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This study characterized the nature and dynamics of interference in mixed red alder (*Alnus rubra* Bong.)/Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands in the Pacific Northwest, USA. Long-term spatial and tree measurements from the Cascade Head (CH) and H.J. Andrews (HJA) Experimental Forests in western Oregon and Delezene Creek (DC), Washington were utilized to investigate neighborhood and population-level measures of interference. Existing neighborhood and population-level measures of interference were modified to evaluate the intensity and importance of intra- and inter-specific interference. The relationship between relative growth rate and population-level and neighborhood interference were examined over 9 years at the CH and HJA study sites and 38 years at the DC study site. In general, the effects of intra-specific interacted with the effects of inter-specific interference to influence the relative growth rates of red alder and Douglas-fir at all of the sites. Performance of the interference measures as predictors of relative growth rates varied between species and with stand structure. In general, population-level indices were the best predictors of relative growth rates for the species with heights greater than the other interacting species over a given interval of time. In contrast, neighborhood indices were the best predictors of relative growth rates for the species with subordinate or equivalent tree heights to the dominant species over a given interval of time. These results were consistent for both species, all three study sites, and all measurement periods when interference occurred and suggest that the importance of neighborhood interference varies with the competitive status of a species. A conceptual model synthesizes the importance of neighborhood and population-level interference as a function of relative dominance of a species. In addition, the literature suggests that this model may also be appropriate for individuals within a population.

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TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF TABLES

LIST OF TABLES (CONTINUED)

Interference Dynamics in Mixed Red Alder/Douglas-fir Forests

CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

This thesis examines the interference dynamics in mixed red alder/Douglas-fir forests in the Pacific Northwest, USA. The first chapter of this thesis presents a summary of the literature pertaining to the objective of this study, which is characterizing the nature and degree of interference in mixed red alder/Douglas-fir stands at different stages of development. Factors addressed in this review include approaches to measuring interference, the use of interference indices to measure the effects of interference on tree growth, and the ecology of mixed red alder/Douglas-fir forests. For the purposes of this literature review and thesis, interference will be defined as any plant-plant interaction influencing the resources available for plant growth (see Goldberg 1990).

The second chapter presents the results of my investigation into the dynamics of interference in mixed red alder/Douglas-fir forests. The overall objective of this study was the characterization of the nature and dynamics of interference in mixed red alder/Douglas-fir in the Pacific Northwest, USA. For this study, long-term spatial and tree measurements from the Cascade Head (CH) and H.J. Andrews (HJA) Experimental Forests in western Oregon and Delezene Creek (DC), Washington were utilized to investigate neighborhood and population-level measures of interference. Existing neighborhood and population-level measures of interference were modified to evaluate the intensity and importance of intra- and inter-specific interference. The relationship between relative growth rate and population-level and neighborhood interference were examined over 9 years at the CH and HJA study sites and 38 years at the DC study site. The results of this study suggest that the importance of neighborhood interference changes with stand structure for red alder and Douglas-fir. I discuss how changes in relative dominance in height between red alder and Douglas-fir may be responsible for this dynamic.

The final chapter of this thesis presents the general conclusions from my research, highlighting areas where future research is needed and recognizing the potential limitations of this study. In addition, the implications of my findings to forest management are discussed.

LITERATURE REVIEW

Introduction

Plant interference has been studied extensively due to its ecological and economic importance. The following literature review examines several topics related to plant interference with special emphasis on experimental approaches for measuring the effects of interference on plant community structure and development. The first part of this review presents various approaches commonly used for studying interference in plant communities. This section begins with a brief historical background of early studies examining interference and is followed by examples of models for predicting the effects of interference on plant size. In addition, additive and replacement series experiments and the neighborhood approach are discussed to illustrate examples of techniques for characterizing interference at the population- and individual plant-level. This section concludes with a discussion of quantifying the importance and intensity of interference.

The second section of this literature review discusses the use of competition indices for predicting the effects of interference on tree growth. This section presents examples of different forms of competition indices commonly used and discusses their performance as predictors of tree growth in various forest ecosystems. The literature review concludes with a section discussing the ecology of the species used in this study, red alder and Douglas-fir.

Measuring Plant Interference

Interference among plants in a population is a dynamic, biologically complex process often challenging to measure (Burton 1993). Individual plant growth is influenced by numerous abiotic and biotic factors, including genetic characteristics and micro-environmental conditions, making it difficult to isolate the effects of interference. Attempts to isolate the influence of interference on individual plant growth require the partitioning of interference into interference effects and responses (sensu Goldberg 1990). This partitioning allows one to evaluate how changes in resource availability resulting from the presence of other plants affect individual plant growth.

Early research examining the role of interference in plant community structure focused on intra-specific interference at the population-level, often utilizing planted monocultures of annual plants (e.g., Harper 1961). Examining the mean plant performance within populations sown at varied densities, numerous studies were able to correlate decreases in mean plant performance with increases in population density (Harper 1961; Obeid *et al.* 1967; Firbank *et al.* 1984). For example, Harper (1961) and Firbank *et al.* (1984) found mean plant weight of *Bromus* sp. was lower in populations with higher sowing densities. Similar results were found by Obeid *et al.* (1967) in their examination of populations of *Linum usitatissimum.* These observed decreases in mean plant size as a result of high population densities have been referred to as the competition-density effect (Firbank and Watkinson 1990).

The effects of plant density on mean plant size in monocultures have been modeled using yield-density models (e.g., Watkinson 1980). These models assume that mean plant size is a function of resource availability per plant (Firbank & Watkinson 1990), with higher densities corresponding to lower resource levels per plant. While these models are adequate at predicting the effects of intra-specific interference on mean plant size in monocultures (e.g., Yoda *et al.* 1963; Watkinson 1980), the differences between species regarding interference effects and responses require an alternative approach for examining inter-specific interference.

To examine the effects of intra- and inter-specific interference on plant growth at the population-level, experimental designs such as the replacement and additive series have been used. In a replacement series design, two or more species are grown in mixtures with varied proportions and a single total density (Joliffe *et al.* 1984). Although this experimental design has been widely used, a common criticism has been that the use of a single population density prevents the isolation of the effects of intra- and inter-specific interference (Joliffe et al. 1984; Firbank & Watkinson 1985; Joliffe 2000). To separate these effects, the additive series design has been used. For this design, the densities as well as the proportions of the mixtures are systematically varied thus allowing for the separation of intra- and inter-specific interference effects (Firbank & Watkinson 1990). Watkinson (1981) presented the following model to predict the influence of intra- and inter-specific interference on mean plant size in two species mixtures, such as in an additive series design:

$$w_x = \overline{w}_x\left[1 + a_x\left(N_x + \alpha_{xz}N_z\right)\right]^{-bx} \qquad \text{eqn 1}$$

where w_x is the mean weight per plant of species x, $\overline{w}_x$ is the mean weight per plant of species x growing in monoculture, a_x represents the area required by a plant of species x to achieve $\overline{w}_x$, N_x and N_z are the density of species x and z, α_{xz} is relative competitive ability of the two species in a mixture, and bx is the efficiency of resource utilization by the population of species x (Watkinson 1981). An advantage of this model is the ability to examine the effects of density on intra- and inter-specific interference.

Additive series have been used to determine the relative importance of intra- and inter-specific interference on plant growth (e.g., Shainsky & Radosevich 1992; Zutter *et al.* 1997). In most cases, the importance of inter-specific interference is greater than intra-specific interference for only one of the two species constituting an additive series (e.g., Shainsky & Radosevich 1992; Zutter *et al.* 1997). This pattern has been attributed to differences between species regarding their effects on resource availability (Shainsky & Radosevich 1992). For example, Zutter *et al.* (1997) demonstrated sweetgum (*Liquidambar sytraciflua* L.) had a significant effect on the light and soil moisture available to loblolly pine (*Pinus taeda* L.), whereas loblolly pine did not have significant effects on the light or soil moisture available to sweetgum. As a result, inter-specific interference was more important than intra-specific interference for loblolly pine but not for sweetgum (Zutter *et al.* 1997). These findings are consistent with Aarssen's (1983) hypothesis that states a species that is a 'superior competitor' will be more affected by intra-specific interference than inter-specific interference. In addition, a 'weaker competitor' will be more affected by inter-specific interference.

While population-level studies provide an estimate of the mean plant response to interference, a limitation of this approach is the inability to account for variation in plant performance among individual plants in a population (Mack & Harper 1977). To examine the influence of interference on plant growth at the individual-level, the neighborhood approach was developed (Mack & Harper 1977; Weiner 1982). Neighborhood experiments examine the performance of a focal plant as a function of the density (e.g., Firbank & Watkinson 1987), size (e.g., Silander & Pacala 1985), cover (e.g., Wagner & Radosevich 1991), aggregation (e.g., Mack & Harper 1977), and/or distance (e.g., Weiner 1984) of neighboring plants. This approach has several advantages over population-level studies, including its ability to quantify the influence of spatial characteristics of neighbor plants (Silander & Pacala 1985; Firbank & Watkinson 1987) and to account for the influence of the local density surrounding each individual plant in a population (Weiner 1984; Firbank & Watkinson 1987).

An important component of neighborhood analyses is the size of neighborhood used to incorporate all of the neighboring plants potentially interfering with the resources available to a focal plant. A common approach for selecting an appropriate neighborhood size is comparisons between regression models predicting plant performance as a function of interference within neighborhoods of various sizes (e.g., Silander & Pacala 1985; Wagner & Radosevich 1991). The neighborhood size that maximizes the R^2 (e.g., Silander & Pacala 1985; Goldberg 1987) or minimizes the residuals (e.g., Wagner & Radosevich 1991) for these models is typically chosen as the optimum neighborhood size for a particular plant community.

Various measures have been integrated into the neighborhood approach to characterize the nature of interference at the individual plant–level in a particular plant community. The distance from neighbors has been used as a measure of the intensity of interference from a particular neighbor on the available resources for a focal plant (Mack & Harper 1977; Silander & Pacala 1985; Wagner & Radosevich 1991). Several studies have weighted the interference effects of neighboring plants within a chosen neighborhood by their distance from the target plant (Mack & Harper 1977; Weiner 1982, 1984; Silander & Pacala 1985; Wagner & Radosevich 1991). This weighting assumes that the effect of a neighbor on the resources available for a focal plant decreases with distance (Weiner 1982). Plants outside of the chosen neighborhood may also influence the resources available for a focal plant (e.g., Silander & Pacala 1985; Wagner & Radosevich 1991). To account for this influence, several studies have weighted the interference effects of plants outside of the chosen neighborhood by the inverse square of their distance from the focal plant (e.g., Silander & Pacala 1985; Wagner & Radosevich 1998). This weighting suggests that neighbors within the chosen neighborhood have a proportionally greater effect on resources available for the focal individual than farther neighbors.

Another measure used in the neighborhood approach is neighborhood density. Neighborhood density provides an estimate of the overall interference effect of neighboring plants on resources available to the focal plant (Harper

1977). In addition, neighborhood density characterizes the degree of local crowding a focal plant experiences. In most cases, focal plant performance has a negative, non-linear relationship with increasing neighborhood density (e.g., Harper 1977; Weiner 1982; Silander & Pacala 1985; Goldberg 1987). This non-linear relationship suggests that there is a large decrease in focal plant performance due to any neighbors at all and smaller effects of adding additional neighbors.

While neighborhood density is adequate to describe the overall interference effect of neighboring plants, it does not account for the size of neighbors and the effect of size on interference for resources (Firbank and Watkinson 1987). The size of neighboring plants relative to the focal plant has been incorporated into neighborhood models to characterize the asymmetry of interference between focal plants and their neighbors (e.g., Thomas & Weiner 1989). These models assume neighbors larger than a focal plant have a disproportionate effect on resource availability (Schwinning & Weiner 1998). In some cases, neighborhood models incorporating only the interference effects of neighbors with sizes equal to or larger than the focal plant have been able to explain more variation in focal plant performance than models incorporating the interference effects of all neighbors irrespective of size (e.g., Thomas & Weiner 1989; Wagner & Radosevich 1998). For example, Thomas and Weiner (1989) found the best model for predicting the relative growth rates of *Impatiens pallida* Nutt. included only the interference effects of neighbors equal to or larger than the focal individuals. They hypothesized that interference in this community was predominantly for light and that smaller neighbors did not strongly interfere with the light available to larger focal plants. However, the degree of asymmetry may vary with the response measure utilized. For example, Wagner & Radosevich (1998) found the best model for predicting Douglas-fir height growth included only the interference effects of neighboring shrub species equal to or larger than focal individuals. However, their best models for predicting Douglas-fir basal area growth included the effects of all neighbors irrespective of size (Wagner & Radosevich 1998). They hypothesized that interference for light was more important for height growth, whereas interference for soil water was more important for basal area growth.

Numerous studies utilizing the neighborhood approach have examined the effect of neighbor spatial arrangement on the interference experienced by a focal plant (Mack & Harper 1977; Waller 1981; Fowler 1984; Weiner 1984; Silander & Pacala 1985; Lindquist *et al.* 1994; Wagner & Radosevich 1998). While several studies have demonstrated the importance of neighbor spatial arrangement in predicting the effects of neighborhood interference (e.g., Mack & Harper 1977; Waller 1981; Silander & Pacala 1985; Lindquist *et al.* 1994), other studies have found a poor relationship (Fowler 1984; Weiner 1984; Wagner & Radosevich 1998). Several reasons have been suggested for this inconsistent performance, including the use of inappropriate neighborhood sizes (Weiner 1984) and the examination of a limited range of neighborhood densities (Silander & Pacala 1985). Both of these factors may bias the importance of other variables such as neighbor size thus resulting in a poor relationship between neighbor spatial arrangement and focal plant performance (Weiner 1984). In addition to these factors, model simulations have demonstrated that spatial arrangement of neighbors may not be an important component of neighborhood interference in plant communities in which the nature of interference is strongly asymmetric (Hara & Wyszomirski1994).

While numerous studies have been able to develop relationships between population- and neighborhood-level interference and plant growth, the relative importance and intensity of interference has often been overlooked (Weldon & Slauson 1986). The importance of interference is related to the amount of overall variation in plant performance that is attributable to interference, whereas the intensity of interference addresses the magnitude of the effects of interference on plant performance (Weldon & Slauson 1986).

The coefficient of determination (R^2) or goodness-of-fit for models predicting plant growth has been suggested as a measure of the importance of interference relative to other factors influencing growth (Weldon & Slauson 1986). However, the use of an inappropriate model form can potentially lead to an over- or under-estimation of the importance of interference (Radosevich & Roush 1990). Alternatively, experimental designs controlling other factors potentially influencing plant performance in a plant community, such as nutrient availability and disturbance, have been used to directly measure the importance of interference. For example, Campbell *et al.* (1991) manipulated the levels of stress and disturbance experienced by pure and mixed stands of *Arrhenatherum elatius*, *Festuca ovina*, and *Poa annua* and were able to directly estimate the proportion of variation in plant growth attributable to interference.

There has been a great deal of debate regarding how the intensity of interference should be measured and calculated (Weldon & Slauson 1986; Campbell *et al.* 1991; Campbell & Grime 1992; Grace 1991, 1995). A common approach to measuring the intensity of inter-specific interference has been to compare plant performance in monocultures versus mixtures along soil nutrient and disturbance gradients (e.g., Campbell & Grime 1992; Turkington *et al.* 1993; Wilson & Tilman 1993). Studies utilizing this experimental approach have calculated the intensity of interference as: (i) the absolute reduction in plant performance of a species grown in a mixture compared to when grown in a monoculture (e.g., Campbell & Grime 1992), and/or (ii) the relative reduction in plant performance of a species grown in a mixture, which is standardized by the species monoculture performance (e.g., Wilson & Tilman 1993). Studies utilizing absolute and relative intensity measures have found conflicting results regarding the relationship between the intensity of interference and resource availability (e.g., Turkington *et al.* 1993), and the usage of solely relative measures has been suggested to separate plant responses to interference from responses to environmental gradients (Grace 1995). As an alternative, the use of slope estimates from regression models predicting relative plant growth as a function of neighborhood interference has been suggested as an approximation of the intensity of interference (Weldon & Slauson 1986). However, similar to the problems associated with using model goodness-of-fit to determine the importance of interference, inappropriate model forms can result in an under- or over-estimation of the intensity of interference.

Use of competition indices to measure the effects of interference on tree growth

The primary mode of interference between trees in a forest community is competition for resources (Oliver & Larson 1996). Because of its ecological and economic importance, various indices for predicting the effects of competition on tree growth have been developed (e.g., Heygi 1974; Martin & Ek 1984; Lorimer 1983; Biging & Dobbertin 1992). These indices are collectively referred to as "competition indices" and are based on the assumption that the degree of resource competition can be described by factors such as stand or neighborhood characteristics (Burton 1993). Using this assumption, competition indices can be utilized to predict the response of focal trees to the effects of resource competition within a forest community (Goldberg 1996).

Competition indices can be divided into two major classes: distance-dependent and distance-independent (Biging & Dobbertin 1995). Distance-dependent indices are based on the assumption that interference in a forest community is a spatially explicit process. These indices take into consideration spatial attributes of the forest community such as inter-tree distances (e.g., Hegyi 1974). In contrast, distance-independent indices generally assume diffuse interference effects with each individual in the population interacting relatively homogenously (Burton 1993). These indices rely solely on population-level measures such as size relative to the population mean (e.g., Glover & Hool 1979) or basal area (e.g., Cao 2000).

Based on the neighborhood approach, distance-dependent competition indices are designed to measure the degree of resource interference around a focal tree as a function of factors such as the density, size, and proximity of neighboring plants. Three major categories of distance-dependent competition indices have been developed for tree-tree competition: (1) indices measuring the "influence area overlap" between trees (Bella 1971; Ek & Monserud 1974); (2) Thiessen or Voronoi polygons representing the area (and resources) potentially available (APA) for tree growth (Moore & Budelsky 1973; Nance *et al.* 1987); and (3) indices incorporating the relative size and distance between a target tree and the neighboring trees within a given radius (Hegyi 1974; Daniels 1976; Lorimer 1983; Weiner 1984; Biging & Dobbertin 1992).

An important component of interference between trees is the degree of interference for above- and below-ground resources due to "overlap" between the crown and root systems of adjacent trees. To characterize these interactions, "influence area of overlap indices" were developed (Bella 1971; Ek & Monserud 1974). These indices are based on the assumption that a tree's ability to interfere with above- and below-ground resources can be represented by an influence area surrounding the tree (Bella 1971). These measures assume the influence area represents all of the resources available to a focal tree (e.g., Bella 1971). In most cases, the open grown crown radius of a focal tree is predicted from its diameter at breast height (dbh) and used to define its influence area (e.g., Bella 1971; Holmes & Reed 1991). In contrast to other neighborhood measures of interference, area of influence indices define the influence of a neighboring tree as a function of the degree of overlap between it and the focal tree's areas of influence. This area of overlap is assumed to represent the degree of interference occurring between interacting individuals for aboveground and belowground resources (Bella 1971; Schwinning & Weiner 1998). A focal tree whose area of influence is not overlapped by neighboring trees is assumed to have access to all of the resources in their respective area of influence.

An alternative approach for expressing the area of resources available for uptake by a focal tree is the use of Thiessen or Voronoi polygons (Mead 1966). These polygons are constructed to represent the growing space or resources available to each focal plant. This approach was originally developed for predicting individual plant yield in agricultural systems (Mead 1966), but has been applied to forest communities in the form of area potentially available (APA) indices (Moore & Budelsky 1973; Nance *et al.* 1987). These indices attribute ground area to each tree based on the spatial location and size of neighboring trees. The resources within each APA are not available for uptake by neighboring trees and the amount of interference for above- and below-ground resources experienced by a particular focal tree can be measured based on the size of its APA.

Influence area of overlap and APA indices provide an indirect measure of the actual area available to a focal tree. In contrast, the most common type of distance-dependent index utilizes the relative sizes and distances of neighboring trees within a given radius to represent the degree of competitive pressure for resources a focal tree experiences (e.g., Hegyi 1974; Lorimer 1983; Biging & Dobbertin 1992; Richardson *et al.* 1999). Based on the neighborhood approach, a neighboring tree's effect on resources is scaled by its distance from the focal tree. With this scaling, closer neighbors are assumed to have a greater effect on resource availability as compared to more distant neighbors. In addition, the use of neighbor size relative to the focal tree allows an expression of the degree to which a focal tree may be suppressed by a neighboring tree.

Distance-independent indices are population-level measures of interference that attempt to predict tree growth as a function of population-level measures such as density, basal area, or relative size. While other approaches for studying the effects of competition at the population level utilize mean tree growth as the response variable (e.g., White and Harper 1970), distance-independent indices are used to predict individual tree growth. In contrast to distance-dependent indices, the majority of distance-independent indices assume the degree of resource competition experience by a focal tree can be described by measures of population size such as density (e.g., Yoda *et al.* 1963) or competitive status such as size relative to the population mean (e.g., Glover & Hool 1978). Measures of population size are assumed to represent overall resource availability throughout the population, whereas measures of competitive status represent the ability of an individual to capture resources relative to other trees in the population (Harper 1977). This approach implies that interference effects on resources in the population are relatively diffuse (Burton 1993). Exceptions to this assumption are distance-independent indices that include a measure of the asymmetry of interference in the population (e.g., Wykoff *et al.* 1982; Wimberly & Bare 1996). This approach results in indices in which only trees in the population larger than a focal tree are influencing resources availability for a focal tree (Wykoff *et al.* 1982).

Numerous comparisons of the ability of competition indices to predict tree growth have been conducted in plantation monocultures (e.g., Hegyi 1974; Daniels *et al.* 1986; Tomé & Burkhart 1989). In many cases, combinations of distance-independent measures such as stand density and distance-dependent measures such as APA have been able to explain significantly more variation in tree growth than distance-dependent or distance-independent measures alone (e.g., Daniels *et al.* 1986; Nance *et al.* 1987; Tomé & Burkhart 1989). These results suggest that the regular spacing of a plantation may result in strong relationships between the area of resources available to a focal tree and the overall population density. In addition, the small amount of variation between individuals in a plantation monoculture may result in an artifact that population measures, such as overall density, can be used to predict the resource availability of individual trees.

Comparisons of competition indices have also been conducted in naturally regenerated mixed-species stands (e.g. Lorimer 1983; Holmes & Reed 1991; Biging & Dobbertin 1992, 1995). Surprisingly, the majority of these studies have found that tree spatial information does not improve the ability to predict the effects of resource competition on tree growth (e.g., Lorimer 1983; Holmes & Reed 1991; Biging & Dobbertin 1995). In many cases, the competitive status (e.g., relative size) of a tree within a forest stand is an equal, if not better predictor of tree growth than more complicated distance-dependent measures (e.g., Biging & Dobbertin 1995). However, these results may be due to the use of absolute growth as a measure of fitness (Biging & Dobbertin 1995). In cases in which absolute growth is used, the use of relative size as an explanatory variable may confound interpretations of the appropriate measures of competition to use due to the strong relationships between size and absolute growth. In addition to the use of absolute growth, these results may also be due to the use of inadequate measures for characterizing the processes involved in resource competition in these forests (Brunner & Nigh 2000).

A criticism of competition indices has been their static nature (Burton 1993). The nature and degree of interference experienced by a focal tree may change over time as forests grow and develop. As a consequence, the ability of a particular index to characterize the nature and degree of interference may also change (Burton 1993). The majority of research evaluating the performance of competition indices has been limited to one or a few years of measurements, even though at various points in stand development (e.g., Lorimer 1983; Tomé & Burkhart 1989; Biging & Dobbertin 1992, 1995). Those studies examining the performance of competition indices over longer time periods have found varying results. For example, Daniels *et al.* (1986) evaluated the correlations between various competition indices and basal area growth for loblolly pine over years 5-13 in stand development. They found the strength of correlation between growth and distance-dependent competition indices was small at younger ages and increased over time. These results suggest that interference may become a more spatially explicit process as trees grow larger. To account for these potential changes in the nature of interference, the repeated calculation of competition indices over longer time periods has been suggested (Mitchell-Olds 1987; Burton 1993); however, few studies have utilized this approach.

In addition to the static nature, another limitation of past research utilizing competition indices has been their single-species approach to measuring interference. The majority of studies in mixed-species forests have relied on competition indices that did not account for possible differences between tree species regarding interference effects (e.g., Gerrard 1969; Lorimer 1983; Holmes & Reed 1991; Biging & Dobbertin 1992, 1995). Studies evaluating the interference effects of shrub and herb species on conifer regeneration have incorporated species differences into competition indices (e.g., Wagner & Radosevich 1998; Richardson *et al.* 1999); however, our understanding of interference within and between tree species in mixed-species forests is still limited.

Ecology of Mixed red alder/Douglas-fir Forests

The management of mixed red alder/Douglas-fir stands has traditionally received a great deal of attention due to red alder's ability to fix nitrogen and potentially improve the growth of Douglas-fir (Binkley 1983). In addition, red alder may also suppress early Douglas-fir growth through competition for resources creating a challenge for landowners managing mixtures of these species (Cole & Newton 1986, 1987). Recent concerns over biodiversity have increased interest in managing mixtures of Douglas-fir with other species such as red alder (McComb 1994). In addition, the increasing market value of red alder wood has led to greater interest in the management of this species (Plank & Willits 1994).

Mixed red alder/Douglas-fir stands typically establish on sites where disturbance, e.g., through clear-cutting followed by slash burning, has resulted in exposure of the mineral soil (Tesch 1995). The rapid initial height growth of the pioneering red alder on these sites often results in overtopping of the shade intolerant Douglas-fir and can lead to reduced growth and substantial morality early on in stand development (Cole & Newton 1986, 1987). Stubblefield and Oliver (1978) reported that the persistence of Douglas-fir under these stand conditions is dependent on canopy gaps, which allow sufficient light penetration for the growth and survival of Douglas-fir. Newton *et al.* (1968) and Miller and Murray (1978) demonstrated that the dominance of red alder in these even-aged stands usually perisists for 25-40 years. At this point in stand development, the height growth of red alder begins to slow down and the sustained rapid height growth of Douglas-fir allows it to reach a dominant position in the canopy (Newton & Cole 1987). As the relatively short-lived red alder continues to senesce, the long-lived Douglas-fir is able to continue vigorous growth and eventually forms a pure overstory (Stubblefield & Oliver 1978; Puettmann *et al.* 1992).

A great deal of research has focused on the interactions between red alder and Douglas-fir due to the nitrogen fixing ability of red alder, which provides for the possibility of positive interaction. Binkley (1992) reported that enhanced Douglas-fir growth due to the presence of red alder is only manifested on sites in which nitrogen is limiting. In addition, competition for other resources such as light and water may override any beneficial effect of nitrogen fixation. For example, Shainsky and Radosevich (1992) demonstrated that intense competition between dense red alder and Douglas-fir for light in young, developing stands resulted in red alder having a negative effect on Douglas-fir growth. In contrast, studies conducted in mature stands on sites with very low soil nitrogen by Tarrant (1961) and Miller *et al.* (1993) reported that the growth and performance of Douglas-fir was enhanced by the presence of red alder. These finding illustrate the influence of soil nitrogen availability on the nature of interactions between these two species at a given point in stand development. However, our understanding of how the nature of these interactions may change over the course of stand development is still limited.

Conclusions from literature

Competition works at various levels throughout the life of a forest stand and over space among individuals at a given point in development. The literature demonstrates the effects of interference on individual plant growth can be measured using population-level and neighborhood analyses. Population-level studies of plant interference are able to estimate the mean competitive effect and response of plants to changes in resource availability. The use of additive series designs allows the partitioning of these effects and responses into intra-specific and inter-specific interactions. To account for the variation in plant performance among individual plants in a population the neighborhood approach was developed. Factors such as neighborhood density, relative size of neighbors, and distance from nearest neighbors have been incorporated into these neighborhood measures of interference to improve our ability to predict the effects of neighborhood interference on plant growth. In addition to measuring the effects of interference on plant growth, the relative importance and intensity of interference can be estimated using statistical techniques and various experimental designs.

The influence of inter-tree competition on tree growth has received a great deal of attention. A variety of competition indices have been developed to predict the influence of inter-tree competition on tree growth. The majority of research testing the ability of these indices to predict tree growth has been conducted in plantation monocultures. Those studies conducted in mixed-species forests have mainly relied on single-species approaches, ignoring the potential for differences regarding the effects of intra- and inter-specific interference on tree growth. The ability of these indices to predict growth has varied between forest types and different points in stand development. Little research has examined how competition in forest ecosystems changes over time. Research evaluating the predictive ability of competition indices over longer time periods is needed to understand the dynamics of interference in long-lived perennial plant populations.

While a great deal of research has examined the interactions between red alder and Douglas-fir early in stand development, there is little information evaluating the outcome of interactions between these two species at later points of stand development or under different spatial conditions. Long-term experiments are needed to characterize how the nature of interference in mixed red alder/Douglas-fir stands changes over the course of stand development and under different spatial conditions.

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CHAPTER TWO

INTERFERENCE DYNAMICS IN MIXED RED ALDER/DOUGLAS-FIR FORESTS

SUMMARY

(1) The effects of interference on the relative growth rates of *Alnus rubra* and *Pseudotsuga menziesii* over 9 and 38 years in planted and natural mixtures in the Pacific Northwest, USA were investigated using two different types of interference measures: (i) neighborhood interference indices (*II)* and (ii) population-level *II.*

(2) To examine the relative intensity and importance of intra- and inter-specific interference over the course of forest development, existing neighborhood and population-level *II* were modified for two-species mixtures. The corrected Akaike Information Criterion (AIC_c) was used to identify the optimum interference measures and model forms for each species and measurement period.

(3) Performance of the interference measures as predictors of relative growth rates varied between species and over time. In general, population-level *II* were the best predictors of relative growth rates for the species with heights greater than the other interacting species over a given interval of time. In contrast, neighborhood *II* were the best predictors of relative growth rates for the species with subordinate or equivalent tree heights to the dominant species over a given interval of time.

(4) The results of this study suggest that the importance of neighborhood interference varies with the relative dominance in size of a species. Using a conceptual model of the importance of neighborhood and population interference as

a function of relative dominance, I hypothesize that changes in the relative dominance of a particular species or individual may result in changes in the importance of neighborhood interference.

INTRODUCTION

The importance of interference in forest community structure and development has been well recognized (Yoda *et al.* 1963; Harper 1977; Duncan 1991; Peterson & Squiers 1995; Oliver & Larson 1996). These interactions may have positive effects on tree growth and survival through processes such as facilitation (Binkley 1983; Walker & Chapin 1987; Peterson & Squiers 1995), or negative effects through processes such as competition for resources (Ford 1975) and allelopathy (Williamson 1990). In general, the predominant mode of interference between trees in a forest community is competition for resources (Oliver & Larson 1996). In many cases, early differences in size among trees due to variation in emergence time (Connolly & Wayne 1996), early growth rates (Turner & Rabinowitz 1983), and/or environmental heterogeneity (Hartgerink & Bazzaz 1984) are magnified as stands develop and competition for resources intensifies. In particular, inequalities in height within a population can result in the pre-emption of resources by larger individuals exacerbating the differences in growth rates among interacting trees (Cannell *et al.* 1984). Often, these asymmetric competitive relationships lead to an increasingly positive correlation between the size of a tree relative to the population and its growth rate (Ford 1975; Cannell *et al.* 1984; Schmitt *et al.* 1987).

While size is often related to resource capturing capacity in populations in which competition is asymmetric (Ford and Diggle 1981; Miller & Werner 1987; Goldberg 1990), the amount of competition a tree experiences is also a function of the size and proximity of its neighbors (Mack & Harper 1977; Weiner 1982; 1984; Silander & Pacala 1985; Goldberg 1987). The role of neighborhood competition as a determinant of tree growth is well documented (e.g., Bella 1971; Weiner 1984; Penridge & Walker 1986; Peterson & Squiers 1995). However, our understanding of the relationship between a tree's size relative to the population and the importance (sensu Weldon & Slauson 1986) of neighborhood competition as a determinant of tree growth is limited. Several authors examining competition in populations with varied size structures have noted that measures of neighborhood competition have only been able to explain the variation in growth of smaller individuals in the population (e.g., Cannell *et al.* 1984; Kubota & Hara 1995; McLellan *et al.* 1997). In these studies, the effects of neighborhood competition on larger individuals has been minimal suggesting that the importance of neighborhood competition as a determinant of tree growth may vary among individuals based on their relative sizes. While neighborhood measures incorporating the effects of competitive asymmetry have been developed to account for this variation (e.g., Penridge & Walker 1986; Thomas & Weiner 1989), these measures have assumed that neighborhood competition is equally important for all individuals in a population irrespective of their size (Thomas & Weiner 1989). Comparative evaluations of the ability of measures of size relative to the population and neighborhood competition to predict tree growth could prove valuable in characterizing the relationships between relative size and the importance of neighborhood competition.

The importance of neighborhood competition may also change over time (e.g., Daniels *et al.* 1986; Stoll *et al.* 1994). Factors such as differences in long-term growth rates among interacting individuals and stochastic events can result in changes to population and neighborhood conditions as a stand develops. As a result, the competitive relationships between interacting individuals may also change (Burton 1993). The use of long-term, repeated measurements of neighborhood and population conditions has been suggested to account for these dynamics (Mitchell-Olds 1987; Burton 1993). However, the logistical difficulty associated with this approach has limited its usage.

In this study, I utilize repeated measurements of tree growth and population-level and neighborhood conditions to characterize the interference dynamics in young and mature mixed red alder (*Alnus rubra* Bong.)/Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco; nomenclature follows Hitchcock & Cronquist 1976) forests in the Pacific Northwest, USA. Mixed red alder/Douglas-fir forests provide an excellent test system for a long-term interference study due to the differences between these species regarding growth rates and resource requirements. Red alder is a fast-growing, early successional species that is often able to attain its mature height within forty years (Newton & Cole 1994). In addition to its rapid early height growth, red alder is also able to fix nitrogen, which provides the opportunity to investigate positive (i.e., facilitation) as well as negative (i.e., competition) interference (Binkley 1983). In contrast, Douglas-fir is a long-lived, early- to late-successional species able to maintain height growth for up to two hundred years (Curtis *et al.* 1974). Red alder and Douglas-fir commonly co-occur throughout the Pacific Northwest and the interference between these two species at different stages of forest development has received a great deal of attention (e.g., Puettmann *et al.* 1992; Shainsky & Radosevich 1992).

The overall objective of this study was to characterize the interference dynamics in mixed red alder/Douglas-fir forests at different stages of stand development. Specific objectives included (i) evaluating the factors influencing interference in mixed red alder/Douglas-fir stands, (ii) assessing the intensity and importance (sensu Weldon & Slauson 1986) of intra- and inter-specific interference, and (iii) determining whether the nature and degree of interference changes with time or population structure.

METHODS

Study sites

This study utilizes data from three mixed red alder/Douglas-fir stands: two replacement series studies at the Cascade Head (124° 00' W, 45° 05' N) and H.J. Andrews (122° 10' W, 44° 14' N) Experimental Forests in western Oregon and a natural, mixed red alder/Douglas-fir stand at Delezene Creek (123° 24' W, 46° 56'

N) in western Washington. The Cascade Head (CH) study site is located on the borders of the *Picea stichensis* and *Tsuga heterophylla* vegetation zones (Franklin & Dyrness 1973) in the Oregon central Coast Range. This region is characterized by a wet, mild, maritime climate with an average annual minimum temperature of 2.2°C and an average annual maximum temperature of 20.9°C. Annual precipitation averages 250 cm and occurs primarily during the winter. Elevations in the CH study site range from 150 to 330 m above sea level and soils are deep, well-drained, fine loams derived primarily from basaltic parent material (Shipman 1997). The H.J. Andrews (HJA) study site is located in the *Tsuga heterophylla* vegetation zone (Franklin & Dyrness 1973) in the Oregon west-central Cascade Range. This region is also characterized by a wet, mild, maritime climate with an average annual minimum temperature of –8.5°C and an average annual maximum temperature of 26.9°C. Annual precipitation averages 230 cm with only 6% occurring between June and August (Halpern 1989). Elevations in the HJA study site range from 500 to 800 meters above sea level and soils are deep, well-drained, coarse loams derived primarily from andesite (Patching 1987) thus the HJA study site has drier soil conditions than the CH study site (D.E. Hibbs, unpublished data). The Delezene Creek (DC) study site is located in the *Tsuga heterophylla* vegetation zone (Franklin & Dyrness 1973) in the Washington southwestern Coast Range. Similar to the other study sites, this region is characterized by a wet, mild, maritime climate with an average annual minimum temperature of 1°C and an average annual maximum temperature of 21.5°C (WRCC 2001). Annual precipitation averages

250 cm and occurs primarily during the winter. Elevations at the DC study site range from 60 to 130 m above sea level and soils are deep, well-drained, fine loams derived from sandstone parent material (Pringle 1986).

Experimental design

The experimental design of the CH and HJA study sites is a replacement series consisting of six proportions of red alder and Douglas-fir replicated three times at each site in a randomized, complete block design (Fuentes-Rodríquez 1994). These sites were prepared for planting by clearcutting and slash burning in 1984 and each site was planted in 1986 with 2-year old red alder and 1-year old Douglas-fir seedlings at 3 x 3 m spacing. Each plot consists of a 15 x 15 m measurement plot (5 x 5 seedlings) surrounded by two rows of buffer trees (Fuentes-Rodríquez 1994). On a subset of the mixed species plots, planting of red alder was delayed until the fifth year. Random mortality has resulted in a range of spatial conditions now existing in these plots. The stand at the DC site is a naturally regenerated, even-aged mixture of red alder and Douglas-fir that was inventoried repeatedly by forest mensuration classes at the University of Washington from 1952-1978 and also in 1990 by D.E. Hibbs and K.J. Puettmann. A complete stem map of the study area was created in 1959. At the time of initial measurement in 1952 the stand was 30 years old.

Field sampling

For the replacement series sites, trees were measured in 15 x 15 m plots, with the CH and HJA sites contributing 36 and 30 plots, respectively. Species, diameter at breast height (dbh), total tree height, height to base of live crown, and crown diameter (average of 2 perpendicular crown diameter measurements) were recorded for each tree from 1991-1993 and also in the years 1995, 1998, and 2001. Locations of trees were mapped in the summer of 2001 and converted to metric coordinates. Stump location and breast height location of each stem were recorded for multiple stemmed individuals occurring in the plots. Only single stemmed trees were used as focal individuals, but a single dbh was estimated for multiple stemmed individuals by summing the basal areas at breast height of each stem and deriving the dbh represented by the basal area total. In the analyses, all multiple stemmed individuals were considered as neighbors. The stand was at age 15 at the time of last measurement.

For the DC site, species and dbh were recorded for each tree in 1952, 1957, 1961, 1965, 1969, 1975, 1978, and 1990. Height measurements were taken from a subset of trees that were representative of the range of tree sizes for Douglas-fir and red alder in the stand at each time of measurement. Missing heights were estimated using ratio estimation (Som 1996). The stand was harvested after the final measurement in 1990.

Interference indices (*II*)

For each site and measurement period, individual tree and population-level measurements were utilized to calculate intra- and inter-specific interference indices (*II*) for each tree. These indices are designed to represent various aspects of the nature and degree of interaction between trees. The set of indices listed in Table 2.1 was selected based on their successful performance in previous studies examining competitive interactions in forest stands. These indices represent a range of complexity (distance independent and dependent, relative diameter or crown sizes of neighboring trees, etc.) and individual tree measurements. Each index was modified to accommodate two-species mixtures allowing for separation of the relative intensity and importance of intra- and inter-specific interactions on individual tree growth.

Several forms of *II* were included to investigate various approaches related to characterizing the nature of interference between trees. These approaches included (i) quantifying the degree of interference a focal tree experienced based solely on the number, size, and proximity of neighboring trees, (ii) estimating the degree of interference for resources occurring due to overlap between the crown and root systems of adjacent trees, (iii) utilizing size of an individual tree relative to the population as a determinant of growth, and (iv) utilizing the size of an individual tree relative to the population and the density of individuals larger in the population as a determinant of growth.

Table 2.1 Neighborhood (N) and population-level (P) interference indices (*II*) used to characterize interference in this study. Each *II* has been modified from the original source to separate intra- and inter-specific interference.

Source	Symbol	Interference Index (*II*)	Type
Hegyi (1974)	H	$II_{i1} = \sum_{j=1}^{n} \left[\left(\frac{(D_{j1} / D_{i1})}{L_{i1j1}} \right) + a\left(\frac{D_{j2} / D_{i1}}{L_{i1j2}} \right) \right]$	N
Lorimer (1983)	L	$II_{i1} = \sum_{j=1}^{n} \left[\left(\frac{D_{j1}}{D_{i1}} \right) + a\left(\frac{D_{j2}}{D_{i1}} \right) \right]$	N
Biging & Dobbertin (1992)	B	$II_{i1} = \sum_{j=1}^{n} \left(\frac{CV_{j1} / CV_{i1}}{L_{i1j1}} \right) + a\left(\frac{CV_{j2} / CV_{i1}}{L_{i1j2}} \right)$	N
Richardson *et al.* (1999)	R	$II_{i1} = \left(\frac{1}{H_{i1}^{2}} \frac{1}{n_1} \sum_{j=1}^{n} (H_{j1})^2 (Af_{j1}) \right) + a\left(\frac{1}{H_{i1}^{2}} \frac{1}{n_2} \sum_{j=1}^{n} (H_{j2})^2 (Af_{j2}) \right)$	N
Bella (1971)	BE	$II_{i1} = \sum_{j=1}^{n} \left[\left(\frac{O_{i1j1}}{AI_{i1}} \right) \left(\frac{D_{j1}}{D_{i1}} \right)^{ex} + a\left(\frac{O_{i1j2}}{AI_{i1}} \right) \left(\frac{D_{j2}}{D_{i1}} \right)^{ex} \right]$	N
Glover & Hool (1979)	G	$II_{i1} = \frac{\left(\left(\frac{B_{i1}}{\overline{B}_1} \right) + a\left(\frac{B_{i1}}{\overline{B}_2} \right) \right)}{2}$	P
Wykoff *et al.* (1982)	W	$II_{i1} = \left(\sum_{j=1}^{n} (D_{jA}{*})^2 \, 0.00007854 \right) + a\left(\sum_{j=1}^{n} (D_{jB}{*})^2 \, 0.00007854 \right)$	P

Table 2.1 (continued)
II_i = interference index for focal tree i
D_i = dbh of focal tree i
D_j = dbh of neighbor tree j
L_{ij} = distance between neighbor j and focal tree i
O_{ij} = area of influence overlap between focal tree i and neighbor j
AI_i = area of influence of focal tree i,
D_j* = dbh of trees larger than focal tree i
CV_i = crown volume of focal tree i
CV_j = crown volume of neighbor tree j
H_i = height of focal tree i
H_j = height of neighbor tree j
n = total number of neighbors
B_i = basal area of focal tree i
$\overline{B}$ = basal area of tree with mean dbh within a stand
Af_j = arc fraction of neighbor *j's* crown, defined as: $Af_j = \left[2 \times \tan^{-1}(R_j / L_{ij}) / 360\right]$
R_j = crown radius neighbor j
a = parameter fit via regression
1, 2 = species
ex = scaling exponent

The first approach was to quantify the degree of interference a focal tree experienced based solely on the number, size, and proximity of neighboring trees. To investigate this approach, several neighborhood *II* were employed (see **L**, **H**, **B**, and **R** in Table 2.1). Each of these indices assumes that the effect of a neighbor tree on the resources available to a focal tree is proportional to its size relative to a focal tree. For all of the indices, except **L**, this effect on resources decreases with distance from the focal tree. Different measures of tree size were used in each of these indices to characterize the nature of interference for resources. **L** and **H** used stem diameter as a surrogate measure of the capacity of an individual tree to utilize resources (Table 2.1). Crown volume was used in index **B** to represent the capacity of an individual tree to absorb photosynthetically active radiation (PAR) (Wang & Jarvis 1990) (Table 2.1). In addition to investigating the influence of neighbor size and proximity on interference, the importance of crown position and stature were investigated utilizing height and crown arc fraction measurements (see **R** in Table 2.1).

The second approach quantified the degree of interference for resources occurring due to overlap between the crown and root systems of adjacent trees. To investigate this approach, an area of influence (AI) neighborhood *II* was utilized (see **BE** in Table 2.1). Each tree was assumed to have a circular area of influence that represented all of the potential resources available to it (Bella 1971). For this study, a focal tree's AI was constructed utilizing crown diameter measurements. In contrast to the other neighborhood *II,* the **BE** index defines the influence of a neighboring tree as a function of the degree of overlap between it and the focal tree's areas of influence. This area of overlap is assumed to represent the degree of interference occurring between interacting individuals for aboveground and belowground resources (Bella 1971). In addition to utilizing this measure of overlap, the **BE** index also utilizes the ratio of diameters between neighboring trees to represent asymmetrical interference. Bella (1971) incorporated a scaling exponent to this term to express the degree to which resources were shared disproportionately (i.e., asymmetrically). Based on the findings of past research (e.g., Bella 1971; Holmes & Reed 1989; Biging & Dobbertin 1992), **BE** indices with scaling exponents set at 1, 1.5, and 2 were used.

The final approaches utilized the size of a focal tree relative to the population as a determinant of growth. To investigate this relationship, two population-level *II* were utilized. Glover & Hool's (1979) (**G** in Table 2.1) utilizes the diameter of the focal tree relative to the mean diameter in the population thus ranking the size of the focal tree in the population relative to the population mean. In contrast to the other *II*, this index assumes that the growth of a focal tree is strictly a function of its relative size and does not incorporate a measure of density. The second population-level index, **W**, developed by Wykoff *et al.* (1982) assumes one-sided competition, i.e., only trees in the population larger than the focal tree have an influence on resource availability. For the calculation of this index, only trees with basal areas larger than the focal tree were utilized.

Because of lack of other measurements, only indices utilizing dbh (to characterize tree size) and inter-tree distances were calculated for the DC study site (**H**, **L**, **G**, and **W** in Table 2.1). To avoid plot edge biases, only trees occurring at least 3 meters from the measurement plot border at the CH and HJA sites and at least 9 meters from the study site border at the DC site were selected for evaluation.

A set of fixed search radii were used to determine neighboring trees for inclusion in the calculation of neighborhood indices, with the exception of the **BE** index, which utilized the area of overlap. For the CH and HJA sites, the maximum radius was restricted to 4.5 m to avoid extending beyond the plot borders. The central tree of each plot was the exception to this restriction with search radii set at 3, 4.5, 6, and 7.5 m, respectively. Search radii set at 3, 4.5, 6, 7.5, 9, and 11.5 m were utilized to calculate the neighborhood indices for the DC study site.

Analysis

The relative diameter growth rate was selected as a surrogate measure of fitness and was calculated for each measurement period as:

$$RGR_i = \frac{D_i - D_0}{D_0} \qquad \text{eqn 1}$$

where RGR_i is the relative diameter growth during the measurement period i, D_i is the diameter at the end of the measurement period, and D_0 is the diameter at the beginning of the measurement period. This measure was chosen to account for differences in initial size among trees at the beginning of a measurement period thus allowing for a more accurate assessment of the relative importance and intensity of interference interactions at different stages of development (Ford & Sorrensen 1992).

A growth model, which incorporated intra- and inter-specific interference, was developed to evaluate the intensity and importance of interference over each measurement period. The main growth model used was:

$$RGR_i = \beta_0 + \beta_{aa} \cdot \ln(II_{aa}) + \beta_{ab} \cdot \ln(II_{ab}) + \beta_{aa \cdot ab} \cdot \ln(II_{aa} \cdot II_{ab}) + \varepsilon \qquad \text{eqn 2}$$

where II_{aa} and II_{ab} are the intra- and inter-specific II at the beginning of the growth interval, $II_{aa} \cdot II_{ab}$ is the intra- X inter-specific II interaction, and ε is the error term. In addition to the full model (Equation 2), models only incorporating intra- or inter-specific interference were evaluated for each growth interval and II using mixed linear regression analyses performed in SAS (PROC MIXED; SAS Institute, Inc. 1999). For the majority of models, non-linearity and non-homogeneous variance was corrected by logarithmic transformation of independent variables. Spatial correlation between trees in each plot was accounted for by including a power spatial correlation structure in each of the models (SP(POW); SAS Institute, Inc. 1999). This structure utilized the x-, y-coordinates of each tree to account for the covariance between trees due to spatial location. For the CH and HJA study sites, random plot effects were also incorporated into the models to account for variation in growing conditions across plots.

The corrected Akaike Information Criterion, AIC_c, was used to determine the best II's and neighborhood sizes for each measurement period and to test the relative fit of each model (Burnham & Anderson 1998). $\mathrm{AIC_c}$ is derived from the maximum log-likelihood estimate and number of parameters in a given model, rewarding models for goodness of fit, but imposing a penalty for multiple parameters. Smaller $\mathrm{AIC_c}$ values indicate better models and $\mathrm{AIC_c}$ values are ranked according to the difference between the $\mathrm{AIC_c}$ value for a given model and the lowest $\mathrm{AIC_c}$ value in a given set of models using the formula:

$$\Delta_i = AIC_{ci} - AIC_{c\min} \qquad \text{eqn 3}$$

where AIC_{ci} is the value for the model i, $AIC_{c\min}$ is the smallest value in the given set of models, and Δ_i is the departure of model i from the model with lowest AIC_c value in the given set. The value, Δ_i, allows a strength of evidence comparison among the models, where increasing Δ_i values correspond with decreasing probability of the fitted model being the best approximating model in the set (Anderson *et al.* 2000). As a rule of thumb, models with a $\Delta_i \leq 2$ have considerable support and should be considered when making inferences about the data (Burnham and Anderson 2001). Models with $\Delta_i > 2$ and ≤ 10 have less support, and those with $\Delta_i \geq 10$ have very little or no support. For this study, only models with a $\Delta_i \leq 2$ are reported.

To approximate the probability of a model being the 'best' in a given set, the Δ_i values were used to calculate Akaike weights (w_i) with the following formula (Burnham and Anderson1998):

$$w_i = \frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^{R} \exp(-\Delta_r / 2)} \qquad \text{eqn 4}$$

where w_i is the Akaike weight for model i and R is the number of models in the set. The ratio of weights (Rw) between competing models was used to provide a measure of the relative strength of evidence for the best model in a given set. This ratio represents the relative likelihood of a model being the best model in a given set as compared to other alternative models (Anderson *et al.* 2000) and was calculated using the formula:

$$R_w = \frac{w}{w_j} \qquad \text{eqn 5}$$

where w is the Akaike weight for the model with the lowest AIC_c value in the set and w_j is the Akaike weight for another given model in the set.

To account for model selection uncertainty, parameters in models containing the same variables as those in the best model were averaged using the model averaging method developed by Buckland *et al.* (1997). An advantage of this method is the ability to make inferences based on the entire set of models, rather than solely on the selected best model (Buckland *et al.* 1997). An additional advantage of this method is the ability to derive more precise, less biased estimates of the parameters in the best model (Burnham & Anderson 1998, 2001).

Model-averaged parameter estimators were calculated using the formula:

$$\hat{\theta}_a = \sum_{i=1}^{R} w_i \hat{\theta}_i \qquad \text{eqn 6}$$

where $\hat{\theta}_a$ is the average of the parameter maximum likelihood estimator, $\hat{\theta}$, w_i is the Akaike weight for model *i* containing the parameter $\hat{\theta}$, and $\hat{\theta}_i$ is the parameter estimate for θ in model *i.* In addition to estimating model-averaged parameters, unconditional estimates of variance ($\hat{\text{var}}(\hat{\theta})$) for the model-averaged parameters from the best model were calculated using the following formula from Buckland *et al.* (1997):

$$\hat{\text{var}}(\hat{\theta}) = \left[\sum_{i=1}^{R} w_i \sqrt{\text{var}\left\langle \hat{\theta}_i \middle| g_i \right\rangle + \left\langle \hat{\theta}_i - \hat{\theta}_a \right\rangle^2} \right]^2 \qquad \text{eqn 7}$$

where $\text{var}\left\langle \hat{\theta}_i \middle| g_i \right\rangle$ is the conditional sampling variance given model *i.* The 95% confidence intervals were calculated for each model-averaged parameter using the unconditional estimates of variance.

A null model was included in each set of candidate models to determine the importance of interference on relative growth rates over the measurement period. The null model stated that the relative growth rate over a given measurement period was solely a function of the spatial correlation among trees in a given population. If models incorporating the measures of interference were ranked higher than the null model, it can be assumed that interference was more important than other unmeasured factors (Anderson *et al.* 2001) such as genetic variation and environmental heterogeneity, which may also affect relative diameter growth rates (Welden & Slauson 1986).

After the 'best' models for each measurement period were determined, the corresponding averaged parameter estimates for these models were evaluated to approximate the relative intensity of intra- and inter-specific interference (Welden & Slauson 1986). Two lines of evidence were used to determine if there was a difference between the intensity of intra- and inter-specific interference: (i) the selected best models (i.e., $\Delta_i \leq 2$) contained the interaction between intra- and inter-specific interference or (ii) the selected best models contained exclusively intra- or inter-specific interference parameters. If the best models for the CH and HJA sites contained a neighborhood *II*, an additional evaluation of appropriate neighborhood size was done for the central tree in each plot to determine the accuracy lost because of the restrictions placed on search radii for these sites.

RESULTS

The number and mean dbh of red alder and Douglas-fir in the young (CH and HJA) and mature (DC) stands for all measurements are shown in Table 2.2. In general, red alder in the young stands had larger heights as compared to the Douglas-fir, whereas Douglas-fir had larger heights in the mature stand (Fig. 2.1). Diameter at breast height followed a similar pattern (Table 2.2). Very little mortality occurred in the young stands (Table 2.2). In contrast, roughly 30 percent of the red alder and

Table 2.2 Mean diameter at breast height (dbh) and number of trees (N) of red alder and Douglas-fir at the CH, HJA, and DC study sites. Standard errors in parentheses.

		Red alder		Douglas-fir	
Site	Age	N	dbh (cm)	N	dbh (cm)
CH	6	85	10.0 (0.47)	142	2.1 (0.08)
	9	85	14.5 (0.51)	142	6.7 (0.16)
	12	85	17.8 (0.56)	142	11.2 (0.29)
	15	84	18.9 (0.50)	137	15.1 (0.48)
HJA	6	51	2.3 (0.27)	63	1.6 (0.14)
	9	51	7.5 (0.50)	63	4.5 (0.20)
	12	51	12.0 (0.58)	63	8.8 (0.30)
	15	50	13.1 (0.50)	60	13.1 (0.43)
DC	30	143	21.5 (0.57)	106	22.9 (0.93)
	35	143	22.5 (0.60)	106	25.5 (1.03)
	39	141	23.1 (0.63)	105	27.0 (1.14)
	43	134	24.5 (0.64)	98	31.2 (1.34)
	47	129	25.3 (0.66)	96	35.1 (1.48)
	53	118	27.8 (0.70)	89	38.0 (1.67)
	56	113	30.3 (0.70)	89	40.3 (1.81)
	68	101	32.8 (0.83)	81	44.9 (2.30)

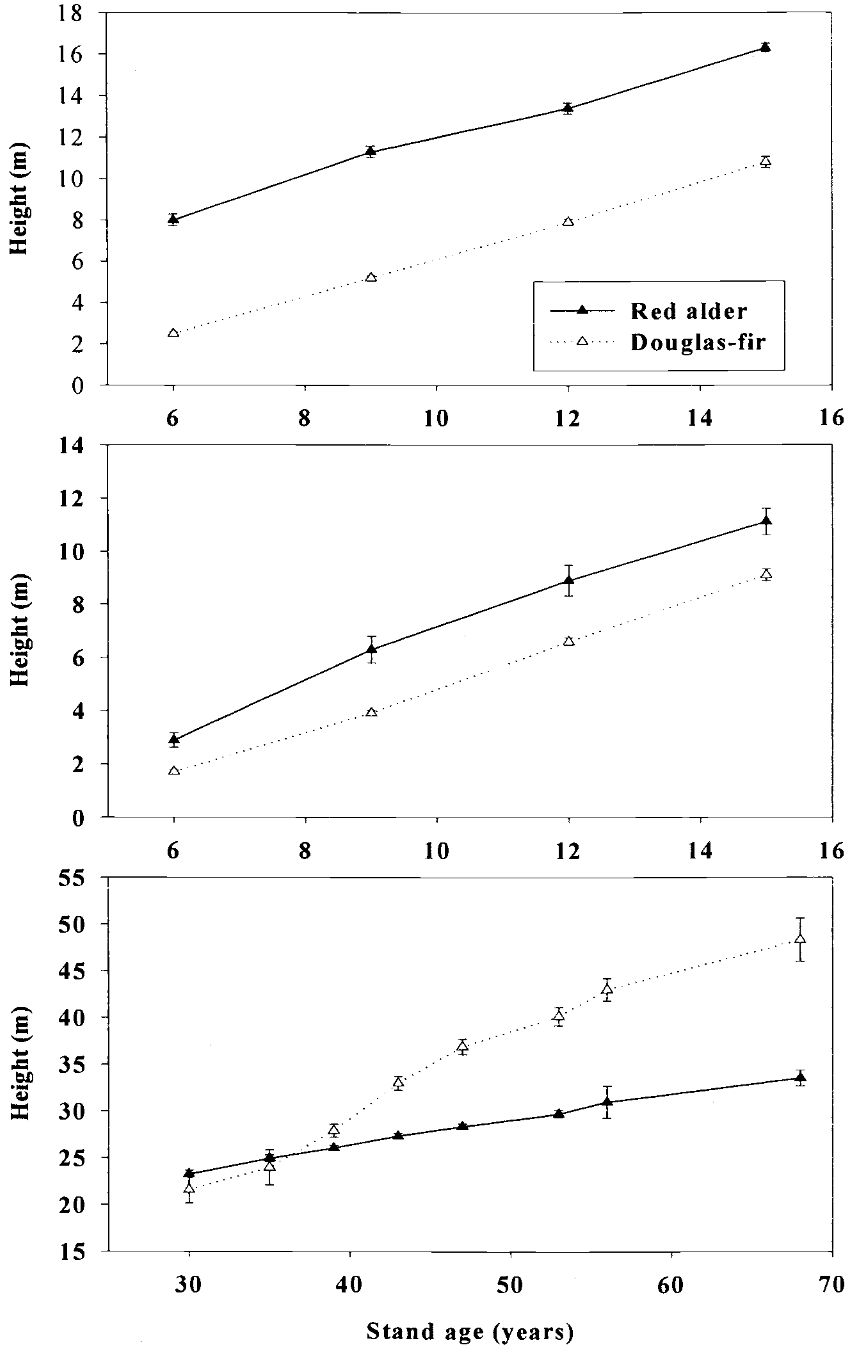

Fig. 2.1 Mean height of red alder and Douglas-fir over time at the (a) CH, (b) HJA, and (c) DC study sites.

22 percent of the Douglas-fir died in the mature stand from stand age 30 to 68 (Table 2.2).

Analysis of interference

Interference and the other factors represented in the growth models (i.e., relative size) were more important to the relative growth rates of red alder and Douglas-fir in the young and mature stands than unmeasured factors, as was the null models had Δ_i values greater than 4.0 for both species in all measurement periods. In addition, the poor performance of the null models (i.e., $\Delta_i > 4.0$) indicates that the set of *II* utilized in this study contained interference measures appropriate for characterizing the factors influencing relative growth rates in young and mature mixed red alder/Douglas-fir stands.

Specific spatial information, i.e., neighbor tree distances, was not beneficial for characterizing the nature of interference in these stands. With few exceptions, models employing a neighborhood *II* that did not weight neighbor tree influence by proximity (**L**, **BE** in Table 2.1) and/or models utilizing a population-level *II* (**G** and **W** in Table 2.1) had stronger evidence of being the best model in the set (i.e., $\Delta_i <$ 2) as compared to models utilizing *II* weighting neighbor influence by distance (**H**, **B**, and **R** in Table 2.1). However, in the young stands several of the best models for both species utilized the AI neighborhood *II* (**BE**) (Tables 2.3 and 2.4). Additional weighting of **BE** for asymmetrical interference was unnecessary as there was no distinguishable difference between the fit of models with the three different

Table 2.3 Parameters, 95% confidence intervals (in parentheses), and AIC model comparisons of selected best models (i.e., $\Delta_i \leq 2.00$) for quantifying the effects of intra- and inter-specific interference on Douglas-fir relative growth rates over the measurement periods examined (years 6-9, 9-12, and 12-15) in the young stands (CH and HJA).

				Model parameters[c]							
Site	Y[a]	*II*[b]	Radius	B_o	B_{aa}	B_{ab}	B_{aa*ab}	K[d]	Δ_i[e]	w_i[f]	Rw[g]
CH	6-9	**G**	-	0.95	-0.36	0.015	0.011	7	0.00	0.651	1.00
				(0.91, 0.99)	(-0.40, -0.32)	(0.014, 0.016)	(-0.043, 0.065)				
		G	-	0.95	-0.36	-	-	5	1.24	0.350	1.86
				(0.91, 0.99)	(-0.40, -0.32)						
	9-12	**BE 1**[*]	AI	0.77	-	-0.12	-	5	0.00	0.194	1.00
				(0.71, 0.83)		(-0.015, -0.086)					
		BE 1.5	AI	0.77	-	-0.011	-	5	0.18	0.177	1.10
				(0.71, 0.83)		(-0.014, -0.085)					
		BE 2	AI	0.77	-	-0.010	-	5	0.74	0.134	1.45
				(0.71, 0.83)		(-0.013, -0.079)					
	12-15	**R**	4.5	0.25	0.081	-	-	5	0.00	0.226	1.00
				(0.16, 0.34)	(0.018, 0.14)						
HJA	6-9	**G**	-	1.08	-0.79	-1.11	0.67	7	0.00	0.99	1.00
				(0.95, 1.20)	(-0.94, -0.64)	(-1.36, -0.86)	(0.11, 1.23)				
	9-12	**L**	3.0	0.92	-0.010	-0.22	0.20	7	0.00	0.51	1.00
				(0.64, 1.19)	(-0.20, 0.18)	(-0.23, -0.21)	(0.10, 0.30)				
		L	4.5	0.92	-0.008	-0.26	0.21	7	0.38	0.42	1.21
				(0.64, 1.19)	(-0.20, 0.19)	(-0.27, -0.24)	(0.31, 0.11)				
	12-15	**BE 2**	AI	0.45	0.014	-0.16	0.074	7	0.00	0.177	1.00
				(0.36, 0.53)	(-0.025, 0.054)	(-0.23, -0.085)	(0.044, 0.10)				
		BE 1.5	AI	0.45	0.016	-0.16	0.082	7	0.17	0.162	1.09
				(0.36, 0.53)	(-0.026, 0.059)	(-0.24, -0.083)	(0.048, 0.12)				
		BE 1	AI	0.45	0.019	-0.16	0.091	7	0.38	0.146	1.21
				(0.36, 0.53)	(-0.027, 0.065)	(-0.24, -0.082)	(0.053, 0.13)				
		L	4.5	0.46	0.011	-0.17	0.10	7	0.76	0.121	1.46
				(0.38, 0.53)	(-0.037, 0.060)	(-0.19, -0.14)	(0.059, 0.15)				

Table 2.3 (continued)

[*] Scaling exponent used (1.0, 1.5, 2.0)

[a] Measurement period

[b] Interference index (*II*) used to measure intra- and inter-specific interference (see Table 2.1)

[c] B_o are equation intercepts, B_{aa} and B_{ab} are model-averaged regression coefficients quantifying the effects of intra- and inter-specific interference, respectively, on Douglas-fir relative growth rates, and B_{aa*ab} is the regression coefficient for the effect of the interaction of intra- and inter-specific interference on Douglas-fir relative growth rates.

[d] number of model parameters including the intercept, variance, and covariance parameters

[e] difference between model AIC_c value and minimum AIC_c value

[f] approximate probability that model is best in the set

[g] relative likelihood of model being best in the set

Table 2.4 Parameters, 95% confidence intervals (in parentheses), and AIC model comparisons of selected best models for quantifying the effects of intra- and inter-specific interference on red alder relative growth rates over the measurement periods examined (years 6-9, 9-12, and 12-15) in the young stands (CH and HJA). For definitions of symbols see Table 2.3.

				Model parameters							
Site	Y	*II*	Radius	B_o	B_{aa}	B_{ab}	B_{aa*ab}	K	Δ_i	w_i	R*w*
CH	6-9	**W**	-	0.97	-0.051	-	-	5	0.00	0.295	1.00
				(0.96, 0.98)	(-0.080, -0.022)						
		W	-	0.97	-	0.14	-	5	0.62	0.217	1.36
				(0.96, 0.98)		(0.042, 0.24)					
		W	-	0.97	-0.051	0.14	18.7	7	1.66	0.129	2.29
				(0.96, 0.98)	(-0.080, -0.022)	(0.042, 0.24)	(5.4, 32.0)				
	9-12	**G**	-	0.17	-0.025	0.13	-0.16	7	0.00	0.910	1.00
				(0.091, 0.249)	(-0.081, 0.032)	(0.020, 0.24)	(-0.31, -0.016)				
	12-15	**L**	3.0	0.16	-	0.19	-	5	0.00	0.299	1.00
				(0.11, 0.20)		(0.082, 0.30)					
		BE 1	AI	0.15	-	0.16	-	5	0.93	0.188	1.59
				(0.11, 0.20)		(0.11, 0.21)					
HJA	6-9	**G**	-	0.54	-0.41	-0.16	0.15	7	0.00	0.666	1.00
				(0.45, 0.63)	(-0.54, -0.29)	(-0.29, -0.026)	(0.091, 0.29)				
	9-12	**W**	-	0.16	0.80	-	-	5	0.00	0.221	1.00
				(0.10, 0.22)	(0.21, 1.39)						
		W	-	0.16	0.80	-1.60	0.82	7	0.39	0.181	1.22
				(0.10, 0.22)	(0.21, 1.39)	(-0.03, -3.17)	(0.12, 1.52)				
	12-15	**L**	3.0	0.23	-0.021	-0.47	0.30	7	0.00	0.180	1.00
				(0.14, 0.32)	(-0.10, 0.058)	(-0.76, -0.18)	(-0.025, 0.62)				
		L	4.5	0.23	-0.015	-0.38	0.26	7	0.63	0.140	1.29
				(0.14, 0.32)	(-0.10, 0.073)	(-0.55, -0.21)	(-0.051, 0.56)				

scaling exponents. Evaluations of appropriate neighborhood sizes with the central trees at the CH and HJA sites indicated neighborhoods with a 3 m and 4.5 m radius were appropriate in the young stands (Tables 2.5 and 2.6). The range of neighborhood sizes utilized in the mature stand was also appropriate, as the neighborhood *II* included in the set of best models had neighborhood sizes less than the maximum neighborhood size utilized ($\leq$ 11.5 m) (Tables 2.7 and 2.8).

Intra- and inter-specific interference

In general, there was strong evidence for both species that the effects of intra-specific interference were not exclusively additive to the effects of inter-specific interference. With few exceptions, the set of best models for predicting relative growth rates for red alder and Douglas-fir contained a model with the interaction term describing the product of intra- and inter-specific interference (Tables 2.3, 2.4, 2.7, and 2.8). As an illustration, Figure 2.2 demonstrates the consequences of this interaction on the effects of intra- and inter-specific interference on relative growth rates over years 30-35 in the mature stand. Increasing interference from Douglas-fir reduced the effect of interference from red alder on the relative growth rates of Douglas-fir. Similarly, increasing red alder interference reduced the effect of Douglas-fir interference on the relative growth rates of red alder. Interestingly, the effects of Douglas-fir interference on red alder relative growth rates shifted from a negative slope at low levels of red alder interference to a positive slope at the highest level of red alder interference.

Table 2.5 Evaluations of appropriate neighborhood sizes with red alder occurring in the plot centers at the CH and HJA sites. For definitions of symbols see Table 2.3.

Site	Y	*II*	Radius	K	Δ_i	w_i	Rw
CH	12-15	**L**	3.0	5	0.00	0.490	1.00
			4.5	5	1.45	0.237	2.07
			6.0	5	2.16	0.167	2.95
			7.5	5	3.05	0.106	4.62
HJA	12-15	**L**	4.5	5	0.00	0.540	1.00
			3.0	5	1.99	0.200	2.70
			6.0	5	2.66	0.142	3.80
			7.5	5	3.04	0.118	4.58

Table 2.6 Evaluations of appropriate neighborhood sizes with Douglas-fir occurring in the plot centers at the CH and HJA sites. For definitions of symbols see Table 2.3.

Site	Y	*II*	Radius	K	Δ_i	w_i	Rw
CH	12-15	**R**	4.5	5	0.00	0.429	1.00
			3.0	5	0.97	0.264	1.63
			6.0	5	1.17	0.239	1.80
			7.5	5	3.69	0.068	6.32
HJA	9-12	**L**	3.0	5	0.00	0.998	1.00
			4.5	5	13.1	0.001	688.28
			6.0	5	15.4	0.000	2217.78
			7.5	5	18.4	0.000	8316.67
HJA	12-15	**L**	3.0	5	0.00	0.326	1.00
			4.5	5	0.00	0.326	1.00
			6.0	5	0.70	0.229	1.42
			7.5	5	2.00	0.120	2.72

Table 2.7 Parameters, 95% confidence intervals (in parentheses), and AIC model comparisons of selected best models for quantifying the effects of intra- and inter-specific interference on Douglas-fir relative growth rates over the measurement periods (years 30-35, 35-39, 39-43, 43-47, 47-53, 53-56, and 56-68) examined in the mature stand (DC). For definitions of symbols see Table 2.3.

			Model parameters							
Y	*II*	Radius	B_o	B_{aa}	B_{ab}	B_{aa*ab}	K	Δ_i	w_i	R*w*
30-35	**H**	4.5	0.12	-0.0022	-0.011	0.0044	6	0.00	0.304	1.00
			(0.11, 0.13)	(-0.0074, 0.0030)	(-0.012, -0.010)	(-0.021, 0.029)				
	G	-	0.090	-1.00	0.98	-0.023	6	0.28	0.264	1.15
			(0.054, 0.12)	(-1.20, -0.80)	(0.95, 1.01)	(-0.021, -0.025)				
	H	3.0	0.12	-0.0010	-0.011	0.025	6	0.88	0.196	1.55
			(0.11, 0.13)	(-0.0058, 0.0042)	(-0.012, -0.010)	(0.0091, 0.041)				
35-39	**L**	9.0	0.21	-0.064	-0.063	0.023	6	0.00	0.864	1.00
			(0.16, 0.26)	(-0.086, -0.043)	(-0.075, -0.052)	(0.012, 0.034)				
39-43	**L**	9.0	0.12	-0.031	-	-	4	0.00	0.260	1.00
			(0.092, 0.14)	(-0.046, -0.015)						
	L	9.0	0.12	-0.031	-0.018	0.0062	6	0.15	0.241	1.08
			(0.092, 0.014)	(-0.046, -0.015)	(-0.025, -0.011)	(-0.0077, 0.020)				
43-47	**G**	-	0.040	3.23	-2.51	-1.92	6	0.00	0.644	1.00
			(0.016, 0.063)	(1.56, 4.90)	(-2.55, -2.47)	(-2.87, -0.97)				
47-53	**W**	-	0.093	-	-0.0037	-	4	0.00	0.387	1.00
			(0.082, 0.10)		(-0.0049, -0.0026)					
	W	-	0.093	0.0025	-0.0037	0.0013	6	0.36	0.322	1.20
			(0.082, 0.10)	(-0.0047, 0.0051)	(-0.0049, -0.0026)	(0.00023, 0.0023)				
	G	-	0.037	3.10	-2.19	-0.22	6	0.59	0.288	1.34
			(0.0094, 0.065)	(1.28, 4.74)	(-2.23, -2.15)	(-0.34, -0.10)				
53-56	**W**	-	0.051	-	-0.0020	-	4	0.00	0.517	1.00
			(0.045, 0.058)		(-0.0027, -0.0012)					
56-68	**W**	-	0.15	-	-0.0064	-	4	0.00	0.691	1.00
			(0.13, 0.16)		(-0.00824, -0.0046)					

Table 2.8 Parameters, 95% confidence intervals (in parentheses), and AIC model comparisons of selected best models for quantifying the effects of intra- and inter-specific interference on red alder relative growth rates over the measurement periods (years 30-35, 35-39, 39-43, 43-47, 47-53, 53-56, and 56-68) examined in the mature stand (DC). For definitions of symbols see Table 2.3.

			Model parameters							
Y	*II*	Radius	B_o	B_{aa}	B_{ab}	B_{aa*ab}	K	Δ_i	w_i	R*w*
30-35	**L**	7.5	0.059	-0.0058	-	-	4	0.00	0.171	1.00
			(0.052, 0.065)	(-0.0078, -0.0038)						
	L	6.0	0.059	-0.0060	-	-	4	0.03	0.168	1.02
			(0.052, 0.065)	(-0.0068, -0.0052)						
	L	4.5	0.059	-0.0062	-	-	4	0.09	0.163	1.05
			(0.052, 0.065)	(-0.0076, -0.0048)						
	L	3.0	0.059	-0.0071	-	-	4	0.12	0.161	1.06
			(0.052, 0.065)	(-0.0075, -0.0067)						
	L	7.5	0.059	-0.0058	0.0035	-0.0023	6	1.50	0.081	2.12
			(0.052, 0.065)	(-0.0078, -0.0038)	(-0.0030, 0.010)	(-0.0053, 0.0010)				
35-39	**L**	6.0	0.050	-0.014	-0.013	0.0057	6	0.00	0.714	1.00
			(0.040, 0.061)	(-0.016, -0.012)	(-0.021, -0.0040)	(0.0009, 0.011)				
39-43	**L**	3.0	0.024	-0.0051	-	-	4	0.00	0.137	1.00
			(0.020, 0.028)	(-0.0057, -0.0045)						
	L	6.0	0.024	-0.0043			4	0.57	0.103	1.33
			(0.020, 0.028)	(-0.0051, -0.0035)						
	L	9.0	0.024	-0.0030	0.0016	-0.0019	6	0.80	0.092	1.49
			(0.020, 0.028)	(-0.0054, -0.0010)	(-0.0019, 0.051)	(-0.0057, 0.0019)				
	L	7.5	0.024	-0.0041	-	-	4	0.96	0.085	1.61
			(0.020, 0.028)	(-0.0047, -0.0035)						
	L	9.0	0.024	-0.0030	-	-	4	1.09	0.080	1.72
			(0.020, 0.028)	(-0.0054, -0.0010)						
	L	7.5	0.024	-0.0041	-0.0004	-0.0012	6	1.41	0.068	2.02
			(0.020, 0.028)	(-0.0047, -0.0035)	(-0.0081, 0.0071)	(-0.0050, 0.0026)				
43-47	**L**	4.5	0.022	-0.0053	-0.0029	-0.0022	6	0.00	0.289	1.00
			(0.017, 0.027)	(-0.0059, -0.0047)	(-0.0042, -0.0016)	(-0.0080, 0.0036)				

Table 2.8 (continued)

			Model parameters							
Y	*II*	Radius	B_o	B_{aa}	B_{ab}	B_{aa*ab}	K	Δ_i	w_i	Rw
43-47	L	6.0	0.022	-0.0058	-0.0049	0.0010	6	0.97	0.179	1.62
			(0.017, 0.027)	(-0.0072, -0.0044)	(-0.012, 0.0018)	(-0.0037, 0.0051)				
	L	4.5	0.022	-0.0053	-	-	4	1.94	0.179	1.62
			(0.017, 0.027)	(-0.0059, -0.0047)						
47-53	L	6.0	0.016	-0.0033	-	-	4	0.00	0.134	1.00
			(0.011, 0.021)	(-0.0037, -0.0029)						
	L	7.5	0.016	-0.0032	-	-	4	0.09	0.128	1.05
			(0.011, 0.021)	(-0.0048, -0.0016)						
	L	9.0	0.016	-0.0030	-	-	4	1.71	0.057	2.36
			(0.011, 0.021)	(-0.0054, -0.0010)						
53-56	L	7.5	0.0020	-	-0.00065	-	4	0.00	0.121	1.00
			(0.0014, 0.0027)		(-0.0012, -0.00010)					
	L	6.0	0.0020	-	-0.00071	-	4	0.82	0.080	1.51
			(0.0014, 0.0027)		(-0.0013, -0.00013)					
	L	4.5	0.0020	-	-0.00080	-	4	1.25	0.065	1.87
			(0.0014, 0.0027)		(-0.0014, -0.00021)					
	L	9.0	0.0020	-	-0.00040	-	4	1.80	0.049	2.46
			(0.0014, 0.0027)		(-0.0010, -0.00020)					
	L	4.5	0.0020	-0.0010	-	-	4	1.99	0.045	2.71
			(0.0014, 0.0027)	(-0.0014, -0.00065)						
56-68	L	11.5	0.032	-	-0.014	-	4	0.00	0.294	1.00
			(0.025, 0.039)		(-0.018, -0.010)					
	L	11.5	0.032	-0.013	-0.014	0.0078	6	0.36	0.246	1.20
			(0.025, 0.039)	(-0.016, -0.010)	(-0.018, -0.010)	(0.00, 0.016)				

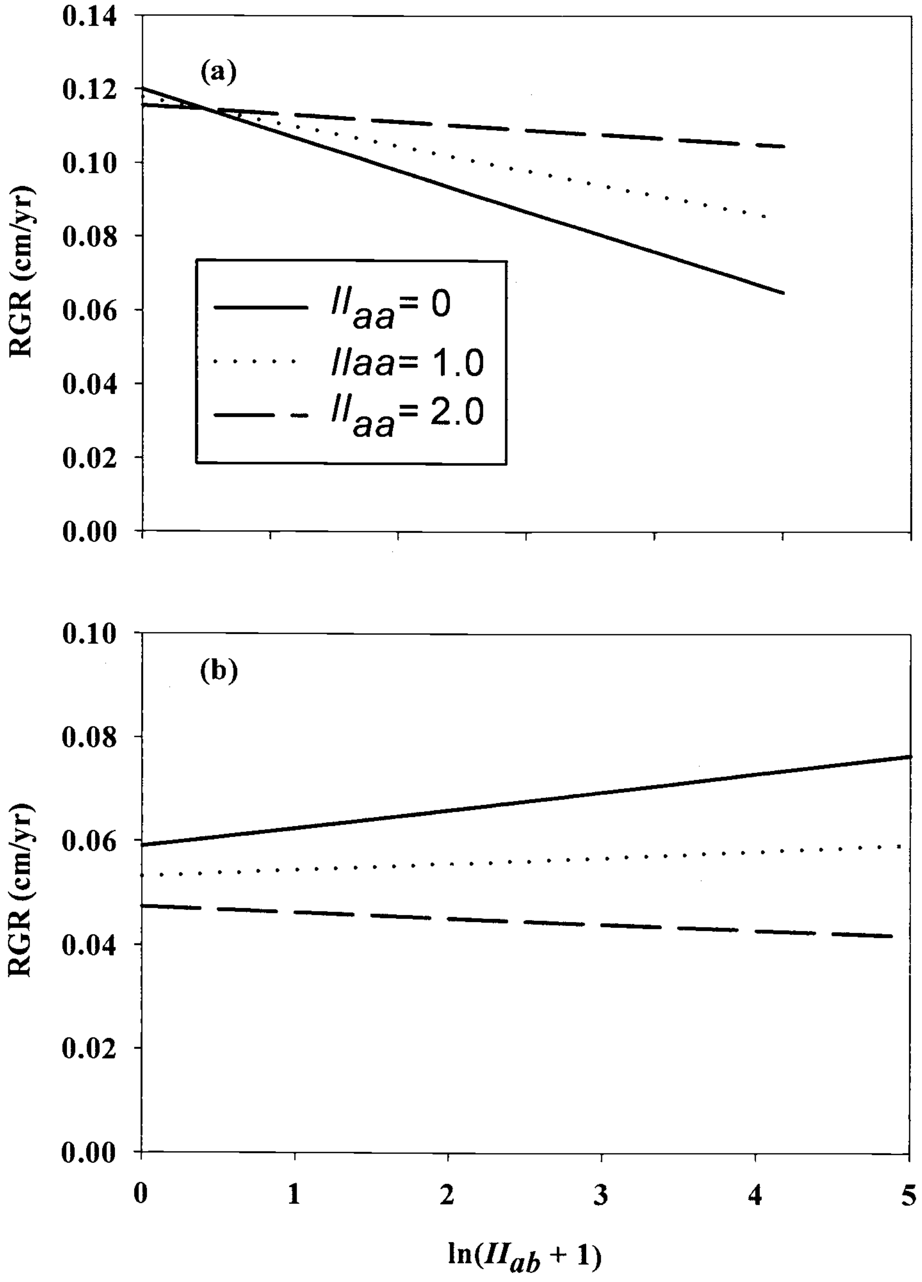

Fig. 2.2 The influence of intra-specific interference (II_{aa}) on the effects of inter-specific interference (II_{ab}) on relative growth rate over years 30-35 at the DC site for (a) Douglas-fir and (b) red alder. II_{aa} and II_{ab} were measured with (a) neighborhood *II* **H** and a neighborhood radius of 4.5 m and (b) neighborhood *II* **L** and a neighborhood radius of 7.5 m (see Table 2.1).

In addition to the selection of models containing the interaction term, other evidence suggested that the effects of intra-specific interference were not exclusively additive to the effects of inter-specific interference. In several cases in the young stands, intra-specific interference had a positive effect on Douglas-fir relative growth rates (Table 2.3). These positive parameter estimates are possibly a function of interference from Douglas-fir being less negative relative to interference from red alder in the young stands, which resulted in individuals with a higher proportion of Douglas-fir in their respective neighborhoods or populations achieving higher relative growth rates. As an illustration, Figure 2.3 demonstrates the relationship between Douglas-fir relative growth rates over years 12-15 at the CH site and neighborhood interference from Douglas-fir (Fig. 2.3a) and red alder (Fig. 2.3b). Increasing interference from Douglas-fir resulted in higher relative growth rates, whereas, increasing interference from red alder depressed Douglas-fir relative growth rates. This relationship was also observed for red alder over this time period as is evident from the positive relationship between neighborhood interference from Douglas-fir and red alder relative growth rates in the best models for years 12-15 at the CH site (Table 2.4).

Due to the non-additive nature of the effects of intra- and inter-specific interference on red alder and Douglas-fir relative growth rates, I was unable to compare the specific intensities of intra- and inter-specific interference. However, the significant interaction between intra- and inter-specific interference in the majority of the selected best models for red alder and Douglas-fir in the young and

Fig. 2.3 Relationships between Douglas-fir relative growth rate (RGR) over years 12-15 at the CH site and (a) intra- and (b) inter-specific interference (II_{aa} and II_{ab}, respectively). (a) II_{aa} was measured with neighborhood *II* **R** and a neighborhood radius of 4.5 m and (b) II_{ab} was measured with neighborhood *II* **B** and a neighborhood radius of 4.5 m (see Table 2.1).

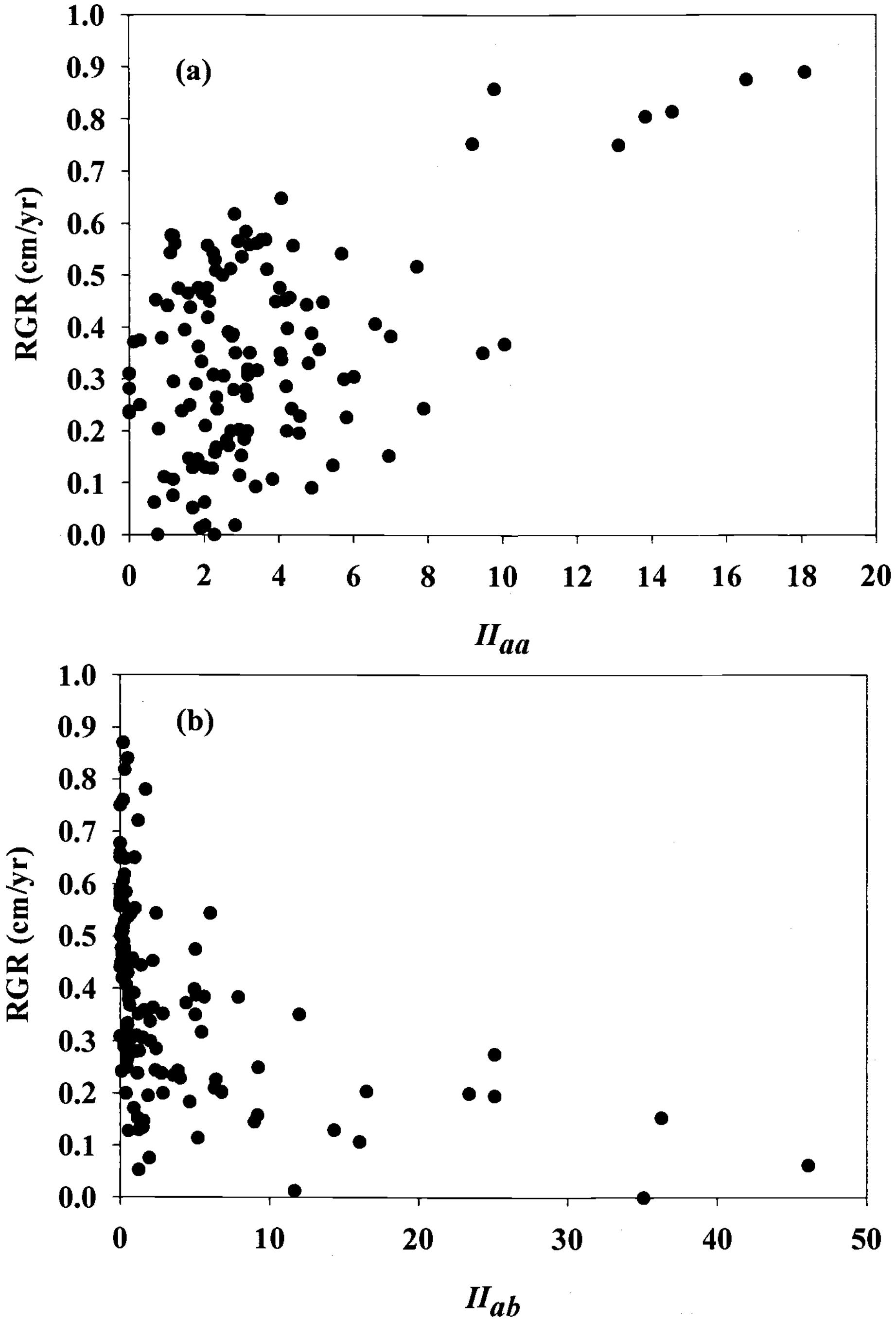

Fig. 2.3 (continued)

mature stands suggests that the intensity of intra- and inter-specific interference differed for both species.

Interference dynamics

Red alder

The importance of size relative to the population and neighborhood interference varied between the young and mature stands. In general, size relative to the population was a better determinant of red alder relative growth rates in the young stands as the majority of best models for predicting red alder relative growth rates used population-level *II* (Table 2.4). It is important to note that the selection of the population-level *II* **W** over the earliest measurement period (years 6-9) at the CH site suggests that population density was also influencing red alder relative growth rates, whereas the selection of the population-level *II* **G** over the same period at the HJA site suggests that solely size relative to the population was determining red alder relative growth rates (Table 2.4). The positive inter-specific interference effects on red alder relative growth rates over years 12-15 at the CH site, as well as and the negative intra- and inter-specific interference effects on red alder relative growth rates over the same period at the HJA site (Table 2.4) suggest that the increased intensity of neighborhood interference from co-dominant red alder at the CH site and co-dominant red alder and Douglas-fir at the HJA site may be correlated with the shift in the nature of interference from the population-level to the neighborhood-level over the final measurement periods in the young stands.

There was strong evidence that neighborhood interference was more important to red alder relative growth rates in the mature stands as all of the best models for predicting red alder relative growth rates used neighborhood *II* (Table 2.8). Similar to the young stands, the importance of neighborhood interference in the mature stand was observed during the periods red alder occupied co-dominant and subordinate canopy positions (Fig. 2.1c).

Douglas-fir

In general, neighborhood interference was more important to Douglas-fir relative growth rates in the young stands as the majority of best models for predicting Douglas-fir relative growth rates used neighborhood *II* (Table 2.3). However, over the earliest measurement period examined (years 6-9) size relative to the population was more important to Douglas-fir relative growth rates than neighborhood or population level interference, as evident by the best models for predicting Douglas-fir relative growth rates over this period containing the *II*, **G** (Table 2.3). In the mature stands, the importance of size relative to the population and neighborhood interference changed as Douglas-fir attained a dominant canopy position. During the measurement periods in which Douglas-fir had co-dominant heights with red alder (years 30-43, Fig. 2.1c), neighborhood interference was a better determinant of relative growth rates (Table 2.7). However, once Douglas-fir had attained a dominant canopy position relative to red alder (years 43-68, Figure

2.1c), size relative to the population became a better determinant of relative growth rates. Over this time period, all of the best models used population *II* (Table 2.7).

Ecological neighborhoods

Neighborhood sizes also changed over time for both species (Tables 2.3, 2.4, 2.7, and 2.8). Measurement periods in which there was little difference between models using different neighborhood sizes, such as years 9-12 for Douglas-fir at the HJA site (Table 2.3), indicate there was no distinguishable difference between neighborhood interference at different scales during that particular interval. However, the measurement periods in which there were significant differences between models containing neighborhood *II* (i.e., $\Delta_i < 2$) indicate a general pattern of increasing neighborhood size with increasing stand age or tree size for both species. For example, the appropriate neighborhood size for Douglas-fir in the mature stand at age 30 was roughly 4.5 m (Table 2.7). The appropriate neighborhood size increased to 9.0 m by age 35 and remained that size through age 39 (Table 2.7). The appropriate neighborhood size also increased with stand age for red alder. In general, the best models for predicting relative growth rates over the earlier years (30-43) examined in the mature stand included neighborhood *II* with radii ranging from 3.0-9.0 m (Table 2.8). However, by age 56 the neighborhood size had increased to 11.5 m as the best models for predicting red alder relative growth rates over years 56-68 exclusively included neighborhood *II* with the largest neighborhood size (Table 2.8).

DISCUSSION

Overall, the growth and interference patterns observed in the young and mature stands in this study are consistent with the findings of other studies examining the development of mixed red alder/Douglas-fir stands in the Pacific Northwest (Newton *et al.* 1968; Stubblefield & Oliver 1978; Shainsky & Radosevich 1992; Puettmann *et al.* 1992). In addition, the growth patterns observed in this study are also consistent with the autoecological characteristics of both species (Harrington 1990; Herman & Lavender 1990) suggesting that all of the sites examined in this study were sites suitable for the growth of Douglas-fir and red alder.

The results of this study suggest that the importance of neighborhood interference (sensu Weldon & Slauson 1986) varies with competitive status (i.e., size relative to the population). The differences in importance of neighborhood competition observed in this study appear linked to changes in the relative dominance in height of red alder and Douglas-fir in the young and mature stands and the patterns can be represented by a conceptual model linking relative competitive status, as quantified by average height of a species in relation to average height of the interfering species, to the importance of neighborhood interference on individual tree growth (Fig. 2.4a). This model suggests that neighborhood interference is an important determinant of individual tree growth for species with subordinate and co-dominant heights in the population, whereas tree size relative to the population is a better determinant of individual tree growth for

Fig 2.4 (a) Conceptual model of the importance of neighborhood interference and size relative to the population for determining tree growth as a function of relative dominance. (b) Relationships between relative dominance and the importance of neighborhood interference and size relative to the population as determinants of red alder (RA) and Douglas-fir (DF) relative growth rates during the early (years 6-15), intermediate (years 30-43), and later (years 43-68) stages of stand development examined in this study.

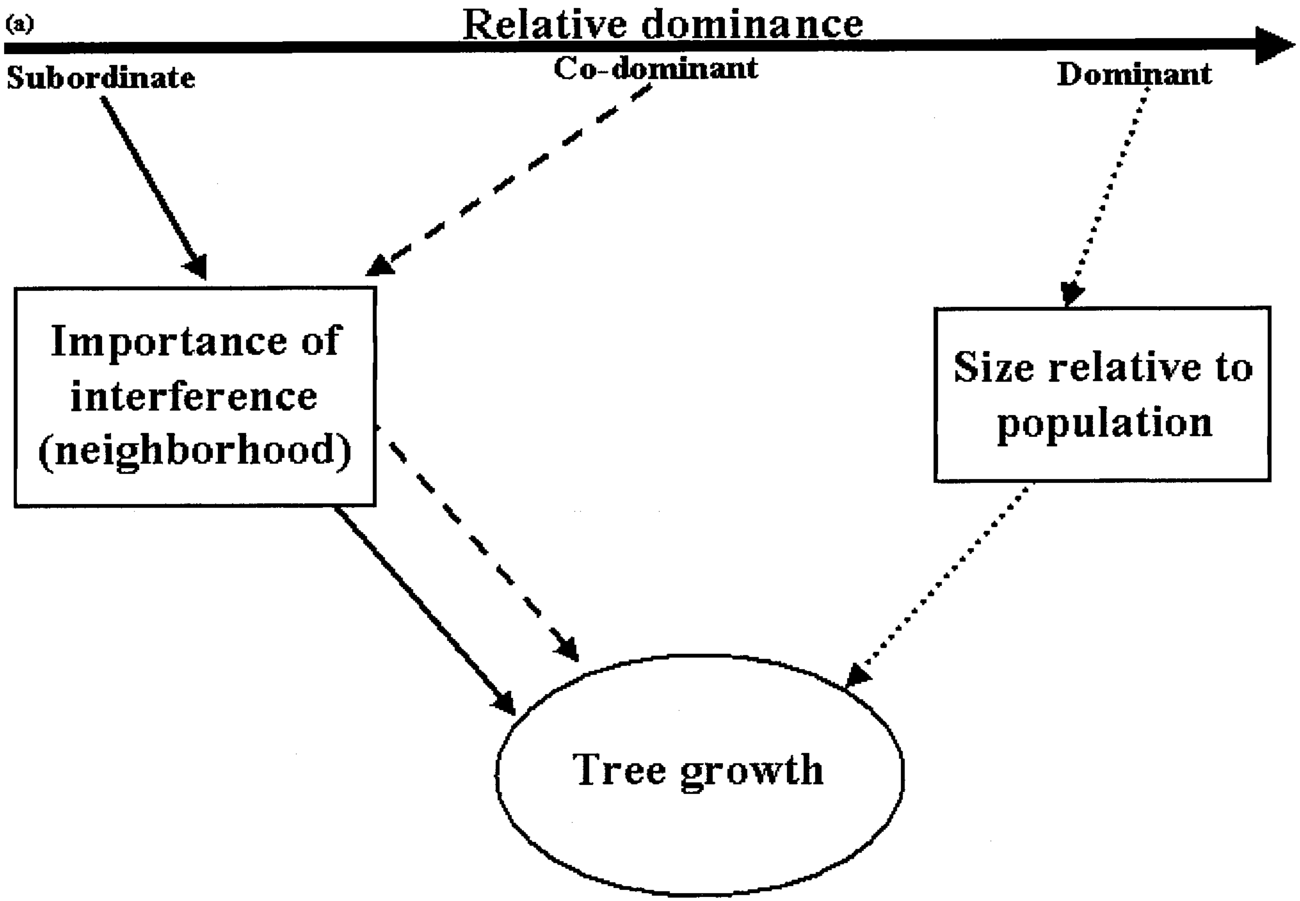

Fig 2.4 (continued)

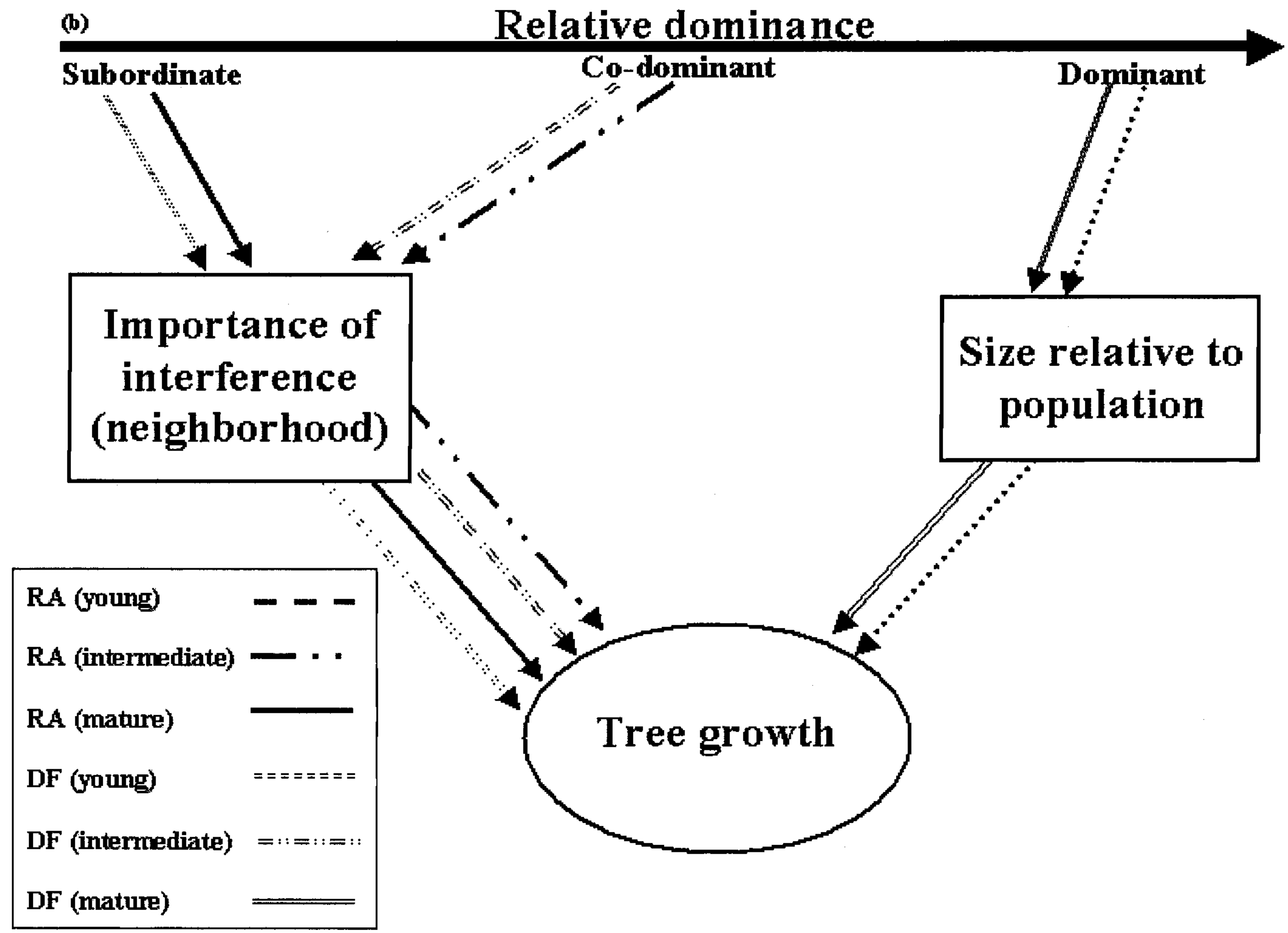
(b)
Relative dominance
Subordinate
Co-dominant
Dominant
Importance of interference (neighborhood)
Size relative to population
Tree growth
RA (young)
RA (intermediate)
RA (mature)
DF (young)
DF (intermediate)
DF (mature)

Fig 2.4

species with dominant heights. The conceptual model suggests that resource competition is size-asymmetric thus linking the size of a tree relative to the population to its resource capturing capacity (Ford and Diggle 1981; Miller & Werner 1987; Goldberg 1990). In addition, the conceptual model assumes that interference is occurring and may not hold true under circumstances in which size is driving relative growth patterns, such as those observed over the earliest measurement period in the young stands.

The findings of other studies that have investigated interference in two-species mixtures support my conceptual model. For example, in an addition series experiment, the taller species, *Liquidambar styraciflua*, had a significant effect on the resources available to the subordinate species, *Pinus taeda*, whereas *P. taeda* did not have significant effects on the resources available to *L. styraciflua* (Zutter *et al.* 1997). These findings suggest that the size of the dominant species, *L. styraciflua*, relative to the population was the most important factor determining their growth, whereas the growth of the subordinate species, *P. taeda*, was strongly affected by the neighboring *L. stryraciflua.* Similar results were also found in a removal experiment, in which the growth of the tallest species, *Plantago lanceolata* and *Sanguisorba minor*, were unaffected by competition from the subordinate species, *Briza media*, *Carex caryophllea*, and *Lotus corniculatus* (McLellan *et al.* 1997). Longer-term studies of neighborhood competition in mixed species populations have also noted that individual tree size becomes a better determinant of growth as relative dominance in height between the focal species and neighboring vegetation changes over time (e.g., Wagner & Radosevich 1998).

The findings of other studies that have investigated aspects of this phenomenon in monocultures also support the conceptual model and suggest that this model also applies to individuals. For example, Cannell *et al.* (1984) noted a weak relationship between measures of neighborhood interference and the relative growth rates of individuals with dominant heights in monocultures of *Picea stichensis* and *Pinus contorta*. In their study, competitive status, as quantified by height relative to the population, was able to explain significantly more variation in the growth of dominant individuals than measures of neighborhood interference (Cannell *et al.* 1984). These relationships have also been observed in population-level studies of competition. For example, Ford (1975), in his examination of size hierarchy development in monocultures of *Tagetes patula*, noted that the dominant individuals in the population all shared higher, similar relative growth rates, whereas there was a great deal of variation in relative growth rates among subordinate individuals. These findings suggest that the dominant plants in this population were less affected by neighborhood interference as compared to the subordinate individuals.

The strong relationships between size relative to the population and the growth of dominant individuals observed in this and other studies are presumably due to the greater access to available resources a dominant size relative to the population confers. Initial size differences among individual plants or species due to factors such as variation in germination time and early growth rates are often extremely important in determining the outcome of competitive interactions among individuals in a population (Fowler 1984; Wilson 1988; Connolly & Wayne 1996). In many cases, a size advantage by an individual plant or species over another results in an asymmetrical relationship in which the larger individuals obtain a disproportionate share of resources and suppress the growth of smaller individuals (Connolly & Wayne 1996). In this study, the differences between inherent height growth patterns of red alder and Douglas-fir resulted in each species having a height advantage at a different stage of development. The results of this study suggest that the trees with greater heights (i.e., size advantage) at a given point in stand development had greater access to available resources and were thus less affected by neighborhood interference. This pattern was found for both species and in both the young and mature stands (Fig 2.4b).

In contrast to the dominant species, the growth of the species with subordinate or co-dominant heights in each stand were strongly affected by neighborhood interference (Fig. 2.4b). The importance of neighborhood interference to smaller individuals in a population is well documented (Ford & Diggle 1981; Weiner & Thomas 1986). In populations in which differences in height among species or individuals are present, the overtopping of shorter individuals by taller neighbors often results in asymmetric competition for light (Ford & Diggle 1981; Cannell *et al.* 1984; Thomas & Weiner 1989; Freckleton & Watkinson 2001) and possibly other resources (Rothe and Binkley 2001). As a result, shorter individuals often grow in neighborhoods with depleted light resources reducing their photosynthetic rate and the amount of resources available for above- and below-ground growth (Keddy 1990). Thus, it is likely that the above-ground and below-ground resources available to the subordinate species in this study were strongly affected by neighborhood interference. In addition, mutual shading between co-dominant individuals can also reduce the amount of light resources available for individual tree growth (Cannell *et al.* 1984). While the competitive interactions between co-dominant red alder and Douglas-fir in this study were probably more symmetric than between dominant and subordinate individuals (Freckleton & Watkinson 2001), the amount of resources available for the growth of each species in these relationships was still strongly related to the amount of neighborhood interference occurring.

Although tree growth is utilized as a measure of fitness in my model, it is possible similar trends may be observed between relative dominance and other factors such as individual plant fecundity. For example, in a community in which light is the limiting resource, it is likely that the species or individuals with dominant heights relative to others plants in the community will have greater access to available resources for defense and reproduction. Conversely, the neighborhood interference experienced by subordinate species or individuals may reduce the resources available for reproduction thus limiting their probability of reproductive success. As a result, the floristic and genetic composition of a community may be strongly influenced by the relative dominance or competitive stature of a given species or individual. This relationship has been demonstrated in studies of competitive hierarchies in which competitive ability as measured by plant height or aboveground biomass has been positively correlated with the relative abundance of a species in a particular plant community (Mitchley & Grubb 1986; Keddy & Shipley 1989).

Despite red alder's nitrogen-fixing ability, none of the results of this study suggest that facilitation was the dominant form of interference occurring between red alder and Douglas-fir. While both competition and facilitation may have been occurring simultaneously between red alder and Douglas-fir (Callaway & Walker 1997), the relationships between relative dominance in height and neighborhood interference observed in this study suggest that competition was the dominant form of interference. The beneficial effects of nitrogen fixation on Douglas-fir growth may only be manifested on sites in which soil nitrogen is limiting (Binkley 1992). Thus, the relatively high soil nitrogen in the young stands (D.E. Hibbs, unpublished data) and the long-term presence of red alder in the mature stand may have limited the beneficial effects of nitrogen fixation on the growth of Douglas-fir over the measurement periods examined. Because nitrogen fixation is a highly energetic process (Tjepkema & Winship 1980), it is possible that competition for light from taller neighbors may have resulted in a reduction in the nitrogen-fixing capacity of subordinate or co-dominant red alder.

Alternative explanations for the relatively poor performance of models incorporating neighborhood interference as compared to models with population-level measures are not likely. The use of a single neighborhood size for all individuals in the population regardless of tree size has been suggested as a reason for the poor performance of neighborhood measures of interference (Burton 1993). However, I examined this issue by plotting the residuals from a variety of models with different neighborhood sizes over individual tree size and found no detectable pattern (data not shown). The use of inappropriate measures of neighborhood interference has also been suggested as a reason for weak relationships between individual plant growth and neighborhood interference in past studies (Thomas & Weiner 1989). However, the variety of measures used and the strong relationships between neighborhood interference and tree growth found for the majority of measurement periods examined in this study suggest that factors such as changes in relative dominance in height are driving the trends observed in this study versus inappropriate measures of neighborhood interference.

In conclusion, interference patterns are dynamic and change with the relative positions of individuals in a population. Data from three different mixed species stands suggest a conceptual model that demonstrates the influence of relative dominance on the importance of neighborhood interference in forest communities. While a two-species mixture was used as a simple example of the influence of relative dominance on the importance of neighborhood interference, this model is likely appropriate for individuals within a population and communities composed of numerous species. Trends similar to those predicted by my model have also been documented in other perennial plant communities

(Mitchley 1988; McLellan *et al.* 1997), suggesting that the application of this model may not be restricted to interference between tree species. The relationships between relative dominance in height and neighborhood interference described by this model are presumably due to the importance of competition for light in the communities examined and an alternative measure of relative dominance may be needed in environments in which competition for other resources is more important.

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CHAPTER THREE

CONCLUSION

INTERFERENCE DYNAMICS IN MIXED RED ALDER AND DOUGLAS-FIR FORESTS

The results of this study suggest that the importance of neighborhood interference to the individual growth rates of red alder and Douglas-fir varies with their size relative to the population. In the three mixed red alder/Douglas-fir stands examined in this study, neighborhood interference was an important determinant of individual tree growth for the species with subordinate or co-dominant heights. In contrast, size relative to the population was a more important determinant of individual tree growth for the species with dominant heights.

These observed relationships suggest that the nature of interference in these communities was relatively asymmetric. The dominance in height of red alder in the young stands and Douglas-fir in the mature stands presumably allowed these dominant species greater access to resources relative to the subordinate species in those populations. While neighborhood interference from subordinate neighbors may have influenced the resources available to the dominant species, the greater access to resources their dominant status conferred was a more important determinant of tree growth. Conversely, due to the pre-emption of resources by larger neighbors, the amount of resources available to the subordinate species in the young and mature stands was strongly influenced by neighborhood interference. In the instances in which both species were co-dominant in height, the mutual shading between species resulted in each species having a strong effect on the resources available for the growth of a given individual. As a result, neighborhood interference was very important for both species in the stages of stand development in which they were co-dominant.

The results of this study suggest that interference patterns are dynamic and change with the relative position of an individual in a population. In addition, the results of this study suggest that the importance of neighborhood interference may be predicted by the relative dominance of an individual plant in a population. Future studies examining the role of interference in plant community structure and dynamics will need to take into consideration the influence relative dominance has on the importance of interference. While past research has recognized the importance of measuring interference at the individual plant level, this study suggests that the importance of interference as a determinant of growth is not constant among individuals in a population.

MANAGEMENT IMPLICATIONS

Mixed red alder/Douglas-fir forests

The results of this study have several implications for the management of mixed red alder/Douglas-fir forests, as well as for other forest ecosystems. A key component of successfully managing mixed-species forests is understanding the interference effects and responses (sensu Goldberg 1990) of the species constituting the mixture. In this study, the autoecological characteristics of red alder and Douglas-fir resulted in each respective species having strong interference effects on the resources available to the other species at a given point in stand development. Because red alder and Douglas-fir have relatively high light compensation points and do not respond well to low light conditions (Harrington 1990; Herman & Lavender 1990), successful management of mixtures containing these two species requires strategies that minimize their interference effects on the resources available to the other species.

In the young stands, the interference effects of red alder on Douglas-fir were greater than interference effects of Douglas-fir on red alder. Depending on the particular management objectives, there are several options that may minimize these interference effects on the resources available to Douglas-fir early in stand development. One option is controlling the spatial distribution of red alder and Douglas-fir. If the objective is to maximize the yield of Douglas-fir while maintaining a small red alder component for nitrogen production and wildlife habitat, planting single red alder amongst mono-specific clumps of Douglas-fir may be a viable option. This strategy will minimize the amount of inter-specific neighborhood interference experienced by Douglas-fir while enhancing the overall structural diversity of the stand. To manage for commercially viable red alder and Douglas-fir, planting row-by-row mixtures, as suggested by Hibbs and DeBell (1994), may be a viable option. Planting a row of red alder for every three rows of Douglas-fir will reduce the interference effects of red alder on the majority of the

Douglas-fir in the plantation. In addition, the row planting of red alder will allow you to commercially thin red alder with minimal damage to the Douglas-fir (Hibbs & DeBell 1994).

Another option is to control the timing of red alder establishment (Newton *et al.* 1968; Hibbs & DeBell 1994). This may be a suitable option if the management objective is to create a tree-by-tree mixture of Douglas-fir and red alder. In order to facilitate the delayed planting of red alder, this strategy would require either planting Douglas-fir at an initial wide spacing or pre-commercially thinning the Douglas-fir to a wider spacing before planting the red alder. Both of these options would require considerable weed control to ensure successful Douglas-fir and red alder establishment (Hibbs & DeBell 1994). A benefit of this approach is the ability to commercially thin both Douglas-fir and red alder in the same entry.

In the mature stand, the interference effects of Douglas-fir were greater than red alder. If the objective is to obtain a commercial harvest of both red alder and Douglas-fir, a potential option to minimize these interference effects on the resources available to red alder is to manage red alder on a shorter rotation than the Douglas-fir component. This strategy would reduce the amount of red alder mortality, while increasing the resources available to the dominant Douglas-fir. To maintain habitat for wildlife, scattered red alder could be left for snag production.

The changes in neighborhood size over the time period observed in this study have important implications for thinning treatments aimed at removing a given red alder or Douglas-fir from the interference effects of its neighbors. These findings suggest that as a stand develops larger canopy openings will be required to release a particular individual from the interference effects of its neighbors.

The relationships between relative dominance and neighborhood interference observed in this study also have important implications for crop tree release treatments. Traditionally, foresters have approached crop tree release treatments with the assumption that the growth of a given tree was determined primarily by competition for resources with its neighbors. However, the results of this study suggest that the importance of neighborhood competition as a determinant of tree growth will vary based on the relative dominance in height of a given individual. The findings of this study suggest that crop trees in subordinate or co-dominant positions will respond more from a crop tree release treatment than a dominant individual.

Measuring interference

There has been a great deal of work devoted to developing indices for predicting tree growth as a function of either population–level or neighborhood interference. The majority of these studies have found that simple population-level measures of interference have performed equally as well or better than more complicated neighborhood measures. In this study, the performance of population-level and neighborhood measures of interference as predictors of tree growth was related to the dominance of an individual relative to the population. These findings illustrate that these measures may not be universally applicable to all conditions within a particular forest stand and that managers may need to take into consideration the vertical structure of their stands before choosing an index to predict tree growth.

STUDY LIMITATIONS

A potential limitation of this study was that the data utilized were from experiments not explicitly designed to test the relationships between neighborhood and population-level interference and tree growth. An evaluation of the importance of competitive status and neighborhood interference in plant populations with a wider range of neighborhood conditions than those examined in this study would be the next logical step to verify some of the hypotheses this study has generated. Another potential limitation of this study was the failure to account for the influence of interference from understory vegetation on individual tree growth. The abundance and composition of understory plants in a particular neighborhood or population can potentially influence individual tree performance. Long-term, repeated measurements of understory cover and composition may help improve our ability to predict individual tree growth as a function of neighborhood interference. Finally, measurements of factors such as soil moisture and photosynthetically active radiation would have allowed a more direct estimate of the effects of neighboring vegetation on the amount of resources available to each tree.

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