AN ABSTRACT OF THE THESIS OF

Sean M. Garber for the degree of Master of Science in Forest Resources presented on September 5, 2002.
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Abstract approved ______________________________
Douglas A. Maguire

Knowledge of stand structure, stand dynamics, and production ecology of species mixtures lags well behind that of single-species, even-aged stands. Two mixed-species spacing trials in central Oregon allowed investigation of mixed-species dynamics in a controlled experimental setting. The first site, Pringle Butte, is a mixture of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). The second site, Lookout Mountain, is a mixture of ponderosa pine and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). Both studies were planted in the early 1970's and established as replacement series under a split-plot design with spacing as the whole plot factor and species composition as the split-plot factor. Plot data have been collected since 1975. In the summer of 2001, 95 trees outside the plots were destructively sampled and 114 plots were intensively sampled. From these data the following were developed and assessed: (*i*) volume growth dynamics; (*ii*) models predicting individual tree vertical foliage distributions; (*iii*) models describing the profile of maximum branch diameter within a tree; and (*iv*) volume growth efficiency.

In both studies, the least shade tolerant species had the fastest early growth rates. Over time, volume development depended on both spacing and composition; *P. ponderosa* was able to catch up with *P. contorta* within the mixtures and between the pure plots at Pringle Butte, whereas *A. grandis* still lags behind *P. ponderosa*, although its relative contribution increases with increasing spacing at Lookout Mountain. Relative yields of mixtures were greater than one, but significantly so only in the *A. grandis* - *P. ponderosa* mixtures.

Branch leaf area equations indicate that, given branch diameter, position in the crown is an important factor in estimating leaf area. Tree leaf area was best predicted by the product of tree basal area and the ratio of crown length above breast height, a surrogate for sapwood area at crown base. Branch- and tree-level predictions differed significantly between sites for *P. ponderosa.* Relative vertical foliage distribution on individual trees of both *A. grandis* and *P. ponderosa* shifted up with an decrease in relative height, while increased spacing resulted in a downward shift in relative foliage distribution on *P. ponderosa* at Lookout Mountain. Spacing and competing species also affected absolute foliage distributions in a manner consistent with expected influence on crown length.

For all species and spacings, profiles of maximum branch diameter were curvilinear, decreasing near the crown base. Tree variables such as diameter, height, and crown length were able to account for spacing. The effect of species composition on branch profiles was more difficult to assess. Profiles of maximum branch diameter

increase with increasing spacing and tree relative height, but the effects of species composition depended on spacing in all species. More pronounced increases in maximum branch diameter profiles with increasing relative height within the crown were found in the subordinate species in mixtures than in adjacent pure plots and in its overtopping competitor. In contrast, the overtopping species had a larger spacing response in the pure plots than in mixed plots.

The ratio of leaf biomass to crown biomass decreased with increasing spacing, but was also influenced by species composition. Growth efficiency decreased with increasing spacing, except in *Abies grandis*, which peaked at the intermediate spacing. Results suggest that plot growth efficiency peaks at intermediate densities depending on composition. At wider spacings, growth efficiency appears to be limited by greater allocation of carbon to branches for both construction and maintenance respiration. At tighter spacings, growth efficiency appears to be limited by competition among individuals, reducing resources per individual and promoting differentiation. In dense, differentiated stands, the poorest individuals contribute leaf area but little growth, reducing stand growth efficiency.

Spacing and species composition play an important role in stand development and resulting crown structure. Mixtures can produce a more diverse array of stand structures and yield similar if not more volume than pure stands of the higher yielding species. Management of mixed-species stands must take into account the interactions

between spacing and species' growth dynamics, but this same interaction opens possibilities for a wide variety of stand structures for a given species composition.

Crown Structure, Stand Dynamics, and Production Ecology of Two Species Mixtures in the Central Oregon Cascades

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorized release of my thesis to any reader upon request.

Sean M. Garber, Author

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CROWN STRUCTURE, STAND DYNAMICS, AND PRODUCTION ECOLOGY OF TWO SPECIES MIXTURES IN THE CENTRAL OREGON CASCADES

CHAPTER ONE: INTRODUCTION

INTRODUCTION

As demands for forest resources increase, the complexity of stand management objectives also increases. Historical demands from forests primarily involved timber-based products. Currently there is more demand on forests to provide clean water, recreational benefits, better wildlife habitat, and timber products. For these objectives, traditional even-aged regulated stand structures are not adequate. This presents a complex problem for industries as ecosystem objectives and production management appear to be conflicting objectives. This is most apparent in single-species, even-aged forests, whether they are planted or natural. Stand development and productivity in these stands are relatively simple and predictable. However, as the complexity of stand dynamics (i.e. survivor growth, mortality, and ingrowth) increases with more complex canopy, species, and age structures, stocking levels are harder to assess, intermediate treatments are harder to apply, and development and productivity become more difficult to predict.

Silvicultural prescriptions are designed and applied to accomplish many of the objectives referred to above. Silvicultural manipulation regulates attributes of trees such as their size, shape, and branching characteristics (Smith et al. 1997). Over time, these manipulations alter stand dynamics and structure (Oliver 1981; Clatterbuck and Hodges 1988; Oliver and Larson 1996). The dominant methods to regulate these attributes involve manipulation of stand density. Density management guidelines have been constructed for the past 70 years in even-aged, single-species stands (e.g., Reineke 1933; Chisman and Schumacher 1940; Gingrich 1967), and are widely used in practice. Some work has been done to expand these concepts to more diverse structures such as mixed-species stands and uneven-aged stands (Puettmann et al. 1992; Sterba and Monserud 1993; Wilson et al. 1999). However, before implementation of intermediate treatments, foresters must be able to predict the changes in stand and crown structure likely to result over time from altered spacing and species composition, as these will influence volume production and wood quality.

In order to accurately predict net biomass or stemwood volume productivity, it is important that more biologically-based models be developed. A biologically-based model would have easily-measured attributes of an ecological system that are indirectly or directly related to the variable of interest. That is, developing predictor variables that are physiologically and ecologically based. In addition, to understand forest productivity, one must account for variability in production caused by diverse stand structures as a result of age, site quality, species, and density (Smith and Long 1989). Quantifying these predictor variables relative to other stand characteristics such as density, age, condition or health, species, and treatments can lead to development of productivity models for any forest structure.

Existing studies on the Pringle Falls Experimental Forest in the Deschutes National Forest, in the Cascade mountains of central Oregon, provide an opportunity to assess and quantify productivity and stand structure development in mixed-species stands. Two mixed-species spacing studies were designed to assess the growth rate and development of pure and mixed stands planted to different densities. Two species mixtures are available: (1) ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and (2) ponderosa pine and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). Each installation contains a range of densities, each with three level of species mixture: species A alone, species B alone, and a 50:50 mix of species A and B.

Results of this study will add new information to the state of our knowledge on stand dynamics and production ecology of species mixtures. More importantly, these study sites represent the few replacement series studies with long-term data for forest species. Quantification of stand structure, stand development, and productivity will significantly aid in the management of mixed-species stands. The results of this study will assist future researchers in developing useful tools for practicing foresters and will aid silviculturists in planning intermediate treatments and predicting the potential responses of various ecosystem components in public and private forests.

OBJECTIVES

The overall objective of this study was to identify and quantify aspects of stand development, productivity, and crown structure that are unique to mixed-species stands in the central Oregon Cascades. To achieve this comprehensive objective, the study addressed five specific questions: (*i*) Does stand growth and development vary by spacing, species composition, or the interaction of spacing and composition? (*ii*) Does spacing, species composition, or their interaction affect vertical foliage distribution? (*iii*) How does spacing and species composition interact to alter expected responses of maximum branch diameter profiles to spacing? (*iv*) Is plot volume growth efficiency responding consistently to spacing regardless of species composition? And (*v*) what are the silvicultural implications of these spacing trials for controlling stand structure through spacing and species composition.

CHAPTER TWO: LITERATURE REVIEW

INTRODUCTION

A study of mixed-species and multi-structured stands should begin with a firm understanding of dynamics and growth of single-species, even-aged stands. Relatively little literature is available on individual tree or stand attributes in stands of multiple species so the literature on single-species stand development becomes extremely valuable as a starting point. Forest structure and forest production can then be related to species composition. However, it is useful to review past literature on the structure of forest stands, namely, individual crown and stem components. First will be a synopsis of crown architecture including, foliage distribution and branches diameters. The second section will address stand dynamics and production ecology in single-species stands and mixed-species stands. This latter section will connect structure and function in the context of stand dynamics and production ecology of mixed-species stand components.

STAND STRUCTURE, DYNAMICS, AND PRODUCTION EFFICIENCY

Net primary production (NPP, the accrual of plant dry matter) is a function of total photosynthetic surface area, photosynthetic rate of foliage, and the proportion of fixed carbon burned in respiration (Waring 1983; Vose and Allen 1988; Perry 1994).

Foliage is the only important source of fixed carbon in temperate trees (Roberts and Long 1992); therefore, the growth of various tree components depends on the ability of foliage to fix carbon and on the allocation of the fixed carbon fixed through photosynthesis. Leaf area determines the capacity of a canopy to absorb photosynthetically active radiation (PAR) (Perry 1994). Predicting leaf area is a difficult task; however, technological advancements and enhanced in knowledge of tree physiology have lead to easier and more precise predictors of leaf area.

Patterns in leaf area distribution and leaf area density within crowns can be variable even within a species (Maguire and Bennett 1996; Maguire and Kanaskie 2002). Foliage distribution is closely linked to light penetration and interception (Sampson and Smith 1993), and both photosynthesis and stomatal conductance have been shown to vary by location within the crown (Woodman 1971; Brooks et al. 1991). As a result, not only is foliage amount and distribution linked to production, but the distribution of foliage is also linked to efficiency of production.

Growth efficiency is defined as some unit of productivity divided by total plant biomass, land area, leaf area, or leaf biomass (Perry 1994). Foresters interested in production of merchantable wood fiber consider stemwood volume increment an important recipient of assimilated carbon. Therefore, growth efficiency has most commonly been defined as stemwood volume increment per unit leaf area. Growth efficiency has been shown to vary with tree leaf area, tree age, stand density, foliage ratio (ratio of foliage weight to total crown weight), canopy architecture, and stand structure.

Stand structure is the arrangement of the various parts of above- and below-ground components of the forest. The specific mix of species can impose a unique structure on forest stands (Kelty 1989; Oliver and Larson 1996; DeBell et al. 1997; Bauhus and Messier 1999; Schmid and Kazda 2001). These unique structure can in turn influence the growth efficiency and therefore forest production.

CROWN STRUCTURE

Foliage distribution

Size, shape, and position of crowns have been shown to significantly affect the production ecology of forests (Roberts et al. 1993; Gilmore and Seymour 1995). Physiological processes proceed at different rates in different places within a crown and among different leaf age classes (Woodman 1971; Teskey et al. 1984; Sprugal 1990; Brooks et al. 1991). As a result, it has been suggested that foliage distribution has influences on gas exchange, light interception, photosynthesis, and respiration (Grace et al. 1987; Russell et al. 1989; Baldwin et al. 1997). Foliage distribution has been shown to be affected by stand structure, season, and site factors (Stephens 1969; Vose 1988; Vose and Swank 1990; Gillespie et al. 1994). Because stands of multiple species have different structures than those of single-species, foliage distribution is probably also affected by competing species. The importance of vertical foliage distribution has been demonstrated in ecosystem process models, but it may also aid in the understanding differences in stand development and the production ecology of species mixtures.

Modeling foliage distribution

Models have been developed for many of the primary commercial species around the world including *Pseudotsuga menziesii* (Mirb.) Franco (Kershaw and Maguire 1996; Maguire and Bennett 1996), *Pinus taeda* L. (Vose 1988; Gillespie et al. 1994; Baldwin et al. 1997), *Pinus radiata* D. Don in New Zealand (Wang et al. 1990), *Pinus sylvestris* L. (van Hees and Bertelink 1993), *Abies grandis* (Dougl. ex D. Don) Lindl. (Kershaw and Maguire 1996), *Tsuga heterophylla* (Raf.) Sarg. (Kershaw and Maguire 1996), and even a few deciduous trees (Yang et al. 1999). Although the discussion will mainly focus on the more common vertical profiles (Vose 1988; Maguire and Bennett 1996; Baldwin et al. 1997), it should also be noted that radial distribution has also been investigated (Wang et al. 1990; Kershaw and Maguire 1996).

Foliage distributions have been modeled using common probability density functions. Distribution parameters have been estimated using nonlinear least squares (Vose 1988; Gilmore and Seymour 1997), however, maximum likelihood is preferable from the standpoint of statistical theory. Maximum likelihood methods have been used by Schreuder and Swank (1974), Baldwin et al. (1997), and Maguire and Bennett

(1996), and others have used method of moments (Kershaw and Maguire 1996). Differences in parameters can be tested among treatments and perhaps even modeled as a function of tree size or stand structure measures (Mori and Hagihara 1991; Maguire and Bennett 1996; Baldwin et al. 1997).

The earliest attempts to characterize foliage distribution applied the normal distribution (Stephens 1969; Schreuder and Swank 1974; Whitehead 1978; Massman 1982). The normal probability density function (pdf) is described by:

$$f\left(x;\mu,\sigma^2\right)=\frac{1}{\sigma\sqrt{2\pi}}e^{\frac{-(x-\mu)^2}{2\sigma^2}}$$

where μ is the location parameter ($-\infty < \mu < \infty$), σ^2 is the scale parameter ($0< \sigma^2 < \infty$), and x is a normal random variable ($-\infty < x < \infty$). Stephens (1969) assessed foliage distribution in 50 *Pinus resinosa* Ait. with a large range in diameter and crown lengths, and concluded that foliage on all trees would conform to a normal distribution. However, his data indicated that intermediate and suppressed trees had foliage distributions that were skewed downward. The normal pdf has the advantage of being well-studied, however, it has several disadvantages: (1) it under predicts foliage at the top of the trees; (2) its domain extends from $-\infty$ to $+\infty$ and tree crowns have distinct bounds on foliage distribution, corresponding to the lowest live branch and tip of the tree; and (3) it is extremely rigid not lending itself to the slight skewness or kurtosis potentially found in trees crowns (Beadle et al. 1982; Massman 1982). Variations on the normal distribution have also been used including a skewed normal distribution (Beadle et al. 1982) and lognormal distribution (Schreuder and Swank 1974). However, as with the normal distribution, these distribution are fairly rigid.

Other distributions that have been applied include the Chi-square distribution (Massman 1982), beta distribution (Massman 1982; Wang et al. 1990; Maguire and Bennett 1996), gamma distribution (Schreuder and Swank 1974; Massman 1982), and the Weibull distribution (Schreuder and Swank 1974; Mori and Hagihara 1991; Gillespie et al 1994). Schreuder and Swank (1974) investigated several density functions for *Pinus strobus* L. and *P. taeda* and concluded that the Weibull was the most useful because it was interpretable, simple, and easy to use. More recently, many investigators have affirmed these findings using a two-parameter Weibull probability density function (Hagihara and Hozumi 1986; Mori and Hagihara 1991; Gillespie et al 1994). The Weibull pdf is:

$$f(x;\gamma,\beta)=\frac{\gamma}{\beta}\left(\frac{x}{\beta}\right)^{\gamma-1} e^{-\left(\frac{-x}{\beta}\right)^{\gamma}}$$

where γ is the shape parameter ($0 < \gamma < \infty$), β is the scale parameter ($0 < \beta < \infty$) and x is a Weibull random variable ($0 \leq x < \infty$). Although many investigators suggest the Weibull distribution works well, it has significantly undesirable properties. It is not constrained at the upper end, that is the domain of x extends to infinity. Baldwin et al. (1997) truncated the Weibull model so that it would nearly terminate at the base of the tree.

The beta distribution has also been a preferred when compared to many other distributions (Masman 1982). It has the greatest flexibility relative to the density functions presented above. The beta distribution also as the appealing property of being constrained between 0 and 1. The beta distribution is described by:

$$f(x;\alpha,\beta) = \frac{1}{B(\alpha,\beta)} x^{\alpha-1}(1-x)^{\beta-1}$$

where

$$B(\alpha,\beta) = \frac{\Gamma(\alpha)\Gamma(\beta)}{\Gamma(\alpha+\beta)} ,$$

$$\Gamma(\alpha) = \int_0^{\infty} e^{-x} x^{\alpha-1} dx \quad \text{for all } \alpha > 0,$$

α and β are shape parameters ($0 < \alpha, \beta < \infty$) and x is a beta random variable ($0 \leq x \leq 1$). Wang et al. (1990) and Maguire and Bennett (1996) have reported good results with this distribution. In contrast to the Weibull distribution which has the advantage of being relatively simple, the gamma integral must to be numerically estimated (Schreuder and Swank 1974; Maguire and Bennett 1996).

Trends in foliage distribution

Studies on foliage distribution have yielded a wide range in results from different species and stand histories. Stephens (1969) suggested that all trees would exhibit the same distribution. However, trees in lower crown classes had a more skewed foliage distribution in his study. Converting his results from foliage mass to leaf area, the normally distributed foliage would become skewed toward the top of the tree due to increasing SLA with depth into the crown (Brooks et al. 1991). Likewise, Maguire and Bennett (1996) and Baldwin et al. (1997) observed that leaf area distribution is shifted slightly downward as compared to the distribution of foliage mass. As crown position increases, the mode of the relative foliage distribution shifts down the stem and the distribution becomes more skewed upward, perhaps as an adaptation to poorer light environments (Maguire and Bennett 1996). This behavior has been observed in *Chamaecyparis obtusa* Sieb. et Zucc.) Endl. (Mori and Hagihara 1991), *P. menziesii* (Maguire and Bennett 1996), and *Abies balsamea* (L.) Mill. (Gilmore and Seymour 1997).

Relatively few studies have assessed changes in foliage distribution with age or stand development. Patterns in *P. sylvestris* indicated modes above the crown midpoint in young trees, with a lowering of the mode with age (van Hees and Bartelink 1993). The same pattern was observed with increasing diameter in *C. obtusa* (Mori and Hagihara 1991). In contrast, Maguire and Bennett (1996) reported an upward shift and more peaking in foliage of *P. menziesii*, especially in trees of higher relative heights within the canopy when comparing tree sizes among plots assumed to represent slightly different points during stand development. Although this trend over time has to be verified with repeated measurements, similar results were found in *P. strobus* and *P. taeda* (Schreuder and Swank 1974). However, this latter study was done at the stand level and the upward shift may be the result of stand density reduction and death of lower crown classes. The inconsistencies may also reflect differences in the stage of stand development or in stand structure. With more competition, one would expect the foliage distribution to shift up as in trees relegated to lower crown classes. Alternatively, it might be expected that open-grown trees would have foliage shifted to lower portions of the crown. Differences in stand foliage distribution may also be attributable to differences in shade tolerance. Early successional stands have showed more foliage near the upper canopy (negative skew) while later successional stands were more symmetric in distribution (Yang et al. 1999).

Silvicultural treatments may also influence the distribution of foliage within the crowns of trees. Effects of thinning are not well-studied, but have resulted in the upward shift of stand-level distributions immediately after thinning, probably due to removal of lower crown classes (Beadle et al. 1982; Bidlake and Black 1989). Siemon et al. (1980) suggested a longer term shift down in the tree-level foliage distribution after thinning, but differences among the different levels of thinning were very small. Fertilization has been shown to impact tree foliage distributions (Vose 1988; Kershaw and Maguire 1995). Vose (1988) concluded that fertilization in *P. taeda* resulted in foliage increases in lower crown positions. In contrast, Gillespie et al. (1994) found no effect of fertilization on relative foliage distributions, while Kershaw and Maguire (1995) observed greater foliage with height above the crown base in fertilized trees. The latter authors also surmise that site affects the total amount of leaf area and not its distribution while fertilization affects total amount and distribution of leaf area.

The limited work in horizontal foliage distribution has shed some light on crown structure. Foliage is generally located further away from the bole with increasing depth into the crown (Wang et al. 1990; Kershaw and Maguire 1996). Furthermore, the distribution changed from a peak in foliage at the main stem at the top of the tree to peak in foliage in the middle of the branch at the crown base (Kershaw and Maguire 1996).

In summary, foliage distribution on individual trees is sensitive to stand structure and stand manipulation. These may also change with time and with stand development. Very little work has investigated the effects of species mixtures on the foliage distribution. Results present by Yang et al. (1999) on the stand level suggest that mixed-species stands have a deeper profiles and crown volume than single-species stands. This may support the idea of niche separation discussed below.

Branch diameter

Branch diameter is the result of duration of branch growth. In many of the species studied, trends of average and maximum branch diameter within crowns is curvilinear, increasing with depth into the crown until near the base of the crown (Colin and Houllier 1991; Gilmore and Seymour 1997; Maguire et al. 1994; Maguire et al. 1999). The peak in maximum branch diameter occurs near the point of maximum crown profile development (Roeh and Maguire 1997). The decrease in branch diameter below maximum crown development is a function of decreased branch radial growth at lower portions of the crown (Kershaw et al. 1990; Mäkinen 1999). However, differences in branch diameters among trees of different social positions (Colin and Houllier 1991; Gilmore and Seymour 1997), density (Magnussen and Yeatman 1987; Ballard and Long 1988; Colin and Houllier 1991; Maguire 1994), thinning (Siemon et al. 1976; Maguire et al. 1991), and tree size (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998), have been reported. As has already been addressed, increasing light conditions provide for greater branch longevity and faster branch growth. Consequently, improved social position, wider spacing, and thinning increase length of the live crown, branch longevity, and attained branch diameter (Kershaw et al. 1990; Colin and Houllier 1991; Mäkinen 1999b). Since the majority of these studies have been done in even-aged stands, increases in branch diameter with tree size is the result of greater crown lengths and perhaps better social position. Despite a great deal of emphasis on modeling branch diameters, little information is available on the relative patterns within trees under different conditions, such as those imposed by species mixtures.

Model forms for trends in branch diameter through the crown have generally been borrowed from stem taper work, including segmented polynomials (Colin and Houllier 1991; Maguire et al. 1994; Roeh and Maguire 1997; Meredieu et al. 1998; Maguire et al. 1999) and variable exponent models (Maguire et al. 1999). Mixed-effects models are desirable due to random tree effects and/or autocorrelation of multiple measurements from a single tree (Mäkinen and Colin 1998; Meredieu et al. 1998; Maguire et al. 1999).

DEVELOPMENT AND PRODUCTIVITY OF SPECIES MIXTURES

Reasons for favoring mixed-species stands are numerous and include protection from insects and diseases, resistance to wind and other abiotic stresses, risk reduction, compensatory growth, landscape aesthetics, and conservation of native plants and animals (Wierman and Oliver 1979; Kelty 1992; Schmid and Kazda 2001). However, knowledge of the relationships between species composition, stand dynamics, and productivity are lacking (Kelty 1992).

Stand development of single-species stands

Even-aged, single-species stand development has generally been divided into four stages (Oliver 1981; Oliver and Larson 1996). Disturbances, large and intense enough to remove all of the existing stands create areas open for the development of a new cohort of vegetation, a stage referred to as stand initiation. Following this, there is a constant increase in the numbers of new individuals to the stand until established plants exclude the addition of any new individuals, at which time the stem exclusion begins. As the stem exclusion stage proceeds, trees become taller and crowns recede. Individuals on poorer microsites, with poorer genotypes, or growing more slowly are relegated to lower strata. Consequently, crown differentiation intensifies and these individuals become overtopped and may eventually die. Overlapping of crowns results in crown abrasion and gaps in canopies. As trees age, crowns become less plastic, and therefore less able to occupy these openings in the canopy. Light availability increases on the forest floor providing for the establishment of a new cohort of vegetation during the understory reinitiation state. Eventually, barring disturbance, the fourth staged is reached, the old-growth stage.

Stand development of even-aged, mixed-species stands

Canopies in mixed-species stands not only differentiate on the basis of genetics and microsite, but also by species grouping (Oliver and Larson 1996; Smith et al. 1997). The process of stratification is a function of many processes and species characteristics. Among species, differences exist in the ability to occupy niches that minimize direct interaction with competitors (Kelty 1989, 1992). For example, intolerant species tend to grow faster in height due to increased photosynthetic rates and perhaps more allocation of fixed carbon to stemwood than more shade tolerant species earlier in their life (Wang et al. 2000). The intolerant species gain dominance and occupy the upper canopy layers, relegating the tolerant species to the lower strata (Oliver 1978; Wierman and Oliver 1979; Larson 1986; Wang et al. 2000). As stand development continues, relative position may change as well (Oliver 1978; Larson 1986; Clatterbuck and Hodges 1988). Other factors, however, can affect these patterns including direct interaction between species (Cobb et al. 1993) and spacing of dominant trees (Clatterbuck and Hodges 1988).

Production in mixed-species stands

Many studies have explored the relative productivity of mixed-species stands using replacement series studies. These studies are designed to hold plant density constant while replacing a proportion of trees with another species. The most common setup is a split-plot design in which the whole-plot factor is spacing and the split-plot factor is species composition. Pure stands are established at each spacing in addition to mixtures, established by replacing every other tree with the opposite species. Variations on this design impose ratios other than 50:50 (i.e., one out of every four planting spots for 75:25 ratios). Analysis of the effects of combining species are generally evaluated by comparing yields of each species in mixture with its yield in pure culture by assessing relative yield total (RYT) of the for each treatment (Harper 1977; DeBell et al. 1997).

Results of these studies have generally shown that mixtures are less productive than monocultures of the highest yielding component (Kelty 1989; Smith and Long 1992). Most of these studies are documented in the agricultural literature and involve annual herbs (Trenbath 1974; Harper 1977). Extensions of true replacement series studies in the forestry literature are relatively rare; most work has been done in plantations or naturally established stands without control over other factors. Several studies in Europe have suggested volume production in mixtures can exceed pure stands of the least productive component, and in some cases, pure stands of the more productive component (Assmann 1970; Frivold and Frank 2002). DeBell et al. (1997) and Bauhus et al. (2000) reported higher biomass production of the *Eucalyptus* spp. component in the mixture than in pure stands of *Eucalyptus* at comparable densities.

Kelty (1992) discusses production in mixtures at length and suggests that for mixtures to have more production would require competition reduction or facilitation. Competition reduction can be achieved if there is significant niche separation, for example, from stratification in canopies (Kelty 1989; Fajvan and Seymour 1999) or in belowground rooting distributions (Schmid and Kazda 2001). Several studies have reported higher production in mixed stands due to stratification, where at least one species makes better use of limited resources under given stand structures (Wierman and Oliver 1979; Larson 1986; Kelty 1989; Fajvan and Seymour 1999); however, none of these studies made comparisons to pure stands and none controlled density of the most productive component. Others however, have found no such result (Smith and Long 1992).

Facilitation is the result of a synergistic interaction whereby one species provides resources for the other. The most common example of this occurs in mixtures with legumous species hosting symbiotic nitrogen fixing bacteria (e.g., *Frankia* spp., *Rhizobia* spp., etc.). Such interactions have been repeatedly demonstrated recently with several mixtures in Hawaii and Australia (DeBell et al. 1997; Bauhus et al. 2000). These types of mixtures may also be beneficial in the temperate forests of the United States and Canada, one example being the combination of conifers and *Alnus* species especially on infertile sites (Binkley 1984a; Binkley et al. 1984).

Literature currently suggests that in replacement series studies, where density is controlled, a mixture will achieve higher rates of volume or biomass growth than pure stands of the less shade-tolerant species. Comparisons between mixtures and the pure stands of the tolerant component are less clear. Spacing, degree of mixing, site quality, and silvicultural treatment may also influence results from comparing species mixtures.

Growth efficiency and stand structure

Growth efficiency is defined here as stemwood production per unit leaf area. It is the net result of quantity of leaf area, the efficiency by which a tree converts carbon dioxide and water into carbohydrates, and the relative allocation of the fixed carbon to stemwood production (Waring and Schlesinger 1985; Roberts et al. 1993). Many factors affect stand growth efficiency including stand structure, site, and age. Tree- and stand-level growth efficiency have been investigated in detail. Many studies have reported that, within a stand, growth efficiency is lower within trees with larger crowns (Assmann 1970; Kuuluvainen 1988; Jack and Long 1992; Roberts and Long 1992; Sterba and Amateis 1998) and greater tree leaf areas (Waring 1983; Binkley and Reid 1984; O'Hara 1988; Long and Smith 1990; Gilmore and Seymour 1996; Maguire et al. 1998). Roberts and Long (1992) speculated that this pattern is in part the result of lower amounts of photosynthetic tissue relative to structural compounds in branches and associate construction and maintenance respiration; that is, trees with larger crowns have a larger proportion of fixed carbon allocated to construction and maintenance of branches, leaving less for stemwood production (Long and Smith 1990). Several studies have found higher individual tree growth efficiencies in thinned stands (Waring et al 1981) and in plantations with wider initial spacing

(Sterba and Amateis 1998). Tree growth efficiency has also been shown to increase with improved canopy position (Waring et al. 1980; O'Hara 1988; Roberts and Long 1992; Roberts et al. 1993; Gilmore and Seymour 1996; O'Hara 1996; Maguire et al. 1998; Kollenberg and O'Hara 1999).

Stand growth efficiency is stand volume per unit stand leaf area, and thus is influenced by individual tree efficiencies and the distribution of trees by growth efficiency or size class. Since trees with small leaf areas have higher growth efficiencies, high density stands may have higher stand growth efficiencies (Smith and Long 1989). This has not been the result in all studies, including stands beyond crown closure (Velazquez-Martinez et al. 1992), of different spacings (Sterba and Amateis 1998), and thinned to various intensities (Waring et al. 1981; Binkley and Reid 1984; Velazquez-Martinez et al. 1992; Garber and Seymour, unpublished data). O'Hara (1989) suggests that stand structure, or the distribution and arrangement of tree sizes, tree crowns, and leaf areas in a stand, may be a more important determinant of growth efficiency than total leaf area. Although high density stands beyond crown closure contain trees with relatively high growth efficiencies, they also contain trees with very low growth efficiencies (i.e., suppressed trees). Consequently, for stands that have not been thinned, stand growth efficiency may peak at some intermediate stand density (Waring et al. 1980), limited by large crown sizes at low densities and low growth efficiencies in poorer crown classes and high densities.

The influence of species mix on stand growth efficiency is largely unknown. One study compared mixtures and monocultures and attributed higher growth on pure stands to higher stand leaf area and higher mean tree growth efficiency (Smith and Long 1992). However, they do not present stand-level growth efficiency data nor did they control spacing.

CHAPTER THREE: STAND PRODUCTIVITY AND DEVELOPMENT IN TWO MIXED-SPECIES SPACING TRIALS IN THE CENTRAL OREGON CASCADES

ABSTRACT

Stand dynamics and productivity were assessed in two mixed-species spacing trials in central Oregon. For the first 30 years, standing volume in pure and mixed plots of *Pinus contorta* Dougl. ex Loud. and *Pinus ponderosa* Dougl. ex Laws. was significantly influenced by spacing, while time and time × species composition were also significant. Standing volume in the second study, pure and mixed plots of *Abies grandis* (Dougl. ex D. Don) Lindl. and *P. ponderosa*, was significantly influenced by spacing, species composition, and an interaction between spacing and composition, while time and all time interaction effects were significant. In both studies, the least shade tolerant species had the fastest early growth rates. However, *P. ponderosa* was able to catch up with *P. contorta* within the mixtures and between the pure plots at Pringle Butte, whereas *A. grandis* still lags behind *P. ponderosa* at Lookout Mountain, although differences have decreased over time. Relative yields in mixtures of *P. contorta* and *P. ponderosa* indicate no overall volume growth benefits. Mixtures of *A. grandis* and *P. ponderosa*, however, resulted in relative yield totals significantly greater than one at the closest and widest spacings. Results suggest spacing and species composition play an important role in stand production and development and

that mixtures can yield similar if not more volume than pure stands of the higher yielding species at some spacings and stages of stand development.

INTRODUCTION

It has long been debated whether even-aged, mixed-species stands produce more stem volume than even-aged, single-species stands. Beyond potential gains in production, reasons for preferring mixed-species stands include potential protection from insects and diseases, resistance to wind and other abiotic stresses, improved aesthetics, and enhanced diversity of associated plants and animals (Wierman and Oliver 1979; Kelty 1992; Schmid and Kazda 2001). However, knowledge of species interactions, the resulting stand dynamics, and total productivity of mixed-species stands lag well behind our understanding of single-species stands (Kelty 1992).

Mixed-species stand development has been explored with a type of controlled experiment referred to as a replacement series study. These studies are designed so that plant density is fixed but one species is replaced with given number of a second species. Most of these studies have been conducted in an agricultural setting with annual herbs (Trenbath 1974; Harper 1977). Results have generally shown that mixtures are less productive than monocultures of the highest yielding component (Trenbath 1974; Kelty 1992). Extensions of true replacement series studies in the forestry literature are rare; however, several semi-controlled studies in northern Europe suggest production in mixtures can exceed those of pure stands of the least shade-tolerant component, and in some cases, the higher yielding species (Assmann 1970; Frivold and Frank 2002). Moreover, several authors have reported higher biomass production of the *Eucalyptus* component in mixture than in pure stands of *Eucalyptus* at comparable densities (DeBell et al. 1997; Khanna 1997; Bauhus et al. 2000).

In the central Oregon pumice region, mixed stands of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) predominate on drier sites at low elevations. On moister sites, ponderosa pine can mix with grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), often but not always forming a stratified mixture (Oliver and Larson 1996; Cobb et al. 1993). Chance differences in seed placement, dispersal, and germination rate, as well as inherent silvical characteristics like growth rate and shade tolerance, can create a wide range of stand structures for a given mix of species. The main goals of this study were to understand productivity patterns and stand development in controlled mixed-species spacing trials and to extend inferences to naturally regenerated stands of similar composition. Specific objectives are: (*i*) to assess whether standing volume and stand productivity varies over time with species composition; (*ii*) to test for any possible interaction between spacing and species composition; and (*iii*) to relate results to current theory on mixed-species stand dynamics.

METHODS

Study Sites

The study was conducted at two sites. The first site, Pringle Butte, is a mixture of *Pinus ponderosa* and *Pinus contorta.* The second site, Lookout Mountain, is a mixture of *P. ponderosa* and *Abies grandis.* Both sites are east of the Cascade Range crest, 35 miles southwest of Bend, in the Pringle Falls Experimental Forest, Deschutes National Forest, Deschutes County, Oregon.

Pringle Butte site

The Pringle Butte study site is located on the northwest-facing slope of Pringle Butte at an elevation of 1,370 m (43^{o}43' N, 121^{o}37' W). Slopes range from 4 to 27 percent, with an average of 10 percent. Mean annual precipitation is only 61 cm and falls predominantly between the months of October and April, with a half-meter snow pack common between January and March. Maximum temperatures occur in July, averaging 26^{o}C, and frosts can occur at any time during the year (Cochran and Barrett 1999a). The soils in this area have been typed as a developing Xeric Vitricryands on 75 cm of dacite pumic from the eruption of Mount Mazama (Cochran and Barrett 1999a). This pumice layer overlays sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments.

The study area is 3.9-ha, clearcut in 1970. The ground cover consists of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus* *velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), scattered Ross sedge (*Carex rossi* Boott), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and western needle grass (*Stipa occidentalis* Trub. ex Wats.). *P. ponderosa* site index (base age 100) has been estimated at 24 m using Meyer's (1961) curves and 33.5 m using Barrett's (1978) method (Cochran and Barrett 1999a).

Lookout Mountain site

The Lookout Mountain study site is located on the northeast-facing slope of Lookout Mountain at an elevation of 1550 m ($43^{o}49'$ N, $121^{o}41'$ W). Slopes average close to 20-percent. Average annual precipitation is approximately 100 cm, most of which falls as snow between the months of September and May. Generally, summers are hot and dry, with temperatures ranging from 21 to 32^{o}C. Nights are predominantly cool with the chance of frost occurring any time during the year (Cochran and Barrett 1999b). Soils are deep, well-drained Typic Cryorthents, developed from dacite pumice originating from the eruption of Mount Mazama, overlaying a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments (Seidel 1985; Cochran and Barrett 1999b).

This study site is 8.1-ha, clearcut in 1974 in a mixed-conifer/snowbrush-chinkapin plant community (Seidel 1985). The ground cover consists primarily of *C. velutinus*, *A. patula*, and golden chinkapin (*Castonopsis chrysophylla* (Dougl.) A. DC.) (Seidel 1985). *C. velutinus* ground cover is very dense over much of the study site. The late successional plant community association is *Abies concolor/Ceanothus velutinus* (Franklin and Dyrness 1973). Site index (base age 100) for *P. ponderosa* (Meyer 1961) is about 27.5 m (Seidel 1985).

The site was planted with 2-0 bare root *P. ponderosa* stock grown at the USDA Forest Service nursery in Bend, OR, and 2-0 *A. grandis* containerized stock. Seed of each species was collected in 1971 from near the study site. Planting took place in the spring of 1974 and during the first two years, any seedlings that died were replaced by transplanted seedlings from outside the plots. In addition, the *C. velutinus*, *A. patula*, and *C. chrysophylla* were sprayed in June of 1976 and 1979 with herbicides to reduce competition (Seidel 1985).

Experimental Design

Each study was established under a completely randomized split-plot design in which the whole-plot factor was tree spacing and the split-plot factor was species composition. Pringle Butte was composed of five initial spacings: 1.8, 2.7, 3.7, 4.6, and 5.5 m (6, 9, 12, 15, and 18 feet). Species composition included pure *P. ponderosa*, pure *P. contorta*, and a 50:50 mix of both species. Treatment combinations were replicated twice, so each of the five spacings were randomly assigned to 10 whole plots, and subplots within each whole plot were randomly assigned a species mix. The size of the whole plots varied by spacing but each contained 147 to 390 measure trees.

Lookout mountain was composed of three initial spacings: 1.8, 3.7, and 5.5 m (6, 12, and 18 feet). The three species combinations in the subplots included pure *P. ponderosa*, pure *A. grandis*, and a 50:50 mix of both species. Each whole plot consisted of three subplots of the same spacing. The whole plots were of variable size, depending on spacing, and were designed so that each subplot had 24 measured trees. Three replications produced a total of nine whole plots and 27 subplots.

Plot Measurements

Data have been collected on each study for the past 20 to 30 years by the USDA Forest Service and more recently by Oregon State University. At Pringle Butte, diameter at breast height (DBH) of all plot trees was measured to the nearest 0.25 cm (0.1 in) in 1982, 1986, and 1992, and to the nearest 0.1 cm in May 2001. Total height (HT) of all plot trees was measured to the nearest 0.03 m (0.1 ft) in 1982, 1986, and 1992, and to the nearest 0.01 m during the summer of 2001, ignoring the current season's leader growth. Height to the lowest living branch (HLB, nearest 0.01 m) was also collected in 2001.

At Lookout Mountain, DBH of all plot trees was measured to the nearest 0.13 cm (0.05 in) in the fall of 1984, 1990, and 1995, and to the nearest 0.01 m in late summer 1999. Total height of all plot trees was measured to the nearest 0.03 m (0.1 ft) in the 1984, 1990, and 1995, and to the nearest 0.1 cm in late summer 1999.

Height to the lowest living branch to the nearest 0.01 m was also collected in late summer 1999.

Missing heights were predicted with a nonlinear regression model fitted to measure trees on the same plot and for the same measurement year:

$$\mathrm{HT} = 1.37 + \beta_1\, e^{\frac{\beta_2}{\mathrm{DBH}}} + \varepsilon$$

where the β_i's are parameters to be estimated from the data and all other variables are defined above. Any missing heights to lowest live branch were predicted using the following model, again fitted to data for the specific plot and year:

$$\mathrm{HLB} = \mathrm{HT}\left[1 + e^{\beta_0 + \beta_1 \mathrm{DBH} + \beta_2 \frac{\mathrm{DBH}}{\mathrm{HT}}}\right]^{-1} + \varepsilon$$

where the β_i's are parameters to be estimated from the data and all other variables are defined above.

Estimation of Productivity

Productivity was defined as the net growth of the initial stem volume (inside bark) expressed as a periodic annual increment. Stem shape has been successfully modeled with a variable exponent taper model (Kozak 1988; Garber and Maguire, in review):

$$\text{dib} = \alpha_1 \text{DBH}^{\alpha_2} X^{C} + \epsilon$$

where dib is the predicted diameter inside bark at some height h, $X = [1 - (Z)^{0.5}] / [1 - (p)^{0.5}]$, Z is the relative height h / HT, p is the relative height where shape of tree changes form neoloid to paraboloid, $C = f$ (Z and other tree variables), ϵ is the random error term, α_1 and α_2 are the parameters estimated from the data, and DBH and HT are defined above.

Individual tree volume was estimated as total (stump to tip) inside bark volume (VOL) by numerically integrating the taper function from 0.15 m to the tree tip:

$$\text{VOL} = (0.00007854) \times \int_{0.15}^{\text{HT}} \left(\hat{\text{dib}}\right)^2 dh$$

where, $\hat{\text{dib}}$ is the predicted diameter inside bark (cm) at height h (m). Plot volume (V) for a given year was then calculated as the sum of all individual tree volumes on the plot ($\text{m}^3\ \text{ha}^{-1}$) and periodic annual increment (PAI) was calculated as the average annual change in plot volume over the growth period ($\text{m}^3\ \text{ha}^{-1}\ \text{yr}^{-1}$).

Species mixtures were evaluated by assessing relative yield total (RYT) for each whole plot (Harper 1977; DeBell et al. 1997):

$$[3.1] \quad \mathrm{RYT} = \frac{Y_{A|B}}{Y_A} + \frac{Y_{B|A}}{Y_B}$$

where Y_A = yield of species A in the pure A subplot, Y_B = yield of species B in the pure B subplot, $Y_{A|B}$ = yield of species A in the mixed subplot, and $Y_{B|A}$ = yield of species B in the mixed subplot. Relative yields totals were computed as the average of all plots at a given spacing.

Statistical Analyses

Plot-level standing volume

The effects of spacing, species composition, and time on estimates of plot-level standing volume over the last *t* measurement periods were tested by two-way repeated measures analysis of variance for split-plot designs using the following mixed-treatment-effects model:

$$[3.2] \quad \mathbf{V}_{ijk} = \mu + \mathbf{SPACE}_i + \delta_{k(i)} + \mathbf{SPPCOMP}_j + (\mathbf{SPACE} \times \mathbf{SPPCOMP})_{ij} + \epsilon_{ijk}$$

where $\mathbf{V}_{ijk}$ is a $t \times 1$ vector containing standing volume at each measurement, μ is a $t \times 1$ vector of mean volumes, $\mathbf{SPACE}_i$ is a $t \times 1$ vector of effects for the ith level of spacing, $\delta_{k(i)}$ is a vector of whole-plot random errors, $\mathbf{SPPCOMP}_j$ is a $t \times 1$ vector of effects of the jth level of the species composition factor, $(\mathbf{SPACE} \times \mathbf{SPPCOMP})_{ij}$ is a $t \times 1$ vector of interaction effects between spacing and species composition, and ϵ_{ijk} is a vector of subplot random errors. Whole-plot and subplot errors are assumed to be random with mean $\mathbf{0}$ and variance σ_δ^2 and σ_ϵ^2, respectively.

Hypotheses of no time effect and time interactions with factors in [3.2] were tested with Wilks' Lambda (Johnson and Wichern 1998). Overall effects of spacing, species composition, and their interaction were tested by *F*-tests. Where the null hypothesis (no differences between the treatments) was rejected by the multivariate analysis of variance, the Bonferroni adjustment multiple range test was used to identify differences at selected ages ($\alpha \leq 0.05$).

Plot-level Periodic Annual Increment

Estimates of plot-level periodic annual increment were tested across three factors - spacing, species composition, and time by two-way repeated measures analysis of variance, with initial standing volume as a covariate. The statistical model was consistent with a split-plot design but was specified with the following mixed-effects model:

[3.3] $\mathbf{PAI}_{ijk} = \mu + \mathbf{SPACE}_i + \delta_{k(i)} + \mathbf{SPPCOMP}_j + (\mathbf{SPACE} \times \mathbf{SPPCOMP})_{ij} + \mathbf{V}_{ijk} + \epsilon_{ijk}$

where $\mathbf{PAI}_{ijk}$ is a $t \times 1$ vector of periodic annual increments for the three time periods, $\mathbf{V}_{ijk}$ is a $t \times 1$ vector containing initial plot volume, and μ, $\mathbf{SPACE}_i$, $\delta_{k(i)}$, $\mathbf{SPPCOMP}_j$, $(\mathbf{SPACE} \times \mathbf{SPPCOMP})_{ij}$, and ϵ_{ijk} are as above. Whole-plot and subplot errors are assumed to be random with mean $\mathbf{0}$ and variance σ_δ^2 and σ_ϵ^2, respectively.

Hypotheses of no time effect and time interactions in [3.3] were tested just as those in [3.2].

Relative yield totals

If there was no effect of each species on the other in the mixed plots, then each species should account for half the relative yield (0.5) and their RYT calculated from [3.1] should be one. Therefore, the null hypotheses of $RY = 0.5$ and $RYT = 1.0$ were tested using a univariate mixed-effects split-plot analysis of variance (Kuehl 2000). Overall effects of spacing, species, and their interaction were tested with contrasts and F-tests. Where the null hypothesis was rejected by the analysis of variance, the Bonferroni adjustment multiple range test was used to identify differences at selected ages ($\alpha \leq 0.05$).

RESULTS

Pringle Butte

Spacing had the most significant impact on standing volume per hectare ($p <$ 0.001). Species composition was only marginally significant ($p = 0.035$) while the interaction between spacing and species composition was marginally insignificant ($p =$ 0.077). In general, standing stand volumes were largest at the narrow spacings and decreased with increasing spacing (Fig. 3.1). Multiple comparisons at age 32 indicated that the 1.8- and 2.7-m spacings had significantly greater volumes then the 3.7-, 4.6-, and 5.5-m spacings (Table 3.1). The pure *P. contorta* and mixed plots

Table 3.1. Results of Bonferoni multiple range tests among the levels of spacing and species compositions at Pringle Butte. Means followed by the same letter indicate no significance at the experimentwise α-level of 0.05.

Factor Level	Means					
Spacing (m)	Stand volume at age 32 (m^3 ha^{-1})		PAI from ages 13-18 (m^3 ha^{-1} yr^{-1})		PAI from ages 23-32 (m^3 ha^{-1} yr^{-1})	
1.8	97.25	a	5.16	a	3.18	a
2.7	83.58	a	4.35	a	2.87	ab
3.7	53.23	b	2.86	b	1.99	bc
4.6	54.27	b	2.63	b	1.91	bc
5.5	44.50	b	2.23	b	1.63	c
Composition						
LP	69.16	a	3.77	a	2.21	a
MX	69.21	a	3.55	a	2.38	a
PP	61.33	a	3.02	b	2.35	a

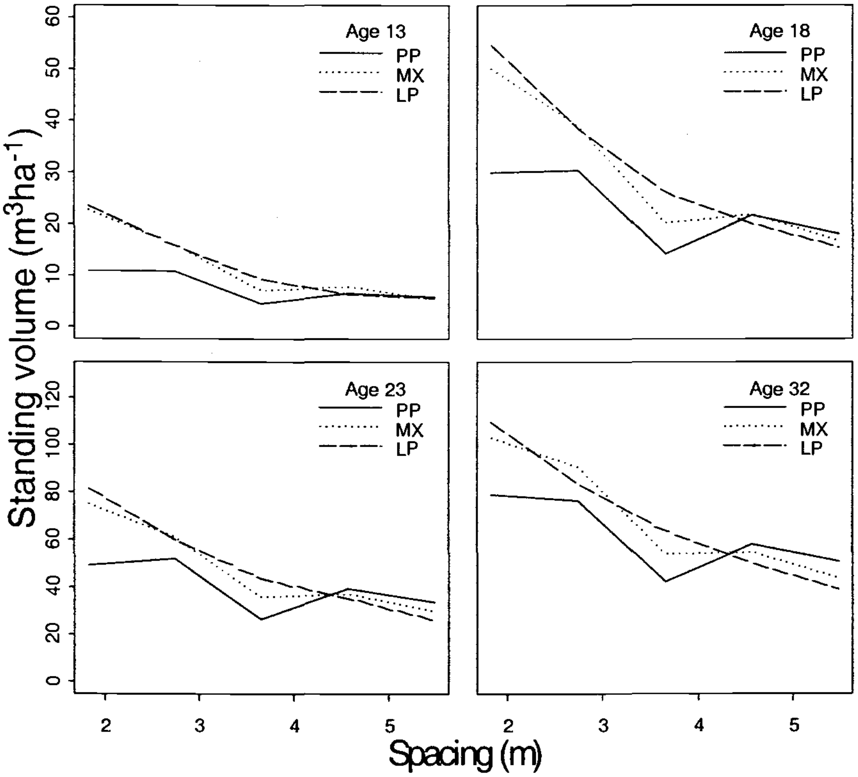

Figure 3.1. Plots of standing volume over treatment spacing for pure *Pinus contorta* (LP, dashed line), pure *Pinus ponderosa* (PP, solid line), and the mixture (MX, dotted line) at Pringle Butte: (a) age 13, (b) age 18, (c) age 23, and (d) age 32.

generally showed greater standing volumes than pure *P. ponderosa* plots at the higher densities through time. This however, was reversed at the wider spacings, where pure *P. ponderosa* plots had slightly greater standing volumes.

Not surprisingly, standing volume increased significantly over time ($p < 0.001$). In addition, the effect of species composition differed by growth period ($p = 0.019$), but the effects of spacing and spacing × species composition interaction did not vary significantly over time ($p = 0.063$ and $p = 0.269$, respectively). These results suggest that trajectories of standing volume for each species composition are somewhat different, but do not depend on spacing. Univariate ANOVA's (at each time period) showed a decreasing significance of SPPCOMP and the SPACE × SPPCOMP interaction over time. For example, total standing volume at age 13 was significantly affected by spacing and species composition, but the interaction was only marginally significant. By age 32, spacing was the only significant factor; species composition and the interaction between the two factors were no longer marginally significant ($p > 0.2$, Table 3.1). Initial differences in growth rates, especially between the pure *P. contorta* plots and pure *P. ponderosa* plots, have decreased with time regardless of spacing.

After correcting for initial volume, periodic annual increment did not differ significantly by growth period or among different levels of spacing and species composition. Similarly, this dependence of PAI on initial volume did not vary across growth periods (no interactions with time). However, if the initial volume was removed from analysis as a covariate, spacing, time, time × SPACE, and time × SPPCOMP all became significant. There was a general decrease in PAI with spacing regardless of time period ($p = 0.003$, Fig. 3.2). PAI also generally decreased over time

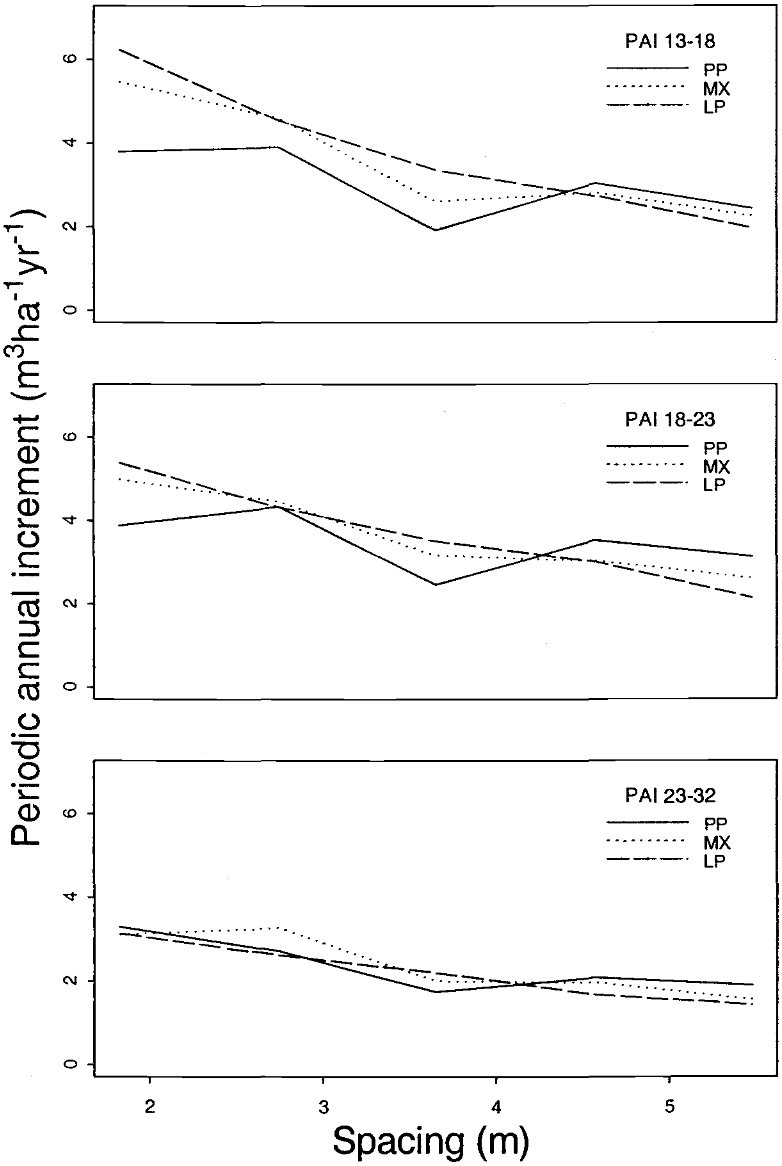

Figure 3.2. Plots of periodic annual increment on spacing for the three time periods for pure *Pinus contorta* (LP, dashed line), pure *Pinus ponderosa* (PP, solid line), and the mixture (MX, dotted line) at Pringle Butte: (a) from age 13 to 18, (b) from age 18 to 23, and (c) from age 23 to 32.

($p < 0.001$), although the effect of time depended on spacing ($p = 0.021$) and composition ($p = 0.005$, Fig. 3.2). Between years 13 and 18, highest PAI's were found on the pure *P. contorta* and mixed plots at the higher densities. PAI decreased for both of these compositions with decreasing density. In contrast, *P. ponderosa* PAI stayed roughly constant across density. Through time, PAI on the *P. contorta* plots and the mixed plots steadily declined at the 1.8- and 2.7-m spacings. PAI on the *P. ponderosa* plots at the 1.8- and 2.7-m spacings and all compositions at the three widest spacings increased during the period between 13 to 18 years old, then decreased thereafter. By the last growth period (23-32 years), PAI's, although still decreasing with spacing, were similar among the compositions at each spacing (Fig. 3.2c, Table 3.1). All spacings and compositions have reached their peak in PAI, although mean annual increments (MAI) are still increasing.

Relative yield totals for these two species were not significantly different than one (Fig 3.3a), indicating no benefits of the mixture in terms of total volume at age 32. At the closest spacing, *P. contorta* makes up the largest portion of the standing volume, although RY is not significantly different from 0.5. At the largest two spacings however, the relative yield of *P. ponderosa* is very similar to *P. contorta*.

Lookout Mountain

In contrast to Pringle Butte, spacing, species composition, and their interaction were all highly significant ($p < 0.001$). As at Pringle Butte, the largest standing

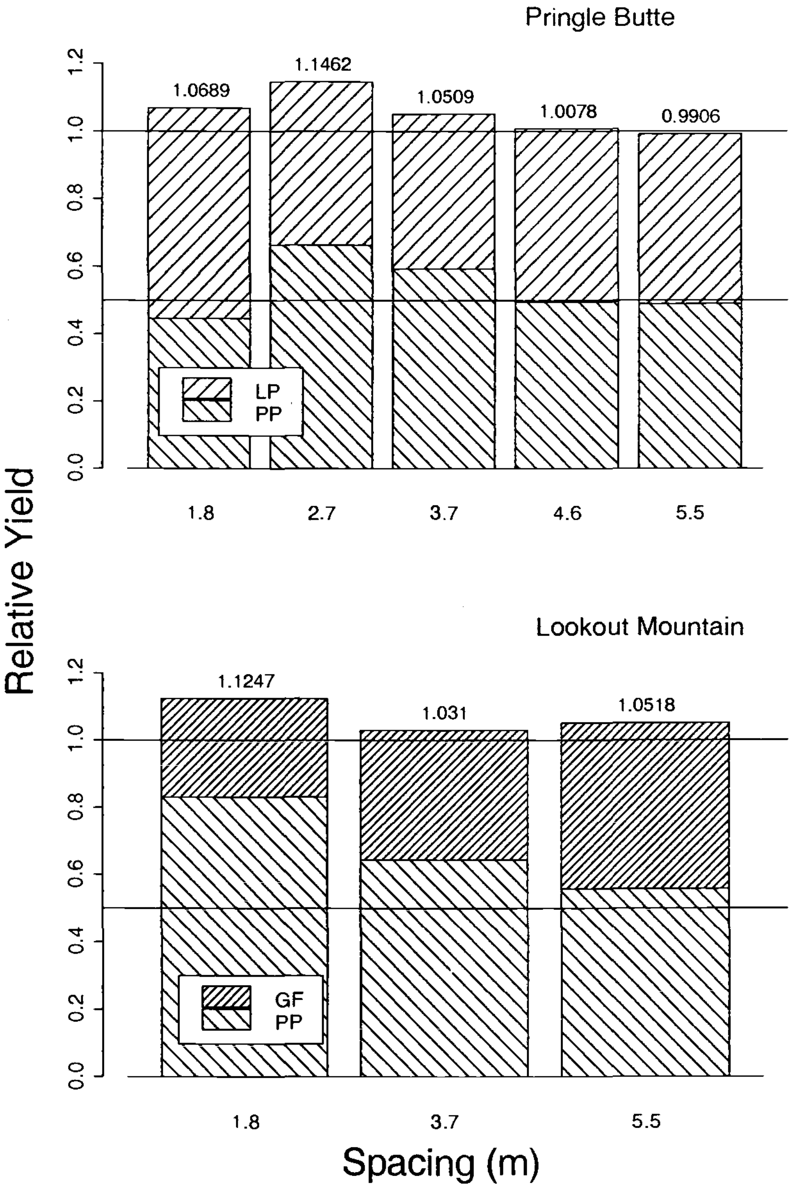

Figure 3.3. Bar plot of combined relative yields across spacings by component species (GF = *Abies grandis*, LP = *Pinus contorta*, and PP = *Pinus ponderosa*): (a) Pringle Butte and (b) Lookout Mountain. Numbers above the bars are relative yield totals.

volumes were present on the densest plots and decreased with increasing spacing at all time periods (Fig. 3.4). Multiple comparisons at age 28 indicated that volume declined significantly with successive increases in spacing (Table 3.2). Although differences in the 3.7- and 5.5-m spacings were small early on, significant differences have developed by age 28 (Table 3.2, Fig. 3.4). Differences between the pure *P. ponderosa* and the mixed plots were too small to distinguish statistically (Table 3.2). However, both had significantly larger standing volumes at age 28 than the pure *A. grandis* plots.

Table 3.2. Results of Bonferoni multiple range tests among the levels of spacing and species compositions at Lookout Mountain. Means followed by the same letter indicate no significance at the experimentwise α-level of 0.05.

Factor Level	Means					
Spacing (m)	Stand volume at age 28 (m^3 ha^{-1})		PAI from ages 13-18 (m^3 ha^{-1} yr^{-1})		PAI from ages 23-28 (m^3 ha^{-1} yr^{-1})	
1.8	128.98	a	5.83	a	9.71	a
3.7	78.10	b	2.77	b	7.23	b
5.5	50.80	c	1.66	c	5.03	c
Composition						
PP	108.00	a	5.05	a	8.05	a
MX	96.20	a	4.13	b	7.85	a
GF	53.69	b	1.08	c	6.08	b

Standing volume increased significantly over time ($p < 0.001$), but the effects of spacing and species composition changed by growth period ($p = 0.002$ and $p <$

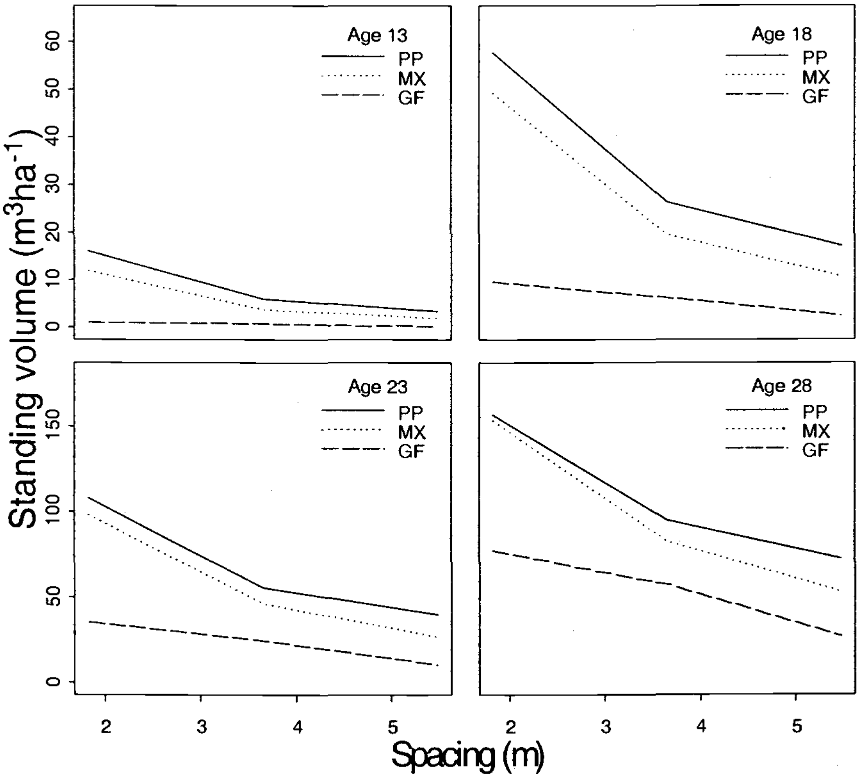

Figure 3.4. Plots of standing volume over treatment spacing for pure *Abies grandis* (GF, dashed line), pure *Pinus ponderosa* (PP, solid line), and the mixture (MX, dotted line) at Lookout Mountain: (a) age 13, (b) age 18, (c) age 23, and (d) age 28.

0.001, respectively). Repeated measures ANOVA on PAI's for the three growth periods reaffirmed these time dependent effects. After accounting for initial volume, overall periodic growth was not significantly affected by spacing, species composition, or their interaction ($p = 0.067$, $p = 0.084$, and, $p = 0.124$, respectively). However, as with *P. contorta* / *P. ponderosa* study at Pringle Butte, analysis without initial volume as a covariate indicated all factors and time interactions were significant.

Multiple comparisons of PAI's show statistical differences among all three spacings regardless of growth period (Table 3.2). Largest PAI's were found in the closest spacings while the plots at the widest spacings had the lowest (Fig. 3.5). Relative and absolute differences in growth rates among the compositions have decreased over time, especially at the closer spacings (Table 3.2, Fig 3.5). For the growth period representing ages 13 to 18, PAI was significantly different among the differing levels of species composition (Table 3.2). PAI's were highest for the pure *P. ponderosa* plots followed successively by the mixture and pure *A. grandis* plots. By the most recent growth period, differences between the mixture and the pure *P. ponderosa* plots were not statistically significant, however were still greater than pure *A. grandis* plots. With the exception of the 1.8-m pure *P. ponderosa* plots, periodic annual increments are increasing through age 28 for all spacings and levels of species composition. MAI is also increasing with time at all spacing and compositions.

Relative yield totals for this study all exceeded one (Fig. 3.3b), and significantly so for the 1.8- and 5.5-m spacings ($p < 0.035$). Relative yield was significantly influenced by species ($p = 0.004$), while the interaction between spacing and species was marginally insignificant ($p = 0.052$). The highest RYT was found in the 1.8-m spacing, suggesting a greater complementary yield effect at close spacings. Of this total, the *P. ponderosa* component made up approximately 83% of the standing

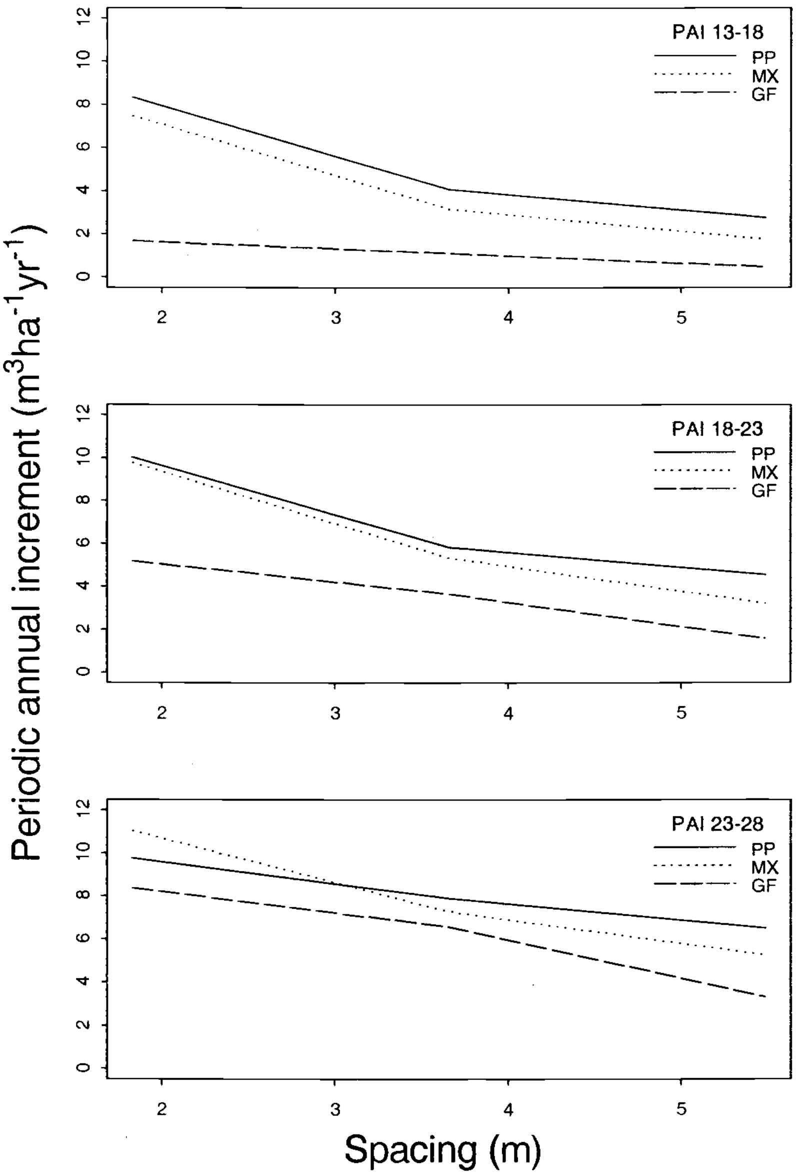

Figure 3.5. Plots of periodic annual increment on spacing for the three time periods for pure *Abies grandis* (GF, dashed line), pure *Pinus ponderosa* (PP, solid line), and the mixture (MX, dotted line) at Lookout Mountain: (a) from age 13 to 18, (b) from age 18 to 23, and (c) from age 23 to 28.

volume at the 1.8-m spacing, which was significantly greater than 0.5. At the 3.7-m and 5.5-m spacings, RY's were not significantly different than 0.5.

DISCUSSION

Much debate surrounds production of mixed-species stands versus monocultures. Results in this study suggest no yield gains in mixtures of *Pinus contorta* and *Pinus ponderosa* relative to pure stands of either. However, there was evidence to suggest otherwise in mixtures of *Abies grandis* and *P. ponderosa*, where relative yield totals were slightly, but significantly, greater than one in the closest and widest spacings (Fig 3.3b). In agronomy, replacement series studies on herbaceous species have generally shown that mixtures are less productive than monocultures of the highest yielding component of the mixture (Trenbath 1974; Harper 1977). Similar trends have also been reported in several studies in forestry. Assmann (1970) described a series of even-aged, mixed-species plantation studies from Switzerland and Germany. In four of the studies, mixtures of *Pinus sylvestris* L. and *Picea abies* (L.) Karst., *P. sylvestris* and *Fagus sylvatica* L., *Quercus patraea* L. and *F. sylvatica*, and *F. sylvatica* and *P. abies*, yields in mixtures exceeded yields of the intolerant species, but were equal to or less than yields (empirical or tabular) of the shade tolerant species. Similar results were reported in mixed stands of *Betula* species (*Betula pubescens* Ehrh. and *Betula pendula* Roth) and either *P. abies* or *P. sylvestris* (Frivold and Frank 2002). Moreover, in a study in Utah, pure *Abies lasiocarpa* Hook

(Nutt.) stands produced more in monocultures than in mixtures with *Pinus contorta* var. *latifolia* Dougl. (Smith and Long 1992). However, because many of these studies were naturally regenerated stands with a limited range of densities, or not strictly controlled, other factors could have complicated the results. Regardless, this has by far been the dominant working hypothesis, and it has been supported by considerable experience within mixed-species production research in agronomy and forestry (Kelty 1992).

Several other studies have reported more standing basal area or volume in mixtures without comparisons to pure stands of the highest yielding species. In mixed stands of *Pinus strobus* L., *Picea rubens* Sarg., and *Tsuga canadensis* (L.) Carr., higher basal areas and volumes were reported in mixtures with a *P. strobus* overstory than without (Fajvan and Seymour 1999). *P. strobus* decreased the yields of the *P. rubens* and *T. canadensis*; however, the gain with respect to the sum of all three species far exceeded the loss in the lower strata. Similarly, Kelty (1989) compared hardwoods stands with and without a *T. canadensis* understory component. Hardwood growth was slightly less in mixtures than in the pure hardwood stands, however, the growth of the understory *T. canadensis* significantly increased stand basal area and volume production, and was considered to be nearly additive. Neither of these studies made comparisons to pure *T. canadensis* stands nor was density or age controlled.

Few studies of herbaceous communities have found larger biomass production from mixtures (Trenbath 1974; Jolliffe et al. 1984). As suggested above, very little experimental work has been done in forestry, although Assmann (1970) also reported that volumes in *Larix decidua* Miller and *F. sylvatica* mixtures exceeded pure stands of *F. sylvatica* by 18%, and *P. abies* and *Abies alba* Miller mixtures exceeded biomass production of pure stands of *A. alba* by 15-37%. Likewise, basal area production of mixtures exceeded basal production of the most shade tolerant component in mixtures of *P. sylvestris* and *P. abies* at all sites and ages (Poleno 1981, cited in Kelty 1989), *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg. (Wierman and Oliver 1979), and *P. menziesii* and *A. grandis* (Larson 1986). It is important to keep in mind, however, that the latter two comparisons were not performed in the context of a controlled experiment. In naturally occurring stands, trends in site productivity may parallel changes in species composition. Recently however, several detailed replacement series studies in the tropics and subtropics have demonstrated large gains in standing volume of *Eucalyptus* species (*Eucalyptus globulus* Labill. and *Eucalyptus saligna* Sm.) when planted with *Acacia mearnsii* de Wild or *Albizia falcataria* (L.) Forberg (DeBell et al. 1997; Khanna 1997; Bauhus et al. 2000). In two cases, relative yield totals were reported greater than 1.6 (Debell et al. 1997; Bauhus et al. 2000).

Kelty (1992) suggested greater production in mixtures would require interactions among the species to be characterized by competition reduction or facilitation. Competition reduction can be achieved if there is significant niche separation between species. Although niche separation encompasses numerous possible mechanisms, some aboveground and some belowground, one of the major concepts is that resources exploited by one are relatively unexploited by the other (Kelty 1989). From an aboveground perspective, species can stratify within the canopy. Intolerant species, such as *P. contorta* and *P. ponderosa*, in the overstory may utilize higher light intensities better than shade tolerant species due to their higher light saturation points (e.g. Fajvan and Seymour 1993, 1999). Presence of a more shade tolerant species, such as *A. grandis*, in the lower stratum may increase stand production due its ability to make use of light that a shade intolerant would not be able to use (Kelty 1989). In this case, the shade tolerant species has a higher light compensation point than the shade intolerant species (Perry 1994).

Niche separation may also occur belowground. For example, if different species tend to root in a different soil horizon, an increase in resource use may occur (Brown 1992; Rothe and Binkley 2001). Schmid and Kazda (2001) examined the rooting architecture of *P. abies* and *F. sylvatica* in pure and mixed stands. Their results suggest that the two species occupy the same soils depths, but at different proportions. Moreover, in mixtures, the species rooting habits changed slightly. Changes in rooting structure may result in more complete use of available soil resources, in turn increasing productivity. Note, however, that for a gain in total production, the species involved have to either make use of some resources that would otherwise remain unutilized, or growth per unit of resource would have to increase. Rooting patterns were not investigated during this study; however, due to the dryness of these sites and different rooting depths of these species, belowground niche separation may be a mechanism increasing resource use, especially in *A. grandis-P. ponderosa* mixtures.

Facilitation is the result of a synergistic interaction among the species whereby one provides resources that otherwise would not be available for the other. The most common example of this occurs in mixtures with legumous species associated with nitrogen fixing bacteria (e.g., *Frankia* spp., *Rhizobia* spp., etc.). For example, mixtures of *Eucalyptus* species and *Acacia* or *Albizia* produce a higher biomass in the *Eucalyptus* species component than in pure stands of *Eucalyptus* at comparable densities (DeBell et al. 1997; Khanna 1997; Bauhus et al. 2000). Such facilitative mixtures may also occur in the temperate forests of the United States and Canada with conifers and *Alnus* species, especially on infertile sites (Miller and Murray 1979; Binkley 1984a, 1984b), but not necessarily on higher sites (Miller et al. 1999). Facilitation may also occur as a result of hydraulic redistribution whereby deep rooting species release water to the surface rooting horizons. Hydraulic redistribution has been shown to be a significant source of daily evapotranspiration in forests that experience prolonged drought periods such as the Oregon pumice region (Brooks et al. 2002). Although data were not available in this study, redistribution of water may be a possible mechanism explaining the slight relative yields gains in mixtures of the deeper rooting *P. ponderosa* and more shallow rooting *A. grandis* at Lookout Mountain.

Even-aged, single-species stand development has generally been classified into four stages (Oliver 1981; Oliver and Larson 1996). Stand initiation ensues from disturbances large and intense enough to remove all of the existing stand, thereby creating for the development of a new cohort of vegetation. Species begin to interact intensely during the stem exclusion stage. This stage occurs when the existing trees usurp site resources and prevent establishment of additional stems on the site. Typically, the most limiting resource is considered to be light (Oliver and Larson 1996), although trenching experiments implicate soil moisture as well, even under closed canopies (Lutz 1945). On drier sites stands like *P. ponderosa* forests of the interior west can be open in canopy structure due to moisture limitations (Cochran et al. 1994; Ryan and Yoder 1997). Regardless, as stands develop, individuals on poorer microsites, with poorer genotypes, or with a slow start lag behind in height growth. Consequently, crown differentiation occurs, and some individuals become overtopped and can eventually die (Oliver and Larson 1996; Smith et al. 1997). Canopies in mixed-species stands not only differentiate on the basis of genetics and microsite, but they also stratify by species grouping (Larson 1986; Kelty 1989; Oliver et al. 1990; Cobb et al. 1993; Oliver and Larson 1996). The process of stratification is a function of many silvical attributes. In mixed stands, differences exist in the ability of species to occupy niches relative to its competitors (Kelty 1989, 1992). For example, intolerant species tend to grow faster in height, due in part to higher photosynthetic rates, but also by allocating more fixed carbon to stemwood than more shade tolerant species earlier in their life (Wang et al. 2000). The intolerant species dominate the upper canopy layers, relegating tolerant species to lower strata. Many of the differences in the Pringle Butte and Lookout Mountain studies can probably be attributed to differences in species shade tolerances and early growth rates. *P. contorta* would be considered the most shade intolerant of the three species studied, and would be expected to exhibit faster early growth rates relative to the other two species (Seidel 1987; Cobb et al. 1993). Shade intolerant species experience intense selective pressure to express rapid early growth to maintained well-lit social positions. At the other end of the spectrum, shade-tolerant species like *A. grandis* reach their exponential growth rate somewhat later, and perhaps for a longer duration, and they are able to survive in shade despite drastic reductions in growth rates (Larson 1986; Cobb et al. 1993). Examples of stratified mixtures are plentiful. *Alnus rubra* Bong. can easily out grow *T. heterophylla* and *Thuja plicata* Donn. ex D. Don in coastal forests of the Pacific Northwest, quickly overtopping them (Stubblefield and Oliver 1978). *P. menziesii* can similarly be overtopped by the intolerant *Larix kaempferi* (Lamb.) Carr. on North Island of New Zealand (West 1991). In stands of *P. menziesii* and *T. heterophylla*, *P. menziesii* is regarded as moderately shade intolerant, and can overtop the *T. heterophylla* component after 20 to 40 years (Wierman and Oliver 1979). Likewise, *Betula papyrifera* Marsh. outgrows *A. lasiocarpa* in the sub-boreal zone of British Columbia (Wang et al. 2000). Stratification in all these studies was attributed to the slightly faster height growth rate of the intolerant species rather than to any age differences among the species.

As stand development continues, these relative positions may change as well. The tolerant species may later catch up with the intolerant species and even displace it from the upper canopy positions. At Pringle Butte, the pure *P. ponderosa* plots have nearly overcome the fast initial growth of the pure *P. contorta* plots. Similar results on the east slopes of the Washington Cascades were reported where shade tolerant *A. grandis* dominated *P. menziesii* in mature stands (Larson 1986). Stand reconstruction demonstrated that *P. menziesii* was the dominant species for the first 50 years due to its faster juvenile growth. *A. grandis* was relegated to the lower canopy layer during those 50 years because it was not able to maintain height growth. However, when these stands reached 50 years of age, the more vigorous codominant and dominant *A. grandis* gradually displaced the *P. menziesii* in the overstory. This same pattern was also observed in central hardwood forests of southern New England (Oliver 1978). *Betula lenta* L. and *Acer rubrum* L. dominated the upper stratum through early stand development, but the more tolerant *Quercus rubra* L. trees caught up and subordinate *B. lenta*.

Pringle Butte and Lookout Mountain studies underscore some variations on the above theory. The rate of stratification in species mixtures is predominately a function of three factors: (*i*) the relative height growth rates of the species in open-grown conditions; (*ii*) the rate of crown closure of shade intolerant species over shade tolerant species; and (*iii*) the proportional height growth reduction of shade tolerant species with a decrease in light intensity from full sun. In most studies of stand dynamics, stand density was not controlled or manipulated, and therefore largely was ignored as a factor in stand development. Results presented here in both *P. contorta* - *P. ponderosa* and *P. ponderosa* - *A. grandis* suggest that spacing is an important factor in the interaction of these species. At high densities, rapid overtopping by the faster growing intolerant species was expected and observed. In contrast, at wider spacings the more shade tolerant species was less rapidly and less completely overtopped. Therefore, the relative contribution of each species to stand growth was dependent on stand density. For example, in the Lookout Mountain study, the *A. grandis* component dramatically increased with a decrease in stand density on mixed plots (Fig. 3.3b). At the higher densities, *A. grandis* was clearly subordinate to *P. ponderosa* in the mixed plots, but at wider spacings, both species were able to maximize their growth and contribute more equally to stand volume production. This concept is also evident at Pringle Butte where *P. contorta* dominates total volume at the densest spacings and the *P. ponderosa* plots dominates total volume at the widest spacings. This difference can be attributed to a dramatic height response of *P. ponderosa* to increased spacing at Pringle Butte, regardless of species composition. Height response of *P. ponderosa* to spacing was not as clear on the more mesic Lookout Mountain sites. Traditionally, dominant height has been found relatively insensitive to stand density (Smith et al. 1997); however, there is some evidence indicating reduced height growth with increasing spacing on xeric sites (Curtis and Reukema 1970; Barrett and Roth 1985). Spacing of interacting trees was also implicated in two different stand development patterns in mixtures of *Quercus falcata* var. *pagodifolia* Ell. and *Liquidambar styraciflua* L. (Clatterbuck and Hodges 1988).

Stand development in mixtures may also be influenced by the composition itself. For example, presence or absence of certain species may influence development and observed stand structure. In the present study, *P. ponderosa* was found in the upper and lower strata depending on whether it was mixed with *A. grandis* or *P. contorta*, respectively. This has also been documented elsewhere. On the east slopes of the Cascades even-aged mixtures of *Larix occidentalis* Nutt., *P. contorta*, *P. menziesii*, and *A. grandis* often form two distinct strata, *L. occidentalis* and *P. contorta* in the upper strata and *P. menziesii*, and *A. grandis* in the lower stratum (Cobb et al. 1993). In stands without a component of *P. contorta*, *P. menziesii* can overtop *A. grandis* forming a third stratum. Moreover, growth of understory *A. grandis* improves in absence of a *P. menziesii* layer. Likewise, the presence of *P. strobus* suppressed the growth of *P. rubens* and *T. canadensis* in the northeast (Fajvan and Seymour 1999). Similarly, *Quercus falcata* var. *pagodifolia* is relegated to a lower stratum in the presence of faster growing *Platanus occidentalis* L. (Oliver et al. 1990) and *Liriodendron tulipifera* L. (O'Hara 1986), but is dominant when grown with *L. styraciflua* (Clatterbuck and Hodges 1988).

Many of the above studies describe processes in stands that exhibit a rather thorough intermixing of species, specifically a random distribution of seed of all species across the stand at stand initiation. However, this may not always be the case. Stands with a high degree of species clumping, would probably develop quite differently than those natural stands investigated in previous studies and in controlled experiments like the Pringle Butte and Lookout Mountain spacing trials. Clumped stands may behave more similarly to an aggregation of even-aged, single-species stands, and may not differentiate as they would under more complete interspersion (Hibbs 1982).

In many studies, relative yields in mixtures have been computed as a ratio of yield in a mixture to an expected yield at the same density derived from yield tables (e.g. Wierman and Oliver 1979). Jolliffe et al. (1984) discusses some of the disadvantages of this approach. Serious shortcomings occur when results are interpreted at the individual tree level or distinguishing between intraspecific and interspecific competition. This may be a source of some discrepancies in literature; estimates of expected yields from yield tables assume accurate estimates of site and density, uniform early stand development, and comparable silvicultural treatments. In contrast, comparisons for the Pringle Butte and Lookout Mountain studies were made to empirical controls on the same site.

Implications of this study for density management in mixed-species stands are far reaching. Conventional stand dynamics and volume production in mixed-species stands may suggest that one species may relegate another species to a subordinate position, for example, *P. ponderosa* mixed with *A. grandis* at tight spacings. In some cases this may be beneficial, for example if some sort of vertical structure is desired for habitat or edge aesthetics, or where natural stratification patterns produce desired wood quality (Clatterbuck and Hodges 1988). On the flip side, if volume production of the two species is of interest, results here suggest density can be altered to obtain the desired yield of each species. For example, wider spacings can be used to obtain more equal production of component species that stratify at close spacings. This however is not universal. Some species, especially hardwoods, stratify more a wider spacings than at close spacings due to crown expansion, which may result in poorer wood quality (Clatterbuck and Hodges 1988). In such cases, higher densities would be desirable. Density can be controlled at planting, as in this study, or later in stand development by precommercial or commercial thinning. Thinning has traditionally been presented as a method to maintain or increase individual tree growth (Nyland 1996; Smith et al. 1997). By changing growth, thinning may also serve to change the growth trajectories of some component species in the stand, thereby changing the structure and dynamics of the stand.

Species mixtures have the ability to equal the growth of pure stands of the highest yielding component of the mixture (Assmann 1970). However, relative performance of the individual component species depends on the stand density and age of the stand. Intolerant species have faster early growth rates which allows them to quickly occupy upper strata. However, results suggest that stand density can be manipulated at planting or perhaps later on in stand development by thinning to alter these patterns, resulting more or less equal growth among the species. As a result, future studies comparing the mixture to monocultures must consider stand density and spatial distribution. Moreover, future work on the effects of thinning on stand dynamics in species mixture is recommended.

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CHAPTER FOUR: INDIVIDUAL TREE VERTICAL FOLIAGE DISTRIBUTIONS IN TWO CENTRAL OREGON SPECIES MIXTURES

ABSTRACT

Allometric equations were developed to estimate branch and tree leaf areas for grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in two mixed-species spacing trials in the central Oregon Cascades. Branch leaf area for a given branch diameter decreased at the base of the live crown in all tree species, reinforcing the importance of accounting for branch position within the crown. Tree leaf area was predicted well using sapwood area at crown base, consistent with the pipe-model theory, but the most consistent predictor was the product of basal area and crown ratio above breast height. This variable is more convenient to measure and circumvents the problem of estimating sapwood taper to crown base if sapwood area is measured at breast height. The performance of sapwood area at breast height was inconsistent among the species, while crown length performed most poorly. Both branch and tree equations differed significantly between the study sites in *P. ponderosa*, suggesting variation in allometric relationships and in leaf area: sapwood area ratios between the two sites. The higher ratio was found on the more xeric, slower-growing site, contradictory to existing theory. Individual tree relative vertical foliage distributions of *A. grandis* and *P. ponderosa* shifted up with a decrease in tree

height relative to the tallest tree on the plot, while increased spacing resulted in a downward shift in relative foliage distribution on *P. ponderosa* at Lookout Mountain. Profiles also indicate the influence of spacing and competing species on absolute foliage distributions. Future studies should account for tree age and stand conditions, in addition to its relative tree height when assessing foliage distributions.

INTRODUCTION

Net primary productivity (NPP) of forest ecosystems is the product of its structure and function. NPP occurs as a result of photosynthesis, whereby plants utilize energy in sunlight to fix or assimilate carbon and build biomass. Leaf area determines the capacity of a canopy to absorb photosynthetically active radiation (PAR) (Perry 1994). Foliage is the predominant source of fixed carbon in temperate trees since the energy absorbed from PAR fuels the process of photosynthesis.

In addition to total leaf area, forest NPP is determined by the photosynthetic efficiency or the net assimilation rate per unit of foliage (Waring 1983; Vose and Allen 1988; Perry 1994). The wide vertical distribution of leaf area and associated attenuation of light cause the distribution of foliage within the crowns of trees and canopies of stands to also be an important determinant of NPP due to its effect on photosynthetic efficiency. Photosynthesis and stomatal conductance have been shown to vary among crown positions and leaf ages (Woodman 1971; Brooks et al. 1991), and foliage distribution is directly linked to light interception and penetration (Grace et al. 1987; Baldwin et al. 1997). In short, foliage distribution plays a large role in tree-level and stand-level production efficiency and NPP.

Stand structure is the distributions and spatial arrangement of above- and below-ground components of the forest. Different combinations of species are known to produce forest structures not generally found in single-species stands (Kelty 1989; Oliver and Larson 1996; DeBell et al. 1997; Bauhus and Messier 1999; Schmid and Kazda 2001). However, foliage distribution and production efficiency are poorly understood in species mixtures. Schmid and Kazda (2001) assessed the belowground distribution of fine roots and found that differences in rooting patterns were accentuated in mixtures relative to monocultures. Much work has been done on developmental patterns in naturally established mixed-species stands, demonstrating stratification patterns and stand structures not generally found in single-species stands (Wierman and Oliver 1979; Oliver and Larson 1996). Vertical foliage profiles for individual trees generally exhibit an upward shift in foliage with decreasing relative height, height of a trees relative to the tallest tree in the stand (Maguire and Bennett 1996; Gilmore and Seymour 1997). Stratification in species mixtures suggests that patterns of foliage distribution may be further exaggerated in mixtures. Such changes in crown structure and foliage distribution can alter the photosynthetic efficiency and forest production.

This study was part of an effort to understand stand dynamics and production efficiency in two mixed-species spacing trials in central Oregon pumice region. The objectives of this study were to test the effects of spacing and species composition on vertical distribution of foliage. Pursuit of these objectives required development of allometric equations for predicting leaf area on individual branches and equations for predicting total tree leaf area.

METHODS

Study sites

The study was conducted at two sites. The first site, Pringle Butte, is a mixture of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). The second site, Lookout Mountain, is a mixture of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and *P. ponderosa.* Both sites are east of the Cascade Range crest, 35 miles southwest of Bend, in the Pringle Falls Experimental Forest, Deschutes National Forest, Deschutes County, Oregon.

Pringle Butte site

The Pringle Butte study site is located on the northwest-facing slope of Pringle Butte at an elevation of 1,370 m ($43^{o}43'$N, $121^{o}37'$W). Slopes range from 4 to 27 percent, with an average of 10 percent. Mean annual precipitation is only 61 cm and falls predominantly between the months of October and April, with a half-meter snow pack common between January and March. Maximum temperatures occur in July, averaging 26^{o}C, and frosts can occur at any time during the year (Cochran and Barrett

1999a). The soils in this area have been typed as a developing Xeric Vitricryands on 75 cm of dacite pumic from the eruption of Mount Mazama (Cochran and Barrett 1999a). This pumice layer overlays sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments.

The study area is 3.9-ha, clearcut in 1970. The ground cover consists of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), scattered Ross sedge (*Carex rossi* Boott), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and western needle grass (*Stipa occidentalis* Trub. ex Wats.). Small amount of dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) was present in the stand. *P. ponderosa* site index (base age 100) has been estimated at 24 m using Meyer's (1961) curves and 33.5 m using Barrett's (1978) method (Cochran and Barrett 1999a).

Lookout Mountain site

The Lookout Mountain study site is located on the northeast-facing slope of Lookout Mountain at an elevation of 1550 m (43°49' N, 121°41' W). Slopes average close to 20-percent. Average annual precipitation is approximately 100 cm, most of which falls as snow between the months of September and May. Generally, summers are hot and dry, with temperatures ranging from 21 to 32°C. Nights are predominantly cool with the chance of frost occurring any time during the year (Cochran and Barrett

1999b). Soils are deep, well-drained Typic Cryorthents, developed from dacite pumice originating from the eruption of Mount Mazama, overlaying a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments (Seidel 1985; Cochran and Barrett 1999b).

This study site is 8.1-ha, clearcut in 1974 in a mixed-conifer/snowbrush-chinkapin plant community (Seidel 1985). The ground cover consists primarily of *C. velutinus*, *A. patula*, and golden chinkapin (*Castonopsis chrysophylla* (Dougl.) A. DC.) (Seidel 1985). *C. velutinus* ground cover is very dense over much of the study site. The late successional plant community association is *Abies concolor/Ceanothus velutinus* (Franklin and Dyrness 1973). Site index (base age 100) for *P. ponderosa* (Meyer 1961) is about 27.5 m (Seidel 1985).

The site was planted with 2-0 bare root *P. ponderosa* stock grown at the USDA Forest Service nursery in Bend, OR, and 2-0 *A. grandis* containerized stock. Seed of each species was collected in 1971 from near the study site. Planting took place in the spring of 1974 and during the first two years, any seedlings that died were replaced by transplanted seedlings from outside the plots. In addition, the *C. velutinus*, *A. patula*, and *C. chrysophylla* were sprayed in June of 1976 and 1979 with herbicides to reduce competition (Seidel 1985).

Experimental Design

Each study was established under a completely randomized split-plot design in which the whole-plot factor was tree spacing and the split-plot factor was species composition. Pringle Butte was composed of five initial spacings: 1.8, 2.7, 3.7, 4.6, and 5.5 m (6, 9, 12, 15, and 18 feet). Species composition included pure *P. ponderosa*, pure *P. contorta*, and a 50:50 mix of both species. Treatment combinations were replicated twice, so each of the five spacings were randomly assigned to 10 whole plots, and subplots within each whole plot were randomly assigned a species mix. The size of the whole plots varied by spacing but each contained 147 to 390 measure trees.

Lookout mountain was composed of three initial spacings: 1.8, 3.7, and 5.5 m (6, 12, and 18 feet). The three species combinations in the subplots included pure *P. ponderosa*, pure *A. grandis*, and a 50:50 mix of both species. Each whole plot consisted of three subplots of the same spacing. The whole plots were of variable size, depending on spacing, and were designed so that each subplot had 24 measured trees. Three replications produced a total of nine whole plots and 27 subplots.

Fieldwork

Destructive sampling

In August and September of 2001 a total of 94 trees was selected for destructive sampling in close proximity to each of the study sites. All trees were selected prior to felling to match the range in local density, age, size, and species corresponding to trees on the study plots. Selected trees were also mostly free of *A. americanum*. Of these 94 trees, 23 were *A. grandis*, 22 were *P. contorta*, and 49 were *P. ponderosa* (Table 4.1). Before felling, four attributes were recorded for each sample tree: (*i*) diameter at breast height, DBH (to the nearest 0.1 cm), (*ii*) total tree height, HT (to the nearest 0.01 m), (*iii*) height to the crown base, HCB (to the nearest 0.01 m), defined as the lowest whorl with three or more living branches (Kenefic and Seymour 1999), and (*iv*) height to the lowest living branch, HLB. Each sample tree was felled in a manner that minimized foliage loss and breakage. A metric tape was stretched along the bole from base to tree tip. Total height from the base of the stump to the tip of the tree was recorded. The crown was then divided into thirds by marking each third on the tree bole. Basal diameters and height of each live branch were measured to the nearest millimeter and centimeter, respectively. Branch measurements were made by whorl, starting from the top whorl and proceeding in a counterclockwise direction from the tape within each whorl. A total of six whorl branches, free of *A. americanum*, two from each crown third, and three interwhorl branches (*A. grandis* only), one from each crown third, were selected at random. Sample branches were then cut at the base. A subsample of approximately 100 fresh needles across each age class were randomly removed in rough proportion to the various ages classes on the sample branch, placed in a plastic bag, and stored in a

Table 4.1. Mean and range for tree characteristics from destructive sampling by study site and species.

Parameter	Pringle Butte *Pinus contorta*	Pringle Butte *Pinus ponderosa*	Lookout Mountain *Abies grandis*	Lookout Mountain *Pinus ponderosa*
Sample size				
Trees	22	24	23	25
Total branches	2490	1266	5041	1309
Subset branches	132	144	207	114
Branch diameter (mm)				
Min.	1.0	2.0	1.0	3.0
Mean	13.5	23.3	9.9	28.1
Max.	59.0	72.0	43.0	78.0
Depth into crown (m)				
Min.	0.04	0.00	0.06	0.16
Mean	3.37	3.21	4.46	3.95
Max.	11.10	10.58	13.43	11.97
Subset branch diameter (mm)				
Min.	1.0	4.0	1.0	3.0
Mean	13.0	21.1	9.2	26.1
Max.	45.0	64.0	32.0	61.0
Subset branch depth into crown (m)				
Min.	0.13	0.20	0.06	0.30
Mean	3.52	2.92	3.83	3.80
Max.	9.71	9.28	13.02	10.69
Subset branch leaf area (m^2)				
Min.	0.00	0.02	0.00	0.01
Mean	0.35	0.96	0.14	1.32
Max.	3.04	7.30	1.99	6.63
DBH (cm)				
Min.	2.60	2.00	2.50	5.00
Mean	14.24	16.05	12.84	19.62
Max.	26.10	32.30	26.80	38.30
Total Height (m)				
Min.	2.41	2.11	2.16	3.26
Mean	8.02	8.27	8.09	9.74
Max.	11.35	13.08	14.52	13.70
Crown length (m)				
Min.	1.94	1.26	1.79	2.02
Mean	6.96	5.77	7.54	7.87
Max.	11.10	10.58	13.43	11.97

cooler for transport to the laboratory. The remaining portions of the branch were clipped into segments and placed in paper bags. After branch sampling, the tree was bucked into sections, and thin (1 cm) disks were removed for sapwood measurement and labeled. Disks were extracted from 0.3 meters, breast height (1.37 meters), crown base, and each third of the crown.

Plot sampling

In June and July of 2001 two sample trees, one from each of the two larger thirds of the diameter range, were selected at random from each subplot at Pringle Butte and Lookout Mountain for a total of 114 trees. Of these trees, 27 were *A. grandis*, 30 were *P. contorta*, and 57 were *P. ponderosa*. Table 4.2 shows the mean sample tree characteristics. For each sample tree, three attributes were recorded: (*i*) diameter at breast height (to the nearest 0.1 cm), (*ii*) total tree height (to the nearest 0.01 m), and (*iii*) height to the crown base (to the nearest 0.01 m), defined as the lowest whorl that has at least one live branch and contiguous with the main crown. On every whorl from the base of the stump to the tree tip, height of attachment (nearest 0.01 m) and basal diameter (nearest mm) of each branch on each sample tree were measured and recorded as living or dead.

Table 4.2. Mean and range for tree characteristics from intensive plot tree sampling by study site and species.

	Pringle Butte		Lookout Mountain	
Parameter	*Pinus contorta*	*Pinus ponderosa*	*Abies grandis*	*Pinus ponderosa*
Sample size				
Trees	30	30	27	27
Total branches	5180	2899	10170	2718
Branch diameter (mm)				
Min.	1.0	1.0	1.0	2.0
Mean	16.4	25.0	8.9	30.6
Max.	57.0	131.0	55.0	77.0
Depth into crown (m)				
Min.	0.08	0.10	1.39	0.23
Mean	6.48	5.88	7.85	7.73
Max.	13.79	14.09	15.73	15.58
DBH (cm)				
Min.	8.50	11.00	9.00	13.60
Mean	18.59	20.65	18.16	26.20
Max.	26.60	33.10	26.80	41.70
Total Height (m)				
Min.	7.52	6.93	6.05	10.04
Mean	10.66	9.91	11.34	12.43
Max.	13.80	14.11	15.68	15.60
Height to lowest live branch (m)				
Min.	0.24	1.43	-0.20	1.07
Mean	1.90	2.98	0.59	3.79
Max.	5.07	4.65	1.36	6.09
Crown length (m)				
Min.	2.46	4.20	5.25	5.12
Mean	8.76	6.93	10.75	8.64
Max.	12.96	11.04	14.96	13.07
Crown width (m)				
Min.	1.41	2.35	1.95	1.80
Mean	4.09	3.92	3.05	4.21
Max.	6.01	6.43	4.75	6.45

Lab analysis

Fresh foliage samples were frozen until they could be analyzed for projected (*A. grandis*) or total (*Pinus* species) leaf area. Surface areas of the sub-samples were determined differently for each species. Projected leaf area was estimated for *A. grandis* with an image analysis system, LI-3500 (LI-COR, Lincoln, NB). For both species of *Pinus*, individual fascicles from the entire subsample were laid out end-to-end after sorting by the number of needles per fascicle. Total length (L), number of needles per fascicle (N), and average diameter of the fascicle were recorded for each batch of fascicles. Diameters were taken with a micrometer on one out of every 15 to 20 needles and surface area was determined by (Fites and Teskey 1988): $A = NLr(\pi + 3)$ and $A = 2NLr(\pi/3 + 1)$ for *P. contorta*, and *P. ponderosa*, respectively, where A is the all-sided leaf area, r is the average batch radius, and all other variables are defined above. A test comparison between image analysis and physical measurements on the *Pinus* species indicated comparable area estimates and precision, so direct measurement was chosen due to its ease and speed. Leaf area of each subsample was measured to the nearest 0.001 cm^2. These sub-samples were then rebagged and dried at 70^oC for at least 72 hours, then weighed to the nearest 0.0001 g. Specific leaf area (SLA) was computed as the ratio of projected or total leaf area to dry weight.

Branch samples were oven-dried at 70^oC for at least 72 hours. Foliage was separated from wood, and foliage and wood (including bark) dry weights were measured to the nearest (0.01 g.). Leaf area for each sample branch (BLA) was estimated by multiplying total foliage dry weight by SLA of the same branch. A branch-level leaf area model was then developed to predict branch leaf area from branch basal diameter and location within the crown. Tree foliage area was then determined by adding up the leaf areas of each branch.

Statistical analyses

Various linear and nonlinear regression models were fitted to the data to develop predictive branch- and tree-level equations applicable to the sampled populations. Final models were chosen on the basis of biological appeal, residual analysis, and Furnival's (1961) index of fit (FI), a modified maximum likelihood criterion allowing concurrent evaluation of root mean square errors, normality, and homoskedasticity across weighting factors.

Branch-level equations

A series of weighted and unweighted, linear and nonlinear models were screened to develop branch-level equations for predicting leaf area from branch diameter and depth into the crown (Maguire and Bennett 1996; Kenefic and Seymour 1999). The general model can be written as:

$$\mathrm{BLA} = f(X\,;\,\theta\,) + \epsilon$$

where BLA is total branch leaf area, X are explanatory variables, θ are the parameters, and ϵ are independently and identically distributed additive random errors:

$$\epsilon \overset{iid}{\sim} N(0, X^{W}\sigma^{2})$$

where W = 0 (unweighted case), -0.5, -1.0, . . . -6.0 in the case of increasing variance.

Tree-level equations

Branch-level equations were applied to sampled trees to estimate tree-level leaf area. After determining projected (*A. grandis*) or total (*Pinus* species) leaf area for sampled trees, predictive equations were developed for estimating total tree leaf area for each species. A number of weighted and unweighted, linear and nonlinear, published and unpublished model forms were tested. The response variable was tree leaf area (TLA), while explanatory variables included: diameter at breast height (DBH), crown length (CL), basal area times crown ratio above breast height (BACR), sapwood area at crown base (SACB), sapwood area at breast height (SABH), height to crown midpoint (HCM), and diameter: height ratio (see Table 4.3 for variable definitions).

Vertical foliage distribution

Observed vertical foliage distribution was characterized on the measured plot trees by dividing the crown into ten segments of equal length and summing the foliage within that segment using the branch-level equations developed. The proportion of total tree foliage area in each of the ten segments was then determined. A standard two-parameter beta distribution was fitted to the empirical distribution for each tree. The beta distribution was chosen because it has the desirable properties of being

Table 4.3. Variable abbreviations and definitions applied to all branch- and tree-level leaf area and foliage distribution models.

Variable	Definition
SITE	Study site indicator (Pringle Butte = 0, Lookout Mountain = 1)
SPACE	Tree spacing (m)
SPPCOMP	Plot species composition (pure = 0, mixed = 1)
BD	Branch diameter (mm)
DINC	Depth into the crown (m)
RDINC	Relative depth into the crown (DINC / CL)
BLA	Branch total leaf area (m^2)
DBH	Tree diameter at breast height (cm)
HT	Tree total height (m)
HTRel	Relative tree height (HT / height of tallest tree on subplot)
CL	Crown length (m)
HLB	Height to the lowest living branch (m)
HCM	Distance to the crown midpoint (m, HT - (CL / 2))
BA	Basal area (cm^2)
SABH	Sapwood area at breast height (cm^2)
SACB	Sapwood area at crown base (cm^2)
BACR	Basal area times crown ratio (cm^2, BA * CL / (HT - 1.37))
TLA	Tree projected or total leaf area (m^2)

extremely flexible and logically defined on an interval with fixed endpoints. Other distributions that have been experimented with, including the normal, chi-square, and Weibull distributions, all lack some of these properties. The interval (0, 1) was rescaled to crown length making the tree tip and lowest live branch the respective endpoints. Estimates of the parameters α and β were determined using maximum likelihood estimation (see Appendix).

Parameter estimates from the beta distribution, α and β, were tested across two factors, spacing and species composition, by two-way multivariate analysis of variance (MANOVA) with unbalanced subsamples under a split-plot design. Overall effects of spacing, species composition, and their interaction were tested using Wilks' Lambda (Johnson and Wichern 1998). Where null hypotheses (no main or interaction effects) were reject by MANOVA, effects on α and β were separated using *F*-tests. Where the null hypothesis (no differences between the treatments) was rejected by the univariate analysis of variance, the Bonferroni adjustment multiple range test was used to identify differences ($\alpha = 0.05$).

Parameter estimates from the beta distribution were also modeled as a linear function of tree (DBH, HT, HTRel, HLB, and CL) and treatment (SPACE and SPPCOMP) variables using least squares regression for the purposes of determining effects of other variables on foliage distribution and prediction. Finally, using the developed regression equations, vertical foliage distributions were predicted for the average-sized trees found on the plots across the range of spacing and species composition.

RESULTS

Branch-level equations

The best model form, defined by FI, for estimating branch foliage area in each species was a model introduced by Maguire and Bennett (1996) for *Pseudotsuga menziesii* (Mirb.) Franco. Final models for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa*, respectively, were:

$$[4.1a] \quad \mathrm{BLA} = \alpha_1 \mathrm{BD}^{\alpha_2} \mathrm{RDINC}^{\alpha_4 - 1} e^{-(\alpha_3 \mathrm{RDINC})^{\alpha_4}}$$

$$[4.1b] \quad \mathrm{BLA} = \beta_1 \mathrm{BD}^{\beta_2} \mathrm{RDINC}^{\beta_4 - 1} e^{-(\beta_3 \mathrm{RDINC})^{\beta_4}}$$

$$[4.1c] \quad \mathrm{BLA} = (\gamma_1 + \gamma_5 \mathrm{SITE}) \mathrm{BD}^{\gamma_2} \mathrm{RDINC}^{\gamma_4 - 1} e^{-(\gamma_3 \mathrm{RDINC})^{\gamma_4}}$$

where BLA is branch leaf area (m^2), BD is branch diameter (mm), RDINC is the relative depth into the crown (0 at the tree tip to 1 at the base of the live crown), and SITE is an indicator variable identifying the study site (Pringle Butte = 0 and Lookout Mountain =1). Models for *A. grandis* and *P. ponderosa* explained greater than 85% of the variation, while the model for *P. contorta* explained 78% of the variation in leaf area. All models were weighted by $\mathrm{BD}^{-3.5}$ to correct for heteroskedasticity. The final models indicated that, for a given BD, foliage area was curvilinear, decreasing at the crown base (Fig. 4.1, Table 4.4). The variable SITE was significant in most *P. ponderosa* branch-level models tested, including [4.1*c*] ($p = 0.015$).

Table 4.4. Parameter estimates and standard errors for the branch leaf area equations for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa*.

Parameter	Estimated value	SE
Equation 4.1*a*		
α_1	0.0043	0.0007
α_2	2.1010	0.0457
α_3	1.3349	0.0456
α_4	2.3094	0.1143
σ	0.0008	
Equation 4.1*b*		
β_1	0.0072	0.0017
β_2	1.8271	0.0610
β_3	1.3040	0.1421
β_4	1.6334	0.1399
σ	0.0013	
Equation 4.1*c*		
γ_1	0.0037	0.0006
γ_2	2.2019	0.0451
γ_3	1.7054	0.4944
γ_4	1.6690	0.0632
γ_5	-0.0004	0.0002
σ	0.0012	

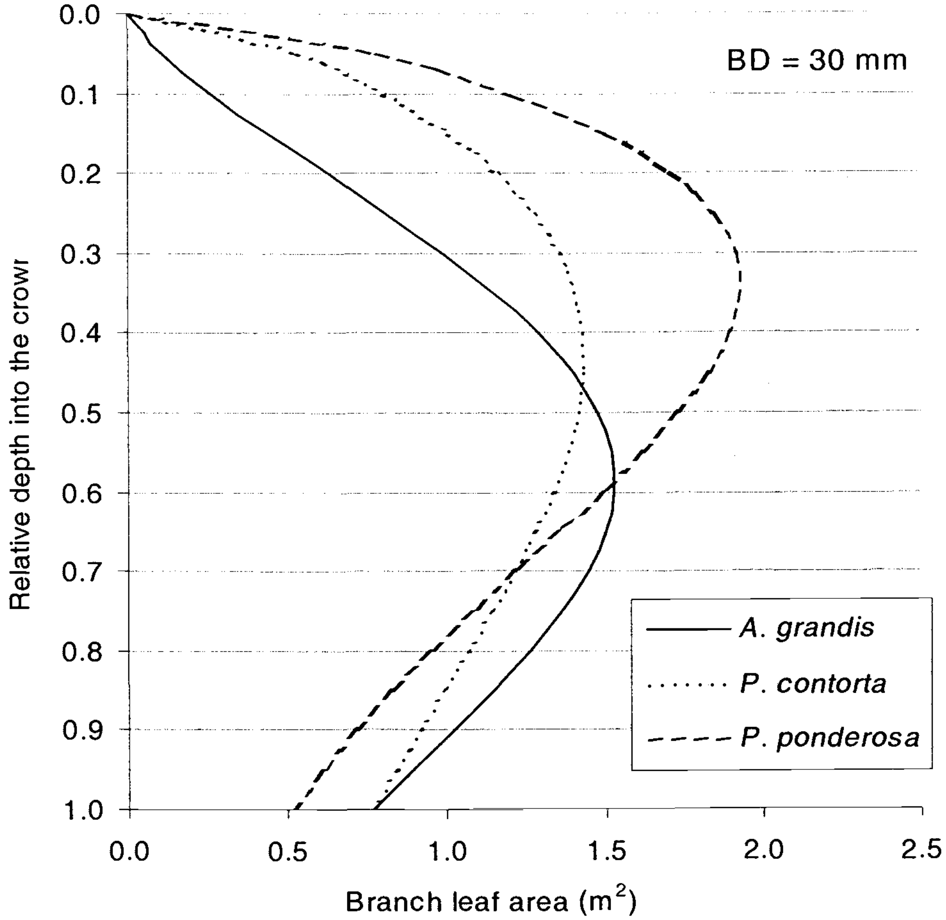

Figure 4.1. Profiles of branch leaf area with relative depth into the crown and a branch diameter of 30 mm for *Abies grandis* (solid line), *Pinus contorta* (dotted line), and *Pinus ponderosa* (dashed line).

Tree-level equations

Nearly all models performed statistically and biologically well for each of the species (Tables 4.5-4.8). In general, nonlinear models performed slightly better than simple linear models due to the curvilinear form of leaf area across the range of most explanatory variables. Model 4.7, a nonlinear function of BACR, performed

Table 4.5. Model forms, weighting factors, and fit statistics for linear and nonlinear sapwood- and crown-based models screened for prediction of total leaf area in *Abies grandis*.

Model	Model form	Weight	R^2[§]	s[†]	FI[*]	Source
4.2*a*	$TLA = \alpha_{11}SACB$	$SACB^{-2.5}$	0.87	0.0156	4.9626	Marchand 1984
4.3*a*	$TLA = \alpha_{21}SABH$	$SABH^{-1.5}$	0.94	0.2247	5.5921	Marchand 1984
4.4*a*	$TLA = \alpha_{31}BACR$	$BACR^{-1.5}$	0.95	139.2987	4.6865	Kenefic and Seymour 1999
4.5*a*	$TLA = \alpha_{41}SACB^{\alpha_{42}}$	$SACB^{-2.5}$	0.83	0.0158	4.9969	Maguire et al. 1998
4.6*a*	$TLA = \alpha_{51}SABH^{\alpha_{52}}$	$SABH^{-1.5}$	0.94	0.2299	5.7198	Maguire et al. 1998
4.7*a*	$TLA = \alpha_{61}BACR^{\alpha_{62}}$	$BACR^{-1.5}$	0.95	132.8005	4.4679	Maguire and Bennett 1996
4.8*a*	$TLA = \alpha_{71}CL^{\alpha_{72}}$	CL^{-5}	0.71	0.0871	10.0484	
4.9*a*	$TLA = \alpha_{81}SABH^{\alpha_{82}}HCM^{\alpha_{83}}$	$SABH^{-1.5}$	0.96	0.1971	4.9042	Dean and Long 1986
4.10*a*	$TLA = \alpha_{91}SABH^{\alpha_{92}}CL^{\alpha_{93}}$	CL was not significant				Gilmore et al. 1996
4.11*a*	$TLA = \alpha_{101}CL^{\alpha_{102}}e^{\alpha_{103}(DBH/HT)}$	CL^{-5}	0.96	0.0340	3.9236	Maguire and Bennett 1996

TLA, Tree leaf area (m^2); SACB, sapwood area at crown base (cm^2); SABH, sapwood area at breast height (cm^2); CL, crown length (m); BACR, basal area times modified live crown ratio (CL / (tree height - 1.3)) (Valentine et al. 1994); HCM, height to crown midpoint (m) (Tree height - (CL / 2)) (Dean and long 1986)

[§] Kvalseth's (1985) generalized R^2

[†] Root mean square error

[*] Furnival's (1961) index of fit ($FI = [f'(TLA)]^{-1}[s]$)

Table 4.6. Model forms, weighting factors, and fit statistics for linear and nonlinear sapwood- and crown-based models screened for prediction of total leaf area in *Pinus contorta*.

Model	Model form	Weight	$R^{2\S}$	$s^{\dagger}$	FI*	Source
4.2*b*	$TLA = \beta_{11}SACB$	$SACB^{-2}$	0.92	0.0606	5.6166	Marchand 1984
4.3*b*	$TLA = \beta_{21}SABH$	$SABH^{-1}$	0.95	0.6332	5.8820	Marchand 1984
4.4*b*	$TLA = \beta_{31}BACR$	$BACR^{-2}$	0.93	385.3344	4.9074	Kenefic and Seymour 1999
4.5*b*	$TLA = \beta_{41}SACB^{\beta_{42}}$	$SACB^{-2.5}$	0.96	0.0143	4.1078	Maguire et al. 1998
4.6*b*	$TLA = \beta_{51}SABH^{\beta_{52}}$	$SABH^{-1}$	0.96	0.5619	5.2202	Maguire et al. 1998
4.7*b*	$TLA = \beta_{61}BACR^{\beta_{62}}$	$BACR^{-2}$	0.93	389.5069	4.9606	Maguire and Bennett 1996
4.8*b*	$TLA = \beta_{71}CL^{\beta_{72}}$	$CL^{-4.5}$	0.86	0.1205	7.6860	
4.9*b*	$TLA = \beta_{81}SABH^{\beta_{82}}HCM^{\beta_{83}}$	HCM was not significant				Dean and Long 1986
4.10*b*	$TLA = \beta_{91}SABH^{\beta_{92}}CL^{\beta_{93}}$	CL was not significant				Gilmore et al. 1996
4.11*b*	$TLA = \beta_{101}CL^{\beta_{102}}e^{\beta_{103}(DBH/HT)}$	$CL^{-4.5}$	0.93	0.0846	5.3945	Maguire and Bennett 1996

TLA, Tree leaf area (m^2); SACB, sapwood area at crown base (cm^2); SABH, sapwood area at breast height (cm^2); CL, crown length (m); BACR, basal area times modified live crown ratio (CL / (tree height - 1.3)) (Valentine et al. 1994); HCM, height to crown midpoint (m) (Tree height - (CL / 2)) (Dean and long 1986)

§ Kvalseth's (1985) generalized R^2

† Root mean square error

* Furnival's (1961) index of fit ($FI = [f'(TLA)]^{-1}[s]$)

Table 4.7. Model forms, weighting factors, and fit statistics for linear and nonlinear sapwood- and crown-based models screened for prediction of total leaf area in *Pinus ponderosa*.

Model	Model form	Weight	R^{2}[§]	s[†]	FI[*]	Source
4.2*c*	$TLA = (\gamma_{11}+\gamma_{12}SITE)SACB$	$SACB^{-2}$	0.83	0.1294	11.3202	Marchand 1984
4.3*c*	$TLA = (\gamma_{21}+\gamma_{22}SITE)SABH$	$SABH^{-2}$	0.81	0.0922	12.5288	Marchand 1984
4.4*c*	$TLA = (\gamma_{31}+\gamma_{32}SITE)BACR$	$BACR^{-2}$	0.88	617.6183	9.9224	Kenefic and Seymour 1999
4.5*c*	$TLA = (\gamma_{41}+\gamma_{43}SITE)SACB^{\gamma_{42}}$	$SACB^{-2}$	0.93	0.0856	8.7235	Maguire et al. 1998
4.6*c*	$TLA = (\gamma_{51}+\gamma_{53}SITE)SABH^{\gamma_{52}}$	$SABH^{-2}$	0.89	0.0879	11.9511	Maguire et al. 1998
4.7*c*	$TLA = (\gamma_{61}+\gamma_{63}SITE)SABH^{\gamma_{62}}$	$BACR^{-2}$	0.92	496.3997	7.9750	Maguire and Bennett 1996
4.8*c*	$TLA = \gamma_{71}CL^{\gamma_{72}}$	$CL^{-4.5}$	0.86	0.3053	16.1075	
4.9*c*	$TLA = (\gamma_{81}+\gamma_{84}SITE)SABH^{\gamma_{82}}\,HCM^{\gamma_{83}}$	$SABH^{-2}$	0.91	0.0753	10.2298	Dean and Long 1986
4.10*c*	$TLA = (\gamma_{91}+\gamma_{94}SITE)SABH^{\gamma_{92}}\,CL^{\gamma_{93}}$	$SABH^{-1.5}$	0.93	0.2758	10.9764	Gilmore et al. 1996
4.11*c*	$TLA = (\gamma_{101}+\gamma_{104}SITE)CL^{\gamma_{102}}\,e^{\gamma_{103}(DBH/HT)}$	CL^{-6}	0.92	0.0377	7.4612	Maguire and Bennett 1996

TLA, Tree leaf area (m^2); SACB, sapwood area at crown base (cm^2); SABH, sapwood area at breast height (cm^2); CL, crown length (m); BACR, basal area times modified live crown ratio (CL / (tree height - 1.3)) (Valentine et al. 1994); HCM, height to crown midpoint (m) (Tree height - (CL / 2)) (Dean and long 1986)

[§] Kvalseth's (1985) generalized R^2

[†] Root mean square error

[*] Furnival's (1961) index of fit ($FI = [f'(TLA)]^{-1}[s]$)

Table 4.8. Parameter estimates and asymptotic standard errors of the Total Leaf Area equations for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa*.

Parameter	Estimated value	SE
α_{11}	0.2174	0.0094
α_{21}	0.3021	0.0148
α_{31}	2101.9033	83.6023
α_{41}	0.1931	0.0295
α_{42}	1.0304	0.0368
α_{51}	0.3153	0.0779
α_{52}	0.9913	0.0494
α_{61}	2799.1600	459.9940
α_{62}	1.0729	0.0417
α_{71}	0.4035	0.1074
α_{72}	2.1352	0.1501
α_{81}	0.3198	0.0642
α_{82}	1.2748	0.1058
α_{83}	-0.8951	0.3013
α_{101}	0.0958	0.0159
α_{102}	1.4095	0.0986
α_{103}	1.8039	0.1781
β_{11}	0.2942	0.0129
β_{21}	0.3324	0.0117
β_{31}	2128.3641	82.1536
β_{41}	0.1563	0.0208
β_{42}	1.1372	0.0301
β_{51}	0.1558	0.0493
β_{52}	1.1457	0.0597
β_{61}	2385.7000	375.5340
β_{62}	1.0263	0.0355
β_{71}	0.2872	0.0799
β_{72}	2.4719	0.1405
β_{101}	0.2178	0.0405

Table 4.8. (Continued).

β_{102}	1.8439	0.1563
β_{103}	0.8474	0.1703
γ_{11}	0.4055	0.0227
γ_{12}	-0.0501	0.0317
γ_{21}	0.3218	0.0188
γ_{22}	-0.0603	0.0266
γ_{30}	-0.8457	0.3143
γ_{31}	2740.0565	140.6129
γ_{32}	-431.9031	180.1138
γ_{41}	0.1825	0.0298
γ_{42}	1.1771	0.0330
γ_{43}	-0.0338	0.0110
γ_{51}	0.1932	0.0411
γ_{52}	1.1058	0.0411
γ_{53}	-0.0409	0.0417
γ_{61}	5267.8900	659.7230
γ_{62}	1.1707	0.0300
γ_{63}	-925.3170	321.2240
γ_{71}	0.3642	0.1020
γ_{72}	2.6684	0.1430
γ_{73}	0.3036	0.0509
γ_{81}	1.3741	0.0803
γ_{82}	-1.0416	0.2604
γ_{83}	-0.0633	0.0211
γ_{91}	0.1220	0.0324
γ_{92}	0.9031	0.1233
γ_{93}	0.7823	0.3177
γ_{94}	-0.0207	0.0087
γ_{101}	0.2155	0.0209
γ_{102}	1.8489	0.0664
γ_{103}	1.0803	0.0851
γ_{104}	-0.0491	0.0091

consistently well across species as did [4.5], a nonlinear function of SACB. Model 4.11, a nonlinear function of CL and exponential function of DBH/HT provided the best fits on the basis of FI for *A. grandis* and *P. ponderosa* (Tables 4.5, 4.7). Mixed results across species occurred with SABH [4.6], SABH with HCM [4.9], and SABH with CL [4.10]. SABH worked moderately well for *A. grandis* and *P. contorta*, but not for *P. ponderosa*. Model 4.8, based on CL, was consistently the poorest across all species. The variable SITE was significant ($\alpha \leq 0.05$), in all models tested for *P. ponderosa* except for [4.8*c*] (Table 4.7).

Vertical foliage distribution

Multivariate analysis on the parameters of the beta distribution indicate that the only significant experimental factor affecting the relative vertical distribution of foliage was spacing for *P. contorta*. Likewise, individual tree variables performed poorly in predicting parameters of the beta distribution. Although most predictive equations accounted for less than 50% of the variation of the beta parameter estimates, HLB and HTRel accounted for greater than 97% of the variation in the α and β parameter estimates for *P. contorta* (Tables 4.9 and 4.10). The estimate of β was partially explained by HTRel in *A. grandis* ([4.17]), but α had no apparent relationship to any predictors. HTRel, HLB, and treatment variable SPACE accounted for 37% and 46% of the variation in the α and β parameter estimates, respectively, for *P. ponderosa* at Lookout Mountain ([4.18]).

Table 4.9. Model forms, weighting factors, and fit statistics for linear models predicting foliage distribution parameters for *Pinus contorta*, *Pinus ponderosa* at Pringle Butte, *Abies grandis*, and *Pinus ponderosa* at Lookout Mountain.

Model	Model form	Weight	$R^{2\,\S}$
Pinus contorta			
4.12	$\alpha = \eta_{11}\mathrm{HTRel} + \eta_{12}\mathrm{HLB}$	$\mathrm{HLB}^{-1.5}$	0.97
4.13	$\beta = \eta_{21}\mathrm{HTRel} + \eta_{22}\mathrm{HLB}$	HLB^{-1}	0.98
***Pinus ponderosa* (Pringle Butte)**			
4.14	$\alpha = \eta_{30}$	NA	NA
4.15	$\beta = \eta_{40}$	NA	NA
Abies grandis			
4.16	$\alpha = \eta_{50}$	NA	NA
4.17	$\beta = \eta_{60} + \eta_{61}\mathrm{HTRel}$	NA	0.20
***Pinus ponderosa* (Lookout Mountain)**			
4.18	$\alpha = \eta_{70} + \eta_{71}\mathrm{DBH}$	NA	0.37
4.19	$\beta = \eta_{80} + \eta_{81}\mathrm{HTRel} + \eta_{82}\mathrm{HLB} + \eta_{83}\mathrm{SPACE}$	NA	0.46

§ Kvalseth's (1985) generalized R^2.

DISCUSSION

Branch-level equations

Results of this study reaffirm the importance of accounting for crown position when developing branch-level equations. Many models have included a variable representing position within the crown (Ek 1979; Gillespie et al. 1994; Maguire and Bennett 1996; Baldwin et al. 1997). Maguire and Bennett (1996) showed that foliage on a branch of fixed diameter tends to decrease as the crown base is approached. This peaking behavior was found for each of the three species studied at Pringle Butte and Lookout Mountain. Branch leaf area (BLA) must decrease gradually as shading increases, as branch growth ceases, and as the branch approaches mortality. Several mechanisms may be involved, including water stress in lower branches (Waring and

Table 4.10. Parameter estimates and standard errors for linear models predicting foliage distribution parameters for *Pinus contorta*, *Pinus ponderosa* at Pringle Butte, *Abies grandis*, and *Pinus ponderosa* at Lookout Mountain.

Parameter	Estimated value	SE
η_{11}	3.1307	0.1476
η_{12}	0.4357	0.1361
η_{21}	1.8765	0.0804
η_{22}	0.1896	0.0530
η_{30}	2.8640	0.1386
η_{40}	1.8605	0.0591
η_{50}	3.2955	0.0968
η_{60}	2.4226	0.2289
η_{61}	-0.6460	0.2603
η_{70}	7.6858	0.9659
η_{71}	-0.1604	0.0418
η_{80}	4.7784	0.6587
η_{81}	-1.1079	0.5158
η_{82}	-0.2099	0.0741
η_{83}	-0.2516	0.0643

Silvester 1994; Protz et al. 2000) and light intensities falling below the light compensation point (Perry 1994), both of which can reduce photosynthesis. Moreover, as branch elongation decreases and older foliage is lost closest to the main stem (Assmann 1970; Kershaw and Maguire 1995), there is less surface area for the growth of new foliage. Many of these branches have generally been thought of nonfunctional; that is, they are not contributing to overall tree NPP (Sprugel et al. 1991; Fujimori 1993). Results on BLA have varied probably due to differing shade tolerance among species. Crown position is also an important factor influencing BLA in species considered tolerant of shade (Kershaw and Maguire 1995; Maguire et al. 1998; Kenefic and Seymour 1999). However, the decrease in BLA in the bottom part of the crown would be expected to be less dramatic in shade tolerant versus in shade intolerant species. This trend was corroborated by comparison of the three species at Pringle Butte and Lookout Mountain. The *Pinus* species reached a peak at relative depths into the crown of lower than 0.5, whereas the most shade tolerant *A. grandis* peaked at greater than 0.5 (Fig. 4.1). In *Pinus taeda* L., another shade intolerant species, one study found a peak in foliage very high in the crown (Gillespie et al. 1994). In contrast, two very shade tolerant species, *Picea rubens* Sarg. (Maguire et al. 1998) and *Tsuga heterophylla* (Raf.) Sarg. (Kershaw and Maguire 1995), maintained large branch leaf areas for a given diameter deep into the crown. In contrast, leaf area of *Tsuga canadensis* (L.) Carr. branches apparently continued to increase with depth into the crown for a given diameter (Kenefic and Seymour 1999).

Tree-level equations

Sapwood area models, especially those at crown base, have traditionally worked well for predicting tree leaf area (Waring et al. 1977; Waring et al. 1982; Marchand 1984; Coyea and Margolis 1992). Sapwood has considerable biological significance given its function as water conducting tissue servicing a fixed amount of leaf area (Shinozaki et al. 1964a,1964b; Waring et al. 1982). The sapwood area-leaf area relationship in *P. ponderosa*, however, differed between the two sites. Many studies have demonstrated differences in leaf area: sapwood area ratios among species, particularly those that differ by shade tolerance (Kaufmann and Troendle 1981). However, leaf area: sapwood area ratios also vary within a species, particularly across gradients in site moisture regime (Waring et al. 1982; White et al. 1998), vapor pressure deficit and maximum summer temperatures (Mencuccini and Grace 1995; Mencuccini and Bonosi 2001), site quality (Dean and Long 1986), fertilization and thinning (Brix and Mitchell 1983), stand density (Keane and Weetman 1987; Long and Smith 1988), canopy position (O'Hara and Valappil 1995), and absolute tree height (McDowell et al., in press). Moreover, work on sapwood anatomy has demonstrated differences in water conducting properties of the sapwood tissues across environmental gradients (Pothier et al. 1989a; Pothier et al. 1989b) and tree growth rates (Whitehead et al. 1984; Pothier et al. 1989a). In this study, Pringle Butte was more a more xeric site than Lookout Mountain; however, leaf area: sapwood area ratios for Pringle Butte were slightly higher, suggesting less sapwood area is required to supply water to a given amount of leaf area, a relationship expected usually expected on a moister site (Waring et al. 1982; White et al. 1998). Pringle Butte was also the site with slower growth rates (see Chapter Three). Smaller leaf area: sapwood area ratios would be expected on slower growing sites due to lower saturated sapwood permeability (Pothier et al. 1989a).

Sapwood area at breast height was not as strong a predictor as sapwood area at crown base. Others have reported similar findings (Marchand 1984; Hungerford 1987; Barker 1998). Although a linear relationship existed between the weight of foliage and the weight of nonphotosynthetic tissue above the base of the live canopy, below the live crown no fixed relationship exists (Shinozaki et al. 1964a, 1964b). Many authors have demonstrated sapwood area flare below the base of the live crown (Waring et al. 1982; Hungerford 1987; Maguire and Hann 1987; Ryan 1989; Maguire and Batistia 1996; Barker 1998). Therefore, across stands of widely varying density the ratio of leaf area to sapwood area at crown base is expected to be more stable, or a correction must be introduced for height to crown base. Although it is unknown why sapwood taper exists, Becker et al. (2000) suggest that individual tracheids taper from the top to the base of the tree to increase hydraulic conductivity. Changes in tracheid size may be a physiological response to increasing tree height by buffering effects of increased hydraulic stress within the tree (Becker et al. 2000). Consequently, relationships between breast height sapwood area and tree leaf area may vary quite a bit among species, but also within species, height to crown base, and local climate.

Sapwood area at crown base is much more difficult to measure in the field than sapwood area at breast height. As a result, other measures have been devised to augment or serve a surrogates for sapwood area at crown base. Dean and Long (1986) estimated leaf area as a function of breast height sapwood area and height to the center of the live crown. This model, [4.9], worked well for *A. grandis* and moderately well for *P. contorta* across spacings because it implies that, for a given leaf area, sapwood area increases with an associated increase in the distance from breast height to the center of the live crown (Long and Smith 1988; Long and Smith 1989). However, some caution must be exercised when applying this model form, since tall trees with small crowns can be predicted to have negative leaf areas (O'Hara and Valappil 1995).

The most consistent predictions were obtained from the product of basal area and crown ratio above breast height (BACR), a surrogate for sapwood area at crown base. Valentine et al. (1994) suggested the proportion of tree basal area at crown base that is sapwood should be related to the percentage of the tree height above breast height covered by the live crown. Thus, sapwood area at breast height (without taper) would be equal to the cross-sectional area of the bole at breast height times a modified live crown ratio (CL/(HT - 1.37)). An alternative explanation for the efficacy of BACR is that crown ratio above breast height is a surrogate for taper to crown base. Shinozaki (1964a, 1964b) similarly showed that diameter at crown base performed better than diameter at breast height for predicting foliage mass. Other studies have also demonstrated BACR-based models predict leaf area as well as or better than sapwood area at crown base (Valentine et al. 1994; Maguire and Bennett 1996; Barker 1998; Kenefic and Seymour 1999). However, crown length and sapwood area predictors were found superior to BACR-based models in *Abies balsamea* (L.) Mill. (Gilmore et al. 1996).

Vertical foliage distribution

Relative vertical foliage distribution was most strongly related to tree height relative to the height of the tallest tree on the plot (HTRel). In *A. grandis* and *P. ponderosa* the negative parameter estimate on HTRel in predicting β indicated an upward shift in foliage with decreasing position of the tree with in the stand. In contrast, for *P. contorta* the positive parameter estimate on HTRel for α and β suggested that foliage shifts up and becomes more peaked with increasing position of the tree with in the stand. Stephens (1969) observed that trees in lower crown classes exhibited a slight upward skew in the distribution of foliage, although, his results were for foliage mass distribution rather than leaf area. Leaf area distributions are shifted slightly downward relative to leaf mass distributions (Maguire and Bennett 1996; Baldwin et al. 1997), due to increasing SLA with depth into the crown (Brooks et al. 1991). Pronounced downward shifts in foliage distribution with increasing social position have been observed in *Chamaecyparis obtusa* Sieb. et Zucc.) Endl. (Mori and Hagihara 1991), *P. menziesii* (Maguire and Bennett 1996), and *A. balsamea* (Gilmore and Seymour 1997). These results would suggest that *A. grandis* and *P. ponderosa* at

Lookout Mountain trees in lower canopy positions shift foliage to higher levels in the crown, perhaps as an adaptation to poorer light environments (Maguire and Bennett 1996). In contrast, several hardwood species have displayed an upward shift in foliage with increasing canopy position (Meadows and Hodges 2002), similar to *P. contorta* at Pringle Butte. This may be due in part to the extreme shade intolerance of *P. contorta* packing as much foliage in full sun as possible in higher canopy positions.

Spacing had a direct influence on relative foliage distributions in *P. ponderosa* at Lookout Mountain and an indirect influence in *P. contorta* through the effect of height of the lowest living branch. In both species, parameter estimates suggest a downward shift in foliage with increased spacing as expected. Wider spacings result in better light environments for individual trees and thus lower and wider crowns (Curtis and Reukema 1970), although this does not necessarily translate directly into a downward shift in relative foliage distribution. Absolute foliage distributions are presented for comparison (Fig. 4.2). In *P. contorta* and *P. ponderosa* at Lookout Mountain absolute distributions shifted down with increased spacing (Fig. 4.2a, 4.2d). In contrast, slight upward shifts in foliage were observed in *P. ponderosa* at Pringle Butte and *A. grandis* (Fig. 4.2b, 4.2c). *P. ponderosa* at Pringle Butte did show a downward shift between 1.8- to 3.7-m spacings, however, due to its dramatic height response between 3.7- and 5.5-m spacings, foliage distribution exhibited an upward shift (Fig. 4.2b).

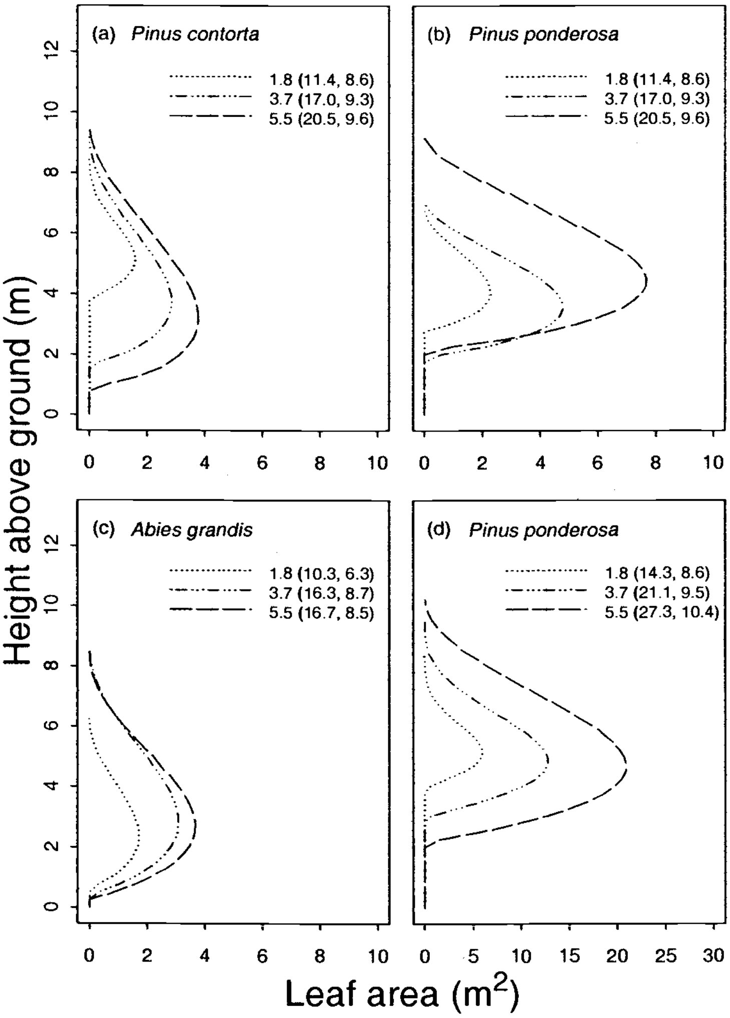

Figure 4.2. Profile of foliage distribution with tree height for three trees of average height, diameter, and crown length at 1.8-, 3.7-, and 5.5-m spacing for pure plots of: (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis*, and (d) *Pinus ponderosa* at Lookout Mountain. Tree diameter and height are given in parentheses.

Although species composition did not influence relative foliage distributions (Table 4.9), profiles of absolute distributions show slight differences between the pure and mixed stands (Fig. 4.3). Differences were probably the due to stratification in mixtures. For the dominant species, *P. contorta* at Pringle Butte and *P. ponderosa* at Lookout Mountain, competition was less pronounced in mixtures, therefore exhibited more leaf area and, in the case of *P. contorta*, a lower peak in foliage distribution in mixtures than in pure stands where competition is higher. The opposite trend was observed in *P. ponderosa* at Pringle Butte, the subordinate species (Fig. 4.3b). No differences were apparent in *A. grandis* (Fig. 4.3c).

Many other factors may play a role in foliage distribution, including shade tolerance, tree size, tree age, and treatments. Shade tolerant species have lower light compensation points and can maintain longer crowns with more foliage than shade intolerant species. An analysis of an even-aged *C. obtusa* plantation by Mori and Hagihara (1991) suggested foliage distributions also change with size of the tree, shifting downward and becoming more normal with diameter at breast height. Although relatively few studies have assessed changes in relative foliage distributions with age or stand development, patterns observed in *Pinus sylvestris* L. indicated a shift in foliage down the stem with increasing age (van Hees and Bartelink 1993). Also, early successional hardwood stands had more foliage near the upper canopy, while later successional stands had more symmetric foliage distributions (Yang et al. 1999). However, the opposite trend was shown in pure even-aged stands of *Pinus*

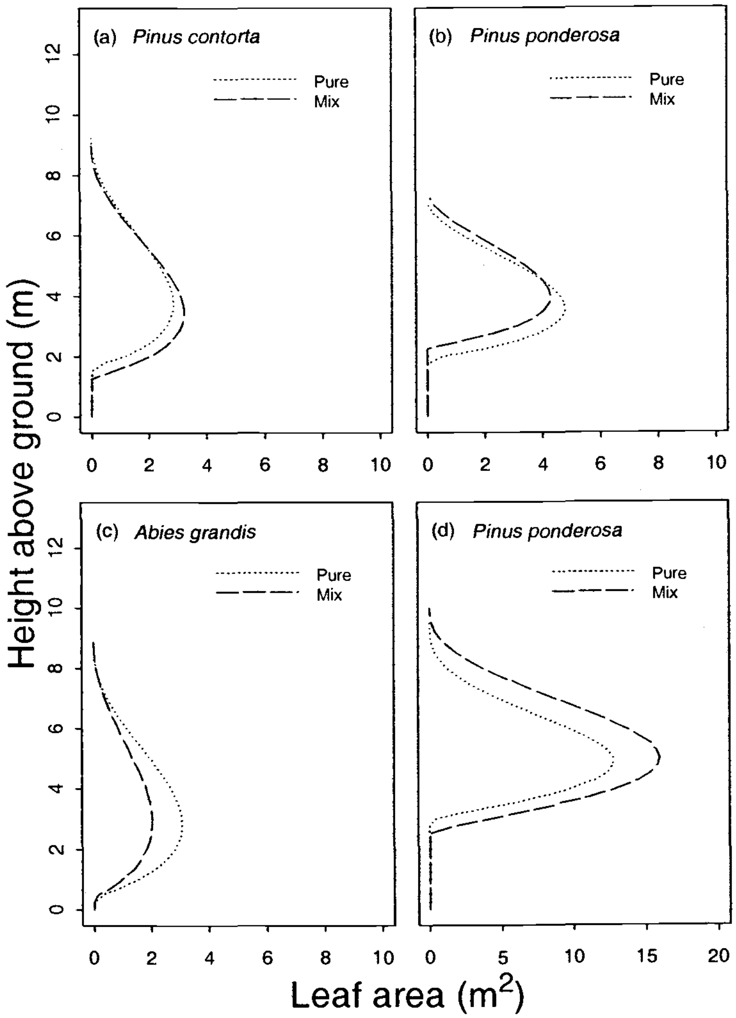

Figure 4.3. Profile of foliage distribution with tree height for three trees of average height, diameter, and crown length at 3.7-m spacing for pure (Pure, dotted line) and mixed (Mix, dashed line) plots of: (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis*, and (d) *Pinus ponderosa* at Lookout Mountain.

strobus L. and *P. taeda* (Schreuder and Swank 1974). These latter two stand-level studies probably reflected changes in stand structure, stand density reduction from mortality in lower crown classes, rather than changes in within-tree foliage distribution. In *P. menziesii*, Maguire and Bennett (1996) reported an upward shift and stronger peak in foliage among plots assumed to represent advancing stages of stand development. The effects of thinning are not well-studied, but studies have suggested an upward shift of stand-level distributions (Beadle et al. 1982; Bidlake and Black 1989). In contrast, Siemon et al. (1980) suggested a slight downward shift in the tree-level foliage distribution after thinning, but differences among the different levels of thinning were very small. In a *Pinus radiata* D. Don thinning study, foliage distribution at all spacings were not significantly different from normal (Whitehead 1978), suggesting no change in relative distribution. Response of absolute foliage distribution would depend strongly on the type of thinning, and would also be affected by time since thinning. Although spacing effects should not be confused with thinning effects, results here would suggest that changes in foliage distributions after thinning would also depending on species composition. Clearly the impact of stand structure and intervention requires more study.

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CHAPTER FIVE: VERTICAL TRENDS IN MAXIMUM BRANCH DIAMETER IN PURE AND MIXED-SPECIES STANDS IN CENTRAL OREGON

ABSTRACT

The influence of spacing and competitor species on vertical trends in maximum branch diameter was assessed in two spacing studies in the central Oregon Cascades with nonlinear mixed-effects models. One study involved a mix of *Pinus contorta* Dougl. ex Loud. (lodgepole pine) and *Pinus ponderosa* Dougl. ex Laws. (ponderosa pine), the other a mix of *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir) and *P. ponderosa*. The impact of autocorrelation on the precision of parameter estimates was reduced to below $\alpha = 0.05$ with a single random tree effect. In general, models including treatment variables representing spacing and species composition were significantly better than the best models without these explicit treatment variables. Tree variables such as diameter, height, and crown length were able to account for most stand conditions. The most difficult stand condition to account for was the variation due to competing species. For all species, spacings, and compositions, profiles of maximum branch diameter were curvilinear, decreasing near the crown base, even in plots where crown closure has not occurred suggesting other mechanisms slowing branch growth in addition to self-shading. Profiles of maximum branch diameter increase with increasing spacing and tree relative height, but the effects of species composition depended on spacing in all species. Increases in

spacing resulted in a more pronounced increase in maximum branch diameter profiles in the subordinate species in mixtures than its adjacent pure plots and its overtopping competitor. In contrast, the overtopping species had a larger spacing response in the pure plots than in mixed plots. Previous work in these studies have reported a spacing effect on stratification. These results suggest the same effect on maximum branch diameter profiles. Furthermore, results suggest that wood quality, in terms of knot size, may be improved in more dense pure stands or for the subordinate species in mixed stands, analogous to development in uneven-aged management schemes.

INTRODUCTION

Branch size and distribution are important aspects of crown structure. Branches support foliage necessary for photosynthesis and influence the interception of light by the crown. However, several tradeoffs exist between the size of branches and physiological processes directly and indirectly related to production efficiency (Roberts and Long 1992). Larger branches generally support a larger quantity of foliage and therefore have greater photosynthetic potential. However, larger branches can also have increased hydraulic resistance (Waring and Silvester 1994; Protz et al. 2000) and perhaps larger rates of respiration relative to boles (Kinerson 1975; Sprugel 1990), especially at higher crown positions (Ryan et al. 1996). Larger trees with larger crowns typically produce thicker and longer lived branches, resulting in larger knots and more juvenile wood (Maguire et al. 1991); hence, a tradeoff exists between photosynthetic capacity and wood quality (Kershaw et al. 1990; Houllier et al. 1995). In short, crown structure has a major impact on growth efficiency and forest productivity, and also on the quality of wood produced in the bole.

Crown architecture has also been related to wildlife habitat (Morrison et al. 1987; McComb et al. 1993; Hamer 1995), fire intensity potential (Agee 1993; Keyes and O'Hara 2002), tree behavior under wind stress (Moore 2002), tree shape (Burkhart and Walton 1985; Ballard and Long 1988), stand occupancy (Krajicek et al. 1961), and net primary production (Smith and Long 1989; Long and Smith 1990; Hynymen 1995).

Branch diameter is determined largely by the duration of branch growth. Older branches in whorls near crown base therefore can reach greatest diameters. However, the largest branches within a tree are often found slightly above crown base, indicating that average and maximum branch diameter within crowns is curvilinear, increasing with depth into the crown until near the base of the crown (Colin and Houllier 1991; Gilmore and Seymour 1997; Maguire et al. 1994; Maguire et al. 1999). However, differences in branch diameters among trees growing in different social positions (Colin and Houllier 1991; Gilmore and Seymour 1997), in different stand densities (Magnussen and Yeatman 1987; Ballard and Long 1988; Colin and Houllier 1991; Maguire 1994), under varying thinning regimes (Siemon et al. 1976; Maguire et al. 1991), and to different absolute sizes (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998) have been reported for even-aged, single-species stands.

Relatively little work has been conducted in stands with more complex structures, such as species mixtures. Since patterns of stand development in species mixtures are more diverse than in single-species, even-aged stands (Oliver and Larson 1996), patterns in crown structure, particularly branch diameter, would be expected to vary with species composition and stand density.

The influence of spacing and species composition on the vertical patterns of maximum branch diameter was assessed in two existing mixed-species spacing studies in the central Oregon pumice region. This region is characterized by mixed stands of *Pinus ponderosa* Dougl. ex Laws. and *Pinus contorta* Dougl. ex Loud. on drier sites at low elevations, while on moister sites, *P. ponderosa* can mix with *Abies grandis* (Dougl. ex D. Don) Lindl., often but not always forming a stratified mixture (Oliver and Larson 1996; Cobb et al. 1993). The primary objectives of this study were to: (*i*) verify the effect of spacing on branch diameter in these three species; (*ii*) to test whether the effect of spacing on maximum branch diameter at a given height in the crown does not differ by competitor species; and (*iii*) to outline the implications of these spacing trial results for controlling stand structure through spacing and species composition. To test the effect of spacing and species composition at multiple levels within the crown, the statistical model had to address within-tree autocorrelation and/or random tree effects. Likewise, it was of biological and practical significance to know whether any effects of spacing and species composition were exerted beyond their effects on tree diameter, height, and live crown length. Therefore, two secondary objectives were to: (*i*) test whether random tree effects were sufficient to eliminate within-tree autocorrelation of branch diameters; and (*ii*) test for any residual spacing and species composition effect on branch diameter profiles beyond that accounted for by introducing tree diameter, height, and crown length as covariates.

METHODS

Study Sites

The study was conducted at two sites. The first site, Pringle Butte, is a mixture of *Pinus ponderosa* and *Pinus contorta*. The second site, Lookout Mountain, is a mixture of *P. ponderosa* and *Abies grandis*. Both sites are east of the Cascade Range crest, 35 miles southwest of Bend, in the Pringle Falls Experimental Forest, Deschutes National Forest, Deschutes County, Oregon.

Pringle Butte site

The Pringle Butte study site is located on the northwest-facing slope of Pringle Butte at an elevation of 1,370 m (43°43'N, 121°37'W). Slopes range from 4 to 27 percent, with an average of 10 percent. Mean annual precipitation is only 61 cm and falls predominantly between the months of October and April, with a half-meter snow pack common between January and March. Maximum temperatures occur in July, averaging 26°C, and frosts can occur at any time during the year (Cochran and Barrett 1999a). The soils in this area have been typed as a developing Xeric Vitricryands on

75 cm of dacite pumic from the eruption of Mount Mazama (Cochran and Barrett 1999a). This pumice layer overlays sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments.

The study area is 3.9-ha, clearcut in 1970. The ground cover consists of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), scattered Ross sedge (*Carex rossi* Boott), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and western needle grass (*Stipa occidentalis* Trub. ex Wats.). *P. ponderosa* site index (base age 100) has been estimated at 24 m using Meyer's (1961) curves and 33.5 m using Barrett's (1978) method (Cochran and Barrett 1999a).

Lookout Mountain site

The Lookout Mountain study site is located on the northeast-facing slope of Lookout Mountain at an elevation of 1550 m (43°49' N, 121°41' W). Slopes average close to 20-percent. Average annual precipitation is approximately 100 cm, most of which falls as snow between the months of September and May. Generally, summers are hot and dry, with temperatures ranging from 21 to 32°C. Nights are predominantly cool with the chance of frost occurring any time during the year (Cochran and Barrett 1999b). Soils are deep, well-drained Typic Cryorthents, developed from dacite pumice originating from the eruption of Mount Mazama, overlaying a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments (Seidel 1985; Cochran and Barrett 1999b).

This study site is 8.1-ha, clearcut in 1974 in a mixed-conifer/snowbrush-chinkapin plant community (Seidel 1985). The ground cover consists primarily of *C. velutinus*, *A. patula*, and golden chinkapin (*Castonopsis chrysophylla* (Dougl.) A. DC.) (Seidel 1985). *C. velutinus* ground cover is very dense over much of the study site. The late successional plant community association is *Abies concolor/Ceanothus velutinus* (Franklin and Dyrness 1973). Site index (base age 100) for *P. ponderosa* (Meyer 1961) is about 27.5 m (Seidel 1985).

The site was planted with 2-0 bare root *P. ponderosa* stock grown at the USDA Forest Service nursery in Bend, OR, and 2-0 *A. grandis* containerized stock. Seed of each species was collected in 1971 from near the study site. Planting took place in the spring of 1974 and during the first two years, any seedlings that died were replaced by transplanted seedlings from outside the plots. In addition, the *C. velutinus*, *A. patula*, and *C. chrysophylla* were sprayed in June of 1976 and 1979 with herbicides to reduce competition (Seidel 1985).

Experimental Design

Each study was established under a completely randomized split-plot design in which the whole-plot factor was tree spacing and the split-plot factor was species composition. Pringle Butte was composed of five initial spacings: 1.8, 2.7, 3.7, 4.6, and 5.5 m (6, 9, 12, 15, and 18 feet). Species composition included pure *P. ponderosa*, pure *P. contorta*, and a 50:50 mix of both species. Treatment combinations were replicated twice, so each of the five spacings were randomly assigned to 10 whole plots, and subplots within each whole plot were randomly assigned a species mix. The size of the whole plots varied by spacing but each contained 147 to 390 measure trees.

Lookout mountain was composed of three initial spacings: 1.8, 3.7, and 5.5 m (6, 12, and 18 feet). The three species combinations in the subplots included pure *P. ponderosa*, pure *A. grandis*, and a 50:50 mix of both species. Each whole plot consisted of three subplots of the same spacing. The whole plots were of variable size, depending on spacing, and were designed so that each subplot had 24 measured trees. Three replications produced a total of nine whole plots and 27 subplots.

Data Collection

In June and July of 2001 two sample trees, one from each of the two larger thirds of the diameter range, were selected at random from each subplot at Pringle Butte and Lookout Mountain for a total of 114 trees. Of these 114 trees, 27 were *A. grandis*, 30 were *P. contorta*, and 57 were *P. ponderosa*. For each sample tree, four attributes were recorded: (*i*) diameter at breast height, DBH (to the nearest 0.1 cm), (*ii*) total tree height, HT (to the nearest 0.01 m), (*iii*) height to the lowest live branch, HLB (to the nearest 0.01 m), and (*iv*) two perpendicular crown widths (to the nearest 0.01

Table 5.1. Mean tree characteristics from sample trees by study site and species.

	Pringle Butte		Lookout Mountain	
Parameter	*Pinus contorta*	*Pinus ponderosa*	*Abies grandis*	*Pinus ponderosa*
Sample size				
Trees	30	30	27	27
Total branches	5180	2899	10170	2718
Branch diameter (mm)				
Min.	1.0	1.0	1.0	2.0
Mean	16.4	25.0	8.9	30.6
Max.	57.0	131.0	55.0	77.0
Depth into crown (m)				
Min.	0.08	0.10	1.39	0.23
Mean	6.48	5.88	7.85	7.73
Max.	13.79	14.09	15.73	15.58
DBH (cm)				
Min.	8.5	11.0	9.00	13.60
Mean	18.6	20.7	18.16	26.20
Max.	26.6	33.1	26.80	41.70
Total Height (m)				
Min.	7.52	6.93	6.05	10.04
Mean	10.66	9.91	11.34	12.43
Max.	13.80	14.11	15.68	15.60
Height to lowest live branch (m)				
Min.	0.24	1.43	-0.20	1.07
Mean	1.90	2.98	0.59	3.79
Max.	5.07	4.65	1.36	6.09
Crown length (m)				
Min.	2.46	4.20	5.25	5.12
Mean	8.76	6.93	10.75	8.64
Max.	12.96	11.04	14.96	13.07
Crown width (m)				
Min.	1.41	2.35	1.95	1.80
Mean	4.09	3.92	3.05	4.21
Max.	6.01	6.43	4.75	6.45

m). On every whorl from ground level to the tree tip, height of attachment (nearest 0.01 m) and basal diameter (nearest mm) of each branch on each sample tree were measured and recorded as living or dead. Basal branch diameters were measured by caliper at horizontal and vertical axes relative to the standing tree, at a distance from the bole approximately equal to one branch diameter. Branch diameter used in analysis was the geometric mean of the two perpendicular measurements. Table 5.1 gives the mean sample tree and branch characteristics.

Model development

Crown width

To assess the absolute effect of spacing and species composition on maximum branch diameter, crown width (CW) was modeled as a function of spacing (SPACE) and species composition (SPPCOMP). Assuming maximum stand-grown crown width would be equal to the spacing at close spacings, then reach a maximum at wider spacings, the relationship can be described by:

$$[5.1] \quad CW = [a_1 SPACE + a_2 SPPCOMP][1 - \log(a_3 SPACE + a_4 SPPCOMP)]$$

where a_i are parameters to be estimate from the data, log is the natural logarithm, and other variables are explained above (see Table 5.2 for variable definitions).

Maximum branch diameter

Various regression models were explored for describing the trend in maximum branch diameter (BD) over depth into the crown. In addition, other tree, stand, and site variables were added to the models to account for the influence of each on maximum branch diameter.

Table 5.2. Variables associated with modeling crown width and maximum branch diameter.

Variable	Definition
BD	Diameter of largest whorl branch (mm)
MBD	Maximum branch diameter attainable on a tree (mm)
SPACE	Tree spacing (m)
SPPCOMP	Plot species composition (pure = 0, mixed = 1)
DBH	Diameter at breast height (cm)
HT	Total tree height (m)
HLB	Height to lowest living branch (m)
CL	Crown length (m, HT - HCB)
CR	Crown ratio (CL/HT)
CW	Crown width (m, geometric mean of two measurements)
h	Height of whorl above crown base (m)
p	Reference point
DINC	Depth into crown (m)
RDINC	Relative depth into crown (DINC/CL)

Several basic model forms were tested by Maguire et al. (1999) for describing maximum branch diameter trends in young coastal *Pseudotsuga menziesii* (Mirb.) Franco. Reasonable biological behavior and unbiased residuals were obtained from a variable exponent equation originally introduced for describing stem taper (Kozak 1988; Kozak 1997):

$$[5.2] \quad Y = X^{C}$$

where Y is a ratio of diameter inside bark at some height h_i to diameter inside bark at reference point p, $X = [1 - (Z)^{0.5}] / [1 - (p)^{0.5}]$, $Z = h_i / \mathrm{HT}$, HT = total height, and $C = f$ (Z and other tree and site variables). This model was formulated so that the ratio X ranges from 0 at the tree tip and 1 and the reference point p (Kozak 1988). This equation was modified by Maguire et al. (1999) so that branch diameters of a particular tree were expressed as proportion of the predicted maximum diameter (MBD) attainable for a tree of a given diameter, height, and crown length. Branch diameter was constrained to equal zero at tree tip and predict MBD at relative height p. Maguire et al. (1999) assumed p varied as a function of CR, yielding the following modification of [5.2]:

$$[5.3] \quad \frac{\mathrm{BD}}{\mathrm{MBD}} = X^{C}$$

where $X = [1 - (\mathrm{Z})^{0.5}] / [1 - (p)^{0.5}]$, $Z = h / \mathrm{CL}$, $p = f(\mathrm{CR})$, $h = \mathrm{CL} - \mathrm{DINC}$ = height of the branch above crown base (m), C is a function of branch position (Z) and other tree and stand predictors such as DBH, HT, CL, CR, HLB, SPACE, and SPPCOMP, and ϵ is the random error term. Expressing MBD as a nonlinear function of empirical stand-grown CW (Maguire et al. 1999), [5.3] can be rewritten as:

[5.4] $\mathrm{BD} = \gamma_1 \mathrm{CW}^{\gamma_2} X^C + \epsilon$

where BD, CW, X, and C are defined above and γ_1 and γ_2 are parameters to be estimated from the data. In this model, absolute trends in maximum branch diameter are represented in the nonlinear function of CW, a function of maximum attainable crown width, DBH, HT, and CR (Hann 1997), and the relative trends are represented in the X^C component.

Statistical Analyses

Crown width

A series of weighted and unweighted nonlinear models in the form of [5.1] above were screened to explore the relationship of spacing and species composition on CW:

$$\mathrm{CW} = [\alpha_1 \mathrm{SPACE} + \alpha_2 \mathrm{SPPCOMP}][1 - \log(\alpha_3 \mathrm{SPACE} + \alpha_4 \mathrm{SPPCOMP})] + \epsilon$$

where CW, SPACE, and SPPCOMP are defined above, and

$$\epsilon \overset{iid}{\sim} N(0, \mathrm{SPACE}^{W}\sigma^{2})$$

where W = 0 in the unweighted case and -0.5, -1.0, . . . -3.0 in the case of increasing variance. Final models were chosen on the basis of residual analysis and Furnival's (1961) index of fit (FI).

Maximum branch diameter

Multiple observations of branch diameter were collected from each of the 114 sample trees; therefore, the data violated the assumption of independence (Neter et al. 1996; Rawlings et al. 1998). Moreover, preliminary residual analysis indicated the presence of autocorrelation. Some success in reducing the impact of autocorrelation in longitudinal forestry data using mixed-effects models has been demonstrated (Biging 1985; Gregoire et al. 1995; Tassisa and Burkhart 1998; Fang and Bailey 2001). Mixed models have also been implemented for modeling branch diameters (Meredieu et al. 1998; Mäkinen and Colin 1998, 1999; Maguire et al. 1999), so the selected statistical model was a nonlinear mixed-effects model with a random tree effect:

$$[5.5] \quad \mathbf{BD}_i = f_i(\theta_i\, ; \mathbf{X}_i) + \epsilon_i$$

where $\mathbf{BD}_i$ is a $n \times 1$ vector of branch diameters observed on a subject tree i, f_i can be any nonlinear function, θ_i is a $n \times p$ vector of fixed and random effects, and ϵ_i is a $n \times 1$ vector of within subject errors. Lindstrom and Bates (1990) suggest formulating θ_i by specifying design matrices $\mathbf{A}_i$ and $\mathbf{B}_i$ ($n \times p$ and $n \times q$, respectively):$\theta_i = \mathbf{A}_i\,\alpha + \mathbf{B}_i\,\delta_i$, where α is a $p \times 1$ vector of fixed effects parameters and δ_i is $q \times 1$ vector of random effects parameters. These design matrices contain zeros and ones to turn fixed effects and random effects off and on, respectively. For example, if all the covariates specified in $\mathbf{X}_i$ are to have a single fixed and random effect, $\mathbf{A}_i = \mathbf{B}_i = \mathbf{I}_i$. For this application a single random tree effect was introduced, therefore, $q = 1$.

To complete the specification of [5.5], it is necessary to characterize the distribution of ϵ_i and δ_i. It is assumed that both are multivariate normal and have variance and covariance

$$\begin{bmatrix}\delta \\ \varepsilon\end{bmatrix}_i \sim N\left(\begin{bmatrix}0 \\ \mathbf{0}\end{bmatrix}_i, \begin{bmatrix}\sigma^2\Lambda & \mathbf{0}_{\varepsilon\delta} \\ \mathbf{0}_{\delta\varepsilon} & \sigma^2\mathbf{I}\end{bmatrix}_i\right)$$

where 0 is a null scalar, $\mathbf{0}$ is a $n \times 1$ null mean vector, $\mathbf{0}_{\delta\epsilon}$ and $\mathbf{0}_{\epsilon\delta}$ are the null covariance matrices, Λ_i is a $q \times q$ correlation matrix for the random tree effects, $\mathbf{I}_i$ is an

$n \times n$ within-tree correlation identity matrix, and σ^2 is a scalar representing the mean square error.

Since the relative rankings of subset models are not influenced by autocorrelation, relative performance of different predictor variables was assessed by running an all-subsets regression on a logarithmic transformation of [5.4], assuming a multiplicative rather than additive error term. Assuming positive autocorrelation, more variables would become significant in the model. The best subsets, with and without the treatment covariates SPACE, SPPCOMP, and SPACE × SPPCOMP, were then refitted in nonlinear form with random effects using maximum likelihood. Evaluation of assumptions for testing parameters were assessed using empirical autocorrelation plots (Monserud 1986; Pinheiro and Bates 2000). Models with alternative sets of fixed covariates and random tree effects were compared using Akaike's (1969) information criterion (AIC):

$$\text{AIC} = -2l(\theta) + 2k$$

where $l(\theta)$ is the log-likelihood and k is the number of parameters in the model. Nested models, including tests on random effects and covariates, were compared using likelihood ratio tests (Pinheiro and Bates 2000). All models were also evaluated on the basis of residual plots, bias, standard error of estimates, and biological behavior. All final predictor variables were significant at $\alpha \leq 0.05$-level.

RESULTS

Crown width models

Three models were developed, as *P. ponderosa* data were pooled between sites. Crown width was significantly related to spacing for each species:

Abies grandis

[5.6*a*] $CW = [\alpha_{11}SPACE][1 - \log(\alpha_{12}SPACE)]$

Pinus contorta

[5.6*b*] $CW = [\alpha_{21}SPACE + \alpha_{22}SPPCOMP][1 - \log(\alpha_{23}SPACE)]$

Pinus ponderosa

[5.6*c*] $CW = [\alpha_{31}SPACE][1 - \log(\alpha_{32}SPACE)]$

where CW, SPACE, and SPPCOMP are defined above, and parameter estimates are given in Table 5.3. The effect of species composition was only significant on the slope in *P. contorta*. Models for the two *Pinus* species accounted for greater than 50% of the variation in CW, where as [5.6*a*] accounted for 39% of the CW variation in *A. grandis*. Models confirm the relationship between CW and spacing is asymptotic, increasing with spacing at a decreasing rate, until maximum crown width is obtained.

Table 5.3. Parameter estimates and standard errors for the crown width models 5.6*a*, 5.6*b*, and 5.6*c*.

Parameter	Estimated value	SE
α_{11}	0.7182	0.0894
α_{12}	0.2124	0.0287
α_{21}	0.4002	0.1217
α_{22}	0.2206	0.1049
α_{23}	0.0488	0.0374
α_{31}	0.5976	0.0843
α_{32}	0.1082	0.0269

Maximum branch diameter models

Four models using tree and treatment variables were developed, one for each species on each site, i.e., *P. ponderosa* was modeled separately for each site. Overall, models fit well with all coefficients of determination above 0.70. In particular, best fits were obtained for both *P. ponderosa* data sets ($R^2 > 0.85$), while *Abies grandis* provided the greatest challenge and consequently had the poorest fit ($R^2 = 0.71$). Final models had well-distributed, homogeneous residuals, and therefore did not require weighting (Fig. 5.1). Autocorrelation was evident in the data for each species. However, a single random tree effect on the CW term was adequate for reducing the autocorrelation below the point where it would have a significant impact on standard error estimation ($\alpha \leq 0.05$). The most dramatic example of this was *P. ponderosa* at Pringle Butte (Fig. 5.2). The generalized nonlinear least squares fit suggested high-order autocorrelation (Fig. 5.2a). A single random tree effect rendered this autocorrelation insignificant at an α-level of 0.05 (Fig. 5.2b). All models were curvilinear, peaking just above the base of the live crown, but covariates differed by species and location:

Pinus contorta, Pringle Butte

$$[5.7a]\quad \mathrm{BD} = \gamma_{11}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{12}}}\right)^{\gamma_{13}e^{-Z}+\gamma_{14}\mathrm{HT}+\gamma_{15}\mathrm{CL}+\gamma_{16}\mathrm{SPACE}+\gamma_{17}\mathrm{SPPCOMP}}$$

Pinus ponderosa, Pringle Butte

$$[5.7b]\quad \mathrm{BD} = \gamma_{21}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{22}\mathrm{CR}}}\right)^{\gamma_{23}Z^{\gamma_{24}}+\gamma_{25}\mathrm{CL}+\gamma_{26}\mathrm{SPACE}\times\mathrm{SPPCOMP}}$$

Abies grandis, Lookout Mountain

$$[5.7c]\quad \mathrm{BD} = \gamma_{31}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{32}\mathrm{CR}}}\right)^{\gamma_{33}Z^{\gamma_{34}}+\gamma_{35}\mathrm{SPPCOMP}+\gamma_{36}\mathrm{SPACE}\times\mathrm{SPPCOMP}}$$

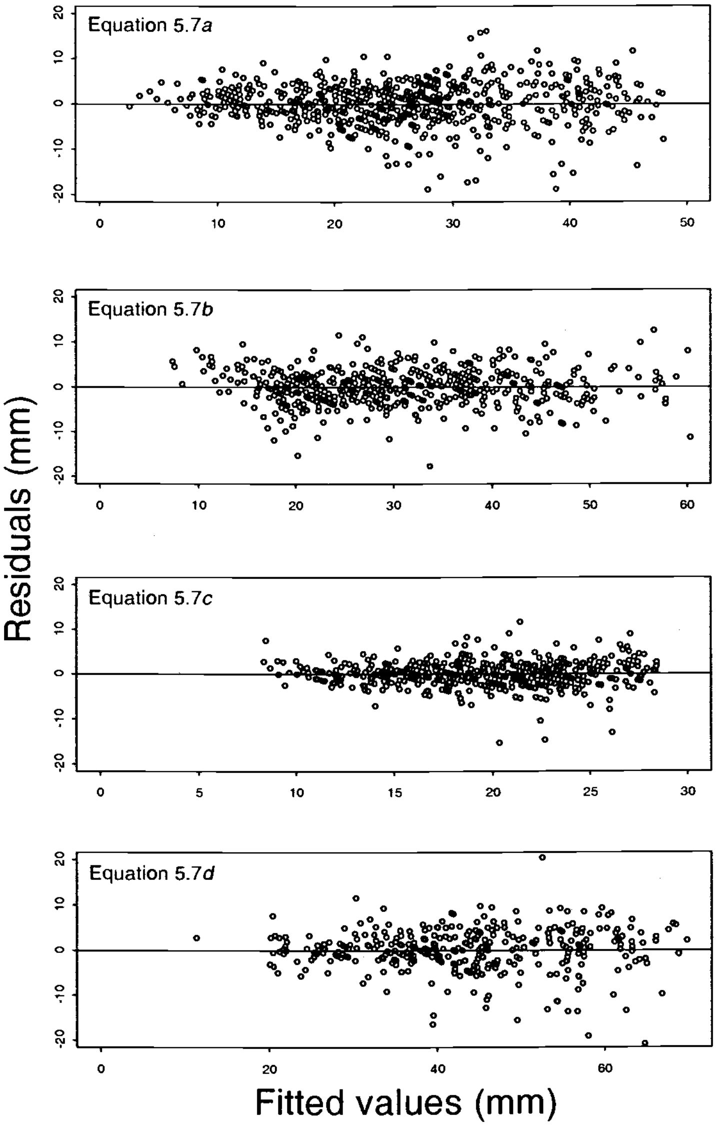

Figure 5.1. Plots of residuals on fitted values for equations 5.7*a*, 5.7*b*, 5.7*c*, and 5.7*d* corresponding to *Pinus contorta*, *Pinus ponderosa* at Pringle Butte, *Abies grandis*, and *Pinus ponderosa* at Lookout Mountain, respectively.

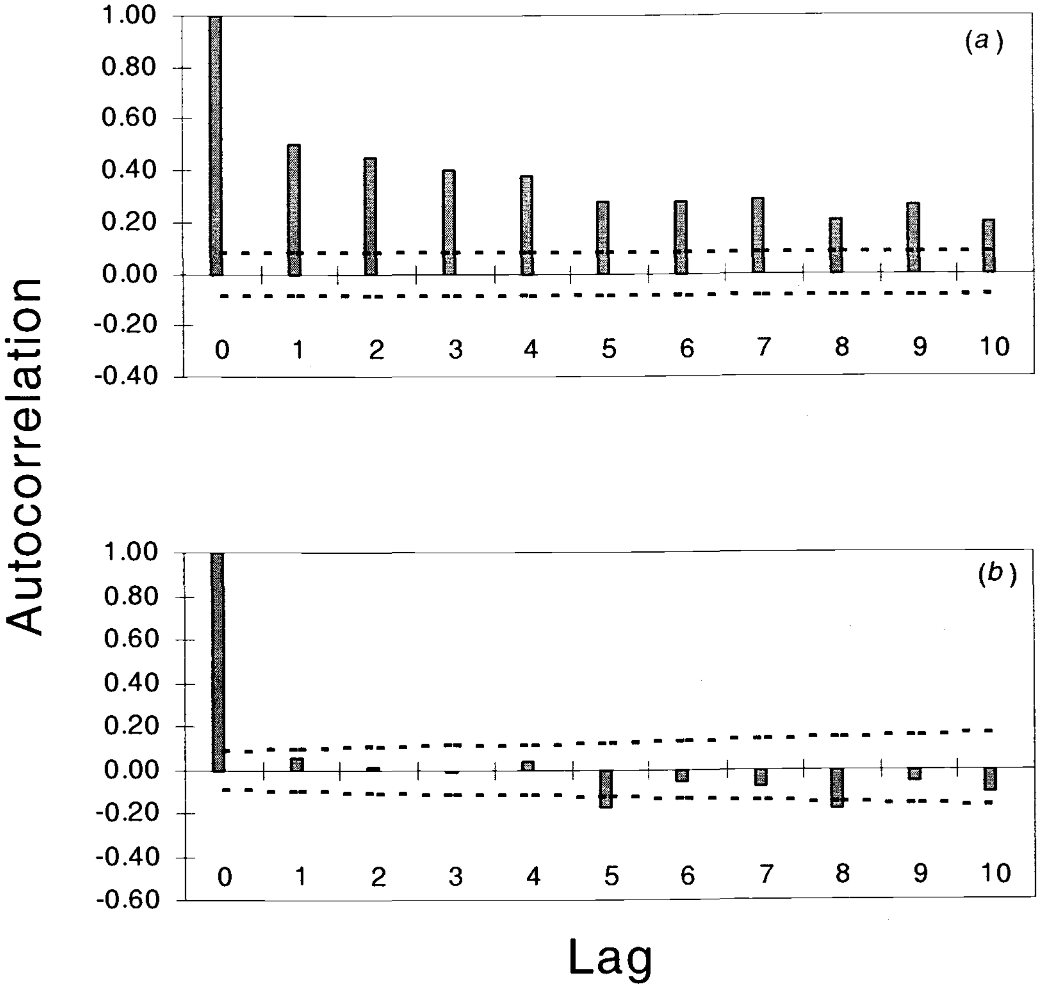

Figure 5.2. Autocorrelation plots for the two different runs of model 5.7*b* for *Pinus ponderosa* at Pringle Butte: (a) generalized nonlinear least squares run (GNLS, no random effect); (b) nonlinear mixed-effects model run with random tree effects (NLME). Estimates of the parameters for each run were obtained using the method of maximum likelihood. Dotted lines represent 95% confidence region.

Pinus ponderosa, Lookout Mountain

$$[5.7d] \quad \mathrm{BD} = \gamma_{41}\mathrm{CW}^{\gamma_{42}}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{43}\mathrm{CR}}}\right)^{\gamma_{44}Z+\gamma_{45}\frac{\mathrm{HT}}{\mathrm{DBH}}+\gamma_{46}\mathrm{CL}}$$

Smallest biases were generally at the base of the live crown. Equation 5.7*c* produced consistently positive bias that increased with relative height above the crown base. All biases however, were below 2.0 mm, with most below 1.0 mm. Standard errors of the estimate were all under 8.0 mm, and generally decreased with relative height above the crown base. Parameter estimates and asymptotic standard errors for [5.7*a*], [5.7*b*], [5.7*c*], and [5.7*d*] are given in Table 5.4.

Tree-level covariates

For all but *P. ponderosa* at Lookout Mountain, MBD was a linear function of CW (i.e., the exponent was not significantly different from unity). The value *p* was modeled as a linear function of CR for each species except *P. contorta* (equation 5.7*a*), which was reparameterized as a constant estimated from the data. The variable exponent was also slightly different for each species. All equations contained a single function of *Z* allowing the exponent to change among observations. In addition, several other tree-level variables, including HT, CL, and DBH/HT, were also significant. At Pringle Butte, HT and CL significantly affected relative

Table 5.4. Parameter estimates and asymptotic standard errors of the best variable exponent maximum branch diameter models for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa* at Pringle Butte and Lookout Mountain.

Pringle Butte			**Lookout Mountain**		
Parameter	Estimated value	SE	Parameter	Estimated value	SE
Equation 5.7*a*: *Pinus contorta*			**Equation 5.7***c*: *Abies grandis*		
γ_{11}	7.4646	0.3808	γ_{31}	5.4002	0.2794
γ_{12}	0.0772	0.0490	γ_{32}	0.7776	0.0351
γ_{13}	-1.8563	0.1202	γ_{33}	0.4575	0.0511
γ_{14}	0.1537	0.0136	γ_{34}	0.5102	0.0885
γ_{15}	-0.0668	0.0150	γ_{35}	-0.3210	0.0745
γ_{16}	0.0564	0.0117	γ_{36}	0.0589	0.0047
γ_{17}	0.0696	0.0248	$SD(\delta_{31})$	0.7080	0.2177
$SD(\delta_{11})$	0.5766	0.2407	$SD(\varepsilon)$	3.0220	0.0477
$SD(\varepsilon)$	4.7212	0.0397			
Equation 5.7*b*: *Pinus ponderosa*			**Equation 5.7***d*: *Pinus ponderosa*		
γ_{21}	8.3974	0.6295	γ_{41}	13.7854	1.3385
γ_{22}	0.6854	0.0947	γ_{42}	0.7210	0.0758
γ_{23}	0.4945	0.0437	γ_{43}	0.7949	0.0447
γ_{24}	0.5557	0.0871	γ_{44}	0.4105	0.0380
γ_{25}	0.0153	0.0058	γ_{45}	-0.2603	0.0873
γ_{26}	0.0139	0.0052	γ_{46}	0.0261	0.0039
$SD(\delta_{21})$	1.1187	0.1940	$SD(\delta_{41})$	0.8851	0.2585
$SD(\varepsilon)$	4.2315	0.0462	$SD(\varepsilon)$	4.9732	0.0554

maximum branch diameters in *P. contorta* (equation 5.7*a*). CL was also significant for *P. ponderosa* at Pringle Butte. At Lookout Mountain, only *P. ponderosa* had significant tree-level variables, including CL and DBH/HT. No functions of tree variables explored explained any additional variation in the relative branch diameter profiles of *A. grandis*.

Treatment effects

At Pringle Butte, treatment covariates representing spacing ($p < 0.001$) and species composition ($p = 0.005$) were significant in *P. contorta* whereas only the interaction ($p = 0.007$) between the two covariates was significant in *P. ponderosa*. The parameter estimate on SPACE in *P. contorta* was positive indicating relative maximum branch diameter increased with spacing. The parameter estimate on SPPCOMP was also positive. Since SPPCOMP was an indicator variable that equaled one in the mixed-species plots, this parameter estimate suggests larger relative branch diameters for *P. contorta* when growing with *P. ponderosa*, especially at lower crown positions (i.e., $X > 1.0$). In contrast, the spacing effects on relative maximum branch diameter in *P. ponderosa* depended on the SPPCOMP (equation 5.7*b*). The parameter estimate on the interaction was positive indicating that the spacing effect on relative maximum branch diameters was greater for mixed-species plots; that is, branch size increased more rapidly with spacing in mixtures than in pure culture (Table 5.4).

At Lookout Mountain, SPPCOMP exhibited a significant effect on *A. grandis* relative branch diameters ($p < 0.001$). The negative parameter estimate indicated a negative effect of *P. ponderosa* competition on relative maximum branch diameters in

A. grandis. The interaction between SPACE and SPPCOMP was significantly positive in *A. grandis* ($p < 0.001$), suggesting an increase in relative branch diameter with increasing spacing in the mixture, but no spacing effect in pure stands, analogous to *P. ponderosa* at Pringle Butte. In contrast, *P. ponderosa* branch diameters responded only to spacing ($p < 0.001$). SPACE was excluded from the final model ([5.7*d*]) in favor of CL because increases in branch diameter resulting from spacing were directly proportional to the increase in CL with spacing.

Necessity for treatment variables

When data were reanalyzed without the treatment variables SPACE and SPPCOMP, the resulting were functions of only tree-level covariates:

Pinus contorta, Pringle Butte

$$[5.8a] \quad \mathrm{BD} = \gamma_{51}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{52}}}\right)^{\gamma_{53}e^{-Z}\gamma_{54}\mathrm{HT}+\gamma_{55}\mathrm{CL}}$$

Pinus ponderosa, Pringle Butte

$$[5.8b] \quad \mathrm{BD} = \gamma_{61}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{62}\mathrm{CR}}}\right)^{\gamma_{63}Z^{\gamma_{64}}+\gamma_{65}\mathrm{CL}}$$

Abies grandis, Lookout Mountain

$$[5.8c] \quad \mathrm{BD} = \gamma_{71}\mathrm{CW}\left(\frac{1-\sqrt{Z}}{1-\sqrt{\gamma_{72}\mathrm{CR}}}\right)^{\gamma_{73}Z^{\gamma_{74}}}$$

These models were significantly inferior to [5.7*a*], [5.7*b*], and [5.7*c*], respectively (Table 5.5). In a few cases, tree variables were able to account for the same variation accounted for by treatment variables. For example, in *P. ponderosa* at Pringle Butte, using either CL or SPACE resulted in a nearly identical AIC. Consequently, CL was able to account for the same variation as SPACE. In the case of *P. ponderosa* at

Table 5.5. Akaike's information criterion, log-likelihood, and likelihood ratio tests comparing models with tree and site variables and models with only tree-level variables for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa* at both study sites.

Equation No.	Number of estimated parameters	AIC	Log-likelihood	Likelihood ratio statistic	*p*-value
Abies grandis					
5.7*a*	8	2447.84	-1215.92	20.87	0.000029
5.8*a*	6	2464.71	-1226.35		
Pinus contorta					
5.7*b*	9	4005.29	-1993.65	24.20	0.000006
5.8*b*	7	4025.49	-2005.74		
Pinus ponderosa (Pringle Butte)					
5.7*c*	8	2957.14	-1470.57	7.74	0.005413
5.8*c*	7	2962.88	-1474.44		
Pinus ponderosa (Lookout Mountain)					
5.7*d*	8	2179.69	-1081.85		

Lookout Mountain, CL explained more variation than the treatment variable SPACE. In contrast, no tree-level variables tested were able to account for the effects of competitor species in either *A. grandis* or *P. contorta*, nor were there adequate tree-level variables to replace the spacing effect on *P. contorta*. As reported above, CL and SPACE were significant in the *P. contorta* model, although unexpectedly, they had opposite signs (Table 5.4). Even without SPACE in the model, CL had a negative effect branch size at a given crown depth for *P. contorta*, but a positive effect in *P. ponderosa* (Table 5.6).

With respect to bias, standard error of the estimates, and branch diameter profiles, changes after dropping treatment variables are actually quite small, especially for *P. ponderosa* at Pringle Butte (Fig. 5.3). While patterns in bias and precision for [5.8*a*], [5.8*b*], and [5.8*c*] were nearly identical to [5.7*a*], [5.7*b*], and [5.7*c*], slight discrepancies in profiles were evident for *P. contorta* on mixed plots when $Z > 0.5$ (Fig. 5.3b) and *A. grandis* on mixed plots when $Z < 0.5$ (Fig. 5.3c). These latter differences underscore the inability of tree-level attributes to account for variation due to species composition.

Table 5.6. Parameter estimates and asymptotic standard errors of the best variable exponent maximum branch diameter model for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa* at Pringle Butte.

Parameter	Estimated value	SE
Equation 5.8*a*		
γ_{51}	7.8570	0.1349
γ_{52}	0.1813	0.0479
γ_{53}	-1.6719	0.1006
γ_{54}	0.1442	0.0144
γ_{55}	-0.0266	0.0141
$SD(\delta_{51})$	0.5769	0.2491
$SD(\varepsilon)$	4.8199	0.0397
Equation 5.8*b*		
γ_{61}	8.3179	0.6297
γ_{62}	0.6974	0.0933
γ_{63}	0.4934	0.0439
γ_{64}	0.5427	0.8395
γ_{65}	0.0179	0.0057
$SD(\delta_{61})$	1.1133	0.2006
$SD(\varepsilon)$	4.2652	0.0462
Equation 5.8*c*		
γ_{71}	5.1622	0.2880
γ_{72}	0.7944	0.0335
γ_{73}	0.4526	0.0512
γ_{74}	0.5148	0.0914
$SD(\delta_{71})$	0.8115	0.2162
$SD(\varepsilon)$	3.0619	0.0477

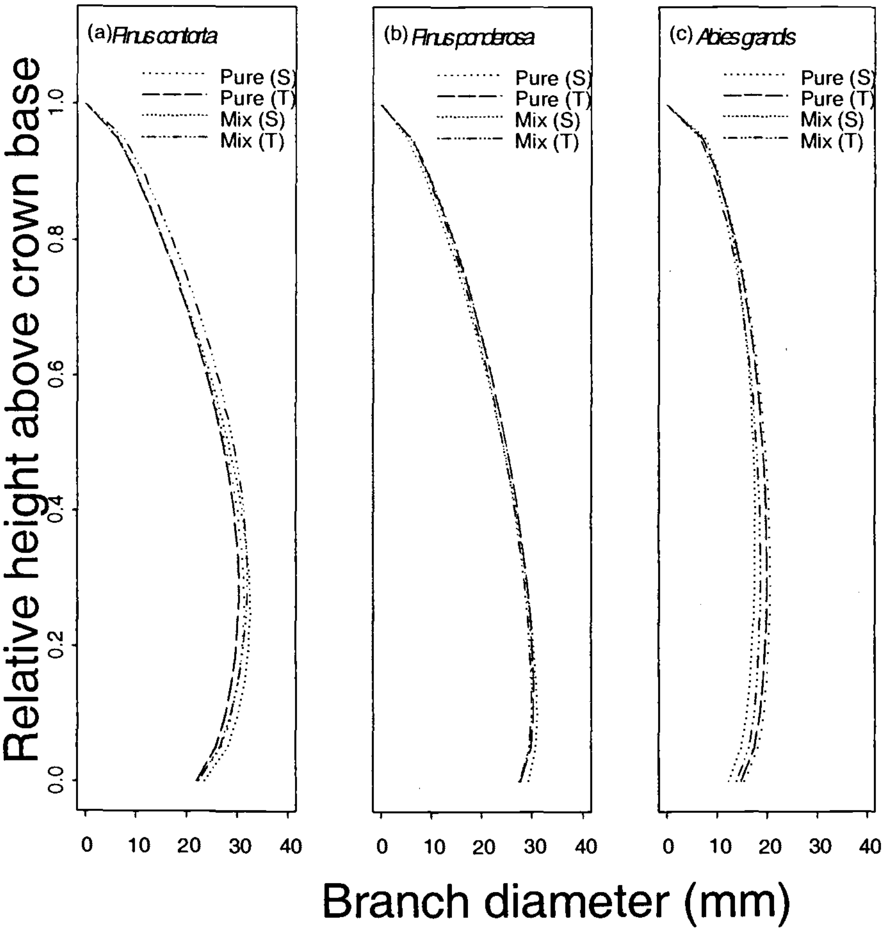

Figure 5.3. Profiles of maximum branch diameter with relative height above the crown base for average-sized trees at 3.7-m spacing in pure (Pure) and mixed (Mix) plots using model developed with tree and treatment variables (S) and model developed with only tree-level variables (T) for (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, and (c) *Abies grandis*.

DISCUSSION

Crown width

Spacing accounted for most of the variation in crown width in all three species. In general, as spacing increased, crown width increased at a decreasing rate. In only one case, *P. contorta*, did species composition influence crown width. The parameter estimate on species composition was positive suggesting *P. contorta* had greater crown widths for a given spacing in mixtures. *P. contorta* overtopped *P. ponderosa* in mixtures at Pringle Butte, therefore had better canopy positions and greater ability to expand crowns than in pure *P. contorta* plots.

The effect of spacing and in the case of *P. contorta*, species composition, on absolute maximum branch diameter is also demonstrated through crown width. Wider spacings result in large crowns and larger attainable maximum branch diameter (MBD) within a tree.

Maximum branch diameter

Autocorrelation

Maguire et al. (1999) assumed a random tree effect would eliminate any significant autocorrelation among branches within trees, and verified this assumption qualitatively by residual analysis. Similar assumptions were made in modeling branch diameters on *Pinus sylvestris* L. and *Pinus nigra* Arnold ssp. *Laricio* (Poiret) Maire, but without mention of the residual analysis (Meredieu et al. 1998; Mäkinen and Colin

1998). Recent work on taper equations for these central Oregon sites indicated random effects were not enough to eliminate within-tree autocorrelation in stem diameters (Garber and Maguire, in review). However, results suggest a random tree effect is adequate for eliminating autocorrelation among branch diameters on a single tree, even in cases where multi-order autocorrelation is initially present (Fig. 5.2).

Selection of covariates

Selection of covariates is an important process for the development of predictive models. Ideally, tree level variables would be most useful in predicting crown architecture of trees grown under varying stand structures, especially for incorporation into growth models. Most previous studies have relied on tree-level variables exclusively (Colin and Houllier 1992; Doruska and Burkhart 1994; Maguire et al. 1994; Gilmore and Seymour 1997; Roeh and Maguire 1997; Maguire et al. 1999). In some cases, intertree variation was very high, making the model building process difficult (Doruska and Burkhart 1994). In other cases, stand variables such as site index and competition index have been included, but have not contributed much additional predictive power to the models (Maguire et al. 1991; Mäkinen and Colin 1998). Variables representing tree size, such as diameter, height, and crown length, have adequately represented the effects of relative canopy position, stand density, and site quality on tree allometrics, including branch size (Roeh and Maguire 1997; Mäkinen and Colin 1998; Maguire et al. 1999). However, most of these studies have taken place in even-aged, single-species stands, where stand structures are relatively simple and homogeneous. In this context, total height serves as an indicator of relative tree height within the canopy, while crown length reflects local stand density and spacing. In more complex stand structures, size variables would not as effectively indicate relative position and cumulative effects of past competition. Since trees of the same size, but grown under different conditions have different crown architectures (O'Connell and Kelty 1994), tree size variables such as diameter and height may be inadequate for predicting branch size in more complex stands. In the Pringle Butte and Lookout Mountain spacing studies, accounting for the effects of growing conditions with tree variables proved to be difficult, but it is important to recognize that much, if not most of the influence of diameter, height, and crown length, is imposed by the portion of the model predicting MBD; that is, the function of crown width. In some cases, such as in *P. ponderosa* at both sites, crown length was able to account for additional variation in branch profiles due to spacing, and, at Pringle Butte, precluded the need for addition of diameter and height as covariates. In this latter case, crown length was apparently highly correlated with tree diameter and height, whereas at Lookout Mountain, branch size responded to variation in height over diameter for a given crown length. As indicated in other studies, branch size increased with diameter at a given height and crown length (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998).

In *P. contorta*, crown length and spacing were significant in the model, but had opposite effects. With height and spacing in the model, the marginal effect of increasing crown length was a decrease in branch diameter at a given relative height in the crown. However, crown length also had a positive effect on crown width, so the net effects of crown length must take both portions of the model into account. In *A. grandis*, the relative profile of branch diameter varied by spacing and species composition, but in a manner that did not influence diameter-height-crown length combinations. It would appear that tree size variables in Lookout Mountain *P. ponderosa* were adequate.

Vertical profiles for average plot trees

Vertical profiles of maximum branch diameter indicated that each species exhibited a peak between 0.1 to 0.4 relative height above the crown base, regardless of spacing or composition (Fig. 5.4 and 5.5). Location of the maximum branch diameter varied with species, spacing, and relative height. *P. ponderosa* appears to have its largest branch diameters at lower relative crown heights than its competitor, *P. contorta*, at Pringle Butte (Fig. 5.4a versus Fig. 5.4b). At Lookout Mountain, *P. ponderosa* branch diameters peaked at lower relative crown heights than *A. grandis* (Fig. 5.4c versus Fig. 5.4d).

At Pringle Butte and Lookout Mountain effects of increased spacing resulted in larger branches on pure plots for all species (Fig. 5.4). This was most evident for *P.*

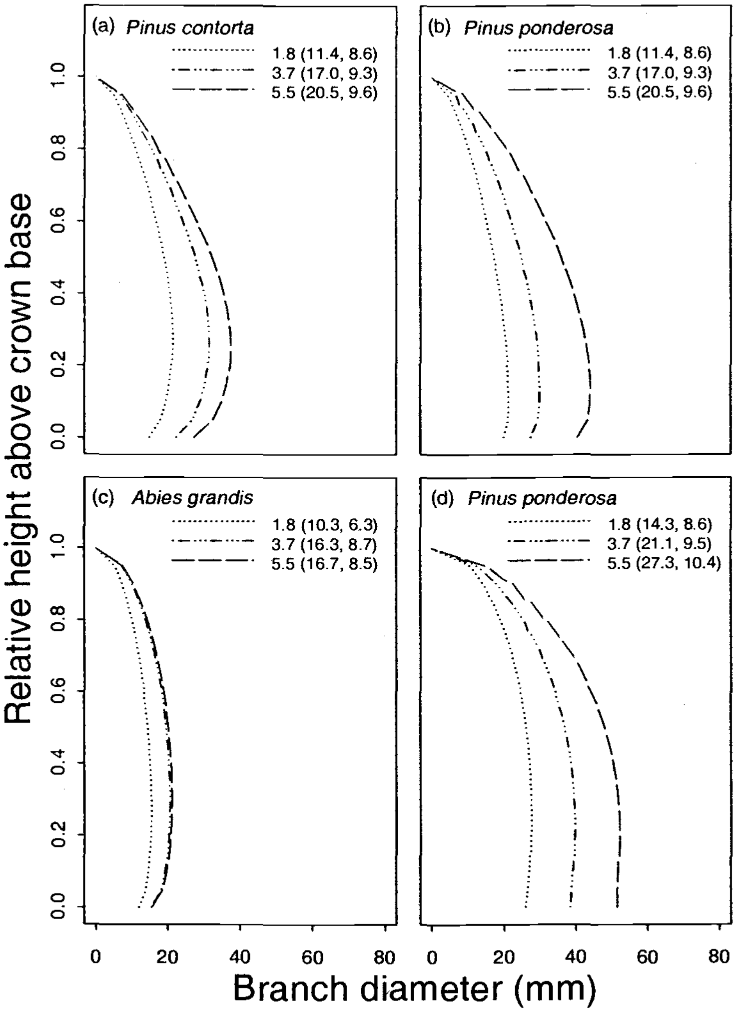

Figure 5.4. Profiles of maximum branch diameter with relative height above the crown base for a tree of average height, diameter, and crown length at 1.8-, 3.7-, and 5.5-m spacing for pure plots of: (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis*, and (d) *Pinus ponderosa* at Lookout Mountain. Tree diameter (cm) and height (m) are given in parentheses.

ponderosa at both locations (Fig. 5.4b, 5.4d). In contrast, there was little response in branch size for *A. grandis* at spacings greater than 3.7 m (Fig. 5.4c).

Effects of species composition across spacing were also evident (Fig. 5.5). As with pure plots, maximum branch diameters for each species in mixtures responded to the increase in spacing, however, these responses were different than in monocultures. In *P. ponderosa* at Pringle Butte (Fig. 5.5a-5.5c) and *A. grandis* (Fig. 5.5d-5.5f), pure plots had wider maximum branch diameter profiles at tighter spacings than mixed plots. As spacing increased, the difference between pure and mixed plots diminished; that is, the trees in mixtures had a greater response to the increase in spacing than trees in pure plots. In contrast, *P. contorta* at Pringle Butte and *P. ponderosa* at Lookout Mountain had wider branch diameter profiles in mixture than in pure plots at the closest spacing. As spacing increased, differences became smaller in *P. contorta* but not in *P. ponderosa* at Lookout Mountain (Fig. 5.5a-5.5f). In this case, the pure plots responded more to the increased spacing than did the mixed plots.

Although not a primary focus in this study, increasing relative height, height of the subject tree relative to the tallest tree on the subplot, a measure of social position within the stand, resulted in an increase of maximum branch diameter in all species except for *P. contorta* (Fig. 5.6). Relative profiles for *P. contorta* overlap to a large degree depicting larger branch diameters at high relative positions within the crown with decreasing social position (Fig. 5.6b). However, when plotted on an absolute scale, overlapping only occurs near the crown base, with the highest relative height

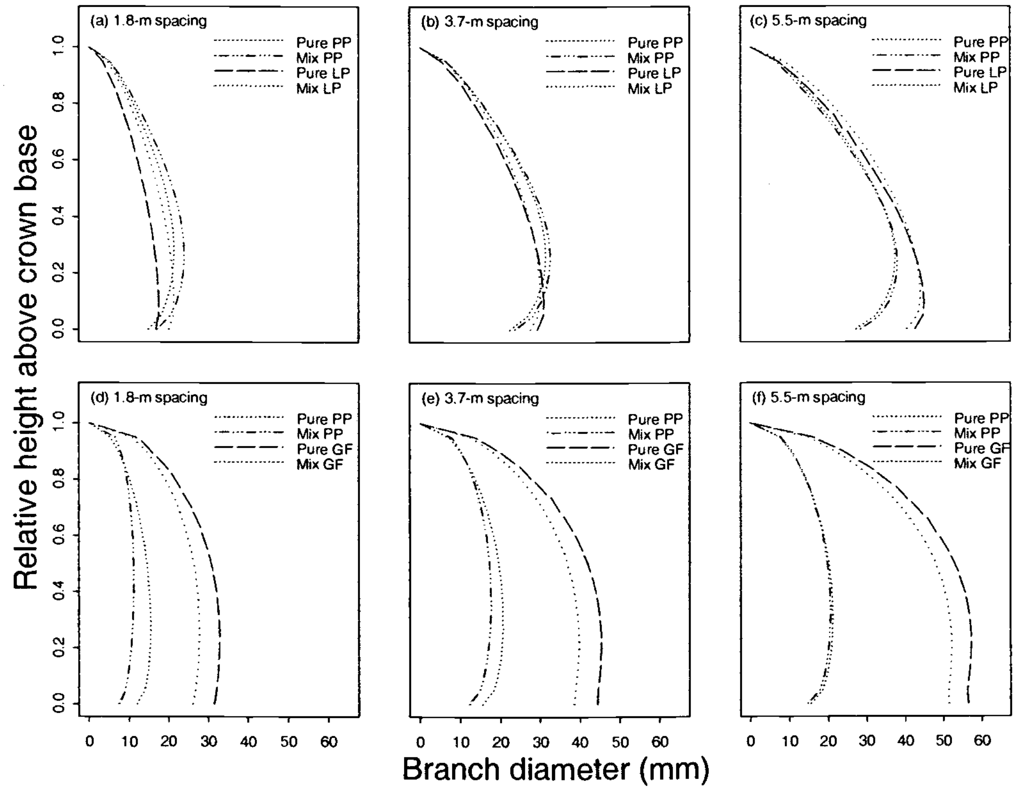

Figure 5.5. Profiles of maximum branch diameter with relative height above the crown base for two trees of average diameter, height, and crown length for each species on pure (Pure) and mixed (Mix) plots for *Abies grandis* (GF), *Pinus contorta* (LP), and *Pinus ponderosa* (PP): (a) 1.8-m (Pure PP DBH=12.7, HT=6.8, Mix PP 10.4, 6.5, Pure LP 11.4, 8.6, Mix LP 12.9, 8.5), (b) 3.7-m (Pure PP 16.7, 7.1, Mix PP 16.89, 7.5, Pure LP 17.0, 9.3, Mix LP 17.8, 9.0), and (c) 5.5-m (Pure PP 23.6, 9.3, Mix PP 22.9, 9.2, Pure LP 20.5, 9.6, Mix LP 21.1, 9.5) spacings at Pringle Butte and (d) 1.8-m (Pure PP 14.3, 8.6, Mix PP 17.7, 9.4, Pure GF 10.3, 6.3, Mix GF 7.7, 5.7), (e) 3.7-m (Pure PP 21.1, 9.5, Mix PP 23.9, 10.1, Pure GF 16.3, 8.8, Mix GF 14.7, 9.0), and (f) 5.5-m (Pure PP 27.3, 10.4, Mix PP 28.7, 10.4, Pure GF 16.7, 8.5, Mix GF 16.8, 8.3) spacings at Lookout Mountain.

having the highest height to crown base (not shown). As with spacing, relative tree social position has previously been shown to influenced profiles of maximum branch diameter (Colin and Houllier 1991; Gilmore and Seymour 1997).

Branch diameter development

Existing branch diameter depends on the rate and duration of past branch growth. Growth of a branch depends on position of the branch within the crown, tree social position, and stand structure (Mäkinen 1999a). In general, branch diameter growth begins rapidly, then decreases markedly as a negative exponential function of branch age (Kershaw et al. 1990; Mäkinen 1999b). As a result, older branches, such as those deeper in the crown, are generally growing slower than younger branches at the top of the tree. Branch growth at a given height is also positively correlated with growth of the main stem (Mäkinen 1999a). Faster tree growth suggests better social position within a stand. Lower social positions, and consequently lower relative heights, can result in rapid deceleration of branch growth (Fujimori 1993; Mäkinen 1999a; Mäkinen and Colin 1999).

This growth patterns would be expected to result in largest branches at the base of the live crown. However, the curvilinear form, with branch diameter decreasing near the base of the live crown found in these three species, has also been found in several other species, regardless of shade tolerance, including *P. nigra* (Meredieu et al. 1998), *P. sylvestris* (Mäkinen and Colin 1998), *Picea abies* (L.) Karst. (Colin and

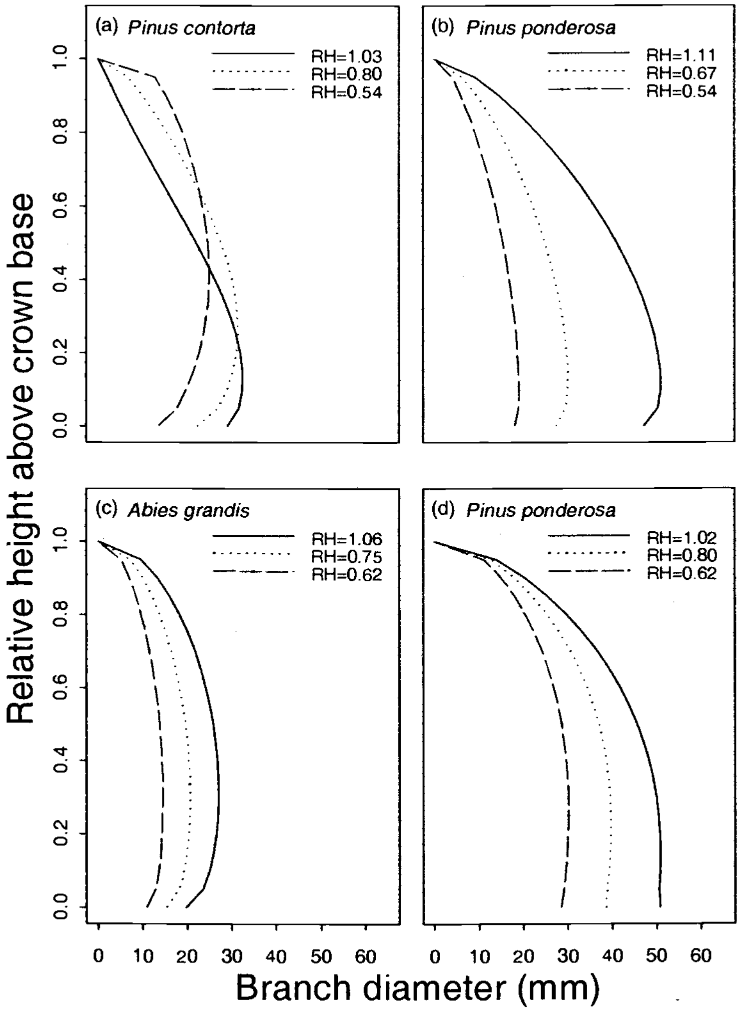

Figure 5.6. Profiles of maximum branch diameter with relative height above the crown base for three trees of different social positions (RH = HT / maximum HT on plot) and corresponding diameters, heights, and crown lengths at 3.7-m spacing: (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis*, and (d) *Pinus ponderosa* at Lookout Mountain.

Houllier 1991), *Abies balsamea* (L.) Mill. (Gilmore and Seymour 1997), and *P. menziesii* (Maguire et al. 1994; Maguire et al. 1999). Although the decrease in branch size near the base of the live crown has been attributed to a poorer light environment (Kershaw et al. 1990; Mäkinen 1999b), this growth pattern was also evident in the widest spacings at Pringle Butte and Lookout Mountain where crown closure has not occurred. Likewise, Roeh and Maguire (1997) reported a decrease in branch diameter at the base of the live crown in stands of young *P. menziesii* that have not reached crown closure. These results suggest that branch growth slows before crown closure, due in part to self-shading and shading by adjacent trees, but also perhaps due to the growth rate of the tree (Colin and Houllier 1991; Maguire et al. 1994; Mäkinen and Colin 1998). Another possible mechanism for relatively slower growth in lower branches after accounting for age is the higher number of whorl branches found at the base of the crown, increasing competition among branches.

Effects of density have also been observed in previous studies of branch diameters (Magnussen and Yeatman 1987; Ballard and Long 1988; Colin and Houllier 1991; Maguire 1994). Since, wider spacings result in faster tree growth (Chapter Three) and larger crowns (Curtis and Reukema 1970), branches would have faster early growth rates longer longevity (Mäkinen 1999a). Effects of stand density have also previously been shown to vary among crown positions in *P. sylvestris* (Mäkinen 1999b). Branch growth in the upper crown is thought to be more influenced by regional conditions, whereas local stand conditions have increasing effects in the lower portion of the crown (Mäkinen 1999b). *P. ponderosa*, at both sites, responded more dramatically to spacing than the other two species. A recent study on these same plots reported a dramatic height and volume response to spacing by *P. ponderosa* at Pringle Butte (see Chapter Three). Clearly, spacing has a profound effect on the development of *P. ponderosa*. Only *A. grandis* did not show an increase in maximum branch diameter at the between the two widest spacings at Lookout Mountain (Fig. 5.4). Crown closure has not occurred on either one of these two spacings for *A. grandis* and the live crowns extend to the ground. Consequently, the trees at both spacings were essentially still open-grown.

In the mixtures, however, affects of spacing different among the species. In contrast to single-species stands, canopies in mixed-species stands not only differentiate on the basis of within species genetics and microsite, but they also stratify by species grouping (Cobb et al. 1993; Oliver and Larson 1996; Smith et al. 1997). The process of stratification is a function of many silvical attributes including shade tolerance and height growth. Consequently, when different species are well-interspersed as individuals, multiple strata can form (Cobb et al. 1993), resulting in wider vertical foliage profiles (Yang et al. 1999), different light environment, and an alteration of tree growth dynamics. Alterations in tree growth dynamics are manifested by changes in crown architecture. At Pringle Butte and Lookout Mountain, both species had different branch diameters depending on whether they were in a pure or mixed stand. In some cases, such as *P. contorta* at Pringle Butte and *P. ponderosa* at

Lookout Mountain, trees in mixtures had wider maximum branch diameter profiles due to the lower stature of their competitors. In contrast, species relegated to a lower social position, *P. ponderosa* at Pringle Butte and *A. grandis* at Lookout Mountain, had narrower profiles in mixtures than in pure plots. Stratification has therefore influenced branch diameter development over time, causing prolonged branch growth in the overtopping species and faster suppressed growth in subordinate species. In addition, the effects of competing species changed with increasing spacing, resulting in fewer differences in the profiles between trees in pure and mixed plots. Spacing effects on stand development in these plots suggest that increasing spacing improves growth for the superior and the subordinate species, but the improvement is more marked for the subordinate species due to increased light availability going from understory to open-grown conditions. Wider spacing resulted in less stratification in both spacing trials (see Chapter Three). Maximum branch diameter responded in a similar way. Although at narrow spacings the competitive effect of the overtopping species in mixtures resulted in narrower branch diameter profiles in the subordinate species, as spacing increased the subordinate species gained better canopy positions, and subsequently their branch growth response to spacing was greater than in the pure stands; that is, differences between branch diameters in pure and mixtures decreased. In contrast, the response in branch diameter profiles of the overtopping species to spacing was smaller in the mixed plots than pure due to less competition with increasing spacing in pure plots.

After initial rapid growth reduction, branch growth continues slowly, if at all, although the branch continues to survive for many years (Andrews and Gill 1939; Mäkinen 1999b). As branches develop, they are relegated to lower crown positions and poorer light conditions due to self-shading (Brooks et al. 1991; Sampson and Smith 1993). These poorer light conditions result in poorer branch growth, especially less earlywood production (Kershaw et al. 1990; Mäkinen 1999a; Mäkinen and Colin 1999; Protz et al. 2000). Since water transport is a function of tracheid anatomy, differences in tracheid diameter causes changes in permeability. Moreover, since most water transport occurs in the earlywood tracheids, hydraulic resistance increases (Pothier et al. 1989; Protz et al. 2000). Water stress results in a decrease in stomatal conductance (i.e., stomatal closure), foliage mortality, and reduced photosynthesis in lower canopy positions. Despite increasing stress, these branches remain alive. Half or more of the life of a branch can be spent without perceivable increment (Andrews and Gill 1939; Kershaw et al. 1990; Mäkinen 1999a). Senescent branches are assumed to satisfy there own maintenance costs, but do not contribute to net tree production (Sprugel et al. 1991), and therefore are considered nonfunctional for tree growth (Fujimori 1993). Eventually, with the passage of time and increasing shade, the branch dies.

Silvicultural implications

Wood quality is strongly related to crown architecture, particularly as crown architecture influences the proportion of juvenile wood, knot size, and earlywood/latewood ratio (Maguire et al. 1991; Agestam et al. 1998; Björklund and Moberg 1999; Moberg 2001; Gartner et al. 2002). It has long been known that local stand density controls crown length and width (Assmann 1970; Curtis and Reukema 1970; Rouvinen and Kuuluvainen 1997). Although crown length has an obvious impact on the size of the crown wood core (Maguire et al. 1991), others have not found corresponding differences in wood properties to equate crown wood with juvenile wood (Gartner et al. 2002). Regardless, stand density does influence the length of crownless bole and also influences the size of the branches, and therefore knot size and distribution. Moreover, competing species also influence the size of branches. Two major strategies have been adopted in the past to improve wood quality. The first is to maintain high densities resulting in smaller crowns (Curtis and Reukema 1970) and therefore longer branchless boles. The second is to grow at wide spacing and prune (Nyland 1996; Smith et al. 1997). The first strategy generally will result in higher wood production at early ages (see Chapter Three), as well as smaller branches; however, the average size of the stems will be smaller. If large piece size is of interest, this approach will require thinning at some stage to reduce density before crown lengths are too small. Thinning can increase upper crown branch growth, while lengthening lower branch longevity; however, previous results also suggest that thinning cannot stimulate branch growth in those branches that have already become suppressed (Mäkinen 1999a,1999b). Impact on wood quality is minimal except for the potential persistence of lower branches after thinning. In some circumstances, thinning can be costly, especially when rotation lengths are short and there no market exists for small logs. Thinning can also result in considerable residual stand damage, depending on the equipment used. The second approach is also costly, especially if several prunings are required. An alternative strategy involves cultivation of stratified, mixed-species stands in which subordinate species serve as trainers, accelerating the growth reduction and self-pruning of branches on the overtopping species (Smith et al. 1997). This approach can also yield wood of high quality in the subordinate species, analogous to development in uneven-aged stands where younger cohorts develop under partial shade (Nyland 1996; Smith et al. 1997).

Several additional factors, including spacing, species ratio, and stand dynamics, should be addressed when considering managing species mixtures. The results presented here from Pringle Butte and Lookout Mountain represent several spacings, but only one mixture ratio (50:50), and a single point in time. Spacing influences stand development (see Chapter Three), and therefore will affect crown structure. Wider spacings will result in less stratification, longer branch durations, and larger branch diameters than tighter spacings, especially for the subordinate species. Small changes in spacing will likely result in rather large reductions in branch sizes in the subordinate species. With this in mind, spacings in mixtures can be fine-tuned to obtain the desired log size, log quality, and stand volume. For example, if 3.7-m spacing provides desired log size by age 50, but longer crowns, larger branches, and less stand volume than wanted, interplanting a slower-growing tolerant species may yield the desired crown dimensions and stand volume with little sacrifice in log size.

Changes in the ratio of each species will change the local competition and therefore will also alter crown architecture. For example, one *P. ponderosa* to every two *A. grandis*, will likely increase the branch sizes in both species, while two *P. ponderosa* to every one *A. grandis* may decrease the branch sizes in both species. As with spacing, species ratio would have to be fine tuned for objectives.

Finally, just as with spacing, species ratio will alter stand dynamics. A higher ratio of the overtopping and subordinate species will likely increase and decrease, respectively, the stratification between the species. The choice of species will affect the dynamics of the stand due to differences in growth rates over time. Two similar species, such as the *Pinus* species at Pringle Butte, will result in less stratification than two dissimilar species, such as the *Abies-Pinus* mixture at Lookout Mountain.

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CHAPTER SIX: STAND-LEVEL GROWTH EFFICIENCY IN TWO MIXED-SPECIES SPACING STUDIES IN THE CENTRAL OREGON CASCADES

ABSTRACT

Stand and tree growth efficiency were assessed across a range of spacing and species compositions in two mixed-species spacing trials on the eastside of the Oregon Cascades. One study involved a mix of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), the other a mix of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and ponderosa pine. As spacing increased, LAI generally decreased in *A. grandis*, but leveled out in the two *Pinus* species at the widest spacings. Plot branch masses also decreased in all but pure *P. ponderosa* and *A. grandis-P. ponderosa* plots. Foliage ratio, ratio of foliage mass to crown mass, generally decreased with increasing spacing in all but pure *P. contorta* and *P. contorta-P. ponderosa* mix, where it was roughly constant across spacings. Growth efficiency decreased slightly with spacing for all compositions at Pringle Butte, however varied with species composition at Lookout Mountain. While pure *P. ponderosa* and the *A. grandis-P. ponderosa* mixture exhibited a decrease with increasing spacing, *A. grandis* increased between 1.8- and 3.7-m spacing beyond which it decreased. Results suggest that plot growth efficiency peaks at intermediate densities, which depend on species composition. At wider spacings, growth efficiency appears to be limited by higher proportions of respiring tissue, while at tighter

spacings, growth efficiency appears to be limited by competition among individual reducing resources per individual and resulting in differentiation, where the poorest individuals contribute leaf area but proportionally less growth reducing stand growth efficiency.

INTRODUCTION

Net primary productivity is the accrual of biomass through the process of photosynthesis (Perry 1994). In photosynthesis, trees absorb light energy and reduce carbon dioxide to carbohydrates. This fixed carbon then serves as the raw material for further biochemical synthesis (Waring and Schlesinger 1985; Perry 1994). Although photosynthesis may occur in several parts of the tree including foliage and bark (Waring and Schlesinger 1985), the most important location of carbon fixation in temperate species is the foliage (Waring and Schlesinger 1985; Roberts and Long 1992). Carbon is allocated to different parts of tree (Waring and Schlesinger 1985; Perry 1994; Smith et al. 1997), depending on the tree's environment (Mooney et al. 1978; Waring 1983). Allocation patterns have evolved through natural selection to increase the tree's ability to survive and reproduce (Smith et al. 1997). Maintenance respiration is the first priority for carbon allocation, since the tree must first survive (Waring and Pitman 1985). Leaf area is also considered a fairly high priority to ensure continued capacity to fix carbon, but stem growth is commonly thought of as a low priority (Waring and Pitman 1985; Waring and Schlesinger 1985; Smith et al. 1997).

Because stemwood is commercially important, relative allocation to this component has attracted much attention (Waring et al. 1980; Waring et al. 1981; Waring 1983; O'Hara 1988; O'Hara 1989; O'Hara 1996; Maguire et al. 1998).

The rate at which carbon is assimilated into biomass is often expressed per unit leaf area, and this rate has been labeled growth efficiency (Assmann 1970; Waring 1983). Growth efficiency has been measured in various other ways, but is generally expressed as some unit of productivity per unit total plant biomass, land area, leaf area, or leaf biomass (Perry 1994). Growth efficiency is defined here as stemwood volume increment per unit leaf area for individual trees or stands.

At the tree-level, growth efficiency has been shown to decline with increasing leaf area of the tree (Long and Smith 1990; Smith and Long 1992; Maguire et al. 1998) and increase with higher canopy position (Waring et al. 1980; O'Hara 1988; Roberts and Long 1992; Roberts et al. 1993; Gilmore and Seymour 1996; O'Hara 1996; Maguire et al. 1998; Kollenberg and O'Hara 1999). Density effects, however, are not very well understood, and have been confounded by effects of canopy position and silvicultural treatments. Long and Smith (1990) reported higher growth efficiency in tighter spacings, while Waring et al (1981) and Sterba and Amateis (1998) have found higher growth efficiencies at wider spacings.

Many factors influence growth efficiency, including shifts in allocation to stemwood production, increase or decrease in net photosynthesis, and increase or decrease in respiratory losses. Stand growth efficiency is a function of individual tree growth efficiencies, so for a given site quality and age, stand growth efficiency is primarily influenced by stand structure. Trees spaced at tighter spacings would be expected to form stands with higher leaf areas at an earlier age, more self-shading, and a decrease of light penetration into the canopy (Sinclair and Knoerr 1982; Pierce and Running 1988; Vose and Allen 1988; Vose and Swank 1990; Sampson and Smith 1993). Less light interception per unit leaf area results in decreasing photosynthesis in the lower canopy strata, reducing average tree growth efficiency and therefore stand growth efficiency. Moreover, if density increases, competition for scarce soil and water resources increases, perhaps resulting increased allocation to other tree components (Keyes and Grier 1981; Haynes and Gower 1995). Several studies have documented results in which growth efficiency has decreased with increasing stand leaf area or stand density (Waring et al. 1981; Waring and Pitman 1983; Binkley and Reid 1984; Velazquez-Martinez et al. 1992).

It has also been suggested that, at equal total stand leaf area, higher density stands will have greater growth efficiencies. Trees with smaller crowns may be more efficient due to higher foliage mass to crown mass ratios and lower sapwood volumes and associated respiratory losses (Smith and Long 1989). Since higher densities result in trees with smaller crowns (Curtis and Reukema 1970), higher density stands may have higher mean tree growth efficiency, and thus greater stand growth efficiency (Smith and Long 1989; Smith and Long 1992). Growth efficiency has been found to increase with increasing stand density before and after crown closure in *Pseudotsuga* *menziesii* (Mirb.) Franco (O'Hara 1989), *Pinus contorta* var. *latifolia* Dougl. (Smith and Long 1989; Long and Smith 1990), and *Abies balsamea* (L.) Mill. (Lavigne 1988).

Relatively few studies have addressed the effects of species composition on stand growth efficiency. In even-aged, mixed-species stands, stand structure develops not only as a result of differentiation within a species, but also stratification among species, yielding more complex canopy architectures than found in single-species stands. Smith and Long (1992) investigated mixtures of *P. contorta* var. *latifolia* and *Abies lasiocarpa* (Hook) Nutt. and found higher individual tree growth efficiencies in pure *A. lasiocarpa* stands than in either mixtures or pure *P. contorta* var. *latifolia* stands. They attributed this to the lower mean tree leaf area in *A. lasiocarpa*, however, they did not report on stand-level growth efficiency, nor was density or species mix controlled.

Past work in spacing and thinning studies suggests the influence of spacing on stem volume growth is a tradeoff between resource availability and costs of crowns. Wider spacing reduces competition among individuals but also increases construction and maintenance respiration of branchwood. Several important questions arise. First, is the improved resource availability enough to offset the increases in maintenance costs? How does species composition affect stand growth efficiency at the stand level? Finally, how do individual trees behave within stands of varying density and species composition? These questions were addressed in two mixed-species spacing trials in the central Oregon Cascades. The main objective of this study was to assess patterns in growth efficiency across spacing and species composition in two controlled spacing trials. Specific objectives were: (*i*) to assess whether stand growth efficiency varies with spacing; (*ii*) to test for any possible interaction between spacing and species composition on stand growth efficiency; (*iii*) to relate results in growth efficiency to crown size, sapwood volume, and stand density; and (*iv*) to qualify the distribution of individual tree growth efficiencies in monocultures and mixtures.

METHODS

Study Sites

The study was conducted at two sites. The first site, Pringle Butte, is a mixture of *Pinus contorta* Dougl. ex Loud. and *Pinus ponderosa* Dougl. ex Laws. The second site, Lookout Mountain, is a mixture of *P. ponderosa* and *Abies grandis* (Dougl. ex D. Don) Lindl. Both sites are east of the Cascade Range crest, 35 miles southwest of Bend, in the Pringle Falls Experimental Forest, Deschutes National Forest, Deschutes County, Oregon.

Pringle Butte site

The Pringle Butte study site is located on the northwest-facing slope of Pringle Butte at an elevation of 1,370 m (43^{o}43' N, 121^{o}37' W). Slopes range from 4 to 27 percent, with an average of 10 percent. Mean annual precipitation is only 61 cm and falls predominantly between the months of October and April, with a half-meter snow pack common between January and March. Maximum temperatures occur in July, averaging 26^{o}C, and frosts can occur at any time during the year (Cochran and Barrett 1999a). The soils in this area have been typed as a developing Xeric Vitricryands on 75 cm of dacite pumic from the eruption of Mount Mazama (Cochran and Barrett 1999a). This pumice layer overlays sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments.

The study area is 3.9-ha, clearcut in 1970. The ground cover consists of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), scattered Ross sedge (*Carex rossi* Boott), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and western needle grass (*Stipa occidentalis* Trub. ex Wats.). *P. ponderosa* site index (base age 100) has been estimated at 24 m using Meyer's (1961) curves and 33.5 m using Barrett's (1978) method (Cochran and Barrett 1999a).

Lookout Mountain site

The Lookout Mountain study site is located on the northeast-facing slope of Lookout Mountain at an elevation of 1550 m (43^{o}49' N, 121^{o}41' W). Slopes average close to 20-percent. Average annual precipitation is approximately 100 cm, most of which falls as snow between the months of September and May. Generally, summers are hot and dry, with temperatures ranging from 21 to 32^{o}C. Nights are predominantly cool with the chance of frost occurring any time during the year (Cochran and Barrett

1999b). Soils are deep, well-drained Typic Cryorthents, developed from dacite pumice originating from the eruption of Mount Mazama, overlaying a sandy loam paleosol developed in older volcanic ash with cinders and basalt fragments (Seidel 1985; Cochran and Barrett 1999b).

This study site is 8.1-ha, clearcut in 1974 in a mixed-conifer/snowbrush-chinkapin plant community (Seidel 1985). The ground cover consists primarily of *C. velutinus*, *A. patula*, and golden chinkapin (*Castonopsis chrysophylla* (Dougl.) A. DC.) (Seidel 1985). *C. velutinus* ground cover is very dense over much of the study site. The late successional plant community association is *Abies concolor/Ceanothus velutinus* (Franklin and Dyrness 1973). Site index (base age 100) for *P. ponderosa* (Meyer 1961) is about 27.5 m (Seidel 1985).

The site was planted with 2-0 bare root *P. ponderosa* stock grown at the USDA Forest Service nursery in Bend, OR, and 2-0 *A. grandis* containerized stock. Seed of each species was collected in 1971 from near the study site. Planting took place in the spring of 1974 and during the first two years, any seedlings that died were replaced by transplanted seedlings from outside the plots. In addition, the *C. velutinus*, *A. patula*, and *C. chrysophylla* were sprayed in June of 1976 and 1979 with herbicides to reduce competition (Seidel 1985).

Experimental Design

Each study was established under a completely randomized split-plot design in which the whole-plot factor was tree spacing and the split-plot factor was species composition. Pringle Butte was composed of five initial spacings: 1.8, 2.7, 3.7, 4.6, and 5.5 m (6, 9, 12, 15, and 18 feet). Species composition included pure *P. ponderosa*, pure *P. contorta*, and a 50:50 mix of both species. Treatment combinations were replicated twice, so each of the five spacings were randomly assigned to 10 whole plots, and subplots within each whole plot were randomly assigned a species mix. The size of the whole plots varied by spacing but each contained 147 to 390 measure trees.

Lookout mountain was composed of three initial spacings: 1.8, 3.7, and 5.5 m (6, 12, and 18 feet). The three species combinations in the subplots included pure *P. ponderosa*, pure *A. grandis*, and a 50:50 mix of both species. Each whole plot consisted of three subplots of the same spacing. The whole plots were of variable size, depending on spacing, and were designed so that each subplot had 24 measured trees. Three replications produced a total of nine whole plots and 27 subplots.

Plot Measurements

Data have been collected on each study for the past 20 to 30 years by the USDA Forest Service and more recently by Oregon State University. At Pringle Butte, diameter at breast height (DBH) of all plot trees was measured to the nearest

0.25 cm (0.1 in) in 1992 and to the nearest 0.1 cm in May 2001. Total height (HT) of all plot trees was measured to the nearest 0.03 m (0.1 ft) in 1992 and to the nearest 0.01 m during the summer of 2001, ignoring the current season's leader growth. Height to the lowest living branch (HLB, nearest 0.01 m) was also collected in 2001.

At Lookout Mountain, diameter at breast height of all plot trees was measured to the nearest 0.13 cm (0.05 in) in 1995 and to the nearest 0.01 m in late summer 1999. Total height of all plot trees was measured to the nearest 0.03 m (0.1 ft) in 1995 and to the nearest 0.1 cm in late summer 1999. Height to the lowest living branch to the nearest 0.01 m was also collected in late summer 1999.

Estimation of Productivity

Productivity was defined as the net growth of the initial stem volume (inside bark) expressed as a periodic annual increment. Stem shape has been successfully modeled with a variable exponent taper model (Kozak 1988; Garber and Maguire, in review):

$$\text{dib} = \alpha_1 \text{DBH}^{\alpha_2} \; X^{C} + \epsilon$$

where dib is the predicted diameter inside bark at some height h, $X = [1 - (Z)^{0.5}] / [1 - (p)^{0.5}]$, Z is the relative height h / HT, p is the relative height where shape of tree changes form neoloid to paraboloid, $C = f$(Z and other tree variables), ϵ is the random error term, α_1 and α_2 are the parameters estimated from the data, and DBH and HT are defined above.

Individual tree volume was estimated as total (stump to tip) inside bark volume by numerically integrating the taper function from 0.15 m to the tree tip (see Chapter Three). Plot volume for a given year was then calculated as the sum of all individual tree volumes on the plot and periodic annual increment (PAI) was calculated as the average annual change in plot volume over the growth period (cm^3 ha^{-1} yr^{-1}).

Estimation of tree leaf area

Leaf area equations were developed from the same trees destructively sampled for the taper equations (see Chapter Four). The models developed for *A. grandis*, *P. contorta*, and *P. ponderosa*, respectively were:

$$[6.1a] \quad \mathrm{TLA} = \alpha_{11}\mathrm{CL}^{\alpha_{12}}\, \mathrm{e}^{\alpha_{13}(\mathrm{DBH/HT})}$$

$$[6.1b] \quad \mathrm{TLA} = \beta_{11}\mathrm{BACR}$$

$$[6.1c] \quad \mathrm{TLA} = (\gamma_{11} + \gamma_{14}\mathrm{SITE})\mathrm{CL}^{\gamma_{12}}\, e^{\gamma_{13}(\mathrm{DBH/HT})}$$

where TLA is tree leaf area, CL is crown length (m), DBH is diameter at breast height, HT is total height, BACR is basal area (m^2) times crown ratio above breast height (BA

× CL / (HT-1.37)), SITE is an indicator variable representing the study site (PB = 0 and LM = 1), and α_{11}, α_{12}, α_{13}, β_{11}, γ_{11}, γ_{12}, γ_{13}, and γ_{14} are parameters estimated from the data (Table 6.1).

Estimation of tree leaf and branch mass

Leaf and branch mass equations were developed by subsampling branches from the trees destructively sampled for taper and leaf area equations (see Chapter Four). The final tree leaf mass models developed for *A. grandis*, *P. contorta*, and *P. ponderosa*, respectively were:

[6.2*a*] $\mathrm{TLM} = \alpha_{21}\mathrm{CL}^{\alpha_{22}}\, e^{\alpha_{23}(\mathrm{DBH/HT})}$

[6.2*b*] $\mathrm{TLM} = \beta_{21}\mathrm{BACR}$

[6.2*c*] $\mathrm{TLM} = (\gamma_{21} + \gamma_{24}\mathrm{SITE})\mathrm{CL}^{\gamma_{22}}\, e^{\gamma_{23}(\mathrm{DBH/HT})}$

where TLM is tree leaf mass (Mg), α_{21}, α_{22}, α_{23}, β_{21}, γ_{21}, γ_{22}, γ_{23}, and γ_{24} are parameters estimated from the data (Table 6.1) and all other variables are defined above. Final

Table 6.1. Parameter estimates and standard errors for the tree leaf area, leaf mass, and branch mass equations for *Abies grandis*, *Pinus contorta*, and *Pinus ponderosa*.

Parameter	Estimated value	SE
α_{11}	0.0958	0.0159
α_{12}	1.4095	0.0986
α_{13}	1.8039	0.1781
α_{21}	0.0265	0.0045
α_{22}	1.4516	0.1028
α_{23}	1.8802	0.1815
α_{31}	0.0048	0.0012
α_{32}	1.8423	0.1421
α_{33}	2.1817	0.2662
β_{11}	2128.3641	82.1536
β_{21}	347.8272	13.8461
β_{31}	0.0042	0.0026
β_{32}	1.6478	0.1160
γ_{11}	0.2155	0.0209
γ_{12}	1.8489	0.0664
γ_{13}	1.0803	0.0851
γ_{14}	-0.0491	0.0091
γ_{21}	0.0263	0.0027
γ_{22}	1.9119	0.0700
γ_{23}	1.0921	0.0088
γ_{24}	-0.1487	0.0540
γ_{31}	0.0106	0.0016
γ_{32}	2.5003	0.0964
γ_{33}	1.2945	0.1208
γ_{34}	-0.2838	0.0726

tree branch mass models developed for *A. grandis*, *P. contorta*, and *P. ponderosa*, respectively were:

$$[6.3a] \quad \mathrm{TBM} = \alpha_{31}\mathrm{CL}^{\alpha_{32}}\, e^{\alpha_{33}(\mathrm{DBH/HT})}$$

$$[6.3b] \quad \mathrm{TBM} = \beta_{31}\mathrm{DBH}^{\beta_{32}}$$

$$[6.3c] \quad \mathrm{TBM} = (\gamma_{31} + \gamma_{34}\mathrm{SITE})\mathrm{CL}^{\gamma_{32}}\, e^{\gamma_{23}(\mathrm{DBH/HT})}$$

where TBM is tree branch mass (Mg), α_{31}, α_{32}, α_{33}, β_{31}, β_{32}, γ_{31}, γ_{32}, γ_{33}, and γ_{34} are parameters estimated from the data (Table 6.1) and all other variables are defined above.

Statistical Analyses

Since leaf area for *A. grandis* determined from [6.1*b*] is projected, while leaf area for *P. contorta* and *P. ponderosa* from [6.1*a*] and [6.1*c*] were all-sided values, TLA for *A. grandis* was converted to an all-sided value by multiplying projected leaf area by 2.50. Growth efficiencies, however, were based on projected values for *A. grandis*. Plot leaf area index (LAI) was calculated as the sum of all individual tree leaf areas on the plot divided by the plot area in the same units ($m^2\ m^{-2}$), while plot leaf and branch masses were scaled to a per hectare basis. Plot foliage ratio (FR) was determined by dividing foliage mass by crown mass (plot foliage mass + plot branch mass) (Roberts and Long 1992). Plot-level growth efficiency was then defined as PAI per unit plot leaf area (cm^3 m^{-2} yr^{-1}). Estimates of plot LAI, branch mass, foliage ratio, and growth efficiency were tested across two factors (spacing and species composition) by two-way split plot analysis of variance using a mixed-treatment-effects model (Kuehl 2000). Where the null hypothesis of no differences between the treatments was not supported by the analysis of variance, the Bonferroni adjustment multiple range test was used to identify which means were different. Tests on simple effects were assessed with orthogonal polynomial contrasts and *F*-tests. An α-level of 0.05 was used in all tests of significance.

RESULTS

Leaf area index

At Pringle Butte, spacing ($p = 0.034$) and species composition ($p = 0.003$) had a significant effect on LAI, while the interaction did not ($p = 0.115$). LAI's ranged from 2.3 to 5.1 m^2 m^{-2} and was separated into two groups across spacing, 1.8 to 2.7 m and 3.7 to 5.5 m (Fig. 6.1a; Table 6.2). LAI's on pure *P. ponderosa* and the mixture were significantly higher than the pure *P. contorta* plots (Fig. 6.1a; Table 6.2), but the interaction between spacing and species composition was not significant. LAI on the pure *P. contorta* plots showed a constant decrease across densities. Likewise, the mixtures exhibited a similar trend, albeit, not as dramatic. In contrast, the pure *P.*

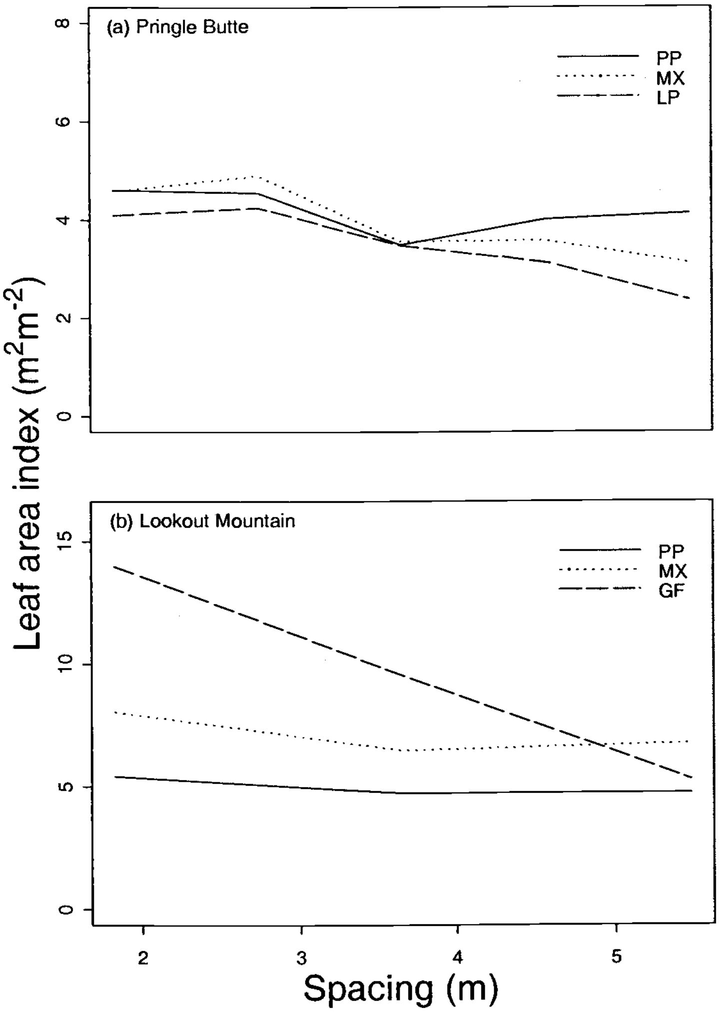

Figure 6.1. Trends in all-sided LAI over spacing for the three species mixtures at (a) Pringle Butte and (b) Lookout Mountain. GF, *Abies grandis*, LP, *Pinus contorta*, PP, *Pinus ponderosa*, MX, Mix.

ponderosa plots exhibited a decrease in leaf area between 1.8- and 3.7-m spacing, and then an increase from 3.7- to 5.5-m, although not significant (Fig. 6.1a).

Table 6.2. Results of Bonferoni multiple range tests among the levels of spacing and species composition at Pringle Butte. Means followed by the same letter indicate no significance at the experimentwise α-level of 0.05.

Factor Level	Response means							
Spacing (m)	Leaf area index (m^2 m^{-2})		Branch mass (Mg ha^{-1})		Foliage ratio		Growth efficiency (m^{3}m^{-2}yr^{-1})	
1.8	4.4334	a	13.98	a	0.3323	a	71.37	a
2.7	4.5675	a	14.00	a	0.3336	a	62.51	ab
3.7	3.5085	b	11.51	a	0.3199	a	56.53	ab
4.6	3.5689	b	12.55	a	0.3011	b	53.30	b
5.5	3.2017	b	11.49	a	0.2932	b	52.25	b
Composition								
LP	3.4606	a	14.03	a	0.2877	a	63.11	a
MX	3.9469	b	13.16	a	0.3107	b	58.78	a
PP	4.1605	b	10.93	b	0.3497	c	55.69	a

At Lookout Mountain, after converting projected leaf area to all-sided leaf area in *A. grandis*, spacing ($p = 0.004$), species composition ($p < 0.001$), and their interaction ($p < 0.001$) were all significant. LAI's ranged from 4.01 to 14.92 m^2 m^{-2}, and largest were consistently found on the closest spacing (Table 6.3). *A. grandis* held the most leaf area in generally, and was significantly higher than the mixed and pure *P. ponderosa* plots (Table 6.3). LAI's on the mixed plots were also significantly higher than on the pure *P. ponderosa* plots. The effect of spacing on LAI depended on species composition. LAI on pure *P. ponderosa* and mixed plots decreased between 1.8- and 3.7-m spacing then remained constant between 3.7- and 5.5-m, whereas LAI dramatically decreased with increasing spacing in the pure *A. grandis* plots (Fig. 6.1b).

Table 6.3. Results of Bonferoni multiple range tests among the levels of spacing and species composition at Lookout Mountain. Means followed by the same letter indicate no significance at the experimentwise α-level of 0.05.

Factor Level	Response means							
Spacing (m)	Leaf area index ($m^2 m^{-2}$)		Branch mass (Mg ha^{-1})		Foliage ratio		Growth efficiency ($m^3 m^{-2} yr^{-1}$)	
1.8	9.1448	a	11.55	a	0.5146	a	175.49	a
3.7	6.9063	b	12.23	a	0.4501	b	165.51	a
5.5	5.5911	c	12.80	a	0.4240	c	138.36	b
Composition								
GF	9.5930	a	9.11	a	0.5861	a	159.29	a
MX	7.0849	b	13.99	b	0.4313	b	157.09	a
PP	4.9644	c	13.48	b	0.3714	c	162.99	a

Plot branch mass

At Pringle Butte and Lookout Mountain the only significant effects on plot branch mass were from species composition and the interaction between species composition and spacing (Table 6.2, 6.3; Fig. 6.2). Plot branch masses ranged from 7.3 to 18.2 Mg ha^{-1} and 4.7 to 22.5 Mg ha^{-1} at Pringle Butte and Lookout Mountain, respectively. At Pringle Butte, significantly larger branch masses were found on the pure *P. contorta* and mixed plots at close spacings. Conversely, at Lookout Mountain,

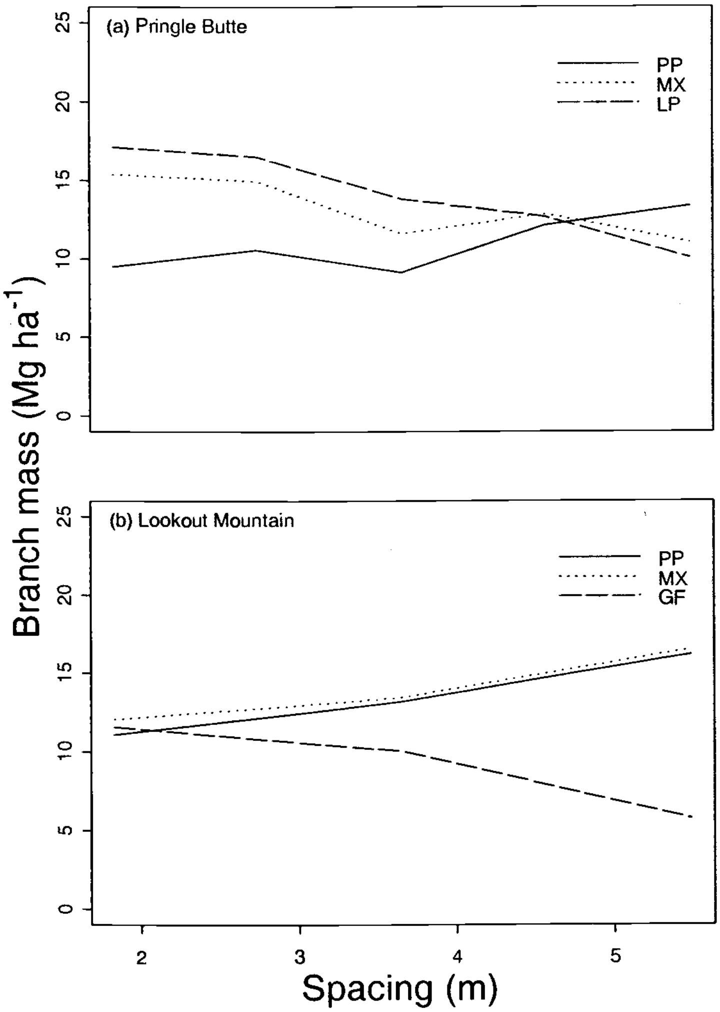

Figure 6.2. Trends in plot branch mass over spacing for the three species mixtures at (a) Pringle Butte and (b) Lookout Mountain. GF, *Abies grandis*, LP, *Pinus contorta*, PP, *Pinus ponderosa*, MX, Mix.

pure *P. ponderosa* and mixed *A. grandis* and *P. ponderosa* plots supported significantly larger branch masses at wider spacings. The trend in branch mass was quite similar for pure *P. ponderosa* at both sites, increasing with spacing, the primary difference was the behavior of *P. contorta* and *A. grandis* branch mass, both of which decreased with increasing spacing (Fig. 6.2).

Plot foliage ratio

Foliage mass to total crown mass, or FR, ranged from 0.27 to 0.41 at Pringle Butte. Spacing ($p = 0.009$), species composition, and their interaction had significant effects on FR ($p < 0.001$). FR generally decreased with increasing spacing, with the three closest spacings significantly higher than the two widest spacings, indicating a significantly higher proportion of branch wood at wider spacings (Fig. 6.3a, Table 6.2). Across species at Pringle Butte, *P. ponderosa* FR was significantly higher than the mixture which was significantly higher than *P. contorta* (Table 6.2). These differences generally increased from wider to narrower spacings (Fig. 6.3a).

The FR range at Lookout Mountain was from 0.31 to 0.63. The main ($p <$ 0.001) and interaction ($p = 0.020$) effects were significant. Although FR's were higher than at Pringle Butte, FR similarly decreased with increasing spacing (Fig. 6.3b). At Lookout Mountain, *A. grandis* had the highest FR and *P. ponderosa* had the lowest (Table 6.3). Regardless of species composition, FR decreased from the 1.8- to

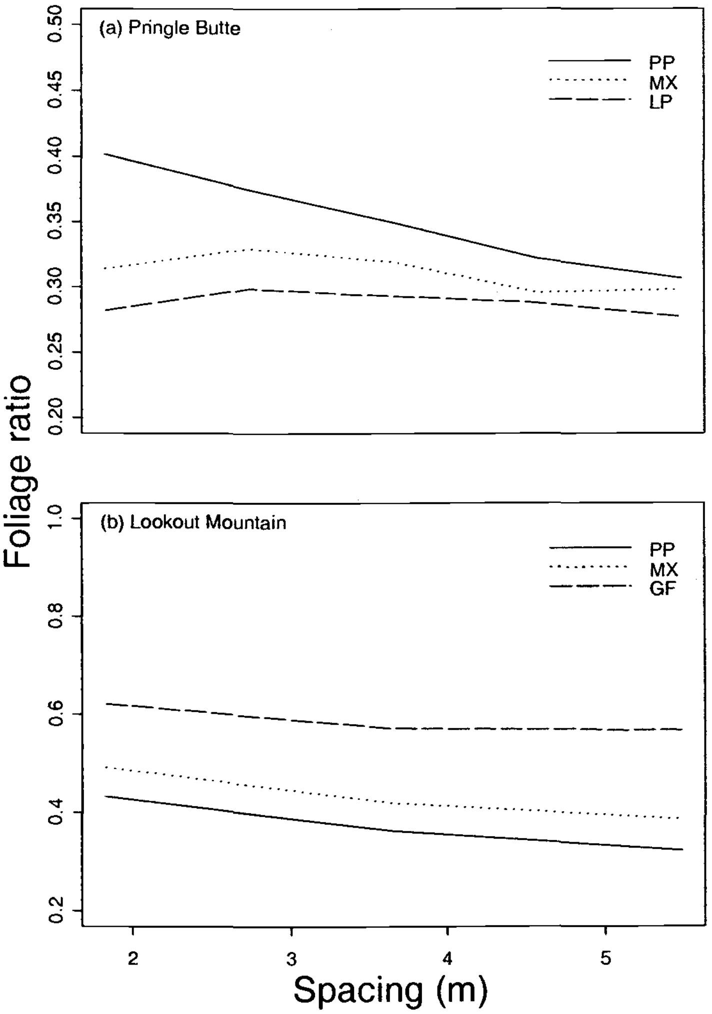

Figure 6.3. Trends in stand foliage ratio (foliage mass / crown mass) over spacing for the three species mixtures at (a) Pringle Butte and (b) Lookout Mountain. GF, *Abies grandis*, LP, *Pinus contorta*, PP, *Pinus ponderosa*, MX, Mix.

the 3.7-m spacing, although *A. grandis* declined more slowly (Fig. 6.3b). FR of *P. ponderosa* for a given spacing was surprisingly similar between the two sites (Table 6.3, Fig. 6.3).

Plot growth efficiency

Plot growth efficiency (GE) ranged from 46.7 to 85.2 cm^3 m^{-2} yr^{-1} at Pringle Butte. The only significant effect on GE was attributable to spacing ($p = 0.012$). Plot GE consistently declined with increasing spacing for the pure *P. contorta*, pure *P. ponderosa*, and the mix (Fig. 6.4a, Table 6.2). Plot GE's at Lookout Mountain ranged from 96.3 to 205.3 cm^3 m^{-2} yr^{-1}. At this site, spacing and the interaction between spacing and composition were significant ($p = 0.009$ and $p = 0.020$, respectively). The interaction effect emerged as significant because *A. grandis* at the closest spacing had a unusually low GE (Fig. 6.4a). As with Pringle Butte, GE decreased with increasing spacing on the pure *P. ponderosa* and mixed plots, with GE at the 1.8- and 3.7-m spacing both significantly greater than the 5.5-m spacing (Table 6.3).

DISCUSSION

Leaf area index

Plot LAI's were low relative to published numbers in both *Pinus* species due largely to the fact that the wider spacings have not yet reached crown closure and maximum leaf area for the site. All-sided LAI's for *Pinus contorta* have been

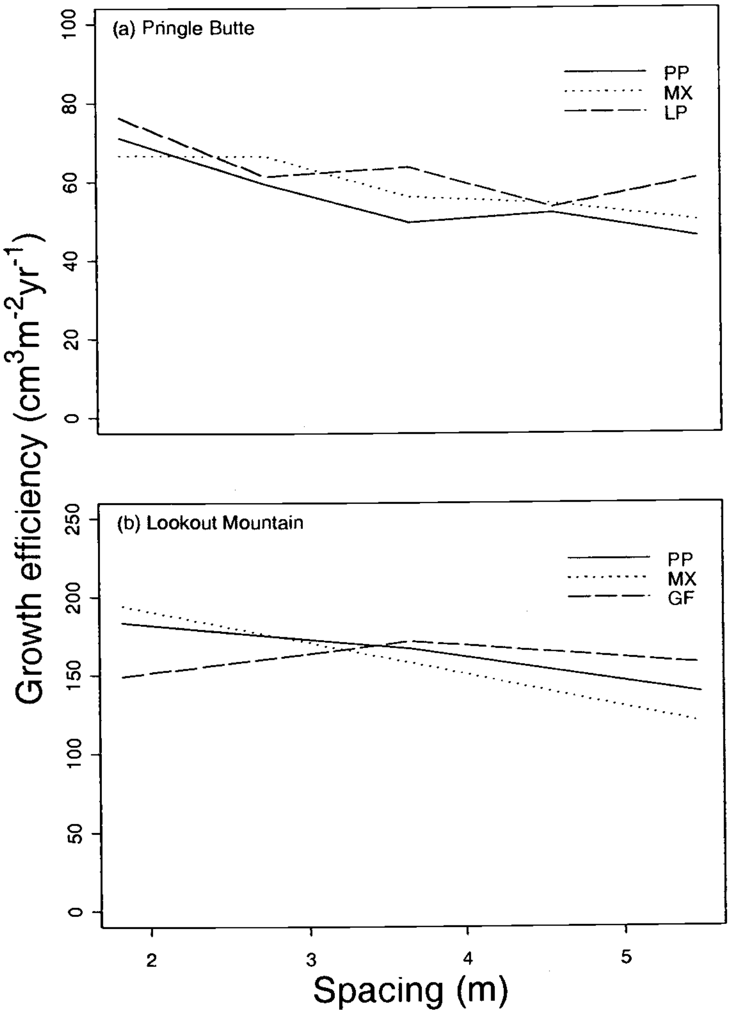

Figure 6.4. Trends in stand growth efficiency over spacing for the three species mixtures at (a) Pringle Butte and (b) Lookout Mountain. GF, *Abies grandis*, LP, *Pinus contorta*, PP, *Pinus ponderosa*, MX, Mix.

estimated to range from 2.3 to 13.4 $m^2 m^{-2}$ (Keane and Weetman 1987). However, within the range of stem densities at Pringle Butte, LAI would be expected to reach between 8.8 to 13.4 $m^2 m^{-2}$ (Keane and Weetman 1987), which is quite a bit higher than those obtained at Pringle Butte. Other studies have reported LAI for *P. contorta* based on projected or one-sided leaf area. Assuming the constant π as the conversion factor from one-sided to all-sided leaf area (Grace 1987), all-sided LAI's have ranged from 2.3 to 20.4 $m^2 m^{-2}$ (Smith and Long 1989; Long and Smith 1992; Kollenberg and O'Hara 1999). All-sided LAI estimates for *Pinus ponderosa* in this study, 2.8 to 6.0 $m^2 m^{-2}$, were also low compared to the previously published range of 3.9 to 23.2 $m^2 m^{-2}$ (Larsson et al. 1983; McLeod and Running 1988; O'Hara 1996). Several studies of *P. ponderosa* stands in central Oregon averaged LAI's around 7.0 $m^2 m^{-2}$ (Gholz 1982; O'Hara 1996), which is slightly higher than those at Pringle Butte and Lookout Mountain. Although few estimates of LAI have been published for *A. grandis*, projected LAI for *Abies lasiocarpa* ranges from about 3.0 to 14.2 $m^2 m^{-2}$ (Jack and Long 1991a; Jack and Long 1992; Smith and Long 1992). Projected LAI's for *A. grandis* on Lookout Mountain, 1.7 to 6.0 $m^2 m^{-2}$, were at the low end of that range.

Part of this discrepancy may be due to the age and the stage of stand development of many of these plots, and the stand densities found in this and previous studies. The Pringle Butte and Lookout Mountain plots were around 30-years-old and, as already mentioned, the widest spacings have not reached crown closure. LAI therefore increases in direct proportion to the increase in stem density at closer spacings. The tightest spacings at both sites have reached crown closure, and therefore should have reached their maximum leaf area (Long and Turner 1975; Grier and Running 1977). Maxima for these sites were therefore inferred to be approximately 4 m^2 m^{-2} for *P. contorta*, 14 m^2 m^{-2} for *A. grandis*, and 5 m^2 m^{-2} for *P. ponderosa* (slightly less at Pringle Butte and slightly more at Lookout Mountain). It is generally thought that once crown closure has occurred, LAI is independent of stand density (Pearson et al. 1984; Long and Smith 1990). Although an effect of stem density has been documented in the past whereby LAI's decrease with increasing stem densities after crown closure (Keane and Weetman 1987). Site quality and water balance have been shown to influence maximum attainable leaf area (Grier and Running 1977), so the pumice region of central Oregon would be expected to have somewhat lower LAI's than other regions receiving more rainfall, having solid with better water holding capacity, and experiencing lower potential evapotranspiration.

Plot branch mass

The range of branch masses found at Pringle Butte and Lookout Mountain were within published ranges. The range for *P. contorta* at Pringle Butte was 9.7 to 18.2 Mg ha^{-1} well within the general range of 4.1 to 23.5 Mg ha^{-1} (Pearson et al. 1984; Comeau and Kimmins 1989). Branch masses have not been reported for *A. grandis* or *P. ponderosa*. Plot branch mass increased with plot leaf area (Fig. 6.5), but the

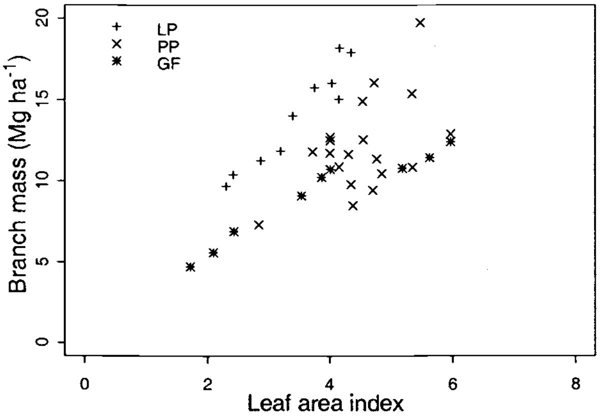

Figure 6.5. Scatterplots of stand branch mass on plot LAI for pure plots of *Pinus contorta* (LP), *Pinus ponderosa* (PP), and *Abies grandis* (GF) at Pringle Butte and Lookout Mountain.

differed by species composition. *P. contorta* had the largest had the largest branch mass for a given LAI (Fig. 6.5). Although there were fewer trees per unit area and same or less leaf area at wider spacings, *P. Ponderosa* branch mass continued to increase (Fig. 6.2). A study of crown architecture of *P. ponderosa* on these same study sites reported a dramatic response of maximum branch diameter profile to increased spacing (see Chapter Five), suggesting that the longer crown lengths and larger branches at wider spacing more than compensate for the fewer trees (Fig. 6.6).

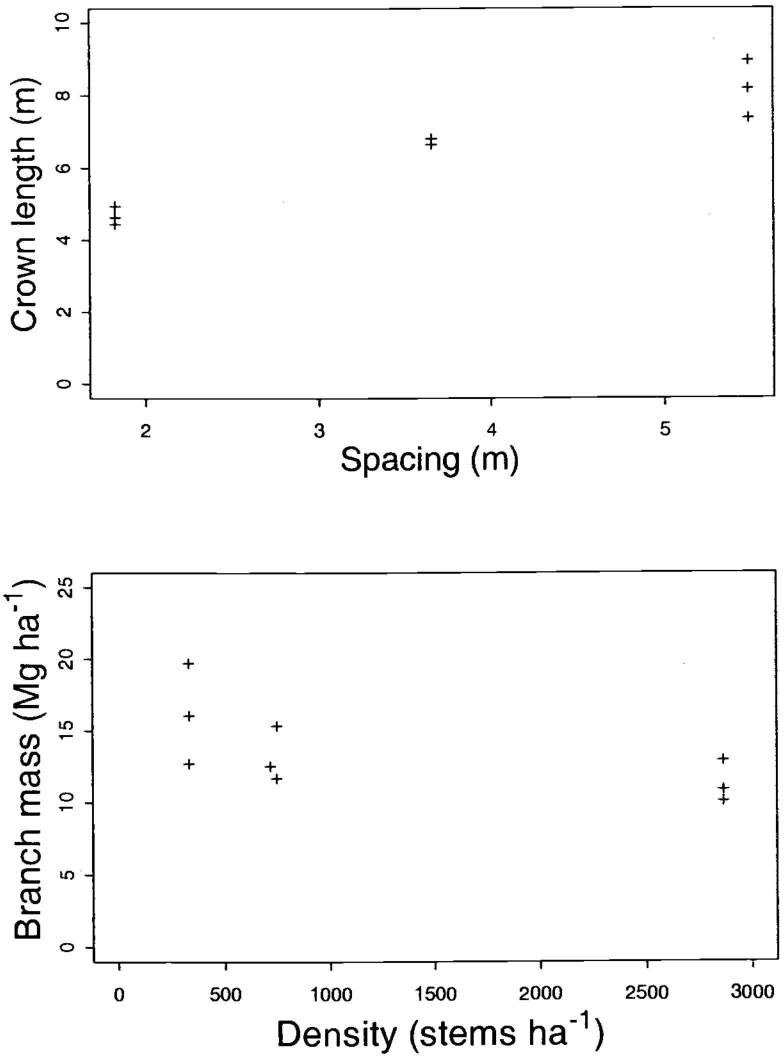

Figure 6.6. Scatterplots of (a) average crown length over spacing and (b) plot branch mass over stem density for *Pinus ponderosa* at Lookout Mountain.

Plot foliage ratio

FR values for individual trees have been reported in the central Rockies and range between 0.3 to 0.5, 0.3 to 0.9, and 0.15 to 0.45 for *P. contorta* var. *latifolia*, *Abies lasiocarpa* and mixtures of the two species, respectively (Smith and Long 1992; Roberts and Long 1992). Generally ratios were slightly higher for *A. lasiocarpa* than for *P. contorta* var. *latifolia* and mixtures. Likewise, results at Lookout Mountain indicate higher ratios in *A. grandis* than in either of the other two species or the mixtures at both sites. Clearly less branch wood is required to hold a given amount of leaf areas in *Abies* species than in *Pinus* species. *Pinus* species tend to be shade-intolerant pioneer species, which tend to be fast-growing but inefficient users of growing space (Daniel et al. 1979). *Pinus* species tend to have higher light saturation and compensation points than more shade-tolerant species (Perry 1994). These species may have evolved a crown architecture that distributes foliage in a manner that minimizes self-shading and maximizes intensity of intercepted light. In contrast, *A. grandis* tends to be a more shade-adapted species with lower light saturation and compensation points, allowing it to hold more leaf area per unit branch mass.

Plot growth efficiency

Growth efficiency has been calculated in many different ways at the tree- and stand-level. The range of stand values presented here for *P. ponderosa* were very similar to those reported for *P. ponderosa* on similar sites (O'Hara 1996), but growth efficiency values for *P. contorta* were lower than those reported for *P. contorta* on slightly better sites (Smith and Long 1992; Kollenberg and O'Hara 1999). *Abies grandis* growth efficiency at Lookout Mountain were similar to values reported for *A. lasiocarpa* in Utah (Smith and Long 1992) and *Abies balsamea* in Maine (Gilmore and Seymour 1996).

Patterns in LAI, branch mass, and FR at Pringle Butte and Lookout Mountain demonstrate how changes in spacing and species composition cause large changes in stand structure, crown geometry, and canopy architecture (Curtis and Reukema 1970; Rouvinen and Kuuluvainen 1997). Changes in crown and canopy architecture in turn influence the production ecology of trees and forest ecosystems (Kuuluvainen 1988; O'Hara 1988; O'Hara 1989; Jack and Long 1992; Roberts and Long 1992). Most previous studies of growth efficiency focus on either the tree-level or stand-level. Relatively few studies have integrated growth efficiency at both scales, leaving some ambiguity about general patterns. For example, trees and stands with high leaf areas are generally thought to have lower growth efficiency (Smith and Long 1989; Long and Smith 1990). However, trees with high leaf area are generally found in stands with lower LAI's, while stands with high LAI's generally contain trees with low mean tree leaf area. Consequently, a separate understanding of tree and stand growth efficiency relationships with stand structure are necessary to understand production ecology of forests.

Tree and stand growth efficiency

Assuming site quality is constant, leaf area has been considered a primary driver of growth efficiency in trees (Waring 1983; Binkley and Reid 1984; O'Hara 1988; Long and Smith 1990; Gilmore and Seymour 1996; Maguire et al. 1998) and stands (Waring et al. 1981; O'Hara 1989; Velazquez-Martinez et al. 1992; O'Hara et al. 1999). The effect of leaf area on growth efficiency however is indirect, working via three things: (*i*) foliage ratio and (*ii*) sapwood volume, and (*iii*) self-shading.

Tree growth efficiency

FR has been suggested as an important factor in tree and stand growth efficiency (Smith and Long 1989; Roberts and Long 1992; Smith and Long 1992; Roberts et al. 1993). Trees with larger crowns. i.e., trees with larger leaf areas, tend to have smaller foliage ratios (Smith and Long 1989; Long and Smith 1990; Jack and Long 1991b; Roberts and Long 1992; Smith and Long 1992). This general result is consistent with results for all three species at Pringle Butte and Lookout Mountain (Fig. 6.7). Smaller FR suggests proportionally more branch wood is required to support a given unit of tree leaf area. Many studies have reported lower growth efficiency in trees with large crowns (Assmann 1970; Kuuluvainen 1988; Jack and Long 1992; Roberts and Long 1992; Sterba and Amateis 1998) and greater tree leaf areas (Waring 1983; Binkley and Reid 1984; O'Hara 1988; Long and Smith 1990;

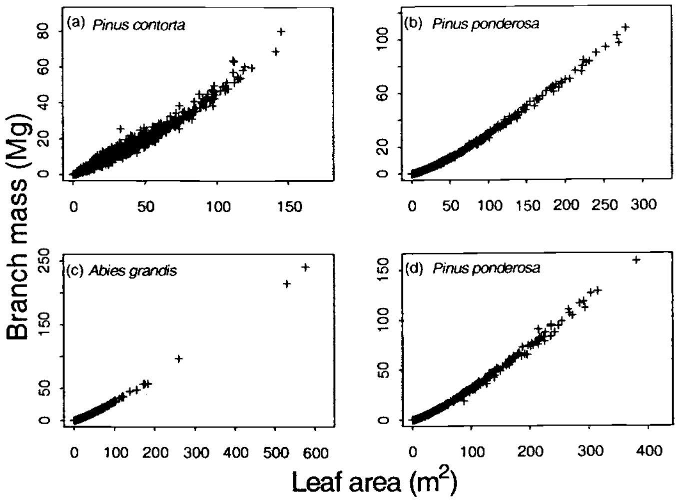

Figure 6.7. Scatterplots of individual tree branch mass on tree leaf area for pure plots of (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis* and (d) *Pinus ponderosa* at Lookout Mountain.

Gilmore and Seymour 1996; Maguire et al. 1998). Roberts and Long (1992) speculated that this pattern is in part the result of lower FR's; that is, a lower ratio of photosynthetic tissue to construction costs and respiring tissue in branches. It is significant to note that branches tend to have higher respiration rates than boles for a given amount of living tissue (Kinerson 1975; Sprugel 1990), especially at higher crown positions (Ryan et al. 1996). It follows that trees with larger crowns have a larger proportion of fixed carbon allocated to construction and maintenance of branches, leaving less for stemwood production.

Sapwood is the water conducting portion of the main stem and the only portion of the stemwood that contains living cells. Although sapwood volume was not estimated in this study, it is thought to be exponentially related to tree leaf area, increasing with increasing leaf area and stand height (Ryan 1989; Maguire and Batista 1996). Therefore, trees with higher leaf area would have proportionally more sapwood volume and, as with living branches, a higher maintenance respiration load (Ryan 1989; Ryan 1990; Sprugel 1990; Ryan and Waring 1992). Therefore, for a given LAI greater sapwood volumes would reduce the amount of fixed carbon available for stemwood production.

Stand growth efficiency

FR and sapwood volume also influence stand-level growth efficiency. With increases in mean tree branch mass per unit of tree leaf area associated with increasing spacing, stand FR would be expected to decrease with increasing spacing. Results at Pringle Butte and Lookout Mountain confirm this trend, with the possible exception of *P. contorta* at the closest spacing (Fig. 6.3). Sapwood volume per unit area would be expected to decrease or remain roughly constant due its relationship with mean tree leaf area (Ryan 1990; Maguire and Batistia 1996). These responses would impose lower growth efficiencies at lower densities. In both *Pinus* species, higher growth efficiencies were found at the tightest spacings, and growth efficiency decreased with increasing spacing. Contrary to this theory, growth efficiency remained fairly similar across spacing in *A. grandis.* Moreover, others have reported increases in growth efficiency with increasing spacing after thinning (Waring et al. 1981; Waring and Pitman 1983; Binkley and Reid 1984; Velazquez-Martinez et al. 1992; Garber and Seymour, unpublished data), and possibly peaking at some intermediate leaf area after crown closure (Waring et al. 1980).

Although stands with lower mean tree leaf areas have lower mean tree branch mass, they also generally carry a large number of trees, forming closed canopies at an earlier stand age. At this stage of stand development, typically referred to as stem exclusion (Oliver 1981; Oliver and Larson 1996), competition decreases essential resources, such as nutrients, water, and light, limiting individual tree growth (Waring et al. 1981; Waring and Schlesinger 1985). Lower foliar concentrations of nitrogen, potassium, and magnesium have been found associated with high leaf area indices and high densities in *Pseudotsuga menziesii* plantations (Velazquez-Martinez et al. 1992). Foliar concentrations of these elements and growth efficiency have been reported to increase with decreasing density (Velazquez-Martinez et al. 1992) and artificial reductions in leaf area (Jose and Gillespie 1997). Reductions in leaf area increases individual leaf nutrition, average light intensity, and photosynthetic efficiency (Jose and Gillespie 1997). Moreover, better nutrient availability may translate into lower fine root production, a shift in allocation from root to shoot (Keyes and Grier 1981;

Haynes and Gower 1995; Albaugh et al. 1998). This shift in allocation would increase stemwood production and growth efficiency (Binkley and Reid 1984; Waring and Pitman 1985; Velazquez-Martinez et al. 1992; Jose and Gillespie 1997; Albaugh et al. 1998).

Water availability affects the quantity of leaf area and photosynthesis (Perry 1994). In studies of leaf area dynamics, maximum leaf area accumulated where moisture stress was lowest, thus total leaf area of temperate forests is related to a water balance at the site (Grier and Running 1977; Mooney et al. 1978; Waring et al. 1978). Leaf area is also limited by the capacity of the sapwood to supply water, in turn a function of the water availability (Kaufmann et al. 1982). Water stress in trees may initiate stomatal closure decreasing carbon dioxide uptake (between -1.0 and -2.5 megapascals soil water potential) (Waring and Schlesinger 1985; Yoder et al. 1994; Ryan and Yoder 1997). This reduced carbon uptake may also decrease the ratio of carbon dioxide to oxygen in foliage, increasing photorespiration, and decreasing photosynthetic capacity (Waring and Schlesinger 1985). In addition, increases in water availability may alter allocation patterns, shifting allocation to above ground components (Comeau and Kimmins 1989; Albaugh et al. 1998). In short, increases in water availability can also enhance growth efficiency.

Synthesis

Low density stands are essentially a collection of individuals with high mean tree leaf area, branch mass, and sapwood volume, resulting in trees with low ratios of photosynthetic to nonphotosynthetic tissue. Consequently, these stands have lower foliage to branch biomass (Fig. 6.3) and lower growth efficiencies (Fig. 6.4). As density increases and crown closure occurs, mean tree leaf area, branch mass, and sapwood volumes decrease, and consequently photosynthetic to nonphotosynthetic tissue ratio increases. However, competition among individuals increases and differentiation begins, whereby some trees exert dominance to the demise of others, as a result of resource limitation (Oliver and Larson 1996). Many studies have documented an influence of crown class or relative social position of a tree within a stand on tree growth efficiency, which generally increases with relative crown position (Waring et al. 1980; O'Hara 1988; Gilmore and Seymour 1996; Barker 1998; Maguire et al. 1998), as an improved crown position results in better light capture and less shaded foliage. However, as discussed above, larger crowns result in lower tree growth efficiency, which seems at odds with growth efficiency-crown position relations. Several studies have uncovered two different patterns of tree growth efficiency with leaf area. Some species exhibit an increase in mean tree increment with mean tree leaf area but at a decreasing rate, suggesting a decrease in mean tree growth efficiency with increasing leaf area (Long and Smith 1990). In contrast, several other species have exhibited an increase in growth efficiency with leaf area up to a point, thereafter growth efficiency decreased with leaf area (Roberts et al. 1993; Maguire et al. 1998). The latter pattern was evident in the three species at Pringle Butte and Lookout Mountain (Fig. 6.8).

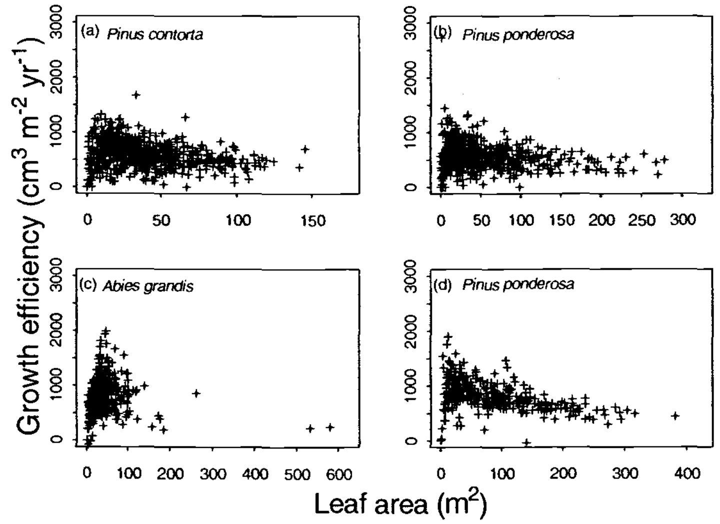

Figure 6.8. Scatterplots of individual tree growth efficiency on tree leaf area for pure plots of (a) *Pinus contorta*, (b) *Pinus ponderosa* at Pringle Butte, (c) *Abies grandis* and (d) *Pinus ponderosa* at Lookout Mountain.

Roberts et al. (1993) proposed a general model to describe these trends in growth efficiency with canopy structure. For stands of a given age and site quality, if increases in leaf area are not associated with substantial increases in height, and thus the light environment is not improved to offset the effects of increases in foliage ratio, growth efficiency decreases as leaf area increases (Roberts and Long 1992; Roberts et al. 1993). If, however, a greater leaf area is associated with substantial increases in height and the light environment is improved to offset the effects of increases in foliage ratio, growth efficiency increases as leaf area increases (Roberts and Long 1992; Roberts et al. 1993). Later, there is a point at which additional increases in leaf area and height, and therefore light environment is not able to offset the effects of the increasing foliage ratio, thus growth efficiency will decline with further increases in leaf area (Roberts et al. 1993).

Higher density stands contain trees with higher growth efficiency than lower density stands (O'Hara 1988). This was also the case in all the species at Pringle Butte and Lookout Mountain. However, when viewing the distribution of individual tree growth efficiencies (Fig. 6.9-6.12), the high density stands also contain trees with some of the lowest growth efficiencies (O'Hara 1988). As a result, the range in individual tree growth efficiencies is larger in higher density stands than in lower density stands. This is most evident in the pure *Pinus* plots at both study sites (Fig. 6.9, 6.10, and 6.12). *A. grandis* shows the opposite trend, whereby the distribution of individual tree growth efficiencies increase with spacing and the largest tree growth efficiencies are found in the widest spacing (Fig. 6.11).

These patterns have been confounded by thinning, which should not be confused with a pure spacing effect. Several studies have reported increases in stand

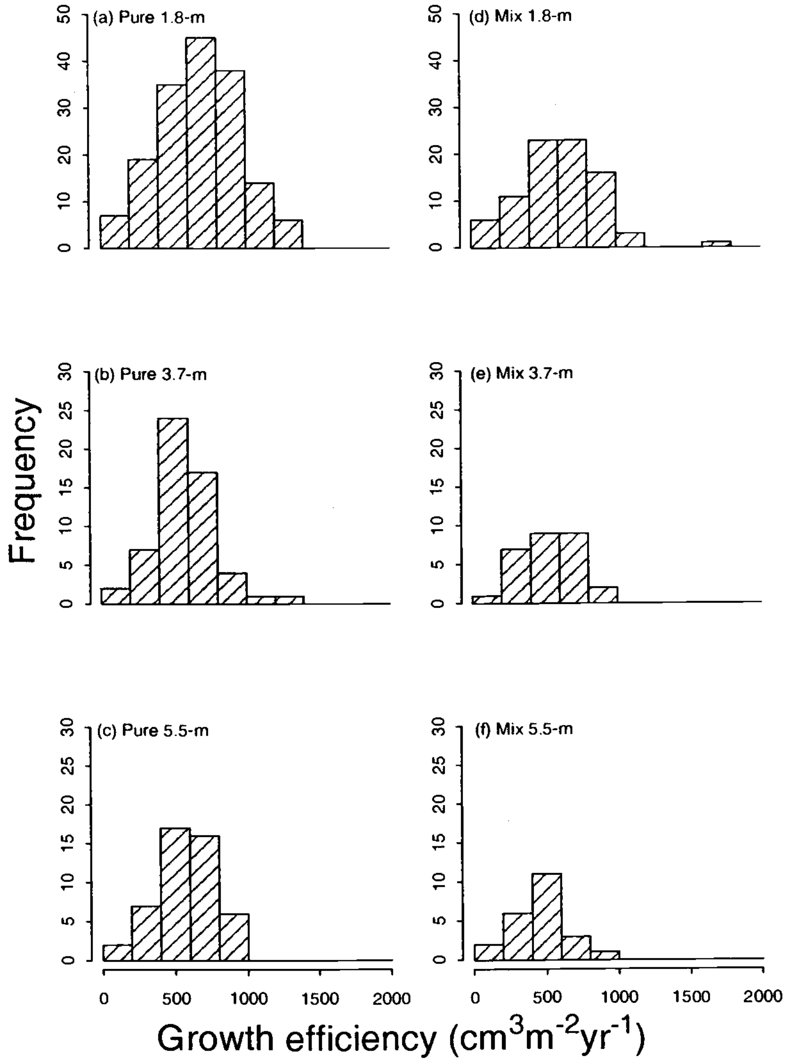

Figure 6.9. Distribution of individual tree growth efficiencies for pure and mixed *Pinus contorta* plots at Pringle Butte: (a) Pure 1.8-, (b), Pure 3.7-, (c) Pure 5.5-, (d) Mix 1.8-, (e), Mix 3.7-, and (f) Mix 5.5-m spacing.

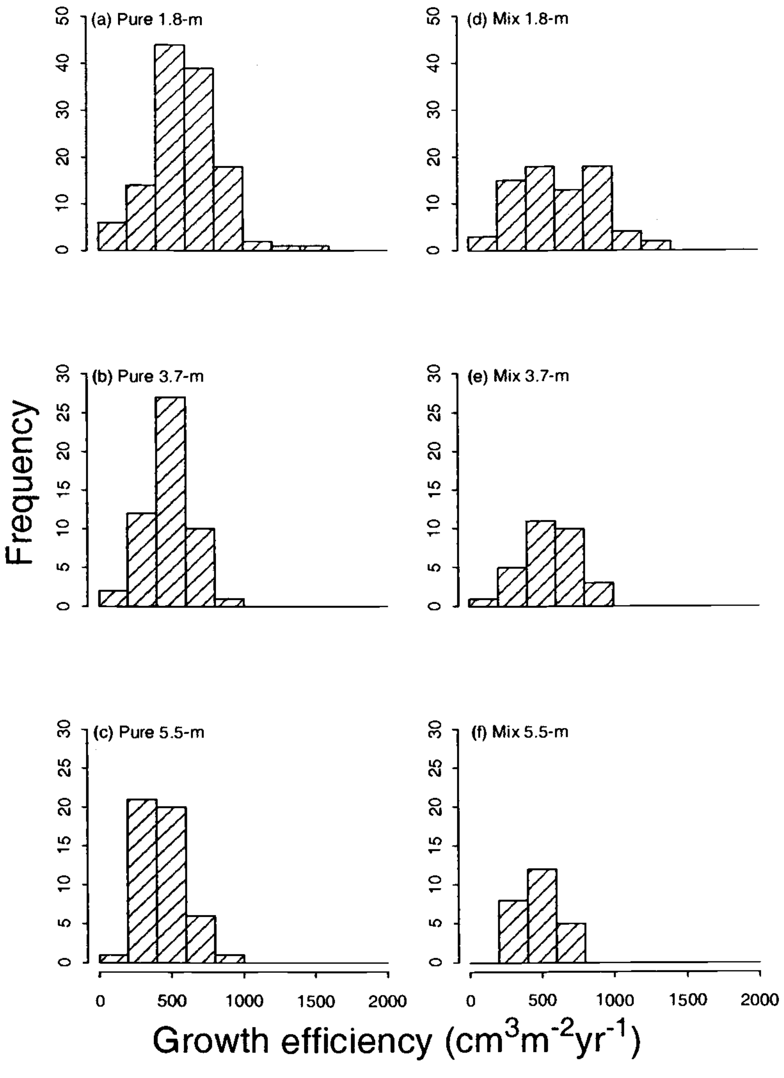

Figure 6.10. Distribution of individual tree growth efficiencies for pure and mixed *Pinus ponderosa* plots at Pringle Butte: (a) Pure 1.8-, (b), Pure 3.7-, (c) Pure 5.5-, (d) Mix 1.8-, (e), Mix 3.7-, and (f) Mix 5.5-m spacing.

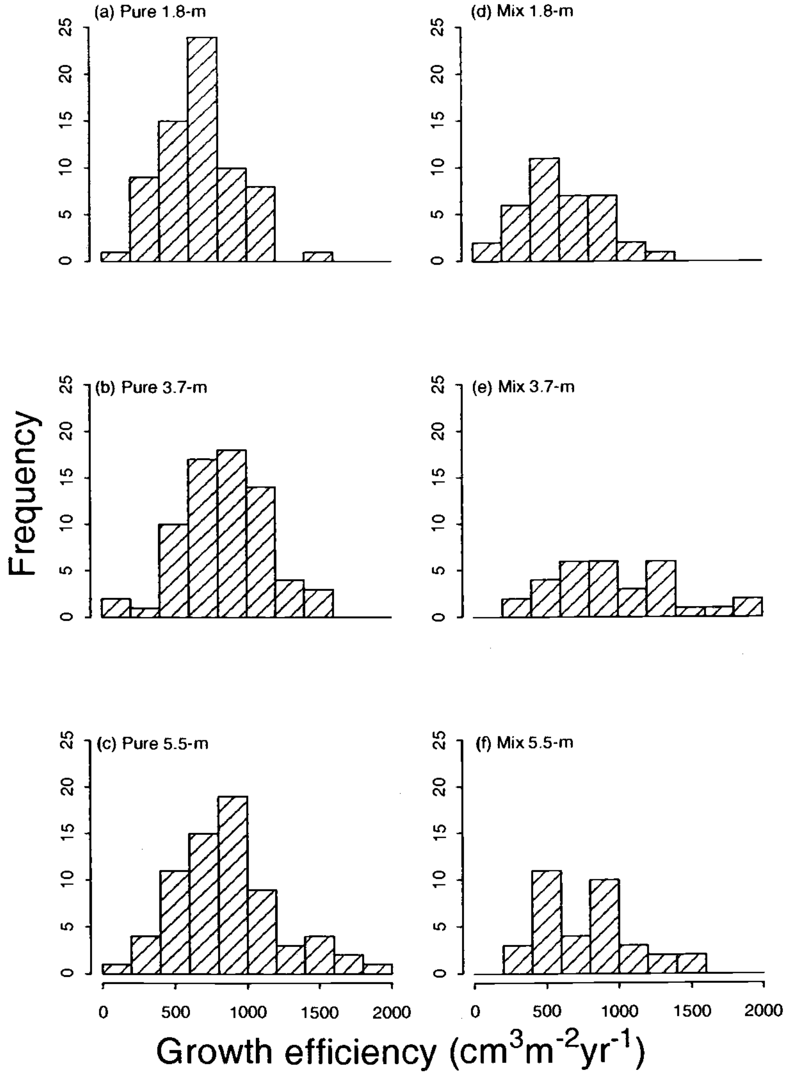

Figure 6.11. Distribution of individual tree growth efficiencies for pure and mixed *Abies grandis* plots at Lookout Mountain: (a) Pure 1.8-, (b), Pure 3.7-, (c) Pure 5.5-, (d) Mix 1.8-, (e), Mix 3.7-, and (f) Mix 5.5-m spacing.

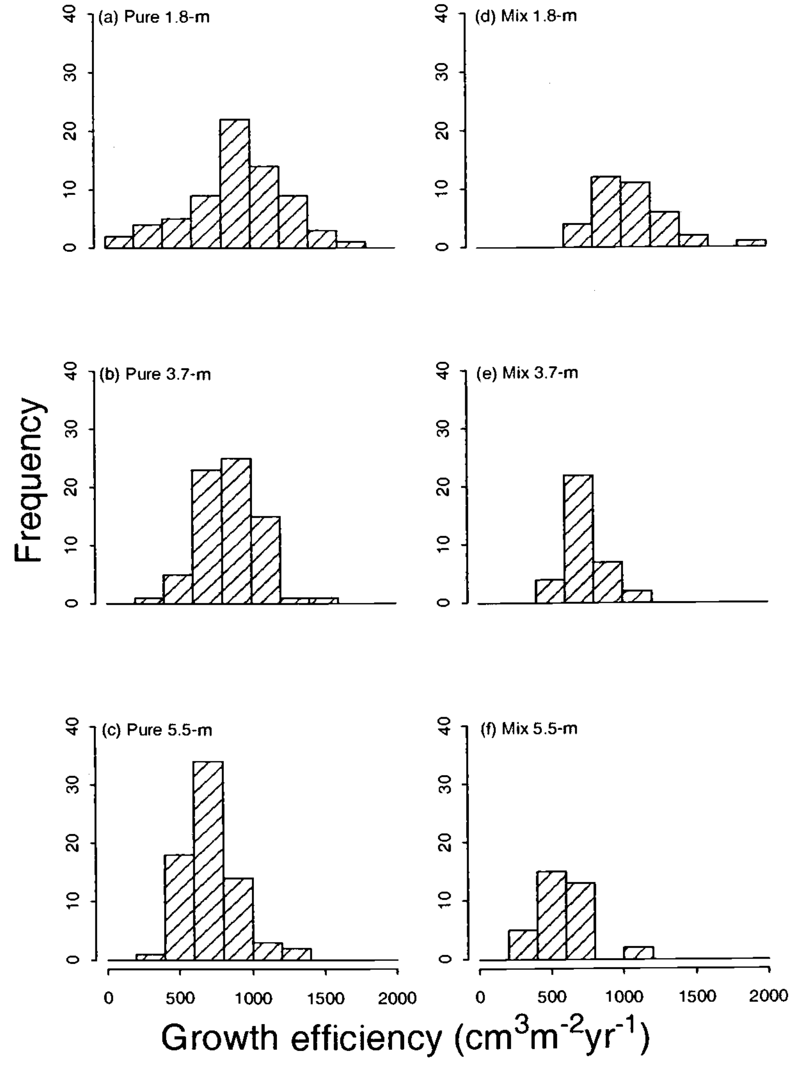

Figure 6.12. Distribution of individual tree growth efficiencies for pure and mixed *Pinus ponderosa* plots at Lookout Mountain: (a) Pure 1.8-, (b), Pure 3.7-, (c) Pure 5.5-, (d) Mix 1.8-, (e), Mix 3.7-, and (f) Mix 5.5-m spacing.

growth efficiency after thinning (Waring et al. 1981; Waring and Pitman 1983; Binkley and Reid 1984; Velazquez-Martinez et al. 1992; Garber and Seymour, unpublished data), others have not (Lavigne 1988). Thinning in the short term reduces leaf area and competition, but reallocates leaf area to fewer stems (O'Hara 1988). Consequently, this improves light capture per unit foliage area in the short term. Short term growth efficiency would depend on the type of thinning and the relative responses of stem growth and leaf area. In the long term, growth efficiency will depend on canopy closure, as this will influence the stand foliage ratio.

CONCLUSIONS

As demonstrated at Pringle Butte and Lookout Mountain in both *Pinus* species, growth efficiency increases with increasing density apparently due to decreasing stand-level branch mass to foliage mass ratio. However, when differentiation becomes more extreme with increasing density or stand development, the impact of the subordinate trees on stand growth efficiency becomes greater. These trees contribute relatively more leaf area than they contribute growth, thereby reducing stand growth efficiency. Consequently, as stand density increases, if the improvement in stand photosynthetic to nonphotosynthetic ratio is not enough offset reductions in individual tree growth efficiencies from increases in competition and differentiation, stand-level growth efficiency will stay the same or fall, as it did at Lookout Mountain in *A. grandis*.

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CHAPTER SEVEN: CONCLUSIONS

Managing stands requires knowledge of stand development and resulting stand structures. It is not always clear how stand components will interact. This study focused on the influence of spacing and species composition on elements of individual tree crown structure, stand development and production, and growth efficiency in two approximately 30-year-old mixed-species spacing studies. Decreasing spacing resulted in more stemwood production per unit area due to more stems. However, decreasing spacing also reduced the time to crown closure where stand dynamics change. With decreasing spacing, crowns generally became shorter, with upward shift in absolute foliage distributions, and smaller maximum branch diameters. In mixed-species stands, these general patterns remain the same, however, there are relative differences among the species that increase the complexity of stand structure. Early stand development in these plots resulted in predictable stratification patterns, whereby the more shade intolerant species exhibited the faster early height growth rate, overtopping the more shade-tolerant species. However, spacing largely influenced this process though its effect on the development of the subordinate component. Closer spacings result slower growth response than what wider spacings and pure stands at the same density would suggest. Likewise, increasing spacing in mixtures resulted in a more dramatic shift upward in absolute foliage distributions and increasing maximum branch diameters than their overtopping competition or in pure stands.

Such processes have a tradeoff as far as production efficiency. Larger crowns carry larger ratio of branchwood to foliage. This increases construction respiration costs at the time of production and also increases the amount of living tissue, requiring larger maintenance respiration costs. Higher densities in the two *Pinus* species studied resulted in both higher production and growth efficiency. *Abies grandis* in contrast, suggests higher densities may also have tradeoffs; limitations associated with competition and differentiation whereby suppressed individuals bring down stand-level growth efficiency. In contrast to production and crown structure, no effects of species composition on growth efficiency could be detected during this study.

The results of this study have many practical implications related to silviculture. A tradeoff exists between high stand production and production of large piece sizes. A similar tradeoff exists regarding wood quality. Mixed-species stands may be a way to alleviate these tradeoffs, producing large, high quality wood and obtaining larger standing volumes. Both spacing and species composition can be altered to potentially obtain a larger array of desired end-products. Stratification among species may eliminate the necessity for pruning under certain circumstances, while delaying thinning in others. Likewise, knowledge of stand development in mixtures can also be put to use manipulating forests to obtain desired structures for habitat or aesthetic objectives (e.g. vertical distribution of foliage, branch sizes for nesting platforms, etc.). Theories underlying growth efficiency can be used in intermediate treatments, especially thinning, reallocating leaf area to more efficient trees. One of the forest managers primary tools are density management diagrams and growth models. These are prevalent for many single-species stands. However, less is known regarding the behavior of stand trajectories in mixed-species stands. Results at Lookout Mountain suggest larger production in mixtures relative to monocultures of the more production species at this point. This may also suggest a potential increase in the maximum size-density line.

The highest densities in these studies were just entering the stem exclusion stand of stand development, whereas the low density plots have not reached stem exclusion. In addition, *A. grandis* growth was just beginning to increase during the last measurement period. The next 20 years will probably see all plots enter the stem exclusion stage, where other dynamic processes take place, primarily self-thinning. The effects of spacing and species composition on crown structure and volume growth are likely to increase with stand development. Response of *A. grandis* growth over time, effects of composition on growth efficiency, and trends in growth efficiency across spacing over time will be points of interest. In addition, dynamic responses of foliage distributions, branch diameters, and crown recession are also points of study as stand development continues in these spacing trials.

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APPENDIX

BETA PROBABILITY DENSITY FUNCTION

The standard form of the Beta probability density function is:

$$f(x;\alpha,\beta) = \frac{1}{B(\alpha,\beta)} x^{\alpha-1}(1-x)^{\beta-1}$$

where

$$B(\alpha,\beta) = \frac{\Gamma(\alpha)\Gamma(\beta)}{\Gamma(\alpha+\beta)} ,$$

$$\Gamma(\alpha) = \int_0^\infty e^{-x} x^{\alpha-1} dx \quad \text{for all } \alpha > 0,$$

α is the location parameter ($0 < \alpha < \infty$), β is the shape parameter ($0 < \beta < \infty$), and x is a beta random variable ($0 \leq x \leq 1$).

LIKELIHOOD ESTIMATION

Given $x_1, \ldots, x_n$ are identically independent samples from a Beta(α, β) distribution, their joint probability can be described by:

[A1] $$\prod_{i=1}^{n}\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)}x_i^{\alpha-1}(1-x_i)^{\beta-1}$$

Likelihood estimates for α and β were chosen such that this function is at its maximum. Since no closed form of maximum likelihood solution exists for the beta distribution, they were derived numerically. The log-likelihood function for [A1], $l(\alpha,\beta;x_i)$, is given by

[A2] $$\sum_{i=1}^{n}[\log\Gamma(\alpha+\beta)-\log\Gamma(\alpha)-\log\Gamma(\beta)+(\alpha-1)\log x_i+(\beta-1)\log(1-x_i)]$$

where $\log\Gamma$ is the natural log of the gamma integral. Given initial values for α and β, the Fisher-Scoring method was used to obtain iterative solutions (Mielke 1975). The five partial derivatives of [A2] for this method are as follows:

[A3] $$\frac{\partial l}{\partial\alpha}=\sum\left[\psi(\alpha+\beta)-\psi(\alpha)+\log x_i\right]$$

[A4] $$\frac{\partial l}{\partial\beta}=\sum\left[\psi(\alpha+\beta)-\psi(\beta)+\log(1-x_i)\right]$$

[A5] $$\frac{\partial^2 l}{\partial^2 \alpha} = n\left[\psi'(\alpha+\beta) - \psi'(\alpha)\right]$$

[A6] $$\frac{\partial^2 l}{\partial^2 \beta} = n\left[\psi'(\alpha+\beta) - \psi'(\beta)\right]$$

[A7] $$\frac{\partial^2 l}{\partial\alpha\partial\beta} = n\left[\psi'(\alpha+\beta)\right]$$

where $\psi(.)$ and $\psi'(.)$ are the digamma (first derivative of the gamma integral) and trigamma (second derivative of the gamma integral) functions, respectively. [A3] and [A4] comprise the score vector:

$$U(\alpha,\beta;x_i) = \begin{bmatrix} \dfrac{\partial l}{\partial\alpha} \\ \dfrac{\partial l}{\partial\beta} \end{bmatrix}.$$

[A5], [A6], and [A7] represent the elements of the Fisher Information matrix:

$$-\mathcal{I}_x(\alpha,\beta) = \begin{bmatrix} \frac{\partial^2 l}{\partial^2 \alpha} & \frac{\partial^2 l}{\partial \alpha \partial \beta} \\ \frac{\partial^2 l}{\partial \beta \partial \alpha} & \frac{\partial^2 l}{\partial^2 \beta} \end{bmatrix}.$$

Given this, the Fisher Scoring algorithm is as follows:

$$\begin{bmatrix} \hat{\alpha} \\ \hat{\beta} \end{bmatrix}_{new} = \begin{bmatrix} \hat{\alpha} \\ \hat{\beta} \end{bmatrix}_{old} - \mathcal{I}_x(\hat{\alpha},\hat{\beta})^{-1} U(\hat{\alpha},\hat{\beta};x_i)$$

where new estimates are calculated using the old estimates.

DISTRIBUTION OF PARAMETER ESTIMATES

With large *n*, asymptotic theory suggests the estimates of the parameters are:

$$\begin{bmatrix} \hat{\alpha} \\ \hat{\beta} \end{bmatrix} \sim CAN\left(\begin{bmatrix} \alpha \\ \beta \end{bmatrix}, \mathcal{I}_x(\hat{\alpha},\hat{\beta})^{-1} \right)$$

where *CAN* is continuously asymptotically normal (Mukhopadhyay 2000).