primarily dominated by highgrading (Day 1996). The practice of highgrading removes the larger and more valuable seral species and leaves a degraded stand that is more susceptible to pest attacks (Schmidt 1990). Currently, there is an increasing emphasis on thinning to rehabilitate these stands in order to increase individual tree growth rates while decreasing the risk of pest attacks (Vyse *et al.* 1990).

The silvicultural system options often depend on the stand structure characteristics. In stands where interior Douglas-fir is seral with a single or two layer structure, clearcutting, shelterwood and seedtree systems are viable choices. When interior Douglas-fir is climax with an uneven-aged structure, individual tree selection or group selection may be more appropriate (Schmidt 1990). Most stands in the IDF zone are harvested using some form of partial cutting and are restocked by natural regeneration (Vyse *et al.* 1990 in Newsome *et al.* 1990). It has been argued that interior Douglas-fir occurs naturally as unevenaged stands and should be managed accordingly (Bonner 1990). However, partial cutting and shelterwood systems have been criticized because they put regeneration at increased risk of pest attacks and partial cutting has been found to increase mortality in residual stands (Hagle and Goheen 1988 in Vyse *et al.* 1990).

Even-aged systems may be less susceptible to pest attacks, but often result in regeneration problems. In dry regions or on south facing slopes, interior Douglas-fir regeneration in large gaps often fails or has slow growth because of competition with grasses for soil moisture and high surface temperatures (Schmidt and Larson 1989 in Jay and Hutton 1990). Strip cut and shelterwood systems can reduce regeneration problems but are also more prone to the same pest problems as partial cutting systems (Jay and Hutton 1990). Even-aged systems often conflict with other management values that require continuous cover such as wildlife and visual quality values.

#### 2.1.2.2 Wildlife

The ecological diversity of the IDF zone creates a variety of stand structures that provide a wide range of habitat niches, supporting many species of wildlife (Hope *et al.* 1991). Ungulates such as elk (*Cervus elaphus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and mountain sheep (*Ovis canadensis*); predators such as mountain lions (*Felis concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*); and numerous species of birds and small mammals can all be found in interior Douglas-fir forests. The dense multistoried stands provide cover to the animals and the grasslands and forest gaps provide forage (Schmidt 1990).

The short, cool winters and variable canopy closure attract many animals to overwinter in the low elevation sites and south facing slopes of the IDF zone. Mule deer, white-tailed deer, mountain sheep and elk all can migrate long distances to spend the winter in interior Douglas-fir forests (Hope *et al.* 1991). These stands provide forage, thermal cover and shallow snow which are all necessary for these animals to maintain their energy balance on an annual basis (Armleder *et al.* 1986). Current management has concentrated on maintaining this winter habitat for large ungulates, but biodiversity concerns will likely shift the management focus to include small birds and mammals (Vyse *et al.* 1990).

#### 2.1.2.3 Range

The grasslands and forests in parts of the IDF zone are valued as cattle range. Management actions that favour the growth of dense stands can decrease the amount of forage available to cattle (Schmidt 1990). Cattle grazing itself has been suspected of contributing to the growth of dense stands when the cattle remove the grasses that compete with interior Douglas-fir regeneration (Jay and Hutton 1990). Grazing

has also contributed to problems with regeneration when the seedlings are trampled by cattle (Newsome *et al.* 1990).

#### 2.1.2.4 Water

Water quality is rarely a concern in interior Douglas-fir forests. Moderate precipitation and temperatures in the IDF zone result in most of the water being used up by vegetation before it reaches the lower soil depths. Therefore, the effects of stand treatments on water yields are limited (Swank *et al.* 1989 in Schmidt 1990).

#### 2.1.2.5 Recreation

The low elevation and proximity to population centers makes interior Douglas-fir stands important for recreational use (Day 1996). Roads allow easy access for hunting and fishing (Vyse *et al.* 1990). The hardiness of interior Douglas-fir stands makes them tolerant to high levels of recreational use. The ability to manage the forests using partial cutting systems allows managers to maintain a high aesthetic quality for visitors (Schmidt 1990).

#### 2.2 Studies of Competition

The term competition refers to the mainly negative effect on the growth rate and form of a plant due to the presence and behaviour of neighbouring plants (Harper 1961 in Weiner 1982). Competition is often defined as a form of plant to plant interference. This interference is mediated through the use of shared environmental resources, such as light, water and soil nutrients (Bazzaz 1990 in Tremmel and Bazzaz 1993).

This definition implies that competition only occurs when the supply of shared resources falls below the combined demands of the plants within a population (Cannell and Rothery 1984). Before competition occurs, individual plant growth rates can vary because of individual differences in microsite conditions and the genetic compositions of the plants. Once the resource demand of the population passes the amount available and competition begins, the variation in growth rates increases and the population begins to develop a wider distribution of plant sizes (Penridge and Walker 1986). These changes occur as each plant reacts to having its access to resources limited by other plants and, in turn, as it makes

resources limited to other plants (Bazzaz 1990 in Tremmel and Bazzaz 1993). A plant's response to competition varies depending on the spatial relationship between the plant and its neighbours and its ability to react to competitive losses through changes in architecture and physiology (Tremmel and Bazzaz 1993).

Many studies have been conducted in order to investigate the connection between a plant's competitive response and its spatial relationship with its neighbours (e.g., Benjamin 1993, Bonan 1988, Weiner 1982). Most studies of competition have focused on the effects of competition at a population level by manipulating the density of the population in regularly spaced experimental growth plots. From these studies, observations can be made on the effects of competition on population total values of yield, reproduction, and mortality (Barclay and Layton 1990). Competition processes are inferred, but the underlying competitive mechanisms are seldom elucidated. This shortfall is due to the fact that interplant distances are scarcely ever regular in 'natural' growing conditions. Therefore, density is a very crude measure of the level of competition experienced by an individual plant. Plants react to the activity of neighbouring plants, not population density (Mack and Harper 1977). If a study only looks at density, important variation due to plant size and competitive ability are obscured (Penridge and Walker 1986)

Other factors that influence the growth and form of a plant such as initial size, vigour, microsite, and genetic characteristics can all contribute to the difficulty in isolating the effects of competition alone (Brand and Magnussen 1988). Therefore, neighbourhood experiments that aim to isolate and study the effects of local neighbours on a plant have been established. In these experiments, various spatial arrangements of neighbouring plants are grown around a focal plant under controlled conditions (e.g., homogenous site quality, uniform initial size, low genetic diversity seed). From these experiments, the effects of the distance between plants and the number of neighbours on the growth of the plant can be observed (Thomas and Weiner 1989).

Neighbourhood experiments are not only established to look at the effects of competition on plant growth and form, but also to try to answer some of the long standing questions about the underlying biological processes of competition. Plants interact in several ways that can be observed, such as the shading of plant canopies by other canopies or the amount of area a species is able to occupy compared to another species. However, many of the processes cannot be observed (e.g., below ground root interactions). Therefore, researchers must try to infer the underlying mechanisms from experimental results. Because every plant species seems to have its own specific reaction and strategy towards competitive growing conditions, it is difficult to generalize experimental results. There are several issues that must be

examined and, if possible, tested in order to understand the particular competitive strategy of the species and to infer the underlying mechanisms.

The first and most widely debated issue is the spatial extent to which a plant can be assumed to exert a competitive influence. Often a region is defined around a subject plant to represent the reach of its competitive influence. By doing this, neighbouring plants that are located within this region can be identified as competitors. The method used to define this region is a very important consideration, because it is often used as the underlying foundation for investigative studies and models of competition.

Four main approaches have been proposed as methods for defining the region of competitive influence for a plant. The first approach is that there is no competitive region around a plant and that competition is only a diffuse population effect. Only the number of plants in the population is relevant and the distance to the neighbouring plants is not considered. The second approach is that there is a region around a plant, but it does not have a definable boundary. The third approach is that there is a boundary for this region, but the region cannot overlap with the regions of the neighbouring plants. The size of the region around a plant is therefore limited by the proximity of its neighbours. The last approach is that the region is bounded, but can overlap with other regions (Benjamin and Hardwick 1986 in Benjamin 1993).

All of these approaches are based on assumptions of the biological processes that enable the root system of a plant to access and compete for resources. No one approach can be accepted as superior over the others because each plant species will have its own unique way of interacting with the root systems of other plants when growing in a specific environment. However, it is possible to test which approach is most appropriate for a species under specific conditions using neighbourhood competition experiments (Benjamin 1993). For example, the diffuse approach can be tested by evaluating whether or not the proximity of a set of neighbours has any effect on the growth of a focal plant. The non-overlapping approach can be tested by evaluating whether neighbours that are located beyond the plant's immediate neighbours can have any influence on the growth of a focal plant.

Once a region of competition has been defined, the second issue that must be addressed is how the limited resources within that region are shared. Many theories suggest that resources should be partitioned between a plant and its neighbours based on their relative sizes (Weiner 1984, Cannell and Rothery 1984). This resource sharing is usually referred to in terms of symmetry. If it is proposed that all of the resources are divided equally between the plants regardless of size, the relationship is referred to as absolute symmetry. If it is proposed that resources are shared directly proportional to plant size,

the relationship is termed as relative symmetry (Thomas and Weiner 1989). However, it has also been hypothesized that there can be inequalities in this proportional sharing. For example, large plants may be able to access disproportionately more resources than smaller plants. In this case, the relationship is termed asymmetrical (Weiner 1984)

Like the concepts of competitive regions, these theories are used to describe the possible biological processes occurring not only among the root systems of the plants, but also among their leaf canopies. The term resource depletion can be used interchangeably with symmetry and is hypothesized to represent a situation where the majority of competition occurs for below ground resources. The term resource preemption can be used interchangeably with asymmetry and often implies situations where canopy competition for light is occurring. In this situation, large plants are able to shade out smaller plants causing the characteristic disproportionate allocation of resources (Newton 1993).

Different degrees of symmetry or asymmetry can be expected on different sites and in different stages of stand development (Thomas and Weiner 1989). However, when a relationship of asymmetry is occurring, it can be observed in the development of increased inequality in plant sizes. Asymmetry assumes that there is a relationship of "dominance and suppression", where disproportionate sharing results in size differences being accentuated over time (Bonan 1988).

Another issue discussed in plant competition studies concerns the relationships between large and small plants. When small plants are growing in the competitive region of a large plant but are considered to have no effect on the large plant, the relationship is defined as one-sided. If all the plants growing within the region of the large plant have some influence on its growth, the relationship is termed two-sided (Brand and Magnussen 1988). As with symmetry and asymmetry, each term can be associated with relationships where a different resource is limiting. It is often hypothesized that below ground resources are limiting when a two-sided relationship is observed, because the small plants are able to use the below ground resources at the expense of their larger neighbours. A one-sided relationship is often suggested as representing competition for light because small plants below the canopy of a larger plant will likely have no effect on the larger plant if below ground resources are not scarce (Thomas and Weiner 1989). However, a competitive relationship is rarely found to be one extreme or the other, as both competition for light and below ground resources can occur simultaneously.

Like an asymmetrical relationship, a one-sided relationship will tend to accentuate size inequalities within a population. Over time these relationships tend to form hierarchies within a population. This process is

especially evident in even-aged populations where there is a trend for a normally distributed mass of seedlings to develop over time into a positively skewed distribution in which there are a few large dominants and many small suppressed individuals (Weiner 1982, Thomas and Weiner 1989). The role of competition in the formation of these hierarchies and the competitive interactions between the individuals within each hierarchy are not fully understood and are often of particular interest to researchers (Bonan 1988).

Mack and Harper (1977) studied the effect of spatial patterns and neighbourhood effects between dune annuals. Their objective was to find how much plant-to-plant variation could be related to small differences in species proximity and pattern of arrangement of neighbours. The study found that the size, distance and pattern of neighbour arrangement could account for up to 69% of the variation observed in the focal plant's weight. It was noted that these results disprove the diffuse competition effect approach.

Another neighbourhood competition study was conducted by Weiner (1982) using annual plants. Weiner studied seed production of focal plants while varying the number of neighbours arranged around them in concentric rings. He created a model that considered the spatial arrangement of the neighbouring plants. Weiner found the model to have good predictive ability and hypothesized that the model could be used to study the effects of spatial patterning in crops.

Cannell and Rothery (1984) noted that there are many models of competition in the current literature, but that there are few studies that observe the process of competition in extensive plots. The objective of their study was to observe competition processes within stands of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine. Before making their observations, Cannell and Rothery hypothesized that competition will be a stochastic process if the trees are randomly distributed and the expected outcome would be an even dispersion of large and small plants. However, they also noted that this would only occur if the resources competed for are evenly distributed, which is rarely true in 'natural' environments. Environmental heterogeneity will make observations of dispersion due to competition difficult. In their observations, Cannell and Rothery found a sigmoid relationship between plant size and plant growth. This relationship results in a bimodal frequency distribution of plant sizes. They explained this relationship and distribution as the result of a one-sided relationship between the trees, indicating that light was a limiting factor.

Brand and Magnussen (1988) attempted to quantify competition in even-aged monocultures of red pine (*Pinus resinosa* Ait.). To do this, they measured the vigour of several stands that were all of the same mean diameter, but stocked at different densities. Variation due to differences in age was ignored in the study. Brand and Magnussen found that the small trees had the highest vigour in low density stands. They hypothesized that this was due to lower maintenance respiration levels per unit foliage. As density increased, the vigour of the smaller trees decreased, which they concluded was an indication of an asymmetrical relationship between the trees. They also concluded that competition within the observed stands was two-sided, since the tallest trees also reduced in vigour as density increased.

Models of theoretical plant populations were used by Bonan (1988) to investigate the effects of neighbourhood spatial patterns. He hypothesized that if competition is an important factor in the development of hierarchies, spatial patterns and neighbourhood effects should be an important determinant of size distributions within a population. His study modelled the growth of one plant alone, the growth of a population with a random distribution, and a population with even spacing. The initial masses and growth rates of the plants in the populations were varied in successive model runs, with either uniform or random values assigned to the plants. The competitive relationships between the plants was also varied between symmetrical and asymmetrical. The model was then run for every possible combination of these variables.

Bonan found that the evenly spaced model runs only maintained higher yields than the random spacing until the plants in the population reached a size where they began to compete with each other. When the model runs of uniform initial masses and random initial masses were compared, Bonan found that size inequalities created by the randomly assigned initial size values actually decreased until competition began. The model runs that had randomly assigned growth rates all formed hierarchies before the plants began competing and confounded the effects of spatial pattern. Bonan hypothesized that the randomly assigned growth rates could represent variation due to microsite heterogeneity and genetic differences. In all the simulations, the asymmetrical relationship runs resulted in greater variation in growth rates.

The four different approaches to defining the region of competitive influence around a plant were tested in a neighbourhood experiment using carrots by Benjamin (1993). Carrots were grown in varying numbers of rings around a focal plant at varying radii. Benjamin found that the focal plant mean weight decreased as the number of rings increased, which falsified the non-overlapping region approach. He also found that increasing the radius of the first ring increased the weight of the focal plant which allowed the diffuse population effect approach to be rejected. By observing the growth rate of the focal

plant over time, Benjamin was able to note that the growth rate showed a decrease sooner in trials with close neighbours due to faster complete overlap from the neighbours' competitive regions. He concluded that this would not occur according to the unbounded region approach. Therefore, Benjamin concluded that the bounded region approach was the most appropriate for carrots.

#### 2.3 Incorporating Competition into Growth Models

Models are representations of the way a system is believed to work. Forest growth and yield models can be used to improve the modeller's knowledge of the system or they can be used to make predictions about the future state of the forest. These models are generally divided into two categories: process models and empirical models. Process models tend to be used as exploratory tools to investigate the biological interactions that occur within a forest system. Empirical models are more often relied upon as tools to predict how management actions will affect the development of a forest.

Both types of models can be constructed to incorporate and model the effects of competition. However, since modellers and researchers are in a constant process of debating and attempting to improve their understanding of the mechanisms of competition, there are as many ways of incorporating competition into a model as there are theories on how the processes of competition work.

In process models, competition is often incorporated as a function that allocates stand-level resources among individual trees. The function can take many forms depending on how the modeller believes that the resources are shared. Individual tree growth within the model is then related to the share of the resources allocated to the tree (Korol *et al.* 1995). Empirical models incorporate competition by assigning an index of competitive stress (competition index) to each tree in the model. This index is used to modify the potential growth of each tree according to its level of competitive stress. Competition indices can be calculated in many different ways depending on how the competition experienced by a tree is defined and measured by the modeller.

The use of empirical models and competition indices has been criticized because the prediction made using these models are based on observations of past growth patterns. These patterns can only be used to make short term predictions for trees growing under the same conditions as the trees that were observed (Dhôte 1994). However, there is no guarantee that the patterns observed will continue long into the future because of uncertainty in the future climatic conditions and many other variables (Biondi 1996, Korol *et al.* 1995). Process models try to represent the true functional relationships and biological

processes that occur in a forest so that growth can be predicted under any climatic condition based on these relationships and processes (Korol *et al.* 1995).

The focus of this section will be on empirical models and competition indices, mainly because of their simpler data requirements and practicality in application. Also, it will be shown that as modellers try to improve the performance of the competition indices, the indices have been modified in an attempt to make them more closely represent the underlying biological processes and functional relationships. As competition indices become more complex, the distinction between process models and empirical models becomes more difficult to define.

#### 2.3.1 Competition Indices

Empirical models can be constructed without considering the effects of competition or they can incorporate it using simple measures of competition at the stand-level, such as density or basal area per hectare. However, important variability in individual tree growth due to competition will be ignored if this is done (Daniels 1976). The effects of competition will be averaged over the stand and the relationship between neighbourhood competition and individual tree growth will be obscured (Bella 1971). Stand-level measures of competition can be used for estimating total stand growth, but will not be effective in certain instances, such as when a forest manager or researcher is interested in determining the effects of silvicultural treatments on individual tree growth (Moore *et al.* 1973).

Competition indices are used to quantify the relative competitive stress of each individual tree within a modelled stand. These indices can be calculated by conducting long term, intricate experiments to observe and measure the competition processes occurring between a tree and its neighbours. More often, the index is based on some easily measurable attributes of the tree and its immediate environment, which are assumed to correlate with the actual competitive stress of the tree (Barclay and Layton 1990).

In order to test how well an index correlates with the actual competitive stress experienced by a tree, the growth rate of the individual tree is used to represent the level of competitive stress. If the tree has a very small growth rate, it is assumed that it experiences a large amount of competitive stress. Therefore, when a competition index is being tested, the modeller attempts to find a strong inverse relationship between the index value and the tree's growth rate.

Many competition indices can be calculated from simple attributes of a subject tree and its immediate neighbours. Inventory measures such as dbh and total height of a subject tree and its neighbours can be entered into an equation to calculate an index. In order to try to improve the performance of the index, measurements of less commonly measured attributes can also be added. Attributes such as crown width or the spatial locations of the subject tree and its neighbours have been tested. All of these variables are able to represent aspects of the competitive processes occurring between a subject tree and its neighbours, but often they have a confounding effect on each other when attempting to find a correlation with tree growth rate. Therefore, it is difficult to distinguish between alternative formulas for competition indices (Waller 1981 in Weiner 1984).

Over the last three decades, a wide diversity of approaches to calculating competition indices have been developed (e.g., Armstrong 1993, Bella 1971, Daniels *et al.* 1986). Because of the difficulty in evaluating the different formulae and the variation in results found using different species and locations, none of the approaches have proven to be clearly superior. As the number of approaches developed increased, categories were formed to help simplify the discussion and comparison of the approaches. Generally, indices have been divided into two main broad categories: approaches that do not explicitly utilize spatial information in their formulation (distance independent) and those that do (distance dependent) (Munro 1974 in Biging and Dobbertin 1995). Many different approaches fall under the distance dependent competition index category and constitute the majority of the available literature. However, distance independent competition indices are still favoured for their minimal data requirements and computational simplicity. They are also relied upon for comparisons with distance dependent indices when attempts are made to evaluate the gains from using the more complicated approaches.

Discussions in the literature comparing different approaches, and the process of constructing an index to find the best predictive formula, often make the procedure sound like an exercise in model fitting (Weiner 1984). However, close observation of each approach will reveal many of the same issues debated in the studies of competition discussed above. Competition indices can be seen as mathematical representations of the hypothesized processes of competition. For example, comparisons between distance dependent and independent indices can be seen as analogous to comparisons between the diffuse competition effect and the bounded competitive region approaches. An understanding of the biological basis on which each approach is founded is important when differentiating and comparing the many approaches to calculating competition indices.

#### 2.3.1.1 Distance Independent Competition Indices

Most measurements of forest stands do not routinely include the spatial locations of the trees as one of the measured attributes. If a modeller is attempting to construct a model of a stand using a data set that does not include spatial data, the options for incorporating competition into the model are limited to distance independent indices (Holdaway 1984).

Simple approaches have been suggested for modellers facing this situation. These indices are usually based on comparisons of an attribute of the subject tree to an average value for the stand. For example, Gloover and Hool (1979 in Lorimer 1983) created an index that is calculated by dividing the dbh of the subject tree by the average dbh of the stand. Variations of the same formula can be easily created to try to improve the performance of the index. For example, the dbh values may be squared or another attribute such as basal area or crown length can be used in its place.

Gloover and Hool's Index = 
$$\frac{D_s^2}{\overline{D}^2}$$

where  $D_S$  is the dbh of the subject tree and  $\bar{D}$  is the average dbh of the stand or plot.

This index is not often favoured due to the poor biological reasoning on which it is based. The index is based on the fact that the cumulative effect of past competition and other factors is expressed in the actual size of the tree at any given point in time (Bella 1971). If the tree is below average, it is a indication that the tree has a history of high competitive stress. The tree will therefore be assigned a larger index value and the model will predict that its growth will continue to be below standard. This way of measuring competition is not based on any real indication of the competitive environment. Rather, the index uses the concept of "large trees grow quickly and small trees grow slowly". This concept can work well, but only in even-aged monocultures in the absence of stand treatments and only over short time horizons (Lorimer 1983).

The first competition indices developed were attempts to measure the density immediately around the subject tree. Stand-level measures such as basal area per hectare or stems per hectare were calculated for a set region around the tree (Bella 1971). When calculated this way, these measures of density become measures of crowding. The difficulty with this approach is that the region around the subject tree within which the degree of crowding is measured must first be defined. In order to do this, the spatial location of the trees must be known in order to evaluate which trees are within the region for a

subject tree. This means that these indices are not technically distance independent, but they are still categorized as distance independent because they do not explicitly contain distance in their formulation.

If spatial data are available, the challenge of how to define the measurement region around the tree still remains. This problem is common to many of the indices in the other categories and is addressed throughout the literature using many different approaches. Usually the region is defined as a circle around the subject tree and the trees that fall within that circle are considered to be competing neighbours. Selecting a set radius for this circle is analogous to defining a boundary for the region of competitive influence discussed in the plant competition studies section above. As in the competition studies, there is no clear way to determine the distance within which a tree is considered to have an influence on the subject tree.

Some distance independent indices are based on distance dependent indices that have had the distance term removed. Because of the inherent use of distance in the process of defining the competitive region and identifying the neighbouring trees, sometimes a modeller may wish to test the necessity of including the actual measurement of distance in an index (Lorimer 1983). Therefore, when the distance term is removed, the index technically becomes distance independent.

Due to the high costs associated with collecting spatial data, Holdaway (1984) presented a distance independent index that could be incorporated into more generalized tree growth models. The index attempts to represent mathematically the effect of the forest community on the growth of a single tree. Stand density, stand structure and stand species composition were used to calculate the index. Holdaway tested the index by incorporating it into the growth model STEMS (Stand and Tree Evaluation and Modeling System) to predict the growth of various tree species in Minnesota, Wisconsin and Michigan.

#### 2.3.1.2 Distance Dependent Competition Indices

#### 2.3.1.2.1 Ratio of Diameters

The ratio of diameters approach to calculating competition indices takes three factors into consideration to describe the competitive environment of a tree: the size of the neighbours, the total number of the neighbours and the distance to each neighbour. In order to select which trees qualify as neighbours, a neighbourhood region must first be defined for each subject tree. The use of a competitive region shows that this approach is based on the bounded area of influence approach. This procedure is an important

step, not only because of the biological theories being represented, but also because the performance of the index can vary greatly depending on how the neighbours are selected (Daniels *et al.* 1986).

The most often cited first example of a ratio of diameters index is Hegyi's (1974 in Lorimer 1983) index. Hegyi's index is calculated using a ratio of the dbh of a neighbouring tree to the dbh of the subject tree. This ratio is then divided by the distance between the subject and neighbouring tree. This distance scaled ratio is then calculated for every neighbouring tree that falls within the defined region around the subject tree. All of the ratios are then summed to produce an index value.

Hegyi's Index = 
$$\sum_{i} \frac{\binom{D_i}{D_S}}{L_i}$$

where  $D_i$  is the dbh of the  $i^{th}$  competing neighbour and  $L_i$  is the distance between the subject tree and the  $i^{th}$  competing neighbour.

The use of a ratio of diameters can be seen as a representation of the degree to which a subject tree is being suppressed by another tree. Conversely, it can also represent the degree to which a subject tree dominates a neighbouring tree. This effect of domination and suppression is then scaled by the distance between the trees. This is a reasonable factor to include since the actual effect a neighbour has on the subject will depend on its proximity. The contribution of a neighbouring tree to the index is directly proportional to its size. Therefore, this approach assumes that there is a symmetrical sharing of resources between the trees. Since trees that are smaller than the subject tree contribute to the total index value, the index also considers the relationship between the trees to be two-sided.

Hegyi's index was originally designed to use a radius of 3.05 meters to define the competitive region around the subject tree. The use of a fixed radius was criticized by Daniels *et al.* (1986). If a fixed radius is used, the index will not include new neighbours over time. As both the subject tree and its surrounding trees grow, their crowns and rooting systems may also grow and will likely begin to interact with other trees at a greater distance. The index will not consider these neighbours and will represent competition with a decreasing value as smaller immediate neighbours die from self thinning.

Daniels *et al.* (1986) proposed the use of an angle gauge sweep that would allow neighbours to be selected within a variable radius plot. A variable radius plot allows the distance within which the trees are selected to be proportional to the size of the trees. Using this system, as distant trees grew they

could eventually reach a diameter above which they would be included in the plot and could be considered as neighbours. Daniels *et al.* favoured Hegyi's index for its computational simplicity. They tested the index using many different basal area factors (BAF) for the angle gauge sweep and they also tried many different variations of the terms used in the formula such as dbh squared and distance squared. From these modifications, Daniels *et al.* were able to find a form of Hegyi's index that worked just as well and sometimes better than other distance dependent indices.

Lorimer (1983) also chose to work with Hegyi's index because of its simple formulation and because of the poor results he observed when using more complicated indices. Lorimer tested Hegyi's index in many modified forms in highly variable hardwood stands. He expressed the same criticism as Daniels *et al.* (1986) over the use of a fixed radius region for identifying neighbours. He noted the problem as one of age dependence because as the stand grows in age, the number of stems decreases and the distances between them increases. Therefore, older and less dense stands will tend to have lower index values even though the levels of competition occurring between the trees may be the same as in younger and more dense stands. Lorimer tested the use of angle gauge sweeps as suggested by Daniels *et al.*. However, Lorimer found this method difficult because his spatial data was collected from predefined plots that only measured the trees within a set area. Therefore, he was wary that the angle gauge sweep for some subject trees would require the inclusion of distant neighbours outside of the plot area for which he would have no measurements.

To overcome this, Lorimer proposed that the search radius for the competitive region should be equal to a constant multiple of the average crown radius of the overstory trees.

Search Radius (R) =  $b \times MCR$ 

where b is a constant and MCR is the mean crown radius.

As the stand opens up with age, the radius will increase as the crowns of the trees expand to fill the gaps. If the number of trees in the stand does not decrease over time, the average crown radius will not change and the search radius will remain the same. In this situation, the increasing competitive stress occurring within the stand will be reflected in the diameter growth of the trees and the index value for a subject tree will increase as the dbh ratios increase.

As crowns expand over time, trees are able to exert an influence on other trees that are further away. However, the distance term will still scale the ratio between two trees in the same way in the index. Therefore, Lorimer suggested that the distance term should be weighted by the search radius.

Lorimer's Index = 
$$\sum_{i} \frac{\binom{D_{i}}{D_{s}}}{\binom{L_{i}}{R}}$$

This modification would keep the scaling effect of the inter-tree distance relative to the age and structure of the stand.

Weiner (1984) built a model that contained a competition index similar in form to Hegyi's index in order to study neighbourhood interference amongst pitch pine (*Pinus rigida* Mill.) trees. Weiner decided to create his own index that was similar to the ratio of diameters approach because he did not consider any other approach to have a theoretical basis.

Weiner's Index = 
$$\sum_{i} \frac{TM_{i}}{L_{i}}$$

where  $TM_i$  is the total mass of the  $i^{th}$  competing neighbour.

Weiner tested various forms of this model and found many had significant correlations with growth rate. His results showed that the form of the index that used distance squared performed best. He hypothesized that this was more than just model fitting and that squaring the distance term reflected the way in which the effect of a competing tree decreases as the distance between it and the subject tree increases.

The model developed by Weiner was modified by Thomas and Weiner (1989) in an attempt to consider asymmetrical competitive relationships between trees. To do this, they included a constant factor that devalued the contribution of a competing tree to the index if it is smaller than the subject tree.

Thomas' Index = 
$$\sum_{i} \begin{cases} \frac{TM_{i}}{L_{i}} & TM_{i} > TM_{s} \\ \frac{TM_{i}}{L_{i}(1-A)} & TM_{i} < TM_{s} \end{cases}$$

where A is constant representing competitive asymmetry and  $TM_S$  is the total mass of the subject tree. This constant was varied to try to find an optimal value to for *Pinus rigida*. Thomas and Weiner found that a value of 0.7 fit the relationship best.

Weiner's (1984) model was later used by Newton (1993) to study competition processes within second-growth black spruce (*Picea mariana* (Mill.) B.S.P.) stands. Newton believed that more could be learned about competition if tree growth response was measured by observing more than just one tree characteristic. Therefore, his objective was to study the effect of competition on the partitioning of above ground growth in several tree components. By looking at the individual components, he hoped to assess which components were most affected by competitive stress. As density stress increased, Newton found that bark mass increased, stem mass decreased, branch mass decreased and foliar mass increased. When he tested Weiner's model for its ability to predict these results, Newton only found significant results in the densest stands.

A second objective of Newton's study was to try to determine if the competitive relationships in the study stands were symmetrical or asymmetrical. Newton hypothesized that the resources were shared symmetrically and therefore, competition would mainly be for below ground resources (resource depletion). In order to determine this, he proposed to look at the growth rate within the size classes in the stands. If the relationship was asymmetrical (resource preemption), greater size variation would be observed in the high density stands. However, if a constant or decreasing size variation was observed and the growth rates showed equivalent declines in all size classes then a relationship of symmetry would be more likely. Newton found the latter to be true. He also observed little difference in the leaf morphology between size classes, which indicates that little competition for light existed which further supports the symmetric relationship.

Newton and Jolliffe (1998) conducted a study with the objective of determining if the competitive relationships in spatially heterogeneous black spruce stands were symmetrical or asymmetrical. Newton and Jolliffe proposed to evaluate these relationships by studying the correlation between measures of stem volume growth for a subject tree and a directional specific competition index. They chose to use

the index created by Weiner (1984) as well as the index created by Silander and Pacala (1985 in Newton 1988). Newton and Jolliffe recognized the fact that these indices are not able to consider the spatial distribution of the neighbouring trees around the subject (i.e. a different degree of competition will be experienced if all of the neighbours are clumped on one side than if they were evenly distributed). Since this is an important consideration in spatially heterogeneous stands, they developed a spatial modifier that reflects the position of the subject relative to the mass concentration of the competitors within the neighbourhood.

Newton's Index = 
$$\left(\sum_{i} \frac{TM_{i}}{L_{i}^{2}}\right) \left(1 - \frac{R_{CM}}{R_{MAX}}\right)$$

where  $R_{cm}$  is the distance between the subject tree and the centre-of-mass of the competitors and  $R_{MAX}$  is the length of the search radius used to select the competing neighbours.

Newton and Jolliffe (1998) calculated three different measures of growth in an attempt to remove the effect of size on growth rate. These measures were used to provide a common basis to compare growth performance among trees of varying sizes. They then tested various transformations of the competition indices to find a form that had the best correlation with each of the growth measures. They went on to develop a framework that could be used to analyze the cumulative amount of competition experienced by a tree from competitors in size classes above it and from competitors in size classes below it. Using this framework, Newton and Jolliffe came to the conclusion that the competition was asymmetrical and directional-specific. They found that decreased growth rates occurred as competition from larger size classes increased. They referred to this relationship as a "dominant resource preemption process".

#### 2.3.1.2.2 Area of Influence

The area of influence approach to calculating competition indices is based on the concept that a tree's ability to compete for all resources can be represented by the area of the competitive region surrounding the tree. The radius of this region would be defined as a function of the tree size (Gerrard 1969 in Daniels 1976). From this region a competition index could be calculated, not by measuring the neighbours within the region, but rather by measuring the degree to which the region is overlapped by the regions of its neighbours. The overlapping of the regions of each tree has been proposed to express the competitive interaction occurring between above-ground parts of a tree as well as among the roots of individual trees (Bella 1971).

The first example of an area of influence index was created by Staebler (1951 in Tennent 1975). In his index, Staebler defined the radius of the influence area to be a function of dbh. In order to simplify the calculation of overlap areas, Staebler only measured the radial width of the overlap regions.

Work on the area of influence approach was continued by Opie (1968 in Bella 1971). In Opie's index, the actual area of overlap was summed and then divided by the total area of the subject tree's region. This modification scaled the amount of overlap to be relative to the size of the tree. This is a crucial factor to include because it recognizes the important fact that a certain degree of overlap can have drastically different effects on a small tree as compared to the effects of the same amount of overlap on a large tree.

Opie's Index = 
$$\sum_{i} \frac{a_i}{A_s}$$

where  $a_i$  is the area of overlap between the regions of influence of the subject tree and the  $i^{th}$  competing neighbour and  $A_s$  is the total area of the subject tree's region of influence.

Shortly after Opie, Gerrard (Gerrard 1969 in Bella 1971) introduced an index he referred to as the "competition quotient" which was very similar to Opie's index. Gerrard defined the function of the index very precisely as follows: "The competitive stress sustained by a tree is directly proportional to the area of overlap of its competition circle with those of its neighbours and inversely proportional to the area of its own competition circle." (Gerrard 1969 in Tennent 1975)

This premise is clearly reflected in the formula of the index:

$$CQ = \frac{1}{A_s} \times \sum_{i} a_i$$

Gerrard tested his index by trying many different sizes of influence areas. He did this by modifying the constant in the function relating the radius of the area of influence region to the subject tree diameter.

In order to avoid the complicated computations required to calculate overlap areas, a simpler version of the previous indices was tested by Newnham (1966 in Bella 1971). In his index, the index value was calculated by measuring the amount of the circumference of the area of influence region of the subject tree that is overlapped by the neighbours.

Bella (1971) found problems with the indices created by Opie, Gerrard and Newnham because they did not consider the size of the tree with which the subject tree overlapped. Therefore, he created his own index that he referred to as the "competitive influence-zone overlap". Under the previous indices, the effect of a set amount of overlap was the same whether it came from one large tree or from several small trees. Bella added weights to his index in order to assign relative importance to the overlap areas of each competitor. He did this by multiplying each overlap area by a ratio of the neighbouring tree diameter over the subject tree diameter.

In doing this, Bella changed the area of influence index from being based on a competition theory of absolute symmetry to one of relative symmetry. In Bella's index, if two trees are found to share resources when their areas overlap, the resources will be distributed according to their sizes. This modification reflects the very high stress experienced by a small tree that has been overtopped by a large tree. Conversely, it also shows the minimal effect that a small tree has on the large tree as it grows under its canopy. Because the small tree still contributes to the competition index of the large tree, the index considers the relationship to be two-sided.

After making this modification, Bella went on to acknowledge the fact that large dominant trees often require disproportionately more resources than suppressed trees due to the differences in the metabolic processes associated with each state (Baskerville 1965 in Bella 1971). To represent this disproportionate sharing, Bella included a term that would allow the index to represent an asymmetrical relationship between the trees. This term was added in the form of a scaling exponent to the newly added ratio of diameters. This exponent could be varied in order to find the degree to which the resources are shared disproportionately. This value is likely to be species and location specific and therefore can only be determined during the testing process.

Bella's Index = 
$$\sum_{i} \left( \frac{a_i}{A_S} \right) \left( \frac{D_i}{D_S} \right)^{EX}$$

where EX is the scaling exponent for asymmetrical relationships.

Bella's index set the radius of the influence area based on the open grown crown radius of the trees. A regression equation was used to predict the open grown crown radius for a tree using the dbh of the tree as the independent variable. In order to investigate the effect of varying the size of the influence area from the open grown crown size, an adjusting factor was also added to the formula that could be modified during the testing process.

Bella tested his index using data from even-aged fully stocked stands of Douglas-fir, jack pine (*Pinus banksiana* Lamb.), red pine and aspen, as well as data from an even-aged stand of *Eucalyptus* species. During the testing process, Bella was able to find an optimal value for both the exponent and the radius adjusting factor. Because the optimal value was greater than the open grown crown radius, Bella hypothesized that the optimal radius represented the far-reaching effects of the below ground competition processes. Once these values were found for a species, Bella noted that they were robust over the range of site and stand conditions that were tested.

A similar index to Bella's was created by Arney (1973 in Daniels 1976) that also used open grown crown radius to define the area of influence. Ek and Monserud (1974 in Daniels 1976) created an index that assigned weights to the overlap areas like Bella's index. However, instead of using dbh, the ratio was calculated as the product of crown radius and height of the neighbouring tree over the same product calculated for the subject tree.

Ek and Monserud's Index = 
$$\sum_{i} \binom{a_i}{A_s} \binom{D_i H_i}{D_s H_s}$$

where  $H_i$  is the height of the  $i^{th}$  competitor and  $H_S$  is the height of subject tree.

Gerrard's competition quotient was tested by Tennent (1975) using stands of young radiata pine (*Pinus radiata* D. Don). Tennent criticized the use of crown radius to define the area of influence. He believed that this method overlooked the fact that a stand-grown tree with a similar dbh to an open-grown tree may have already had its dbh growth restricted through competition. Therefore, its hypothetical open-grown crown radius based on this restricted dbh may be underestimated and could have little relationship to its competition zone. Instead of using open-grown crown radius, Tennent tested a range of radii until an optimal value was found. Tennent found that the R<sup>2</sup> value of the regression equation using the competition quotient and dbh to predict growth increment reached an asymptotic maximum as the radius was increased.

Keister and Tidwell (1975) used an index similar to Arney's to estimate of the probability of a tree dying within a five year period. They hypothesized that the trees with higher index values were more likely to die. To test this, they calculated the index for each remeasurement of study stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.). They found that the index values closely represented the crown classes of the studied trees. Because the index was calculated several times for each tree over time, they were also able to make observations of whether a tree was able to maintain a

constant index value or if the index was gradually increasing over time representing a progression towards mortality.

The influence of competition on the thinning response of white pine (*Pinus strobus* L.) trees was studied by Gillespie and Hocker (1986). The objective of the study was to test the ability of a competition index and other variables to predict which trees in a stand will produce the best response to thinning if selected as residuals. They used an index similar to Arney's, with the area of influence radius defined as a multiple of diameter. The index was used in a regression equation along with percent live crown, crown class, pre-thinning diameter growth and age to predict post-thinning diameter growth as a percentage of pre-thinning diameter. Gillespie and Hocker found the competition index and crown class made the largest contributions to the predictive ability of the regression equation.

Arney's index was also used by Barclay and Layton (1990) to predict the response of Douglas-fir stands to thinning and fertilizer experiments. The index values were regressed with initial diameter to predict the growth of the stands that had occurred over the 12 year period since the treatments were applied. They found that the index decreased as the fertilizer level increased in unthinned plots. In the thinned plots, the competition index increased as the fertilizer level increased. They hypothesized that the index values decreased in the unthinned plots due to mortality caused by the application of the fertilizer. Also, in the thinned plots, the increasing index values are likely to be a reflection of the faster growth and resulting increased competition. Overall, Barclay and Layton found that initial diameter performed far better at predicting growth than Arney's index.

#### 2.3.1.2.3 Area Potentially Available

The area potentially available approach was developed based on a more flexible method of defining the competitive region around a tree for use in a competition index. Instead of using circles of various radii to represent this area, the area potentially available approach defines a polygon around each tree. The shape and extent of this polygon is defined by the spatial locations of the neighbouring trees. The polygon area assigned to each tree can be seen as representing the growing space available to the tree (Moore *et al.* 1973). The amount of crown and root competition can therefore be estimated based on the limits of the available growing space. Therefore, a competition index can be calculated simply as the area within the polygon defined for each tree.

Growing space polygons are formed using a map on which each plant or tree is represented by a point. Lines are drawn between a point and all its neighbouring points. Polygons borders are formed by placing perpendicular bisectors on these lines. The closest of these bisecting lines are then joined to form a closed polygon. In this process, the trees that act as neighbours are also defined as those that contribute to the border of the polygon (Mithen *et al.* 1984). In order to reflect the relative sizes of the subject and neighbouring trees, the bisecting lines can be positioned at different points along the line between two trees relative to their sizes. The polygon boundaries would then be shifted towards the smaller trees in order to reflect the greater competitive stress caused by larger neighbours.

Growing space polygons, often referred to as Thiessen or Voronoi polygons, have been studied in plant competition experiments (Mead 1966 in Mithen *et al.* 1984) and have also been used in forestry applications as a method for measuring density. The local density of a plant can be thought of as the inverse of its polygon area and the density of the stand can be estimated using the reciprocal of the mean polygon area of the trees.

The area potentially available approach has been favoured for its ability to represent the spatial development of a tree in non-uniform patterns. This allows the index to represent growing conditions such as when a tree is growing on the edge of a clearing. The ratio of diameters and area of influence approaches are calculated under the assumption that the neighbouring trees are evenly distributed around the subject tree. Using area potentially available, the absence of neighbours on one side is represented by assigning a portion of the open area to the polygon of the subject tree. This approach also recognizes the trees on the other side of the opening as the neighbours of the subject tree. These trees would not be given consideration in the other approaches if they were outside of the defined competitive region.

Another advantage of the area potentially available approach is the ability of the index to decrease over time in order to represent a tree that is experiencing increasing competitive stress. If a tree stops growing, but its neighbours continue to grow, the polygon boundaries will be shifted towards the smaller tree as the difference in their sizes increases. This allows for observations of tree dynamics not obvious in other approaches. The rate of change in competitive stress and the direction of the changes can be observed for trees.

The area potentially available approach may not be appropriate for use in all stand types. In the same way that it has the potential to represent stands with uneven spatial distributions well, it can also be

constrained by the same situation. If a large tree is surrounded by many small trees growing in its understory, the polygon area of the large tree may be unrealistically constrained by those small trees (Lorimer 1983). Even if the boundary between the large and small trees is weighted towards the small tree, it is not possible for the boundary to extend beyond the location of the small tree. Therefore, if many small trees are growing immediately around the base of a large tree, its polygon area will be severely restricted and it will appear to have a greater competitive stress than is actually caused by the presence of the small trees.

The constraining effect of immediate neighbours can also prevent the area potentially available approach from considering the influence of trees beyond the immediate neighbours. For example, if a small tree is located between two large trees, the small tree will be selected as the neighbour for each tree and the effect of the two large trees on each other will be obscured. This inability to consider trees beyond the immediate neighbours demonstrates that this approach is based on the competition theory of non-overlapping bounded competition regions. This theory can be quite appropriate in some stand conditions, such as even-aged structures; however, it may be an unrealistic assumption in other conditions such as uneven-aged stands. One possible solution to these problems is to make the index one-sided by only selecting neighbours that are of equal or greater size than the subject tree. However, this is not a satisfactory solution if the modeller believes that the studied trees have a two-sided relationship and is unwilling to make the assumption of one-sidedness.

The same difficulty of age dependence discussed by Lorimer (1983) in the area of influence approach can be applied to the area potentially available approach as well. As stands develop over time and density decreases, the index values will appear to decrease even though competition levels may still be the same.

The term "area potentially available" was first used to refer to this approach by Brown (1965 in Tennent 1975). He used polygons with fixed bisecting boundaries as a measure of local density. Brown's measure of density was modified by Moore *et al.* (1973) for use as a competition index. They added weights to the perpendicular boundary lines to represent the differences in the relative sizes of the neighbours. Moore *et al.* tested their index by including it in a regression equation predicting the growth of tolerant hardwoods. They found significant results and also found that it was able to account for more variation in growth than Bella's (1971) area of influence index. Moore *et al.* were particularly interested in the ability of Brown's index to represent both increasing and decreasing changes in competitive stress. They calculated the difference between the competition index for each tree at each time period to create a value they termed the "change in competitive status". They hypothesized that the change in

competitive status would be useful as an interaction term with the area potentially available index for predicting future growth.

Pelz (1978 in Biging and Dobbertin 1992) modified the index by Moore *et al.* to use tree height instead of diameter to weight the location of the polygon boundary. In order to prevent excessively large index values being calculated for trees next to or in clearings, Smith (1987 in Smith *et al.* 1992) used estimated open-grown crown width to put a limit on the unbounded sides of the polygon.

The area potentially available approach was studied by Mithen *et al.* (1984) in a controlled experiment using *Lapsana communis* seedlings grown in a greenhouse. The objective of the study was to observe the growth and mortality of the individual plants in relation to the area potentially available to each plant. Two plots of seeds were planted and mapped after germination. The first plot was harvested right before the plants began self thinning and the second plot was allowed to grow several weeks longer before being mapped again and harvested. In the first plot at harvest, the distribution of polygon sizes was very skewed with many small polygons. The second plot at the later harvest showed a much more even distribution of polygon sizes. The distribution of plant weight from the two harvests both were skewed to form hierarchies. Mithen *et al.* found that the plot of the logarithm of harvest polygon area versus the logarithm of plant weight had a slope of negative 3/2 which is what they expected to observe based on the negative 3/2 thinning law (Yoda *et al.* 1963 in Mithen *et al.* 1984). They also found that the area of the polygon for a plant before self thinning was the best predictor of plant weight at the second harvest. Mithen *et al.* hypothesized that this was due to the fact that competition from neighbouring plants that died from thinning have a lasting effect until the second harvest.

A "pixel based" approach to calculating the area potentially available to a tree was proposed by Armstrong (1993). Armstrong criticized the other distance dependent approaches for the inability to consider how the neighbouring trees are distributed around the subject tree. He also found a problem with the way in which the existing area potentially available indices represent the processes of crown expansion. When a tree dies, the existing indices immediately assign the area of the newly formed gap to the neighbouring trees. Armstrong believed that this does not realistically represent the actual expansion of the neighbouring crowns into the gap. To solve this problem, Armstrong suggested that the stand area should be divided into a fine grid and the pixels within the grid would be grouped to represent the growing area of a tree. At each cycle of the model, each pixel would be selected and the immediate surrounding pixels would be checked to identify those that are already assigned to trees. The pixel would then be awarded for that cycle to the neighbouring tree that would be tallest at the center of the pixel.

The rate of expansion would be controlled by only allowing trees to expand by one pixel per cycle. Armstrong found that the pixel based approach produced more reasonable estimates than the existing indices for the prediction of growth and the effects of thinning in deciduous forests in eastern North America.

#### 2.3.1.2.4 Crown Models

Crown models have been used extensively in process modeling. Measurements of crown characteristics were usually ignored in empirical models in the past because computational limitations made them impractical to include. As computational power grows with improving technology, empirical modellers can include more variables in their models in an attempt to improve the predictive ability of their models. Variables such as spatial information and crown parameters have been found to make very good contributions to the predictive ability of an equation (Smith 1994, Biging and Dobbertin 1995), but will still be limited in large scale applications due to the difficulty in measuring these attributes on the same scale.

The dimensions of the crown of a tree are used in process models to represent the foliage mass within the crown. This mass can then be used to indicate the ability of the tree to access solar radiation for energy input and its consequent growth. Process modellers have found that stem volume increment and crown dimensions are interrelated. This relationship has been described as the "pipe model theory", which states that there is a constant ratio between foliar biomass and the sapwood cross-sectional area of a tree (Raulier *et al.* 1996). This strong relationship has been imported into empirical models for use as a competition index. This was done using the assumption that the crown dimensions can represent the competitive status of the tree instead of its ability to access to solar radiation. For example, if a tree has a large crown with branches along the length of its stem, it is associated with open growing conditions and low competitive stress. If the crown is small and short, it can be used as an indication of suppressed growth and high competitive stress.

The use of a three dimensional model of crown competition for predicting volume growth was studied by Smith (1994). The objective of the study was to present and test a three dimensional geometric model of crown competition that would represent the processes that occur within tree crowns such as light interception and photosynthetic production. The output from this model for each tree could then be used as a competition index in an empirical growth model. The model was kept simple to ensure that it remained practical and therefore it only requires data on the spatial location, total height and height to the base of the live crown of the tree. Smith used the crown model to predict crown volume, crown

surface area, and non-shaded surface area for loblolly pine trees. He then tested these measures for their ability to act as competition indices in an equation predicting volume growth. Smith found that the estimate of non-shaded surface area was the best predictor of volume growth. However, all of the values performed better than just using crown length alone as a competition index.

The use of crown models as competition indices was tested along with a range of established distance dependent and independent indices by Biging and Dobbertin (1995). Biging and Dobbertin tested the indices using mixed species stands of Douglas-fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl), red fir (*Abies magnifica* A. Murr.), and sugar pine (*Pinus lambertina*) in multiple-aged stands. They hypothesized that the advantages of distance dependent indices would become apparent when testing spatially heterogeneous stands. The crown model was used to calculate crown surface area, volume, and cross sectional areas for each tree. Biging and Dobbertin used the estimated crown parameters to form both distance independent indices (by comparing the crown measures to a stand total) and dependent indices (by comparing the crown measures to those of selected neighbours). They also tested various indices based on the cross sectional areas of all the competing neighbour's crowns sliced at a set height calculated as a proportional distance up the crown of the subject tree.

Neighbours were selected for the distance dependent indices using a height angle gauge. This is a similar process to selecting neighbours using a horizontal angle gauge to create a variable radius plot. However, instead of selecting neighbours based on the size of their diameters relative to their distance from the subject, the height of the neighbours relative to their distance is used.

Height Angle Gauge Critical Distance = 
$$\frac{H_i}{\tan(\Theta)}$$

where  $\theta$  is the search angle from the horizontal.

Theta can be varied to find an optimal search angle. This method was favoured by Biging and Dobbertin because it represents the fact that small trees will be shaded by tall trees that are further away. Also, they were wary of using a horizontal angle gauge sweep based on diameter because diameter itself is affected by competition (Biging and Dobbertin 1992).

The indices were tested by including them with height and diameter squared in an equation predicting growth. Biging and Dobbertin found that the cross sectional area at a percent of subject tree height, when calculated as a distance independent index, performed the best. They hypothesized that it

performed better than the distance dependent form because the subject tree's crown position relative to the whole plot is more relevant than when it is compared to its neighbours in a small area of the plot. Biging and Dobbertin also found that the differences between the indices using crown surface area and the indices using crown volume were smaller than anticipated. They suggested that it may have been due to the fact that both were derived from the same variables and were highly correlated.

Raulier *et al.* (1996) studied the influence of social status on crown geometry and volume increment in stands of black spruce. They hypothesized that using a crown model by itself to predict growth is not enough due to the fact that tolerant species such as black spruce are able to modify their crown architecture and leaf physiology in response to decreased light conditions. Therefore, a suppressed tree will require far more shade leaves to produce the same growth as a dominant tree. To account for this difference, Raulier *et al.* tested the ability of their crown model to predict tree growth in conjunction with three different competition indices. The indices were based on the heights of the subject tree and its neighbours instead of their diameters. The first index was based on a distance dependent index developed by Ford and Diggle (1981 in Raulier *et al.* 1996) and the last two indices were distance independent and similar to the index created by Gloover and Hool (1979 in Lorimer 1983). Raulier *et al.* found that the indices were significant when included with the crown model, but contributed very little to the prediction of tree growth. They hypothesized that this may be due to the fact that the dimensions of the crown are a product of competition and already strongly represents its competitive status.

## 2.3.1.3 Comparison Tests of Competition Indices

With the wide diversity of approaches to calculating competition indices available, it is a very difficult task for a modeller to decide which index is most appropriate for a specific tree species and location of interest. When a new index is published, the author always includes information about the species for which the index was designed and where the index was tested. However, unless an index was published for the forest region and species that a modeller intends to work with, this information may not be useful to the modeller in making a decision. Therefore, a portion of the literature concerning competition indices focuses on comparing the existing indices for use with certain species, structures and locations.

The objective of these studies is to determine which index is able to best represent the competitive stress for a selected tree species. This is evaluated by testing which index is able to explain more of the variation in the observed growth of the selected species. In order to be able to test this, the study must have a data set containing measurements of the individual tree growth of a stand studied over time, as

well as measurements of the various individual tree attributes that are needed to calculate the indices. Once the index values have been calculated for each tree using this information, observed growth is regressed on the indices, either alone or in combination with other individual tree attributes. The performance of each index can then be compared using the  $R^2$  values of the regressions. The index used in the regression that produced the highest  $R^2$  value is then considered to be the best for the specific conditions studied.

The comparison test literature often contains discussions of whether distance dependent indices are better than distance independent indices. In most studies, this comparison is made automatically if the study tests representative indices from both categories. The study is able to propose an answer based on whether the index that was found to have the best performance is distance dependent or independent. However, the discussions can become much more subjective if the gain in performance is compared against the costs and extra work of calculating a distance dependent index.

One of the earlier comparison tests was conducted by Daniels (1976). The focus of the study was on the ratio of diameters and area of influence approaches. Daniels tested the indices created by Hegyi (1974 in Lorimer 1983), Arney (1973 in Daniels 1976), Bella (1971), and Ek and Monserud (1974 in Daniels 1976) using data from loblolly pine plantations. He found Hegyi's index performed better than Arney's and at least as well as Ek and Monserud's. Daniels noted that Hegyi's index also had the benefit of a much simpler computation.

Lorimer (1983) tested a wide range of indices for use in natural hardwood stands. He compared indices representing each of the approaches in both the distance dependent and independent categories. Lorimer also tested many of his own variations on each approach. For the ratio of diameters approach, he found that squaring the distance measure reduced the performance of the index. However, he also found that eliminating distance (turning it into a distance independent index) had little effect. Lorimer also studied the effects of using different methods to select neighbouring trees for the various indices. He compared the performance of several indices when neighbours were selected using angle gauge sweeps of various factors and when neighbours were selected using a competitive region with various radii. He tested the radii set as a multiple of the subject tree crown width and also as a multiple of the mean crown width of the stand. Tests were also conducted that limited the selection of neighbours based on crown classes. Overall, a distance independent index similar to Glover and Hool's (1979 in Lorimer 1983) was favoured. Lorimer also found better results when only neighbours within crown classes of equal or greater size than that of the subject tree were selected.

Ten different indices were tested by Daniels *et al.* (1986) for use in loblolly pine plantations. They recognized that the selected index was ultimately going to be used in a growth model. Therefore, in the tests they regressed the indices with other standard growth model variables such as diameter and stand density. Overall, they found that the best distance dependent indices showed little, if any, advantage over the best distance independent indices. However, of the distance dependent indices, Daniels *et al.* were particularly impressed by the performance of the area potentially available index.

Due to the small difference in predictive ability found in previous comparison tests, Mugasha (1989) decided to focus on simpler indices. He compared seven indices for use in young jack pine and trembling aspen stands. The distance dependent indices were limited to examples of the ratio of diameters approach. Mugasha also included tests where neighbour selection for the indices was limited to trees that were greater in height than the subject tree. After ranking all of the indices based on the test results, Mugasha found Hegyi's index as it was calculated by Daniel *et al.* (1986) was best when neighbours of all heights were selected.

The lack of success of distance dependent indices in past comparisons was hypothesized by Tomé and Burkhart (1989) to suggest that there is still room for improvements in the existing indices. They emphasized the importance of a correct interpretation of the relationship between neighbours, if one wants to quantify competition in a single mathematical expression. Therefore, Tomé and Burkhart created modified versions of the ratio of diameter and area of influence indices based on studies by Yoda (1975 in Tomé and Burkhart 1989) and Harper (1977 in Tomé and Burkhart 1989) to test along with several other existing indices. The indices were tested for use in eucalypt plantations in Portugal. Tomé and Burkhart found that the modified and area potentially available indices were significant when tested in conjunction with other stand-level variables, but contributed little improvement.

A modified version of an area of influence index was created and tested against existing indices by Holmes and Reed (1991). Their modified index proposed to represent root competition by measuring the volume of overlap between three dimensional models of rooting zones for each tree. The rooting zone was defined as a conical shape with a depth based on the tolerance class of the tree and width proportional to the crown class. Holmes and Reed tested this index along with the indices created by Hegyi (1974 in Lorimer 1983), Bella (1971) and Moore *et al.* (1973) for use in mixed northern hardwoods. In order to represent the wide range of crown positions within the study stands, they tried adding weights based on the crown classes to the influence of each tree when calculating the indices. During the tests, Holmes and Reed found that different species worked well using Bella's index when specific

weightings were used. Only one species performed well using the area potentially available index by Moore *et al.* (1973). The modified root index also showed low performance. Hegyi's index showed the most consistent performance across the range of species tested.

Distance dependent indices were tested for use in multi-aged mixed species conifer stands in northern California by Biging and Dobbertin (1992). They hypothesized that it would be evident if distance dependent indices are superior to distance independent indices in these heterogeneous study stands. A wide range of indices from all categories were tested along with several indices modified by Biging and Dobbertin to include measures of geometry. They chose to select neighbours using height angle gauges because they viewed light as an important limiting resource. The indices were tested in conjunction with a growth model that included the variables height and diameter squared. Overall, Biging and Dobbertin found improvements in the predictive ability of the growth model by including the competition indices. The ratio of diameter indices performed poorly in the tested stands, but their modified versions that included crown parameters showed improved results. They also found that removing the distance term from the ratio of diameter indices resulted in improved performance in some tests. The crown parameter models developed by Biging and Dobbertin performed better than the area potentially available and area of influence approaches.

Both distance dependent and independent indices were tested for use in models of basal area growth after silvicultural treatment by Wimberly and Bare (1996). They noted that the subject tree dbh performed very well as a competition index, but only if stand structure has not been changed drastically. After a stand has been thinned, growth rates will vary due to the new spatial pattern and dbh will not be able to predict these new growth rates.

Individual tree models that can make predictions based on the new spatial pattern can be particularly useful for assessing the future stand structure resulting from a treatment. Periodic remeasurement data collected before and after thinning in stands of Douglas-fir and western hemlock were used by Wimberly and Bare. Indices from each category and approach were calculated and tested. They chose to select neighbours for each index using a vertical angle sweep (height angle gauge). Variations of each index were also tested by limiting selected neighbours to trees of equal or greater height than the subject tree. Wimberly and Bare calculated a "thinning index" by finding the difference between each competition index calculated before and after thinning. The thinning index was included in the model to represent the amount of new growing space. The area potentially available index, with neighbour selection limited by height, was found to perform the best, but only by a small amount. Wimberly and Bare hypothesized

that the poor performance may be caused by the very regular spacing resulting from the thinning. They stated that distance dependent indices may not be effective when stands have been thinned from below, but they may be more useful in stands that have been treated with crown thinning or clump retention, are uneven-aged and/or are very dense.

# 3 Methods

# 3.1 Sample Data

The data for this study were collected from a set of six permanent sample plots located in the Knife Creek block of the University of British Columbia's Alex Fraser Research Forest, which is located approximately 15 km southeast of Williams Lake, British Columbia. The plots were established in 1988 and were remeasured in 1992 and 1997. A detailed description of the location, establishment and measurement of the study plots can be found in Marshall and Wang (1996). A brief summary of how the plots were established is presented here as it appears in the Marshall and Wang paper:

Plots 1 and 2 were located in relatively open portions of the block, with the stand structure dominated by large dbh trees. Plots 3 and 4 were located in an area that was quite dense originally, but which had been spaced. These plots represent a stand structure dominated by mid-sized dbh trees. Plots 5 and 6 were established in an area dominated by large numbers of small dbh trees. Plots 1 through 4 are 0.1 ha in size (31.6 m x 31.6 m) and plots 5 and 6 are 0.05 ha (31.6 m x 15.8 m). The smaller size of the latter two plots was necessary to maintain some degree of uniformity of conditions within the plots and to keep the number of trees measured to a manageable size.

All living trees above 1.3 m in height were tagged and measured in these plots. Each tree had the following measurements/observations recorded: species, dbh, total tree height, height to lowest living branch, crown diameter, a subjective rank of tree vigour, angle of lean, distance of lean, direction of lean and tree location. The measurements regarding the lean of the trees were necessary to calculate corrections for the height measurements of the tall, large dbh trees that tend to develop a lean over time. Influence trees (border trees) around each plot were identified based on subjective criteria. They were defined as trees that were of sufficient size and proximity to a plot to possibly affect the growth of the trees within the plot. Only the dbh, height and location were recorded for the border trees.

When the study plots were remeasured in 1992, the same measurements/observations were recorded except for those regarding the lean of the trees and location. At the same time, ten trees were destructive sampled in the vicinity of each plot (Hugh Hamilton 1993 in Marshall and Wang 1995). In total, sixty trees were used to calculate oven dry biomass equations for various tree components (Marshall and Wang 1995). The data collected and the biomass equations were then combined and analyzed in the report by Marshall and Wang (1996).

In Marshall and Wang (1996), the following plot level summary variables were calculated: stems per hectare, basal area per hectare, quadratic mean diameter, Curtis' (1982) relative density index, average vigour, volume per hectare using the British Columbia Provincial volume equations (Ministry of Forests 1976) and the biomass per hectare of various tree components (calculated using the new biomass equations). These variables were calculated for both the first and second measurements. The growth of the stand over the four and a half year period between the measurements was calculated as the difference between the variables at each measurement. In the report discussion, the growth values were related to the initial plot conditions and hypotheses were constructed regarding the impact of stand structure on subsequent growth dynamics.

The third remeasurement in 1997 was conducted in conjunction with this study. The data that were collected from this remeasurement were entered into a Microsoft Excel (Microsoft Corporation 1996) spreadsheet and combined with the data from the previous two measurements. The summary variables calculated in the Marshall and Wang (1996) study were calculated using the new data. The spreadsheet now displays the values of each variable calculated at each remeasurement, as well as the growth that occurred in the two intervals between the three remeasurements. Summary tables showing the structure of the study plots at each remeasurement and the changes observed in the study variables are provided in Chapter 4. The hypotheses constructed in the Marshall and Wang (1996) paper were re-evaluated after the addition of new data in Chapter 5.

The data were reorganized in a new spreadsheet that would facilitate the calculation of the competition indices that were selected for evaluation in this study. Several trees had to be removed from the data set due to missing data or errors in measurement. A total of 1169 trees were used as sample trees in the calculation of each index. An additional 406 border trees were included to be used as potential competing neighbouring trees in the calculations. Because crown width was not measured on the border trees, but was a necessary variable for the calculation of some of the indices, a multiple regression equation predicting crown width using dbh and dbh² was fit using the data from the sample trees. The regression equation was then used to estimate crown width values for the border trees.

In order to visually evaluate the spatial relationships of the trees and their crowns, the plot data was entered into ArcView Geographic Information System (Environmental Systems Research Institute, Inc. 1997). In ArcView it was possible to create a graphic representation of each plot displaying numbered points that represent the location of each tree and rings that represent the crown area of each tree. This plot made it possible to identify which trees were adjacent to a particular tree and also determine if the

crowns of the trees overlapped (see Appendix 1 for an example of the ArcView representation of plot 1). This visual reference was a very important tool during the process of calculating and validating the indices.

# 3.2 Calculation of the Competition Indices

A wide range of competition indices were selected for evaluation in this study. The choice of indices was limited to the individual tree indices discussed in Chapter 2 except for two stand-level measures of density that were selected to be tested for their ability to be used as competition indices.

Representatives of both distance dependent and distance independent indices were selected in order to be able to evaluate the value of using spatial data in the calculation of an index. The choice of distance dependent indices was limited to the ratio of diameters and area of influence approaches only. The area potentially available approaches were excluded because of the concerns discussed by Lorimer (1983) about the constraining effects an uneven-aged stand would have on the function of this approach.

The two stand-level density measures selected were basal area per hectare and Curtis' (1982) relative density index. The individual tree characteristics vigour and basal area were selected to be evaluated for their ability to function as simple competition indices. The index created by Gloover and Hool (1979 in Lorimer 1983), Lorimer's distance independent version of Hegyi's index (1983) and an index calculated using the live crown ratio were selected as representatives of the distance independent indices. The indices selected from the ratio of diameters approach were the indices created by Hegyi (1974 in Lorimer 1983), Weiner (1984), Silander and Pacala (1985 in Newton and Jolliffe 1998), and Newton and Jolliffe's modified versions of the indices by Weiner and Silander and Pacala (1998). The indices selected from the area of influence approach were the indices created by Opie (1968 in Bella 1971), Bella (1971), and Ek and Monserud (1974 in Daniels 1976).

Table 1. Indices selected for evaluation and their formulation.

#### **Distance Independent Indices**

Index	Formula	Variable Definitions
Basal Area Per Hectare	BA/Ha	BA = basal area of the plot
		Ha = size of plot in hectares
Curtis' RDI	SPH/D <sub>q</sub>	SPH = number of stems per hectare
		D <sub>q</sub> = quadratic mean diameter
Vigour	Subjective rank on a scale	0 = dead
	of 0 to 3	1 = little potential for future development
		2 = moderate potential for development
Dorgant Book Area Creater	(PA> Cubio et) (PA	3 = good potential for development
Percent Basal Area Greater than the Subject Tree	(BA>Subject)/BA	BA>Subject = total basal area of all trees in the plot with basal area greater than that of the subject tree
Gloover and Hool's Index	$D_{c}^{2}$	D <sub>S</sub> = dbh of the subject tree
	$\frac{D_S^2}{\overline{D}^2}$	$\bar{D}$ = average dbh of the stand or plot.
Live Crown Ratio		LC = length of the living crown
	$LC_{-}(H_{T}-H_{LLB})$	$H_T$ = total height of the subject tree
	$\frac{LC}{H_T} = \frac{(H_T - H_{LLB})}{H_T}$	H <sub>LLB</sub> = height of the lowest living branch on the
	1	subject tree
Lorimer's Index	$\sum_{i} \binom{D_i}{D_s}$	$D_i$ = dbh of the $i^{th}$ competing neighbour
Lorimer's Index 2	$\sum (D_i^2 / )$	
	$\frac{\sum_{i} \left( \frac{1}{D_s^2} \right)}{\left( \frac{1}{D_s^2} \right)}$	
Distance Depedent Indice	S	
Hegyi's Index	$\sum_{i} \frac{\binom{D_{i}}{D_{S}}}{L_{i}}$	L <sub>i</sub> = distance between the subject tree and the i <sup>th</sup> competing neighbour
Hegyi's Index 2	$\sum_{i} \frac{\binom{D_{i}^{2}}{D_{S}^{2}}}{L_{i}}$	
Weiner's Index	$\sum_{i} \frac{TM_{i}}{L_{i}}$	$TM_i$ = total mass of the $i^{th}$ competing neighbour
Silander and Pacala's Index	$\sum_{i} TM_{i} \left( 1 - \frac{L_{i}}{R_{MAX}} \right)^{2}$	$R_{MAX}$ = length of the search radius used to select the competing neighbours
Newton and Jolliffe's Modification of Weiner's Index	$\left(\sum_{i} \frac{TM_{i}}{L_{i}^{2}}\right) \left(1 - \frac{R_{CM}}{R_{MAX}}\right)$	
Newton and Jolliffe's Modification of Silander and Pacala's Index	$\left[\sum_{i} TM_{i} \left(1 - \frac{L_{i}}{R_{MAX}}\right)^{2}\right] \left[1 - \frac{R_{CM}}{R_{MAX}}\right]$	R <sub>CM</sub> = distance between the subject tree and the centre-of-mass of the competitors
Opie's Index	7	a <sub>i</sub> = area of overlap between the regions of
-p	$\sum a_i$	influence of the subject tree and the i <sup>th</sup>
	$\sum_{i} \frac{a_{i}}{A_{s}}$	competing neighbour
	$\overline{}_i A_S$	A <sub>s</sub> = total area of the subject tree's region of influence
Bella's Index	$\sum_{i} \binom{a_i}{A_S} \binom{D_i}{D_S}^{EX}$	EX = scaling exponent for asymmetrical relationships
Ek and Monserud's Index	$-(\alpha / )(DH / )$	H <sub>i</sub> = height of the i <sup>th</sup> competitor
ING FIGURES AND ANGEN	$\sum_{i} \binom{a_i}{A_S} \binom{D_i H_i}{D_S H_S}$	H <sub>s</sub> = height of subject tree

These indices were calculated for every sample tree in every plot with routines written using Microsoft Visual Basic which were run as macros within Excel (see Appendix 2 for the source code of the routines). A routine functions by selecting the first sample tree in the first plot as a subject tree. It then searches through the rest of the sample trees in the plot and through the plot's border trees to see if any of the trees match the criteria for selection as competing neighbours. If a neighbouring tree qualifies, it is included in the calculation of the index. Once all of the neighbours have been identified and the final index value has been calculated, the routine outputs the index value for the subject tree in a results table. It then moves on to select the next sample tree and repeats the process. The routine continues through the rest of the plot and then through each of the remaining plots until an index value has been calculated for every sample tree in every plot.

The routine was written so that the criteria for identifying competing neighbours could be easily modified. This made it possible to run the routine several times for each index in order to observe what effect varying the criteria had on the index values. These additional calculations made it possible to explore the effects of including trees from various distances from the subject tree. It also made it possible to explore the effects of placing restrictions on which trees qualify as neighbours based on their size relative to the size of the subject tree. From these calculations it was possible to make inferences about the extent to which the neighbouring trees were able to exert an influence over subject trees.

# 3.2.1 Distance Independent Indices

#### 3.2.1.1 Simple Indices using Stand-level Variables

The two stand-level variables were included in order to make comparisons between the performance of simple stand-level measures and the more complicated individual tree indices. The original 1988 measurement values of basal area per hectare and Curtis' (1982) relative density index (see Table 2 in Chapter 4) were selected for use as index values. The value for each plot was assigned to each tree within the respective plot as a competition index value.

# 3.2.1.2 Simple Indices using Individual Tree Characteristics

The simple indices that were selected are very easy to calculate and do not require spatial data. They were included so that their performance could be compared to the performance of the more complicated distance dependent indices. This made it possible to compare the gains in performance against the costs of collecting spatial data.

Individual tree vigour was selected for use as an index because the vigour of a tree is often a good indication of the competitive stress experienced by a tree. If a tree has a low vigour, it is usually a result of stress from competition. The vigour value recorded for each tree in the 1988 measurement was designated as a competition index for each tree.

The basal area of each tree recorded in the 1988 measurement was used to calculate a simple index. The index was calculated by finding the total basal area of all of the trees in a plot that had a basal area greater than the subject tree (Biging and Dobbertin 1995). However, testing this index value when it was calculated for all of the plots was problematic because the index value for a subject tree is relative to its plot. Therefore, it was decided that this value should be divided by the total basal area of the plot to produce a percentage. The final index was named "the percent basal area greater than the subject" (or "BA > subject" as an abbreviated form). This index required a simple routine to be calculated. The routine identified all of the trees in a plot with a basal area larger than that of the subject tree. The basal area of all of these trees was then summed and divided by the total basal area of the plot to create an index in the form of a percentage.

Gloover and Hool's Index (1979 in Lorimer 1983) was included in this study despite the criticisms discussed in Chapter 2. The index compares the characteristics of the subject tree to the plot average instead of making comparisons to trees within a defined competitive neighbourhood around the subject tree. This index was included in an attempt to evaluate the relative gains made by indices that are calculated using a competitive neighbourhood.

Gloover and Hool's Index = 
$$\frac{D_s^2}{\overline{D}^2}$$

where  $D_S$  is the dbh of the subject tree and  $\bar{D}$  is the average dbh of the stand or plot.

The live crown ratio index was included in this study because it is a very simple representation of a crown model. The size of the crown of a tree relative to its height is a good indication of the degree to which a tree is suppressed and can also be related to its growth potential. The index was calculated for each tree in each plot using the 1988 measurement values.

Crown Ratio = 
$$\frac{LC}{H_T} = \frac{(H_T - H_{LLB})}{H_T}$$

where LC is the length of the living crown,  $H_T$  is the total height of the subject tree, and  $H_{LLB}$  is the height of the lowest living branch on the subject tree.

# 3.2.1.3 Lorimer's Modification of Hegyi's Index

Lorimer's (1983) modification of Hegyi's (1974 in Lorimer 1983) index (hereafter referred to as "Lorimer's index" or "Lorimer") is an example of an index calculated with the distance term removed in order to investigate the necessity of using distance in the calculation of an index. Lorimer noted that since the spatial location of the trees and the distances between them must be known in order identify the competing neighbours to be used in the calculation of Hegyi's index, distance is inherently included in the index. This fact led Lorimer to hypothesize that removing the distance term from Hegyi's index would have little effect on the performance of the index and would, by definition, make the index distance independent. Lorimer's index was selected in order to evaluate if his hypothesis was valid when applied to the stands in this study.

Lorimer's 's Index = 
$$\sum_{i} \binom{D_i}{D_S}$$

where D<sub>i</sub> is the dbh of the i<sup>th</sup> competing neighbour.

Lorimer also included a further modified version of Hegyi's index in his study. He hypothesized that if the diameters of the subject and neighbouring trees were squared, the index may show improved performance. This further modified index (hereafter referred to as "Lorimer's index 2" or "Lorimer2") was included in this study to see if an improved performance could also be found.

Lorimer's 's Index 
$$2 = \sum_{i} \begin{pmatrix} D_i^2 \\ D_S^2 \end{pmatrix}$$

When Hegyi (1974 in Lorimer 1983) introduced his index, he suggested that a fixed search radius should be used as the method for identifying competing neighbours. In order to investigate the effect of using a wider or narrower search radius, Lorimer's index and Lorimer's index 2 were both calculated using three different lengths of radii. The maximum length of the radii was restricted by the width of the measured border around the plots. If a radius length was selected that was longer than the border width, it would have resulted in a search area extending beyond the measured border area for some of the sample trees near the edges of the plots. This would have likely resulted in underestimated index values for these trees. When the plots were established, border trees were selected arbitrarily which resulted in an inconsistent width of the measured border. Therefore, the width of the borders on all of the plots had to be evaluated first. This was done using ArcView with which distances can be easily measured on the graphical display of a plot. The general spacing of the trees was also evaluated during this process. From these evaluations it was determined that the maximum search radius should be set at nine meters. It was also decided that a search radius much less than 5 meters would result in a poor representation of the neighbourhood around many of the sample trees. Therefore, the three search radii were set at 5, 7 and 9 meters.

The use of a fixed search radius was criticized by Daniels *et al.* (1986), who suggested that a variable radius plot would be a better method for identifying competing neighbours when calculating Hegyi's index. In order to investigate the claims made by Daniels *et al.*, Lorimer's index and Lorimer's index 2 were both calculated using variable radius plots for neighbour selection. ArcView was again used to evaluate which trees were selected as competing neighbours for a given subject tree when various BAF's were used to define the extent of the variable radius plot. It was determined that a BAF larger than 6 m²/ha would likely have an extent well beyond the measured area of each plot. Any larger value would likely produce biased indices for some trees, especially in plots 1 and 2 where there are many large diameter trees that could be selected by the search criteria but are located outside of the measured area. Therefore, the indices were calculated using BAF's set at 2, 4 and 6 m²/ha. The routines identified if a neighbouring tree was considered to be in a variable radius plot by calculating a critical distance. If the distance between the subject and the neighbouring tree was less than the critical distance calculated for the neighbouring tree, it was selected as a competing neighbour.

Critical Distance = 
$$\frac{D_i}{2 \times \sqrt{BAF}}$$

A third method for identifying neighbours discussed in the literature was the use of a height angle gauge. This method, which was recommended by Biging and Dobbertin (1992), was included to evaluate if competing neighbours should be selected on the basis of their distance and height relative to the subject tree rather than on the basis of their distance and diameter relative to the subject. The indices were calculated using a 30, 45 and 60 degree search angle for the study. Neighbouring trees were selected if their height intercepted a cone projected from the base of the subject tree at the set angle. This was checked for each tree using each angle  $(\theta)$  in the routines by calculating the critical distance.

Height Angle Gauge Critical Distance = 
$$\frac{H_i}{\tan(\Theta)}$$

where  $\boldsymbol{\theta}$  is the search angle from the horizontal.

In order to be able to evaluate if the relationships between the study trees are one-sided or two sided, Lorimer's index and Lorimer's index 2 were calculated again with a height restriction placed on the potential neighbours. In order to qualify as a competing neighbour with this restriction, the neighbouring tree must be taller than the subject tree. The indices were calculated using the three methods described above and this restriction.

# 3.2.2 Distance Dependent Indices

#### 3.2.2.1 Hegyi's Index

Hegyi's (1974 in Lorimer 1983) index is one of the most commonly tested indices in the literature (i.e., Daniels 1976, Lorimer 1983, Pukkala and Kolstrom 1987, Biging and Dobbertin 1992). It has been found to perform very well considering its computational simplicity. Therefore, it was also selected for this study to see if it could provide similar results when applied to the study stands.

Hegyi's Index = 
$$\sum_{i} \frac{\binom{D_i}{D_s}}{L_i}$$

where L<sub>i</sub> is the distance between the subject tree and the i<sup>th</sup> competing neighbour.

When Lorimer (1983) tested Hegyi's index in his study, he also tested a version of Hegyi's index using squared diameter terms. This index (hereafter referred to as "Hegyi's Index 2" or "Hegyi2") was also included in this study to see if the squared terms improve the performance of the index.

Hegyi's Index 
$$2 = \sum_{i} \frac{\binom{D_i^2}{D_s^2}}{L_i}$$

Hegyi's index and Hegyi's index 2 were calculated at the same time as Lorimer's indices using the same routine. Therefore, the same set of search criteria were used to identify competing neighbours (fixed radius plots of 5, 7 and 9 m; variable radius plots using BAF's of 2, 4 and 6 m²/ha; and height angle gauge plots using 30, 45 and 60 degree searches). The indices were also calculated a second time using the height restriction on the competing neighbours.

### 3.2.2.2 Weiner's Index

Weiner's (1984) index may not use an actual ratio of diameters in its formulation, but it was still included with the ratio of diameters approaches because it follows a similar method of calculation. Since Weiner's index was developed for studies of plant competition, the competitive influence of neighbours is measured in terms of their total mass instead of their diameters. The total mass for each tree was estimated using the biomass equations published in Marshall and Wang (1995). This index was included because it was hoped that more information about the influence of competing neighbours would be contained in the total mass measure due to the fact that the total mass is estimated using both the height and diameter of the trees.

Weiner's Index = 
$$\sum_{i} \frac{TM_{i}}{L_{i}}$$

where TM<sub>i</sub> is the total mass of the i<sup>th</sup> competing neighbour.

For this study, competing neighbours were selected using only a fixed radius search because the index was calculated using the same routine as the next three indices which could only be calculated using fixed radius searches. The same radius lengths of 5, 7 and 9 meters that were used to calculate the other ratio of diameter indices were also used to calculate Weiner's index and the next three indices. A

version of the index using the height restriction on competing neighbours was also calculated for Weiner's index.

#### 3.2.2.3 Silander and Pacala's Index

Silander and Pacala (1985 in Newton and Jolliffe 1998) modified Weiner's Index so that the distance measure is scaled relative to the search radius of the plot. The search radius is also the maximum distance that a competitor can be located from the subject tree, which is why the distance scaling term is referred to as  $R_{\text{MAX}}$ .

Silander and Pacala's Index = 
$$\sum_{i} TM_{i} \left(1 - \frac{L_{i}}{R_{MAX}}\right)^{2}$$

where R<sub>MAX</sub> is the length of the search radius used to select the competing neighbours.

This index was included to evaluate if the scaling term could increase the performance of the index when applied to the study stands. Since the maximum search radius is one of the variables used in the equation, only fixed radius plots could be used to identify competing neighbours. A second version of the index was calculated using the restriction on competing neighbours.

# 3.2.2.4 Newton and Jolliffe's Modification of Weiner's Index and Silander and Pacala's Index

Newton and Jolliffe (1998) modified the indices by Weiner and Silander and Pacala to include their centre-of-mass adjustment factor. Newton and Jolliffe created the modified versions of these indices in an attempt to better represent the competitive effects of trees growing in spatially heterogeneous stands.

Newton and Jolliffe's Modification of Weiner's Index = 
$$\left(\sum_{i} \frac{TM_{i}}{L_{i}^{2}}\right) \left(1 - \frac{R_{CM}}{R_{MAX}}\right)$$

Newton and Jolliffe's Modification of Silander and Pacala's Index = 
$$\left[\sum_{i} TM_{i} \left(1 - \frac{L_{i}}{R_{MAX}}\right)^{2}\right] \left[1 - \frac{R_{CM}}{R_{MAX}}\right]$$

where R<sub>CM</sub> is the distance between the subject tree and the centre-of-mass of the competitors.

These equations were included in this study because the uneven-aged structure of the study stands has often resulted in a clumped and heterogeneous spacing of the trees. It was hoped that the adjustment factor would help to improve the performance of the indices in the study stands. The use of  $R_{\text{MAX}}$  in both of the equations limited the method of neighbour selection to only fixed radius plots. Both indices were calculated a second time using the restriction on competing neighbours.

# 3.2.2.5 Opie's Index

The first index representing the area of influence approach selected for this study was Opie's (1968 in Bella 1971) index. It is calculated using a single ratio comparing the amount of overlap between the region of competitive influence of a subject tree and its neighbours over the total area of the subject tree's region.

Opie's Index = 
$$\sum_{i} \frac{a_i}{A_S}$$

where  $a_i$  is the area of overlap between the regions of influence of the subject tree and the  $i^{th}$  competing neighbour and  $A_s$  is the total area of the subject tree's region of influence.

Opie proposed that the region of competitive influence should be defined for a tree relative to its diameter. In order to be able to compare all of the area of influence indices, one method of defining the region was selected for use with all of the area of influence indices tested in this study. The use of dbh to define the region was not used due to the criticisms made by Tennent (1975) that were discussed in Chapter 2. Bella (1971) proposed that an equation estimating the open-grown crown area should be used to define the region. However, this equation would use the current dbh of a tree to estimate the open-grown crown area and would be open to similar criticisms.

Since the crown width of the sample trees was recorded in the data, it was decided that the actual crown area calculated from the 1988 values of these measurements would be the most appropriate definition of the region of competitive influence. In both Bella and Tennent's studies, the size of the region of influence was varied to try to find an optimum that would best represent the trees being studied. Therefore, the area of influence indices in this study were also calculated using varied sizes of regions in an attempt to find an optimal definition for the study stands. The size of the region was varied by multiplying the measured crown radius by incremental constants before it was used to calculate the crown area. The three constants used were 1.0, 1.5 and 2.0.

Area of Competitive Influence = 
$$\pi \times \left[ C \times \left( \frac{CW}{2} \right) \right]^2$$

where C is one of the three constants and CW is the crown width.

In order to continue the investigation of the one-sided or two-sided relationships of the study trees, the height restriction was also applied to Opie's index. A second version of the index was calculated that only considered the overlap from a neighbouring tree if the tree was taller than the subject tree.

#### 3.2.2.6 Bella's Index

Bella (1971) added weights to Opie's index that scaled the amount of overlap relative to the diameter of the competing tree. He also included a scaling exponent that would reflect the competitive asymmetry that exists between large and small trees.

Bella's Index = 
$$\sum_{i} \left( \frac{a_i}{A_S} \right) \left( \frac{D_i}{D_S} \right)^{EX}$$

where EX is the scaling exponent for asymmetrical relationships.

This index was added to investigate if the performance of the index could be improved by adding variables that represent the way in which the resources are shared between trees. The index was calculated using three different values for the scaling exponent to investigate what value best represents the amount of asymmetry that exists between the trees in the study stands. The exponent was set to values of 1.0 (i.e., no scaling effect / symmetry), 1.5 and 2.0. The indices calculated using each of these exponent values were referred to as "Bella 1.0", "Bella 1.5" and "Bella 2.0", respectively. Each of these versions were then calculated using the three different definitions of the competitive region for a total of 9 versions of Bella's index. These 9 versions were then calculated again using the height restriction on competing neighbours.

#### 3.2.2.7 Ek and Monserud

The last index selected for this study was the index by Ek and Monserud (1974 in Daniels 1976). Ek and Monserud added a ratio of diameters weighting to Opie's index to scale the effect of the overlap from

larger or smaller trees. In addition, they added the height of both the subject and competing trees into the ratio in an attempt to include more information representing the competitive influence exerted by the neighbouring trees. This index was included in this study to see if the addition of tree height information could improve the performance of the index.

Ek and Monserud's Index = 
$$\sum_{i} \left( \frac{a_i}{A_S} \right) \left( \frac{D_i H_i}{D_S H_S} \right)$$

where  $H_i$  is the height of the  $i^{th}$  competitor and  $H_S$  is the height of subject tree.

Ek and Monserud's index was calculated using the same three definitions of the region of competitive influence as the other area of influence indices and it was then calculated again with the height restriction.

# 3.3 Evaluation of the Competition Indices

The ability of the indices to represent the competitive environment of a subject tree was evaluated by testing how well each index could explain the variation in individual tree dbh growth observed during the remeasurements of the study plots. This ability was tested by performing a regression using an equation containing the index and dbh as the independent variables and the observed growth in dbh as the dependent variable. The performance of this regression was then compared to the performance of a regression using a base equation containing only dbh as the dependent variable. The increase in the performance of the regression using both the index and dbh equation over the performance of the base equation regression was used as a representation of the ability of the index to explain the variation in tree growth due to competition. This regression test was performed for each index selected so that the performance of each index relative to the performance of the other indices could also be compared.

The first step in the evaluation process was to organize all of the index values generated by the routines for each tree. Forty-eight different indices were selected for testing; however, many of the indices were repeatedly calculated using two or three different search criteria resulting in total of 126 indices to be tested. The 126 different index values generated for each tree were divided into manageable categories and combined with the dbh and growth measurements for each tree in Excel (Microsoft Corporation 1996). The dbh recorded in the original 1988 measurement of the study stands was used as the dbh variable. In order to reduce the effects of year-to-year variation, the total growth in dbh observed between the 1988 measurement and 1997 remeasurement was used as the growth variable. All of the

data were converted to text format files that could be easily imported into SAS (SAS Institute Inc. 1996). The relationships between the index, dbh and growth variables were explored using SAS. These relationships were observed by generating many plots and tables of simple correlations.

The next step was to select the form of the equation to be used in the evaluation regressions. The first equation forms tested were created for use in multiple regression analysis. Several transformations of each variable were calculated based on the observations made while analyzing the relationships between the variables. All of the variables and their transformations were included in a SAS regression procedure that calculated a regression for every possible combination of the variables. This procedure made it possible to select the combination of variables that produced the best performance. From this output, an equation was formed using the optimal combination of the variables and their transformations. However, when it was tested using a range of different index values, this equation generally showed low performance and often resulted in negative predicted growth values.

These unsatisfactory results were addressed by testing forms of equations that could be used in a nonlinear regression analysis. The form of the base equation selected was:

$$dbh \ growth = k_1 \times dbh^{p_1} \times c_1^{dbh} + e$$

where  $k_1$ ,  $p_1$ , and  $c_1$ , are parameters that are calculated by the regression and e is the unexplained error.

The form of the equation used to evaluate the indices selected was:

$$dbh \cdot growth = k_1 \times dbh^{p_1} \times index^{p_2} \times c_1^{dbh} \times c_2^{index} + e$$

where  $p_2$ , and  $c_2$  are parameters that are calculated by the regression.

These equations were selected because, when plotted against dbh, the function forms an arch with a steep incline and a long, drawn out decline. This shape is similar to the pattern observed in the plotted relationship between dbh growth and dbh.

Before the nonlinear regressions could be run to evaluate the indices, initial starting values had to be generated for the parameters ( $k_1$ ,  $p_1$ ,  $p_2$ ,  $c_1$ , and  $c_2$ ) which are iterated during the calculation of the nonlinear regression. This was done by running a simple linear regression using the  $log_{10}$  of dbh and the  $log_{10}$  of the index as independent variables and the  $log_{10}$  of dbh growth as the dependent variable. The coefficients generated by this regression were used as the initial values for the nonlinear regression

parameters. This regression was calculated for each of the indices evaluated and the resulting coefficients were entered into the SAS procedure calculating the nonlinear regression for each index.

The nonlinear regressions for the base equation and each index were run and the output for each regression was analyzed. The sums of squares regression and the sums of squares total for each regression were copied from the SAS output and pasted into an Excel file. From this information the following variables were calculated: the mean squared error of the regression equation (MSE), the coefficient of multiple determination ( $R^2$ ), and the standard error of the estimate ( $SE_E$ ). These variables were organized into tables that are presented in Chapter 4.

Before the results of the regression could be accepted, a diagnostic of the regression equations had to be performed. This diagnostic was performed mostly through visual evaluations of scatter plots. The goodness of fit of the regressions were evaluated by plotting the observed dbh growth values versus dbh on the same graph as the predicted dbh growth values from the regression versus dbh. The residual values from each regression were plotted against the predicted growth values in order to evaluate trends in the variance of the error in the regressions. Finally, the precision and the bias of the regression were calculated by diameter class. This was done to evaluate if the increase in the performance of one regression equation over another was concentrated in particular diameter classes.

# 4 Results

# 4.1 Update of Permanent Sample Plot Data

Overall, the growing conditions over the last growth period were far more favourable than those of the first growing period. Both basal area and volume growth were much higher than in the previous period. Interestingly, the highest growth rate occurred in the plots dominated by mid-sized dbh trees and regeneration, whereas in the first growth period it was found in the plots dominated by large dbh trees. Another interesting trend is the continual decrease in the proportion of each plot that is made up by trees in the smaller diameter classes.

#### 4.1.1 PSP Structural Conditions

#### 4.1.1.1 Structure at the Previous Remeasurements

The results presented in Tables 1 to 4 are adapted from the report published by Marshall and Wang (1996). A few measurement errors were corrected, but the data still display the trends observed and discussed by Marshall and Wang. The unauthorized cutting that occurred in plots 1 and 4 after the first measurement had a much more serious effect on the stand structure of plot 1 than on plot 4. Both the before and after cutting measurements are included in Table 2, but the values measured after the cutting will be used for the calculations in the rest of this section.

Table 2. Summary of PSP structural conditions at the 1988 measurement (adapted from Marshall and Wang 1996).

			,			Percentage Composition								
Plot #	Stems/Ha	BA/Ha	Dq <sup>a</sup>	$RD^{b}$	Average	Stems/Ha	Stems/Ha	Stems/Ha	BA/Ha	BA/Ha	BA/Ha			
		$(m^2)$	(cm)		Vigour	< 10	10 - 20	> 20	< 10	10 - 20	> 20			
1	1520	24.29	14.26	6.43	2.07	75.0	12.5	12.5	7.8	10.8	81.3			
1 *	1610	43.61	18.57	10.12	2.07	72.6	12.4	14.9	4.6	6.4	89.0			
2	1170	47.38	22.71	9.94	2.19	57.2	14.5	28.2	1.5	4.9	93.6			
3	2520	29.45	12.20	8.43	1.88	64.2	31.0	4.8	9.4	41.3	49.3			
4	1530	36.04	17.32	8.66	1.94	32.7	53.6	13.7	4.8	38.5	56.7			
4 *	1540	36.13	17.30	8.69	1.92	32.5	53.9	13.6	4.8	38.6	56.6			
5	5660	41.47	9.66	13.34	1.65	88.0	6.0	6.0	15.9	14.8	69.3			
6	4300	32.33	9.78	10.34	1.71	83.2	10.7	6.0	15.8	17.5	66.7			

<sup>\*</sup> Values based on all trees measured before the unauthorized cutting

<sup>&</sup>lt;sup>a</sup> Quadratic mean diameter

<sup>&</sup>lt;sup>b</sup> Curtis' (1982) relative density

Table 3. Volume and biomass of various components for each of the PSP's at the 1988 measurement (adapted from Marshall and Wang 1996).

Plot #	Volume/Ha (m³)	STEMWOOD (kg)	STEMBARK (kg)	LTWIGS (kg)	LNEEDLES (kg)	STUMWOOD (kg)	STUMBARK (kg)	CROWN (kg)	TOTAL (kg)
1	190.4	106946	22706	28921	8883	3304	1022	37358	165508
1 *	360.9	211509	48032	73808	12481	5918	1855	85447	341809
2	387.1	215408	50381	63251	13479	6431	2022	76624	349147
3	191.5	106329	23904	32012	11055	4038	1212	42022	166218
4	234.2	123055	29271	33525	12963	4939	1493	45536	194090
4 *	234.6	123171	29318	33360	12870	4921	1488	45284	194424
5	270.5	140976	33372	29780	13424	5640	1732	38923	221666
6	205.7	108165	25147	27778	12417	4412	1338	38780	169698

<sup>\*</sup> Values based on all trees measured before the unauthorized cutting

Where STEMWOOD is the biomass of the wood from the stem of the tree, STEMBARK is the biomass of the bark on the stem, LTWIGS is the biomass of the living branches, LNEEDLES is the biomass of the living needles, STUMWOOD is the biomass of the wood from the stump, STUMBARK is the biomass of the bark from the stump, CROWN is the sum of LTWIGS and LNEEDLES, and TOTAL is the sum of the first six biomass components.

Table 4. Summary of PSP structural conditions at the 1992 remeasurement (adapted from Marshall and Wang 1996).

Plot #							, Pe	Percentage Composition						
	Stems/Ha	BA/Ha (m²)	Dq (cm)	RD	Average Vigour	Stems/Ha < 10	Stems/Ha 10 - 20	Stems/Ha > 20	BA/Ha < 10	BA/Ha 10 - 20	BA/Ha > 20			
1	1450	25.95	15.10	6.68	2.10	70.3	15.9	13.8	7.0	12.1	80.8			
2	1140	48.32	23.23	10.02	2.18	56.1	. 14.9	28.9	1.6	5.2	93.2			
3	2440	31.29	12.78	8.75	1.89	62.7	31.1	6.1	9.7	39.5	50.8			
4	1500	37.67	17.88	8.91	1.91	28.7	53.3	16.0	4.5	36.9	58.6			
5	5260	42.48	10.14	13.34	1.68	87.0	5.7	7.2	16.4	11.3	72.2			
6	4140	34.22	10.26	10.68	1.72	82.6	11.1	6.3	16.2	18.2	65.6			

Table 5. Volume and biomass of various components for each of the PSP's at the 1992 remeasurement (adapted from Marshall and Wang 1996).

Plot#	Volume/Ha	STEMWOOD	STEMBARK	LTWIGS	LNEEDLES	STUMWOOD	STUMBARK	CROWN	TOTAL
	(m³)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)
1	208.6	118915	24464	31802	9556	3533	1091	40995	182579
2	407.1	230726	51829	65704	13852	6557	2063	79409	368995
3	209.4	117522	25399	36765	12490	4289	1291	48122	180829
4	250.8	132878	30788	36657	13951	5160	1564	49564	208015
5	285.7	151687	34488	31271	13972	5776	1772	40595	236021
6	220.5	116370	26653	29690	13134	4666	1419	41179	181333

#### 4.1.1.2 Structure at the Current Remeasurement

The summary parameters used by Marshall and Wang (1996) in Tables 2 to 5 were calculated using the data collected from the 1997 remeasurement and are presented in Tables 6 and 7.

Table 6. Summary of PSP structural conditions at the 1997 remeasurement.

Plot #							Pe	rcentage Co	Composition					
	# Stems/Ha 1510 1180 2350 1460	BA/Ha (m²)	Dq (cm)	RD	Average Vigour	Stems/Ha < 10	Stems/Ha 10 - 20	Stems/Ha > 20	BA/Ha < 10	BA/Ha 10 - 20	BA/Ha > 20			
1	1510	28.21	15.42	7.18	2.11	66.9	19.9	13.2	6.7	14.7	78.6			
2	1180	50.39	23.32	10.44	2.04	55.9	15.3	28.8	1.9	5.0	93.1			
3	2350	34.64	13.70	9.36	1.83	57.4	34.9	7.7	7.8	40.8	51.4			
4	1460	40.26	18.74	9.30	1.93	27.4	52.1	20.5	3.8	33.8	62.4			
5	5020	45.08	10.69	13.79	1.62	84.9	7.5	7.6	15.4	12.8	71.8			
6	4000	37.54	10.93	11.35	1.79	80.0	13.0	7.0	15.1	19.2	65.7			

Table 7. Volume and biomass of various components for each of the PSP's at the 1997 remeasurement.

Plot #	Volume/Ha	STEMWOOD	STEMBARK	LTWIGS	LNEEDLES	STUMWOOD	STUMBARK	CROWN	TOTAL
	(m³)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)
1	224.0	127795	26621	32113	9660	3843	1185	41247	197096
2	415.2	232230	53760	65288	13706	6837	2151	78864	374929
3	216.8	114306	27548	32306	12651	4747	1433	43811	181377
4	269.0	141617	33289	32436	13461	5511	1677	44580	221832
5	301.2	159084	36869	33656	14776	6132	1880	45325	249809
6	242.3	127604	29485	29383	13462	5120	1558	40908	199658

In the tables above and Figure 1 below, it can be seen how each set of plot pairs were placed purposefully to represent a different stand structure. Because of the uneven-aged nature and the disturbance history of the stands, there is a disproportionately large number of stems in the less than 10 cm diameter class in almost every plot. These stems represent the shade tolerant regeneration in the understory. By focusing on the two larger classes, differences in the stand structure can be seen in terms of the proportion of mid-sized dbh size trees (10 to 20 cm) and large dbh tress (> 20 cm). A large component of mid-sized dbh trees can be seen in plots 3 and 4. Plots 5 and 6 have a larger component of smaller trees than any of the other plots. The effects of the unauthorized cutting can still be seen in plot 1 where the middle diameter class now makes up a larger proportion of the stand. However, plot 2 is still a good example of a stand structure that has a large component of large dbh trees.

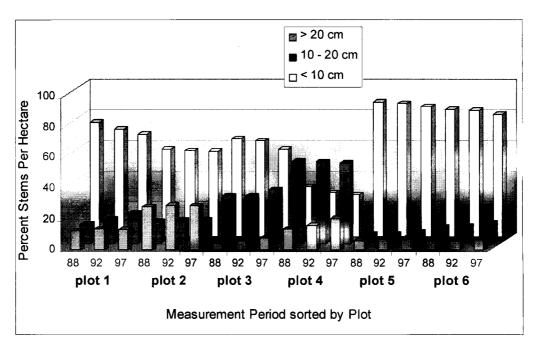


Figure 1. The proportion of the stems divided into diameter classes at each of the measurements for each plot.

The majority of the basal area in every plot is contributed by the trees in the largest diameter class (Figure 2). Therefore, the highest total basal area can be found in plot 2 (50.39 m²/ha) due to the relatively large proportion of the stand being composed of stems greater than 20 cm. A similarly large amount of basal area would have likely been seen in plot 1 if there had been no unauthorized cutting (adding the actual observed growth on to the pre-cutting basal area produces an estimate of 47 m²/ha if no cutting had occurred). As would be expected, a large proportion of the basal area in plots 3 and 4 is contributed by the 10 to 20 cm diameter class and a relatively large proportion of the basal area in plots 5 and 6 is contributed by the smallest diameter class. In terms of total basal area, the paired plots 5 and 6 may each be higher in basal area than paired plots 3 and 4, but plot 3 is closer in basal area to plot 6 and plot 4 is closer to plot 5.

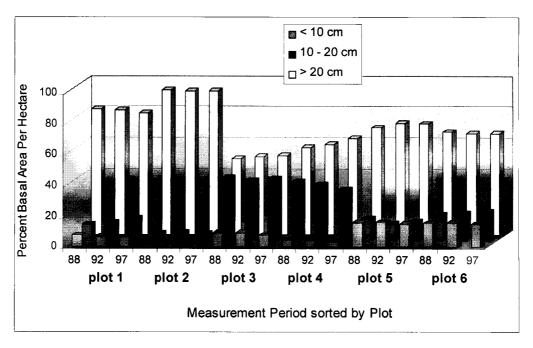


Figure 2. The proportion of the basal area divided into diameter classes at each of the measurements for each plot (Note: the order of the diameter classes has been reversed from Figure 1 for clarity).

The average vigour decreases as the density of the plot increases. Plot 1, which has the lowest density, has the highest average vigour and plot 4, the densest plot, has the lowest average vigour. The low vigour of the dense plots does not imply that the growth performance of the plot will also be low. The low average vigour results from the fact that the smaller stems within the plot are generally suppressed by the dominants in the overstory. Therefore, the large number of smaller, suppressed stems in the dense plots tends to pull the average vigour of the plots down.

The mean diameter of the plots is directly related to the size distribution of the stems within the plots. The plots with a large proportion of trees in the smallest diameter class have lower mean diameters because the number of small trees pull the average down. Plot 2 has the highest mean dbh due to the large proportion of trees in the largest diameter class. Plot 4 also has a high mean dbh, but this is caused more by the relatively few number of trees in the smallest diameter class.

Curtis' (1982) relative density index combines the measures of basal area and stems per hectare to produce an index that can be used to compare the crowding of the trees relative to the stand structure. In these relative terms, plots 3 and 4 appear to have almost identical densities. Plot 2 is slightly more

dense that these two plots and the effects of the unauthorized cutting can be seen in the very low density of plot 1. Plots 5 and 6 have the highest density, which indicates that the plots are overly crowded by the large number of suppressed trees even when measured in terms relative to the stand structure.

Both basal area and total biomass are a function of dbh. Therefore, similar trends among the plots exist for both measures. Plot 2 has the highest biomass because of the many large dbh trees in the plot. Plot 5 has an unusually large biomass, that can be related to the large proportion of the basal area of the plot comprised of trees that are in the greater than 20 cm class. The live needle biomass of each plot is relatively constant across all of the plots. This trend was observed after the previous remeasurement and it was hypothesized by Marshall and Wang (1996) to be an indication of a uniform site quality that exists across all of the plots.

## 4.1.2 Change in PSP Structural Conditions

The growth of the parameters that occurred during the two growth periods that were recorded between the three measurements of the plots are presented in Tables 7 to 10. The results presented in Tables 7 and 8 are adapted from the results published in the report by Marshall and Wang (1996). When comparing the two growth periods, it is important to note that the period between the 1988 and 1992 measurements contained approximately four and a half growing seasons (the half year is used to represent the fact that the 1988 measurement was conducted half way through the growing season of 1988), whereas the growth period between the 1992 and 1997 remeasurements contained only four growing seasons. Therefore, in order to compare any results, the growth should be divided by the number of growing seasons in the period to find an average value of growth per year. Overall, it appears that the growing conditions over the second growth period were more favourable.

Table 8. Change in PSP structural conditions (1992 values - 1988 values) expressed in absolute units and as percentages of 1988 values (adapted from Marshall and Wang 1996).

Plot #	Stems/Ha	Stems/Ha	BA/Ha	BA/Ha	Dq	Dq	RD	RD	Vigour	Vol/Ha	Vol/Ha
	(count)	(%)	(m²)	(%)	(cm)	(%)		(%)		(m³)	(%)
1	-70	-4.6	1.66	6.9	0.83	5.8	0.25	3.9	0.03	18.1	9.5
2	-30	-2.6	0.94	2.0	0.52	2.3	0.08	0.8	-0.01	20.0	5.2
3	-80	-3.2	1.85	6.3	0.58	4.8	0.32	3.8	0.01	18.0	9.4
4	-30	-2.0	1.63	4.5	0.56	3.3	0.25	2.9	-0.03	16.6	7.1
5	-400	-7.1	1.02	2.4	0.48	5.0	0.00	0.0	0.03	15.2	5.6
6	-160	-3.7	1.89	5.8	0.47	4.8	0.35	3.4	0.01	14.8	7.2

Table 9. Change in PSP structural conditions (1992 values - 1988 values) expressed in absolute units and as percentages of 1988 values (adapted from Marshall and Wang 1996).

Plot #	STEMWOOD (kg)	STEMBARK (kg)	LTWIGS (kg)	LNEEDLES (kg)	STUMWOOD (kg)	STUMBARK (kg)	CROWN (kg)	CROWN (%)	TOTAL (kg)	TOTAL (%)
1	11969	1759	2881	674	228	69	3637	9.7	17070	10.3
2	15317	1447	2453	373	127	41	2784	3.6	19848	5.7
3	11193	1495	4753	1435	251	78	6100	14.5	14611	8.8
4	9822	1517	3132	989	221	70	4028	8.8	13925	7.2
5	10711	1115	1490	548	137	41	1672	4.3	14355	6.5
6	8205	1506	1912	717	254	80	2399	6.2	11635	6.9

Table 10. Change in PSP structural conditions (1997 values - 1992 values) expressed in absolute units and as percentages of 1988 values.

Plot #	Stems/Ha (count)	Stems/Ha (%)	BA/Ha (m²)	BA/Ha (%)	Dq (cm)	Dq (%)	RD	RD (%)	Vigour	Vol/Ha (m³)	Vol/Ha (%)
1	60	4.1	2.26	8.7	0.33	2.2	0.50	7.5	0.02	15.5	7.4
2	40	3.5	2.08	4.3	0.09	0.4	0.41	4.1	-0.13	8.1	2.0
3	-90	-3.7	3.35	10.7	0.92	7.2	0.60	6.9	-0.05	7.4	3.5
4	-40	-2.7	2.59	6.9	0.86	4.8	0.39	4.4	0.02	18.2	7.3
5	-240	-4.6	2.59	6.1	0.55	5.4	0.44	3.3	-0.06	15.5	5.4
6	-140	-3.4	3.32	9.7	0.67	6.6	0.67	6.3	0.06	21.8	9.9

Table 11. Change in PSP structural conditions (1997 values - 1992 values) expressed in absolute units and as percentages of 1988 values.

Plot #	STEMWOOD	STEMBARK	LTWIGS	LNEEDLES	STUMWOOD	STUMBARK	CROWN	CROWN	TOTAL	TOTAL
	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(kg)	(%)	(kg)	(%)
1	8880	2156	311	104	310	94	253	0.6	14517	8.0
2	1505	1931	-415	-146	280	88	-545	-0.7	5934	1.6
3	-3215	2149	-4458	161	458	143	-4312	-9.0	548	0.3
4	8739	2500	-4221	-490	351	113	-4983	-10.1	13817	6.6
5	7397	2382	2385	805	356	108	4729	11.7	13788	5.8
6	11234	2832	-307	328	454	139	-271	-0.7	18325	10.1

In the first growth period, there was a decrease in stems per hectare in every plot. In the last growth period, increases were observed in plots 1 and 2. The new growth in plot 1 may be explained by the fact that the regeneration released by the unauthorized cutting may not have reached the minimal height limit for measurement by the second measurement. At the third measurement, however, vigourous growth was observed in the gaps and several new trees that had passed the limit were added to the plot. Changes in the stand structure can be seen over time by observing the distribution of the stems by diameter class at each measurement period shown in Figures 1 and 2. It can be seen that the percentage of trees in the less than 10 cm class was decreasing in all of the plots.

The basal area growth in the last growth period ranged from 0.52 to 0.84 m²/ha/yr. These values are approximately 0.4 m²/ha/yr higher than the values of 0.19 to 0.38 m²/ha/yr observed in the first growth period. There are large differences in growth within the plot pairs. In Figure 2, it can be seen that the amount of basal area in each diameter class changes in a similar pattern to the number of stems per hectare. There is no clear trend between basal area growth and relative density (Figure 3). Basal area growth was highest in plots 3 and 6.

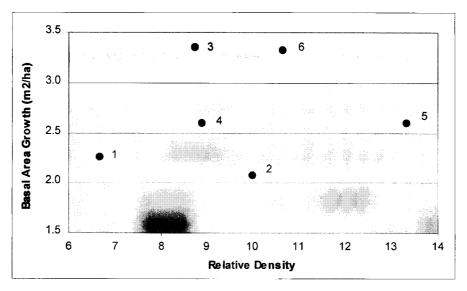


Figure 3. Percent basal area growth (1997 to 1992) versus the 1992 relative densities for all plots.

Only small changes were observed in the vigour of the plots. The changes were both positive and negative and indicated no clear trend. A similar result was also observed in the first growth period. Vigour is a subjective measurement and may only show trends over many measurement periods, if at all.

The quadratic mean diameter increased in all of the plots over the last measurement period. Plots 1 and 2 increased by a smaller amount than they did in the last growth period, probably as a result of the ingrowth. The rest of the plots increased by larger increments than observed in the last period. The increasing mean dbh can be related to the growth trend observed in the stems per hectare. If the number of small trees is continually decreasing, the mean dbh would be expected to reflect this by increasing.

Curtis' (1982) relative density index increased in all of the plots by larger increments than observed in the last growth period. The largest growth occurred in plot 1 which reflects the increase in stems per hectare also observed. The density of plot 1 can be seen to be slowly recovering from the unauthorized cutting.

The volume growth in the last growth period ranged from 4.33 to 5.53 m³/ha/yr. These values are approximately 1.0 m³/ha/yr higher than the values of 3.38 to 4.18 m³/ha/yr observed in the first growth period. Similar to basal area, there are large differences in growth within the plot pairs. Volume growth was highest in plot 6 and the next highest values were in plots 4 and 5. This result varies from the observations made in the first growth period where volume growth was highest in plot 2 and the next highest values were in plots 1 and 3. There is now a slight positive trend between total volume growth and relative density (Figure 4).

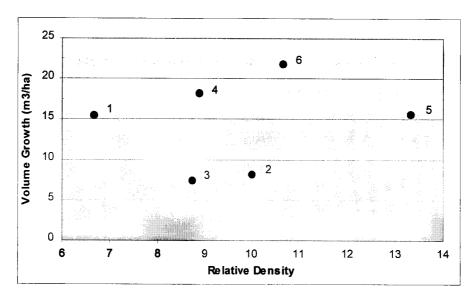


Figure 4. Total volume growth (1997 to 1992) versus the 1992 relative densities for all plots.

The changes in the calculated biomasses were of the same scale as those observed in the last growth period, but are now changing in both positive and negative directions (Figures 5 and 6). In the first growth period, total biomass growth ranged from 2327 to 3970 kg/ha/yr and in the last growth period it ranged from 137 to 4581 kg/ha/yr.

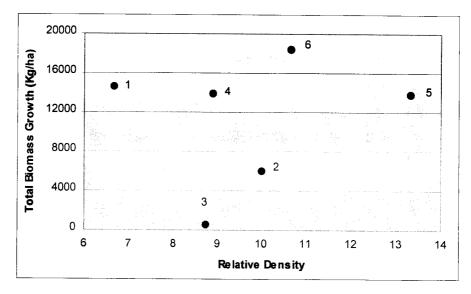


Figure 5. Total biomass growth (1997 to 1992) versus the 1992 relative densities for all plots.

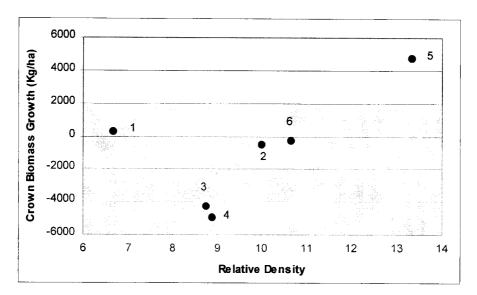


Figure 6. Total crown biomass growth (1997 to 1992) versus the 1992 relative densities for all plots.

## 4.1.3 PSP Mortality between 1992 and 1997

There was a large amount of ingrowth over the last growth period compared to the first growth period, where only one ingrowth tree in plot 2 was recorded. Mortality was not only limited to small trees (Table 12).

Table	12.	Summary	of th	e PSP	mortality.
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Plot#	Number of Ingrowth Trees/Ha	Number of Mortality Trees/Ha	Average Diameter of Mortality (cm)	Min Diameter of Mortality (cm)	Max Diameter of Mortality (cm)
1	90	30	11.4	2.4	28.2
2	60	20	1.4	0.9	1.8
3	0	90	2.2	0.9	4.3
4	0	40	7.1	5.6	8.0
5	0	240	1.9	0.3	3.3
6	0	140	1.7	8.0	2.4

One tree, with a dbh of 28 cm died in plot 1, and all of the trees that died in plot 4 were above 5 cm dbh. A large amount of mortality in plot 3 shows that mortality was not necessarily concentrated in the denser plots 5 and 6. However, Figure 7 shows that a trend of increasing mortality with increasing relative density still exists.

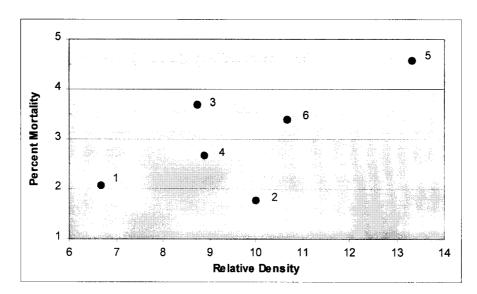


Figure 7. Percent mortality (1997 to 1992) versus the 1992 relative densities for all plots.

## 4.1.4 Relative Growth Rates

By calculating the proportion of the volume growth that occurred in each diameter class relative to the proportion of the basal area in each class, a relative volume growth (R.V.G.) term can be used to compare the contribution made by each class. A similar term representing the proportion of the basal area growth that occurred in each diameter class relative to the proportion of basal area in each class was also calculated (R.B.G.)

Table 13. Gross volume and basal area growth (1997-1992) partitioned into diameter classes, expressed in both absolute units and relative to the proportional representation by basal area of each diameter class.

Plot	DBH Class	Stems	Percent of 1992 BA	Volume Growth (m³/ha)	Volume Growth (%)	R.V.G.	BA Growth (m²/ha)	BA Growth (%)	R.B.G.
1	< 10	910	6.4	1.3	6.6	1.0	0.5	17.0	2.6
	10 - 20	310	14.9	5.0	24.6	1.6	0.9	30.2	2.0
	>20	200	78.6	13.9	68.8	0.9	1.5	52.8	0.7
	Total	1420	100.0	20.2	100.0		2.9	100.0	
2	< 10	620	1.9	0.6	3.3	1.7	0.2	9.7	5.1
	10 - 20	150	4.5	1.4	8.0	1.8	0.3	12.4	2.8
	>20	350	93.6	15.4	88.6	0.9	1.6	77.9	0.8
	Total	1120	100.0	17.3	100.0		2.1		
3	< 10	1350	7.8	1.4	6.5	0.8	0.4	11.0	1.4
	10 - 20	820	39.8	11.7	55.1	1.4	1.9	46.4	1.2
	>20	180	52.4	8.2	38.4	0.7	1.7	42.6	0.8
	Total	2350	100.0	21.3	100.0	,	4.0	100.0	
4	< 10	390	3.6	0.5	2.5	0.7	0.1	4.6	1.3
	10 - 20	770	33.9	9.7	47.8	1.4	1.4	49.3	1.5
	>20	300	62.4	10.1	49.8	0.8	1.3	46.1	0.7
	Total	1460	100.0	20.2	100.0		2.8	100.0	
5	< 10	4260	15.4	2.6	14.3	0.9	0.7	25.6	1.7
	10 - 20	380	12.8	2.9	16.1	1.3	0.4	15.8	1.2
	>20	380	71.8	12.6	69.5	1.0	1.6	58.6	0.8
	Total	5020	100.0	18.1	100.0		2.7	100.0	
6	< 10	3200	15.1	4.4	11.5	0.8	0.7	21.0	1.4
	10 - 20	520	19.2	12.0	31.3	1.6	1.1	31.5	1.6
	>20	280	65.7	22.0	57.1	0.9	1.6	47.5	0.7
	Total	4000	100.0	38.5	100.0		3.4	100.0	

It can be seen that the 10 to 20 cm diameter class consistently makes the largest contribution in relative volume growth in every plot (Table 13). This likely results from the fact that a large number of the trees in the smallest diameter class are suppressed and making very little contribution to the growth of the

stand. Growth in the largest diameter class may be reduced by the small contributions made by some of the large dbh trees that are slowing in growth with old age. The relative basal area growth of each class is highest in the smallest diameter class for all plots except for plots 4 and 6.

Table 14. Gross crown biomass and total biomass growth (1997-1992) partitioned into diameter classes, expressed in both absolute units and relative to the proportional representation by basal area of each diameter class.

Plot	DBH Class	Percent of 1992 BA	CRW-GR (kg/ha)	CRW-GR (%)	R.C.G.	TOTAL-GR (kg/ha)	TOTAL-GR (%)	R.T.G.
1	< 10	6.4	-483.63	-67.0	-10.4	989.55	5.6	0.9
	10 - 20	14.9	-2191.28	-303.5	-20.3	4178.70	23.7	1.6
	>20	78.6	3396.84	470.5	6.0	12469.65	70.7	0.9
	Total	100.0	721.92	100.0		17637.89	100.0	
2	< 10	1.9	-105.30	19.3	10.1	397.76	6.7	3.5
	10 - 20	4.5	-1474.31	270.6	60.7	742.82	12.5	2.8
	>20	93.6	1034.73	-189.9	-2.0	4794.25	80.8	0.9
	Total	100.0	-544.87	100.0		5934.83	100.0	
3	< 10	7.8	125.69	-2.9	-0.4	998.91	166.8	21.4
	10 - 20	39.8	-2390.57	55.6	1.4	8566.10	1430.1	35.9
	>20	52.4	-2036.27	47.3	0.9	-8966.03	-1496.9	-28.6
	Total	100.0	-4301.15	, ,		598.98	100.0	
4	< 10	3.6	-205.04	4.2	1.2	349.79	2.5	0.7
	10 - 20	33.9	-4464.65	90.9	2.7	6223.38	43.9	1.3
	>20	62.4	-240.92	4.9	0.1	7597.41	53.6	0.9
	Total	100.0	-4910.61	100.0		14170.58	100.0	
5	< 10	15.4	854.51	18.0	- 1.2	1743.79	12.6	0.8
	10 - 20	12.8	1103.61	23.3	1.8	3475.94	25.1	2.0
	>20	71.8	2787.00	58.7	0.8	8644.75	62.4	0.9
	Total	100.0	4745.12	100.0		13864.47	100.0	
6	< 10	15.1	-1045.49	392.6	26.0	1748.11	9.5	0.6
	10 - 20	19.2	-3208.02	1204.7	62.6	5635.23	30.7	1.6
	>20	65.7	3987.22	-1497.3	-22.8	10966.15	59.8	0.9
	Total	100.0	-266.30	100.0		18349.48	100.0	

The biomass values changed over the last growth period in both positive and negative directions (Table 14). Therefore, the percent growth of some of the biomass values becomes meaningless when calculated with negative values and makes it impossible to calculate a relative growth rate. For the plots that showed positive changes in all diameter classes, the relative growth rates in crown biomass and total biomass seems to be highest in the 10 to 20 cm diameter class. The one exception is the total biomass growth of plot 2, where growth was much higher in the smallest diameter class.

## 4.2 Evaluation of the Competition Indices

The results from the evaluation of the competition indices are presented in three sections. The first section displays the output from the regression analysis for every index tested using the selected search criteria for each index. In the next section, a table is presented that compiles the version of each index calculated with the search criteria that produced the best performance. The last section presents a summary table showing the best indices representing each approach ranked in order of performance.

## 4.2.1 Results from the Regression Analysis

The regression results are organized in tables that display a row for each index with the corresponding  $R^2$  and  $SE_E$  values. If more than one search criteria was tested for an index, the resulting  $R^2$  and  $SE_E$  values for each search criteria tested are presented across the row under the column headings "1", "2", and "3". These numerical headings will be referred to as the 'scope' used to calculate the index. The 'scope' values were used so that the different search methods used could easily be compared in the same table. If a fixed radius plot was used, the 'scope' values 1, 2 and 3 refer to radius lengths of 5, 7 and 9 m respectively. For a variable radius plot, the 'scope' values 1, 2 and 3 refer to BAF values of 2, 4 and 6 respectively. For height angle gauge plots, the 'scope' values 1, 2 and 3 refer to 30, 45 and 60 degree angles respectively. The 'scope' that produced the best results for each index is highlighted in bold in each table.

### 4.2.1.1 The Base Equation

The base equation shows how well dbh by itself can predict diameter growth. When dbh growth was regressed on dbh alone, the regression produced an  $R^2$  value of 0.36 and a  $SE_E$  of 0.7 cm. This  $R^2$  value is the minimum value that can be expected from all of the other regressions, because the base model is included in all of the equations. The increase in the performance that results from the addition of a competition index can be measured relative to this base  $R^2$  value.

## 4.2.1.2 Distance Independent Indices

## 4.2.1.2.1 Simple Indices using Stand-level Variables

With the addition of either BA/ha or Curtis' (1982) relative density index, the performance of the prediction equation increased by 10 and 9 percent, respectively (Table 15). These R<sup>2</sup> values will also serve as base values for comparisons with other indices. If a more complicated individual tree index is not capable of producing better results, it may not be worth the trouble of calculating the more complex index when these stand-level variables could be used instead.

Table 15. Growth in dbh regressed on the stand-level indices and dbh.

		R <sup>2</sup>	SE <sub>E</sub>
			(cm)
BA/ha	Stand-level	0.46	0.6
Curtis' RDI	Stand-level	0.45	0.6

## 4.2.1.2.2 Simple Indices using Individual Tree Characteristics

Only the individual tree characteristic of vigour was able to show a slightly better performance than the stand-level variables (Table 16). The R<sup>2</sup> value for live crown ratio was below those of the stand-level indices and both basal area greater than the subject tree and Gloover and Hool's (1979 in Lorimer 1983) index showed no increase from the base equation.

Table 16. Growth in dbh regressed on the individual tree characteristic indices and dbh.

		$R^2$	$SE_E$
			(cm)
Vigour	Individual Tree	0.50	0.6
BA > Subject	Individual Tree	0.37	0.7
Gloover and Hool	Individual Tree	0.36	0.7
Live Crown Ratio	Individual Tree	0.41	0.6

### 4.2.1.2.3 Lorimer's Modification of Hegyi's Index

The performance of the many versions of Lorimer's (1983) index that were tested ranged from no increase over the base equation to a 20 percent increase (Table 17). Both versions calculated using a fixed radius plot performed better than the variable radius plot versions. The height angle gauge versions performed almost equally well as the variable radius plot versions. In all versions, the indices

that were calculated using all possible neighbours performed better than those that were limited to selecting only neighbours taller than the subject tree.

Table 17. Growth in dbh regressed on Lorimer's index and dbh.

		$\frac{1}{R^2}$	SE <sub>E</sub>	2 R <sup>2</sup>	SE <sub>E</sub>	$\frac{3}{R^2}$	SE <sub>E</sub>
			(cm)		(cm)		(cm)
Lorimer	Fixed Radius All Neighbours	0.51	0.6	0.56	0.6	0.56	0.6
Lorimer	Fixed Radius Neighbours > Subject	0.51	0.6	0.54	0.6	0.53	0.6
Lorimer	Variable Radius All Neighbours	0.44	0.6	0.49	0.6	0.52	0.6
Lorimer	Variable Radius Neighbours > Subject	0.42	0.6	0.46	0.6	0.46	0.6
Lorimer	Height Angle Gauge All Neighbours	0.38		0.41	0.6	0.51	0.6
Lorimer	Height Angle Gauge Neighbours > Subject	0.37	0.7	0.38	0.7	0.43	0.6

The modifications made in Lorimer's index 2 resulted in a decrease in the performance of the fixed radius plot and height angle gauge versions (Table 18). The R<sup>2</sup> values of the fixed radius version were reduced to approximately the same values as the variable radius plot versions, which were unaffected by the modifications. The height angle gauge versions dropped to be the poorest performer of all of the versions.

Table 18. Growth in dbh regressed on Lorimer's index 2 and dbh.

		1		2	2			
		R <sup>2</sup>	SE <sub>E</sub> (cm)	R²	SE <sub>€</sub> (cm)	R²	SE <sub>∈</sub> (cm)	
Lorimer 2	Fixed Radius All Neighbours	0.45	0.6	0.52	0.6	0.52	0.6	
Lorimer 2	Fixed Radius Neighbours > Subject	0.41	0.6	0.42	0.6	0.39	0.7	
Lorimer 2	Variable Radius All Neighbours	0.42		0.48	0.6	0.51	0.6	
Lorimer 2	Variable Radius Neighbours > Subject	0.41	0.6	0.44	0.6	0.44	0.6	
Lorimer 2	Height Angle Gauge All Neighbours	0.36	0.7	0.37	0.7	0.44	0.6	
Lorimer 2	Height Angle Gauge Neighbours > Subject	0.36	0.7	0.37	0.7	0.39	0.7	

## 4.2.1.3 Distance Dependent Indices

## 4.2.1.3.1 Hegyi's Index

Hegyi's (1974 in Lorimer 1983) index performed very well over all. All versions of the index showed improved performance over the stand-level indices (Table 19). The fixed radius and height angle gauge versions performed almost identically and the variable radius version performed only slightly more poorly. The height restriction on competing neighbours did not affect the performance of the fixed radius version, but it resulted in a reduced performance in the other versions. It is important to note the 4 percent increase in Hegyi's index over the best performing version of Lorimer's index resulting from the addition of inter-tree distance to the equation.

Table 19. Growth in dbh regressed on Hegyi's index and dbh.

		1		1 2		3		
		R²	SE <sub>E</sub> (cm)	R²	SE <sub>E</sub> (cm)	R <sup>2</sup>	SE <sub>E</sub> (cm)	
Hegyi	Fixed Radius All Neighbours	0.53	0.6	0.60	0.5	0.60	0.5	
Hegyi	Fixed Radius Neighbours > Subject	0.54	0.6	0.59	0.5	0.59	0.5	
Hegyi	Variable Radius All Neighbours	0.55	0.6	0.56	0.6	0.57	0.5	
Hegyi	Variable Radius Neighbours > Subject	0.54	0.6	0.55	0.6	0.54	0.6	
Hegyi	Height Angle Gauge All Neighbours	0.57	0.6	0.59	0.5	0.60	0.5	
Hegyi	Height Angle Gauge Neighbours > Subject	0.49	0.6	0.53	0.6	0.57	0.5	

Similar to the results seen for Lorimer's index 2, the modifications in Hegyi's index 2 resulted in a decrease in performance (Table 20). All of the versions tested decreased from 2 to 13 percent in R<sup>2</sup> value. However, the best version of Hegyi's index 2 still performed better than the unmodified version of Lorimer's index.

Table 20. Growth in dbh regressed on Hegyi's index 2 and dbh.

		1		1 2		3	
		R²	SE <sub>E</sub> (cm)	R <sup>2</sup>	SE <sub>E</sub> (cm)	R <sup>2</sup>	SE <sub>E</sub> (cm)
Hegyi 2	Fixed Radius All Neighbours	0.47	0.6	0.56	0.6	0.58	0.5
Hegyi 2	Fixed Radius Neighbours > Subject	0.43	0.6	0.46	0.6	0.43	0.6
Hegyi 2	Variable Radius All Neighbours	0.46	0.6	0.51	0.6	0.54	0.6
Hegyi 2	Variable Radius Neighbours > Subject	0.45	0.6	0.48	0.6	0.47	0.6
Hegyi 2	Height Angle Gauge All Neighbours	0.43	0.6	0.47	0.6	0.53	0.6
Hegyi 2	Height Angle Gauge Neighbours > Subject	0.39	0.7	0.40	0.7	0.44	0.6

## 4.2.1.3.2 Weiner's Index

The version of Weiner's (1984) index calculated with neighbour's taller than the subject tree did not perform better than the stand-level indices (Table 21). The all possible neighbours version did show improved performance, but was still less than the best versions of either Hegyi's or Lorimer's indices.

Table 21. Growth in dbh regressed on Weiner's index and dbh.

		1 R²	SE <sub>E</sub>	2 R <sup>2</sup>	SE <sub>E</sub>	$\frac{3}{R^2}$	SE <sub>E</sub>
Weiner	Fixed Radius All Neighbours	0.44	0.6	0.51	0.6	0.50	0.6
Weiner	Fixed Radius Neighbours > Subject	0.41	0.6		0.6	0.42	0.6

## 4.2.1.3.3 Silander and Pacala's Index

The modifications to Weiner's index made by Silander and Pacala (1985 in Newton and Jolliffe 1998) resulted in a slight decrease in the performance of the all possible neighbours version when compared to the unmodified Weiner's index (Table 22).

Table 22. Growth in dbh regressed on Silander and Pacala 's index and dbh.

		1		2		3	
		R <sup>2</sup>	SE <sub>E</sub> (cm)	R <sup>z</sup>	SE <sub>E</sub> (cm)	R²	SE <sub>E</sub> (cm)
Silander and Pacala	Fixed Radius All Neighbours	0.43	0.6	0.49	0.6	0.50	0.6
Silander and Pacala	Fixed Radius Neighbours > Subject	0.42	0.6	0.42	0.6	0.42	0.6

## 4.2.1.3.4 Newton and Jolliffe's Modification of Weiner's Index and Silander and Pacala's Index

The centre-of-mass modifications added by Newton and Jolliffe (1998) to Weiner's index and Silander and Pacala's index resulted in a small decrease in the performance of each index (Table 23). The performance of the versions calculated using only neighbours taller than the subject was unaffected.

Table 23. Growth in dbh regressed on Newton and Jolliffe's modification of Weiner's index and dbh / Silander and Pacala's index and dbh.

		1		1 2		3	
		R²	SE <sub>E</sub> (cm)	R <sup>2</sup>	SE <sub>E</sub> (cm)	R²	SE <sub>E</sub> (cm)
Newton / Weiner	Fixed Radius All Neighbours	0.44	0.6	0.49	0.6	0.50	0.6
Newton / Weiner	Fixed Radius Neighbours > Subject	0.42	0.6	0.43	0.6	0.42	0.6
Newton / Sil & Pac	Fixed Radius All Neighbours	0.43	0.6	0.46	0.6	0.48	0.6
Newton / Sil & Pac	Fixed Radius Neighbours > Subject	0.42	0.6	0.43	0.6	0.42	0.6

## 4.2.1.3.5 Opie's Index

Opie's (1968 in Bella 1971) index, which is the simplest of the area of influence indices, performed almost as well as Hegyi's index. It performed better than all of the other indices except for Hegyi's index and Hegyi's index 2 (Table 24).

Table 24. Growth in dbh regressed on Opie's index and dbh.

		1		2	2		
		R <sup>2</sup>	SE <sub>E</sub> (cm)	R²	SE <sub>E</sub> (cm)	R²	SE <sub>E</sub> (cm)
Opie	All Neighbours	0.44	0.6	0.53	0.6	0.57	0.6
Opie	Neighbours > Subject	0.46	0.6	0.53	0.6	0.58	0.5

#### 4.2.1.3.6 Bella's Index

The modifications added to Opie's index by Bella (1971) resulted in a slight decrease in performance (Table 25). As the scaling exponent was increased in the Bella 1.5 and Bella 2.0 versions, the performance of the index decreased further. The versions of the index calculated using only neighbours taller than the subject also showed lower performance than the equivalent version using all possible neighbours.

Table 25. Growth in dbh regressed on Bella's index and dbh.

		1		2		3		
		R <sup>2</sup>	R² SE <sub>E</sub>	$R^2$ $SE_E$ $R^2$	R <sup>2</sup>	SE <sub>E</sub>	R <sup>2</sup>	SE <sub>E</sub>
			(cm)		(cm)		(cm)	
Bella 1.0	All Neighbours	0.46	0.6	0.51	0.6	0.55	0.6	
Bella 1.0	Neighbours > Subject	0.44	0.6	0.48	0.6	0.51	0.6	
Bella 1.5	All Neighbours	0.46	0.6	0.50	0.6	0.52	0.6	
Bella 1.5	Neighbours > Subject	0.44	0.6	0.46	0.6	0.46	0.6	
Bella 2.0	All Neighbours	0.45	0.6	0.48	0.6	0.50	0.6	
Bella 2.0	Neighbours > Subject	0.43	0.6	0.45	0.6	0.45	0.6	

#### 4.2.1.3.7 Ek and Monserud's Index

Ek and Monserud's (1974 in Daniels 1976) index also showed a decrease in performance when compared to Opie's index (Table 26). However, it still performed better than Lorimer's index. Similar to Bella's index, the version calculated using only neighbours taller than the subject showed lower performance than the all possible neighbours version.

Table 26. Growth in dbh regressed on Ek and Monserud's index and dbh.

		1		2		3		
		R²	SEE	R²	SE <sub>E</sub>	R²	SE <sub>E</sub>	-
	·	K	(cm)		(cm)		(cm)	
Ek	All Neighbours	0.48	0.6	0.53	0.6	0.50	0.6	-
Ek	Neighbours > Subject	0.45	0.6	0.50	0.6	0.45	0.6	•

### 4.2.2 Comparison of the Performance of the Indices

The best performance of each index is presented in Table 27 along with the number representing the 'scope' at which the best performance was achieved. The performance of each index has been ranked in terms of "percent mean squared error" (percent MSE). This method was used by Biging and Dobbertin (1995) as a simple way to compare the performance of several regression equations relative to the

performance of a base equation. The percent MSE for a regression equation is calculated by dividing the MSE of the tested equation by the MSE of the base equation. The mean square error represents the amount of variation that was not explained by the regression. If the competition index in a regression equation is able to explain more of the variation, it will decrease the amount of unexplained variation and will result in a smaller percent MSE. If the index is not able to explain any more of the variation than the base equation, it will result in a percent MSE of one hundred percent.

The indices are presented in the table in the same order as they were presented in the regression analysis results section. The version of the index with the lowest percent MSE in each subsection is highlighted in bold.

Table 27. The mean square error as a percentage of the base equation mean square error for each index tested.

		Scope	Percent MSE
DBH alone	No Index - Base Equation	-	100.0
BA/ha	Stand-level	-	83.3
Curtis' RDI	Stand-level	-	85.5
Vigour	Individual Tree	-	78.7
BA > Subject	Individual Tree	-	98.7
Gloover and Hool	Individual Tree	-	99.6
Live Crown Ratio	Individual Tree	-	93.2
Lorimer	Fixed Radius, All Neighbours	2	69.6
Lorimer	Fixed Radius, Neighbours > Subject	2.	72.3
Lorimer	Variable Radius, All Neighbours	3	74.7
Lorimer	Variable Radius, Neighbours > Subject	3	84.7
Lorimer	Height Angle Gauge, All Neighbours	3	77.5
Lorimer	Height Angle Gauge, Neighbours > Subject	3	88.6
Lorimer2	Fixed Radius, All Neighbours	3	75.2
Lorimer2	Fixed Radius, Neighbours > Subject	2	90.2
Lorimer2	Variable Radius, All Neighbours	3	76.9
Lorimer2	Variable Radius, Neighbours > Subject	2	87.6
Lorimer2	Height Angle Gauge, All Neighbours	3	88.4
Lorimer2	Height Angle Gauge, Neighbours > Subject	3	95.8
Hegyi	Fixed Radius, All Neighbours	3	62.8
Hegyi	Fixed Radius, Neighbours > Subject	3	64.0
Hegyi	Variable Radius, All Neighbours	3	67.2
Hegyi ·	Variable Radius, Neighbours > Subject	2	70.6
Hegyi	Height Angle Gauge, All Neighbours	3	62.6
Hegyi	Height Angle Gauge, Neighbours > Subject	3	67.0
Hegyi2	Fixed Radius, All Neighbours	3	66.1
Hegyi2	Fixed Radius, Neighbours > Subject	2	84.0
Hegyi2	Variable Radius, All Neighbours	3	72.3
Hegyi2	Variable Radius, Neighbours > Subject	2	82.1
Hegyi2	Height Angle Gauge, All Neighbours	3	73.6
Hegyi2	Height Angle Gauge, Neighbours > Subject	3	88.4

Table 27. Continued.

Weiner	Fixed Radius, All Neighbours	2	77.1
Weiner	Fixed Radius, Neighbours > Subject	2	90.0
Silander and Pacala	Fixed Radius, All Neighbours	3	78.7
Silander and Pacala	and Pacala Fixed Radius, Neighbours > Subject		90.2
Newt/Wein	Fixed Radius, All Neighbours	3	79.0
Newt/Wein	Fixed Radius, Neighbours > Subject	2	89.2
Newt/S&P	Fixed Radius, All Neighbours	3	81.4
Newt/S&P	Fixed Radius, Neighbours > Subject	2	90.1
Opie	All Neighbours	3	67.6
Opie	Neighbours > Subject	3	66.4
Bella 1.0	All Neighbours	3	70.9
Bella 1.0	Neighbours > Subject	3	77.2
Bella 1.5	All Neighbours	3	75.0
Bella 1.5	Neighbours > Subject	3	84.4
Bella 2.0	All Neighbours	3	78.4
Bella 2.0	Neighbours > Subject	2	86.2
Ek	All Neighbours	2	73.3
Ek	Neighbours > Subject	2	78.3

The versions of the indices from each subsection highlighted in Table 27 are compiled in Table 28, sorted from smallest percent MSE (best performance) to largest percent MSE (lowest performance / base equation).

Table 28. The best representatives of each index sorted from smallest to largest percent MSE.

		Scope	Percent MSE
Hegyi	Height Angle Gauge, All Neighbours	3	62.6
Hegyi2	Fixed Radius, All Neighbours	3	66.1
Opie	Neighbours > Subject	3	66.4
Lorimer	Fixed Radius, All Neighbours	2	69.6
Bella 1.0	All Neighbours	3	70.9
Ek	All Neighbours	2	73.3
Lorimer2	Fixed Radius, All Neighbours	3	75.2
Weiner	Fixed Radius, All Neighbours	2	77.1
Sil and Pac	Fixed Radius, All Neighbours	3	78.7
Vigour	Individual Tree	-	78.7
Newt/Wein	Fixed Radius, All Neighbours	3	79.0
Newt/S&P	Fixed Radius, All Neighbours	3	81.4
BA/ha	Stand-level	-	83.3
DBH	No Index - Base Equation	-	100.0

Hegyi's index clearly shows the largest reduction in unexplained variation from the base equation with a decrease of more than 20 percent. Hegyi's index is followed by its modified version, Hegyi's index 2, which is closely followed by Opie's index. It is interesting to note that there are representatives from both the ratio of diameters approach (Hegyi's index) and the area of influence approach (Opie's index) in the top three indices. The distance independent Lorimer's index is ranked next in the table with a large

difference in performance between it and its modified version, Lorimer's index 2. In the gap between the two versions are the remaining two representatives of the area of influence approach, Bella's index 1.0 and Ek and Monserud's index. Weiner's index and Silander and Pacala's index are found just above the individual tree index of vigour. The two indices modified by Newton and Jolliffe fell below the individual tree index, but above the stand-level index of basal area per hectare.

For the ratio of diameter indices, the versions of the indices calculated using fixed radius plots to identify competing neighbours all produced the best performance except for Hegyi's index which performed fractionally better using a height angle gauge plot. These same top performing indices were also calculated using all possible neighbours. Two of the three area of influence indices performed best when calculated using all possible neighbours. The exception was Opie's index which performed fractionally better using only neighbours taller than the subject tree. Most of the top performing versions of each index were calculated using the largest 'scope' for each index. The three that did not were calculated using the second largest search 'scope'.

## 4.2.3 Diagnostics of the Regression Equations

The diagnostic tests presented here were performed for every regression equation tested. The results of the tests for the equations created for each index were often similar. For simplicity, only the results from the base equation and the best performing equation, Hegyi's index, are presented. These equations represent the two extremes in performance and can be studied with the knowledge that all of the other indices fall somewhere in between the two.

## 4.2.3.1 Relationships Among the Variables

Before the regressions can be evaluated for how well they fit the data, the relationships among the variables must be known. These relationships were investigated during the process of selecting the best form of the regression equations to use. Examples of the scatter plots generated during that process are presented below (Figures 8 to 10). The three plots presented show all of the possible combinations of the three variables used in the regression equation for Hegyi's index: observed dbh growth, dbh and Hegyi's index.

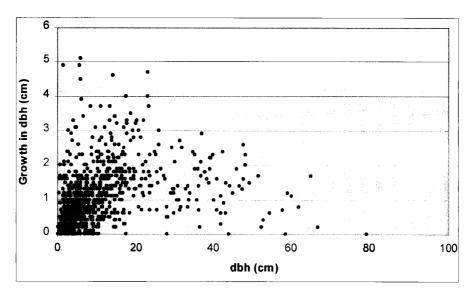


Figure 8. Scatter plot of growth in dbh versus dbh.

In the plot of dbh versus observed dbh growth an arched shape can be seen. There is a high concentration of points surrounding the steep incline of the arch. The points then become more scattered at the peak and throughout the gradual decline. Growth in dbh varies widely for the smaller values of dbh. Between 0 and 20 cm dbh, the dbh growth varies from 0 to 5 cm.

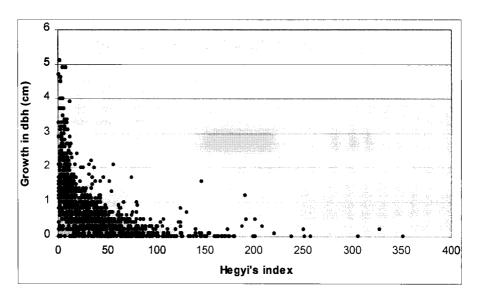


Figure 9. Scatter plot of growth in dbh versus Hegyi's index.

The relationship between Hegyi's index and dbh growth is hyperbolic in shape. At the extremes of the graph, it is possible to see the expected relationships where trees with large index values have small dbh growth and trees with large dbh growth have small index values. However, as the hyperbolic shape passes close to the origin, it can be seen that a large proportion of the observations are in the contradictory position of having both low competition index values and low dbh growth values.

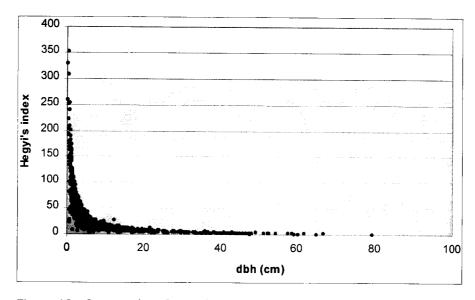


Figure 10. Scatter plot of Hegyi's index versus dbh.

The relationship between dbh and Hegyi's index is also hyperbolic in shape. This shape is expected because of the uneven-aged structure of the stand and the way in which Hegyi's index is calculated. In order to more clearly evaluate this relationship, Figure 10 was divided at the 10 cm dbh point of the x-axis to produce Figures 11 and 12.

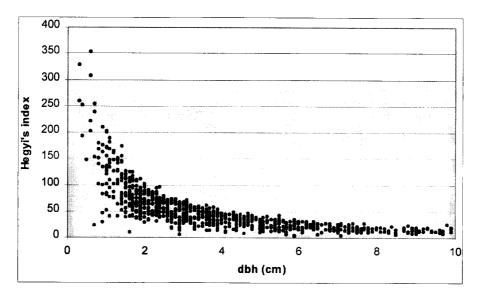


Figure 11. Scatter plot of Hegyi's index versus dbh for observations with  $dbh\ values < 10\ cm.$ 

The observations with dbh values less than 10 cm represent the small, often suppressed, trees in the understory of the stands. It is reasonable to expect the competition index value for these trees to be high in order to represent this suppressed state. Figure 11 shows more clearly that the index values begin to climb drastically for trees with dbh values less than 5 cm. However, there are still a few observations with low index values that are less than 5 cm in dbh. These observations likely represent the small trees growing in gaps or clearings with little competition.

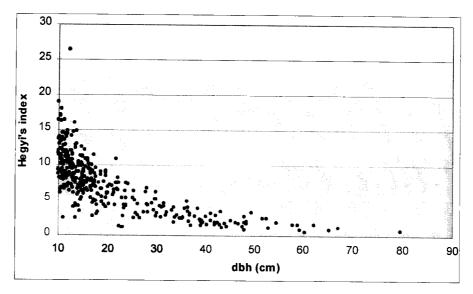


Figure 12. Scatter plot of Hegyi's index versus dbh for observations with dbh values  $\geq$  10 cm.

The competition index values of the trees with dbh values greater than 10 cm gradually decreases as the dbh value increases. This relationship is expected because the competition index is calculated based partly on the assumption that trees with larger dbh values are generally taller and are able to compete more strongly.

#### 4.2.3.2 Goodness of Fit

The goodness of fit of the regression equations was evaluated visually using two scatter plots. Figure 13 contains two plots overlaid on the same graph. The plot of dbh versus predicted dbh growth is overlaid on the plot of dbh versus observed dbh growth (which is the same plot as Figure 8). This plot shows how closely the predicted values represent the variation in the observed values. Figure 14 displays the predicted values plotted against the residual values from the regression. This plot is essential in order to evaluate trends in the variance of the error in the regression.

### 4.2.3.2.1 Base Equation

When the predicted values from the regression of the base equation are plotted, they form a single line because only one variable is used in the equation. This line clearly displays the shape of the selected regression function. The arched shape formed by the observed data is followed fairly closely by the line of predicted values.

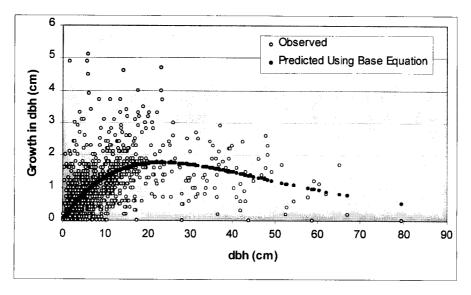


Figure 13. Growth in dbh predicted using the base equation versus dbh plotted with the observed dbh growth versus dbh.

However, there is wide variation in the observed dbh growth between 0 and 20 cm dbh. The line simply passes through the densest part of the cluster and peaks at a diameter growth of less than 2 cm.

Figure 14 shows that the amount of variation in the residuals increases as the size of the predicted values increases (heteroscedasticity). There is a distinct straight line boundary on the bottom half of the graph that angles away from the zero line as the predicted values increase.

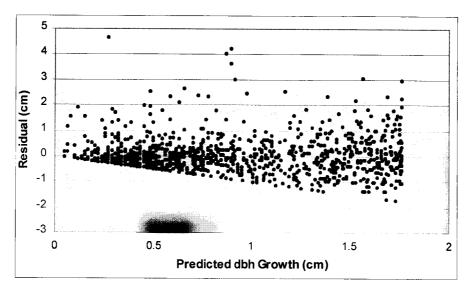


Figure 14. The residuals from the base equation regression plotted against predicted dbh growth using the base equation.

This boundary line is the result of the many observations that had an actual observed dbh growth value of zero and were overestimated by the regression equation. As the regression equation predicts larger values, the residual values calculated as the difference between the predicted values and zero increases accordingly. A straight line is formed on the residual plot because the observed dbh growth can never be less than zero. Therefore, the size of the residuals can never be bigger than the predicted dbh growth at the corresponding point. There is no distinct boundary to the positive side of the residual plot and some of the observations are underestimated by more than four centimeters.

## 4.2.3.2.2 Hegyi's Index

The plot of the predicted dbh growth values generated by the regression equation for Hegyi's index are scattered over a wider range (Figure 15). The majority of the values follow the same shaped curve as the base equation, but many observations are spread around this line to represent the variation seen in the observed dbh growth values. The limit to the predicted dbh growth values is no longer two centimeters. Despite this wide range of values, there is still a large amount of unrepresented variation in the observed growth values.

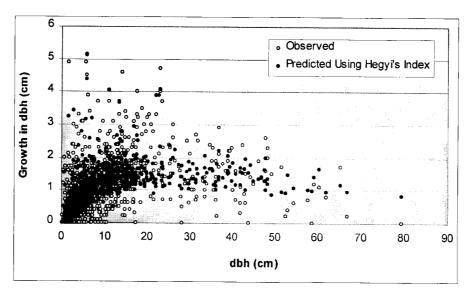


Figure 15. Growth in dbh predicted using the equation including Hegyi's index versus dbh plotted with the observed dbh growth versus dbh.

The first difference between the residual plot of the base equation (Figure 14) and the residual plot of the regression equation for Hegyi's index (Figure 16) is the wider scale of the x-axis. Since the predicted dbh growth values are no longer restricted to two centimeters, the range of predicted values has increased. The same large amount of heteroscedasticity appears to exist in this plot and a straight line boundary on the bottom half remains. The size of the largest negative residual increased because of one tree that was overestimated by three centimeters. However, the size of the underestimated errors was reduced considerably. The several trees that were underestimated by the base equation regression are now better represented, resulting in no positive residual values larger than three centimeters.

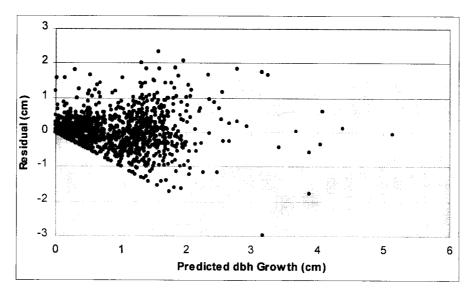


Figure 16. The residual values from the regression equation including Hegyi's index versus predicted dbh growth using Hegyi's index.

## 4.2.3.3 Analysis by Diameter Class

The final diagnostic test performed was to analyze the performance of the regression equations within individual diameter classes. This test indicates if the gains in the performance of one regression equation over another are concentrated in a particular diameter class or if the gains were made at the cost of the performance in another diameter class. It is important to evaluate if the regression equation is able to represent all of the diameter classes evenly.

The precision of the equation was evaluated for each diameter class using the standard error of the estimate again. The bias was calculated as the sum of the residual values for each of the observations in a diameter class divided by the number of observation in the class.

Table 29. Standard error of the estimate and bias of the base equation of Hegyi's index equation presented by diameter class.

Diameter Class (cm)	Number of Observations	Base Equation SE <sub>E</sub>	Hegyi's Index Equation SE <sub>E</sub>	Base Equation Bias	Hegyi's Index Equation Bias
0 to <5	593	0.515	0.443	0.001	0.067
5 to < 10 <sub>.</sub>	226	0.826	0.583	0.013	-0.049
10 to < 15	157	0.779	0.652	-0.023	-0.049
15 to < 20	76	0.785	0.641	0.047	0.101
20 to < 30	51	0.957	0.792	0.057	0.062
30 to < 40	31	0.667	0.669	-0.019	-0.016
> 40	35	0.708	0.657	-0.027	-0.081

The precision values listed in Table 29 are tend to increase towards the middle diameter classes and then decrease in the larger classes. The bias values for the base equation follow a similar pattern to the precision values. However, the equation containing Hegyi's index showed no clear pattern in the bias values.

The values presented in Table 29 can be made clearer by calculating them as percentage values instead (Table 30). Since both values are presented in the same units as the observed dbh growth values (cm of diameter growth), they can be converted to percentage values relative to the observed dbh growth values. This is calculated by dividing the values in Table 29 by the respective average observed dbh growth for the diameter class.

Table 30. Percent standard error of the estimate and percent bias of the base equation of Hegyi's index equation presented by diameter class.

Diameter Class (cm)	Average Observed Growth of Class	Base Equation Percent SE <sub>E</sub>	Hegyi's Index Equation Percent SE <sub>E</sub>	Base Equation Percent Bias	Hegyi's Index Equation Percent Bias
0 to <5	0.4	128.63	110.64	0.26	16.81
5 to < 10	1.0	82.55	58.27	1.26	-4.88
10 to < 15	1.4	55.63	46.58	-1.66	-3.49
15 to < 20	1.7	46.16	37.68	2.76	5.95
20 to < 30	1.8	53.15	44.00	3.16	3.42
30 to < 40	1.6	41.68	41.80	-1.16	-1.01
> 40	1.2	59.03	54.72	-2.27	-6.74

It can be seen in Table 30 that the equation containing Hegyi's index produced a lower percent  $SE_E$  values in all of the diameter classes except for the 30 to < 40 class when compared to the base equation. At the same time, the percent bias values for the Hegyi's index equation were all much higher than the base equation values except in the 30 to < 40 class.

# 5 Discussion

## 5.1 Trends in Permanent Sample Plot Data

Growth of the measured attributes in the study stands continued in every dbh class of each plot over the second growth period. The growth rates were higher than those recorded in the first period, but the same trend towards increasing mean dbh and higher relative densities was observed. The percent composition of the plots made up by stems less than 10 cm dbh continued to decrease as more trees grew bigger than 10 cm or died. Although some ingrowth occurred in plots 1 and 2 in the second growth period, this was not enough to offset the decline in the proportion of the plots composed by smaller trees.

Interior Douglas-fir is adapted to growing as a pioneer species after a disturbance (Arno 1990). Therefore, it is possible that the stands are still increasing in the occupancy of the site since the last stand replacing event. Minor disturbances over time from disease, insects, or windthrow have created gaps in the stands that encouraged new growth. Although there was little evidence of past harvesting in the plots, it is also possible that the stands were subject to periodic selective harvesting over the last century and are still recovering.

In their report on the first growth period, Marshall and Wang (1996) observed that the total growth of all of the calculated attributes was remarkably similar among the plots, given the wide range of stand structures represented by the plots. The growth of these same attributes over the second period, although higher in magnitude, was still quite similar among the plots.

A major difference between the observations from the first and second growth periods was which plots produced the highest volume growth. In the first growth period, plots 1, 2 and 3 had the highest growth, but in the second growth period plots 4, 5 and 6 showed the largest volume growth. This change can easily be explained by the sporadic mortality that was observed in all plots and across all diameter classes within the plots. The volume growth for a plot was calculated as the difference between the total volume of the plot at each remeasurement. This produces a growth value that is net of any losses to the existing volume that occurred over the growth period. Since the growth values in the study stands were generally low, random events such as the loss of a tree through mortality or snow damage to the top of a tree can have a large impact on the calculated volume growth for a plot. Also, as it was noted above, the growth was very similar among the plots; therefore, it would not have required a very large volume

loss in one plot to result in it switching from producing the highest volume growth in one period to the lowest growth in the next.

Marshall and Wang (1996) identified trends in the attributes that were calculated for the first growth period and tried to make connections between the trends and the stand structures of the plots. They found that mortality increased with relative density while basal area growth, volume growth, and total biomass growth decreased with relative density. In the second growth period, the same positive relationship between mortality and relative density was observed. Since plots 5 and 6 have the highest relative density, the changes in volume growth discussed above caused the trend between volume growth and relative density to switch from a negative relationship to a positive one (See Figure 4 in Chapter 4). The growth of the other attributes formed patterns in which no clear trends with relative density could be discerned.

Marshall and Wang (1996) also hypothesized that the trends would become clearer when more data were collected from the next growth period. However, after analyzing the data from the second growth period, this hypothesis does not seem to have been supported. Perhaps the trends will only become clearer after several more remeasurements. In the meantime, the current results simply continue to support the final observations made by Marshall and Wang that stand structure appears to have very little effect on the overall growth of the stands.

## **5.2 Regression Analysis**

The results of the regression analysis showed that the equation that included Hegyi's (1974 in Lorimer 1983) index was able to predict dbh growth best. However, it is important to remember that the objective of the analysis was not to create an equation for modelling growth. The large biases observed in the goodness of fit evaluations performed for each regression equation clearly indicate that the equations would produce poor estimates if they were used as growth models in their current forms. Proper growth equations could have been created by adding weights to the equations to balance out the heteroscedasticity observed in Figures 14 and 16. However, the objective of the analysis was to study the correlations between the indices and dbh growth. Heteroscedasticity has no effect on the ability of the regression analysis to calculate these correlations because it does not affect the accuracy of the regression coefficients that were used to calculate the results. Therefore, it was not necessary to correct the heteroscedasticity and the biases to meet the objectives of this study.

The use of dbh growth as the dependent variable makes the regression analysis seem deceptively similar to a model fitting exercise. Dbh growth was selected as a representative of competitive stress but many other attributes could have been selected in its place. Basal area growth, height growth or even various measures of relative growth could have been used. If the validity of using dbh growth to represent competitive stress is ever questioned, the regression analysis could be performed again using one or more of the other attributes as the dependent variable to see if there is a large difference in the relative ranking of the indices.

Another deceptive step in the regression analysis was the use of dbh in the base equation. Including dbh in the equation with each index may seem like a step in model fitting, but it was necessary for other reasons in this study. Dbh was included in each equation in order to remove the predictive effects of dbh from every index. It was found that the indices that use dbh in their formula tended to have higher simple correlations with dbh growth than those that do not. Dbh is an excellent predictor of dbh growth because the cumulative effects of competition and other factors is expressed in the size of the tree (Bella 1971). However, dbh alone is not able to represent the current competitive stress experienced by a tree. Growth is predicted accurately by dbh under the assumption that the competitive stress experienced by the tree up until the measurement point will continue into the future. However, this assumption is only valid over the short term and only if the stand structure is not drastically altered. Any disturbance or management treatment that alters the spatial pattern of a stand will result in a new growth pattern that dbh will not be able to predict. Therefore, it was necessary to remove the predictive effects of dbh to reveal the ability of the index to represent the current competitive environment around the tree. This was done by including dbh in every regression equation and then comparing all of the results to the base equation containing dbh alone. The difference between the performance of the two equations represented the predictive ability of the index by itself.

## 5.3 Biological Processes

## 5.3.1 Extent of Competitive Influence

More can be learned from the regression analysis than simply which index best explained the variation in dbh growth caused by competition. As was discussed in Chapter 2, each of the indices and the methods of identifying neighbours can be seen as representations of different hypothetical relationships that exist among the trees. By studying which indices and methods worked and which did not, inferences can be

made about the nature of the competition processes occurring within interior Douglas-fir stands and perhaps also about the underlying biological mechanisms through which competition occurs.

The first aspect of competition that can be deduced from the results is the extent to which interior Douglas-fir is able to exert an influence on its neighbours. When a study that is comparing competition indices finds that the distance dependent indices tested did not perform much better than the distance independent indices, it is often hypothesized that the poor performance of the distance dependent indices can be attributed to the relative homogeneity of the study stands (Lorimer 1986). If the stands tested are even-aged and uniformly spaced, the range of index values generated for the trees is not likely to be very wide. Therefore, the ability of the indices to represent the extent to which the trees are able exert an influence will be obscured in these studies. Biging and Dobbertin (1995) hypothesized that the advantages of distance dependent indices would only become apparent when testing spatially heterogeneous stands. From the results of the regression analysis, it appears that the spatial heterogeneity in the uneven-aged stands used in this study have supported Biging and Dobbertin's hypothesis.

In Chapter 2, four approaches to conceptualizing the region over which a tree is able to exert a competitive influence were defined (Benjamin and Hardwick 1986 in Benjamin 1993). The first approach theorizes that the competitive influence of the trees is a diffuse effect that is uniform throughout the stand. The results from the regression analysis did not appear to support this approach. If competition was a diffuse phenomenon, then the stand-level indices would have performed just as well as the other indices because the uniform competitive effect would have been adequately represented by one stand-level index value. Further contrary evidence can be seen in the fact that the distance dependent indices performed better than the distance independent indices. If the competition effect was diffuse throughout the stand, the distance between the subject tree and its neighbours would be irrelevant. However, when the distance term was removed from Hegyi's index to produce Lorimer's index, the performance of the index dropped. This indicated that the distance between the subject tree and a neighbour has an effect on the amount of competitive influence that the subject tree is able to exert on the neighbour.

The second approach theorizes that the extent to which a tree is able to exert a competitive influence can be represented by a region around the tree with a defined boundary. In this approach, the regions of the trees overlap so that extent of the influence of a tree is not limited by its immediate neighbours. This approach is used as the theoretical basis for the area of influence indices and the ratio of diameters indices when they are calculated using the fixed radius method for identifying competing neighbours.

Usually the area of influence indices define the size of the region of influence for each tree relative to the size of the tree crowns. The extent of the influence is therefore very large for trees with large crowns and very small for trees with small crowns. When the competing neighbours are defined for the ratio of diameters indices using a fixed radius plot, it is assumed that the size of the region of influence is the same for all trees. This may not seem to be a reasonable assumption at first, but it is necessary to remember that the region of influence is used in different ways by the two types of indices. In the area of influence indices, the region is used directly to produce index values for the trees by calculating the amount of overlap between the regions. In the ratio of diameters indices, the region is only used in the first step to identify potential competing neighbours. If the size of the region was scaled to the size of the subject tree, small trees would have a small region that would not include distant large trees and therefore would not be able to consider their influence. Therefore, one size of region is used to identify all of the potential competing neighbours. After the neighbours have been identified, their relative sizes and degree of influence on each other are considered in the calculation of the index using their relative diameters.

From the regression analysis results, the optimal size of the fixed radius plot was not identified nor was the optimal scaling factor for the crown width in the area of influence indices. According to the bounded region of influence approach, if a neighbouring tree is located beyond the boundary defined for a subject tree, it will have no competitive influence on the subject tree. Therefore, if neighbours are selected from beyond this boundary, the trees from outside of the boundary will not be able to explain any of the competitive stress experienced by the subject tree and will only reduce the performance of the index. For most of the indices tested, the largest 'scope' that was tested produced the best results. Therefore, it is unclear where this boundary is located. If a larger range of 'scopes' are tested, perhaps the performance of the index will begin to decrease after a certain 'scope' indicating the border of the region has been passed. However, as the 'scope' values are increased, the number of neighbours selected increases or the area in the area of influence increases for each tree. This results in the magnitude of the index values increasing, but the relative differences between the values remains the same. Since the regression analysis is calculated based on the relative values of the indices, past a certain point, any increases in the magnitude of the index values will have little or no effect on the regression results. This effect will result in a leveling off in the performance of the indices as the 'scope' is increased and it would make it difficult to determine an optimal 'scope' value.

The third approach is very similar to the second approach, except that it theorizes that the bounded regions of influence cannot overlap. The area potentially available indices (i.e., Brown 1965 in Tennent

1975 and Moore *et al.* 1973) are based on this theoretical approach. The non-overlapping approach assumes that the competitive influence of a subject tree cannot extend beyond its immediate neighbours. If this were true, the largest 'scopes' used to identify competing neighbours would have produced the poorest results because they are including neighbours that are well beyond the immediate neighbours. This was clearly not the case in the regression analysis results and confirms the concerns discussed by Lorimer (1983) about the applicability of this approach to uneven-aged stands. Perhaps this approach is best reserved for uniformly spaced, even-aged stands where the influence of distant neighbours is less relevant.

The last approach is based on the theory that the region of competitive influence does not have a defined boundary. It is assumed that the boundary is diffuse and that the extent to which a tree is able to exert an influence simply dimishes with increasing distance. This approach is used as the theoretical basis for the ratio of diameter indices that were calculated using variable radius plots and height angle gauge plots to identify competing neighbours. These methods do not require a region of influence to be defined for a subject tree. Neighbours are selected instead from various distances based on their diameters or height. This approach makes sense because neighbouring trees should not be selected because the subject tree exerts an influence on them. Rather, the neighbouring trees should be selected based on their ability to exert an influence on the subject tree. In effect, the critical distance calculated for each neighbour used in both of these methods is a representation of the extent of the influence of the neighbouring trees. If the distance between the subject and the neighbour was larger than this extent, then the neighbour was not considered to exert an influence on the subject.

These methods, which were supported by Daniels *et al.* (1986), Lorimer (1983) and Biging and Dobbertin (1992), would be expected to more accurately represent which trees in the study plots are contributing to the competitive stress of a subject. However, the results from the regression analysis showed that neither of these methods performed much better than the fixed radius plot method. This relatively poor performance may be attributed to the small border around the plots. The size of the BAF values selected as the 'scope' values for the variable radius plots were kept small so that the search routine would not produce biased results by searching outside of the measured plot area. However, due to the large size of some of the study trees, it is likely that for some sample trees neighbours were selected from distances that were larger than the border width. The absence of such neighbours from the dataset produced biased index values. This problem could be addressed by mirroring the plot on all sides as an approximate representation of the area surrounding the plot or only using a subset of trees near the center of the plot.

Similar to the indices discussed in the bounded, over-lapping region approach, an optimal 'scope' value could not be found. Again, the largest 'scope' values often produced the best results. Larger BAF values could be tested to find an optimum if the mirroring technique discussed above is used. It is interesting to note that the largest 'scope' value used in the height angle gauge plots represents the steepest search angle. Unlike the other indices that showed the best performance with the broadest search 'scope', the height angle plots performed the best using the most restrictive criteria for defining neighbours. The largest 'scope' represented a 60 degree angle which means that in order to qualify as a neighbour, a tree must be closer than half its height from the subject tree. These results seem to imply that the height angle gauge method is very efficient at identifying the neighbouring trees that exert a competitive effect on the subject. This method likely deserves more investigation by testing the effects of using even steeper angles.

## 5.3.2 Sharing of Resources

In Chapter 2, the ways in which resources are shared were categorized into three relationships: absolute symmetry (resources evenly shared regardless of size), relative symmetry (resources shared proportional to size) and asymmetry (resources shared disproportionately) (Cannell and Rothery 1984, Thomas and Weiner 1989, Weiner 1984).

A relationship of absolute symmetry is assumed to exist when competition is quantified at the stand-level using measures of density. If competition is measured in terms of crowding using measures such as stems per hectare or basal area per hectare, no consideration is given to the relative sizes of the trees in the stand. Every tree in the area is assumed to draw from the resource pool equally. Curtis' (1982) relative density index measures the degree of crowding relative to the total basal area of the stand, but it still assumes that the resources are being shared evenly by every tree regardless of the individual tree sizes. This assumption may be more safely applied to uniform, even-aged stands where most trees are similar in size and likely use similar amounts of the available resources. However, the results from the regression analysis indicate that this assumption may not be relevant when applied to the uneven-aged study stands. Some of the effects of competition were explained by the stand-level indices, but even better results were found in the indices that considered the relative sizes of the trees.

Most of the indices tested were based on the assumption that a relationship of relative symmetry exists in the study stands. When a comparison is made between the size of the subject tree to the size of the plot total, plot average or various definitions of its immediate neighbours, an assumption is made that the

amount of resources that the subject tree receives will be determined by its size relative to the surrounding trees. If the subject is relatively small when compared to the surrounding trees, it will receive a proportionately small amount of the available resources and will therefore experience a higher level of competitive stress.

This relationship is implicit in the ratio of diameters indices because it is the ratio of the neighbouring tree dbh over the subject tree dbh used in these indices that gives the category its name. The same ratio was added to Bella's index and Ek and Monserud's index in order to represent the same relationship. Considering the fact that a ratio of diameters index produced the best performance of all of the indices tested, it is interesting to note that the area of influence index, which did not contain this ratio, performed better than the two to which it was added. This may be due to the fact that the relative size of the trees is already represented well by the size of the area of influence calculated for each tree. It could be possible that the relative sizes of the crown widths are already a good representation of how the resources are shared and adding the ratio of dbh's just added confounding variation.

A similar confounding effect was seen in Ek and Monserud's index and Newton and Jolliffe's modified indices. In these indices, extra information was added in an attempt to more accurately represent the ability of the subject tree to access available resources. Ek and Monserud added a ratio of the neighbour and subject tree heights to their index. This extra information only reduced the performance of the index, indicating that perhaps the height of the a tree has little influence on its ability to access resources and only added unnecessary variation. Newton and Jolliffe's modifications to Weiner's index and Silander and Pacala's index reduced the index value for the subject tree proportional to its distance from the focus point of the competing neighbours. If the stands were simply not spatially heterogeneous enough for these modifications to have any effect, the index should have performed at least as well as the unmodified versions of the indices. However, a decrease in performance was found, which was surprising because Hegyi's index had already shown that the spatial location of the neighbours is an important determinant of the subject tree's ability to access resources. It was expected that more information about the spatial arrangement of the neighbours would improve the performance. Perhaps the distance term in the unmodified versions of the indices already represented the sharing of resources well enough and the modifications only added confounding variation.

Bella's index and the modified versions of Lorimer's index and Hegyi's index are all based on the assumption that the relationship between the study trees is asymmetrical. These indices assume that larger trees are be able to access disproportionately more resources than smaller trees. Bella's index

represents this disproportionate sharing of resources by adding a variable exponent to the ratio of diameters in the equation. With the addition of this exponent, any difference in size between the diameters of the neighbour and subject trees will be accentuated exponentially in the index. The same premise was used for squaring the diameter terms in Lorimer's index 2 and Hegyi's index 2. In the regression analysis, the performance of Bella's index only decreased as the size of the exponent increased from 1.0 and Hegyi's index 2 and Lorimer's index 2 both showed lower performance than the unmodified versions. The poor performance of these indices indicates that the relationships between the trees in the study stands was not likely asymmetrical.

In Chapter 2 these relationships were also characterized in terms of resource depletion and resource preemption (Newton 1993). The term resource depletion, synonymous to a symmetrical relationship, is often used to represent a stand where below ground resources are the most limiting factor to growth. Resource preemption, synonymous to an asymmetrical relationship, is often used to represent stands where there is high competition for light. Considering the fact that water is often the most limiting resource in the IDF zone (Lopushinsky 1990) and the evidence supporting a symmetrical relationship seen in the regression analysis results, the study stands would be accurately categorized as being in a state of resource depletion.

A final aspect of competition that can be analyzed from the regression analysis results is the relationship between the small and large trees. If small trees are growing within the region of competitive influence of a large tree and they appear to have no competitive effect on the large tree, the relationship between the trees is termed one-sided. If the small trees appear to have some effect on the large trees, it is termed two-sided (Brand and Magnussen 1988). Similar to the resource depletion and resource preemption terms, a two-sided relationship is associated with a state where below ground resources are limiting and a one-sided relationship is associated with competition for light.

From the discussion above, it would be safe to assume that the relationships in the study stands are two-sided because competition appeared to be occurring mainly for below ground resources. However, even more conclusive evidence can be found by evaluating how the performance of each index changed when it was calculated using only neighbours that were taller than the subject tree. In the results of the regression analysis, Opie's index was the only index that performed better when the restriction was placed on the selection of neighbours. Otherwise, the performance of every index dropped when the trees that were smaller than the subject tree were ignored. These results clearly show that the small trees must have some competitive effect on the large trees and that the relationship is two-sided.

#### 5.4 Final Evaluation of the Results

Comparison of the competition indices indicated that the simplest competition indices performed best. The performance of the indices generally dropped when extra information was added, when restrictions were placed on which neighbours qualified, or when modifications were made to the index. However, the one exception was the addition of information on inter-tree distances which clearly was an important variable for quantifying competitive stress.

The importance of inter-tree distance can be seen in the increase in the performance of Hegyi's index over Lorimer's index. The addition of the distance term to the equation increased the R<sup>2</sup> value by 2 percent. However, Lorimer's index is not a good representative of distance independent indices because it uses inter-tree distance in the process of identifying competing neighbours. The next closest, truly distance independent index was individual tree vigour which had an R<sup>2</sup> value 3 percent lower than Lorimer's index and 5 percent lower than Hegyi's index.

The spatial data proved useful for the exploratory purposes of this study and provided insights into the relationships among the trees in the study stands. However, it would be difficult to recommend the collection of spatial data solely to allow for the use of distance dependent competition indices in a growth model. As was discussed in Chapter 2, collecting spatial data can be time consuming and costly. Although, the introduction of technologically advanced field measurement tools, such as distance measuring lasers, have made the process much faster and easier. The potential increase in the performance of the model would have to be large enough to justify these costs. A statistical test could be used to find out whether the increases are significantly large; however, the biases encountered in the regression analysis would prevent this test from being performed using the output from this study. Therefore, this issue will have to be independently investigated to draw any clear solutions.

#### 6 Conclusions

The third measurement of the study plots revealed that the growth rates were higher over the second growth period. Similar to the trends observed in the first growth period, the mean dbh and relative density of each plot continued to increase. The growth of the various measured attributes was still similar among the plots despite the differences in stand structures. The trends between the growth of the attributes and the stand structures became more obscured over the second growth period. Therefore, the conclusion made by Marshall and Wang (1996) in their previous study that the growth of the attributes appears to be robust to differences in stand structures within the densities studied still holds true.

From the range of competition indices selected for testing, the least complicated indices tended to produce the best performance. Overall, the distance dependent index created by Hegyi (1974 in Lorimer 1983) performed best. It was closely followed by Opie's (1968 in Bella 1971) index indicating that the ratio of diameters approach used by Hegyi and the area of influence approach used by Opie, although very different in formulation, are capable of similar performance. Individual tree vigour was found to work surprisingly well as a competition index.

The fixed radius plot method for selecting competing neighbours for the ratio of diameters indices generally produced the best results. The height angle gauge plot method also performed well and deserves further investigation. The variable radius plot method did not perform very well, but should also be investigated further after adding modifications that eliminate plot boundary biases.

From the performance of the various indices, inferences were made about the nature of the competitive relationships in the study stands. The results indicated that a relationship of relative symmetry, also termed resource depletion, exists among the trees in the study stands. This implies that competition occurs mainly for below ground resources. The relationship between the trees was found to be two-sided due to the influence that small trees had on larger trees.

The results from the evaluation of the various competition indices could simply be used as a recommendation of which competition index would produce the best performance if incorporated into a growth model. However, the insights into the nature of the competitive relationships that were revealed by the tests should not be confined to the modelling stage of management planning. The increased understanding of the growth dynamics should be considered by forest managers during every step of the

management planning process. An understanding of how the trees interact within a stand and how they will respond to various treatments can be used to find creative solutions to the many challenges faced by forest managers today.

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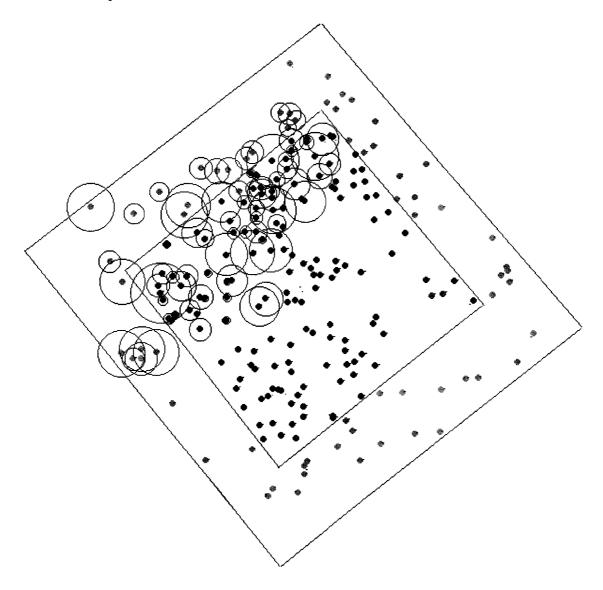
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### **Appendix 1**

#### **ArcView Representation of Plot 1**



Each point represents the location of a tree (the tree number labels are too small to read at the pictured scale).

The dark points represent the sample trees and the light points represent the border trees.

The rings represent the crown area of each tree (the crown areas have only been displayed for a portion of the stand for clarity).

The inner set of lines approximates the location of the plot boundary.

The outer set of lines were drawn in order to estimate the average width of the boundary.

## Appendix 2 a

#### **Code for Routine Calculating the Ratio of Diameters Indices**

```
Sub Hegyi()
Sheets("Hegyi").Select
' fixed radius selection
radius = 9
' BAF selection
' BAF = 6
r = 2
' Select Plots
For plot = 1 To 6
If plot = 1 Then
    p = "Plot 1"
   k = 153
    n = 220
End If
If plot = 2 Then
   p = "Plot 2"
   k = 117
   n = 174
End If
If plot = 3 Then
   p = "Plot 3"
   k = 252
   n = 328
End If
If plot = 4 Then
   p = "Plot 4"
   k = 153
   n = 239
End If
If plot = 5 Then
   p = "Plot 5"
   k = 284
```

n = 344

```
End If
If plot = 6 Then
    p = "Plot 6"
    k = 216
    n = 276
End If
    For j = 2 To k
    heg = 0
    heg2 = 0
    lor = 0
    lor2 = 0
    1 = 10
    Sheets(p).Select
    treej = Cells(j, 1).Value
    xj = Cells(j, 3).Value
    yj = Cells(j, 4).Value
    diaj = Cells(j, 5).Value
    grwthj = Cells(j, 34).Value
    htj = Cells(j, 7).Value
        For i = 2 To n
        treei = Cells(i, 1).Value
        xi = Cells(i, 3).Value
        yi = Cells(i, 4).Value
        diai = Cells(i, 5).Value
        hti = Cells(i, 7).Value
        ' critical distance for BAF
        'CD = diai / (2 * (Sqr(BAF)))
        ' critical distance for height angle guage
        'CH = hti / Tan(60)
        ' distance between the trees
        dist = ((xi - xj) ^2 + (yi - yj) ^2) ^0.5
        ' Competition from above only
        'If hti < htj Then dist = 0 Else
        ' calculate the index
        If dist < radius And dist > 0 Then
        'If dist < CD And dist > 0 Then
        'If dist < CH And dist > 0 Then
            heg = heg + ((diai / diaj) / dist)
```

```
heg2 = heg2 + (((diai ^ 2) / (diaj ^ 2)) / dist)
            lor = lor + (diai / diaj)
            lor2 = lor2 + ((diai ^ 2) / (diaj ^ 2))
            ' list neighbours
            'Sheets("Hegyi").Select
            'Cells(r, 1).Value = treei
            '1 = 1 + 1
            'Sheets(p).Select
        End If
        Next i
    ' Report
    Sheets("Hegyi").Select
    Cells(r, 1).Value = plot
    Cells(r, 2).Value = treej
    Cells(r, 3).Value = heg
    Cells(r, 4).Value = heg2
   Cells(r, 5).Value = lor
   Cells(r, 6).Value = lor2
   r = r + 1
   Next j
Next plot
```

End Sub

# Appendix 2 b

### **Code for Routine Calculating the Area of Influence Indices**

```
Sub Opie()
' Select Plots
g = 2
For plot = 1 To 6
If plot = 1 Then
   p = "Plot 1"
   k = 153
   n = 220
End If
If plot = 2 Then
   p = "Plot 2"
   k = 117
   n = 174
End If
If plot = 3 Then
   p = "Plot 3"
   k = 252
   n = 328
End If
If plot = 4 Then
   p = "Plot 4"
   k = 153
   n = 239
End If
If plot = 5 Then
   p = "Plot 5"
   k = 284
   n = 344
End If
If plot = 6 Then
   p = "Plot 6"
```

k = 216

```
n = 276
End If
For j = 2 To k
Sheets(p).Select
tree = Cells(j, 1). Value
RSUB = Cells(j, 11).Value
Aj = RSUB ^ 2 * 3.141593 / 2
xj = Cells(j, 3).Value
yj = Cells(j, 4).Value
diaj = Cells(j, 5).Value
grwthj = Cells(j, 34).Value
htj = Cells(j, 7).Value
If diaj = 0 Then
    bel25 = 0
   bel5 = 0
    be175 = 0
    bel2 = 0
    opie = 0
Else
1 = 7
    For i = 2 To n
    treei = Cells(i, 1).Value
    xi = Cells(i, 3).Value
    yi = Cells(i, 4).Value
    diai = Cells(i, 5).Value
    hti = Cells(i, 7).Value
    ' for competition from above
    'If hti < htj Then
    'ai = 0
    'Else
    ' distance between the trees
    d = ((xi - xj) ^2 + (yi - yj) ^2) ^0.5
    If d = 0 Then
        ai = 0
        Else
        ' determine which radius is larger
        r = Cells(i, 11).Value / 2
        If r > RSUB Then
```

'End If 'for compt from above

```
r1 = r
               r2 = RSUB
End If
If r < RSUB Then
              rl = RSUB
               r2 = r
End If
If r = RSUB Then
              r1 = RSUB
              r2 = r
End If
If r1 + r2 < d Then
               ai = 0
              Else
               If d + r2 < r1 Then
                              ai = 3.141593 * r2 ^ 2
                              Else
                              s = (r1 + r2 + d) / 2
                              c = (2 / d) * (s * (s - r1) * (s - r2) * (s - d)) ^ 0.5
                              x1 = (r1 ^2 - c ^2) ^0.5
                              If d > x1 Then
                                             ai = r1 ^2 * Atn((c / r1) / Sqr(-(c / r1) *
                                                     (c / r1) + 1)) + r2^2 + Atn((c / r2) /
                                                     Sqr(-(c / r2) * (c / r2) + 1)) - c * d
                              End If
                              If d = x1 Then
                                               ai = 3.141593 * r2 ^ 2 + r1 ^ 2 * Atn((r2 / r1) / r1) / r2 * Atn((r2 / r1) / r2) * Atn
                                                     Sqr(-(r2 / r1) * (r2 / r1) + 1)) - d * r2
                              End If
                              If d < x1 Then
                                              ai = r2 ^2 \times (3.141593 - Atn((c / r2) / Sqr(-(c / r2) / Sqr(-(c / r2) / r2) / Sqr(-(c / r2) / r2)))
                                                    r2) * (c / r2) + 1))) + r1 ^ 2 * Atn((c / r1) /
                                                     Sqr(-(c / r1) * (c / r1) + 1)) - c * d
                              End If
               End If
End If
```

```
End If
                'If ai > 0 Then
                'Worksheets("Arney").Select
                'Cells(j, l).Value = treei
                '1 = 1 + 1
                'Cells(j, 1).Value = ai
                 '1 = 1 + 1
                 'Worksheets("p").Select
                 'End If
    ' Opie
    opie = opie + (ai / Aj)
    'Bella 1.25
    bel25 = bel25 + ((ai / Aj) * (diai / diaj))
    'Bella 1.50
    bel5 = bel5 + ((ai / Aj) * ((diai / diaj) ^ 1.5))
    'Bella 1.75
    bel75 = bel75 + ((ai / Aj) * ((diai * hti) / (diaj * htj)))
    bel2 = bel2 + ((ai / Aj) * ((diai / diaj) ^ 2))
    Next i
End If
' write report
Sheets("Opie").Select
Cells(g, 1).Value = plot
Cells(g, 2).Value = tree
'Cells(g, 3).Value = opie
Cells(g, 3).Value = ((arn + Aj) / Aj)
Cells(g, 4).Value = bel25
Cells(g, 5).Value = bel5
Cells(g, 7).Value = bel75
Cells(g, 6). Value = bel2
g = g + 1
bel2 = 0
bel25 = 0
bel5 = 0
bel75 = 0
arn = 0
opie = 0
Next j
```

Next plot

End Sub

# Appendix 2 c

#### **Code for Routine Calculating the Newton's Modified Indices**

```
Sub Newton()
Sheets("Newton").Select
' fixed radius selection
rmax = 5
' Select Plots
For plot = 1 To 6
If plot = 1 Then
   p = "Plot 1"
    k = 153
   n = 220
End If
If plot = 2 Then
   p = "Plot 2"
   k = 117
   n = 174
End If
If plot = 3 Then
   p = "Plot 3"
   k = 252
   n = 328
End If
If plot = 4 Then
   p = "Plot 4"
   k = 153
   n = 239
End If
If plot = 5 Then
   p = "Plot 5"
   k = 284
   n = 344
```

End If

```
If plot = 6 Then
   p = "Plot 6"
    k = 216
   n = 276
End If
    For j = 2 To k
    heg = 0
    heg2 = 0
    lor = 0
    lor2 = 0
    1 = 10
    sumx = 0
    sumy = 0
    tm = 0
   w1 = 0
    s1 = 0
    Sheets(p).Select
    treej = Cells(j, 1).Value
   xj = Cells(j, 3).Value
   yj = Cells(j, 4).Value
    diaj = Cells(j, 5).Value
   grwthj = Cells(j, 34).Value
   htj = Cells(j, 7).Value
        For i = 2 To n
        treei = Cells(i, 1).Value
        xi = Cells(i, 3).Value
        yi = Cells(i, 4).Value
        diai = Cells(i, 5).Value
       hti = Cells(i, 7).Value
        massi = Cells(i, 74).Value
        ' critical distance for BAF
        ' CD = diai / (2 * (Sqr(BAF)))
        ' critical distance for height angle guage
        'CH = hti / Tan(60)
        ' distance between the trees
        rm = ((xi - xj) ^2 + (yi - yj) ^2) ^0.5
        ' Competition from above only
        If hti < htj Then rm = 0 Else
```

```
' calculate the index
    If rm < rmax And rm > 0 Then
    'If dist < CD And dist > 0 Then
    'If dist < CH And dist > 0 Then
         sumx = sumx + (massi * xi)
        sumy = sumy + (massi * yi)
        tm = tm + massi
        w1 = w1 + (massi / (rm^2))

s1 = s1 + (massi * (1 - (rm / rmax))^2)
        ' list neighbours
         'Sheets("Hegyi").Select
         'Cells(r, 1).Value = treei
         '1 = 1 + 1
         'Sheets(p).Select
    End If
    Next i
' final calculations
If tm = 0 Then tm = 1 Else
xbar = (sumx / tm)
ybar = (sumy / tm)
rcm = ((xj - xbar)^2 + (yj - ybar)^2)^0.5
wein = w1 * (1 - (rcm / rmax))
sil = s1 * (1 - (rcm / rmax))
' Report
Sheets("Newton").Select
Cells(r, 1).Value = plot
Cells(r, 2).Value = treej
Cells(r, 3).Value = w1
Cells(r, 4).Value = s1
Cells(r, 5).Value = wein
Cells(r, 6).Value = sil
r = r + 1
```

Next j

Next plot

End Sub