AN ABSTRACT OF THE DISSERTATION OF

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Forest growth models in the Pacific Northwest are predominantly empirical. Predictions of yield under alternative silvicultural regimes cannot rely completely on field trials; yet empirical growth models are often inadequate for extrapolating untested regimes and genotypes. The limitations of current models include (1) long time-steps (e.g. 5-10 years); (2) insufficient detail for characterizing crowns; and (3) inability to capture physiological mechanisms. The overall goal of this dissertation was to test the ability of a hybrid model (empirical + process-based) to predict the growth of intensively managed plantations.

The first step of model development was to refine current characterizations of Douglas-fir crown structure across several silvicultural treatments. The effects of fertilization, thinning, precommercial thinning, vegetation control, and disease intensity (Swiss needle cast) were found to influence important structural attributes of the crown. Among the crown attributes affected, maximum branch size and total- and nonfoliated-crown profile were the most dynamic attributes. Conversely, treatments had no effect on the number of branches or on branch angle. Equations based solely on bole and crown variables predicted crown structural attributes reasonably well across these varied stand conditions.

Annualized empirical equations for individual tree diameter and height growth were developed next and found to outperform similar models with a longer time-step. The parameters of these empirical equations showed very few meaningful relationships with physiography, soil, or climate, suggesting that representation of key physiological processes was a necessary next step.

Individual branch growth and mortality were significantly influenced by fertilization, thinning, precommercial thinning, vegetation control, and Swiss needle cast. Dynamic equations developed from this dataset significantly improved predictions of crown recession, compared to a traditional empirical approach. The improvements, however, had a relatively minor impact on short-term stand volume growth.

The combination of these equations into a hybrid framework showed improvements in leaf area index and periodic annual increment when compared to other stand-level hybrid models. At the individual tree-level, the use of both empirical and mechanistic components was necessary to achieve a level of bias slightly better than that of a purely empirical approach. Beyond growth predictions, this hybrid model offers many other uses.

Development of a Hybrid Modeling Framework for Intensively Managed Douglas-Fir Plantations in the Pacific Northwest

by

Aaron R. Weiskittel

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

Aaron R. Weiskittel, Author

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DEVELOPMENT OF A HYBRID MODELING FRAMEWORK FOR INTENSIVELY MANAGED DOUGLAS-FIR PLANTATIONS IN THE PACIFIC NORTHWEST

CHAPTER 1: INTRODUCTION

Models, a series of linked relationships that quantitatively or qualitatively define the behavior of a system, serve several purposes in forestry. Their most important function is to provide predictions of probable future conditions, allowing for planning and hypothesis testing. Second, models provide a conceptual framework for understanding the key processes driving a system. Finally, models are useful for identifying areas of future research, because full knowledge of a system is seldom available, and the sensitivity of a model to its various components helps identify priorities.

The development and use of quantitative models in forestry has a long history (e.g. Munro, 1974). Quantitative models have varied widely in form and function (Monserud, 2003), but two classes of models have dominated the forestry literature: empirical and process-based models. Empirical models use equations fitted to extensive data sets, and the forms of the equations are often based on principles of tree and stand growth. Process-based models simulate the mechanisms behind those principles, so they often contain numerous ecophysiological processes and their response to environmental conditions. Although significant advances have recently been made in the use of empirical and process-based models, both modeling approaches have disadvantages. For example, empirical models rely on large amounts of data to cover the environmental and silvicultural conditions of interest, and the resulting equations generally do not extrapolate well beyond the climatic or edaphic characteristics for which they were developed. On the other hand, process-based models often require physiological data that are relatively expensive to collect and are therefore typically not collected by private or industrial landowners. Hybrid growth models, constructed by combining empirical observations of tree growth with fundamental mechanisms or processes driving growth, were first proposed in the context of forest nutrition (Kimmins, 1985). The hybrid modeling approach may be an important advancement in broadening the capability of models to serve as a tool for both silvicultural decisions and research questions (Monserud, 2003).

Although relatively few hybrid models have been reported in the literature (Baldwin *et al.*, 2001; Pinkard and Battaglia, 2001; Milner *et al.*, 2003; Sampson *et al.*, 2006), a variety of approaches have been utilized. The majority of hybrid models have focused only on stand-level attributes (Peng *et al.*, 2002; Pinjuv *et al.*, 2006; Sampson *et al.*, 2006), but a few simulate growth at the individual-tree level (Baldwin *et al.*, 2001; Milner *et al.*, 2003). One of the most widely used hybrid models to date has been 3-PG (Landsberg and Waring, 1997). It has been successfully parameterized for several important commercial species such as *Eucalyptus grandis* (Almeida *et al.*, 2004a), *Pseudotsuga menziesii* (Waring and

McDowell, 2002), *Pinus taeda (*Landsberg *et al.*, 2000), *Pinus sylvestris* (Landsberg *et al.*, 2005), and *Picea sitchensis* (Waring, 2000). A recent review, however, concluded that 3-PG oversimplifies the representation of several key physiological processes (e.g. Schwalm and Ek, 2001). 3-PG also requires information on stand biomass amount and distribution, and it estimates growth only at the stand level, limiting its applicability in intensively- managed plantations of the Pacific Northwest (PNW).

In both empirical and process-based models, the influence of crown structure and dynamics on growth and wood quality has been underutilized. Growth is a hierarchical process that occurs at multiple levels, and models that represent the hierarchy of the system and the interactions between the scales may perform significantly better than models that operate at only one level (Mäkelä, 2003). For example, models that simulate basic physiological mechanisms of light interception, gas exchange, and branch growth can predict the influence of climate on annual photosynthesis, or they can estimate branching structure and stemwood characteristics.

The inclusion of crown structure and its dynamic response to growth conditions provides an excellent opportunity for representing the hierarchical processes that determine growth in the modeling framework. A few models such as TASS (Mitchell, 1975) and MAESTRO (Wang, 1990) have represented the crown in good detail, but they have required information that is typically unavailable across a region. Opportunities exist to reconstruct the crown of an individual tree through basic allometrics (e.g. Mäkinen *et al.*, 2004) and better incorporate this information into a modeling framework.

A hybrid modeling approach may help to better predict and understand the influence of intensive management activities on plantation growth, yield, and wood quality. Over the last decade, rotation lengths in the PNW have significantly decreased and are currently ranging from 30 to 50 years for managed plantations (Adams *et al.*, 2005). Growth and yield models in the region, however, continue to use a 5- to 10- year time-step (Mitchell, 1975; Curtis *et al.*, 1981; Hann, 2005). With shorter rotations and increasing pressure for economic efficiency, the timing of silvicultural activities such as fertilization, thinning, and pruning have become more critical, often rendering a 5-year resolution inadequate on the higher sites in particular. Likewise, these model time-step make it difficult to link responses to silvicultural treatments with weather patterns during and after treatment (e.g. Henning and Burk, 2004). Johnson (2005) recently found a very wide range (1.3- to 2.3-fold difference) of predicted responses to thinning, fertilization, and the combination of these treatments from 6 widely used PNW empirical growth models. Although some of this variation undoubtedly resulted from differences in modeling databases, a large amount can also be attributed to implicit or explicit assumptions about model forms and associated growth responses to intensive silvicultural treatments.

Dissertation Objectives and Structure

The overall goal of this dissertation was to examine the influence of intensive management activities on coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) crown dynamics and incorporate the results into a hybrid modeling framework in which crown and canopy structure heavily influence ecophysiological processes and individual-tree morphology. Specific objectives were to (1) model the influence of intensive management on crown structure; (2) fit individual-tree diameter and height growth models that operate on an annual resolution; (3) quantify the effects of intensive management on individual branch growth and mortality; and (4) develop a modeling framework that incorporates both basic physiological processes and empirical observations on diameter growth, height growth, and crown dynamics.

The context of the dissertation is more fully set in Chapter 2 by critically examining and summarizing the literature on hybrid models and their key physiological components. Objectives 1-4 of the dissertation are addressed in Chapters 3-6, respectively. Chapter 3 assesses the influence of vegetation management, precommercial thinning, fertilization, and commercial thinning on number, angle, maximum diameter, and length of branches in Douglas-fir and develops predictive models for each of these responses. Chapter 4 documents the development of empirical individual-tree diameter and height growth equations that operate on an annual resolution and enable a closer link to annual changes in environmental conditions. The predictive ability of these equations was then compared to an existing growth and yield model with a 5-year time-step. Chapter 5 describes the diameter growth and mortality rate of branches that were initially marked and managed under varying silvicultural regimes (Chapter 3). The resulting equations for branch diameter growth and probability of mortality were then incorporated into a simulation model that included the annualized tree diameter and height growth equations developed in Chapter 4. Chapter 6 develops a modeling framework that predicts stand leaf area index, estimates daily net photosynthesis, and simulates growth and mortality at multiple scales and then test predicted responses to a range of intensive management regimes. Finally, Chapter 7 summarizes the key findings of the study and discusses the future research that is needed to improve the modeling framework for predicting the growth and yield of intensively managed plantations in the PNW.

CHAPTER 2: WHERE EMPIRICAL AND PROCESS-BASED MODELS OF FOREST GROWTH AND YIELD MEET: A CRITICAL EXAMINATION OF HYBRID MODELING

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Abstract

Hybrid models of forest growth and yield offer the potential of combining the strengths of empirical growth models and process-based models, thereby surmounting the weaknesses of each type alone. The three primary advantages of a hybrid model framework are (1) representation of key physiological processes that are sensitive to stand conditions, climate, and site edaphic characteristics; (2) minimal data requirements when compared to purely empirical or process-based modeling approaches, particularly for those species whose parameters can largely be gleaned from the literature; and (3) capability for model outputs that exceed basic bolewood predictions with estimates of detailed wood quality attributes, total carbon sequestration, and water use. This review summarizes the various processes represented in previous hybrid models, outlines a framework for future hybrid modeling in Douglas-fir, and demonstrates several applications of the recommended framework. Existing models differed significantly in their representation of several important processes, particularly respiration, carbon allocation, and growth. The models tended to converge, however, on techniques for simulating light interception, photosynthesis, and stomatal conductance. Overall, the hybrid modeling framework showed strong potential for linking tree and stand growth to environmental conditions that are either fixed or changed due to silvicultural manipulation or natural variation. This feature of the growth model

enables greater versatility for achieving multiple objectives. In future applications of the hybrid model, certain modifications may improve its efficacy; refinements include better connecting soil water and nutrients to key physiological processes, refining predictions of stand leaf area, and more parsimoniously linking empirical predictions of individual-tree growth and morphology to simulated ecophysiological processes.

Introduction

Empirical and process-based forest growth models are important tools for forest managers and researchers, respectively. However, empirical models require large datasets for the target species and region, and they don't typically extrapolate well beyond the conditions covered by the data. Process-based models present a different set of challenges to researchers: the majority of process-based models are very complex, require detailed information on environmental conditions, and are developed to address fundamental questions about patterns in net primary productivity rather than management questions about the relative merits of alternative silvicultural regimes. Hybrid models have been suggested by Kimmins (1985), Monserud (2003) and Landsberg (2003a) as an alternative modeling framework to (1) increase the flexibility of empirical models accommodating the variability of climate and physical site resources among regions; (2) simplify the required amount of input relative to process-based models; and (3) mechanistically represent the influence of silvicultural treatments such as thinning and fertilization. Although hybrid models are more rare than strictly empirical or process-based models, they have attracted renewed interest. Reconsideration of the model has primarily resulted from heightened awareness of both natural and anthropogenic changes in climate, increased availability of weather data from automated weather stations, and other advances in instrumentation for monitoring soil water availability, temperature, gas exchange, nutrient fluxes, etc. The hybrid framework presented by Landsberg and Waring (1997), Physiological Principles for Predicting Growth (3-PG), has been applied to a number of different forest types throughout the world and led to increasingly widespread application of hybrid models. Several reviews have appeared in the forestry literature, but they have generally focused on purely process-based models (Schwalm and Ek, 2001; Landsberg, 2003b).

Hybrid models result from the combination of empirical and mechanistic approaches and are usually motivated by a set of forest-management questions. The model's objective is to utilize physiological principles as much as possible, while relying on allometrics and other accepted empirical modeling conventions to calibrate predictions and observed performance. The model is particularly attentive to components such as tree morphology, for which there are only limited principles and theory. Hybrid models typically operate at the stand-level and on a monthly time-step, although a few run at the individual-tree level and on a daily time-step.

These models have been developed for a variety of applications, including predicting the effects of climate change on tree growth (Baldwin *et al.*, 2001)and characterizing the influence of silvicultural treatments on external log characteristics (Mäkelä and Makinen, 2003). However, two primary classes of hybrid model frameworks are apparent, namely (1) empirical growth equations updated internally or externally by process-based growth modifiers and (2) mechanistic equations that rely on theoretical assumptions. The degree of hybridization within each of these classes varies greatly, so exact classification of hybrid models is difficult. This review summarizes models that have adopted both frameworks and delineates areas in which improvements could drive significant advances. The three parts of the review cover (1) mechanistic modeling of key physiological processes; (2) predicting growth from physiological processes; and (3) applications of hybrid models in silviculture and forest management.

Key Physiological Processes

Process-based models have a long history, and Mäkelä *et al.* (2000a), Le Roux *et al.* (2001), Kirschbaum and Mueller (2001), and Schwalm and Ek (2001) offer more comprehensive reviews of the model framework. This brief review will focus only on key mechanisms omitted in these previous reviews and on the mechanisms critical to the future success of hybrid models.

Light interception

Light interception in nearly all mechanistic models derives from the Beer-Lambert law (Wang, 2003). This law assumes exponential decay of radiation through the canopy, and the rate of this decay depends on the amount of leaf area. Goudriaan and van Laar (1994) refined the Beer-Lambert law by modifying the extinction coefficient to account for the fact that nonblack materials comprise plant canopies. Other mechanistic models have used the two-stream approximation, in which the dependence of the reflection and the transmission of the canopy rely upon the angle of the incident radiation and on the angular dependence of the scattering phase function (Sellers, 1985). Both the Beer-Lambert law and the method of Goudriaan and van Laar (1994) assume isotropic scattering, which means they predict light will scatter with equal efficiency in all possible directions. However, the Beer-Lambert law does not account for the loss of scattered radiation (Wang, 2003). Regardless of its limitations, the Beer-Lambert law has been preferred for its simplicity (Wang, 2001). In a recent validation, Wang (2003) found that the Beer-Lambert law accurately estimated the amount of absorbed visible radiation only if the absorption of direct beam and diffuse light is considered separately and the extinction coefficients are modified appropriately. Most mechanistic models, however, do not separate direct from diffuse radiation, creating an inherent bias in light-absorption estimates.

Most mechanistic models use a fixed extinction coefficient of 0.52 that is based on the work of Pierce and Running (1988) and implies that all radiation is attenuated at this same rate through any forest canopy. Sensitivity analyses have indicated that the models are moderately sensitive to this assumption (Kirschbaum, 1999; Esprey *et al.*, 2004). Hale (2003) indicated that thinned stands had a significantly lower extinction coefficient (~0.3) than the commonly used value for closed stands of *Picea sitchensis* (0.6). Similarly, Smith (1993) indicated that the extinction coefficient for stands of *Pseudotsuga menziesii* varied significantly with solar geometry, leaf area index (LAI), and stand relative density. A constant extinction coefficient is therefore particularly problematic for simulating the growth of stands undergoing intensive silvicultural treatments such as thinning. Goudriaan (1988) presented a method for approximating the direct extinction coefficient from total (direct+diffuse) extinction, and Campbell and Norman (1998) estimated the diffuse extinction coefficient using solar geometry and an assumed leaf angle distribution. Therefore, future models of canopy light interception would benefit from separate extinction coefficients for direct and diffuse radiation based on solar angle and stand structure.

Estimates of diurnal radiation distribution and integrated daily total radiation from daily mean radiation levels are commonly calculated using the sine-curve assumption. In a recent analysis of this assumption, Wang *et al.* (2002) found that this approach can lead to significantly overestimated radiation and an unrealistic diurnal pattern. Instead, they recommend distinguishing direct and diffuse radiation and using a cosine function solar angle, two methods that result in a much better fit to observed data (Wang *et al.*, 2002).

Models of light interception have generally been constructed for the stand-scale, although some have been developed for individual trees (Wang, 1990; Brunner, 1998). The latter models require extensive detail and computational power, but they provide an excellent prediction of individual-tree growth (Wang *et al.*, 1991; Brunner and Nigh, 2000). Schwalm and Ek (2004) recently applied a simplified stand-level light interception model to individual trees and obtained a mean absolute prediction error of 0.20 m^2 ha^{-1} and 0.12 m for basal area and height growth, respectively. Theoretically, this approach should significantly overestimate light interception, because the model does not take into account the relative social position of each tree within the stand (e.g. Korol *et al.*, 1995). Grote and Pretzsch (2002) addressed this problem by modifying the Beer-Lambert law to account for competition directly, in contrast to the indirect solution of Korol *et al.* (1995), who allocated stand-level net primary production to individual trees based on their leaf area. Realistic simulation of stand differentiation and structural dynamics will depend on future improvements in estimating light interception by individual trees.

Estimation of incident radiation and its interception by individual tree crowns is one of the most critical calculations in mechanistic models, because it drives photosynthesis. Complex models of the light-interception process exist, but simplified calculations can be used if (1) direct and diffuse radiation are separated; (2) extinction coefficients are allowed to vary by radiation type, sun angle, and stand structure; and (3) the sine-curve assumption is replaced by alternative calculations. Other important considerations that models generally omit include penumbra effects, the clumping of foliage, and interception by nonfoliated woody elements. Bernier (2001) indicated that bias introduced by ignoring penumbra effects was small when the diffuse fraction is high, and Kucharik *et al.* (1998) concluded that branches did not intercept a significant amount of radiation in boreal forests. The clumping of foliage, however, can have significant effects on estimates of intercepted radiation, and models should incorporate correction factors (Kucharik *et al.*, 1999). Campbell and Norman (1998) presented a simplified equation to estimate a stand-level clumping factor from the ratio of crown length to crown diameter, crown porosity, and a within-shoot clumping factor.

Photosynthesis

Simulation of photosynthesis is the most important calculation in mechanistic models, yet it is also one of the most difficult calculations. The Farquhar *et al.* (1980) biochemical equation has become the standard for most research models (Landsberg, 2003b), although the concept of radiation use efficiency (RUE) is still widely used in forest production models (e.g. Landsberg and Waring, 1997). This latter concept may be adequate for long temporal periods and large geographic regions, but it is too limited to predict photosynthesis under climate change or intensive forest management. For example, Medlyn (1998) indicated that daily RUE was highly variable regardless of canopy structure and that estimates of annual RUE varied significantly across sites with different LAI or light climates. In addition, Schwalm *et al.* (2006) recently indicated that the RUE was sensitive to the ratio of diffuse to total photosynthetically active radiation (PAR) across a variety of ecosystems in Canada. Accordingly, Duursma (2004) recently indicated that using a mechanistic canopy photosynthesis model increased the precision of predictions for stemwood volume growth by 21% when compared to the RUE approach. The ability to condition the critical parameters in the Farquhar *et al.* (1980) equation on ambient CO_2 concentration, leaf nutritional status, and temperature makes this approach much more effective for addressing the influence of climate change or silvicultural treatment on net photosynthesis.

While the Farquhar *et al.* (1980) model provides an adequate estimate of net photosynthesis at the leaf level, the resulting value is difficult to integrate over an entire canopy and throughout the course of a day. Three general approaches have been used to scale up to an entire canopy: (1) big-leaf (the canopy is considered as one leaf); (2) single-layer sunlit/shaded leaves; and (3) multi-layer. In a recent analysis of several single-layer canopy photosynthesis models, Medlyn *et al.* (2003) found that the sunlit/shaded approach worked best at all temporal scales (daily, weekly, and monthly) examined. In addition, Wang and Leuning (1998) found that the sunlit/shaded approach produced values within 5-10% of a multilayered model and was 10 times more computationally efficient. Wang (2000) recently suggested a slight refinement to the sunlit/shaded approach that reduced discrepancies within multilayered models to <3% while increasing the required computing time by only approximately1%. The distinction between sunlit and shaded LAI derives from ray penetration theory and requires the canopy extinction coefficient, LAI, and solar angle (Campbell and Norman, 1998). Wang *et al.* (2000) offered an important refinement of this equation in noting that site aspect and slope can significantly alter the fraction of the canopy LAI that is sunlit; however, those who use the equation rarely apply this crucial adjustment. As also concluded by Landsberg (2003b) and Medlyn *et al*. (2003), the sunlit/shaded approach appears to be the best option for future forestry mechanistic models.

As they are in scaling up to individual tree crowns and the stand canopy, efforts to integrate net photosynthetic rates to total daily net photosynthesis are frustrated by the highly nonlinear nature of photosynthesis during a normal day. Three primary approaches have been adopted for estimating total daily net photosynthesis: (1) hourly time-step; (2) Gaussian integration; and (3) analytical solutions to the daily integral of the Farquhar *et al.* (1980) equation. Research models, particularly, have resorted to using hourly or even half-hour time-steps, while Gaussian integration and analytical solutions have proved more efficient for most forestry applications. Gaussian integration involves breaking the day into 5 relative times and assigning a specific weight to each of the intervals. This approach captures the diurnal variation in net photosynthesis in a more computationally efficient manner than hourly time-step (Goudriann, 1986; Leuning *et al.*, 1995; Duursma, 2004). An analytical solution for the Farquhar *et al.* (1980) equation is presented in Chen *et al.* (1999) and used in the model of Schwalm and Ek (2004). This analytical solution involves estimating canopy photosynthesis at solar noon and multiplying this derived value by the day length. Both Gaussian integration and analytical solution of the Farquhar *et al.* (1980) equation provide more accurate estimates than simply applying a mean empirical value for the entire day.

Another important aspect of modeling canopy photosynthesis, particularly for conifers, is adjusting net photosynthetic rates by leaf age. This variation by needle age class has largely been ignored, despite important changes that can occur in the foliage age class structure in response to disease (Weiskittel *et al.*, 2006a) or silvicultural treatment (Balster and Marshall, 2000; Shibuya *et al.*, 2005). Bernier *et* *al.* (2001) indicated that canopy net photosynthesis was overestimated by 9% when foliage age effects were not accounted for in the model. A similar conclusion was reached by Ogeé *et al.* (2003) in a model developed for *Pinus pinaster* in France. In the Ogeé *et al.* (2003) model, root mean square errors increased by 40-70% when calculations didn't distinguish between foliage age classes (Ogeé *et al.*, 2003). Given these limited, yet striking results, differences in net photosynthetic rates between foliage age classes in conifers can be important for simulating growth responses to silvicultural treatment. Little research has been conducted on determining the Farquhar *et al.* (1980) parameters by foliage age class, but Ethier *et al.* (2006) is one recent exception.

Stomatal conductance

Stomatal conductance is an important parameter in mechanistic models, because it largely determines both net photosynthesis and canopy evapotranspiration. The following three dominant approaches are all, at least in part, empirical: (1) Ball-Berry (Ball *et al.*, 1986); (2) Leuning (1995); and (3) Jarvis-Loustau (Jarvis, 1976; Loustau *et al.*, 1997). Leuning (1995) and Ball-Berry (Ball *et al.* 1986) simultaneously solve for both net photosynthesis and stomatal conductance, while the Jarvis-Loustau approach begins with a maximal value that is reduced by environmental scalars. Three factors control stomatal conductance in the Ball-Berry model: net assimilation, CO_2 concentration in the leaf boundary layer, and relative humidity in the leaf boundary layer (Ball *et al.*, 1986). Leuning (1995) modified this model by substituting vapor pressure deficit at the leaf surface for relative humidity. In contrast to the Ball-Berry and Leuning models, the Jarvis-Loustau model incorporates a soil water stress by including a response function of stomatal conductance to soil water deficit. Van Wijk *et al.* (2000) compared the performance of all three models in a *Pseudotsuga menziesii* stand in The Netherlands and found that relative humidity in the Ball-Berry model was ineffective, but all three models simulated stomatal conductance over the range of soil-water content that was examined with reasonable accuracy. The Jarvis-Loustau model, in particular, reduced the root mean square error by 33% and 14% when compared to the Ball-Berry and Leuning models, respectively (Van Wijk *et al.* 2000). Hence, models that, like the Jarvis-Loustau approach, incorporate links between soil water availability, atmospheric conditions, and stomatal conductance show the most promise for forest production models.

None of these models, however, deal with the influence of soil nutrient availability on stomatal conductance, which may be required to accurately simulate fertilization effects. For example, Ewers *et al.* (2001) indicated that *Picea abies* and *Pinus taeda* that received both irrigation and fertilization increased mean stomatal conductance relative to trees that received only one of these treatments. In this experiment, the accuracy of even long-term predictions of transpiration degraded significantly when maximum stomatal conductance was estimated at experimentally raised soil water availability (Ewers *et al.* 2000). Ewers *et al.* (2000) recommended obtaining mean maximum canopy stomatal conductance under nonlimiting light conditions, low vapor pressure deficit, and highest native soil moisture; they also recommended considering the effects of soil fertility.

Respiration

Respiration is a very important process in the carbon balance and growth of trees, but it has received significantly less attention in mechanistic models than photosynthesis. Hence, there is little consensus on appropriate techniques to model respiration, particularly maintenance respiration. Growth or construction respiration to build woody and foliage tissue can be estimated from empirical relationships based on heat of combustion, ash, and organic nitrogen content of the tissue (Williams *et al.*, 1987) or on tissue carbon and ash content (Vertregt and Penning de Vries, 1987). Generally, the assumed value of this estimate is between 0.25 and 0.35 kg kg^{-1}. Five primary approaches have been proposed in the literature for estimating maintenance respiration: (1) daily Q_{10} (rate doubles for every 10° change in temperature) per unit of biomass carbon (Running and Coughlan, 1988); (2) annual Q_{10} per unit of biomass nitrogen (Battaglia *et al.*, 2004); (3) annual nitrogen content and temperature (Ryan, 1991); (4) constant fraction of gross primary production (Waring *et al.*, 1998); and (5) isometric scaling based on nitrogen content and plant mass (Reich *et al.*, 2006).

Although short-term (i.e. hourly to daily) temperature responses are inadequately described by a constant Q_{10} for respiration, many mechanistic models make this assumption for the purpose of simplification. However, respiration acclimates to temperature (Wythers *et al.*, 2005), so assuming a constant Q_{10} can lead to significantly overestimated respiration. Kirschbaum (1999) presents a daily respiration model that accounts for temperature acclimation, but few datasets currently exist to parameterize it correctly. Estimating respiration on an annual time-step circumvents temperature acclimation but doesn't capture the inherent seasonal variation of respiration (Vose and Ryan, 2002). Predicting maintenance respiration as a function of nitrogen content rather than carbon has been preferred; typically 90% of the nitrogen in plant cells is found in protein, which requires energy for repair and replacement. Nitrogen is also tightly linked with cellular activity (Ryan *et al.*, 1996a). Basing maintenance respiration on nitrogen content also accounts for the effects of nitrogen fertilization in this process (Stockfors and Linder, 1998; Maier, 2001). Further, trees contain a significant amount of structural carbon that is no longer supporting live respiring tissues (e.g. stem and branch heartwood). Nitrogen content is a good predictor of respiration because it also correlates with the amount of live tissue.

Given the great variability in respiration rates by season and tissue type, Waring *et al.* (1998) suggested that net primary production (NPP) is a constant fraction (0.47 ± 0.04) of gross primary production (GPP). However, studies by Mäkelä and Valentine (2000) that indicated that this ratio decreased with increasing tree height have stimulated skepticism about the suggestion. Similarly, Lai *et al.* (2002) found that the ratio of NPP to GPP can vary between 0.35 to 0.65 for young *Pinus* stands, decreasing exponentially with increasing aboveground biomass. Two extensive reviews by Gifford (2003) and Litton *et al.* (in review) have concluded that allocation of carbon to respiration is conservative across a variety of forest ecosystems and does not vary with changes in resource availability or forest age within a site. Thus, a model that assumes a constant ratio between NPP and GPP appears to be the best approach until better estimates of respiration and its variability are established. However, the dearth of information about respiration is directly attributable to the difficulty of measuring and scaling it with any level of confidence and accuracy.

Carbon allocation

After estimating net photosynthesis for a tree or stand, the carbon must be allocated to different parts of the tree for growth and maintenance. Cannell (1989), Cannell and Dewar (1994), Lacointe (2000), Barton (2001) and Litton *et al.* (in review) have presented comprehensive reviews of this topic from a modeling perspective. The four primary approaches to allocating carbon in the context of modeling are (1) pipe-model theory; (2) functional balance; (3) optimal partitioning; and (4) allometrics. Although these approaches are rather similar in nature, their differences and level of refinement are noteworthy. The pipe-model and functional balance theories concentrate on the structural constraints a tree must meet, but they don't identify the exact physiological mechanisms that allocate carbon. Both theories were applied by Mäkelä (1986; 1997; 2002) and Valentine (1985; 1988; 1997). Valentine and Mäkelä (2005) recently presented a hybridization of their approaches in an attempt to better connect empirical models with their process-based counterparts. The current amount of foliage and crown recession drives the amount of carbon allocated to foliage, while the functional balance maintains that a constant proportion of carbon must be allocated to match foliage growth. Carbon is then allocated to the woody compartments of the tree (stem, branches, and coarse roots), according to constant allometric relationships. This process is very similar to the use of allometric equations for predicting allocation in 3-PG (Landsberg and Waring, 1997). These models have not directly incorporated fertilization effects on carbon allocation, but factors such as LAI increase and change in carbon allocation to roots vs. above-ground components should account for the effects.

These hybrid approaches insufficiently address three key factors, however: (1) trees do not maintain a constant relationship between foliage and sapwood area; (2) the effects of climate are not represented; and (3) there is no mechanistic connection to above- or below-ground resource availability (light, water, nutrients). Le Roux *et al.*, (2001) concluded that these shortcomings limit the models' abilities to simulate responses to forest management activities. Several other studies also emphasize the need for refinements. First, the ratio between sapwood cross-sectional area and foliage biomass is not constant; rather, it increases with tree height (McDowell *et al.*, 2002a). Magnani *et al.* (2000) included the principle of functional homeostasis in a refined pipe-model theory; in this approach, allocation shifted from foliage to transport tissues as the plants grew taller, including a notable shift to fine roots. Future refinements of the pipe model may also have to account for the effect of climatic variability, which has a large influence on foliage biomass and sapwood area relations (e.g. Berninger and Nikinmaa, 1997). A recent review by Magnani *et al.* (2002) suggested that greater allocation to foliage would occur with increasing temperature, but lower allocation would correlate with increasing vapor pressure deficit and soil drought. Similarly, allocation to fine roots responded more strongly to drought, and the effect was magnified by coarse soil textures (Magnani *et al.*, 2002). In a recent meta-analysis of the results from the literature, Mencuccini (2003) concluded that any change in environmental parameters that increases the availability of resources (either above- or below-ground) results in the long-term acclimation of a less efficient (per unit leaf area) hydraulic system. The pipe-model and functional balance theories are useful conceptual models of tree growth, but they need further refinements to accommodate forest response to climatic variability or silvicultural treatments in a mechanistically sound manner.

Optimal partitioning offers a more flexible approach to carbon allocation by closely linking the tree, its immediate environment, and resource availability, while maintaining certain structural constraints on growth. The approach minimizes the imbalance between carbon acquisition by foliage and water and nutrient uptake in fine roots, while also ensuring sufficient transport and structural organs (Battaglia *et al.*, 2004). Thus, carbon, water, and nutrients maintain interdependency, thereby preventing a carbon-reliant system. Daily (Battaglia *et al.*, 2004; Schwalm and Ek, 2004), monthly (Battaglia *et al.*, 2004) and annual (Running and Gower, 1991) time-step have used optimal partitioning. It may be biologically reasonable to assume that daily and monthly time-step are most appropriate for deciduous species, while an annual time-step is adequate for most conifer species. Although their internal structures vary, models based on optimal partitioning have the common property of constraining growth by the most limiting factor of carbon, water, or nitrogen. Differences among these models arise primarily from varying objects of optimal partitioning. The objects of optimization have included growth, water transport (Magnani *et al.*, 2000), and uniform bending stress along the stem (Dean, 2001). If the context of a hybrid modeling effort is simulation of tree growth in response to different climate scenarios and silvicultural regimes, optimal partitioning offers considerable promise.

Because datasets that describe carbon allocation patterns across a range of environmental and stand conditions are rare, a hybridized carbon allocation approach may best represent this complex process. Raich and Nadelhoffer (1989) found a strong relationship between annual litterfall and total root allocation across numerous species and geographic locations, although limited to strictly unmanaged forests. Several models, including those of Law *et al.* (1999), Giardina and Ryan (2002), and Duursma (2004), have applied this relationship with apparent success. Relationships defined by Magnani *et al.* (2000) could determine the ratio of foliage to root biomass, and pipe-model theory could allocate between the woody components to maintain structural integrity. Carbon allocation is inherently difficult to model accurately, in part because it is very plastic and responsive to environmental conditions and silvicultural manipulations; however, research has indicated that fixed allocation coefficients are inadequate (Lacointe, 2000). An equally important consideration, however, is that the complexity of models such as transport resistance are often unwarranted (Mäkelä and Sievänen, 1987).

Water transport

Although hydraulic transport and dynamics have been increasingly recognized as primary drivers of forest productivity (e.g. McDowell *et al.*, 2002b), their representation in mechanistic models has been limited. In most models, hydraulic constraints are usually only imposed on stomatal conductance indirectly, through soil water availability. However, certain aspects of the tree hydraulic system are sensitive to site conditions and silvicultural manipulation. For example, stem sapwood permeability varies by crown dominance (Shelburne and Hedden, 1996; Reid *et al.*, 2003), site quality (Shelburne and Hedden, 1996), and tree age (Ryan and Yoder, 1997), but it also responds to thinning (Liu *et al.*, 2003) and fertilization (Amponsah *et al.*, 2004). A complex, mechanistic model for describing the influence of hydraulic transport on canopy gross primary production has performed well across a range of vegetation types (Williams *et al.*, 1996). Although the data needed to parameterize this model are becoming more common, maintaining homeostasis in water transport better represents hydraulic transport and dynamics in mechanistic models (Magnani *et al.*, 2000). Achieving homeostasis in water transport involves the combination short-term stomatal regulation and the optimal allocation of resources between transpiring foliage, conductive sapwood, and absorbing roots (Magnani *et al.*, 2002). These equations require estimates of (1) specific leaf area; (2) stand height; (3) fine root and sapwood longevity; (4)

stem hydraulic resistance per unit of projected leaf area; and (5) specific hydraulic conductance of fine roots and sapwood (Magnani *et al*., 2000). To address the short-term physiological regulation of hydraulic constraints, stomatal conductance could be estimated from equations that utilize leaf-specific hydraulic conductance (Bond and Kavanagh, 1999). Leaf-specific hydraulic conductance could be kept constant or allowed to vary with stem size or with environmental factors. For example, Manter *et al.* (2003a) found that the percent latewood in each sapwood annual ring best estimates leaf-specific hydraulic conductance. Manter's overall canopy net photosynthesis model was rather insensitive to this variable, however, so conductance was assumed to be a constant. Neither of these approaches accounts for the ability of the stem to store water, although sapwood storage can represent between 1.5-25% of the total water transpired in a given day (Phillips *et al*., 2003).

Mortality

Tree mortality is typically the weakest component of both empirical and process-based growth models. Hawkes (2000) enumerates many of the problems that arise from predicting tree mortality in simulation models. Most stand-level models have relied on the -3/2 power law of self-thinning or some similar maximum size-density constraint to simulate mortality (Valentine, 1988; Landsberg and Waring, 1997). Although this approach ignores variation in mortality due to environmental factors (Zeide, 2001), it works reasonably well at the stand level.

However, Pinjuv *et al.* (2006) recently indicated that use of the -3/2 power law of self-thinning in 3-PG on several independent validation plots throughout New Zealand incurred a significant amount of bias.

Individual-tree mechanistic models have predicted mortality from (1) a minimum crown ratio (Valentine and Mäkelä, 2005); (2) a function of crown coverage (Mäkelä, 1997); (3) empirical functions of tree size (Schwalm and Ek, 2004); and (4) carbon-based algorithms. Despite their appealing mechanistic basis, carbon-based algorithms have poorly predicted individual tree mortality (Hawkes, 2000). Mäkelä and Hari (1986) found that their mechanistic approach to mortality reduced accuracy when compared to empirical approaches. Running (1994) indicated that FOREST-BGC should not be run over 100 years because mortality predictions became unrealistic. Conversely, Korol *et al.* (1996) found that an individual-tree mortality model based on the logic of FOREST-BGC simulated stand dynamics that were consistent with the self-thinning rule, even over extended time periods. In virtually all mechanistic models, tree mortality is predicted to occur when maintenance respiration of the tree exceeds available carbon. The primary problems facing this approach, therefore, are (1) predicting respiration accurately and (2) estimating the carbon storage capacity of a tree. An underutilized approach previously suggested by Hawkes (2000) predicts mortality after growth efficiency falls below a designated minimal threshold (Waring, 1983). The advantages of this approach are (1) it is not site- or species-specific; (2) it recognizes that low growth efficiency is a sign of a stressed tree; (3) it inherently reflects climatic variation; and (4) growth efficiency decreases with time, so age or size parameters would not be needed to be explicit (Hawkes, 2000).

Soil water and nutrients

Homann *et al.* (2000), Kirschbaum (2001), and Saint-Andé (2004) provided comprehensive reviews of incorporating soil water and nutrient availability into mechanistic models. Although soil processes may be the dominant process controlling the long-term response of forest net primary productivity to climate change (Medlyn *et al.*, 2000), few growth models represent soil water and nutrients adequately, because of their inherent complexity. Most models estimate soil water availability by adding rainfall and subtracting transpiration, evaporation, and runoff from the soil water holding capacity, usually estimated as rootable depth multiplied by volumetric water holding capacity. Although this tipping bucket approach simplifies calculations and provides a fairly reasonable estimate of seasonal water availability, it doesn’t account for the daily interaction of soil texture, temperature, and vegetation in a mechanistic manner. For example, STAND-BGC can calculate a soil moisture value that is up to 56% greater than a physically possible value, when precipitation is frequent (Conklin, 2004). Neilson (1995) presented a simplified approach that might improve estimates of soil moisture by dividing the soil into 3 layers, constraining roots to the top two layers and dividing surface water between runoff and infiltration. In addition, this model uses empirical equations to relate soil texture to soil water potential (SWP) (Neilson 1995). Soil water potential is preferred over water content in models of plant physiology; however, in a recent review of water availability indices, Eamus (2003) concluded that an adequate measure of site water balance is not yet available. Paul *et al.* (2003) presented a soil water availability model that should suffice for most forestry applications and for predicting daily water content of litter, three-surface soil layers, and the rest of the tree-root zone. On the other hand, a simple soil water balance model of Rötzer (2004) performed comparably to a more complex model of Grote and Pretzsch (2002) in simulating daily soil water content on a site in southern Germany (T. Rötzer, per. comm.).

Nutrient cycling still remains the most difficult soil attribute for accurate modeling. The nutrient supply is composed of three fundamental pools, namely (1) mass of an element that is readily available in the soil solution; (2) mass of an element in labile pools that may be accessed through the activity of microbes and plants; and (3) mass of an element acquired by plants (Fisher and Binkley, 2000). The tremendous variability of nutrient pool size and dynamics, their inherent sensitivity to environmental conditions, and limited physiological understanding of roots complicate representation of these pools in forest growth models. The

Nutrient Budget Model (NUTREM) represents one modeling approach, a simplified model of nutrient uptake, retranslocation, and removal in *Pinus taeda* (Ducey and Allen, 2001). Starting with basic stand-level data (e.g. age, dominant height, basal area per ha), NUTREM estimates the annual uptake for each major nutrient and the total nutrient content of the stand in three stages. First, NUTREM estimates stemwood biomass increment and canopy structural variables using empirical equations. The model then estimates the amount of nutrients needed for construction of woody and non-woody tissues from gross stemwood increment. Finally, the model calculates uptake from the soil for each nutrient as total construction cost minus retranslocation from foliage. In contrast, the Nutrient Cycling Model (NuCM; Verburg *et al.*, 2001) estimates forest nutrient requirements from a specified optimal growth rate. This model simulates the cycling of nitrogen, phosphorous, potassium, calcium, magnesium, sodium, and sulfur based on user-defined stand growth, litterfall, weathering, nitrogen and sulfur mineralization rates, soil mineral composition, initial litter, soil organic matter pools and carbon to nitrogen ratios. In addition, the model treats fertilization and changing atmospheric deposition of nutrients in a mechanistic manner. Other characteristics that are unique to NuCM include division of the soil into 10 layers, simulation of water movement with the continuity equation, decomposition as a 3-stage process (i.e. litter moves into fine litter and two-soil organic fractions), and dependence of mineral weathering rates on the mass of present mineral and the dissolved proton concentration raised to a fractional power. Kirschbaum and Paul (2002) and Corbeels *et al.* (2005a; 2005b) developed similarly detailed mechanistic models of soil nutrient dynamics. Because primary production in most forests is limited by nitrogen availability, Paul *et al.* (2002) developed a simplified model to predict daily nitrogen mineralization as a specific basal rate modified by soil temperature and relative soil water availability. CABALA (Battaglia *et al.*, 2004) has incorporated this approach and shows promise for future mechanistic modeling efforts.

Growth Prediction Based on Physiological Processes in Hybrid Models

Empirical growth equations with physiological growth modifiers

Hybrid model growth equations have included both internal and external modifiers. Baldwin *et al.* (2001) linked an annualized, individual-tree empirical growth model (PTAEDA2; Burkhart *et al.*, 1987) to a highly detailed canopy radiation transfer and photosynthesis model (MAESTRO; Wang, 1990). Total leaf area and its vertical distribution were predicted with empirical equations (Baldwin *et al.*, 1997), then MAESTRO simulated net photosynthesis for a given climatic scenario. This simulated value for net photosynthesis determined site index, one of the primary predictors in the empirical diameter and height growth equations (Burkhart *et al.*, 1987). The model predicted that site indices across the region would increase by 0.0847 m year^{-1} due primarily to increased ambient CO_2 concentrations, resulting in a 97% reduction in mean bias when compared to the empirical-only approach over a 15 year growth period (Baldwin *et al.*, 2001).

Although not a physiologically-derived growth modifier on empirical equations, the use of allometric equations to predict diameter and height growth from volume increment has been utilized in TREE-BGC (Korol *et al.*, 1995), STAND-BGC (Milner *et al.*, 2003), and CenW (Kirschbaum, 1999). These models assume a constant stem shape and wood density then derive growth equations for a given initial diameter and height and initial and current stem weight. Korol *et al.* (1995) found an accuracy of 0.02 m^2 ha^{-1} for stand basal area growth and 0.4 m for tree height growth over a 5-year period. Both empirical approaches are significantly better than estimating the volume of the mean tree by dividing total stem weight by wood density and the number of trees per unit area.

External growth modifiers have produced acceptable results in several species (Pinkard and Battaglia, 2001; Snowdon, 2001; Henning and Burk, 2004). Growth is predicted from an empirical equation and then adjusted by an additive or multiplicative growth index that is derived from either climatic variables (Woollons *et al.*, 1997; Snowdon, 2001) or a combination of simulated physiological processes and climatic variables (Pinkard and Battaglia, 2001; Henning and Burk, 2004). The latter method is preferred because it represents the response of physiological processes to climate rather than more remote correlations between climatic variables and growth. Snowdon (2001) achieved reductions in root mean square error of up to 23%, while Henning and Burk (2004) reduced root mean square error between 7 and 11%. However, Snowdon (2001) updated the empirical growth estimates annually, whereas Henning and Burk (2004) retained a 5-year time-step for the growth equations. An annual time-step ensures the sensitivity of physiological processes to relevant environmental conditions and provides a tighter link between growth and weather conditions. This approach may be better suited to young, monospecific, even-aged stands than to mature, mixed species forest (Henning and Burk 2004). These external growth modifiers have rarely been applied at the individual tree-level, but they have strong potential to improve growth and yield estimates at this resolution (Henning and Burk 2004). However, it is important to distinguish between being able to improve estimates of past growth through knowledge of the corresponding weather during the growth period versus the relative performance of these approaches for predicting future growth. Thus, it is possible to oversell hybrid models to forest managers by citing better performance over past growth periods when in fact this superior performance should be obvious given the amount detail required by the model.

Mason *et al.* (in press) compute potentially-useable-light-sum as a surrogate for time in an otherwise empirical growth model that operates at the stand-level.

This approach conveniently avoids the pitfalls of carbon allocation, allometric assumptions, and the complexity of accurately estimating absorbed photosynthetically-active radiation. Mason *et al.* (in press) were able to simulate the growth of young Douglas-fir stands with varying levels of competing vegetation control quite satisfactorily.

Mechanistic equations

Mechanistic equations use theoretical derivations rather than empirical coefficients to estimate diameter and height growth. Pipe-model theory, as refined by Mäkelä (1997),Valentine (1985), and most recently, Valentine and Mäkelä (2005) exemplifies the most notable equations of this kind. The model predicts growth from variables that describe the initial state of the tree within the constraints of several dimensional relationships. For example, estimating cross-sectional growth at given locations on the stem is a function of the initial and the predicted heights of the tree and crown. This approach is not limited by the need for large datasets covering all the desired conditions, a common criticism empirical models. The drawback of the model is its increased sensitivity to a few theoretically derived variables, particularly the ratio of specific growth rates and the ratio of mean pipe length in the main stem of crown-to-crown length. Valentine and Mäkelä (2005) have refined many quantitative aspects of the pipe model theory, which is widely applicable due to the biological necessity of a functional balance between foliage quantity and the cross section of conducting tissue (Büsgen and Münch, 1929). As with any theory, further refinements are necessary for successful application to specific forest types and growing conditions. Although adequate simulations of tree and stand growth with pipe model assumptions are possible, simulation results do not validate the functional basis of the theory; hence, many of the theory's tenets and corollaries await rigorous testing. Further, theories like the pipe-model and uniform stress hypothesis are teleonomic in nature, meaning that they imply a conscious strategy by the tree to met perceived constraints.

The uniform-stress theory provides an alternative constraint by requiring the stem growth layer to ensure uniform distribution of bending stress along the entire bole. Dean *et al.* (2002) found a close agreement between predictions based on this theory and observed stem taper in 8 commercially important conifer species in North America. *Pseduotsuga menziesii* was the only species that did not support the theory, perhaps because the trees available for analysis were relatively small and young. Mäkelä (2002) found that a modified version of the pipe-model produced results quite similar to those obtained with uniform-stress theory.

In one other approach, Thornley (1999) developed a model of stem height and diameter growth based on a transport-resistance model of partitioning that was modified by foliage turgor pressure. The transport-resistance model combines the movement of carbon and nitrogen in opposite directions with bisubstrate dry matter growth kinetics, which helps provides an explanation for the functional balance in terms of substrate fluxes and dynamics. This approach avoids the inflexibility associated with the empirical and teleonomic methods that are described above, but requires variables that are not easily simulated. Hence, this approach has not been used extensively in tree growth models, due to its complexity and difficulties in determining its parameters (Le Roux *et al.*, 2001). Grote and Pretzsch (2002) presented an interesting reformulation of this idea by replacing the difference in activity between the foliage and stem tissue with net carbon gain at the top and bottom parts of the crown, but did not test the performance of this formulation. Thornley (1999) found that the transport-resistance model predicts the effects of varied stand conditions well, so further research into this approach may be warranted.

Applications of Hybrid Models

Carbon sequestration

The rate and magnitude of carbon sequestrated by forests is still an open scientific question (de Jong, 2001; Cannell, 2003). Economic studies have shown that greenhouse gas mitigation activities can be profitable with appropriate management techniques (Sohngen and Mendelsohn, 2003; Richards and Stokes, 2004). Hybrid models have been extensively used to estimate carbon sequestration potential of forests over a rotation and the influence of management activities on this potential because they have the capacity to estimate net primary production on annual basis. For example, a hybrid model was used to estimate the carbon sequestration of *Picea stichens* in the United Kingdom and continual thinning was found to reduce the carbon storage potential of these plantations by 15% (Dewar and Cannell, 1992). Similarly, Seely *et al.* (2002) used a hybrid model to indicate that application of fertilizer can increase carbon sequestration of aspen (*Populus tremula.*) by 9% in the boreal region of Canada. Waterworth *et al.* (2007) recently developed a generalized hybrid model for the sole purpose of estimating carbon storage of plantations in Australia. The use of hybrid model to estimate and evaluate carbon sequestration potential of forests will likely increase in the upcoming years as more companies become interested in balancing fiber production with greenhouse gas credits.

Climate change

Examining patterns of growth under varying scenarios of future climate change has been one of the primary motivators and applications of hybrid models. Schwalm and Ek (2004) concluded that water use efficiency in north central United States would increase as a result of climate change, resulting in an average increase in net basal area increment of 0.17 m^2 ha^{-1} $year^{-1}$ relative to projections under the current climate. Similarly, Medlyn *et al.* (2000) predicted that a doubling of ambient CO_2 would cause a large (~20%), short-lived increase in NPP for both

Picea abies in Sweden and *Pinus radiata* in Australia, while increasing temperature by 2°C resulted in a long-term increase in NPP of 10-15%. Hybrid models such as 3-PG, however, have limited potential to predict changes in stand productivity with changing climate scenarios because it doesn't mechanistically represent the key processes that will be influenced (Schwalm and Ek, 2001). Thus, for a hybrid model to accurately represent the influence of changing climate on tree growth, four key features are needed: (1) separation of direct and diffuse radiation because of the possible change in cloud cover conditions; (2) a photosynthesis equation sensitive to temperature and ambient CO_2; (3) representation of climatic effects on soil processes; and (4) carbon allocation algorithms dependent on site resource availability. While soil processes have emerged as the dominant process governing forest response to climate change in some studies (Medlyn 2000), shifts in carbon allocation have also been a dominant influence in others (DeLucia *et al.*, 2000). Future efforts should concentrate on understanding the relative importance of these factors and how the relative performance of all factors varies across different climatic regions.

Silvicultural prescriptions

Empirical models often rely on data-derived modifiers to boost stand growth immediately following silvicultural treatments like thinning, with provision for decay in the boost as tree growth becomes commensurate with tree attributes and stand density. This modifier function is necessitated by the lack of mechanisms representing the increase in resource availability and growth efficiency of crowns and foliage. Hybrid models offer an opportunity to account for factors that govern responses to silvicultural treatments and the interaction of these treatments with weather conditions during and after treatment. Although several hybrid models have a framework for evaluating these responses, few have been explicitly used for this purpose. CABALA was designed for this purpose, however, and has performed well in providing decision support for silvicultural prescriptions (Battaglia *et al.*, 2004). This model can predict the influence of different planting arrangements (spacing within blocks, spacing between blocks, and orientation of the blocks) on canopy light interception (Battaglia *et al.*, 2004). Mäkelä (1997) used a hybrid model to compare the effectiveness of different thinning regimes for *Pinus sylvestris* in Finland. Hybrid models need to have an accurate simulation of incoming radiation and canopy light interception to predict growth responses to thinning. These simulations require extinction coefficients that consider LAI and stand density, account for clumping and total canopy cover, and distinguish between direct and diffuse radiation. Provisions for soil water and nutrient dynamics are likewise essential for predicting tree responses to silvicultural manipulation.

Nutrition

Our understanding of the role of nutrition in controlling or constraining plant growth has been limited by the complexity of simulating weathering, litter decomposition, nutrient availability in the soil solution, and uptake, distribution, and re-distribution of nutrients in the tree. Hybrid models are rather limited in their current capacity to simulate growth responses to changes in nutrient availability, including response to fertilization. FORCYTE was one of the first hybrid models and was developed specifically to look at the effects of forest harvesting and other silvicultural activities on nutrient capital and nutrient fluxes in coniferous forests of southwestern British Columbia (Kimmins and Scoullar, 1979). The previously described NUTREM model accounts for nutrient uptake and translocation, as well as the effects of fertilization in *Pinus taeda* (Ducey and Allen, 2001). Likewise, CABALA was recently linked with a model that estimates the supply and uptake of phosphorous and base cations (Smethurst *et al.*, 2004). This approach allows the simulation of nitrogen and phosphorous dynamics simultaneously with other factors that limit productivity. A variant of 3-PG has also been used to predict wood production following nutrient amendments, and was found to perform better than an empirical model (Stape *et al.*, 2004). The drawback of 3-PG in this context, however, is the need to adjust its subjective site fertility rating rather than an explicit treatment of soil nutrient dynamics. Accounting for the relationship between soil nutrient availability, tree nutrition, and growth dynamics is an important but somewhat daunting task for developers of hybrid growth models.

Genetics

Simulating the effects of genetic improvement may be even more difficult than effects of nutrient availability, primarily because of the many potential physiological and morphological mechanisms by which stem volume growth may be enhanced. Likewise, various structural modifications brought about by genetic manipulation interact, changes at the tree level have largely unknown effects at the stand level, and interactions with environmental conditions may be difficult to predict. Although crown architecture and carbon allocation have been the two tree features most amenable to genetic engineering (Martin *et al.*, 2005), few process-based models can explicitly evaluate differences in productivity between trees or stands of different genetic composition. In fact, Almeida *et al.* (2004b) listed incorporation of the genetic effects into hybrid models as one of the most important current needs for applying this type of model to urgent management questions. Mäkelä *et al.* (2000b) used the model PipeQual to analyze differences in growth and wood quality between *Pinus sylvestris* trees of different geographic origin, and found that four structural parameters explained a significant amount of the observed variation: (1) ratio of foliage to active pipe area in stems; (2) ratio of foliage to active pipe area in branches; (3) density of foliage in crowns; and (4) mean branch length relative to a standard value. The 3-PG model has been parameterized and tested for intensively managed *Pinus taeda* plantations managed under a variety of densities, fertilization regimes, and genetic origins (Landsberg *et al.*, 2000). Simulations from the calibrated model agreed well with observed growth. A highly detailed hybrid model developed for the sole purpose of evaluating the genetic influence on growth was ECOPHYS (Rauscher *et al.*, 1990). The model allowed the user to modify morphological, phonological, and physiological clonal characteristics, which can be used to screen clones and help breeders in constructing ideotypes (Host and Isebrands, 1994). The capability to test the effects of genetic manipulation on tree and stand growth requires hybrid models with components that can allow changes in carbon allocation and crown structure.

Wood quality

Several hybrid models can simulate the influence of environmental conditions on wood quality. Few, however, have been designed to explicitly examine wood properties. Instead, stem features controlling wood quality are often by-products of detailed crown and canopy components necessary for simulation of ecophysiological processes. Mäkelä and Mäkinen (2003) generated the 3D geometry of stems and their internal knot structure as input into a sawing simulator. Similarly, CABALA (Battaglia 2004) and the model presented by Pinkard and

Battaglia (2001) give estimates of log and branch size in *Eucalyptus* plantations. Although branches may be the primary factor influencing wood quality in *Pinus spp.* (Grace *et al.*, 1999), branches may have a small influence on simulated grade recovery from logs of other commercially important species such as *Pseduotsuga menziesii* (Todoroki *et al.*, 2005); however, mill studies have suggested the importance of both knot size and juvenile wood content for lumber and veneer grade recovery from logs (Fahey *et al.*, 1991). More detailed models of internal wood properties, similar to those presented by Deleuze and Houllier (1998) and Deckmyn *et al.* (2006), may be required to accurately assess the effect of environmental conditions and silvicultural regime on wood quality.

Conclusions

Hybrid models have been developed with a wide variety of approaches, but all represent key physiological processes in a much simplified form and all produce stand and tree output directly relevant to forest management. Although simple application of physiological principles have met with some success (e.g., 3-PG), a review of the literature suggests a more functional and mechanistic links are warranted between environmental conditions and individual-tree growth.

Several physiological processes have been successfully modeled at a level that is suitable to their incorporation into hybrid growth models and in a way that is widely accepted among scientists, particularly light interception, photosynthesis, and stomatal conductance. On the other hand, little consensus currently exists for approaches to modeling respiration, carbon allocation, water transport, tree mortality, and soil processes. The recommended framework for addressing these issues involves: (1) optimal carbon allocation theory to recognize the importance of maintaining a solid hydraulic architecture (not captured in the pipe-model or functional balance theories); (2) prediction of mortality from growth efficiency thresholds rather than carbon balance; and (3) soil water and nitrogen dynamics simulated with simplified yet mechanistic models that include only that level of complexity meeting the minimal standards required. Mechanistic predictions of growth, however, are still limited. Constraints imposed by allometric equations and modification of empirical growth rates with physiological parameters currently appear to be the best approaches. The value of hybrid models is most fully realized when the need arises to examine the influence of climatic variation, silvicultural treatments, genetic manipulation, and nutrient availability on tree and stand growth. The acceptance and use of these models by the forestry community will require maintaining a transparent, explicit, parsimonious and mechanistically sound modeling framework.

CHAPTER 3: MODELING CROWN STRUCTURAL RESPONSES TO COMPETING VEGETATION CONTROL, THINNING, FERTILIZATION, AND SWISS NEEDLE CAST IN COASTAL DOUGLAS-FIR OF THE PACIFIC NORTHWEST, USA

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Abstract

Crown structure is a key variable influencing stand productivity, but its reported response to various stand factors has varied. This can be partially attributed to lack of a unified study on crown response to intensive management or stand health. In this analysis of several Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) branch data sets, a significant treatment effect of fertilization, thinning, pre-commercial thinning, varying levels of vegetation control, and intensity of a foliar disease (Swiss needle cast) were all found to influence several key crown structural attributes. Maximum branch size and total and non-foliated crown profiles were found to be the most dynamic and sensitive crown variables to the various stand factors as no treatment effects were found for the number of branches within an annual segment or branch angle. When the datasets were combined and used to develop a single predictive equation, treatment effects were largely accounted for by changes in bole and crown size as mean bias was relatively low despite the large range in tree ages examined (4 - 450 years at breast height). While crown structure is highly variable and sensitive to a variety of stand factors, general empirical equations perform quite well and should be better integrated into models of forest growth and yield.

Introduction

Conifer plantation growth and yield can be manipulated through intensive silvicultural practices such as vegetation control (Rose and Ketchum, 2002; Thompson and Pitt, 2003), thinning (Harrington, 2001; Talbert and Marshall, 2005), and fertilization (Dickens *et al.*, 2003). Growth responses to silvicultural treatment are largely mediated by changes in crown structure, including total leaf area (Vose, 1988; Gough *et al.*, 2004), foliar nutrient concentration or amount (Brix, 1981a), and crown length, crown width, and corresponding spatial distribution of foliage (Gillespie *et al.*, 1994). Fertilization also promotes greater photosynthetic rates per unit leaf area, at least temporarily (Brix, 1971; Gough *et al.*, 2004). Accurate quantification of these and other crown responses to specific treatments should enhance our ability to predict stand and tree performance under a wide variety of silvicultural regimes. In addition, it has become increasingly important in commercial species such as Douglas-fir to understand the effect of silvicultural treatments and regimes on wood quality, some attributes of which are controlled in part by crown structure and its dynamic responses over time (Maguire *et al.*, 1991b). In particular, branch size, vigor, and location have direct implications for several components of wood quality (Zobel and van Buijtenen, 1989).

Branch response to intensive silvicultural treatments has varied. Fertilization generally induces its strongest effect on the top half of the crown, whereas thinning affects the bottom half (Brix, 1981b). Both thinning and fertilization have been shown to increase the number of branches on a tree (Brix, 1981b; Mäkinen *et al.*, 2001); however, other studies have concluded that the number of branches per whorl is independent of tree size, site index, and stand density (Briggs and Turnblom, 1999; Woollons *et al.*, 2002; Grotta *et al.*, 2004).

Response of branch diameter and branch length to fertilization and thinning has also been inconsistent. For example, Mäkinen *et al.* (2001) found that diameter growth of both newly initiated and older branches in *Picea abies* were significantly enhanced by fertilization, but more recently Mäkinen *et al.* (2004) concluded that site fertility and fertilization did not significantly influence branch radial growth. In Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), Brix (1981b) found that thinning did not influence branch size, although this treatment did allow branches in the lower part of the crown to grow for a longer period of time before suppression. In contrast, Gary (1978) found that the largest 20-yr-old branches on *Pinus contorta* were nearly 1.6 times greater in thinned vs. unthinned stands 30 years after treatment. Branch elongation has received less attention, but in Douglas-fir was shown to increase throughout the crown with fertilization while remaining insensitive to thinning (Brix, 1981). However, this result contrasts directly with the more general increase in crown length and width with lower stand density (Curtis and Reukema, 1970). Madgwick *et al.* (1986) found that fertilized *Picea abies* had a more rapid decrease in branch extension with increasing depth in crown, resulting in a narrower relative crown profile.

The variability in results to date can be attributed to site and species differences, as well as to the lack of comparable sampling designs in these few studies. The most notable differences among these studies are: (a) thinning intensity; (b) time since treatment; (c) number and location of sample branches; and (d) the statistical model (particularly with respect to use of covariates). In addition, interactions with other factors such as early competing vegetation control and disease or insect defoliation have not been examined in any detail. Defoliation imposes a relatively rapid change in foliage amount and distribution, so branches and stems are expected to respond accordingly. One example in Douglas-fir is Swiss needle cast (SNC), a disease that has become increasingly important in north coastal Oregon by drastically altering both foliage age class structure (Weiskittel *et al.*, 2006a) and stand productivity (Maguire *et al.*, 2002).

The goal of this study was to test for and quantify the effect of silvicultural treatments (competing vegetation control, thinning, fertilization) and Swiss needle cast on crown structural attributes directly relevant to growth, yield, and wood quality in Douglas-fir. Specific responses included: (a) the number of whorl branches within an annual segment; (b) number of interwhorl branches within an annual segment; (c) maximum branch diameter within a whorl; (d) angle of branch insertion; (e) crown profile (trend in crown radius over height within the crown); and (f) profile of non-foliated crown core. The following three hypotheses were tested for each of these six crown structural attributes: (1) the crown attribute is not influenced by silvicultural treatment or SNC; (2) any significant response of the crown attribute to treatment or SNC can be accounted for indirectly by its effect on tree diameter, height, and/or crown length; and (3) existing models developed for estimating these attributes in Douglas-fir are adequate for a wider variety of silvicultural regimes and more variable disease conditions than were sampled previously (Maguire *et al.*, 1994; Roeh and Maguire, 1997; Maguire *et al.*, 1999), particularly in regard to competing vegetation control, thinning, fertilization, and SNC severity. In short, the allometric relationships that determine crown morphology are tested for their sensitivity to changes imposed by any of these silvicultural treatments or by SNC severity. The results will help guide the design of silvicultural regimes that yield the desired quantity and quality of wood from Douglas-fir stands.

Methods

Study sites

The majority of the sites utilized in this study were located in the northern half of the Oregon Coast Range. Other study site locations included two installations in the Oregon Cascade foothills, one installation in the southern Washington Cascade foothills, and one installation in the Willamette Valley (between the Oregon Coast Range and Cascades). The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 100 to 300 cm year^{-1} and January mean minimum and July mean maximum temperatures range from -2 to 2˚C and from 20 to 28˚C, respectively. Variation in precipitation and temperature for this area is strongly correlated with elevation and proximity to the coast. Elevation ranged from sea level to 825 m and all topographical aspects were represented in the database.

The sampled plantations ranged in age from 8 to 60-yrs-old at breast height and contained ≥75% Douglas-fir by basal area, so included varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and other conifer and hardwood species (Table 3.1).

Data collection

Several datasets were combined to test the above hypotheses. The first was collected from 122 sample trees in 33 Douglas-fir plantations with varying levels of SNC in 2002 and 2003 (Weiskittel *et al.*, 2006a). The second was based on 19 sample trees in three pre-commercial thinning (PCT) installations established to test the effect of thinning on SNC symptom development and Douglas-fir growth loss (Maguire *et al.*, 2004). The third dataset was collected from 52 trees on 16 plots designed to test the effects of thinning and fertilization on growth, yield, and wood quality (Maguire *et al.*, 1991a). The fourth and final dataset was built from 30 trees on 10 plots designed to test the effects of competing vegetation control on early tree growth (Vegetation Management Research cooperative (VMRC, Oregon State University); (Rose *et al.*, 1999). The SNC dataset was collected in 2002 and 2003, while the remaining data were collected in 2004. All sample trees were measured for diameter at breast height (DBH), total height (HT), and height to crown base (HCB; lowest live branch; Table 3.2).

The SNC dataset included measurements from 86 trees in 24 young plantations (15-35 yrs at breast height) and 36 trees in nine older plantations (35-65 yrs at breast height). All trees in this dataset (3-4 per stand) were felled and every living branch (at least one green needle and ≥ 1 mm in diameter) was measured for insertion height (nearest 0.01 m) and diameter (nearest 0.1 mm). All measured branches were also coded by north vs. south side of the tree.

The three sampled PCT installations contained a set of three square 0.08-ha plots. Treatments were implemented in 1998 and included a control, moderate thinning (494 residual trees ha^{-1}), and heavy thinning (247 residual trees ha^{-1}). At each installation, the control plot and one randomly selected thinning plot were sampled (heavy thinning at one installation (~254 trees ha^{-1}) and moderate thinning at the other two (~500 trees ha^{-1}). One sample tree was randomly selected from each of the diameter classes containing the 25th, 63rd, and 93rd percentiles of the diameter distribution. Each tree was climbed and every branch (living + dead) from stem base to the 3rd whorl from tree tip was measured for height of insertion (nearest 0.01 m) and diameter (nearest 0.1 mm). All measured branches were also coded for north vs. south side of the tree. A sub-sample of branches was also measured for azimuth of insertion, angle of insertion (º from vertical), total length (nearest 0.01m), and non-foliated length (nearest 0.01m).

Three SMC installations were selected from a set representing young plantations that were respaced to varying degrees well before crown closure (Type I installations; (Maguire *et al.*, 1991a). One was located in the northern Oregon Coast Range, southern Washington Cascades, and central Oregon Cascades. One other SMC installation from the Willamette Valley was also selected from a set representing initial spacing trials (Type III installations; (Maguire *et al.*, 1991a). On four plots at each installation, three sample trees were selected, one each from the diameter classes containing the 25th, 63rd, and 93rd percentiles of the diameter distribution. The four plots from respacing trials (Type I) included the control (C), fertilized (FERT), thinned (THIN), and fertilized + thinned (F+T) plots. The FERT plots received 448 kg ha^{-1} of nitrogen as urea and time since treatment varied from

1 to 4 yrs. Residual tree density in the THIN plots was 50% of initial trees ha^{-1}, so ranged from 455 to 865 trees ha^{-1}. The four plots sampled at the initial spacing trial (Type III) included initial densities of 247, 762, 1865, and 3048 trees ha^{-1}. Each sample tree on the SMC plots was climbed and every branch (living + dead) from stem base to the 3rd whorl from tree tip was measured for height of insertion (nearest 0.01 m) and diameter (nearest 0.1 mm). All measured branches were also coded for north vs. south side of the tree, and a sub-sample was also measured for azimuth of insertion, angle of insertion (º from vertical), total length (nearest 0.01m), and non-foliated length (nearest 0.01m).

VMRC

Five plots were sampled from each of two VMRC installations, one in the mid-Oregon Coast Range and the other in the lower Oregon Cascade foothills. Treatments were defined by area around each subject tree receiving competing vegetation control, including: no treatment (control), 3.34 m^2 of total vegetation control (TVC), 9.29 m^2 of TVC, complete removal of woody only vegetation (WDY), and complete removal of herbaceous only vegetation (HRB) (Rose *et al.*, 1999). Plots at each installation were randomly selected from the three receiving the same treatment, and three trees were randomly selected from the diameter classes containing the 25th, 63rd, and 93rd percentile of the diameter distribution. Each tree was climbed and every branch (living + dead) from stem base to the 3rd whorl from tree tip was measured for height of insertion (nearest 0.01 m) and diameter (nearest 0.1 mm). All measured branches were also coded for north vs. south side of the tree. A sub sample of branches was measured for azimuth of insertion (nearest °), angle of insertion (nearest °), total length (nearest 0.01 m), and nonfoliated length (nearest 0.01m).

Data analysis

The four datasets described above were supplemented with four additional Douglas-fir branch datasets previously analyzed by Maguire *et al.* (1994), Roeh and Maguire (1997), Maguire *et al.* (1999), and Ishii and McDowell (2002). Various linear and nonlinear regression models were fitted to the data to develop a series of equations describing crown structural attributes. The basic modeling unit was either an annual segment of the main tree stem, or primary branches attached to these annual segments. Each dataset was analyzed separately and treatment effects were tested by including indicator variables for discrete treatments. After assessing treatment effects, a global model for each crown structural attribute was developed from the combined datasets. Final models were chosen on the basis of residual analysis, Furnival's (1961) index, Akaike's information criterion (AIC) and biological interpretability.

The data had a distinct hierarchical structure (multiple measurements within trees within plots within installations) and as a result, violated the assumption of independence and zero correlation. A multilevel, mixed-effects model (Pinherio and Bates, 2000) was therefore employed to account for random effects of plots within each installation, trees within each plot, and measurements within each tree. When heteroskedasticity was detected in the residual plots, the final equation was weighted by a power variance function of the primary independent variable. In addition, the degree of within-tree autocorrelation was evaluated by plotting the residuals with the autocorrelation function (ACF) in S-Plus v6.2. If needed, a continuous, first-order, autoregressive function of distance from tree tip was introduced to correct for any remaining autocorrelation. Nested model forms were compared with likelihood ratio tests, and bias was calculated as observed minus predicted.

Number of branches within annual segment

While the total number of whorl and interwhorl branches on an annual segment has been modeled using the Poisson distribution (e.g. Mäkinen and Colin, 1999), the normal distribution was assumed in this analysis because Douglas-fir typically has at least 15 branches within an annual segment. The initial model had a form similar to the one presented by Maguire *et al.* (1994):

$$[3.1]\quad \begin{aligned} \mathrm{NB_i} &= \beta_{10}\mathrm{SEGLEN}^{\beta_{11}} * \mathrm{SEGAGE}^{\beta_{12}} * \mathrm{SEGHT_{REL}}^{\beta_{13}} * \mathrm{SEGDINC}^{\beta_{14}} \\ &\quad * \exp(\beta_{15} * \mathrm{SEGDINC}) * \mathrm{CR}^{\beta_{16}} + \varepsilon_1 \end{aligned}$$

where NB_i is the total number of branches, SEGLEN is segment length (m), SEGAGE is segment age (years), SEGDINC is segment depth into the crown or distance between tree tip and top of the annual segment (m), $SEGHT_{REL}$ is the relative height of the segment in the stem (SEGHT/HT), SEGHT is the absolute height of the segment tip above ground (m), CR is tree crown ratio, the β_i's are parameters to be estimated from the data, and $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$. In each dataset, this model was fitted separately to four classes of NB_i, namely the total number of branches (live + dead; NB_T), the number of whorl branches (NB_W), the number of interwhorl branches (NB_I), and the number of live branches (NB_L). For the NB_L model, the four datasets described above were merged with the datasets previously analyzed by Maguire *et al.* (1994) and Ishii and McDowell (2002).

Maximum whorl branch size

A modified Kozak (1988) variable-exponent model was fitted to the data representing vertical trends in maximum branch size (Maguire *et al.* 1999, Garber and Maguire 2005). A simple power function of DBH performed better than predicted crown width for scaling maximum branch size (cf. Maguire *et al.* 1999). Both live and dead branches were included during parameter estimation and the form of the equation was:

$$[3.2] \quad \mathrm{BD}_{\max} = \beta_{21}\mathrm{DBH}^{\beta^{22}} \frac{1-\sqrt{\mathrm{BHT}_{\mathrm{rel}}}}{1-\sqrt{\beta_{23}\mathrm{CR}^{\beta_{24}}}}^{\left(\begin{array}{l}\beta_{25}\sqrt{\mathrm{BHT}_{\mathrm{rel}}}+\beta_{26}\exp(-\frac{\mathrm{DBH}}{\mathrm{HT}}) \\ +\beta_{27}(\mathrm{Z}^{*}\frac{\mathrm{DBH}}{\mathrm{HT}})+\beta_{28}\mathrm{CL}+\beta_{29}\mathrm{CR}\end{array}\right)} + \varepsilon_2$$

where $\mathrm{BD}_{\max}$ is maximum branch diameter within a whorl (mm), CL is crown length (m), $\mathrm{BHT}_{\mathrm{rel}}$ is branch relative height (branch height/total tree height), the β_i's are parameters to be estimated from the data, $\varepsilon_2 \overset{\mathrm{iid}}{\sim} \mathrm{N}(0, \sigma_2^2)$, and all other variables have been defined above. The final equation was fitted to a dataset constructed by merging the data collected for this study with the datasets previously analyzed in Maguire *et al.* (1994), Maguire *et al.* (1999), and Ishii and McDowell (2002).

Branch angle of insertation

Branch angle of insertation (relative to vertical) was predicted using the function suggested by Roeh and Maguire (1997):

$$[3.3] \quad \begin{array}{l}\mathrm{BA} = (\beta_{31} + \beta_{32}\mathrm{HT}) * (1 - \exp(\beta_{33}\mathrm{DINC} \\ \qquad + \beta_{34}\mathrm{BHT}_{\mathrm{rel}} + \beta_{35}\mathrm{SI})^{(\exp(\beta_{36}\mathrm{BD}))} + \varepsilon_3\end{array}$$

where BA is branch angle (°), DINC is depth into the crown (total tree height – branch height), SI is Bruce's (1981) site index (m), BD is branch diameter (mm), the β_i's are parameters to be estimated from the data and $\varepsilon_3 \overset{\mathrm{iid}}{\sim} \mathrm{N}(0, \sigma_3^2)$.

Total and non-foliated crown profile

Crown profile was estimated using the three-stage approach outlined by Roeh and Maguire (1997). First, insertion angle of every live branch was estimated with equation [3.3] fitted separately to each plot by including a random installation and plot effect, similar to the procedure given by Robinson and Wykoff (2004) for imputing missing tree heights. Similarly, total and foliated branch length was predicted for every measured live branch by fitting the following total branch length model (Roeh and Maguire 1997) and non-foliated branch length model (Weiskittel, 2003) to each plot separately:

$$[3.4] \quad \mathrm{BL} = (\beta_{41}\mathrm{DINC}^{\beta_{42}}) * \exp(\beta_{43}\mathrm{DINC} + \beta_{44} * \mathrm{BHT}_{\mathrm{rel}}) * \mathrm{BD}^{\beta_{45}} * \mathrm{CR}^{\beta_{46}} + \varepsilon_4$$

$$[3.5] \quad \mathrm{NFBL} = \frac{\mathrm{BL}}{1 + \exp(\beta_{51} + \beta_{52}\mathrm{BD} + \beta_{53}\mathrm{BHT} + \beta_{54}\mathrm{BHT}_{\mathrm{rel}} + \beta_{55}\mathrm{CL})} + \varepsilon_5$$

where BL is total branch length (m), NFBL is non-foliated branch length (m), BHT is branch height above ground (m), the β_i's are parameters to be estimated from the data, $\varepsilon_i \overset{iid}{\sim} N(0, \sigma_i^2)$, and all other variables are defined above. Equations 3.3, 3.4, and 3.5 were fitted to the data collected for this study combined with those previously analyzed by Roeh and Maguire (1997) and Ishii and McDowell (2002).

From equations [3.4] and [3.5], the crown radius at the height of each live whorl was estimated from the following geometric relationship:

$$[3.6] \quad \mathrm{CRD}_{\mathrm{i}} = \mathrm{BL} * (\pi * \sin(\frac{\mathrm{BA}}{180}))$$

where $\mathrm{CRD}_{\mathrm{i}}$ is crown radius (m) and all other variables have been defined above. Total and non-foliated crown radii ($\mathrm{CRD}_{\mathrm{TOT}}$ and $\mathrm{CRD}_{\mathrm{NFOL}}$, respectively) were estimated at each whorl height as the simple mean of all live whorl branches. Crown profile and unfoliated crown core were described with a model similar to equation [3.2]. The model was numerically integrated to estimate volumes of the total crown, unfoliated crown core, and the foliated shell of the crown for each sample tree.

Results

Number of branches within annual segment

Annual segments from the main stem of coastal Douglas-fir held on average 3.8 whorl branches and 9.9 interwhorl branches. In general, the number of branches increased with segment age, segment length, segment relative height in crown, segment depth into the crown, and crown length, while it decreased with depth into the crown and crown ratio (Table 3.3). No treatment effects could be detected on the number of whorl or interwhorl branches, after accounting for segment length, segment depth into the crown, segment age, segment relative height in the stem, and crown ratio. The south-facing side of an annual segment held up to 14% more branches than the north-facing side. Mean bias for equation [1] was -0.45 ± 1.34.

The model presented by Maguire *et al.* (1994) tended to overpredict the number of branches within an annual segment by 3.1 ± 8.1 branches

Maximum branch size within annual segment

Silvicultural treatments significantly affected maximum diameter of whorl branches in each of the datasets (Figure 3.1). In the SMC dataset, fertilization increased maximum branch size in the upper stem third (p=0.0662), while thinning significantly increased maximum branch size in the lower stem third (p=0.0164). The combination of fertilization and thinning caused a mean maximum branch size profile very similar to the control tree, indicating that these treatments negated each other's effects, at least with respect to the behavior of maximum branch size over relative height in the crown. However, thinning significantly increased crown length, so on an absolute scale the effect of the combined treatments was unique. Also, the effect of both treatments diminished with time since treatment (TST), primarily because the longer term responses of tree diameter, height and crown length eventually account for the change in branch diameter at a given depth into the crown. In the PCT dataset, precommerical thinning significantly increased maximum branch sizes in the lower 50% portion of the stem (p=0.0022) and there was a significant difference between the moderate and heavy thinning treatments (p=0.0235). For a given bole and crown size, there was very little difference, however, between the treatments. In the VMRC dataset, the 9.29 m^2 TVC treatment showed moderate evidence of significantly decreasing maximum branch sizes in the upper relative crown third when compared to the control (p=0.0606). In the SNC dataset, foliage retention had a significant effect (p<0.0001) on maximum branch size, but the effect differed by relative position in the stem (p<0.0001). Greater levels of SNC increased maximum branch sizes in the lower third of the stem and reduced the variability in maximum branch diameter among different heights.

Aspect had no significant effect on maximum diameter of whorl branches, but tree diameter, height, and either crown length or crown ratio were always significant covariates. The overall maximum branch diameter profile equation performed well across these varied stand conditions after the inclusion of height to crown midpoint (HCM) rather than CR. In general and for a given bole size, decreasing the crown length by 50% is related to a 21.2% mean reduction in maximum branch size in the lower half of the stem. Mean bias for the final model was -2.01 ± 9.53 mm. The equation previously presented by Maguire *et al.* (1999) equation tended to underpredict maximum branch size by an average of 6.8 mm.

Branch angle of insertation

No treatment effects could be detected on the insertion angle of branches. Branch angle increased with greater HT/DBH, BD, SI, and BHT, and decreased with increasing relative height on the tree (Table 3.4). Mean bias for the final model (equation [3.3]) was 1.7°. The model previously developed by Roeh and Maguire (1997) underpredicted branch angle by an average of 10°. For this larger dataset, predictors HT/DBH and branch height (BHT) performed better than HT and DINC (cf. Roeh and Maguire 1997).

Total and non- foliated crown profile

Silvicultural treatments significantly affected crown profile in all of the datasets (Figure 3.2). In the SMC dataset, thinning and its interaction with fertilization had a significant effect on crown profile (p=0.0004 and 0.0002, respectively); however, fertilization had no effect (p=0.1694). For a given bole and crown size, thinning decreased crown radii in the lower relative third of the crown and the combination of thinning and fertilization produce crown radii similar to the control. The profiles did not vary significantly by time since treatment (p=0.2256). In the SNC dataset, foliage retention had a significant effect on crown profile (p=0.0023), but its effect varied by relative position in the crown (p=0.0151). Crown radii in the near the crown midpoint were slightly greater on healthy trees (FOLRET=3.5 yrs), while heavily diseased trees (FOLRET=1.5 yrs) had relatively greater crown radii in the lower 10% of the crown. In the PCT dataset, precommerical thinning significantly increased crown radius in the lower half of the crown (p=0.0279). There was no significant difference between the heavy and moderate thinning treatments. In the VMRC dataset, complete removal of only herbaceous ($p<0.0001$) or only woody vegetation caused a significant treatment effect ($p<0.0001$ and 0.0002, respectively), while the area treated around subject trees had no significant effect on subject tree profile. Both complete removal treatments increased crown radius at all crown heights relative to the control treatment, with herbaceous removal producing slighter greater crown radii woody removal. Complete removal of both herbaceous and woody vegetation, however, had the greatest effect on crown profile. Mean bias for the final equation fitted was 0.09 m. Mean bias for the regional crown profile model for Douglas-fir (Hann, 1999) underpredicted crown radius on average by 0.81 m (se 0.85).

On average, north-pointing branches were 10% longer than otherwise identical south-pointing branches, although, the effect varied by relative height in the stem. Non-foliated branch length, however, did not differ by branch aspect. The effect of branch aspect, however, was not incorporated into the final models because it was not measured on all branches.

Silvicultural treatments also significantly affected non-foliated crown radius in all datasets (Figure 3.3). In the SMC dataset, both fertilization and thinning had a significant negative effect on non-foliated crown radii ($p<0.038$ and 0.0001, respectively), while the interaction between treatments and the time since treatment were not significant. For a given bole and crown size, fertilization and thinning had little relative influence on non-foliated crown radii in the upper two thirds of the crown when compared to the control, while thinning caused longer non-foliated crown radii in the lower third of the crown. The combination of fertilization and thinning, however, significantly reduced non-foliated crown radius in the upper two thirds of the crown. In the SNC dataset, the disease has resulted in greater non-foliated crown radii in the upper two thirds of the crown ($p=0.0160$), while the profiles are quite similar in the lower third of the crown. In the PCT dataset, thinning significantly reduced non-foliated crown radii throughout the crown ($p=0.0017$), but no difference was detected between 247 and 494 residual trees per ha. In the VMRC dataset, the amount of area treated with vegetation control (ATRT), the herbaceous vegetation only removal, and the woody vegetation only removal each had a significant effect on non-foliated crown radii $p=0.0086$, 0.0001, and 0.0008, respectively). The complete and herbaceous vegetation only treatments modified the non-foliated crown radii very little when compared to the control. Removal of woody vegetation only, however, significantly increased non-foliated crown radii, particularly in the lower crown third. Mean bias for the overall equation was -0.01 m and the fitted equation explained 69% of the original variation.

Mean foliar volume was 232 m^3, while the mean proportion of total crown volume occupied by foliage was 0.90. A significant treatment effect was found in the SMC and PCT datasets, while neither SNC nor competing vegetation control had any effect on foliar volume after accounting for DBH, HT, and CR. For a given bole and crown size, pre-commercial and commercial thinning increased foliar volume by 41 and 20%, respectively. Foliar volume was modeled as a simple power function of DBH, HT and CR:

$$[3.7] \quad FV = 24.2969 * \frac{DBH}{HT}^{1.7911} * CR^{4.4125}$$

where FV is foliar volume (m^3) and the other variables have been defined above. The equation explained 76% of the original variation in FV and had a residual standard error of 0.13 m^3.

Discussion

Documented crown responses to silvicultural treatments have varied tremendously. A recent study on crown characteristics of juvenile loblolly pine (*Pinus taeda* L.) six years after thinning and fertilization concluded that branch and crown attributes had little response to these treatments (Yu *et al.*, 2003); however, Zhang *et al.* (2004) found very significant responses from the same species. In our study of plantation-grown Douglas-fir, crown structure was found to be highly responsive to intensive management, as well as to premature foliage loss under Swiss needle cast. Previously published equations describing Douglas-fir crown structure, however, performed remarkably well under conditions well beyond those under which they were originally parameterized, and little improvement was achieved by introducing alternative model forms. In general, crown structural attributes were readily predicted from DBH, HT, and HCB, because specific combinations of these variables reflect the silvicultural regime under which the tree was grown, and because the allometric relationships between these tree-level variables and the crown structural attributes are not severely altered by the treatments per se. The adequacy of DBH, HT, and HCB was consistent with results from many other studies of branch size and distribution coniferous species (Mäkinen and Colin, 1998; Meredieu *et al.*, 1998).

Number of branches within annual segment

The number of branches on an annual segment is largely influenced by segment length, or the height increment of the tree for that year (Mäkinen and Colin, 1999). The number of branches can be further modified by the competitive status of the tree - trees at the upper end of the diameter distribution yield a higher density of branches per unit length of segment, most likely due to increased levels of light (Maguire *et al.*, 1994). This also explains why the number of branches per segment slowly decreases with depth in the crown as was observed in this study. Mäkinen (1996) found that this trend may also be related to competition as the number of branches in the uppermost whorls, contrary to the older whorls, was not correlated with competition However, Wichmann (2002) found a strong positive relationship between competition and the number of branches in whorl five (from tree tip) in a recent study of Sitka spruce plantations (*Picea sitchensis* (Bong.) Carr). This result may underscore the need to distinguish between resource competition (procurement of light, water, nutrients) and interference competition (physical exclusion) at the branch-level (Wichmann, 2002). On the other hand, total tree size has generally been sufficient to describe past and present competitive interactions at the tree-level in shade-tolerant conifers (Colin *et al.*, 1992; Maguire *et al.*, 1994); hence, in our study, crown length and crown ratio served as useful surrogates for local stand density and competition.

The relationship between branch number and height increment of the stem may change with tree age. Mäkinen and Song (2002) found their model for number of branches was biased when applied to stands averaging 100 years older than the stands used in the construction of the model. Ishii and McDowell (2002) confirmed that branching density declined with age as epicormic branches become more prominent in older trees. Segment age, therefore, was included in the equation to account for this effect The age of the whorl was also expected to account for the inherent genetic component of the branch number per segment While there is relatively little genetic variation in the number of branches per whorl in Douglas-fir (e.g. St. Clair, 1994), significant differences among provenances and families within provenances have been found in several other species (Cannell, 1974; Li *et al.*, 1997; Xiao *et al.*, 2003). The significant effect of aspect on branch density per segment length on the analyzed Douglas-fir was contrary to results from Sitka spruce (Cochrane and Ford, 1978) and loblolly pine (Doruska and Burkhart, 1994). Douglas-fir trees in this study held fewer branches on the north side, probably due to the effect of light or temperature on branch initiation or survival. A similar but weak trend was reported for Sitka spruce in a more recent study (Wichmann, 2002).

At the stand-level, the number of branches has been found to increase with greater tree density within the stand (Kellomäki and Tuimala, 1981) and with greater site fertility (Lämmä *et al.*, 1990); however, other studies found that the number of branches per whorl was independent of tree size, site index, and stand density (Mäkinen, 1996; Briggs and Turnblom, 1999; Woollons *et al.*, 2002). Assuming that all these results hold across species, the differences in total number of branches per unit stand area must be attributable to one or both of the following: (1) different density of interwhorl branches; or (2) different summed crown lengths. Stand treatments such as thinning and fertilization have been shown to increase the number of branches on a tree (Brix and Ebell, 1969; Mäkinen *et al.*, 2001), the former through increasing crown length and the latter through increasing branch density per unit crown length. Consistent with the positive fertilization effect, Lämmä (1990) found that the number of branches on Scots pine (*Pinus sylvestris* L.) was positively correlated with foliar nitrogen concentration and fine soil fraction, but Mäkinen and Colin (1999) found that site index was not significant in their model for predicting the number of whorl branches in the same species. In our study, no explicit treatment or site effects were observed, which is most likely a result of each of these stand factors being well accounted for by segment length and location. The overall branch number model performed well given the wide range of stand conditions and ages.

The influence of other stand factors such as species composition and pruning, however, may not be fully captured in this model. Grotta *et al.* (2004) found that the number of Douglas-fir branches on the first 5.2 m of the stem was unaffected by either the proportion of red alder (*Alnus rubra* (Bong.)) in the stand. Garber and Maguire (in review), however, reported that both species composition and stand spacing influence the number of branches in a whorl for some *Pinus ponderosa* and *Pinus contorta* in central Oregon. Likewise, significant amounts of epicormic branching can occur after pruning Douglas-fir, which tends to become more severe as more live crown is removed, irrespective of stand density (Collier and Turnblom, 2001).

Maximum branch size within annual segment

In general, branch diameter growth begins rapidly, then decreases markedly as a negative exponential function of branch age (Kershaw *et al.*, 1990; Mäkinen, 1999). It has been estimated that half or more of the life of a branch can be spent without perceivable increment (Kershaw *et al.*, 1990; Mäkinen and Colin, 1999) due to self-shading (Brooks *et al.*, 1991; Sampson and Smith, 1993) and competition (Mäkinen, 1996). While branch size may be influenced by other factors such as growth hormones, water transport, and respiratory load, light has consistently been found to be the primary driving factor (Mäkinen, 2002). Hence, branch position within the crown was the best variable for describing variation in maximum branch size because it integrated the effects of branch age, light environment, and local competition. Maximum branch diameter followed a curvilinear relationship over distance from the tree tip, even prior to canopy closure, due to self-shading and shading by adjacent trees (Garber and Maguire, 2005b). This general relationship was further modified by tree social position and crown size; that is, a tree receiving more light tended to grow larger branches for a given depth into crown. In contrast to our results, Wichmann (2002) found that maximum branch diameter was greater on the south side of Sitka spruce stems growing in Denmark; however, this relationship has been found highly variable in other species (Grace *et al.*, 1999).

Annual variation in radial increment of branches has previously been shown commensurate with radial increment in the main stem (Cannell, 1974; St. Clair, 1994; Mäkinen, 1999), and this relationship was not noticeably changed by different stand conditions (Mäkinen and Colin, 1999). Maximum branch profiles should therefore be readily predictable from DBH and HT, and changes imposed by silvicultural treatments should be captured by tree-level characteristics. In fact, many studies have shown that additional variables describing tree-level competition have had little influence on describing branch size, at least in even-aged stands composed of a single species (Maguire *et al.* 1994, Mäkinen, 1996; Wichmann, 2002). In mixed-species and/or uneven-aged stands, however, response of branch diameters appears more complicated. In mixed-species spacing trials in central Oregon, Garber and Maguire (2005) have shown that the response of branch diameter was best accounted for by explicit treatment variables representing spacing and species composition, even after accounting for DBH, HT, and HCB. A similar conclusion was reached in our analysis because a significant treatment effect was detected in each of the field trials examined, despite accounting for the effects of treatments on stem diameter, tree height, and crown size directly by including them as predictor variables.

Fertilization and complete removal of vegetation were the only treatments that significantly influenced branch size in the upper crown, while the other treatments primarily influenced branches in the lower crown. Others have similarly concluded that branch size in the upper crown is influenced more by regional conditions, in contrast to the lower portion of the crown which responds more strongly to local stand conditions created by silvicultural treatments (Mäkinen, 1996). However, the influence of fertilization on coastal Douglas-fir in Oregon differed slightly from responses of Norway spruce in Finland (Mäkinen *et al.* 2001; 2004). Branch diameter growth of both newly initiated and older branches in Norway spruce was significantly increased with fertilization (Mäkinen *et al.* 2001). In our analysis of coastal Douglas-fir, diameter growth of relatively young branches in the upper crown accelerated in response to fertilization, but diameter growth of older branches in the lower crown decelerated slightly relative to the control trees. This shift in the pattern of branch diameter growth was most likely caused by the greater foliage biomass on branches of fertilized trees (Kershaw and Maguire, 1995), and the correspondingly greater shading of lower branches. Also contrary to our results for coastal Douglas-fir, Mäkinen *et al.* (2004) concluded that variables describing site fertility and fertilization regime had no significant effect on branch radial growth beyond that accounted for by responses of DBH, HT, and HCB.

Both pre-commercial (Ruha and Varmola, 1997; Fahlvik *et al.*, 2005) and commercial thinning (Gary, 1978; Medhurst and Beadle, 2001) have been shown to increase maximum branch size. Thinning allows branches in the lower parts of residual tree crown to receive more light (and other resources), stimulating growth and facilitating greater longevity (Brix, 1981; Mäkinen, 1999). The mean increase in branch size for the lower half of the crown between thinned and unthinned trees was 2.4 mm after pre-commercial thinning and 1.9 mm after commercial thinning.

These increases are much lower than values given in Ruha and Varmola (1997) as well as Gary (1978). This difference in degree of response may be attributable to the way that each investigator corrected for thinning effects on DBH, HT, and HCB, or to differences in thinning intensity, response time, or relative shade tolerance of the species. Most work on response of branch size to thinning has been done with shade-intolerant pine species (*Pinus spp.)*, but Douglas-fir is a more shade tolerant species and holds a great amount of leaf area for given tree size (DBH, height, crown length). Thus, Douglas-fir branches in the lower crown may not be able to respond as vigorously to thinning as the pine species because of greater levels of self-shading or the steeper changes in foliage attributes such as specific leaf area.

To our knowledge, the effects of defoliation and competing vegetation control on branch size have not been previously reported. The tendency of SNC to reduce branch size in the middle portion of the crown and increase branch size in the lower portion of the crown was indicative of the disease biology. Manter *et al.* (2003b) indicated that, within individual trees, fungal colonization was consistently higher in the upper portions of the crown where needle retention was reduced nearly 15% compared to a healthy tree. This loss of foliage in the top portion of the crown may have reduced self-shading and increased branch radial growth below this portion, leading to a peak in maximum branch diameter lower in the crown.

The reduction in maximum branch size in the upper crown of the trees with intensive vegetation control was not expected, but was consistent with narrower relative diameter of the upper stem under the same set of treatments (Weiskittel *et al.*, 2006b). This indicates that very intensive vegetation control may significantly alter tree allometry and growth dynamics. However, the results of intensive vegetation the effects of vegetation management agree with the finding of Campbell (1963) who indicated that Douglas fir growing faster in height tend to have smaller diameter branches after stem volume is accounted for.

Genetics and climate may modify maximum branch profiles, but were not accounted for in this study. Cannell and Bowler (1978) observed proportionally thicker branches on certain families Sitka spruce, and these differences were independent of tree growth vigor as measured by cumulative size of the main bole. Similarly, exposure to greater windspeeds increased mean branch diameter by 26% in radiata pine (*Pinus radiata* D. Don), an increase that was additional to the increase expected from the effects of wind on stem diameter and height (Watt *et al.*, 2005).

In short, responses of branch diameter to silvicultural treatments and environmental conditions can to a large extent be predicted from corresponding responses in DBH, HT, and HCB; that is, the treatments and conditions do not dramatically change the allometric relationships between tree dimensions and branch dimensions. However, some fine-tuning of branch diameter predictions may be possible or even necessary to account for effects of silvicultural treatments on wood volume, quality, or value.

Branch angle of insertation

The angle at which branches are attached to the stem has a major influence on crown form as well as wood quality. Using a computer model, Honda (1971) demonstrated that slight changes in branch angle that may appear to be trivial resulted in major changes in crown shape after being repeated over many orders of branching. Furthermore, branch angle can influence carbon allocation patterns within the crown as the caloric cost of horizontal branches is higher than that of vertical branches of the same length (Horn, 1971). On an individual tree, branch angle is largely determined by the effects of gravity and light availability. The initial branch angle of newly formed branches is determined by the angle of the lateral bud on the stem and elongating branches tend to orient according to the light source, gravitational fields, and the effects of growth regulators produced by the dominant leader. Hence, branch angles (from vertical) increase from the apex towards the base of the crown (Roeh and Maguire, 1997), due in part to gradients in growth regulators paralleling distance from the tree apex, in part to the increasing proportion of light received from the side vs. top, and in part to the increasing mass of foliage and lateral branches carried by the branch (Kershaw and Maguire, 1995).

The deflection of the branch tip due to gravity is largely a function of branch length, however, but also depends on the taper of the branch (Castera and Morlier, 1991). Branch angle, therefore, was concluded to be largely a function of location and size as corroborated by the behavior of coastal Douglas-fir.

Tree social position had a particularly strong influence on branch angle. Balsam fir (*Abies balsamea* (L.) P. Mill.) branches have been shown to become flatter with decreasing relative tree height in the stand (Gilmore and Seymour, 1997). We observed the same response in coastal Douglas-fir, with branch angle declining over increasing height to diameter ratio of the tree (and by inference the relative height of the tree in the stand). Of all the models developed in this study, the branch angle model had the poorest fit, indicating a high degree of variability in this crown structural response. In Scots pine relatively little within-whorl but considerable between-tree variation in branch angle has been observed (Duursma, 1998). Previous work in Douglas-fir has suggested that little of the variation in branch angle can be attributed to genetics variation, so this trait is not strongly heritable; however, branches in whorls formed at relatively young ages seemed to express family differences more strongly (St. Clair, 1994).

Stand density appeared to exert little control over branch angle in coastal Douglas-fir, consistent with previous work (e.g. Roeh and Maguire, 1997); however, it must be kept in mind that considerable stand density effects are implicit in diameter, height, and crown length of the tree. Field trials that have explicitly tested silvicultural treatments such as fertilization (Brix, 1981b; Mäkinen *et al.*, 2001) or thinning (Medhurst and Beadle, 2001) have suggested little influence of these treatments on branch angle. Although we observed no treatment effects on branch angle in coastal Douglas-fir, branch angle did increase slightly with increasing site index, as previously observed in this species (Roeh and Maguire 1997). This pattern may be a result of greater amounts of foliage on a given branch and the corresponding implications for source direction of light, gravitational effects on the greater mass, and gradients in growth regulators as discussed above in the case of increasing depth into the crown.

Crown profile and non-foliated crown core

Crown profile and non-foliated crown core were the two crown structural attributes most sensitive to silvicultural treatment and SNC disease severity. The sensitivity to direct manipulation of stand density was expected because inter-tree competition typically restricts crown expansion (Deleuze *et al.*, 1996). Maximal crown expansion requires rapid leader growth on both terminal and lateral shoots, with minimal interference from neighboring trees (Ottorini, 1991). The rate of branch elongation declines exponentially from the top whorl toward the base of the crown commensurate with reductions in light intensity (Schoettle and Smith, 1991). As a results, crown shape resembles a paraboloid rather than a cone (Mitchell, 1975). Branch length also tends to decrease along the stem to tip because of bud ageing, the increased distance for water and nutrient translocation, greater mechanical constraints, and more unfavorable carbon balance (Deleuze *et al.*, 1996).

Branch elongation varies greatly both within individual whorls (Mäkinen, 1999) and among years due to the fluctuations in the climate (Pensa and Jalkanen, 1999). However, in this study, between-year variation in branch length was much greater than the variation within an individual whorl. Schoettle and Smith (1991) found that branches on the south side of lodgepole pine crowns had a significantly greater increment in length than those on the north side. In contrast, the longest branch was most often found on the east and north-east side of Sitka spruce crowns (Wichmann 2002), and no differences were detected by aspect in first year growth of Scots pine branches (Duursma 1998). We found the longest branch most commonly on the north or north-west side of the crown in coastal Douglas-fir, leeward to the prevailing winter storms in western Oregon and Washington.

Important variables influencing crown profile were the ratio of DBH to HT and crown size. Generally, trees in lower social position tend to allocate proportionally more to branch elongation rather than height increment (Gilmore and Seymour, 1997), which is mostly capture in the combination of covariates used in this analysis. Similar to maximum branch profile, a treatment effect in each separate dataset was found for crown profile. Several key differences between maximum branch diameter profiles exist, suggesting a change in branch allometry with different treatments. First, fertilization had no significant effect on total crown profile, while thinning led to a reduction of crown radii in the lower crown. This differs slightly from the findings of both Brix (1981) as well as Madgwick (1986). Brix (1981) found that fertilization increased branch elongation at all crown levels in the first growing season following treatment and the effect lasted for 2-4 years, while thinning caused a decreased for 1-3 years and increase thereafter with an end result of no overall effect. Madgwick (1986), on the other hand, found that fertilized trees had a more rapid decrease in branch elongation with increasing depth in the crown, resulting in a narrower relative crown profile. The results of this study were more aligned with the findings of Madgwick (1986). Second, the influence of commercial thinning was different than the effect of pre-commercial thinning as the latter led to the more expected increase in lower crown radii. This difference may be attributable to the size and age of the trees at the time of treatment. Since the pre-commercial thinnings usually occur at an age when the canopy isn’t completely closed, the lower crowns of the residual trees haven’t been exposed to extensive shading and are more vigorous, which allows them to utilize the increased growing space more effectively than the commercially thinned residual trees. Third, there is very little relative change in crown profiles for heavily diseased trees when compared to healthy ones of the same size despite a rather significant change in their maximum branch diameter profiles. This may caused by branches at the lower crown levels using their photosynthates to refoliate rather than elongate since light is no longer a limiting factor. Finally, similar to the pre-commercial thinning, all levels of vegetation control caused an increase in crown radii throughout the crown despite little change in maximum branch profiles when compared to the control. This change is expected due to the increases in growing space caused by the vegetation control treatments.

In contrast to crown profile, the non-foliated crown core has rarely been quantified despite important implications for growth efficiency (Mitchell, 1975; Jack and Long, 1992), and despite its key role in understanding and simulating light interception (Brunner, 1998). In one class of growth and yield models, Douglas-fir crowns have been represented as a foliar shell (total crown radius –radius of non-foliated crown core) roughly equal in width to the last 5 years of branch and stem elongation (Mitchell, 1975). Five years is appealing as a limit because this period represents a reasonable average foliage longevity, net assimilation rates decline rapidly with needle age, and foliage older than five years comprises a very small portion of total foliage amount. Strictly interpreted, however, this approach would likely underestimate foliar volume of coastal Douglas-fir because higher order branches attached near the base of primary branches still contained considerable amounts of one- to five-year foliage and, hence, non-foliated crown cores occurred only in the lower 30% of some larger crowns. Further, various stand factors significantly modified the profile even after accounting for changes in DBH, HT, and HCB. In contrast to crown profile, the combination of fertilization and commercial thinning had a greater effect on the size of the non-foliated crown core than the individual treatments by themselves. Although fertilization has been reported to decrease needle longevity because of greater rates of self-shading (e.g. Balster and Marshall, 2000), it can significantly increase branch sapwood permeability in lower branches (Amponsah *et al.*, 2004), which may allow a longer foliated branch length to be maintained for a longer period of time, particularly when light conditions are significantly improved by thinning. The overall influence of fertilization on both crown profile and non-foliated crown core, however, resulted in little change in the foliated crown radius throughout the crown, consistent with the results of Balster and Marshall (2000). Second, residual trees in pre-commercially thinned stands were able to maintain longer foliated branch lengths throughout the crown compared to the control, but trees in commercially thinned stands had non-foliated crown cores quite similar to the control trees. This again is likely a function of stand age and the degree of canopy closure prior to the thinning treatment. Although the effects of SNC and vegetation management had a significant effect on the non-foliated crown core, there was relatively little change for a given tree size. The complete control of woody vegetation, however, significantly increased non-foliated crown core, particularly in the lower portion of the crown when compared to the other treatments.

Pre-commercial and commercial thinning were the only silvicultural treatments that significantly increased foliar volume. The change in crown volume following thinning has largely been attributed to greater light availability lower in the crown and a corresponding increase in branch longevity and crown length (Brix, 1981b). However, the increase we observed in coastal Douglas-fir accounted for the increase associated with thinning responses of diameter, height, and crown length. Hence, other factors such as wider crown profile and smaller non-foliated core were important factors influencing crown structural responses to thinning.

The mean ratio of foliar to total crown volume calculated in coastal Douglas-fir was significantly higher than values reported for older (66- to 134-yr-old) conifers in Utah (Jack and Long 1992). The latter conifers included both shade tolerant and intolerant species with a mean ratio of foliar volume to total crown volume of 0.3 to 0.5 (Jack and Long, 1992). Differences in site conditions, species, or stand age probably contribute to these relatively low ratios. The mean breast height age for our coastal Douglas-fir was 15 years, or young enough to have crown volumes composed primarily of fully foliated branches.

Conclusion

All the stand factors examined in this study, which included fertilization, pre-commercial thinning, commercial thinning, extended defoliation caused by a foliar disease, and various levels of vegetation management, had a significant effect on key crown structural attributes above and beyond changes in DBH, HT, and HCB. The most sensitive crown structural features were maximum branch size, crown profile, and non-foliated crown core. The number of branches held by annual segments of the main stem and the angle of branch attachment were not influenced by silvicultural treatments or disease severity after accounting for size and location in the stem. Silvicultural treatments affected primarily the lower portion of the crown; however, both fertilization and complete removal of competing vegetation significantly influenced branch sizes in the upper crown. In addition, some of the changes in crown structural attributes induced by silvicultural treatments were highly dependent on the time since treatment, highlighting the variation in response time of crown structural attributes. Overall, models including only tree diameter, height, and crown length performed well across a very wide range in silvicultural regime, stand structure, and disease severity; hence, important crown attributes can be predicted to a degree of accuracy sufficient for most applications from standard tree measurements.

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Table 3.1. Attributes of the installations and plots sampled in 2002-2003 (SNC), and 2004 (PCT, SMC, VMRC).

Attribute	**Mean**	**Std. Dev.**	**Min**	**Max**
PCT ($n_{install}$ = 3, n_{plot} = 6)				
Total basal area (m^2 ha^{-1})	20.7	6.6	9.7	28.6
Douglas-fir quadratic mean diameter (cm)	20.4	4.6	14.4	26.3
Trees per ha	691.6	262.5	456.9	1111.5
Average breast-height age (year)	12.3	1.8	9.6	14.4
Site index	51.7	1.7	48.5	53.5
SMC ($n_{install}$ = 4, n_{plot} = 16)				
Total basal area (m^2 ha^{-1})	26.5	7.8	6.4	38.5
Douglas-fir quadratic mean diameter (cm)	23.5	5.5	11.9	33.7
Trees per ha	743.2	592.8	245.0	2800.5
Average breast-height age (year)	19.8	1.9	16.0	21.5
Site index	39.2	1.5	37.5	41.1
SNC ($n_{install}$ = 33)				
Total basal area (m^2 ha^{-1})	37.8	15.3	10.4	76.83
Douglas-fir quadratic mean diameter (cm)	29.9	10.6	11.4	53.49
Trees per ha	524.4	307.9	150.0	1222.6
Average breast-height age (year)	28.8	14.4	11.0	62.4
Site index	39.3	3.9	26.6	46.2
VMRC ($n_{install}$ = 2; n_{plot} = 10)				
Total basal area (m^2 ha^{-1})	14.9	5.0	2.7	24.84
Douglas-fir quadratic mean diameter (cm)	13.4	2.4	5.9	17.49
Trees per ha	1014.2	94.1	719.0	1101.0
Average breast-height age (year)	7.9	0.1	7.8	8.17
Site index	38.8	2.0	37.0	41.1
ALL				
Total basal area (m^2 ha^{-1})	21.0	15.2	0.6	76.86
Douglas-fir quadratic mean diameter (cm)	19.4	10.0	5.1	53.49
Trees per ha	763.5	500.0	150.0	2800.5
Average breast-height age (year)	15.0	11.9	7.8	62.4
Site index	38.8	4.4	26.3	53.5

Table 3.2. Attributes of 223 Douglas-fir sampled in 2002-2004 by dataset.

Attribute	Mean	Std. Dev.	Min	Max
		PCT (n_{tree} = 19)		
DBH (cm)	23.3	6.3	11.6	32.6
HT (m)	14.75	3.19	9.19	19.93
HCB (m)	2.14	2.15	0.30	6.80
		SMC (n_{tree} = 52)		
DBH (cm)	27.1	6.9	12.2	42.7
HT (m)	18.34	3.12	10.15	23.97
HCB (m)	6.01	3.47	0.20	12.58
		SNC (n_{tree} = 122)		
DBH (cm)	30.4	10.2	12.5	66.6
HT (m)	23.95	7.89	11.90	45.80
HCB (m)	10.02	5.83	0.50	28.33
		VMRC (n_{tree} = 30)		
DBH (cm)	14.8	2.9	9.8	21.2
HT (m)	10.55	1.62	7.46	14.67
HCB (m)	0.85	0.62	0.10	2.34
		ALL		
DBH (cm)	26.9	9.9	9.8	66.6
HT (m)	20.06	7.81	7.46	45.80
HCB (m)	7.18	5.83	0.10	28.33

Table 3.3. Equation form, parameter estimates, R^2, and residual standard error (RSE) for number of branches and maximum branch size. All parameters are significant at $\alpha = 0.1$.

Model	Equation form	R^2	RSE
1a, total number of live branches	$NB_L = 21.8035 * SEGAGE^{-0.3123} * SEGLEN^{0.1679} * SEGHT_{rel}^{0.4332} * SEGDINC^{0.2142}$ $* \exp(-0.1212 * SEGDINC) * CL^{0.4728}$	0.58	6.10
1b, total number of whorl branches	$NB_W = 8.9097 * SEGAGE^{-0.2199} * SEGLEN^{0.0402} * SEGHT_{rel}^{0.4080} * SEGDINC^{0.3218}$ $* \exp(-0.0600 * SEGDINC) * CR^{0.2377})$	0.36	1.70
1c, total number of interwhorl branches	$NB_I = 29.7614 * SEGAGE^{-0.4039} * SEGLEN^{0.4883} * SEGHT_{rel}^{0.3692} * SEGDINC^{0.3091}$ $* \exp(-0.2011 * SEGDINC) * CR^{0.2873} * CL^{0.4465}$	0.61	5.73
1d, total number of branches	$NB_{TOT} = 12.4144 * SEGLEN^{0.1693} * SEGHT_{rel}^{0.0954} * SEGDINC^{0.0856}$ $* \exp(-0.0478 * SEGDINC) * CR^{0.4021}$	0.55	6.36
2, maximum branch size	$BD_{max} = 0.6839 * DBH^{0.9142} \frac{1 - \sqrt{BHT_{rel}}}{1 - \sqrt{0.8934 * CR^{-0.0566}}}^{\left(\begin{array}{l} 0.8872 * \sqrt{BHT_{rel}} + 0.2244 * \exp(-\frac{DBH}{HT}) - 0.05895 * (Z * \frac{DBH}{HT}) \\ -0.2483 * \log(HCM) + 0.1988 * \log(CL) \end{array}\right)}$	0.80	4.45

Table 3.4. Equation form, parameter estimates, R^2, and residual standard error (RSE) for branch angle, total and foliated branch length and total and foliated crown radius. All parameters are significant at $\alpha = 0.1$.

Model	Equation form	R^2	RSE
3, branch angle	$BA = (92.2171 - 7.2944 * \frac{HT}{DBH}) * (1 - \exp(-0.1114 * BHT + 2.4781 * Z - 0.0683 * SI)^{(\exp(0.0146 * BD))}$	0.30	16.98
4, total branch length	$BL = (0.1444 * DINC^{0.3995}) * \exp(-0.0125 * DINC + 0.2007 * BHT_{rel}) * BD^{0.7068} * HCM^{-0.1229}$	0.66	0.33
5, non-foliated branch length	$NFBL = \frac{BL}{1 + \exp(-2.1105 + 0.0163 * BD - 0.1726 * BHT + 8.6618 * BHT_{rel} + 0.0622 * CL)}$	0.52	0.05
6, total crown radius	$CRD_{TOT} = 0.0703 * DBH^{0.9749} \frac{1 - \sqrt{BHT_{rel}}}{1 - \sqrt{0.8405 * CR^{0.1917}}}^{\left(\begin{array}{l} 0.3101 * \sqrt{BHT_{rel}} + 0.9574 * \exp(-\frac{DBH}{HT}) \\ + 0.1203 * (Z * \frac{DBH}{HT}) + 0.2541 * CR \\ - 0.0078 * CL \end{array}\right)}$	0.73	0.42
6, non-foliated crown radius	$CRD_{NFOL} = 0.1574 * DBH^{0.5331} \frac{1 - \sqrt{BHT_{rel}}}{1 - \sqrt{0.3445 * CR^{1.3567}}}^{\left(\begin{array}{l} 0.8872 * \sqrt{BHT_{rel}} - 0.6250 * \exp(-\frac{DBH}{HT}) + 0.1283 * (Z * \frac{DBH}{HT}) \\ - 0.05132 * CL + 2.2559 * CR - 0.0098 * HCM \end{array}\right)}$	0.69	0.15

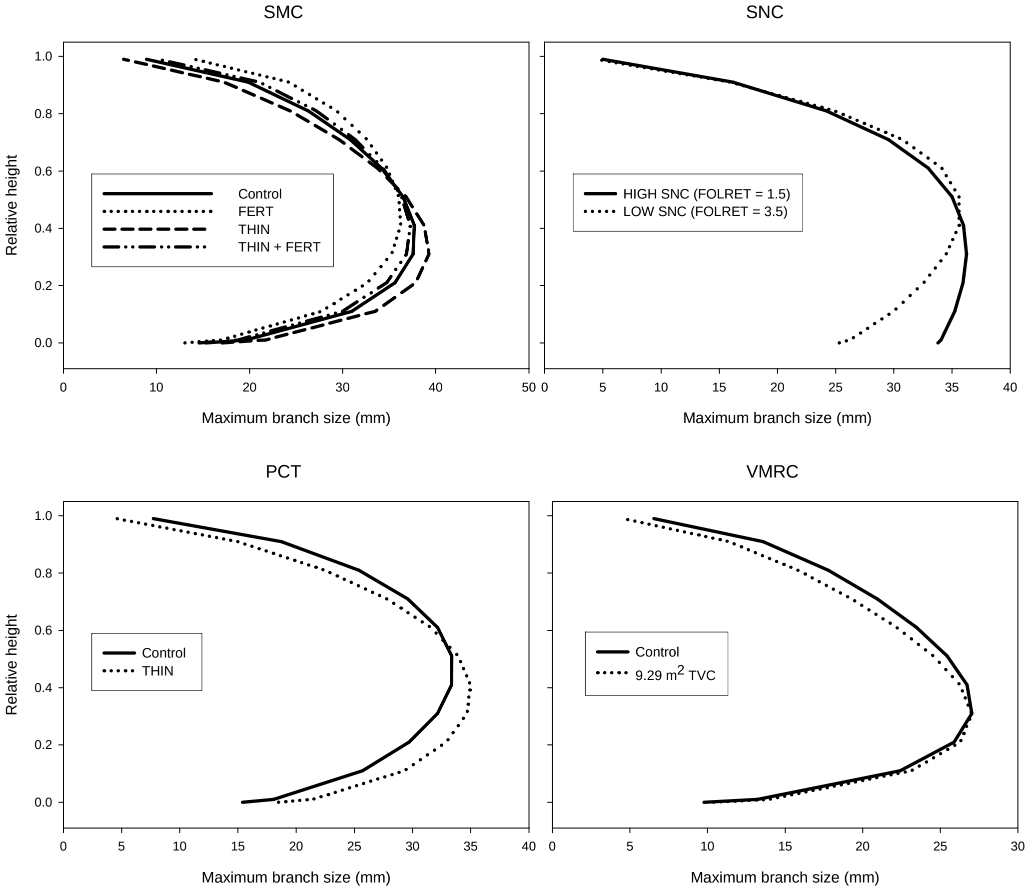

Figure 3.1. Trend in maximum branch diameter over relative height in the crown, estimated from equation [3.2] for the mean tree in each individual dataset. For the SMC graph, the time since treatment (TST) was assumed to be 3 years for both fertilization and thinning.

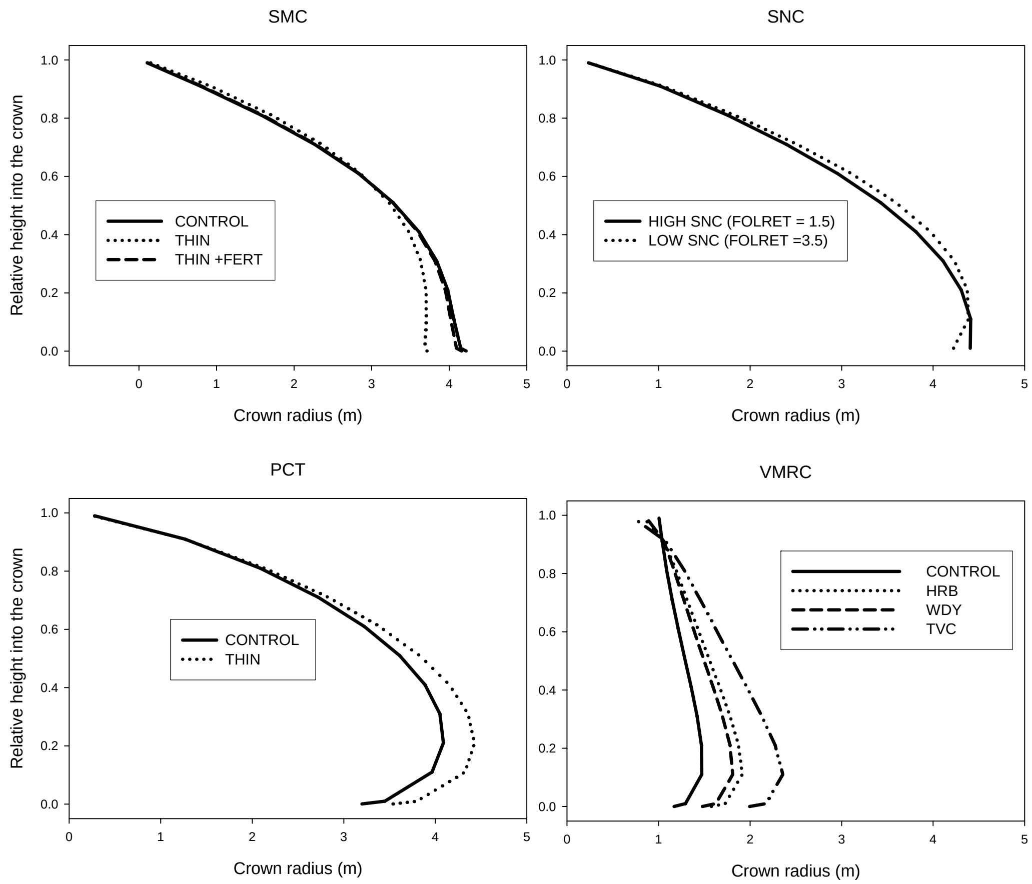

Figure 3.2. Trend in crown radius over relative height in the crown (crown profile) estimated from equation [3.6] for the mean tree in each individual dataset. For the SMC graph, the time since treatment was assumed to be 3 years.

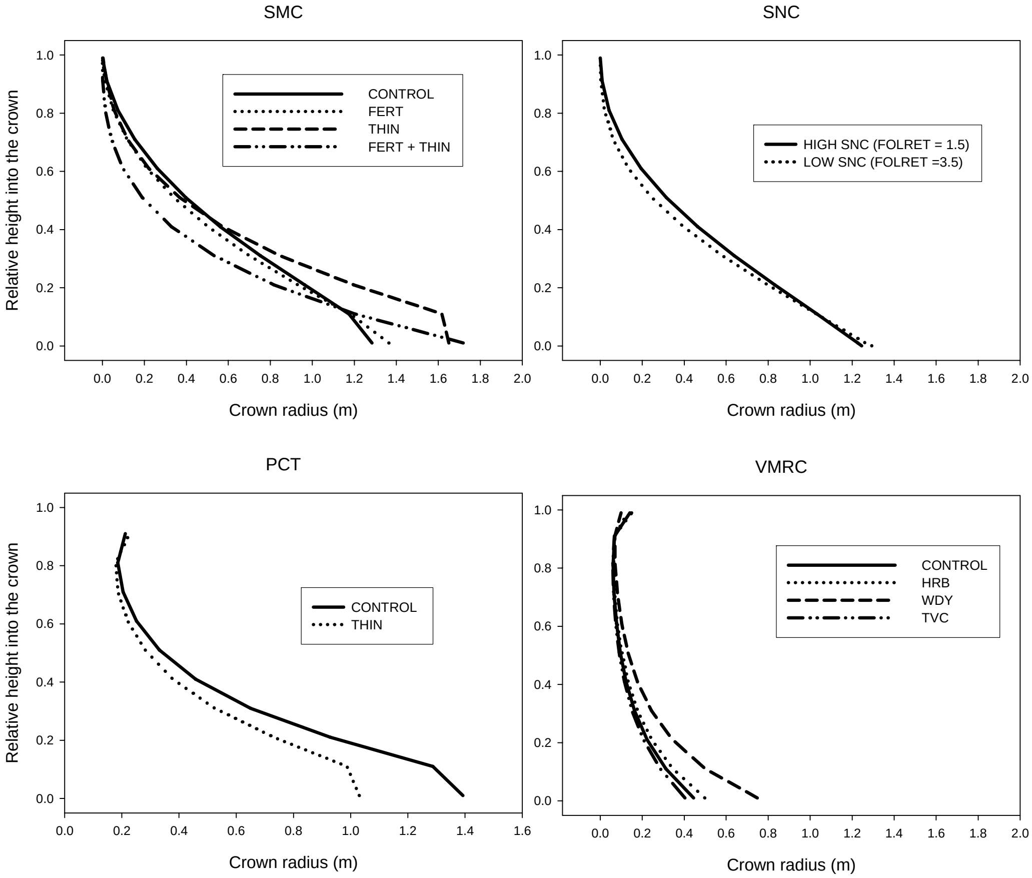

Figure 3.3. Non-foliated crown profile (unfoliated core of crown) estimated from equation [3.6] for the mean tree in each individual dataset.

CHAPTER 4: ANNUALIZED DIAMETER AND HEIGHT GROWTH EQUATIONS FOR PACIFIC NORTHWEST PLANTATION-GROWN DOUGLAS-FIR, WESTERN HEMLOCK, AND RED ALDER

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Abstract

Predicting the influence of intensive management and climate on tree growth through simulation requires a shorter time-step than currently employed by most regional models. Extensive plantation data sets in the Pacific Northwest exist, but have been collected on inconsistent remeasurement cycles varying from 2 to 12 years in length. This can make it quite difficult to fit growth models because interpolation is required or often, only measurement cycles equal to the length of the model time-step are used. This analysis utilized an innovative technique of Cao (2002; CJFR 32: 2051-2059) to estimate annualized diameter and height growth equations for pure plantation-grown Douglas-fir, western hemlock, and red alder. Cao's (2002) technique was statistically improved for all three species by the use of a multilevel mixed effects framework. Behavior of the models was consistent with biological expectations (i.e. parameter estimates are of the correct magnitude and sign). The random effects showed some correlation with key physiographic variables such as slope and aspect for Douglas-fir and red alder, but these relationships were nonexistent for western hemlock. Further, the random effects were more correlated with physiographic variables than actual climate or soils information. Long-term simulations on an independent dataset using these equations showed that multilevel mixed effects were more precise than those fitted with maximum likelihood, but the level of bias was comparable and even smaller

than an existing growth model with a longer time-step. These models will prove to be quite useful for understanding the interaction of climate and silviculture in the Pacific Northwest and refining the precision of future growth model projections.

Introduction

Over the last decade, rotation lengths in the Pacific Northwest (PNW) have significantly decreased and are currently ranging from 30 to 50 years for managed plantations (Adams *et al.*, 2005). Growth and yield models in the region, however, continue to use a 5-10 year time-step. With the shorter rotations, treatment windows for silvicultural activities such as fertilization, thinning, and pruning are also shortening, and are often less than five years, especially on higher sites. Likewise, these model time-step also make it difficult to forecast silvicultural treatment effects accurately or investigate the role of annual climate fluctuations on growth (e.g. Henning and Burk, 2004). For example, Johnson (2005) recently found a very wide range (1.3 – 2.3 fold difference) of predicted responses to thinning, fertilization, and the combination of these treatment using six commonly used PNW empirical growth models. These large differences among models can partially be attributed to their inability to capture the short-term stand dynamics following intensive treatment. As management practices continue to intensify and rotations become even shorter in this region, the need for annual diameter and height growth equations increases.

The primary difficulty in developing annual equations is that most permanent plots are remeasured on a 2-6 year cycle. Shorter measurement cycles are usually not favored because the effect of measurement error can greatly bias results (e.g. Snowdon, 1987). McDill and Amateis (1993) evaluated several different methods to fit annual growth models from periodic measurement and found two interpolation methods to work better than averaging. Cao *et al.* (2002) generalized these conclusions and recently presented a method to simultaneously develop annual individual-tree diameter and height growth and survival equations from periodic measurements (Cao, 2004). This method has been successfully used for European beech [*Fagus sylvatica* L.] (Nord-Larsen, 2006), loblolly pine [*Pinus taeda* L.] (Cao, 2000; Cao *et al.*, 2002; Cao, 2004), longleaf pine [*Pinus palustris* Mill.] (Cao *et al.*, 2002), Norway spruce [*Picea abies* (L.) H. Karst] (Johannsen, 1999), and oak [*Quercus robur* L. and *Quercus petraea* L.] (Johannsen, 1999). However, these analyses have not accounted for the hierarchical and repeated measurements nature of typical growth data, for which mixed-effects models have proven to be quite useful (e.g. Hall and Bailey, 2001). An additional benefit of this approach is partitioning out the sources of variation and allowing the influence of covariates not typically included in these models to be evaluated in a parsimonious manner.

The primary objective of this study was to develop annualized diameter and height growth equations from periodic measurements of Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], western hemlock [*Tsuga heterophylla* (Raf.) Sarg], and red alder [*Alnus rubra* Bong.] grown in pure, unmanaged plantations. In addition, a comparison of models fit with simple maximum likelihood (ML) and multilevel mixed effects (MLME) was made. Finally, the random effects from the MLME approach were used to identify influential factors that govern site to site variation in growth.

Methods

Data Sets

Data for this study came from existing permanent plots established by three PNW research cooperatives. The Douglas-fir growth data were from the Stand Management Cooperative (SMC; University of Washington) and Swiss Needle Cast Cooperative (SNCC; Oregon State University), while western hemlock data were derived solely from the SMC database. The red alder growth data came from the SMC and the Hardwood Silviculture Cooperative (HSC; Oregon State University). In all cases, only pure, healthy control plots with a sufficient number of breast-height age, height (HT), and height to crown base (HCB) measurements were used. A brief description of each database is given below.

Stand Management Cooperative (SMC)

Since being established in the mid-1980's, the SMC has maintained a database on 435 installations in Vancouver Island, British Columbia and west of the Cascade crest in Washington and Oregon. The installations are primarily in Douglas-fir plantations, but also include a limited number of western hemlock and red alder plantations. The Douglas-fir and western hemlock growth data used in this study come from the Type I and III installations. Type I installations were established as square 0.2-ha plots in existing plantations and have received intensive silvicultural regimes since plot establishment in the 1980s. The Type III installations are 30 plantations established in the 1990s and have at least five square 0.2-ha plots with varying stocking levels, ranging from 247 to 3048 trees per ha. In addition to these installations, four western hemlock installations established in 1980 and part of the Regional Forest Nutrition Research Project (RFNRP; University of Washington) Phase IV project on fertilizing precommercially thinned plantations were also included in the analysis. The red alder data comes from two installations that were part of a Department of Energy project and were established in 1980 to examine the implications of whole tree harvesting.

Swiss Needle Cast Cooperative (SNCC)

The SNCC has a total of 76 permanent installations (one 0.08 ha plot per installation) established in relatively young (10-30-years old) Douglas-fir plantations with varying levels of SNC in 1998 throughout the northern Oregon Coast Range (Maguire *et al.*, 2002). In addition, there are 22 younger plantations (10-15-years old in 1998) and 30 older plantations (30-60-years old in 2002) with a precommercial thinning installation (two 0.08 ha plots per installation; thinned to 494 trees per ha + control) and commercial thinning installation (two 0.2 ha plots per installation; thinned + control; (Mainwaring *et al.*, 2005), respectively. Each plot has been annually assessed for SNC severity and measured for growth every two years. Preliminary analysis found very little bias across a range of SNC severities with a fitted regional growth equation and hence, all control plots were included in the final analysis.

Hardwood Silviculture Cooperative (HSC)

The HSC was first established in 1988 and maintains the oldest and most extensive red alder growth database in existence. The growth data used in this analysis came from 26 Type 2 installations testing various management options from Coos Bay, Oregon to Vancouver Island, British Columbia that were established between 1989 and 1997. Each installation has at least five 0.13 ha plots planted with initial densities ranging from 254 to 3048 trees per ha across a range of site fertility classes.

Data analysis

HT and HCB were estimated for trees where these attributes were missing with a model fit by species. Preliminary analysis indicated that a mixed models framework similar to the one described by Robinson and Wykoff (2004) significantly improved imputation. The models were of the following form:

[4.1] $HT = 1.37 + \exp(\beta_{10} + b_{1i} + b_{1j} + \beta_{11}DBH^{\beta_{12}}) + \varepsilon_1$

[4.2] $HCB = HT / [1 + \exp(\beta_{20} + b_{2i} + b_{2j} + \beta_{21}HT + \beta_{22}CCFL + \beta_{23}\log(SBA) + \beta_{24}(DBH/HT) + \beta_{25}(SI - 1.37))] + \varepsilon_2$

where DBH is diameter at breast height (1.37 m), CCFL is crown competition factor in trees of larger diameter than subject tree (Krajicek *et al.*, 1961; Hann *et al.*, 2003), SBA is stand basal area per hectare, SI is species-specific site index, β_{ij}'s are model fixed parameters, b_{1i}, b_{1j}, b_{2i}, and b_{2j}, are random intercept terms for the *i*th installation and *j*th plot, and ε_1 and ε_2 are within plot random error terms. All random effects were tested for significance with likelihood ratio tests at significance level of 0.05 (Pinherio and Bates, 2000). These equations were then applied to trees with missing HT and HCB by calculating best linear unbiased predictors from the subsample of trees with HT and HCB for each installation and plot. Crown ratio (CR) was then calculated as 1 – HCB/HT.

Varying definitions of crown base were used in each of the databases, even for a given species. For example, Douglas-fir HCB in the SMC database was defined as the lowest contiguous whorl of at least two live branches (compacted crown ratio), while HCB in the SNCC database was defined as the lowest live branch (uncompacted crown ratio). After predicting missing CR's from [2], all plots where compacted crown ratio was measured and predicted were converted to uncompacted crown ratio using the equations of Monleon *et al.* (2004).

In addition to SBA and CR, several other growth predictor variables were derived including SI, basal area in trees with a DBH larger than the subject tree (BAL), and the percent crown closure of the plot at the tip of the subject tree (CCH) (Hann *et al.*, 2003). SI values were determined using equations that require breast height age and top height for the 100 largest-diameter trees per ha of the target species. SI at 50-yr base age for Douglas-fir was calculated by solving Bruce's (1981) dominant height equation. The Bonner *et al.* (1995) equation was used for western hemlock. The three most prevalent red alder site index equations were tested to ascertain the best results because no previous growth equation existed prior. The equation of Nigh and Courtin (1998) was used in the final equations because it was base age 25-yr and preliminary analysis suggested they have higher correlation with growth than equations presented in Harrington (1986) and Harrington and Curtis (1986).

SBA was determined by summing tree cross-sectional areas at breast height on the plot of interest and multiplying by the plot’s expansion factor. Basal area in larger trees (BAL) was calculated for each tree by summing tree cross-sectional areas at breast height of all trees on the plot of interest that have larger DBH than the subject tree and multiplying by the tree’s expansion factor. For each tree, CCH was calculated by estimating crown widths for all other trees on the plot at the height of the subject tree. Crown profile equations presented in Hann (1999), Marshall *et al.* (2003), and Hann (1997) for Douglas-fir, western hemlock, and red alder, respectively, were used to calculate crown width, which was converted to crown area by using the formula for the area of a circle. The crown areas were multiplied by the tree expansion factor, summed across all sample trees on the plot with a height greater than the height of the sample tree, and expressed as a percentage of ground area covered. This procedure was repeated for all trees on the plot.

Diameter growth

After evaluating several parameterizations, diameter growth was modeling using the form suggested by Hann *et al.* 2003:

$$[4.3]\ \Delta DBH = \boldsymbol{e}\left(\begin{array}{l}\beta_{30}+\beta_{31}\log(\mathrm{DBH}+1)+\beta_{32}\mathrm{DBH}^{2}+\beta_{33}\log\left(\dfrac{\mathrm{UCR}+0.2}{1.2}\right)+\beta_{34}\log(\mathrm{SI}\text{-}1.37)\\ +\beta_{35}\dfrac{\mathrm{BAL}^{2}}{\log(\mathrm{DBH}+5)}+\beta_{36}\sqrt{\mathrm{SBA}}+\beta_{37}\mathrm{I}_{\mathrm{CR}}\end{array}\right)+\varepsilon_{3}$$

where ΔDBH is the annual diameter growth in cm, UCR is uncompacted crown ratio, I_{CR} is an indicator crown ratio measurement (1 if CR wasn't measured, 0 otherwise), the β_i's are parameters to be estimated from the data using the method of Cao (2000), $\varepsilon_3 \sim N(0, \sigma_3^2)$, and all other variables are defined above.

Height growth

Height growth was modeled as the product of potential height growth, the theoretical estimate of height growth of a dominant tree of that size (Wensel *et al.*, 1987), and a height growth modifier:

[4.4] $\Delta HT = PHG \times HMOD$

where ΔHT is the annual height growth, PHG is potential height growth, and HMOD is the height growth modifier. PHG was calculated as follows:

[4.5] $PHG = f_{SPP}(SI_{SPP}, GEA + 1.0) - HT$

where f_{SPP} is the dominant height growth equation for species, GEA is the calculated growth effective age (Hann and Ritchie, 1988). Dominant height growth equations for the three species were Bruce's (1981), Bonner *et al.*'s (1995), and Nigh and Courtin (1998) for Douglas-fir, western hemlock, and red alder, respectively. GEA is defined as the age of a dominant tree with the same height and site as the tree of interest:

[4.6] $GEA = f_{SPP}^{-1}(SI_{SPP}, HT)$.

The following modifier equation form was used for each species (Hann and Ritchie 1988; Hann *et al.* 2003):

$$[4.7]\quad \mathrm{HMOD} = \beta_{70}\left[\begin{array}{l} \beta_{71}\, e^{\beta_{72}\,\mathrm{CCH}} + (e^{\beta_{73}\sqrt{\mathrm{CCH}}} - \beta_{71}\, e^{\beta_{72}\mathrm{CCH}}) \\ e^{-\beta_{76}(1-\mathrm{UCR})^2}\; e^{\beta_{75}\sqrt{\mathrm{CCH}}} \end{array}\right] + \varepsilon_7$$

where the β_i's are parameters to be estimated from the data using the iterative method of Cao (2000), $\varepsilon_7 \sim N(0, \sigma_7^2)$, and all other variables are defined above.

Initial parameter estimates were obtained using SAS v8.2 PROC MODEL assuming that tree and stand variable were constant during the period. Final equations were fitted in SPLUS v6.2 with tree and stand variables being assumed to linearly change during the growth period. Also, it was assumed that there was no dependence between the equations (seemingly unrelated regression would have significantly reduced the data sets because diameter and height growth were not measured on all plot trees). The response variables were the diameter and height growth during the intervening growth period (1-15 years), while the right side of the equation was predicted growth based on the updated parameter estimates. In order to get parameter estimates for annual growth, the right side was made a function that calculates the predicted growth for the period by summing up the annual growth estimates using the updated parameter estimates and, for simplicity, assuming a linear change in the independent variables during the course of the growth period (Appendix A). Given the relatively short remeasurement period of most of the plots (2-4 years), a linear change was deemed appropriate for this analysis. Further, preliminary analysis suggested little difference in the prediction bias achieved using different techniques for estimating the change in the independent variables. The equations were fitted with and without multilevel random intercept. When random effects were estimated it was done at two levels, namely installation and plot. In this case, ε_3 and ε_7 represent the within tree error (i.e. multiple measurements on a tree). When heteroskedasticity was detected in the residual plots, a power variance function of the initial diameter and crown ratio was incorporated into the fitting function for the diameter and height growth equations, respectively. The power variance function in this analysis was defined as $s^2(v) = |v|^{(2x)}$, where v is the variance covariate, $s^2(v)$ is the variance function evaluated at v, and x is the variance function coefficient. In addition, a significant amount of autocorrelation was detected in the residuals of the diameter growth equation and a continuous first-order autoregressive error structure as function of initial diameter was added to appropriately estimate parameter standard errors (Chi and Reinsel, 1989). The variation attributed to the three levels examined in this study (i.e. between installation, between plot, within tree) were analyzed using SAS PROC VARCOMP.

The final equations were evaluated by comparing mean bias (observed – predicted), mean square error, and a fit index, which is analogous to R^2 in linear regression. Although the use of R^2 in MLME has been debated, a generalized form of it was used in this analysis (Xu, 2003). This measure effectively partitioned the variance explained by the fixed effects and the random effects at each level. When MLME was used, parameters β_{30} and β_{70} were made random because preliminary analysis suggested them to be the most variable. Parameter estimates, variance functions, correlation structures, and random effects were evaluated using likelihood ratio tests at a significance level of 0.05 (Pinherio and Bates, 2000).

Following model fitting, the random coefficients were extracted for the installation level and were regressed on physiographic (longitude, latitude, elevation, slope, aspect), soil (depth, texture, rock content, water holding capacity), and mean climate variables (temperature, precipitation, vapor pressure deficit) to identify influential factors on growth variation. Slope and aspect were transformed using the suggestions of Stage (1976), while soil water holding capacity was estimated as outlined in Schwalm and Ek (2004). Mean climate variables were derived from 23-year daily weather records obtained from DAYMET (http://www.daymet.org). A more traditional analysis would have included these variables directly into the fitted equation such as those exemplified in Wykoff *et al.* (1982), but this often leads to model over parameterization. In this analysis, assessing the influence of these variables on the random effects was more justified because of the marginal effect of these variables and it was a more parsimonious solution

Validation of models and fitting technique

Model validation is often an important aspect of constructing a new model, but is often hampered by the lack of large, independent datasets. This remains true for the western hemlock and red alder equations developed in this study. For Douglas-fir, the diameter and height growth equations were paired with previously developed individual-tree static height to crown base (Hann *et al.*, 2003) and mortality (Flewelling and Monserud, 2002) equations. This set of equations was used to predict 12 to 16 years of growth and mortality on the control plots on 12 SMC installations, which were not used during model fitting. The installations were evenly distributed through the Pacific Northwest with initial breast-height age ranging from 23.5 to 46.5 and site index varied from 29.3 to 48.0 m at base age 50. For comparison, the SMC version of the ORegon Growth ANalysis and projectiON (ORGANON; Hann, 2005) model was also used to simulate growth on these plots. ORGANON uses a 5-year time-step so linear interpolation was used to growth for remeasurement periods that did not cover this time-step. Mean bias (observed – predicted), % bias, and mean square error (MSE) were estimated for every simulation.

Results

Diameter growth

A large range of tree sizes were available for the Douglas-fir and red alder diameter growth model, while the western hemlock data were more limited (Table 4.1). The models fit well with R^2 falling between 0.66 and 0.88 for the fixed effects. Likelihood was significantly improved with a variance power function on DBH ($p<0.0001$), a first-order autoregressive error structure ($p<0.0001$), and the inclusion of multilevel mixed effects ($p<0.0001$) in each of the three species. The parameter estimates were consistent with biological expectations; that is, they of the correct sign and approximate magnitude (Table 4.2). Diameter growth increased with initial diameter (curvilinearly), crown ratio, and site index, but decreased with basal area in larger trees and stand basal area (Figure 4.1). For a site index of 35.0 m and a basal area of 10 m^2 ha^{-1}, diameter growth peaked at a diameter of 30.5, 25.0, and 14.8 cm for Douglas-fir, western hemlock, and red alder, respectively. Western hemlock and red alder were more responsive to increasing crown ratio ($\beta_{33}>1.0$). Likewise, red alder diameter growth increased more rapidly with site index ($\beta_{34}>1.0$). When compared to Douglas-fir and western hemlock, the parameter estimates for BAL and SBA (β_{35} and β_{36}) for red alder suggested it was more responsive to symmetrical and asymmetrical competition.

Height growth

Similar to diameter growth, a large range of tree sizes were available for the Douglas-fir and red alder height growth model, while the western hemlock was quite limited. In general, the parameter estimates were consistent with biological expectations (Table 4.4; Figure 4.2). The model fits were adequate as R^2 values were between 0.53 and 0.85 for the fixed effects. Likelihood was significantly improved with a variance power function on CR ($p<0.0001$) and the inclusion of multilevel mixed effects ($p<0.0001$), while a first-order autoregressive error structure was not significant.

For red alder and western hemlock, compacted crown ratio provided a significantly better fit than uncompacted crown ratio and final fits were consequently fit using this definition. However, uncompacted crown ratio was significantly better than compacted crown ratio for Douglas-fir. The asymptote (β_{70}) for western hemlock was not significantly different than one regardless of the estimation procedure. In contrast, the asymptote was significantly less than one in alder and much greater than one in Douglas-fir (Table 4.4). All species showed strong height growth responses to crown ratio. Douglas-fir exhibited slow height growth below a crown ratio of 0.3 and dramatically increased above. In contrast, Red alder and western hemlock were responsive across the range of crown ratio.

The pattern across CCH was strongly dependent on CR for western hemlock and red alder but not for Douglas-fir.

Analysis of random effects

Diameter growth

The installation level random effect was more variable than the plot level random effect and contributed to 5-15% of the variation in diameter growth in the three species. In contrast, the plot to plot variation was 1-2%. This was especially the case in red alder**.** Regressing the installation random effects on physiographic features uncovered a few interesting relationships. The intercept of the Douglas-fir diameter growth equation showed a significant trend with annual precipitation (PRCP), elevation (ELEV), slope (%SLOPE), and aspect (Table 4.5). Parameter estimates suggested diameter growth peaked on north-east facing slopes and at 220 cm of precipitation. The intercept of the red alder equation was related to elevation, slope, and aspect. The parameter estimates indicate that the intercept tends to be highest on north-east facing areas. Western hemlock showed no significant relationship with any physiographic variables.

Height growth

Similar to diameter growth, installation-level random effect contributed to 5-20% of the observed variation in height growth while the plot-level random effect account for 1-2% of the additional variation. The installation random effects for height growth were highly variable and provided fewer meaningful relationships with physiographic features than the diameter growth random effects. The Douglas-fir equation showed a significant relationship with slope, aspect, and percent rock content in the soil B horizon (%ROCK.B; Table 4.5). The parameter estimates indicated that asymptote of the height growth modifier was greatest on north-west facing sites. The asymptote of the red alder equation was related to slope, aspect, and elevation. The parameter estimates indicated that the asymptote was highest on east facing slopes. Western hemlock showed no significant relationship with any physiographic variables.

Validation of models and fitting technique

Mean bias, percent bias, and mean square error for the three equations were within reason and are given in Table 6. The equations fitted with MLME performed significantly better than the ML equations or MLME with predicted random effects. There were some trends in the residuals using ML, while no obvious trends were present in the MLME simulations (Figure 4.3). In comparison to a model with a longer time-step, the biases achieved with the equations presented in this analysis were similar in magnitude and actually smaller than ORGANON's.

Discussion

The procedure of Cao (2002) used here worked well for the development of annual diameter and height growth equations in three primary commercial species of the PNW. Despite its complexity, it has the advantage of using data across many remeasurement intervals without additional manipulation of the dependent variable (such as linear interpolation) to achieve a desired time-step. Further, the use of MLME significantly improved the performance of this technique.

The diameter growth models presented for Douglas-fir and western hemlock and height growth models for Douglas-fir fit well and were generally consistent with observed growth patterns. The parameter estimates for Douglas-fir and, in part, western hemlock were consistent with Hann *et al.* (2003) fits. The western hemlock equation presented here showed a significant effect of site index and the negative influence of predicted crown ratio not seen by Hann *et al.* (2003).

The alder models and the height growth model for western hemlock did not result in fits as good as Douglas-fir. Two reasons were identified to explain this. First, the Douglas-fir data sets were fairly extensive, covering a wide range of growing conditions found in commercial plantations in the region. In contrast, the hemlock and alder data sets were less extensive and did not cover the larger, older end of plantation growing conditions. In particular, the current alder datasets have limited data from late in the stem exclusion stage of stand development (Oliver and Larson, 1996) where density-related effects appear. Second, Douglas-fir growth patterns are well-known and, hence, model forms are well-established. Model forms for other species have been borrowed from Douglas-fir, but, there is evidence that these forms may not be adequate for other species (Hann and Hanus, 2002; Hann *et al.*, 2003). Moreover, it is known that there are density affects on dominant height growth (e.g. Flewelling *et al.*, 2001; Bluhm and Hibbs, 2006) not accounted for in the dominant height growth curves used in this analysis. Several attempts were made to address this; however, the residuals showed no bias with stand density or other variables of importance. These alder equations, however, are the first individual-tree diameter and height growth models for plantation-grown red alder that have been published to our knowledge.

Random effects have been previously demonstrated to reduce the impact of autocorrelation in longitudinal forestry data: tree growth (Gregoire *et al.*, 1995; Fang and Bailey, 2001), site index (Biging, 1985), stem profile (Gregoire and Schabenberger, 1996; Garber and Maguire, 2003), and branch architecture (Garber and Maguire, 2005b). While random effects were successful in reducing the effect of autocorrelation in the height growth equations, they were not sufficient in accounting for the autocorrelation present within the diameter growth data. The addition of the first-order autoregressive process was necessary and successful at reducing the impact of autocorrelation in testing covariates. The combination of random effects and a continuous autoregressive process was also necessary in reducing the impact of autocorrelation in fitting taper equations in small plantation trees (Garber and Maguire, 2003). Although a poor model fit may be the cause of autocorrelation, the fits presented were quite high and other model forms did not perform any better.

Although the primary purpose of the present study was to further develop a process for fitting annualized growth equations and understand influence of physiographic features on growth, these equations are also intended for future use in growth models, especially in light of the absence of such equations for red alder. There is little information on the performance of the fixed-effects parameter estimates from mixed models with regard to prediction. Some evidence suggests that height predictions from mixed effects height-diameter models using the best linear unbiased predictor techniques performed more poorly than regionally and locally developed models when extended to plots with no prior measurements (Monleon *et al.*, 2004). Several recent growth equations, presumably to be used for prediction, have been parameterized using mixed-effects models with no assessment of their performance on an independent dataset in comparison to ordinary least squares (e.g. Fahlvik *et al.*, 2005; Nothdurft *et al.*, 2006). This analysis indicated that diameter and height growth equations fitted with MLME performed significantly better on an independent dataset than similar equations fitted with ML. This was especially true for the height growth model. The height growth modifier augments the expected height growth for a tree, assuming it was a dominant tree, based on its crown size (CR) and crown position (CCH). The expected height growth is dependent on site index which has error associated with its estimation. A random effect on the modifier asymptote may account for some of this error possibly leading to better parameter estimates. Although not as straight forward, an analogous process may occur when fitting the diameter growth model with a random intercept. An additional use of the multilevel mixed-effects technique is for developing site-specific equations using information from other sites and partitioning the variation in growth. Using the predicted random effect with the MLME growth equation parameters, however, resulted in a bias that was between that achieved by the MLME and ML parameters.

An ancillary advantage of the mixed effects model approach was the ability to assess the variation in the installation effects across physiographic, soils, and climate factors. Nord-Larsen (2006) performed a similar type of analysis for European beech, but used an indicator variables for each installation. These relationships were limited for Douglas-fir and red alder, while non-existent for western hemlock. These relationships suggested that diameter and height growth were significantly influenced by installation slope and aspect. Surprisingly, these variables often showed a higher correlation with the random effects than actual climatic or soil variables. Both Douglas-fir and red alder showed the highest growth on north-facing aspects. The results for Douglas-fir are consistent with Hill *et al.* (1948) and McArdle *et al.* (1949) who also found north-facing slopes to be superior for productivity. Although the effects of soil water holding capacity (Hill *et al.*, 1948) and parent material (Carmean, 1954; Steinbrenner, 1981) on height growth have also been reported for Douglas–fir in this region, no significant influence of either factor was found in this analysis. The lack of a significant influence of physiographic effects on western hemlock growth is perplexing. This trend still occurs after the 7 plantation installations used in this analysis are combined with information from 48 other installations established in pure, natural stands. These results are in contrast to those of Steinbrenner (1981) who found trends in western hemlock dominant height growth to be adequately explained ($R^2 > 0.8$) by three variables, namely depth of the A soil horizon, soil texture, and elevation. The negative effects of increasing elevation and slope on red alder growth as well as growth being the slowest on south-facing aspects, however, were all similar with the results of Harrington (1986). Overall, physiographic variables were more powerful descriptors of variation in growth than soils or climate information, but this may be an artifact of using regional soils or climate data rather than site-specific.

Conclusion

The technique presented by Cao (2000) provided a good parameter estimation procedure for annualized equations for both a well-modeled (Douglas-fir) and lesser-modeled species (red alder) in the PNW. It permitted the inclusion of larger and unmanipulated datasets for the development of diameter and height growth equations across a range of remeasurement periods. The inclusion of multilevel mixed effects improved the model fits, but the random effects had a limited relationship with physiographic features, mean climate, and soil properties. Compared to equations fitted with maximum likelihood, prediction biases on an independent dataset were, however, lowest for the multilevel mixed effect parameter estimates. Annualized equations are advantageous in that they provide a finer resolution of stand dynamics over time needed for the making decisions on the timing and degree of silvicultural intervention in high-intensity plantation forestry, but achieve a similar degree of bias as models with a longer time-step. The finer temporal resolution of the annualized equations also allows for the assessment of annual climate variations on individual tree and stand growth dynamics, which can be effectively achieved by hybridization of these equations with a physiological model (e.g. Baldwin *et al.*, 2001).

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Table 4.1. Description of the diameter growth rate data sets for Douglas-fir, western hemlock, and red alder trees. Variables are: diameter at breast height (DBH), uncompacted crown ratio (UCR), basal area in larger trees (BAL), stand basal area (SBA), breast height age (BH AGE), and site index (SI).

Variable	Douglas-fir		Western hemlock		Red alder	
	Mean	Range	Mean	Range	Mean	Range
Individual Tree	N = 57,074		N = 11,479		N = 46, 546	
DBH (cm)	10.7	0.1 – 97.5	6.2	0.1 – 35.1	5.9	0.1 – 28.2
UCR	0.75	0.10 – 0.99	0.96	0.47 – 0.99	0.73	0.1 – 0.99
BAL (m^2 ha^{-1})	10.4	0.0 – 178.0	3.9	0.0 – 36.9	4.7	0.0 – 25.9
Individual Plot	N = 356		N = 7		N = 132	
SBA (m^2 ha^{-1})	16.8	4.0 – 178.2	6.2	2.0 – 37.0	6.8	0.5 – 26.0
BH AGE	12.3	0.1 – 60.4	15.4	6.1 – 33.6	8.5	3.0 – 20.0
SI (m at 50-yr)	40.1	16.6 – 60.3	36.1	27.2 – 39.3	29.3	23.0 – 41.3
length of growing period (years)	4.7	1 – 12	2.5	2 – 4	3.0	1 – 15

Table 4.2. Parameters and asymptotic standard errors for predicting the diameter growth rate (equation [4.3]) of untreated Douglas-fir, western hemlock, and red alder fitted using maximum likelihood and multilevel mixed effects. Fit index, residual standard error, and AIC value for each model are also given.

Parameter/ Standard error	Maximum likelihood			Multilevel mixed effects		
	Douglas-fir	Western hemlock	Red alder	Douglas-fir	Western hemlock	Red alder
β_{30}	-3.6865	-3.0984	-3.6166	-2.9553	-2.3867	-3.4805
SE(β_{30})	(0.0392)	(0.0479)	(0.0592)	(0.4009)	(0.8991)	(0.4566)
β_{31}	0.2121	0.4617	0.3847	0.4222	0.5818	0.3953
SE(β_{31})	(0.0081)	(0.0059)	(0.0125)	(0.0063)	(0.0076)	(0.0065)
β_{32}	-0.00046	-0.00032	-0.0015	-0.00005	-0.00041	-0.0008
SE(β_{32})	(0.00002)	(0.00001)	(0.00009)	(0.00002)	(0.00001)	(0.0003)
β_{33}	0.1878	4.2445	1.3000	0.3488	1.7334	1.5890
SE(β_{33})	(0.0202)	(0.0767)	(0.0179)	(0.0219)	(0.0650)	(0.0249)
β_{34}	1.0778	0.9399	1.3619	0.8932	0.7173	1.2685
SE(β_{34})	(0.0098)	(0.0144)	(0.0276)	(0.1052)	(0.2507)	(0.1402)
β_{35}	-0.0069	-0.0010	-0.0085	-0.0036	-0.0009	-0.0022
SE(β_{35})	(0.00007)	(0.00003)	(0.0003)	(0.00005)	(0.00003)	(0.00007)
β_{36}	-0.1257	-0.2488	-0.2426	-0.2873	-0.3074	-0.3926
SE(β_{36})	(0.0028)	(0.0021)	(0.0058)	(0.0041)	(0.0033)	(0.0043)
β_{37}	0.0145	0.0099	-0.0648	0.0412	-0.0452	-0.0193
SE(β_{37})	(0.0043)	(0.0041)	(0.0068)	(0.0041)	(0.0053)	(0.0037)
Fit index	0.88	0.86	0.66	0.97	0.95	0.83
Residual standard error	2.58	0.62	1.23	1.24	0.40	1.04
AIC	139,083	70,973	157,431	127,780	46,133	147,099

Table 4.3. Description of the height growth rate data sets for Douglas-fir, western hemlock, and red alder trees.

Variable	Douglas-fir		Western hemlock		Red alder	
	Mean	Range	Mean	Range	Mean	Range
Individual Tree	N = 20,709		N = 8,077		N = 11, 816	
DBH (cm)	14.7	0.2 – 97.5	5.4	0.1 – 33.8	5.6	0.1 – 28.2
HT (m)	10.83	0.50 – 52.48	4.95	0.20 – 20.72	6.18	0.20 – 22.60
CCH	7.9	0.0 – 303.5	6.0	0.0 – 207.3	31.16	0.0 – 464.1
UCR	0.77	0.1 – 0.99	0.97	0.49 – 0.99	0.78	0.1 – 0.99
Individual Plot	N = 345		N = 7		N = 132	
BH AGE	10.8	0.1 – 60.4	15.4	6.1 – 33.6	8.5	2.0 – 24.0
SI (m at 50-yr)	39.7	16.6 – 60.3	36.1	27.2 – 39.3	29.3	23.0 – 41.3
length of growing period (years)	3.8	1.0 – 12.0	2.2	2.0 – 4.0	3.0	1.0 – 15.0

Table 4.4. Parameters and asymptotic standard errors for predicting the height growth rate (equation [4.7]) of untreated Douglas-fir, western hemlock, and red alder fitted using maximum likelihood and multilevel mixed effects.

Parameter/ Standard error	Maximum likelihood			Multilevel mixed effects		
	Douglas-fir	Western hemlock	Red alder	Douglas-fir	Western hemlock	Red alder
β_{70}	1.5673	1.0033	0.9286	1.3020	0.9880	0.9415
SE(β_{70})	(0.0065)	(0.0060)	(0.0067)	(0.1643)	(0.0282)	(0.0230)
β_{71}	0.2928	0.5722	0.6176	0.4794	0.5501	0.3833
SE(β_{71})	(0.0085)	(0.0298)	(0.0411)	(0.0388)	(0.0238)	(0.0816)
β_{72}	-0.00047	-0.0125	-0.0050	-0.0018	-0.0130	-0.0075
SE(β_{72})	(0.00003)	(0.0019)	(0.0015)	(0.0008)	(0.0016)	(0.0063)
β_{73}	-0.0021	-0.0015	-0.0048	0.0187	-0.0040	-0.0089
SE(β_{73})	(0.00021)	(0.0002)	(0.0024)	(0.0018)	(0.0016)	(0.0020)
β_{74}	6.0425	5.2812	4.1802	2.7961	6.4301	2.9185
SE(β_{74})	(0.2013)	(0.4440)	(0.8516)	(0.3484)	(0.4793)	(0.6589)
β_{75}	0.0569	0.0	0.0418	0.1126	0.0	0.0
SE(β_{75})	(0.0089)	(NA)	(0.0298)	(0.0126)	(NA)	(NA)
Fit index	0.85	0.53	0.54	0.94	0.62	0.65
Residual standard error	1.04	0.82	1.14	0.77	0.69	0.96
AIC	52,578	55,832	37,584	39,812	50,019	34,943

Table 4.5. Model, equation form, R^2, and root mean square error (RMSE) for model predicting the influence of physiographic features on the random effects of each model. All parameter estimates were significant at $\alpha = 0.05$.

Model	Equation form	R^2	RMSE
Douglas-fir diameter growth	-26.6559 + 0.3792*ln(ELEV) + 0.4470*ASP22 – 0.0260*PRCP + 5.6702*ln(PRCP)	0.36	0.51
Douglas-fir height growth	0.0301 + 0.0983*ASP1 – 0.0018*%ROCK.B	0.07	0.14
Red alder diameter growth	0.5138 + 0.3748*ASP22 – 0.0896*ELEV	0.29	0.12
Red alder height growth	0.0844 – 0.0052*%SLOPE + 0.0419*COSA – 0.3495*ASP12	0.41	0.07

Table 4.6. Mean bias (observed – predicted), percent bias, and mean square error (MSE) for predicted and observed diameter at breast height (DBH; cm) and height (HT; m) after 12 to 16 years of simulation on twelve Stand Management Cooperative (SMC) planted control plots using the maximum likelihood (ML) and multilevel mixed effects (MLME) equations developed in this analysis as well as the ORGANON growth model, which uses a 5-year time-step. Initial breast height age of the plots was between 23.5 and 46.5 years, while site index ranged from 29.3 to 48.0 m at base age 50.

Model	DBH (cm; n = 1767)			HT (m; n = 472)		
	Mean bias	Mean square error	% bias	Mean bias	Mean square error	% bias
ML	1.6479	2.4881	6.1035	1.2157	1.7256	4.0544
MLME	0.1102	2.1665	0.4508	-0.1993	1.3567	1.1695
MLME with predicted random effects	1.2199	3.2797	5.1555	0.7156	2.0154	2.0503
ORGANON	-1.7883	2.6229	-7.0704	-1.4959	2.1820	-5.6759

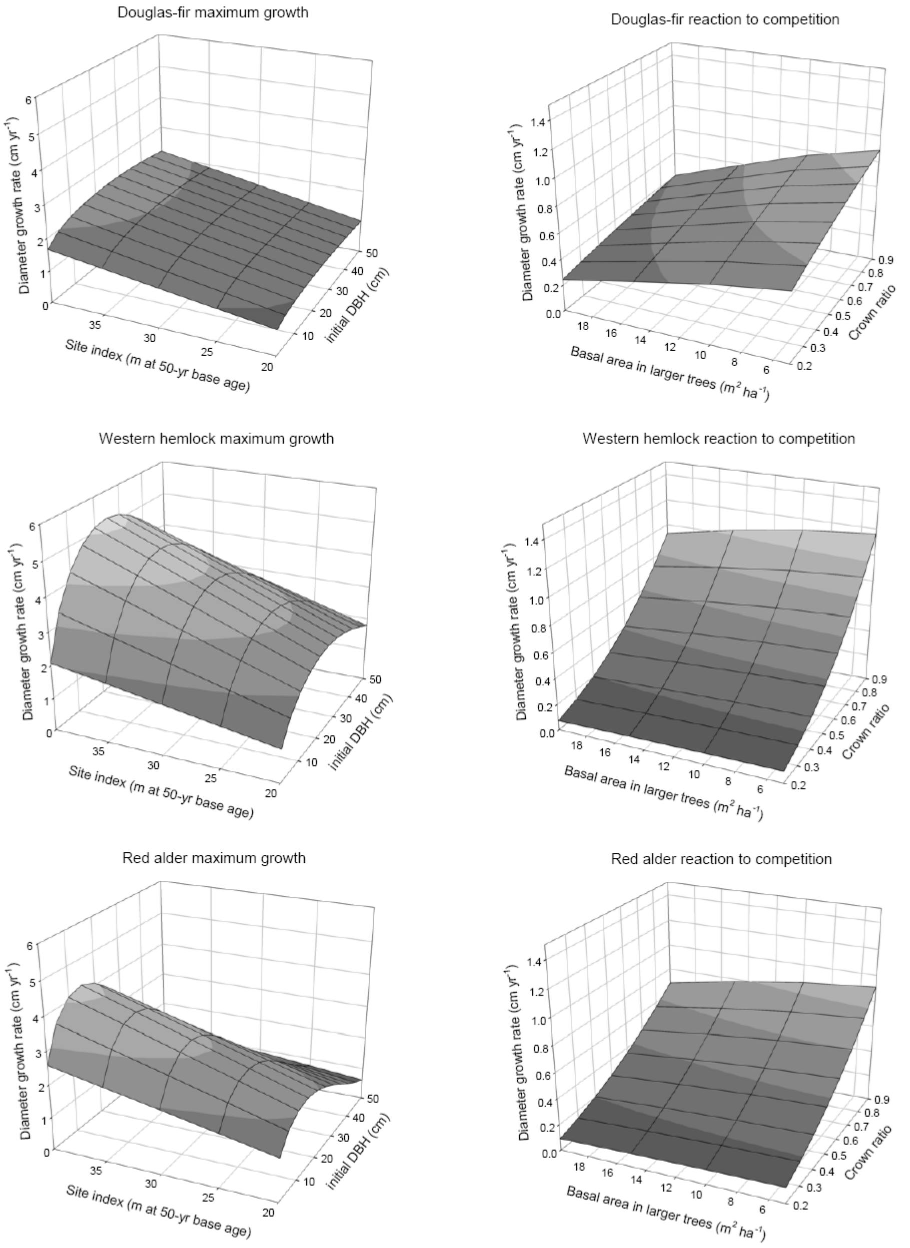

Figure 4.1. Predicted surface response for annual diameter increment using equation [4.3] for an open-grown tree at varying levels of site index (left panel) and for an average size tree with increasing competition (right panel) by species.

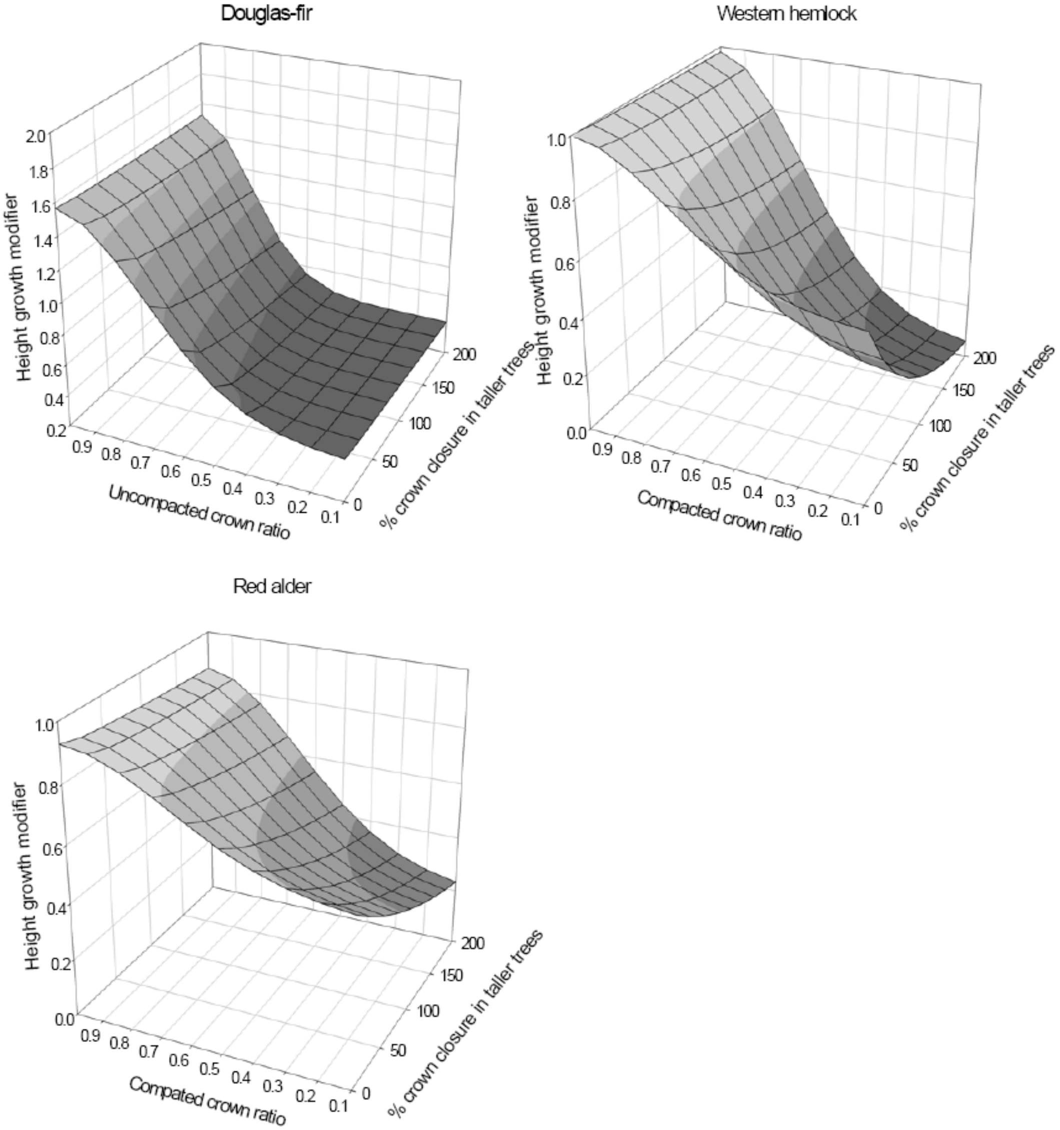

Figure 4.2. Predicted surface response of the height growth modifier using equation [4.7] across a range of crown ratios and percent crown closure in taller trees for Douglas-fir, western hemlock, and red alder.

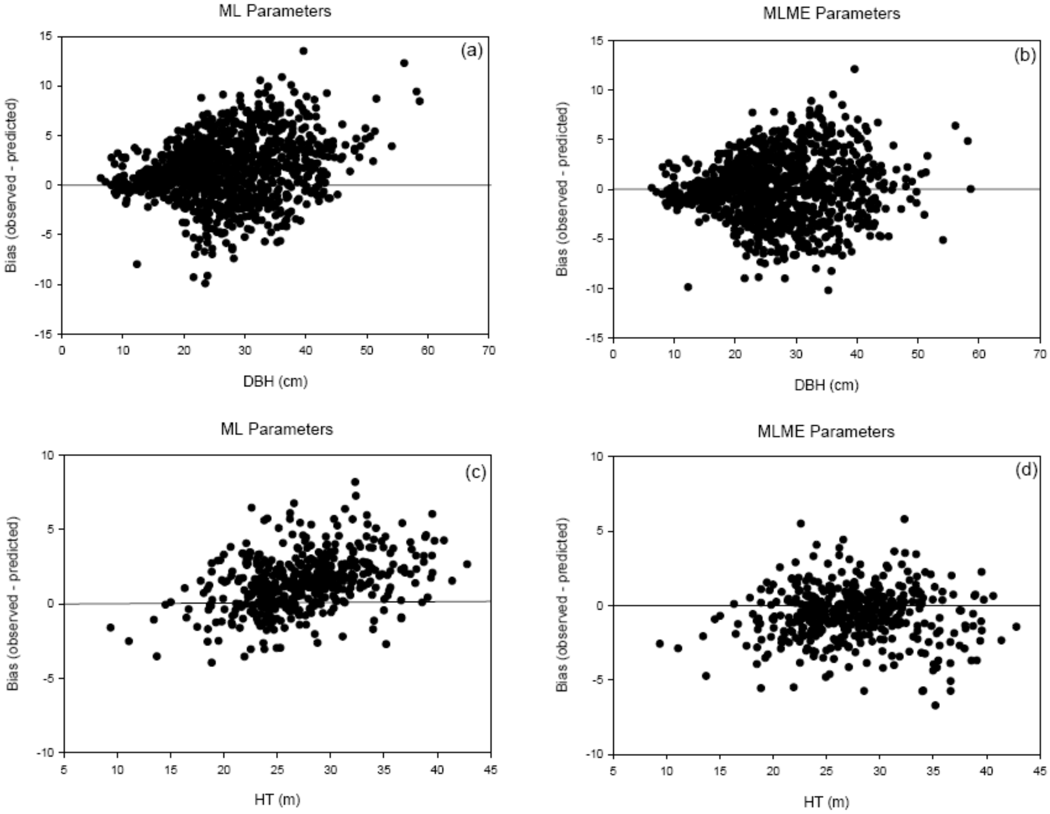

Figure 4.3. Bias (observed – predicted) over observed diameter at breast height (DBH; cm) and total height (HT; m) after 12- 16 years of simulation with the diameter and height growth equations fitted using maximum likelihood (ML; b, d) and multilevel mixed effects (MLME; a, c) on 12 Stand Management Cooperative installations not used during the fitting process.

CHAPTER 5: RESPONSE OF BRANCH GROWTH AND MORTALITY TO SILVICULTURAL TREATMENTS IN COASTAL DOUGLAS-FIR PLANTATIONS: IMPLICATIONS FOR PREDICTING TREE GROWTH

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Abstract

Static models of individual tree crown attributes such as height to crown base and maximum branch diameter profile have been developed for several commercially important species. Dynamic models of individual branch growth and mortality have received less attention, but have generally been developed retrospectively by dissecting felled trees; however, this approach is limited by the lack of historic stand data and the difficult in determining the exact timing of branch death. This study monitored the development of individual branches on 103 stems located on a variety of silvicultural trials in the Pacific Northwest, USA. The results indicated that branch growth and mortality were significantly influenced by precommerical thinning, commercial thinning, fertilization, vegetation management, and a foliar disease known as Swiss needle cast [*Phaeocryptopus gaeumannii* (T. Rohde) Petr.]. Models developed across these datasets accounted for treatment effects through variables such as tree diameter growth and the size and location of the crown. Insertion of the branch growth and mortality equations into an individual-tree modeling framework, significantly improved short-term predictions of crown recession on an independent series of silvicultural trials, which increased mean accuracy of diameter growth prediction (reduction in mean bias). However, the static height to crown base equation resulted in a lower mean square error for the growth predictions. Individual branches were highly responsive

to changes in stand and site conditions imposed by silvicultural treatments, and therefore represent an important mechanism explaining tree and stand growth responses.

Introduction

Growth is controlled at multiple scales in forests, but is typically simulated at the whole-stand or individual-tree levels. The amount of leaf area and its display on individual branches have a significant influence on individual-tree growth (Vose *et al.*, 1994). In addition, the number and size of branches on a stem control lumber recovery potential (e.g. Maguire *et al.*, 1991b), contribute critical features of habitat for some wildlife species (Hayes *et al.*, 1997; Sullivan *et al.*, 2000), and influence interception of both incoming radiation (Kucharik *et al.*, 1998) and precipitation (Keim, 2004). Although several models have been developed for predicting the dynamic growth and mortality of individual branches (Mitchell, 1975; Ford *et al.*, 1990; Ford and Ford, 1990; Gavrikov and Karlin, 1992; Sorrensen-Cothern *et al.*, 1993), these dynamic crown models remain relatively few and have not been incorporated into forest growth models.

Studies of branch growth and development have most often been based on either age chronosequences (e.g. Ishii and McDowell, 2002) or retrospective growth analysis on a limited sample of harvested branches (e.g. Kershaw *et al.*, 1990). The former approach is limited by the difficulty of removing the effects of factors other than age, because the chronosequence is assembled with stands or trees from many sites to create an artificial time series. Retrospective growth analysis is restricted by the extremely narrow growth rings, or lack of growth rings, in the lower branches of a crown (e.g. Reukema, 1959) and the difficulty of identifying the exact year of death. A branch can fail to form a perceivable increment for half or more of its total life span in at least some and probably many conifer species (Andrews and Gill, 1939; Kershaw *et al.*, 1990; Mäkinen and Colin, 1999). Remeasurement of individual branches on standing trees provides the most accurate estimates of branch growth and mortality, but the cost and safety risks of repeatedly climbing trees to measure branches has prevented wide applications of this approach.

Static models of branch size and number exist for several species including silver birch [*Betula pendula* Roth.; (Mäkinen *et al.*, 2003)], Scots pine [*Pinus sylvestris* L; (Mäkinen and Colin, 1999)], Norway spruce [*Picea abies* (L.) Karst.; (Mäkinen *et al.*, 2004)], radiata pine [*Pinus radiata* D. Don.; (Grace *et al.*, 1999)], and Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco; (Maguire *et al.*, 1994)]. These models have generally been based on data from managed stands, but not typically across a wide variety of intensive silvicultural regimes. Conflicting responses to some silvicultural treatments have also been reported. Mäkinen *et al.* (2001), for example, found that branch diameter growth of both newly initiated and older branches in Norway spruce were significantly enhanced with fertilization, while Mäkinen *et al.* (2004) concluded that variables describing site fertility and fertilization regime did not significantly influence branch radial growth in the same species.

Weiskittel *et al.* (2006b) recently examined the impacts of intensive management on Douglas-fir branch characteristics and found maximum branch diameter to be significantly influenced by vegetation management, precommerical thinning (PCT), fertilization, and commercial thinning. Because a wider array of stand conditions was represented, predictive equations developed from this dataset with only bole and crown variables performed significantly better than branch equations previously developed by Maguire *et al.* (1994; 1999). This result also suggested that branch radial growth patterns are highly correlated with tree growth, even across a wide range of silvicultural treatments, and that the basic allometric relationships between branch, crown and stem dimensions are not altered even by fertilization. Both fertilization (e.g. Brix, 1981b) and thinning (e.g. Short and Burkhart, 1992) have been shown to significantly influence crown recession rates, but validation of this process at the individual branch-level has been minimal. However, Albaugh *et al.* (2006) recently did find that fertilization reduced individual branch longevity.

Forest growth models represent crown dynamics at varying levels of detail. Some models predict the growth of individual branches and others represent the development of different crown segments. Mitchell (1975) represents the growth of individual Douglas-fir branches by empirical growth equations, while Ford and Ford (1990) base their branch growth equations on theoretical relationships between foliage development, biomass production, phenology, and branch morphology. In contrast, Grote and Pretzsch (2002) and Sorrensen-Cothern *et al.* (1993) divide the crown into segments of equal length, simulate physiological processes in each segment, and sum the estimates to predict tree-level production. Traditional empirical growth and yield models generally represent crown dynamics by statically estimating height to crown base from initial tree, stand, and site conditions and again from predicted tree, stand, and site conditions, with crown recession represented by the difference (Hann and Hanus, 2004). Both initial crown size and the rate of crown response to silvicultural treatments control stem growth response to intensive forest management. Improved modeling of crown dynamics, therefore, may lead to better predictions of tree growth across a wide range of stand conditions.

Our overall goal was to examine growth and mortality responses of individual Douglas-fir branches to intensive management regimes in the Pacific Northwest, USA. Specific objectives were to: (1) test the effects of vegetation management, PCT, fertilization, and commercial thinning, as well as Swiss needle cast (SNC; foliar disease caused by [*Phaeocryptopus gaeumannii* (T. Rohde) Petr.]) on Douglas-fir individual branch growth and mortality; (2) develop equations for predicting branch responses to silvicultural treatments based on initial tree and stand conditions; and (3) compare the individual-tree growth predicted under the dynamic equations developed in this study to growth predicted under application of static equations developed previously for Douglas-fir.

Methods

Study sites

Study sites were located over four installations in the Oregon Coast Range, two installations in the Oregon Cascade foothills, one installation in the southern Washington Cascade foothills, and one installation on the fringe of Willamette Valley in the foothills of Oregon Coast Ranges. The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 100 to 300 cm year^{-1} and January mean minimum and July mean maximum temperatures range from -2 to 2˚C and from 20 to 28˚C, respectively (Franklin and Dyrness, 1973). Variation in precipitation and temperature for this area is strongly correlated with elevation and proximity to the coast. Elevation ranged from sea level to 825 m. Aspects facing all cardinal directions were represented in the data.

The sampled plantations were 8- to 22-years-old at breast height and contained ≥75% Douglas-fir by basal area, with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and other conifer and hardwood species (Table 5.1). A more complete description of the stands was outlined by Weiskittel *et al.* (2006b).

Data collection

Several datasets were combined to address the above objectives (Tables 5.2, 5.3). The first was based on 19 sample trees in three PCT installations and 3 sample trees from one growth impact study plot that form part of the SNC cooperative permanent plot network (SNCC, Oregon State University) (Maguire *et al.*, 2004). The second dataset comprised 52 trees in four Stand Management Cooperative installations (SMC; University of Washington) (Maguire *et al.*, 1991a). The third dataset represented 30 trees in two Vegetation Management Research Cooperative installations (VMRC; Oregon State University) (Rose and Rosner, 2005; Rose *et al.*, 2006). All sample trees were measured for diameter at breast height (DBH), total height (HT), and height to crown base (HCB; lowest live branch).

At each research installation, three trees per plot were measured in at least two different plots. Plots sampled from the PCT installations included a control, one thinned in 1998 to 494 trees per ha, and one thinned in 1998 to 247 trees per ha. Plots sampled from each SMC installation included a control (CONT), fertilized

(FERT), thinned (THIN), and fertilized + thinned (THIN+FERT). Plots were fertilized one to four years prior to sampling with 224 kg N ha^{-1} as urea, and were fertilized at the same rate four years prior to the most recent fertilization; therefore, the plots received a total of 448 kg N ha^{-1} as urea over a period of five to eight years prior to branch measurement. Thinning prescriptions were defined by relative stand density (Curtis, 1982) and called for thinning to either 35 or 40 relative density after reaching 55 and 60, respectively. The sampled VMRC plots included: the control, 3.34 m^2 of total vegetation control (TVC) per tree, 9.29 m^2 of TVC per tree, complete removal of woody only vegetation (WDY), and complete removal of herbaceous only vegetation (HRB).

Within each plot, three trees were randomly selected at the 25th, 63rd, and 93rd diameter percentile. Each tree was then climbed in the summer of 2004 and every branch (living + dead) between the stem base and the 3-yr-old whorl was measured for height at insertion and diameter. Branch diameter was measured both horizontally and vertically approximately 5 cm from the bole to avoid the basal swell. All measured branches were also coded as either north or south. A subsample of branches was measured for aspect (azimuth to nearest degree), angle of insertion, total length, and non-foliated length, then were tagged for future reference. In the summer of 2006, each tree was reclimbed and all tagged branches were remeasured for growth and condition (live vs. dead).

Data analysis

Treatment effects

Treatment effects on branch mortality and growth were tested by analysis of covariance with initial branch size, branch location, and tree size as the covariates. The sampling scheme a distinct hierarchical structure (multiple measurements within trees, within plots, and within installations), so violated the assumption that error terms were independent and uncorrelated. A multilevel, mixed-model analysis allowed for three random effects on branch growth and mortality: installation effects, plot effects, and tree effects. When heteroskedasticity was detected in the residual plots, the final equation was weighted by a power variance function of the primary independent variable. A continuous first-order autoregressive term on distance from the tree tip to reduce any remaining significant autocorrelation was tested, but likelihood ratio test indicated that it did not significantly improve the performance of the final models. Nested model forms were compared with likelihood ratio tests. Models were fitted with the NLME and glmmPQL package of S-PLUS v6.2 (Mathsoft, Seattle, WA).

Predictive equations

Initial model forms for branch dynamics were based on nonlinear diameter growth equations and logistic mortality equations developed for individual trees (Hann *et al.*, 2003). Influential variables were identified by all subsets regression from an initial set that included bole and crown size, tree social position in the stand, observed tree growth, and stand density. Severity indices for Swiss needle cast included mean plot-level foliage retention (yrs), tree-level crown sparseness (CLSA, ratio of crown length to sapwood area at crown base), and mean plot-level crown sparseness (Maguire and Batista, 1996; Maguire and Kanaskie, 2002). Final models were selected on the basis of residual analysis, Akaike's information criterion (AIC) and biological interpretability. Because the data were collected on a two-year remeasurement cycle, the growth parameters were annualized using the technique of Cao (2000).

Simulation

The relative performance of branch growth and mortality equations over the more conventional approach of modeling change in height to crown base at the crown level was assessed by simulating 4-yr growth responses to various silvicultural treatments. Tree growth data for verification and testing were collected from 56 plots from nine SMC installations in Oregon and Washington, USA. The plantations were established between 1971 and 1982 at varying densities and levels of vegetation control, and covered a wide range of growing conditions. Initial planting densities ranged from 905 to 1575 stems per ha, and some plots have received subsequent silvicultural treatments involving both thinning and nitrogen fertilization.

The branch-based simulations were performed by combining the branch growth and mortality equations with annualized diameter and height growth equations developed for individual trees (Weiskittel *et al.*, 2007). In the conventional approach, growth was simulated by forecasting crown size with a static height to crown base equation (Hann *et al.*, 2003). Preliminary analysis indicated that the fertilization and thinning modifiers for diameter growth, height growth, and height to crown base (Hann *et al.*, 2003) did not significantly improve the projections, so they were left out. Height to crown base in the SMC verification dataset was defined as the lowest whorl with at least three live branches. Because the tree growth equations defined height to crown base as lowest live branch (Weiskittel *et al.*, 2007), each SMC height to crown based was converted to height of lowest live branch (Monleon *et al.*, 2004). Preliminary analysis on 2,818 trees from the SMC database with measurements of both compacted and uncompacted crown ratio indicated that the equation of Monleon *et al.* (2004) achieved a level of bias similar to an equation developed from the data. Mean bias (observed – predicted), mean square error (MSE), and mean percent bias were calculated for diameter growth, height growth, and change in height to crown base of each individual-tree in the verification dataset, then these statistics were compared between the two simulation approaches. Validation statistics for diameter growth were computed from all Douglas-fir trees on the 56 plots, and validation statistics for height and height to crown based were computed from only the Douglas-fir height subsample from the same 56 plots.

Results

Branch growth

Treatment effects

Control of competing vegetation on the VMRC plots had no significant effect on branch diameter growth. However, branch growth increased significantly after pre-commercial thinning on the SNCC PCT plots (p = 0.0345), and declined with increasing SNC severity (p = 0.05; Figure 5.1). Branch growth was more closely related to tree-level crown sparseness (Maguire and Kanaskie, 2002) than either foliage retention or stand-level crown sparseness. On average, severe SNC reduced branch growth by 36%, while pre-commercial thinning increased growth by 49%.

In the SMC dataset, both thinning (p = 0.0021) and fertilization (p = 0.0003) had a significant influence on branch diameter growth. The effects of these treatments, however, depended on time since treatment (p = 0.0060; Fig. 5.2). Fertilization initially led to a faster growth rate, while thinning temporarily reduced growth. Several years after treatment, branches on thinned plots were growing similar to the control, while those on fertilized trees were growing more slowly. In contrast, the combination of thinning and fertilization initially elevated branch diameter growth to a rate faster than that of the control but slower than that of the fertilized trees; however, by the fourth growing season after last treatment the trees on thinned and fertilized plots were growing up to 0.5 mm faster than all other treatments.

Predictive equation

Individual branch diameter growth in the comprehensive dataset was significantly correlated with tree DBH growth and volume growth, but was not correlated with tree HT growth. The final model form was:

[5.1] $$BDG = \exp(\beta_{10} + \beta_{11} *BD + \beta_{12} *\ln(BD) + \beta_{13} *W + \beta_{14} *RHACB + \beta_{15} *CLSA + \beta_{16} *BAGR + \beta_{17} *HCM) + \varepsilon_1$$

where BDG is annualized branch diameter growth rate (mm yr^{-1}), BD is initial branch diameter (mm), W is an indicator variable for branch type (1 if whorl branch, 0 otherwise), RHACB is relative height above crown base, HCM is height to crown midpoint (m), BAGR is annualized tree basal area growth rate measured over the same growth period (m^2 yr^{-1}), CLSA is tree crown sparseness index (Maguire and Kanaskie, 2002) predicted using the equation of Maguire and Batista (1996), the β_i's are parameters estimated from the data, and $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$ (Table 5.4; Figure 5.6). The model explained 23% of the original variation in branch diameter growth and had a root mean square error of 1.38 mm. No significant treatment effects were detected after accounting for these covariates.

Branch mortality

Treatment effects

Annual probability of branch mortality was significantly influenced by respective treatments in the PCT/SNC, VMRC, and SMC datasets. Although pre-commercial thinning had no significant effect, the probability of branch mortality increased with increasing SNC severity as measured by mean stand crown sparseness ($p<0.0001$; Fig. 5.3).

All vegetation control treatments on the VMRC plots had a significant effect on branch mortality rate, with the exception of 3.34 m^2 of total vegetation control (TVC). The probability of branch mortality was significantly higher in the herbaceous only treatment ($p = 0.0015$) than in the control, but significantly lower in both the woody only ($p = 0.0014$) and 9.29 m^2 of TVC treatments ($p = 0.0181$; Fig. 5.4).

Branch mortality was particularly sensitive to silvicultural treatments in the SMC dataset. Thinning ($p<0.0001$), fertilization ($p<0.0001$), and the interaction of these treatments ($p = 0.0008$) significantly influenced the probability of branch mortality after accounting for several other covariates. In the first growing season following treatment, the probability of branch mortality was significantly higher in fertilized plots and significantly lower in thinned plots when compared to the control (Figure 5). However, in the fourth growing season after treatment, the probability of branch mortality was significantly lower under all three treatments relative to the control.

Predictive equation

Variables representing branch size, branch height, tree size, stand density, and plot-level SNC severity were significant predictors of annual branch mortality. The final form of the equation was:

[2] $\text{logit}(P_{MORT}) = \beta_{20} + \beta_{21}*BD + \beta_{22}*RHACB + \beta_{23}*\ln(BDA) + \beta_{24}*HCM + \beta_{25}*RD_{DF} + \beta_{26}*CLSA_{mean} + \varepsilon_2$

where $\text{logit}(P_{MORT})$ is $\ln[P_{MORT} /(1- P_{MORT})]$ (Hosmer and Lemeshow, 2000), BDA is the diameter sum of all live branches above the subject branch (mm), RD_{DF} is Douglas-fir relative density in metric (Curtis, 1982), $CLSA_{mean}$ is mean stand-level crown sparseness index (Maguire and Kanaskie, 2002), the β_i's are parameters estimated from the data, and $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$ (Table 5.5; Figure 5.7). This model explained 46% of the original variation in branch mortality. No significant treatment effects were observed after accounting for these variables.

Simulation

Simulation of crown dynamics with branch growth and mortality equations ([5.1] and [5.2]) reduced mean square error (MSE) of crown recession by 15% on the fertilized and thinned SMC plots, when compared to simulation with a static height to crown base equation (Table 5.6). Bias was quite high (-68%) with the static HCB approach, but precision was better. Branch-level crown dynamics improved mean accuracy in both diameter and height growth (reduction in mean bias), but the static HCB resulted in a lower MSE for the growth predictions. At the stand-level, the simulation of crown dynamics led to slight improvements of volume growth for each of the treatments when compared the static HCB equation (Table 5.7).

Discussion

Repeated measurement of tagged branches provided unique insight into the response of branch growth and mortality to silvicultural treatment. On permanent plots, the change in height to crown base or change in crown ratio is the more common attribute to monitor (e.g. Curtis and Marshall, 2005), but change in both of these crown measures is the net outcome of individual branch responses to any increase in the availability of light, water, nutrients, and growing space imposed by treatments. Stem dissection can provide reasonable estimates of past branch growth and mortality (Andrews and Gill, 1939; Maguire and Hann, 1987), but some estimation error is inevitable, and the technique does not allow accurate reconstruction of initial stand conditions.

Branch growth

The profile of maximum branch diameter over height within the live crown has previously been found sensitive to several intensive management practices

(Weiskittel *et al.*, 2006b). Maximum branch diameters, for example, were larger in the upper crown of fertilized trees and smaller in the lower crown relative to untreated trees of similar size. Because the profile of maximum branch size can typically be estimated from tree diameter, height, and crown length, this result suggested that fertilization altered to some degree the allometric relationships between tree and branch dimensions, presumably by altering branch growth and/or mortality for a given set of initial conditions. Maximum branch diameter profiles are important components of individual-tree growth and yield models that simulate silvicultural influences on knot size as one determinant of wood quality (Colin and Houllier, 1991; Maguire *et al.*, 1991b). However, because these static models accommodate the decline in maximum branch diameter near crown base (Colin and Houllier, 1991; Maguire *et al.*, 1999; Mäkinen *et al.*, 2004), their repeated application to simulated or real trees over time can imply negative diameter growth in the lowest branches. Direct modeling of branch growth is therefore more appealing because growth can easily be constrained to a minimum of zero.

In this study of intensively managed Douglas-fir stands, the radial growth of a branch depended on both branch- and tree-level variables. The former included initial branch size, position within the crown, and branch type (interwhorl vs. whorl), and the latter included crown size and diameter growth rate. In general, branch diameter growth accelerated rapidly, peaked when the branch was around 6 mm in size and then decreased markedly as a negative exponential function of branch age. This growth pattern has been observed in other studies and other coniferous species (Kershaw *et al.* 1990; Mäkinen 1999)., However, Mäkinen (2002) observed a different pattern in a broadleaved tree, *Betula pendula*. In this species branch radial increment was higher in the second year than in the first, and was more variable during the first 5-6 years of branch development than in conifer species (Mäkinen, 2002).

Half or more of the life of a branch can be spent without perceivable increment (Kershaw *et al.*, 1990) due both to self-shading within a tree crown (Sampson and Smith, 1993) and to competition from other trees (Mäkinen 1996). Although incompletely understood, branch diameter growth is most likely influenced by a combination of light interception, plant growth regulators, water potentials, and respiratory load (Kozlowski & Pallardy 1997). Light availability; however, appears to be the primary driving factor for branch diameter growth (Mäkinen 2002). In our study of Douglas-fir, relative height of the branch within the crown can be interpreted as a surrogate for light availability, although it may also be related to one or more of the other factors listed above. In fact, relative height of the branch was probably the strongest predictor variable because it integrated the effects of branch age, light environment, and competition for water and nutrients.

If silvicultural treatments have little or no effect on allometric relationships within the tree, and if treatment effects on tree diameter, height, and crown length are known or are predictable, then treatment effects on branch growth are implied by changes in these standard tree dimensions. Several studies have found annual variation in radial increment to be similar in the stem and branches (Cannell, 1974; St. Clair, 1994; Mäkinen, 1999), and this relationship likewise does not change noticeably after a change in stand conditions (Mäkinen, 1999). Consistent with this result, the intensity of inter-tree competition was shown to have little influence on radial growth trends in branches (Mäkinen, 1996; Wichmann, 2002). Branch radial growth in our study of Douglas-fir was likewise related to tree basal area growth, with little additional effect of change in stand conditions imposed by silvicultural treatment. However, other tree-level variables such as height to the crown midpoint and crown sparseness probably represented past and present inter-tree competition and site conditions, respectively, and therefore also accounted for some of the variation in branch radial growth. Tree basal area growth was not sufficient to account for all the variation in branch radial growth across a wide range of stand conditions, so information on local inter-tree competition is desirable for increasing the accuracy and precision of predictions. Some previous research has shown that branch radial growth also varies by aspect in the crown, with growth being greatest in the south-facing half of trees (Wichmann 2002). Only moderate evidence for differential growth by aspect was observed in this study, however, and its high variability was consistent with results for other species (Grace *et al.*, 1999).

In general, branch diameter growth in the upper, free-growing part of the crown is influenced by physical site conditions and genetic potential, whereas growth in the lower portion of the crown is largely controlled by the local competitive environment (Mäkinen 1996). Stand structure, particularly stand density, has been shown to influence branch radial growth (Colin and Houllier, 1991; Makinen, 1999), but as indicated above, past and current competition effects often are sufficiently represented by the combination of tree-level variables, particularly those incorporating relative crown size. The branch diameter growth patterns that we observed in Douglas-fir were significantly influenced by thinning, fertilization, and Swiss needle cast severity. SNC significantly reduces the leaf area held by individual branches throughout the crown (Weiskittel *et al.*, 2006a), leaving the branch with a lower photosynthetic capacity and reduced growth potential. However, even at severe levels of SNC, branch radial growth responded positively to precommerical thinning and could achieve rates similar to those observed in healthy, unthinned stands.

Fertilization has been shown to significantly increase diameter growth of *Picea abies* branches initiated both before and after treatment (Mäkinen *et al.* 2001). Although the corresponding increase in stem diameter suggested that allometric relationships between the stem and branches were maintained, the greater increase in branch growth in the top half of the tree was similar to the response of upper branches of fertilized Douglas-fir observed in this study. Response to fertilization in Douglas-fir, however, depended on time since application. Initially, branch diameter growth was uniformly enhanced by fertilization for a given set of initial branch and tree conditions; however, four years after treatment and for a given set of initial conditions, branch diameter growth was actually slower in the fertilized plots. Because tree diameter growth rate for the same growth period is a predictor variable, a given tree diameter increment represents a greater basal area increment by the fourth year after treatment, particularly if the trees have responded to the fertilizer. Fertilization effects therefore accumulate in the tree basal area growth variable with each year, as well as in variables such as height to crown midpoint and mean CLSA. These cumulative treatment effects on predictor variables change the expectation for branch growth, and interpretation of branch growth is therefore similar to distinguishing between direct and indirect effects on stem growth responses in successive years after fertilization. Part of the change in stem to branch allometry, particularly that related to the faster branch growth in the upper part of the crown and slower growth in the lower part, is probably attributable to the rapid buildup of leaf area after fertilization (e.g. Gough *et al.*, 2004) and the consequent increased levels of self-shading (e.g. Balster and Marshall, 2000). This short term direct effect likely diminishes with increasing time since treatment, leading to the common conclusion that site fertility and fertilization regime do not influence branch radial growth patterns relative to overall tree growth rate (Mäkinen *et al.*, 2004).

The primary effect of thinning on branch radial growth is exerted through the increase in branch longevity and, hence, duration of radial growth before suppression (Brix 1981; Mäkinen 1999). Branch radial growth was significantly greater even 8 years after precommerical thinning in Douglas-fir than in unthinned stands, for a given set of initial conditions. Although commercial thinning also had a significant positive effect on branch radial growth, the increase for a given branch and tree size was quite small. The change in branch radial growth with time since thinning was similar to thinning 'shock' sometimes observed at the tree level; that is, branch growth was initially reduced by the thinning relative to the control, but climbed to a level slightly greater than those on trees from unthinned plots. The combination of thinning and fertilization, however, maintained branch radial growth that was significantly higher than the control and the thinned or fertilized treatments.

Branch mortality

Crown recession has been modeled for a number of different forest types (Krumland and Wensel, 1981; Maguire and Hann, 1987; Short and Burkhart, 1992; Hann and Hanus, 2004). Although branch growth and mortality has been of interest to tree physiologists (Ford and Ford, 1990; Sprugel, 1991), few crown recession models have been driven by simulating suppression mortality of individual branches. This approach has been limited by the lack of long-term monitoring of tagged branches on permanent plots and by several difficulties associated with reconstructing branch mortality by stem dissection. With regard to the latter, branch mortality can be difficult to date exactly because branches can remain alive after annual ring formation has ceased (Mäkinen, 2002). Some hardwood branches can stay alive an average of 2-4 years without producing annual rings (Mäkinen, 2002), while values between 0 to 10 years are common for many conifers (Reukema, 1959; Kershaw *et al.*, 1990; Fujimori, 1993). In addition, xylem in the stem can still be connected directly to the xylem of the branch for several years after the branch has lost all its green needles (Shigo, 1985). From a physiological perspective, branch mortality is generally thought to occur when its net carbon balance becomes negative (Witowski, 1996); however, the concept of negative branches (Larson, 1963) continues to be debated (e.g. Lacointe *et al.*, 2004). The carbon balance of a branch is usually regarded as driven by light availability. However, Portz *et al.*

(2000) found that branch mortality in *Pinus contorta var. latifolia* occurred not only from low light, but also from reduced stomatal conductance and lowered photosynthesis, both of which were imposed by shade-initiated reductions in earlywood, tracheid diameter and branch hydraulic conductivity.

Previous studies have suggested that the timing of branch mortality is largely governed by its distance from the tree tip, relative branch diameter in the whorl, and tree age and social position (Kershaw *et al.*, 1990; Mäkinen and Colin, 1999). In our Douglas-fir trees, branch mortality was likewise a function of its diameter and location in the crown, as well as several tree- and stand-level factors. Whorl and tree age were avoided as a covariates because their proximate effects were assumed to represent other ultimate factors more closely related to the driving mechanisms. The summation of branch diameters above the subject branch simultaneously accounted for factors associated with whorl age, tree age, relative position of the tree in the stand, and relative diameter of the branch within the whorl. The probability of branch mortality was also positively related to two stand–level variables, relative density and mean crown sparseness, representing the degree of canopy crowding and crown deterioration, respectively. Umeki and Kikuzawa (2000) similarly found that branch mortality was related to inter-tree competition, even after accounting for the size of both the branch and the tree.

Stand density and age have been shown to be strong determinants of branch mortality rate. Branches tend to stay alive for a longer time in older and less dense stands than in young and highly dense stands (Kershaw *et al.*, 1990; Fujimori, 1993; Mäkinen and Colin, 1999). The age effect can be largely attributed to the deceleration in height growth and corresponding rate of canopy rise as the trees age. Genetics apparently plays a relatively minor role in determining branch mortality rates, as suggested by lack of significant differences in height to live crown and number of live whorls among families and low estimates of heritability (St. Clair, 1994). Maguire and Kanaskie (2002) suggested that one mechanism leading to greater CLSA in stands with severe SNC could be deeper penetration of light into the lower canopy and slower crown recession. However, the greater probability of branch mortality that paralleled increasing SNC severity in this study was consistent with Weiskittel's (2003) observation that height-to-crown-base was also greater in trees with severe SNC, all other conditions being equal. Although SNC infection levels tend to be highest in the upper crown (Manter *et al.*, 2003b), the disease also drastically reduces branch leaf area in the lower crown (Weiskittel *et al.*, 2006a).

Despite the lack of a significant effect of competing vegetation control on branch radial growth, these treatments did alter branch mortality patterns. Compared to control plots with no treatment of competing vegetation, complete removal of herbaceous species accelerated branch mortality rate, but, both complete removal of woody species and total vegetation removal slowed the branch mortality rate. Hardwood basal area was much higher in the treatments not receiving any woody vegetation control (i.e., control and complete removal of herbaceous species), particularly at the hardwood conversion site in the central Oregon Coast Range (Rose and Rosner, 2005; Rose *et al.*, 2006). The lack of hardwood competition allowed trees receiving complete removal of woody species and total removal of both woody and herbaceous species to maintain their crowns, particularly in the total vegetation control treatment. Although trees in the herbaceous only treatment had to compete with more woody species, so they had higher branch mortality rates than the control. However, volume growth was significantly greater in the herbaceous only treatment (Rose and Rosner, 2005).

Thinning in the intensively managed Douglas-fir stands reduced branch mortality rates immediately after thinning and up to four years later. Fertilization, however, initially accelerated branch mortality relative to the controls, but this effect reversed by year four to a lower rate of mortality. The response to combined thinning and fertilization tracked the response to fertilization only, but with slightly less dramatic departure from control responses. In general, these results agree with those of other studies. Thinning has been found to significantly slow branch mortality rate (e.g. Brix, 1981), and fertilization can significantly accelerate mortality and reduce branch longevity (e.g. Albaugh *et al.*, 2006). The only apparent point of disagreement is lower probability of mortality after four years. The early increase in mortality rate is likely due to the rapid buildup of leaf area, the greater degree of self-shading, and the more rapid rise of the whole canopy caused be accelerated height growth. The later decline in branch mortality rate may be attributable to the greater amount of leaf area on a given branch (Kershaw and Maguire, 1995) and the possibility that this additional leaf area allows the branch to maintain a positive carbon balance for a longer period of time. Fertilization can also significantly increase branch sapwood permeability and hence elevate leaf specific conductivities, even in lower crown branches (Amponsah *et al.*, 2004). The improved water relations may also help to prolong branch longevity following fertilization, but may also reduce the amount of water available to upper branches. The latter response would also help to explain the observed decline in branch radial growth rates compared to the control several years after fertilization.

Simulation

Equations that describe branch size and location and that are capable of predicting their growth and mortality have been integrated into several growth and yield simulators (Mäkelä *et al.*, 1997; Siefert, 2003). The applicability of these models for simulating the effects of silvicultural activities on stem wood quality has been demonstrated (e.g. Mäkelä and Makinen, 2003), but their relative performance for predicting growth has not been tested. In this study of intensively managed Douglas-fir stands, simulating the behavior of individual branches significantly improved short-term predictions of individual-tree crown recession across a wide range of silvicultural treatments. However, the improved crown dynamics did not result in a corresponding significant improvement in diameter and height growth predictions. Improved modeling of crown size dynamics apparently did not fully capture the response mechanisms that explain tree growth responses to silvicultural treatments such as the tree leaf area. Additional work may be necessary to characterize branch- or crown-level leaf area differences, to introduce treatment effects on crown or needle growth efficiencies, or to develop empirical diameter and height growth modifiers for various silvicultural treatments. Better growth predictions also feedback into the simulated crown dynamics because branch growth and mortality are closely linked to tree and stand conditions.

Conclusion

Tree crowns are the key link between silvicultural treatments and various types of tree growth responses; however, detailed studies of long-term crown and branch responses to silvicultural treatments are lacking, particularly across a range of site and stand conditions. A total of 2,828 branches on 103 trees were monitored in this study, representing a variety of silvicultural trials throughout the Pacific Northwest, USA. Individual branch radial growth and/or mortality were sensitive to competing vegetation control, thinning, fertilization, and Swiss needle cast intensity, but their effects were accounted for by inclusion of variables such as tree diameter growth, size and location of the crown, and branch size and relative height in the crown. Patterns in branch growth and mortality were highly dependent on time since silvicultural treatment in this study. Simulations run with the equations developed in this study combined with previously constructed individual-tree growth equations performed better for short-term predictions of crown recession that simulations run with the same growth equations but static models of height to crown base. However, this improvement in simulated crown recession did not translate into significantly better predictions of diameter and height growth. The physiological processes driving both crown dynamics and tree growth responses to silvicultural treatments are poorly understood, but better representation of branch and crown dynamics may help to improve predictions of growth under a wide range of silvicultural treatments and regimes.

Acknowledgments

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Table 5.1. Initial attributes of the plots sampled for branch diameter growth and mortality by dataset in 2004.

Variable	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**
PCT/SNC (n_{plot} = 7)				
Trees per ha	663.4	196.5	456.9	988.0
Basal area ($m^2\ ha^{-1}$)	20.2	5.6	9.7	25.3
Relative density	4.5	0.9	2.5	5.4
Mean BH age (yrs)	12.8	2.1	9.6	15.6
Site index (m at 50 yrs.)	49.5	5.9	36.7	53.5
SMC (n_{plot} = 14)				
Trees per ha	743.3	592.8	245.0	2800.5
Basal area ($m^2\ ha^{-1}$)	26.6	7.9	6.5	38.5
Relative density	5.6	1.9	1.5	9.1
Mean BH age (yrs)	19.9	1.9	16.0	21.5
Site index (m at 50 yrs.)	39.3	1.5	37.5	41.2
VMRC (n_{plot} = 10)				
Trees per ha	1014.2	94.1	719.0	1101.3
Basal area ($m^2\ ha^{-1}$)	14.9	5.1	2.7	24.8
Relative density	4.0	1.1	1.1	5.9
Mean BH age (yrs)	7.9	0.2	7.8	8.2
Site index (m at 50 yrs.)	38.8	2.0	37.0	41.0
ALL (n_{plot} = 31)				
Trees per ha	860.7	396.3	245.0	2800.5
Basal area ($m^2\ ha^{-1}$)	20.1	8.2	2.7	38.5
Relative density	4.7	1.6	1.1	9.1
Mean BH age (yrs)	13.1	5.7	7.8	21.5
Site index (m at 50 yrs.)	40.6	4.7	36.7	53.5

Table 5.2. Tree-level attributes for the sample trees used in this analysis by study. Variable definitions are: diameter at breast height (DBH; cm), total tree height (HT; m), height to crown base (HCB; m; lowest live branch), diameter growth rate (DGR; cm yr^{-1}), and height growth rate (HGR; m yr^{-1}).

Variable	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**
		PCT/SNC (n_{tree} = 21)		
DBH (cm)	24.0	6.1	11.6	32.6
HT (m)	14.89	2.97	9.19	19.93
HCB (m)	1.96	1.73	0.14	6.35
DGR (cm yr^{-1})	1.12	0.48	0.29	1.85
HGR (m yr^{-1})	1.09	0.48	0.39	2.18
		SMC (n_{tree} = 52)		
DBH (cm)	27.9	6.5	12.2	42.7
HT (m)	18.28	3.01	10.15	23.97
HCB (m)	4.49	3.15	0.05	11.75
DGR (cm yr^{-1})	1.19	0.60	0.20	2.91
HGR (m yr^{-1})	0.76	0.41	0.10	2.51
		VMRC (n_{tree} = 30)		
DBH (cm)	14.5	3.2	9.8	21.2
HT (m)	10.35	1.75	7.46	14.67
HCB (m)	0.37	0.48	0.01	1.77
DGR (cm yr^{-1})	1.31	0.55	0.49	2.04
HGR (m yr^{-1})	0.94	0.41	0.20	1.92
		ALL (n_{tree} = 103)		
DBH (cm)	24.7	7.8	9.8	42.7
HT (m)	15.99	4.15	7.46	23.97
HCB (m)	3.12	3.05	0.01	11.75
DGR (cm yr^{-1})	1.17	0.57	0.20	2.91
HGR (m yr^{-1})	0.87	0.45	0.10	2.51

Table 5.3. Attributes of the individual branches remeasured for growth by study. Variable definitions are: branch diameter (BD; mm), branch height above ground (BHT; m), relative height above crown base (RHACB), and branch diameter growth rate (mm yr^{-1}).

Variable	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**
PCT/SNC (n_{branch} = 264)				
BD (mm)	24.03	7.91	2.80	43.25
BHT (m)	8.44	4.42	0.35	17.00
RHACB	0.60	0.27	0.10	1.01
BDG (mm yr^{-1})	1.67	1.68	0.01	13.01
SMC (n_{branch} = 669)				
BD (mm)	26.24	9.17	3.40	56.40
BHT (m)	11.26	4.41	0.63	18.90
RHACB	0.58	0.26	0.10	0.97
BDG (mm yr^{-1})	1.73	1.59	0.01	10.80
VMRC (n_{branch} = 223)				
BD (mm)	18.13	6.62	3.00	37.65
BHT (m)	4.36	2.62	0.30	10.18
RHACB	0.50	0.24	0.11	0.84
BDG (mm yr^{-1})	1.19	1.24	0.01	7.53
ALL (n_{branch} = 1156)				
BD (mm)	24.17	8.99	2.80	56.40
BHT (m)	9.28	4.91	0.30	18.90
RHACB	0.57	0.26	0.10	1.01
BDG (mm yr^{-1})	1.61	1.56	0.01	13.01

Table 5.4. Parameter estimates and standard errors for branch diameter growth (equation [5.1]) determined using nonlinear multilevel mixed effects regression.

Parameter	**Estimate**	**Standard error**
β_{10}	-0.8072	0.6889
β_{11}	-0.0645	0.0119
β_{12}	0.9563	0.2901
β_{13}	0.3291	0.0828
β_{14}	1.1808	0.1174
β_{15}	-0.3367	0.1172
β_{16}	0.1773	0.0542
β_{17}	0.0355	0.0132

Table 5.5. Parameter estimates and standard errors for branch mortality (equation [5.2]) determined using nonlinear multilevel mixed effects regression.

Parameter	**Estimate**	**Standard error**
β_{20}	-11.8914	1.8335
β_{21}	-0.1394	0.0095
β_{22}	-7.2184	0.6241
β_{23}	2.0107	0.2292
β_{24}	-0.0649	0.0271
β_{25}	0.4070	0.0537
β_{26}	0.1299	0.0331

Table 5.6 Mean bias (observed – predicted), mean square error (MSE), and percent bias (%) for diameter at breast height (DBH, cm), height (HT, m), and height to crown base (HCB, m) using the Weiskittel *et al.* (2007) growth model with static HCB and dynamic crown equations on 56 Stand Management Cooperative plots with varying levels of intensive management in Oregon and Washington, USA.

	DBH (cm; n = 9162)			**HT (m; n = 2608)**			**HCB (m; n = 2608)**		
Model	**Mean bias**	**MSE**	**% bias**	**Mean bias**	**MSE**	**% bias**	**Mean bias**	**MSE**	**% bias**
Static HCB equation	-0.19	1.11	-1.57	-0.56	0.96	-3.76	-0.84	0.99	-68.08
Dynamic crown equations	-0.01	1.22	-0.66	-0.63	1.00	-4.09	-0.08	0.92	-22.34

Table 5.7. Mean square error (MSE) and its standard deviation for predicted stand-level volume growth (m^3 ha^{-1}) on the verification dataset representing 56 Stand Management Cooperative plots receiving various silvicultural treatments.

Model	**Control (n = 11)**	**Thinned (n = 9)**	**Fertilized (n = 17)**	**Fertilized + Thinned (n = 19)**
Static HCB equation	3.33 ± 2.62	2.20 ± 1.69	2.45 ± 1.31	1.14 ± 1.27
Branch growth and mortality equations	3.29 ± 2.65	2.17 ± 1.70	2.39 ± 1.31	1.12 ± 1.29

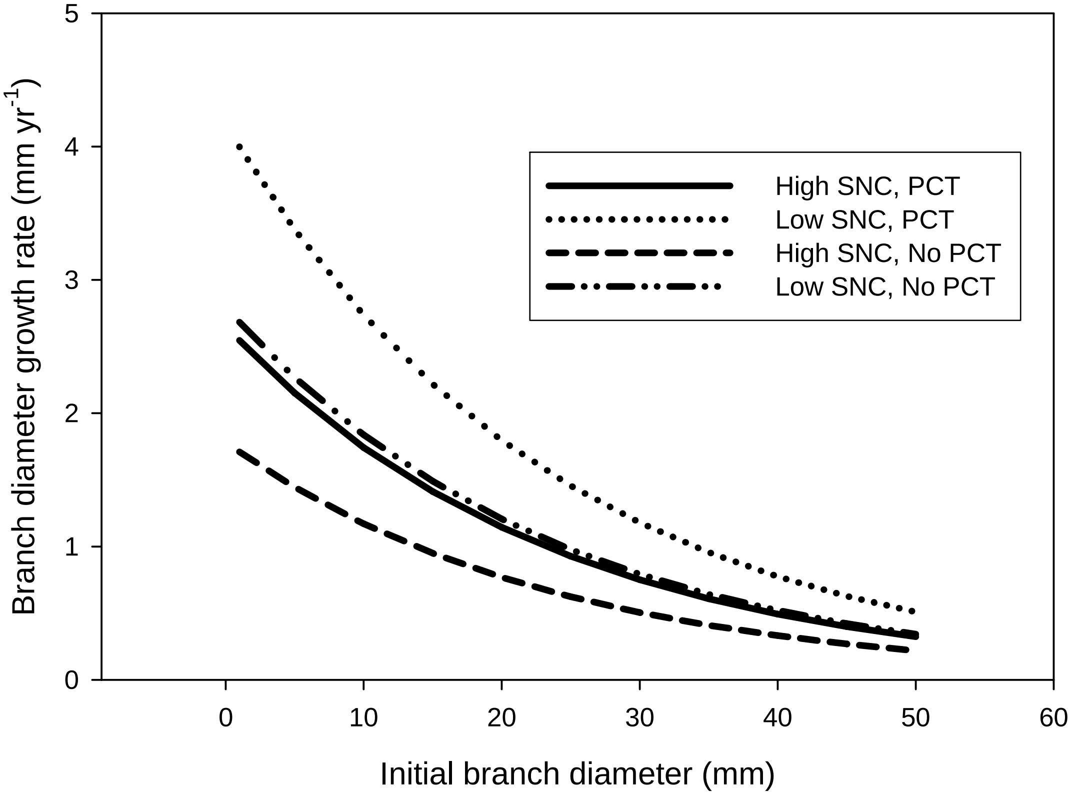

Figure 5.1. Predicted branch diameter growth (mm yr^{-1}) for a mid-crown whorl branch over initial branch diameter (mm**)** at varying levels of Swiss needle cast disease (SNC) with and without precommerical thinning (PCT).

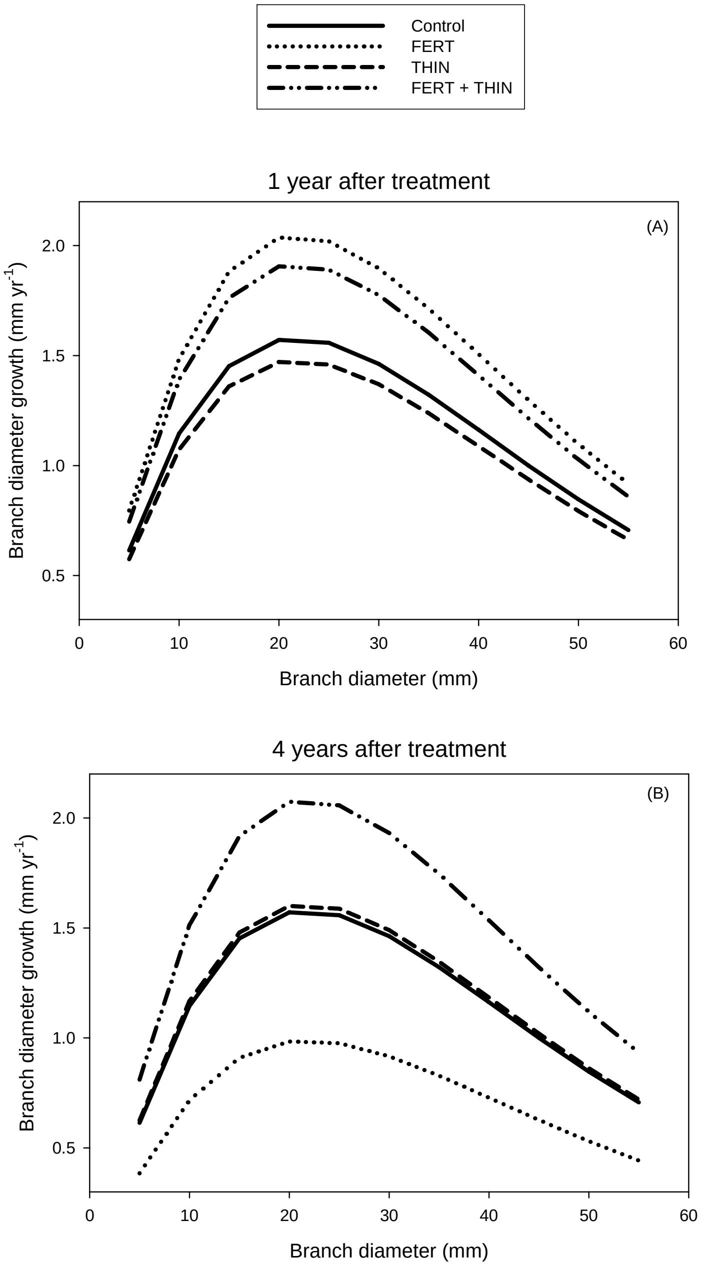

Figure 5.2. Predicted branch diameter growth (mm yr^{-1}) for a mid-crown whorl branch over initial branch diameter (mm) one (graph A) and four (graph B) years following treatment.

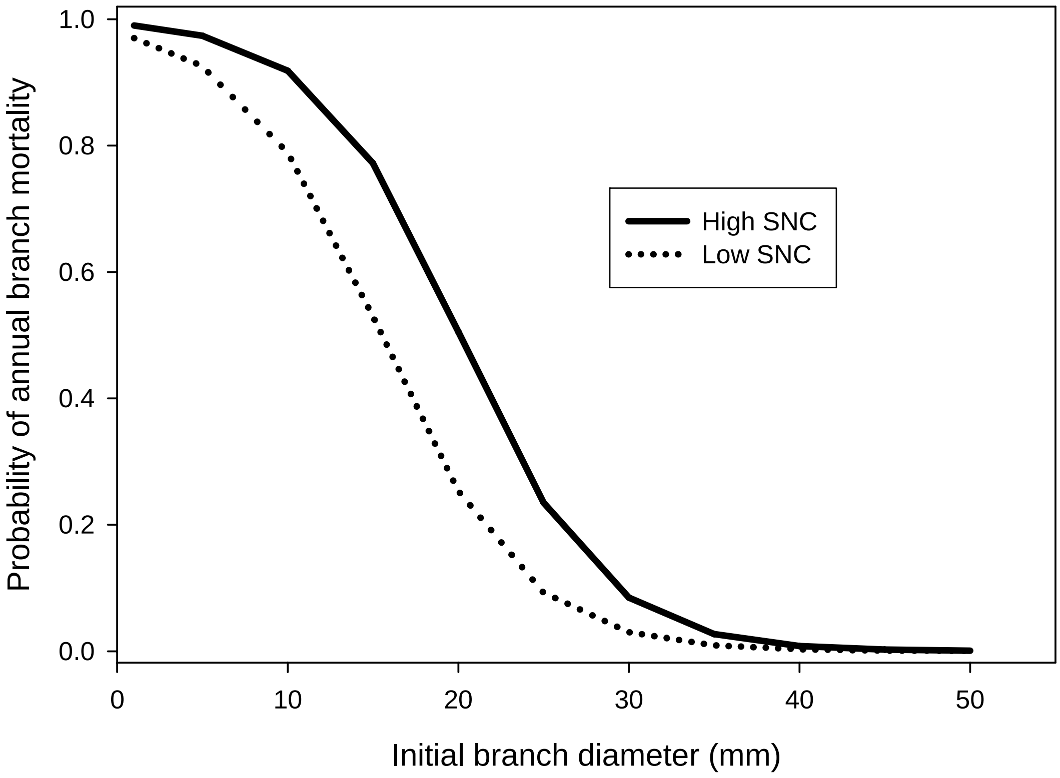

Figure 5.3. Predicted probability of annual branch mortality over initial branch diameter in a stand with high ($CLSA_{mean} = 6$) and low ($CLSA_{mean} = 4$) Swiss needle cast (SNC).

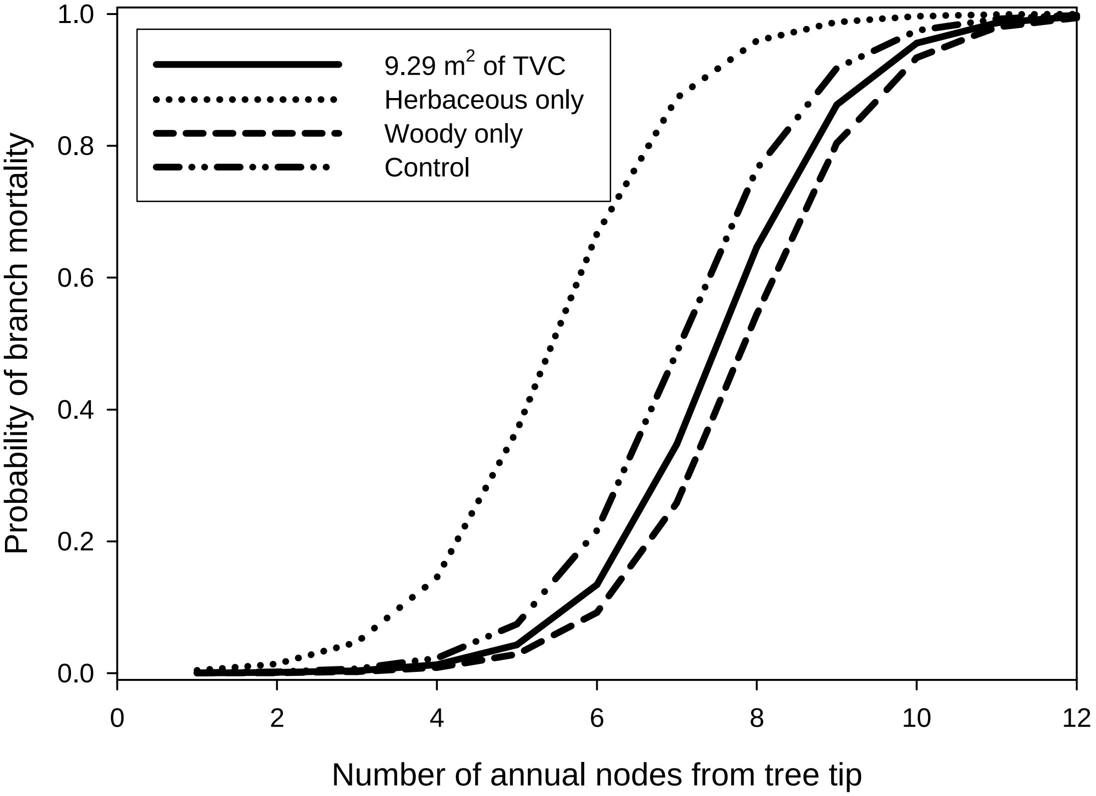

Figure 5.4. Predicted probability of individual branch mortality 14 years after application of several different vegetation management treatments over the number of annual nodes from tree tip at a mean branch and tree size of 15 mm and cm, respectively. The vegetation management treatments included 9.29 m^2 of total vegetation control (TVC), herbaceous only removal, and woody only removal.

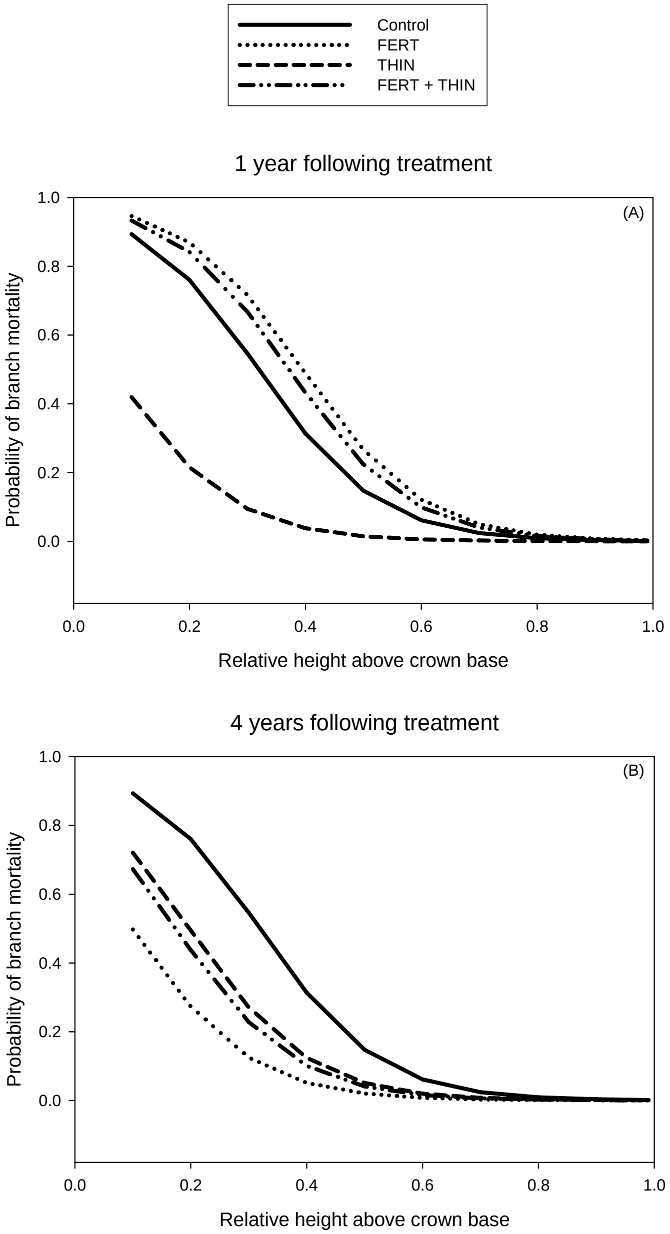

Figure 5.5. Predicted annual probability of individual branch mortality at a mean branch diameter, summation of branch diameters above subject branch, and height to crown midpoint over relative height above crown base one (graph A) and four (graph B) years following treatment.

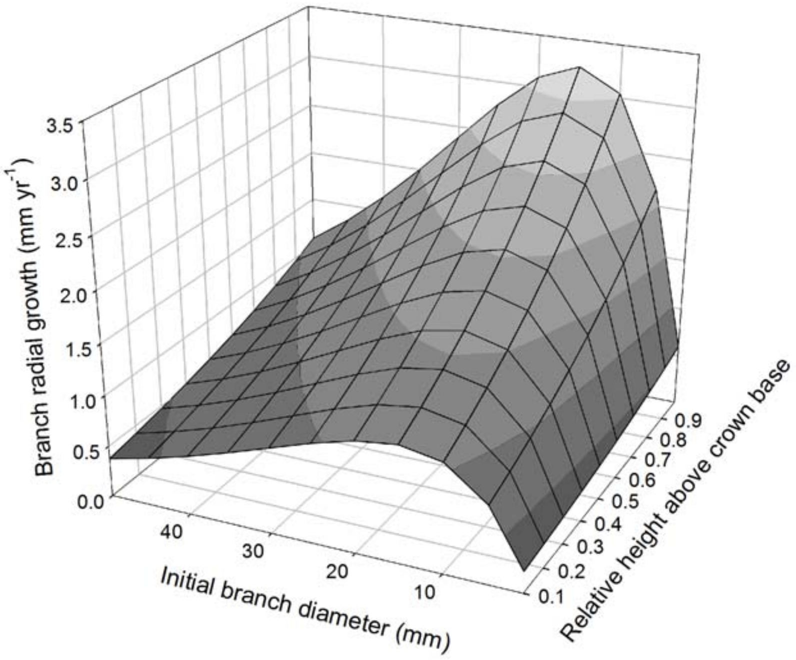

Figure 5.6. Predicted branch radial growth using equation [5.1] over initial branch diameter (mm) and relative height above crown base. The other covariates were set at their mean levels, which were 5 cm cm^{-2}, 50 cm^{2}, and 10 m for crown sparseness, tree basal area growth, and height to crown midpoint, respectively.

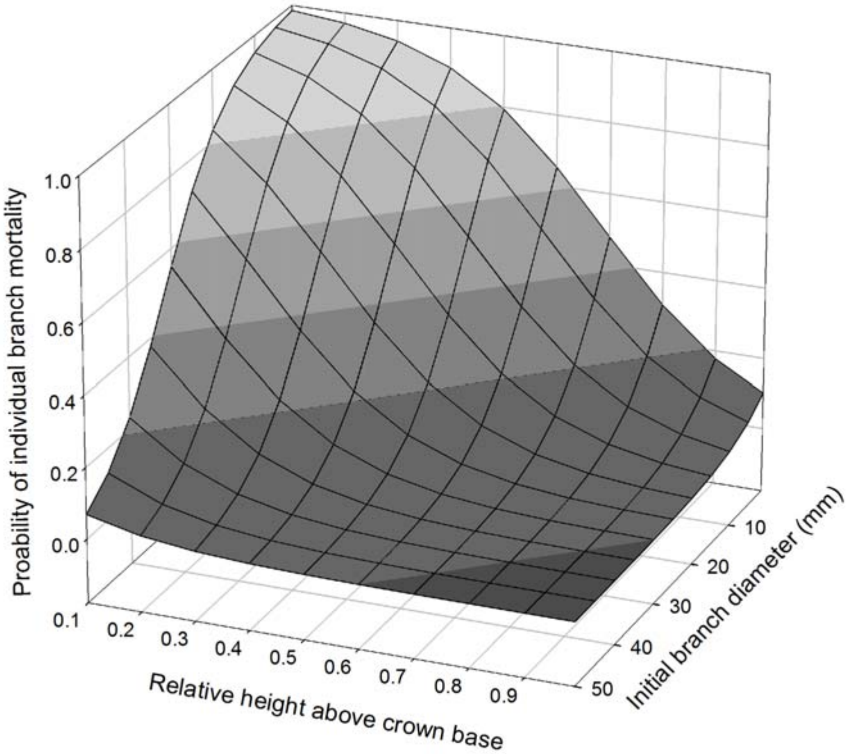

Figure 5.7. Predicted individual branch probability of mortality using equation [5.2] over initial branch diameter (mm) and relative height above crown base. The other covariates were set at their mean levels, which were 180 cm, 12 m, 5, and 5 cm cm^{-2} for summation of branch diameter above the subject branch, height to crown midpoint, relative stand density, and mean crown sparseness, respectively.

CHAPTER 6: DEVELOPMENT OF A HYBRID MODELING APPROACH FOR PREDICTING INTENSIVELY MANAGED DOUGLAS-FIR GROWTH AT MULTIPLE SCALES

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Abstract

Hybrid models offer the opportunity to improve future growth projections by combining advantages of both empirical and process-based modeling approaches. Hybrid models have been constructed in several regions and their performance relative to a purely empirical approach has varied. A hybrid model was constructed for intensively managed Douglas-fir plantations in the Pacific Northwest by embedding a hierarchy of components representing fundamental processes (e.g. light interception, photosynthesis, carbon allocation) into a spatially implicit individual-tree model. Simulated processes operated at a variety of scales from individual branches to trees and stands. The resulting hybrid model improved predictions of stand-level leaf area index (reduction of mean square error (MSE) of 10 – 55%) and current annual increment (28 – 49% MSE reduction), and in reducing the bias of individual-tree growth predictions (3 – 11% MSE reduction) when compared to existing models. These improvements were attributed to a finer resolution of crown structure and dynamics, simple yet mechanistically sound representation of key physiological processes at an appropriate spatial and temporal scale for simulating tree growth, and empirical growth equations that were modified by simulated physiological responses to annual climatic variation and site edaphic characteristics. The probability of individual-tree mortality was predicted equally well as a function of either growth efficiency (stemwood increment per unit

leaf area) or conventional tree dimensions and stand density. Overall, the hybrid modeling framework showed significant potential for predicting growth of trees and stands from fundamental processes mediating tree responses to silvicultural treatments.

Introduction

The long-term effects of intensive management on tree growth and stand yield are difficult to quantify empirically as natural variability necessitates extensive replication. In addition, a thorough understanding of long-term responses to complex treatment regimes requires continuous monitoring over a long period of time and over an entire region (Monserud, 2002). Other difficulties are the constant change of intensive silvicultural practices and the relatively high degree of variability in local site conditions (e.g. soil, climate, aspect). Empirical growth and yield models can predict changes in productivity for management regimes represented in the modeling data, but their performance outside the range of data carries varying degrees of uncertainty. Even in regions with adequate data, predicted responses to management can vary dramatically due to choices made about the form of equations, predictor variables to include, and the manner in which equations are assembled into a growth simulator. Johnson (2005) recently found a very wide range (1.3 – 2.3 fold difference) of predicted responses to standard regimes of thinning, fertilization, and the combination of these treatments among six empirical growth models that are widely available for species in the Pacific Northwest (PNW), USA.

Process-based models have recently found increasing application for decision-making in intensively managed forests (Mäkelä *et al.*, 2000a). These models offer the advantage of simulating growth responses to silvicultural treatments by representing some of the key ecophysiological mechanisms driving growth. As a result, they have a much greater capacity for predicting responses to natural and anthropogenic changes in environmental conditions, for example, annual weather fluctuations, changes in nutrient availability, and strand structural influences on environmental conditions. However, a strong theoretical basis does not currently exist for predicting all aspects of tree growth and morphology from fundamental physiology, and the number of parameters that have to be estimated can sometimes greatly exceed the number required in empirical models. The hybridization of empirical and process-based models has been proposed to retain the desirable attributes of both modeling approaches (Landsberg, 2003a), while keeping parameter requirements to a minimum. Hybrid models have been successful at improving stand-level growth predictions (Woollons *et al.*, 1997; Snowdon, 2001; Pinjuv *et al.*, 2006), but their performance in predicting individual-tree growth has been more varied. Baldwin *et al.* (2001) found that an individual-tree hybrid model was significantly superior to a purely empirical model for predicting growth of *Pinus taeda* trees in the southeastern USA. In contrast, Henning and Burk (2004) achieved only a moderate improvement in short-term predictions for mixed conifer and deciduous stands in north central USA. This type of modeling approach may be best suited for pure even-aged stands of a fast-growing species (Henning and Burk, 2004), but this hypothesis has not been tested. However, it should be pointed out that these specific improvements should be expected as it is not surprising that residual variation around an empirical model can be explained by the use of actual weather information.

One stand-level hybrid model, 3-PG, has been widely used in both research and practical applications (Landsberg and Waring, 1997). Well over 50 publications describe its use for a variety of species in many geographical regions (Landsberg *et al.*, 2003; Almeida *et al.*, 2004a; Landsberg *et al.*, 2005). Although 3-PG offers robust predictions with a fast algorithm and a reasonable list of required parameters, it is built on some fundamental assumptions that are often overlooked and may limit its application. Pinjuv *et al.* (2006) found that 3-PG performed better than a comparable empirical model in predicting basal area growth of *Pinus radiata* stands, but it performed more poorly than an alternative hybrid model primarily due to better representation of key soil water processes.

3-PG relies heavily on the radiation use efficiency (RUE) concept, which assumes that all radiation intercepted by a canopy is converted into a constant amount of carbon. Arguments have recently been raised for abandoning RUE in process-based models for agricultural systems (Loomis and Amthor, 1999; Lizaso *et al.*, 2005). Although 3-PG modifies RUE based on nutrition, temperature, and water availability, this approach is inflexible and does not allow for interactions that can be particularly important for accurately capturing the effects of water stress on canopy processes (Grant *et al.*, 2006). Regardless of the relative merits of RUE in process-based models, canopy light interception is not accurately portrayed in 3-PG because radiation is treated as a homogenous input, absorbance is estimated with a “big-leaf” approach that assumes all foliage receives the same proportion of direct and diffuse light, and light attenuation through the canopy is estimated with a fixed extinction coefficient. In contrast, the sun/shade leaf approach divides the canopy into two foliage types that intercept either mostly direct light (sun foliage) or diffuse light (shade foliage). Because direct radiation must be separated from diffuse radiation for accurate estimates of canopy absorbance (Wang, 2003), the sun/shade leaf approach has been superior to the big-leaf assumption (Medlyn *et al.*, 2003). The monthly time-step of 3-PG has been offered as justification for the simplified process of radiation absorption. Although simulations have shown that this is true to some extent, RUE still varies quite considerably across sites with different leaf area index (LAI) or light climate (Medlyn, 1998). Schwalm *et al.* (2006) found RUE to be quite sensitive to both mean annual temperature and the ratio of diffuse to total photosynthetically active radiation (PAR) across a variety of sites in Canada. 3-PG also requires estimates of tree biomass components that are often not available for a given location. Regional allometric equations for estimating tree biomass components in intensively managed plantations can result in biases between 8-93% (Grier *et al.*, 1984).

The goal of this research project was to compare the performance of 3-PG and a new and more detailed canopy photosynthesis model across a series of several silvicultural trials throughout the PNW. Most previous assessments of 3-PG for predicting response to intensive management have been performed on a limited number of installations and plots (Landsberg *et al.*, 2000; Almeida *et al.*, 2004a; Landsberg *et al.*, 2005). Sampson *et al.* (2006) added some important refinements to the 3-PG model, but did not test its performance relative to the base 3-PG model. This improved model (SECRETS-3PG) still relies on a subjective soil fertility parameter to drive key processes, and soil water has no linkage to estimates of canopy photosynthesis (Sampson *et al.*, 2006). Several other models likewise do not represent this linkage accurately (Grant *et al.*, 2006; Siqueira *et al.*, 2006). A final limitation is the failure of most canopy photosynthesis models to account for the effects of stand slope and aspect, which can be quite significant in complex terrain (Wang *et al.*, 2002). The objectives of this study were to: (1) develop a hybrid model for intensively managed Douglas-fir stands; (2) compare a variety of approaches for mechanistically simulating individual-tree growth and mortality; and (3) to test performance of the model relative to 3-PG and a purely empirical model across a wide range of intensively managed plantations. Recommendations for future work in refining hybrid models are discussed in the context of simulating Douglas-fir responses to silvicultural treatments and annual weather variation in the PNW.

Methods

Model development

The modeling approach emphasized a hierarchical treatment of multiscale processes (Mäkelä, 2003), with predictions made at the individual branch-, tree-, and stand-levels. The desired features of the model included: (1) prediction of annual growth in diameter, height, and crown size of individual trees; (2) characterization of knot size, knot location, crown wood core, and sapwood width as determinants of wood quality; (3) sensitivity to annual climatic variables; (4) representation of soil water availability and its effect on tree growth; (5) representation of nutrient availability and its effect on tree growth; (6) simulation of light interception as influenced by solar geometry and stand density; and (7) prediction of responses to silvicultural regimes through treatment effects on basic ecophysiological processes controlling water and nutrient uptake, carbon assimilation, and carbon allocation. This approach ensured that the model was capable of answering the questions that motivated the modeling effort, i.e., the effect of silvicultural treatments, site conditions, and annual weather on wood yield, wood quality, and tree and stand structure. Likewise, the hybrid structure needed to take advantage of the current state of knowledge at the appropriate scale and offer the flexibility to accommodate future modifications due to improved data availability or physiological modeling. Three primary components comprise the model with characterization of crown structure (BCACS), estimation of annual net primary production (NPP), and allocation of carbon and growth to different parts of the tree (ALOGRO) (Figure 6.1).

Branch, Crown, And Canopy Simulator (BCACS)

The number, size, and location of branches, as well as the implied size and position of the live crown, determine stem, log, and product quality through their effects on micro-anatomical properties and knottiness of the wood (Bowyer *et al.*, 2002). Branches are also an appropriate level to sample and estimate foliage amount (e.g. Kershaw and Maguire, 1995), facilitating estimation of vertical foliage distribution, particularly in coniferous and other species with excurrent form (Maguire and Bennett, 1996; Garber and Maguire, 2005a; Weiskittel *et al.*, 2006a). BCACS (Branch, Crown, And Canopy Simulator) contains a set of empirical equations that predict the location, diameter, and biomass of every branch on each tree on the sample plot being simulated. The input is a tree list containing diameter at breast height (DBH), height (HT), height to crown base (HCB; lowest live branch), and expansion factor (EXPF, in trees per ha) as well as estimates of total age and site index (base age 50 years). Past height growth is reconstructed from the dominant height curves developed by Bruce (1981) to determine the location of annual whorls of branches. Branch diameter, length, and angle were predicted following the approach outlined by Maguire *et al.* (1994), but with the equations developed by Weiskittel *et al.* (in review-a). Branch location was assumed to follow the empirical distribution in Maguire *et al.* (1994). Woody biomass, woody surface area, foliage biomass, and foliage area of all branches were predicted from basal diameter and relative height in the crown (Weiskittel and Maguire, 2006; Weiskittel *et al.*, 2006a) (Appendix A Eqn. 1-3). These attributes were then summed to estimate biomass and surface area at the tree- and stand-levels.

Total stem and sapwood volume were estimated at the tree-level from existing stem volume and sapwood taper equations (Walters *et al.*, 1985; Maguire and Batista, 1996). Volumes were converted to biomass by applying regional values for total and sapwood density (530 and 455 kg m^{-3}, respectively). Belowground biomass at the stand level was estimated from total aboveground biomass assuming the relationship presented by Ranger and Gelhaye (2001) (Appendix A Eqn. 5). Crown projection areas were calculated from estimated crown widths of individual trees and these areas were then summed to determine percent canopy cover (Crookston and Stage, 1999) (Appendix A Eqn. 6).

Net Primary Production (NPP)

Conclusions reached from previous reviews of process-based models (Schwalm and Ek, 2001; Landsberg, 2003b) have converged on a common list of attributes that future models should possess to accurately capture the effects of silvicultural treatments, climate, and their interaction on NPP. These attributes include: (1) daily time-step; (2) separation of direct and diffuse radiation; (3) light extinction coefficients dependent on solar geometry, canopy structure, and type of radiation; (4) separation of sunlit and shaded leaf area; (5) photosynthesis estimates based on the Farquhar *et al.* (1980) biochemical equation, (6) site slope and aspect effects on diurnal distribution of radiation and fraction of sunlit leaf area (particularly in areas with complex terrain); (7) estimates of stomatal conductance as a function of vapor pressure deficit and soil water availability; and (8) canopy gas exchange linked to soil water and nutrition availability.

All of these desired attributes were incorporated into the NPP submodel, as described below. Inputs were kept as simple as possible to capture the fundamental processes, so included: (1) daily climate obtained from DAYMET (http://www.daymet.org); (2) site physiographic features (elevation, slope, aspect); (3) stand structural attributes from BCACS (LAI, biomass, canopy cover, etc.); (4)

basic soils information (rooting depth, texture, rock content), and (5) foliar nitrogen concentration. The model runs on daily time-step and estimates gross primary production (GPP) five times daily based on Gaussian integration (e.g. Leuning *et al.*, 1995). The development of the current-year foliage was assumed to occur linearly for 30 days following bud burst, with date of bud burst predicted from a model developed by Thomson and Moncrieff (1982). Annual foliage litterfall and its seasonal distribution were predicted from an empirical equation (Weiskittel and Maguire, 2007).

Light interception

Although highly detailed light interception models exist (e.g. Brunner, 1998), they still remain quite computer intensive and too complex for application in management-oriented hybrid models. Further, estimating light interception for an individual-tree crown based on canopy-level principles (e.g. Schwalm and Ek, 2004) does not fully account for the competitive position of the tree. Light interception was, therefore, estimated by applying the Beer-Lambert law after accounting for the effects of incomplete canopy closure on the sunlit and shaded portions of the canopy (Appendix A Eqn. 17). Mean daily radiation was separated into direct and diffuse components following the approach outlined by Bristow and Campbell (1985) (Appendix A Eqn. 8), which is based on the ratio of total incoming shortwave radiation to potential shortwave radiation. The amount of direct and diffuse radiation at a given time of the day was estimated from cosine-diurnal distribution following the procedure outlined by Wang *et al.* (2002) (Appendix A Eqn. 11 – 14), in contrast to the more common approach of assuming a sinusoidal pattern to diurnal radiation. Light extinction coefficients for direct and diffuse radiation were based on the relationships described by Smith (1993) (Appendix A Eqn. 15) and Campbell and Norman (1998) (Appendix A Eqn. 16), respectively. The direct radiation extinction coefficient was a function of solar zenith angle, LAI, and stand relative density (Curtis, 1982), while the diffuse radiation extinction coefficient was simply a linear function of LAI. Clumpiness was accounted for by an equation presented in Campbell and Norman (1998) that included the ratio of stand mean crown depth to diameter and the solar zenith angle. A penumbra effect was not simulated because any resulting bias from ignoring this effect was expected to be relatively small when the diffuse fraction is high (e.g. Bernier *et al.*, 2001), as is typical in forest canopies of this region.

Photosynthesis

Net photosynthetic rates were estimated with the Farquhar *et al.* (1980) model for both sunlit and shaded current-year foliage. Maximum Rubisco activity (V_{cmax}), electron transport capacity (J_{max}), and dark respiration rate (R_{dark}) were estimated from their relationship to mean canopy concentrations of foliar nitrogen (Ripullone *et al.*, 2003; Manter *et al.*, 2005). These rates were assumed to be the same for both sunlit and shaded foliage. An alternative approach was found to perform better. First, V_{cmax}, J_{max}, and R_{dark} were estimated at an optimum foliar nitrogen concentration from the equations of Manter *et al.* (2005) (Appendix A Eqn. 19 – 20), net photosynthesis was estimated, and then this rates was multiplied by a modifier that ranged from 0 to 1 and was a nonlinear function of actual foliar nitrogen concentration (Brix, 1993). Temperature modifiers for V_{cmax} and J_{max} were obtained from Manter *et al.* (2003a). Other Farquhar *et al.* (1980) parameters such as CO_2 compensation point in the absence of mitochondrial respiration and the Michaelis-Menten constant of Rubisco were estimated from standard equations. To account for the effects of complex terrain on canopy photosynthesis, sunlit and shaded leaf area were calculated with equation [11] presented by Wang *et al.* (2002) (Appendix Eqn. 18)). Foliage age structure is know to influence total photosynthesis in conifer canopies (e.g. Bernier *et al.*, 2001), but actual V_{cmax}, J_{max}, and R_{dark} measurements for age classes older than the current year were not available. Therefore, the net photosynthetic rates for the 1-, 2-, 3-, and ≥4-year-old foliage age classes were assumed to be 75, 50, 30, and 10% of the net photosynthetic rates of current year foliage calculated from the Farquhar *et al.* (1980) equation based on information available in the literature (Woodman, 1971; Manter *et al.*, 2003a; Ethier *et al.*, 2006).

Water stress effects on canopy photosynthesis are particularly important in the PNW because of high evaporative demand during the warm, dry summer (Waring and Franklin, 1979). In a recent review of models for simulating the effect of water stress on canopy photosynthesis, Grant *et al.* (2006) found approaches ranging from simple scaling factors (Kirschbaum, 1999; Garcia-Quijano and Barros, 2005) to complex iterative solutions (Williams *et al.*, 1996). Although the impact of stomatal conductance on CO_2 fixation is poorly understood, proper behavior requires interactive effects of soil and atmospheric water deficits on CO_2 fixation (Grant *et al.*, 2006). The simplest approach was to predict stomatal conductance from both soil and atmospheric water deficits; however, the equation developed by Bond and Kavanagh (1999) predicts only mean daily values of stomatal conductance. To estimate conductance throughout the day, the mean daily values were modified by the amount of intercepted radiation and time since sunrise (Livingston and Black, 1987) (Appendix A Eqn. 21). Intercellular CO_2 concentration was then estimated from a theoretical relationship to CO_2 compensation point, atmospheric CO_2 concentration, and root water potential (Katul *et al.*, 2003). One limitation of this approach is the assumption that water deficit effects on CO_2 fixation are entirely stomatal, which is not entirely true (Warren *et al.*, 2004). A better understanding of the relationship between stomatal conductance and leaf internal transfer conductance, and the response of both to environment conditions, is required before they can be better integrated into models (Warren and Adams, 2006).

Respiration

One key simplification in 3-PG is the assumption that NPP is a constant fraction of GPP (~0.5). This assumption has generated considerable debate in the literature (Mäkelä and Valentine, 2000; Lai *et al.*, 2002), but results of several studies have supported the generality of this NPP/GPP fraction across a wide range of forest types (Gifford, 2003; Siqueira *et al.*, 2006). Three alternatives to this simplification were tested, including: (1) daily respiration as a function of biomass and temperature (Schwalm and Ek, 2004); (2) daily respiration as a function of nitrogen content and both a short- and long-term response to temperature (Kirschbaum, 1999); and (3) annual respiration as a function of nitrogen content and temperature (Battaglia *et al.*, 2004). Preliminary analysis indicated that estimating NPP as a constant fraction of GPP yielded the strongest correlation with observed stem volume growth.

Soil water and nutrients

Daily soil water balance was calculated similar to Schwalm and Ek (2004). Soil water holding capacity was estimated from rooting depth, texture, and rock content using standard equations (Cosby *et al.*, 1984; Rawls *et al.*, 1992). Daily canopy transpiration and soil evaporation were simulated with modified Penman-

Monteith equations as presented in Waring and Schlesinger (1985) and Kirschbaum (1999), respectively. In the canopy transpiration equation, mean daily stomatal conductance was estimated from leaf and soil water potential, leaf to air vapor pressure gradient, and leaf specific conductance (Bond and Kavanagh, 1999). Based on the data presented by Tan and Black (1976), canopy conductance was estimated by reducing this mean daily stomatal conductance by 88%. In a manner similar to Schwalm and Ek (2004), daily soil water balance was determined by subtracting canopy transpiration and soil evaporation from soil water, and adding daily net precipitation after subtracting interception by canopy leaf and branch surface area (Appendix A Eqn. 7). The amount of intercepted precipitation was based on empirical rainfall attenuation in Douglas-fir stands (Keim, 2004).

For simplicity, daily nitrogen mineralization was the only aspect of nutrient availability that was simulated in the model. Driving variables included temperature, water content, texture, bulk density, and water holding capacity of the soil, as well as daily air temperature, rainfall, and solar radiation (Paul *et al.*, 2002) (Appendix A Eqn. 22). In addition, the mass and height of the litter layer must be known or estimated, as well and the leaf area index and slope. Simulation of daily nitrogen mineralization is achieved by considering the influence of all these factors on the optimum nitrogen mineralization rate estimated from published data (Chappell *et al.*, 1999). Daily soil temperature was calculated from air temperature as modified by the effects of the tree canopy, understory vegetation, litter mass, and depth of soil layer (Paul *et al.*, 2004). Daily nitrogen uptake was estimated as a function of root nitrogen concentration, soil temperature, and the amount of available soil nitrogen (Thornley, 1991) (Appendix A Eqn. 24).

Allocation and Growth (ALOGRO)

Allocation

Several reviews on carbon allocation have outlined the myriad of approaches to quantifying the sources of its variability; however, but no single solution is yet widely accepted (Lacointe, 2000; Barton, 2001; Litton *et al.*, in review). The 3-PG approach of maintaining a fixed NPP/GPP ratio and assuming empirical allometric ratios (Lansberg and Waring, 1997) is robust and provides realistic values; however, the ratio of NPP to GPP is obviously very influential on estimated dry matter productivity, and the allometric ratios available for many if not most species are based on empirical relationships in unmanaged stands. Similarly, Mäkelä (1997) maintained a constant ratio of foliage to fine root biomass to reflect an expected functional balance between the two, regardless of growing conditions. Carbon allocation, however, is highly sensitive to intensive management (e.g. Samuelson *et al.*, 2004), as well as to inherent site resource availability, particularly belowground (e.g. Keyes and Grier, 1981). Allocation conditional on site resource availability was, therefore, initially built into the model. A variety of approaches were examined, including those of Running and Gower (1991), Johnson and Thornely (1987), Kirschbaum (1999), and Landsberg and Waring (1997). Preliminary analysis, however, suggested that a modified 3-PG approach resulted in the highest correlation between simulated above-ground NPP and observed stem volume growth. The modifications to the 3-PG allocation approach involved estimation of the site fertility rating from canopy N percentage (Swenson *et al.*, 2005) and applying Duursma's and Robinson's (2003) correction for inherent bias when estimating stand-level biomass (or its allocation in this case) from stand-level mean tree size (Appendix A Eqn. 25). The site fertility rating estimated the amount of belowground allocation and was predicted with equation [2] of Swenson *et al* (2005):

[6.1] $FR = 0.1 * \ln(\text{soil N content}) - 0.2$

where FR is the soil fertility variable (0 – 1) and the soil N content was expressed as $g\ N\ m^{-3}$.

Disaggregating stand growth to individual trees

Disaggregating stand-level projections of growth to individual trees has been widely debated in the empirical growth and yield model literature (e.g. Qin and Cao, 2006). Process-based models have generally concentrated at the whole-stand level, so little work has been done on mechanistically disaggregating stand NPP to individual trees. Models such as BALANCE (Grote and Pretzsch, 2002) and MAESTRO (Wang, 1990) make highly detailed physiological calculations at the individual-tree level, but a simpler approach was desired for this model. Confronted with the same dilemma, Korol et al. (1995) developed a sophisticated algorithm to disaggregate stand NPP and allocate it to individual trees. Their approach was to divide the canopy into layers of equal leaf area index and within each layer, individual-tree radiation absorbance was estimated as a function of tree leaf area (Korol *et al.*, 1995). Allocation to each tree was based on the amount of radiation absorbed by that particular tree as well as an adjustment for hydraulic architecture (Korol *et al.*, 1995). Brunner and Nigh (2003) ran extensive simulations with a highly detailed light interception model to simulate individual-tree growth. A regression model was fitted to the data presented in Brunner and Nigh (2003). The final model predicted the mean proportion of incoming light absorbed by an individual crown as a function of its size, relative social position, and stand density (Appendix A Eqn. 27). This proportion was then multiplied by the tree leaf area, similar to the weighted leaf areas estimated by Brunner and Nigh (2003). Finally, whole-stand NPP was allocated to each tree based on its proportion of the total stand weighted leaf area. For comparison, disaggregation rules based on each tree’s unweighted proportion of stand leaf area and on the purely empirical approach of Zhang et al. (1993) were also tested.

Individual tree dimensions

Several methods were used to estimate individual tree diameter and height growth based on the portion of net primary production allocated to a tree. These methods included: differentiated allometric equations (Korol *et al.*, 1996; Kirschbaum, 1999; Zhang and Deying, 2003), pipe-model theory (Valentine and Mäkelä, 2005), and transport resistance model (Thornley, 1999). Vertical distribution of annual increment along the bole of an individual tree was predicted with an empirical equation similar in form to Ikonen et al. (2006) but re-parameterized for Douglas-fir (Weiskittel and Maguire, 2004). For comparison, predictions were also made with purely empirical equations (Weiskittel *et al.*, 2007) and the following hybridized form of these equations:

[6.2] $\Delta Y_{adj} = \Delta Y_{EMP} * (\beta_{ij} + \beta_{ij}*NPP + \beta_{ij}*\ln(NPP)) + \varepsilon_1$

where ΔY_{adj} is the adjusted growth rate (diameter or height), ΔY_{EMP} is the predicted growth from the empirical equation, the β_{ij}'s are annualized parameters to be estimated from an independent dataset for the jth equation (diameter vs. height). The modifier was not constrained between 0 and 1 because the original empirical equations of Weiskittel *et al.* (2007) were developed for plantations that had not received any thinning or fertilization treatments and in this study, they were being applied to plots with a variety of intensive management activities. The modifier was, therefore, expected to be above one for several plots. While Henning and Burk (2004) found no difference in predictions made by an additive versus a multiplicative equation form in their hybrid model, the multiplicative form performed better for Douglas-fir. Presumably this modifier represents the environmental effects and fundamental processes that impact site quality not captured in site index. In addition, it is a more parsimonious approach because predicting site index as a function of NPP (e.g. Baldwin *et al.*, 2001) required adjustments for stand density and age to ensure proper behavior.

Previous hybrid models have estimated crown recession as a function of crown coverage (e.g. Mäkelä, 1997), light availability (Nikinmaa and Hari, 1990), or a combination of the two (Valentine and Mäkelä, 2005). In this model, crown recession was predicted as the consequence of simulated individual branch dynamics (Weiskittel *et al.*, in review-b). This approach was shown to perform better than a static height to crown base equation.

Mortality

The literature review by Hawkes (2000) underscored the wide variety of approaches to simulating individual tree mortality. Mortality in ALOGRO was assumed to occur when individual tree growth efficiency (stem biomass increment/tree leaf area) fell below 0.20 kg m^{-2} yr^{-1} (Rosso and Hansen, 1998). Preliminary analysis suggested that this value resulted in excessive mortality so the threshold was reduced to 0.10 kg m^{-2} yr^{-1}. Performance of this approach was compared to that from an empirical model for estimating annual probability of individual tree mortality (Flewelling and Monserud, 2002).

Model verification

Study area

Data from nine Stand Management Cooperative (SMC; University of Washington) installations in Oregon and Washington, USA, comprised the verification and testing dataset (Figure 6.2). These installations covered a wide range of growing conditions that are typical for the region (Table 6.1). The overall climate is humid oceanic, with a distinct dry summer and a cool, wet winter. Twenty-year mean annual rainfall for these locations ranged from 150 to 315 cm and January mean minimum and July mean maximum ranged from -2.2 to 3.5°C and 21.3 to 26.3°C, respectively. Variation in precipitation and temperature were strongly related to elevation and distance from the coast. Elevation ranged from 25 to 300 m above sea level and all aspects were represented. Soils varied from a moderately-deep sandy loam to a very deep clay loam. The plantations were established between 1971 and 1982 at varying densities (905 to 1575 stems per ha) and levels of vegetation control.

Silvicultural regimes

Several sets of 0.2-ha permanent plots were established by the SMC at each installation between 1986 and 1992. Since establishment, the 56 plots have received a variety of silvicultural regimes that have involved thinning, pruning, and nitrogen fertilization (Table 6.2).

Plot measurements

All trees on each plot were remeasured for DBH every 4 years, and at each remeasurement a subsample of at least 40 Douglas-fir trees was also measured for total height and height to crown base. Four to eight years after plot establishment, current-year foliage was sampled from the upper crown of 12 trees in each plot, and analyzed for nutrient content.

Model simulations

The model assembled from BCACS, NPP, and ALOGRO was evaluated by simulating LAI and growth on each of the 56 SMC plots and comparing the predicted stem volume growth to observed periodic annual increment (PAI). Since observed LAI was not available, initial LAI of the plots was derived from BCACS and the three following approaches examined by Turner et al. (2000): (1) allometric function of DBH; (2) ratio of leaf area to sapwood area at breast height; and (3) ratio of leaf area to sapwood area at crown base. Although this assumes that PAI is a good proxy of LAI, this is a valid assumption in Douglas-fir as a previous analysis has found a highly linear relationship between LAI and PAI across a range of LAI values (Schroeder *et al.*, 1982). Given the uncertainty in carbon allocation patterns, the correlation between predicted NPP and PAI was also examined to indicate the relative magnitude of estimation error that may attributable to inaccuracy in estimating NPP vs. allocation of NPP to stemwood production. The same plots were also simulated in 3-PG (Landsberg and Waring, 1997) and SECRETS-3PG (Sampson *et al.*, 2006) after parameterizing for Douglas-fir with information presented by Waring and McDowell (2002). To estimate soil fertility index for 3-PG and SECRETS-3PG, the measured soil nitrogen percentage was converted to nitrogen content based on soil depth and estimated bulk density (Kaur *et al.*, 2002) (Appendix A Eqn. 23). This value for total nitrogen was then converted to the soil fertility index with the equation developed by Swenson *et al.* (2005). Climate information for the growth periods represented on the SMC plots was obtained from DAYMET (http://www.daymet.org).

Results

Stand-level growth

All four methods for estimating LAI led to simulated stem volume increments that were significantly correlated with observed PAI ($p<0.0001$). The relative strengths of these correlations, in descending order, were associated with LAI from the following: (1) sapwood area at crown base ($r = 0.81$; CBSAP); (2) regional allometric equation based on diameter at breast height ($r = 0.79$, Gholz *et al.*, 1979); (3) sapwood area at breast height ($r = 0.78$; BHSAP); and (4) summed branch predictions from BCACS ($r = 0.75$) (Figure 6.3).

Comparison of observed PAI and simulated stem volume increments indicated that LAI predicted from BCACS resulted in the lowest mean bias and lowest mean square error, followed closely by CBSAP (Table 6.3; Figure 6.3). The NPP algorithm described in this study performed significantly better than 3-PG when LAI was estimated by BCACS and CBSAP, but the reverse was true when LAI was estimated by either BHSAP or the regional allometric equation.

Across the silvicultural treatments, the hybrid model developed in this study improved predictions of volume growth in the control and thinned stands, but led to poorer predictions in the fertilized and fertilized + thinned stands (Figure 6.4). The predictions were significantly better than those obtained using 3-PG and SECRETS-3PG across all treatments.

Tree-level growth

Observed volume growth was significantly correlated with predicted volume growth under all four disaggregation methods. The relative strengths of these correlations, in descending order, were associated with disaggregation by: (1) weighted tree leaf area ($p<0.0001$; $r = 0.73$); (2) tree leaf area ($p<0.0001$; $r = 0.62$); (3) competition index (Korol *et al.*, 1995) ($p<0.0001$; $r = 0.49$); and (4) empirical allocation (Zhang *et al.*, 1993) ($p<0.0001$; $r = 0.46$). The level of bias from predicting diameter and height growth by the first three approaches was higher than that from a purely empirical approach; however, the hybrid approach developed in this study produced a level of bias comparable to the empirical approach, in large part due to its empirical basis. The hybrid model predictions modified empirical estimates as follows:

[6.3] $\Delta DBH_{adj} = \Delta DBH_{EMP} * (0.4078 + 0.1846*\ln(NPP))$

[6.4] $\Delta HT_{adj} = \Delta HT_{EMP} * (0.5192 + 0.2133*NPP - 0.0200*\ln(NPP))$

where ΔDBH_{EMP} and ΔHT_{EMP} are predicted diameter and height growing using the equations of Weiskittel et al. (2007). The equations suggest that the diameter growth modifier linearly increased with NPP and ranged from 0.41 to 1.05 (Figure 6.5). The height growth modifier linearly increased up to a NPP of 10 t ha^{-1} and then slowly decreased. These modifiers decreased the mean square error of diameter and height growth prediction by 3 and 12%, respectively. Tree mortality imposed when growth efficiency fell below the threshold produced final stand basal areas that were comparable to predictions with an empirical mortality equation (Figure 6.6); however, both approaches underpredicted mortality in stands with higher density.

Discussion

The goal of this project was to develop the framework for a hybrid model by incorporating features from both empirical and process-based models. These features were selected on the basis of their potential for enhancing the capacity for simulating responses to intensive silvicultural treatments and to variations in environmental conditions. Most of the parameters were gleaned from the literature, and the framework was intended to be useful to both researchers and forest managers. The framework also needed to be flexible enough to accommodate both improvements in modeling techniques and the increasing availability of physiological data. Although 3-PG is a simple and very effective model for simulating stand-level growth (e.g. Pinjuv *et al.*, 2006), its reliance on the radiation-use efficiency concept and environmental modifiers limit the model's capacity to clarify the role of important processes (e.g. nutrient uptake, interaction of water availability and photosynthesis). More explicit treatment of those processes facilitates future refinements and assessment. The framework developed here for Douglas-fir resembles many first-generation process-based models (reviewed by Ryan *et al.*, 1996b), but with some important refinements, including: (1) hierarchical treatment of growth at branch, tree and stand levels; (2) explicit representation of crown structure and function to drive growth processes; (3) incorporation of slope and aspect effects on canopy processes; (4) clear connection between water stress and reductions in photosynthesis; (5) patterns in light extinction that depend on stand structure; (6) net photosynthesis rates specific to foliage age classes; (7) prediction of tree mortality from a threshold growth efficiency; and (8) initiation from readily available information rather than subjective but very influential parameters or detailed and expensive physiological measurements.

The simulation results from the Douglas-fir hybrid model illustrated three important points regarding mechanistic hybrid models, namely: (1) their performance is sensitive and quite dependent on initial LAI estimates; (2) models with more details and finer resolution can significantly increase precision of growth predictions; and (3) a generic modeling approach that works in a variety of geographic regions will be difficult to develop satisfactorily. Process-based models usually require information on tree and stand biomass components other than the main stem, but estimating these components in usually not straightforward. Different methods for estimating LAI in Douglas-fir stands gave generally similar results for younger stands, but differed significantly in the older stands (Turner *et al.*, 2000). However, neither actual LAI nor the effects of intensive management were known or considered in their analysis. Allometric equations based only on DBH were significantly biased in young fertilized Douglas-fir plantations (Grier *et al.*, 1984). Although actual LAI was unknown in this study also, the degree of bias in the growth projections suggested that LAI estimated from crown size and location was superior to LAI estimated solely from DBH. This conclusion was not surprising given that most silvicultural treatments directly affect crown attributes (Brix, 1981b; Weiskittel *et al.*, in review-a).

With accurate estimates of LAI, the NPP model used in the Douglas-fir hybrid model had a much lower level of bias in its growth predictions than 3-PG and SECRETS-3PG (Sampson *et al.*, 2006). Given the range of stand structures and silvicultural treatments simulated in this study, 3-PG performed remarkably well, although it was strongly biased. Since the carbon allocation algorithms were quite similar in both models, the differences appear to be driven by the estimates of NPP. The Douglas-fir hybrid model of this study also benefited from the mean tree correction factor developed by Duursma and Robinson (2003). This correction accounted for variation in stand structure and reduced bias by a significant amount (~10-30%). Regardless, NPP predicted with 3-PG covered a very narrow range compared to the hybrid Douglas-fir model (e.g. Figure 6.4). When LAI is relatively high (>5) nearly 95% of all incoming radiation is intercepted and the RUE concept becomes harder to apply. Moreover, the relationship between intercepted radiation and NPP becomes less clear when stands have significant water stress (e.g. Raison and Myers, 1992), a condition routinely experienced by most Pacific Northwest plantations during the summer months. This prevalence of water limitations underscores the need to properly simulate the effects of soil and atmospheric water deficits on CO_2 fixation. Scalars that vary from zero to one in 3-PG and SECRETS-3PG are insufficiently flexible to capture net effect of daily water relations (Grant *et al.*, 2006). Finally, RUE treats direct and diffuse radiation in the same way, despite the fact that canopies processes behave differently under direct versus diffuse conditions (e.g. Rocha *et al.*, 2004). Schwalm et al. (2006) suggested that the ratio of diffuse to total PAR was a key predictor of the daily RUE across a variety of climate zone and vegetation types.

Unfortunately, many of the shortcomings of the Douglas-fir hybrid model are similar to those found by Ryan et al. (1996) in his assessment of several first-generation process-based models. Missing or poorly represented components include long-term controls on nitrogen mineralization, the uptake and allocation of nitrogen by plants, and the response of belowground allocation and respiration to changes in resource availability. Both CenW (Kirschbaum, 1999) and C&N-CLASS (Arain *et al.*, 2006) address many of the difficulties in modeling soil nutrient dynamics, but their level of required input on soil nitrogen and carbon stores significantly limit their wide application by forest managers. Predictions of nitrogen mineralization and uptake the hybrid model were simple and mechanistically sound, but their performance against observed responses could not be tested. Future refinements to this nutrient availability component and better representation of belowground processes in general will be needed to develop a hybrid model capable of simulating responses to intensive nutrient management.

Adding detail and complexity when modeling key physiological processes is not always a justified solution to improving accuracy. Respiration calculated under the Waring et al. (1998) assumption that NPP is a constant fraction of GPP produced the strongest correlation between NPP and observed stem volume growth. This simplification remains controversial (e.g. Mäkelä and Valentine, 2000; Litton *et al.*, in review); however, it is difficult to separate the effect of NPP/GPP assumptions alone from their interaction with the many other model components. For example, the poorer performance of the other NPP/GPP approaches examined in this study may be attributable to the effects of factors other than temperature on respiration. Guamont-Guay et al. (2006) found that drought played a more important role than temperature in explaining interannual variations in ecosystem respiration and its components (i.e. soil, bole growth and maintenance) in a boreal aspen (*Populus tremuloides*) stand. With regards to soil water balance, the Douglas-fir hybrid model simulated soil water balance with a single-layer tipping bucket approach (Schwalm and Ek, 2004). More complex approaches have been developed (Kirschbaum, 1999; Paul *et al.*, 2003) but their performance relative to simpler approaches has rarely been assessed. A relatively simple soil water balance model developed by Rötzer (2004) was compared to the performance of a more complex model presented by Grote and Pretzsch (2002), and the simpler model was found to be equally effective at predicting observed daily soil water balance (T. Rötzer, per. comm.). This result suggests that the simpler approach is adequate for most practical applications, particularly when detailed information on soil water dynamics is not needed. A major function of future hybrid modeling efforts will be finding the right balance between complexity and simplicity for meeting the objectives of the simulation model.

Current understanding of the key factors driving carbon allocation, dynamics of tree morphology, and mortality of individual trees is lacking. The carbon allocation approaches of many process-based models are built on the assumption that priorities exist for the products of photosynthesis (Running and Gower, 1991; McMurtrie and Landsberg, 1992; Kirschbaum, 1999); however, recent empirical evidence does not support the existence of such a priority (Litton *et al.*, in review). Further, it is commonly assumed that allocation to fine roots is driven by resource availability (Keyes and Grier, 1981; Santantonio and Hermann, 1985), but several studies of carbon allocation to fine roots have concluded that site fertility and fertilization have no effect (Vanninen *et al.*, 1996; King *et al.*, 1999; Retzlaff *et al.*, 2001; Carter *et al.*, 2004), and sometimes even an opposite effect to the generally reported greater allocation under conditions of lower fertility (Nadelhoffer *et al.*, 1985; Majdi and Andersson, 2005). Dean (2001) suggested that stand structure and its apparent influence on stem bending stress may drive belowground allocation processes, but the data to test this in Douglas-fir do not exist. New non-destructive research techniques may allow belowground allocation processes to better quantified in the future (e.g. Johnsen *et al.*, 2007).

Very few studies have linked the dynamics of tree morphology with individual tree net primary production. In this study, diameter growth was much more difficult to predict accurately than height growth. The increment in cross-sectional area of the tree bole has commonly been assumed to be proportional to the leaf area above a given height, implying that increment is constant below crown base (Mitchell, 1975; Mäkelä, 2002); however, empirical evidence has suggested a much more complex pattern along the bole (e.g. Kershaw and Maguire, 2000). Thornley (1999) linked diameter and height growth to carbon and nitrogen fluxes based on theoretical principles, but this approach performed poorly for predicting diameter growth for Douglas-fir. However, the relatively simple treatment of carbon and nitrogen dynamics in the model of this study may have been inadequate to accommodate Thornley’s (1999) approach. Equally limiting may have been the lack of links to climatic factors that actually drive diameter and height growth in this approach (e.g. Yeh and Wensel, 2000). For example, Bouriaud *et al.*(2005) found that the relationship between basal area increment at breast-height and annual stem biomass production was strongly influenced by climate, particularly drought. The Douglas-fir hybrid model circumvents this problem, but relies on an empirically derived modifier function that may not extrapolate well to new conditions. This approach does, however, increase the flexibility of the empirical equations by allowing them to be modified by factors such as climate, soil, and edaphic characteristics, which all directly influence NPP. The modifiers suggest that individual tree diameter growth logarithmically increases with NPP, while height growth peaks at a relatively low NPP (~10 t ha^{-1}) and then decreases. This pattern is consistent with the general observations that diameter growth allocation is increased when conditions are favorable (e.g. fertilization, thinning) and height growth allocation is increased when conditions are less favorable (e.g. high competition). The decrease in the height growth modifier is unexpected, but may suggest that the empirical equation overestimates growth at more productive sites.

The performance of hybrid models relative to purely empirical models has varied. Baldwin (2001) reported a ~97% improvement in the prediction of 15-year stand volume growth by a hybrid model when compared to an empirical counterpart. Pinjuv et al. (2006) reduced mean square error of predicting stand basal area by ~4% moving to a hybrid model. Dzierzon and Mason (2006) achieved a reduction of 14 and 8% with a hybrid model for stand basal area and top height growth, respectively, across *Pinus radiata* plantations in New Zealand. At the individual tree level, Schwalm and Ek (2004) had a level of bias comparable to an empirical model when predicting diameter growth over a 25-yr period with a hybrid model, but the latter significantly improved mean prediction error for height growth. Henning and Burk (2004) showed that a hybrid model did not improve mean square error of predicted diameter growth when compared to an empirical model, but it did significantly decrease the mean bias by nearly 50%. Although they did not compare performance directly to an empirical model, Rötzer *et al.* (2005) simulated diameter growth with the hybrid model BALANCE and obtained discrepancies of 1 to 23% from actual diameters after 7-8 years of simulation. The Douglas-fir hybrid model gave results similar to Schwalm and Ek (2004), with a level of bias in diameter growth comparable to the empirical model, but with significantly improved height growth predictions. Again, it is important to mention that these reported improvements with the use of hybrid models should be expected given that they utilized information (i.e. observed weather records) not used by their empirical counterparts. A real test of a hybrid model should be how well it performs over key variables such as precipitation, soil properties, and foliar N levels.

Neither empirical nor process-based models have found a totally satisfying approach to predicting individual tree mortality with the desired level of accuracy (Hawkes, 2000). In hybrid models, mortality has been predicted from: (1) a minimum crown ratio (Valentine and Mäkelä, 2005); (2) a increasing function of crown coverage (Mäkelä, 1997); (3) empirical functions of tree size (Schwalm and Ek, 2004); and (4) carbon-based algorithms. Despite their appealing mechanistic basis, carbon-based algorithms have not performed well (Hawkes, 2000). Mäkelä and Hari (1986) found that their mechanistic approach to mortality generated a decline in accuracy when compared to empirical approaches. Running (1994) indicated that FOREST-BGC should not be run longer than 100 years because mortality predictions became too unrealistic. The major obstacles to a carbon balance approach are probably the difficulty in accurately estimating respiration and uncertainty about the tree's ability to store reserves. In the Douglas-fir hybrid model, a threshold growth efficiency performed comparably to an empirical model for predicting probability of mortality, at least in the short-term. The growth efficiency threshold has several advantages: (1) thresholds may be less site- or species-specific than other approaches; (2) low growth efficiency is a sign of a stressed tree; (3) growth efficiency inherently reflects climatic variation; and (4) growth efficiency declines with age so size and age do not have to be explicitly included as predictors (Hawkes, 2000). The growth efficiency approach showed promise in the Douglas-fir hybrid model, but similar to the empirical equation, it underpredicted mortality at the higher stand densities. The increased availability of intensively managed Douglas-fir plantation growth and yield data with estimates of individual tree leaf area from LiDAR in the upcoming years will allow further assessment of this approach for predicting long-term trends in mortality.

Although growth projections are similar to a purely empirical model, the hybrid model developed in this study also provides information on stand attributes beyond just growth and mortality. For example, the major aspects of wood quality such as branch number, size, and location as well as bole sapwood and heartwood contents are readily available. However, predictions using the sawing simulator AUTOSAW have shown these attributes to be poorly correlated to wood quality in young Douglas-fir plantations (Todoroki *et al.*, 2005; Weiskittel *et al.*, 2006b). The hybrid model framework presented here also lends itself well to simulating the effects of climate and site edaphic characteristics on tree ring attributes such as earlywood/latewood proportion and wood density, which may be the primary drivers of recovered wood quality in these current plantations. Information was unavailable to parameterize the mechanistic wood quality models of Deckmyn *et al.* (2006) or Deleuze and Houllier (1998). Further, recent empirical evidence has suggested Douglas-fir ring attributes have a complex relationship with variations in climate and site edaphic characteristics (e.g. Bower *et al.*, 2005).

Future improvements for this model at the individual tree level will be the result of: (1) developing growth modifiers from annual growth measurements on destructively sampled stems rather than by annualizing growth from periodic plot remeasurements; (2) better representing the effects of climate and site edaphic characteristics on tree ring characteristics (e.g. Deckmyn *et al.*, 2006), particularly density, thereby refining the conversion of stem biomass increment to volume increment; and (3) further quantifying the relationship between tree growth efficiency and its probability of mortality.

Conclusions

Hybrid models have been proclaimed as the next step forward for improving growth projections for managed stands (e.g. Landsberg, 2003b). The hybrid modeling framework combines the strengths of both empirical and process-based models. The hybrid model constructed here for intensively managed Douglas-fir plantations in the Pacific Northwest significantly improved predictions of LAI and CAI compared to other modeling approaches. At the individual tree-level, disaggregation of NPP and prediction of stem diameter and height growth were improved. In addition, imposing mortality when growth efficiency fell below a threshold value predicted mortality at a level of accuracy comparable to empirical approaches. These improvements resulted directly from: (1) more detailed representation of crown structure and dynamics; (2) inclusion of key physiological mechanisms at an appropriate spatial and temporal resolution; and (3) application of empirical equations modified by simulated NPP to predict diameter and height growth of individual trees rather than relying on allometric or theoretical equations. Areas of future improvement for these types of models include: (1) components that simulate the effects of soil water and nutrients on physiological processes, particularly respiration and carbon allocation, in a simple yet mechanistic manner; (2) components that account for the effects of silvicultural treatment and environmental conditions on foliage age class dynamics, so that seasonal variation in LAI and net photosynthesis can be simulated more accurately; and (3) rigorous assessment of the relationship between growth efficiency and probability of individual tree mortality.

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Table 6.1. Stand physiographic and soils features for the 9 Stand Management Cooperative plots located in Oregon and Washington that were used for model verification in this study.

Stand	Elevation (m)	% Slope	Aspect	Soil depth (m)	% silt in soil	% clay in soil	% rock content in soil
704	182.8	20	270	0.76	35	35	25
705	250.8	30	180	0.76	25	10	30
708	300	5	0	0.64	25	10	35
713	73.4	5	180	0.76	40	20	50
718	102.1	10	180	1.01	55	35	10
722	204.2	10	270	0.66	40	20	20
725	50.9	0	180	0.64	25	10	0
726	27.3	10	225	0.89	55	20	0
736	54.8	40	270	0.61	40	20	35

Table 6.2. Description of the silvicultural regime for 56 Stand Management Cooperative plots used for model verification. ISPA is for initial spacing.

Stand	Plot	Silvicultural regime	Canopy foliar %N 4-8 years after treatment
704	6	ISPA	1.62
	7	ISPA/2, fertilize with 225 kg ha^{-1} every 4 years	1.98
	8	ISPA/4	1.57
	9	ISPA, repeated thinning	1.74
	10	ISPA/2	1.64
	11	ISPA/4	1.85
705	1	ISPA/2	2.41
	3	ISPA, repeated thinning	1.31
	4	ISPA/4	1.94
	6	ISPA/2	1.76
	9	ISPA, repeated thinning, fertilize with 225 kg ha^{-1} every 4 years	2.19
	10	ISPA/4, fertilize with 225 kg ha^{-1} every 4 years	1.67
	12	ISPA	1.66
708	3	ISPA, repeated thinning, fertilize with 225 kg ha^{-1} every 4 years	1.90
	4	ISPA, repeated thinning	1.72
	7	ISPA/2, fertilize with 225 kg ha^{-1} every 4 years	2.14
	9	ISPA/2	1.78
	10	ISPA/4	2.02
	12	ISPA/4, fertilize with 225 kg ha^{-1} every 4 years	2.16
713	1	ISPA	1.26
	2	ISPA/4	1.38
	4	ISPA/2	1.75
	10	ISPA/2, fertilize with 225 kg ha^{-1} every 4 years	2.01
	11	ISPA/4, fertilize with 225 kg ha^{-1} every 4 years	2.19
	12	ISPA, repeated thinning, fertilize with 225 kg ha^{-1} every 4 years	2.25
718	1	ISPA, repeated thinning, fertilize with 225 kg ha^{-1} every 4 years	1.97
	2	ISPA, repeated thinning	2.15

	3	ISPA/2, fertilize with 225 kg ha-1 every 4 years	1.93
	5	ISPA/2	1.60
	7	ISPA/4, fertilize with 225 kg ha-1 every 4 years	2.05
	14	ISPA/4	1.54
722	1	ISPA	1.51
	2	ISPA/4	1.55
	3	ISPA/2	1.42
	10	ISPA, repeated thinning, fertilize with 225 kg ha-1 every 4 years	1.95
	11	ISPA/2, fertilize with 225 kg ha-1 every 4 years	1.79
	12	ISPA/4, fertilize with 225 kg ha-1 every 4 years	1.84
725	1	ISPA	1.38
	3	ISPA/2	1.50
	7	ISPA/4	1.41
	8	ISPA/4, fertilize with 225 kg ha^{-1} every 4 years	1.82
	9	ISPA, repeated thinning, fertilize with 225 kg ha-1 every 4 years	1.82
	10	ISPA/2, fertilize with 225 kg ha-1 every 4 years	1.60
726	4	ISPA, repeated thinning	2.26
	6	ISPA/2	2.37
	7	ISPA/4	2.44
	8	ISPA/2, fertilize with 225 kg ha-1 every 4 years	2.47
	9	ISPA, repeated thinning, fertilize with 225 kg ha-1 every 4 years	2.75
	10	ISPA/4, fertilize with 225 kg ha-1 every 4 years	2.97
736	1	ISPA/4	2.02
	4	ISPA, repeated thinning	1.76
	7	ISPA, repeated thinning, fertilize with 225 kg ha-1 every 4 years	2.30
	8	ISPA/2, fertilize with 225 kg ha-1 every 4 years	2.02
	9	ISPA/4, fertilize with 225 kg ha-1 every 4 years	1.98
	12	ISPA/2	1.95

Table 6.3. Mean bias, mean square error (MSE), and r-square (r^2) for observed and predicted stand-level current annual increment (CAI; $m^3\ ha^{-1}$) on 67 intensively managed Douglas-fir Stand Management Cooperative plots in Oregon and Washington. Predicted CAI was obtained using 4 foliage biomass imputation methods and 3 net primary production models (NPP).

	Method used for estimating foliage biomass											
	Gholz et al. (1979)			**BHSAP[1]**			**CBSAP[2]**			**BCACS[3]**		
NPP Model	**Mean Bias**	**MSE**	**r^2**	**Mean Bias**	**MSE**	**r^2**	**Mean Bias**	**MSE**	**r^2**	**Mean Bias**	**MSE**	**r^2**
This study	6.2544	6.5197	0.60	3.4189	4.5839	0.50	1.7941	3.2703	0.76	0.8078	2.9405	0.67
3-PG[4]	3.1803	4.2468	0.70	2.4066	4.0809	0.71	1.8146	4.1833	0.38	-1.5117	4.1166	0.24
SECRETS 3-PG[5]	-	-	-	-	-	-	-	-	-	1.03475	5.7273	0.32

[1] constant amount of leaf area per unit of predicted sapwood area at breast height (Turner *et al.*, 2000)

[2] constant amount of leaf area per unit of predicted sapwood area at crown base (Turner *et al.*, 2000)

[3] Branch, Crown, And Canopy Simulator (this study)

[4] Landsberg and Waring (1997)

[5] Sampson et al. (2006)

Table 6.4. Mean bias, mean square error (MSE), and percent (%) bias for individual tree predictions of diameter and height growth on 56 Stand Management Cooperative plots with varying levels of silvicultural treatments located throughout the Pacific Northwest, USA.

	DBH (n = 8860)			**HT (n = 2805)**		
Approach	**Mean bias**	**MSE**	**% bias**	**Mean bias**	**MSE**	**% bias**
1. Empirical (Weiskittel *et al.*, 2007)	-0.01	1.22	-0.61	-0.56	0.96	-3.76
2. Allometric (Kirschbaum, 1999)	1.24	1.63	4.97	-0.42	1.30	-3.87
3. Pipe-model (Valentine and Mäkelä, 2005)	3.07	3.25	13.04	-2.52	3.43	-19.78
4. Thornley (1999)	-3.75	3.91	-20.63	-0.06	1.28	-1.41
5. Hybrid	0.53	1.18	1.99	0.15	0.85	1.04

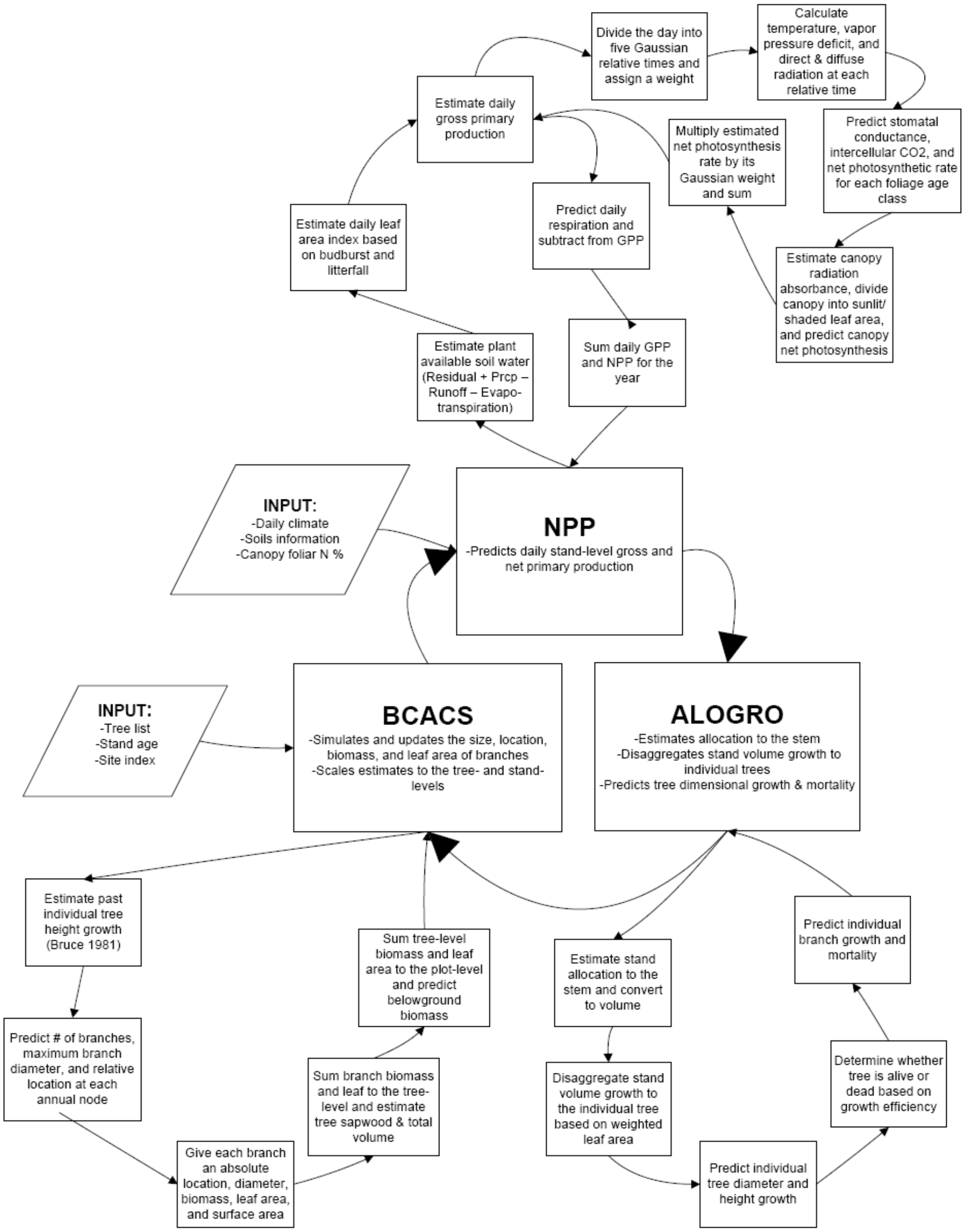

Figure 6.1. Components of the modeling framework used in this study.

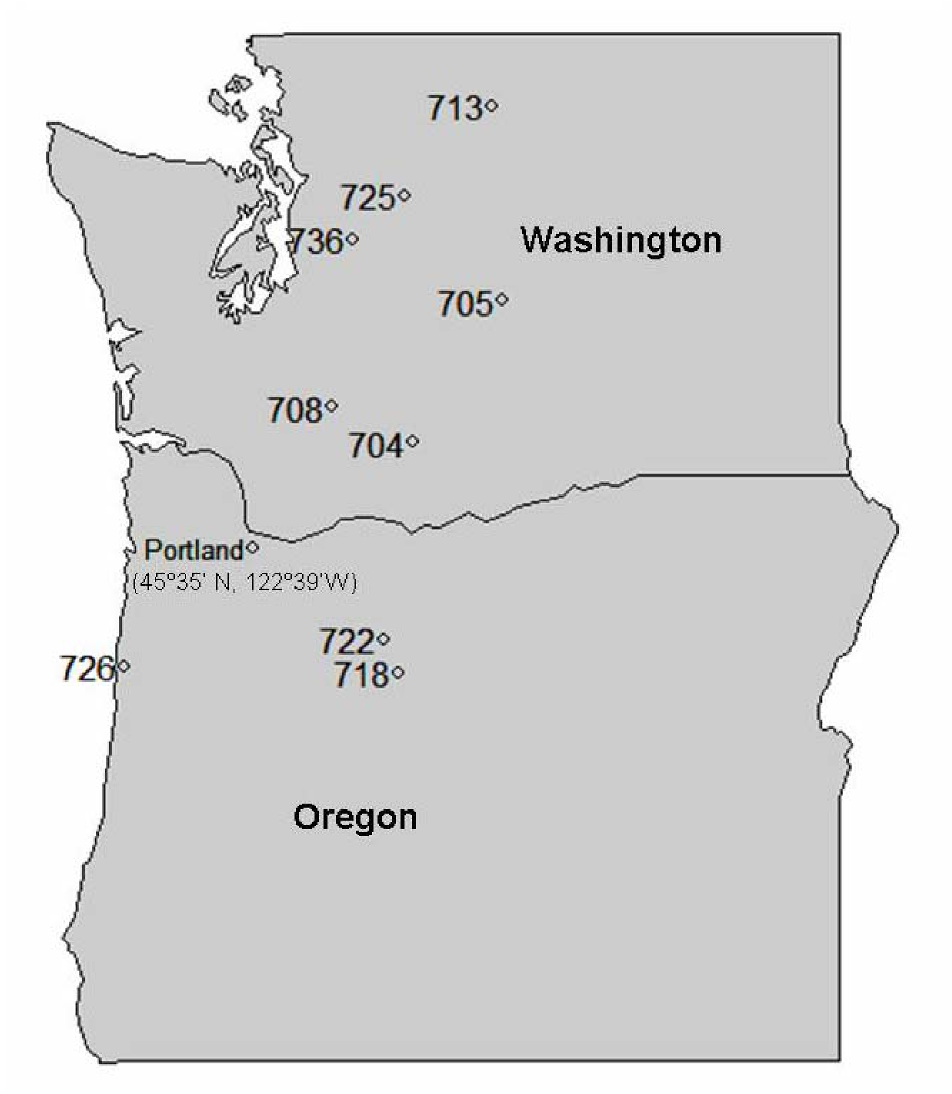

Figure 6.2. Location of Stand Management Cooperative installations in Oregon and Washington used for model verification.

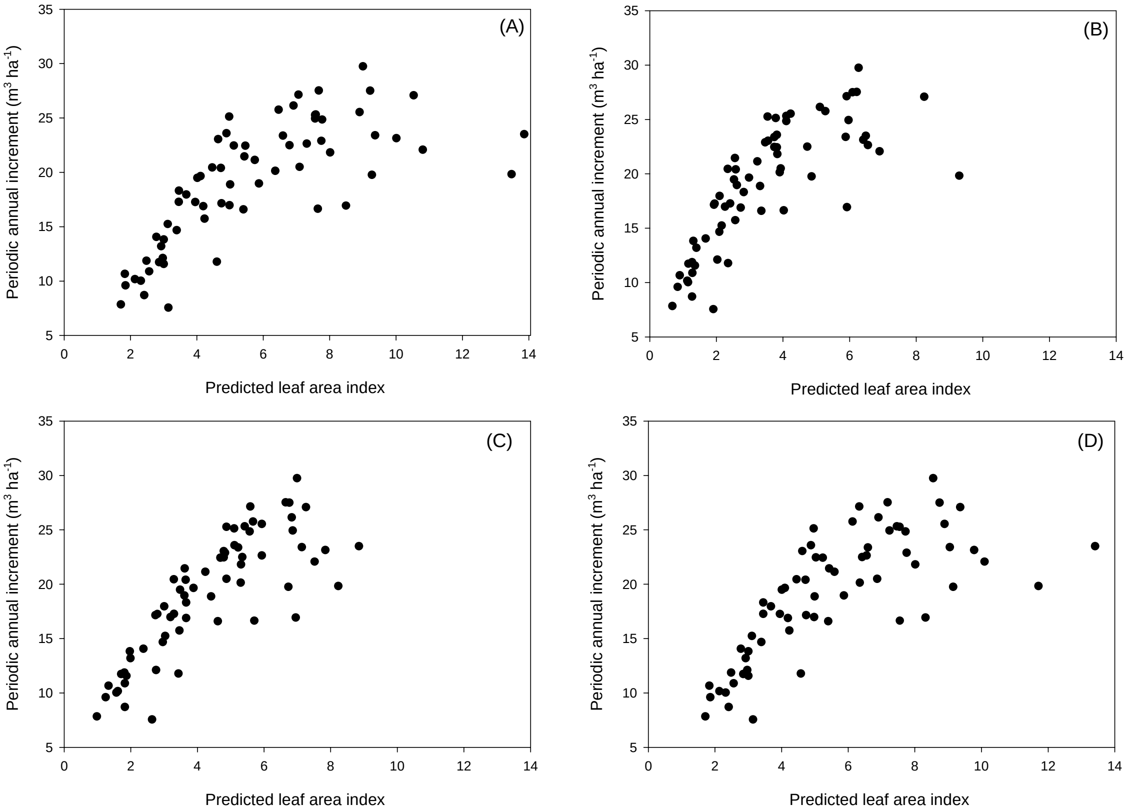

Figure 6.3. Relationship of predicted leaf area index and observed periodic annual increment (PAI; m^3 ha^{-1}) using four different techniques, which included: (1) constant leaf area per unit of sapwood area at crown base (graph A; CBSAP); (2) constant leaf area per unit of sapwood area at breast height (graph B; BHSAP); (3) regional allometric equation on diameter at breast height (graph C; Gholz *et al.* 1979); and (4) output from the Branch, Crown, And Canopy Simulator (graph D; BCACS).

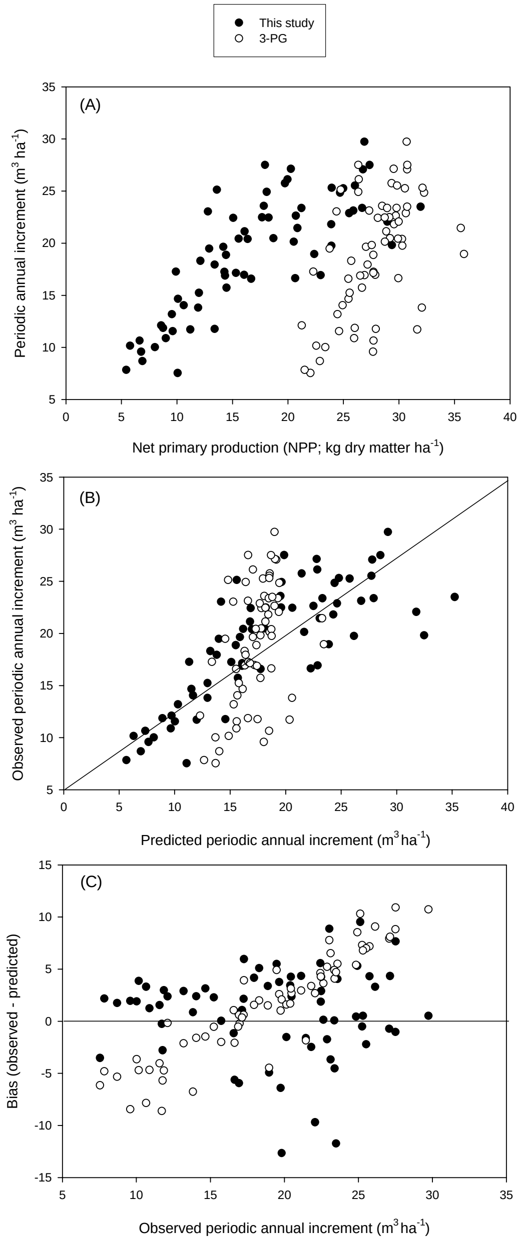

Figure 6.4. Plots of: (A) net primary production (NPP) and periodic annual increment (PAI; m^3 ha^{-1}) for the NPP algorithm described in this study and 3-PG, (B) predicted and observed PAI; and (C) bias (observed – predicted) over observed PAI.

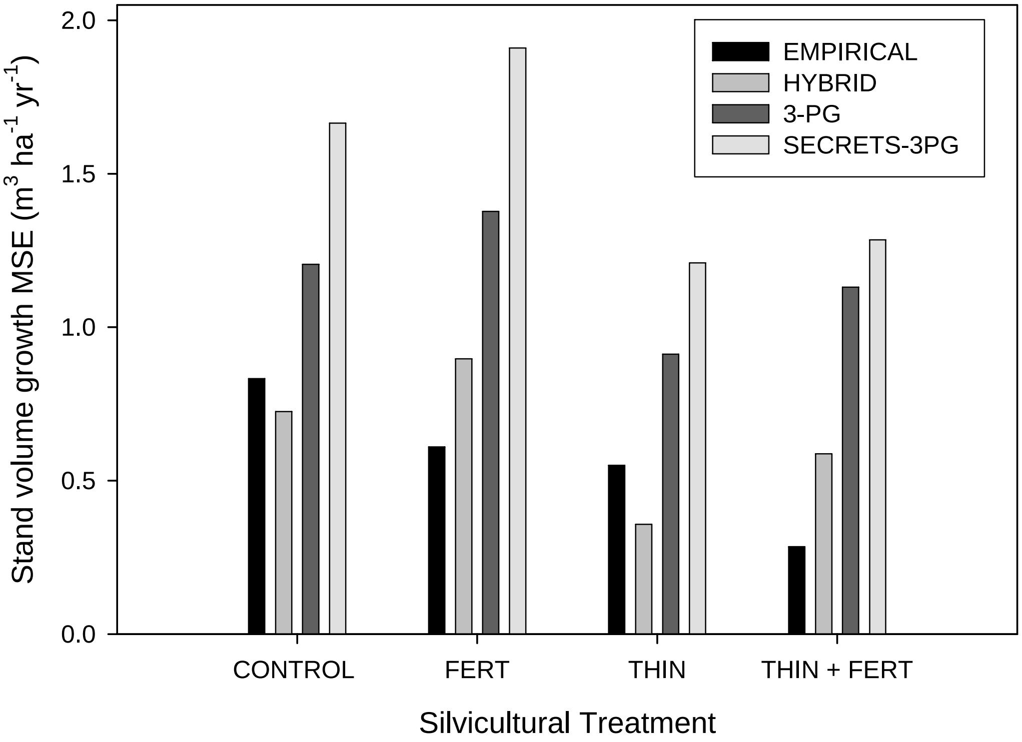

Figure 6.5. Mean square error of predicted 4-year volume growth (m^3 ha yr^{-1}) by silvicultural treatment. The four models used were an empirical one (Weiskittel *et al.*, 2007), the hybrid model developed in this study, 3-PG (Landsberg and Waring, 1997), and SECRETS-3PG (Sampson *et al.*, 2006).

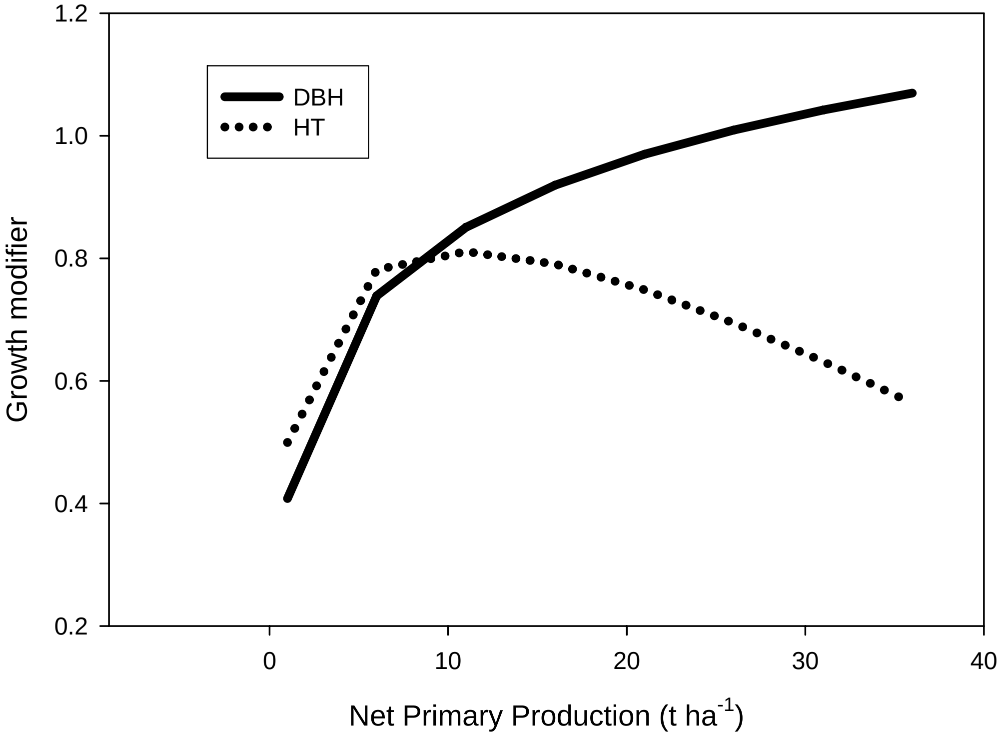

Figure 6.6. Predicted diameter at breast height (DBH) and height growth modifier as a function of simulate net primary production (NPP; t ha^{-1}) using equations [6.3] and [6.4].

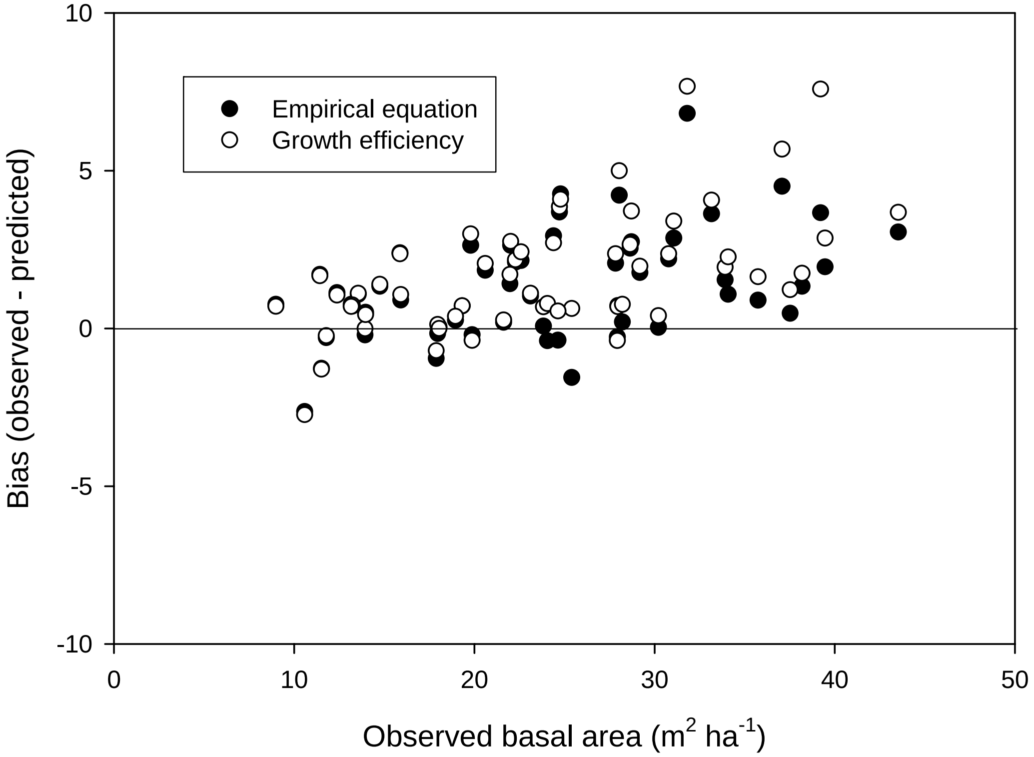

Figure 6.7. Bias (observed – predicted) in stand basal area (m^2 ha^{-1}) on 56 Stand Management Cooperative plots with varying levels of silvicultural treatments located throughout the Pacific Northwest, USA after 4 years of simulation using an empirical mortality equation and the growth efficiency concept.

CHAPTER 7: CONCLUSION

The goal of this dissertation was to improve the ability of individual tree growth and yield models in the Pacific Northwest (PNW) to simulate the effects of intensive Douglas-fir plantation management by testing several alternative formulations. In the process, research on the influence of intensive management on Douglas-fir crown structure and dynamics was initiated and completed. Preliminary hypotheses regarding the inability of current PNW growth and yield models to predict the response of stands to intensive management that motivated this work were: (1) a model time-step (e.g. 5 – 10 years) too long to capture the highly dynamic response of stands following silvicultural treatments; (2) a simplified treatment of crown structure and dynamics; and (3) reliance on site index to capture potential productivity due to favorable climatic, soils, and site edaphic characteristics. Specific objectives of this dissertation were to: (1) annualize diameter and height empirical growth equations; (2) develop equations to describe Douglas-fir crown structure (i.e. branch number, size, angle, and frequency); (3) describe trends in branch diameter radial growth and mortality in intensively managed plantations and fit predictive equations; and (4) synthesize knowledge gained from the previous three objectives with information on key physiological processes in a hybrid modeling framework.

Chapter 2 reviewed the literature on modeling important key physiological processes and their integration into hybrid models. It was found that the models differed drastically in their approach to predicting respiration, carbon allocation, and individual tree dimensional growth and mortality. The models did converge on certain techniques for simulating light interception [Beer's Law], stomatal conductance [Jarvis (1976) style empirical equation], and leaf net photosynthesis [Farquhar *et al.* (1980) biochemical equation]. Overall, hybrid models showed the potential to increase the accuracy of growth predictions relative to purely empirical approaches and offered several other advantages. These included: (1) assessing the effects of climate, soils, and other edaphic characteristics on growth in a mechanistic manner; (2) provide output on plantation attributes beyond just growth and mortality such as carbon sequestration, wood quality, and hydrology budgets; and (3) identify areas of future research across a range of disciplines.

Chapter 3 assessed the influence of fertilization, commercial thinning, precommercial thinning (PCT), Swiss needle cast (SNC), and varying levels of vegetation management on Douglas-fir crown structural attributes. Branch angle and frequency were found to be insensitive to these varied stand conditions, while branch diameter and length were quite sensitive to them. Fertilization increased branch diameter in the upper portion of the crown and thinning led to great branch diameters in the lower portion of the crown, but the effects were highly dependent on the time since treatment. Although statistically significant, the absolute effects of Swiss needle cast and vegetation management on branch size were minimal. The predictive equations developed from this dataset performed significantly better than previous equations presented in Maguire *et al.* (1994; 1999).

Chapter 4 used the extensive PNW plantation datasets to construct annualize individual tree diameter and height growth equations for Douglas-fir, western hemlock, and red alder using the technique of Cao (2000). Model fits and predictive performance were significantly improved with the use of multilevel mixed effects (MLME) regression. This technique also allowed separation of the variance attributable to different hierarchical levels (i.e. installation, plot, year, tree) present in the data. The random effects at the installation level were related to variables describing site mean climate, soils, and edaphic characteristics. The observed relationships were fairly weak for Douglas-fir and red alder ($R^2 < 0.35$) and nonexistent for western hemlock. Both Douglas-fir and red alder diameter growth random effects showed more correlation with these factors than height growth. Overall, site slope, aspect, and soil attributes were better predictors of the installation random effects than climate. Using the developed equations with a previously constructed annual individual tree mortality equation on an independent Douglas-fir dataset indicated that the annualized equations, particularly those fitted with MLME, achieved a level of bias significantly lower than a similar regional model with a 5-year time-step after 12 – 16 years of simulation.

Chapter 5 remeasured a subsample of the branches presented in Chapter 3 to develop dynamic branch growth and mortality predictive equations. In addition, these dynamic branch equations were connected to the individual tree growth equations developed in Chapter 4 to assess their ability to improve estimates of crown recession across a range of stand conditions. Both branch growth and mortality were quite sensitive to stand conditions imposed by intensive management and Swiss needle cast. In the SNC/PCT dataset, branch growth and longevity was significantly reduced by SNC, while PCT only significantly increased branch growth in the heavily thinned treatment (~250 trees per ha) 8 years after the thinning. The influence of fertilization and commercial thinning on both branch diameter growth and mortality were highly dynamic and dependent on the time since thinning. For example, fertilization initially increased branch diameter growth when compared to the control, but led to slower growth rates 2-3 years following the treatment. In contrast, commercial thinning reduced branch diameter growth rates 1 year after the treatment when compared to the control, but growth was significantly higher several years after the treatment. Even 10-12 years following varying levels of vegetation management, significant differences in branch mortality, but not branch growth, were observed. Removal of only the herbaceous 1-2 years following planting significantly increased the probability of individual branch mortality. Complete removal of the woody vegetation and total vegetation control decreased the probability of individual branch mortality. When the datasets were combined, both branch diameter growth and mortality were significantly related to branch- and tree-level variables, particularly branch size and location, tree crown size, and tree social position in the stand. Overall, branch mortality was more predictable than branch diameter growth. Inclusion of the branch diameter growth and mortality into an individual tree growth and yield simulator significantly increased predictions of short-term crown recession. This improvement increased the precision of height growth predictions, but led to poorer predictions of diameter growth. This suggests that better representation of crown dynamics in individual tree models can led to improvements, but diameter and height empirical growth modifiers are likely necessary model components to simulate the effects of silviculture treatments accurately.

Chapter 6 attempted to develop a hybrid modeling framework for intensively managed Douglas-fir plantations in the PNW. The foundation of the model was a hierarchical treatment of key processes at multiple levels including the individual branch-, whorl-, tree-, and stand-levels. This type of approach significantly improved predictions of stand-level leaf area index and current annual increment when compared to other models. At the individual tree-level, the use of empirical growth equations coupled with a process-based derived modifier led to modest improvements in predictions when compared to a purely empirical approach. In addition, the use of growth efficiency as a predictor of individual tree mortality was just as effective as an empirical equation. Overall, the modeling framework showed great potential and can be significantly improved upon by future research.

Future directions

Model development is an effective way for identifying areas for future research. Several areas of future research were identified in this region, namely (1) physiology; (2) wood anatomy; and (3) mechanistically understanding individual tree growth and mortality. Specific needs for each of the research topics is given below.

Physiology

The growth and yield of PNW Douglas-fir plantations has been well studied (e.g. Curtis and Marshall, 2004), but physiological research in these type of stands is lacking. Although physiological research on Douglas-fir seedlings (Warren *et al.*, 2004; Manter *et al.*, 2005) and old-growth stands (Bond and Franklin, 2002; McDowell *et al.*, 2002b) is quite extensive, the number of physiological studies in intensively managed PNW Douglas-fir stand is relatively small. This is in direct contrast to the physiological understanding of the response of southern pines to intensive management (Maier, 2001; Will *et al.*, 2001; Lai *et al.*, 2002; Samuelson *et al.*, 2004). The most important physiological areas needing attention are: (1) photosynthesis; (2) stomatal and transfer conductance; (3) nutrient uptake and allocation; and (4) carbon allocation.

Douglas-fir photosynthesis received a significant amount of attention in the 1960's and 1970's (Helms, 1963; Brix and Ebell, 1969; Woodman, 1971), but the scope of inference is these studies tended to be quite small and predictive equations were rarely presented. Parameters needed for the Farquhar *et al.* (1980) biochemical equation are difficult to find for Douglas-fir when compared to other species (e.g. Wullschleger, 1993), particularly for each individual foliage age class. Ethier *et al.* (2006) recently parameterized the Farquhar *et al.* (1980) biochemical equation for Douglas-fir by foliage age class, but the final predictive equations were not presented. Further, the response of these parameters to changes in foliar nitrogen levels is needed as Manter *et al.* (2005) showed a curvilinear relationship and Ripullone *et al.* (2003) indicated a linear relationship.

Similar to photosynthesis, extensive research on Douglas-fir stomatal conductance was conducted in the 1970's and 1980's (Tan and Black, 1976; Livingston and Black, 1987; Price and Black, 1987). Although these studies generally developed predictive equations that could be easily incorporated into a process-based model, they were limited to stands in British Columbia, which has distinctively different summer precipitation than Oregon or Washington. Give the importance of stomatal conductance for controlling tree response to drought (e.g. Bréda *et al.*, 2006), future research in on this topic needs to address stomatal behavior in Oregon and Washington Douglas-fir plantations. Further, there is increasing evidence that transfer rather than stomatal conductance is the primary limiting processes to photosynthesis under water stress and relatively little research has been conducted on the mechanisms controlling its variation (Warren and Adams, 2006).

Estimates of stand-level nutrient uptake and allocation are scarce for Douglas-fir. Heilman and Gessel (1963) estimated nitrogen uptake on several unfertilized and fertilized stands in the PNW, but the mechanisms driving their observations were not examined. Thus, understanding nutrient uptake requires information on fine root dynamics, decomposition, and nitrogen mineralization, which are difficult, expensive, and tedious research tasks (Tingey *et al.*, 2004; Meehan, 2006). A linear relationship between stand net primary production and nutrient uptake has been found in a variety of forest types (Miller, 1995; Norby and Iversen, 2006). Quantification of this type of relationship in intensively managed PNW Douglas-fir plantation would be very beneficial and an excellent first step.

Numerous studies have examined the distribution of stand biomass in Douglas-fir (Dice, 1970; Ranger *et al.*, 1995; Mitchell *et al.*, 1996). Quantifying

Douglas-fir biomass production and its allocation between stand components has received less attention. The few studies that have examined carbon allocation have been limited to a small range of stand conditions (Keyes and Grier, 1981; Kurz, 1989; Chan *et al.*, 2002). Mechanistically understanding carbon allocation patterns would require several samples at a given site and replication across the landscape. The Stand Management Cooperative Type I installations offer an excellent opportunity to examine the influence of silvicultural treatments and inherent site conditions on carbon allocation. A new non-destructive research techniques (e.g. Johnsen *et al.*, 2007) offers an opportunity to effectively and efficiently quantify this critical process across the landscape.

Physiological research on intensive plantations in the PNW has been relatively slow when compared to other regions. The development of long-term concentrated research plantations such as the 'Garden of Eden' experiment in Northern California (Powers and Ferrell, 1996) and SouthEast Tree Research and Education Site (SETRES) in North Carolina (Albaugh *et al.*, 2004) has helped to strength applied physiological research in these regions. Similar type of study sites in the PNW have been slow to develop, but the Fall River Long-Term Productivity Study in coastal Washington (Harrington *et al.*, 2005) is an excellent example of their potential in this region. Multi-agency efforts such as Fall River will be the most effective and efficient manner for addressing the physiological research shortcoming in this region.

Wood anatomy

Prediction of wood anatomical features with a hybrid model is an important feature of this type of modeling framework. The capacity of hybrid models to accomplish this has been previously demonstrated by Deckmyn *et al.* (2006) and Deleuze and Houllier (1998). Data on important wood properties such as density and early- and late-wood proportion by ring were unavailable for Douglas-fir. Further, the influence of climate and site edaphic features on Douglas-fir wood anatomy has varied. For example, Robertson *et al.* (1990) found that site's annual water deficit accounted for over 50% of the original variation in ring weight, while Bower *et al.* (2005) showed that ring variables are sensitive to drought, but the pattern of their response is highly variable and not very predictable. In addition, Acuna and Murphy (2006) recently concluded that aspect, elevation, and latitude did not significantly influence wood density. A limited amount of research has also been conducted on the influence of intensive management on Douglas-fir wood anatomical features. Jozsa and Brix (1989) found that both thinning and fertilization significantly reduced ring density, but their study was limited to a poor site on Vancouver Island, British Columbia. Collection of this type of information on more sites will help to clarify the mechanisms influencing wood development and allow further incorporation into the hybrid modeling framework presented in this dissertation.

Tree growth and mortality

A mechanistic understanding of individual tree growth and mortality has been limited because it often requires detailed measurements on leaf area and its vertical distribution within the crown, which is difficult, expensive, and tedious. A simple linear relationship between leaf area and growth that is commonly assumed by the pipe-model (e.g. Mäkelä, 2002), however, has a limited predictive ability when compared to actual data (e.g. Kershaw and Maguire, 2000). This suggests that tree growth is a complex interaction between leaf area, climate, and site edaphic characteristics. A similar generalization can also be made about individual tree mortality. The continued development of digital imagery technologies such as LiDAR, which has been shown to be an effective method for assessing individual tree leaf area and growth (e.g. Magnussen and Boudewyn, 1998), offers a potential to collect this type of information over much wider spatial and temporal scales than previously available. The remeasurement of individual tree leaf area, growth, and status (i.e. live or dead) on permanent plots in the PNW should help to identify key factors influencing their relationship and allow them to be better modeled.

Summary

Quantitative models are important tools in forestry that help to predict future conditions, understand important processes, and identify areas of future research. This dissertation explored the potential of a hybrid modeling framework for predicting the influence of intensive management on Douglas-fir growth and yield. In the process, fundamental research on refining the individual tree growth equations and the influence of intensive management on Douglas-fir crown structure and dynamics was completed. The completed hybrid modeling framework presented in this dissertation showed great potential and a number of important uses when compared to a more traditional empirical model, but further research on Douglas-fir physiology, wood anatomy, and individual tree growth and mortality is needed to refine the model.

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APPENDIX A

DETAILED DESCRIPTION OF THE HYBRID MODEL

Branch, Crown, And Canopy Simulator (BCACS)

BCACS first estimates the expected number of years to breast height based on the user supplied site index value and the equation of Nigh and Mitchell (2003). Height of each annual whorl is then estimated based on the Bruce (1981) dominant height growth equation as presented in Nigh and Mitchell (2003). Maximum branch diameter, the total number of branches (live + dead), live branches, whorl, and interwhorl branches were predicted at each whorl with empirical equations of Weiskittel *et al.* (in review-a). The relative location of branches along the bole were predicted using the empirical distribution presented in Figure 6 of Maguire *et al.* (1994) with whorl branches are assumed to be located at annual node height. The first whorl branch is given a random azimuth and each subsequent whorl branch is expected to be equidistant around the circumference of the tree (e.g. Doruska and Burkhart, 1994). Interwhorl branches are given a random azimuth and absolute location in the bole based on their relative location in the annual segment and the number of north- vs. south-facing interwhorl branches. Branch diameter is predicted from relative branch diameter within the whorl with equation [2] presented in Maguire *et al.* (1994). Individual branch angle and length (total and foliated) are predicted from Weiskittel *et al.* (in review-a) equations. Branch foliage (eqn. [1]) and woody biomass (eqn. [2]), foliage age class structure (eqn. [3]), and specific leaf area (eqn. [4]) are estimated using equations built from the data presented in (Weiskittel *et al.*, 2006a).

[1] $$\mathrm{FOL_{BRNCH}} = 11.1824 * \mathrm{BD}^{1.9444} * \mathrm{DINC}^{0.3069} * \mathrm{BHT}^{-1.1964} * (\mathrm{BHT/HT})^{2.4636} * \mathrm{FOLRET}^{0.1539}$$

[2] $$\mathrm{WOD_{BRNCH}} = 0.2952 * \mathrm{BD}^{2.4449} * \mathrm{BHT}^{-0.2907}$$

[3] $$\begin{aligned}
\mathrm{CF_1} &= \exp(-0.3391 * \mathrm{DIN\_CAN}^{0.3372} + 0.3211 * \mathrm{MAX.LAI}) \\
&\quad * {\frac{\mathrm{BHT}}{\mathrm{HT}}}^{1.8250} * \mathrm{FOLRET}^{-0.2841} * \mathrm{CL}^{0.1632} \\
\mathrm{CF_2} &= \exp(-0.0617 * \mathrm{DIN\_CAN}^{0.6224} + 0.1336 * \mathrm{MAX.LAI}) \\
&\quad * {\frac{\mathrm{BHT}}{\mathrm{HT}}}^{0.7961} * \mathrm{FOLRET}^{-0.2552} * \mathrm{CL}^{0.1150} \\
\mathrm{CF_3} &= \exp(-0.0008 * \mathrm{DIN\_CAN}^{1.6100} + 0.0781 * \mathrm{MAX.LAI}) \\
&\quad * {\frac{\mathrm{BHT}}{\mathrm{HT}}}^{0.3046} * \mathrm{FOLRET}^{-0.1594} * \mathrm{CL}^{0.04345} \\
\mathrm{CF_4} &= \exp(-0.0002 * \mathrm{DIN\_CAN}^{1.7487} + 0.0315 * \mathrm{MAX.LAI}) \\
&\quad * {\frac{\mathrm{BHT}}{\mathrm{HT}}}^{0.0794} * \mathrm{FOLRET}^{-0.0749} * \mathrm{CL}^{0.0212}
\end{aligned}$$

[4] $$\begin{aligned}
\mathrm{SLA} &= \exp(4.1237 + 0.2302 * \mathrm{FOL_1} + 0.1571 * \mathrm{FOL_2} + 0.0924 * \mathrm{FOL_3} \\
&\quad + 0.06686 * \mathrm{FOL_4} + 0.0196 * \mathrm{DIN\_CAN} - 0.2261 * \frac{\mathrm{BHT}}{\mathrm{HT}})
\end{aligned}$$

where $\mathrm{FOL_{BRNCH}}$ is foliage branch biomass (g), $\mathrm{WOD_{BRNCH}}$ is branchwood mass (g), BD is branch diameter (mm), BHT is branch height above ground (m), HT is total tree height (m), FOLRET is plot mean foliage retention, $\mathrm{CF_i}$ is the cumulative amount of foliage in age class i, DIN_CAN is depth into the canopy (m; maximum tree height in the stand – BHT), MAX.LAI is an indicator variable for maximum leaf area (1 if max leaf area, 0 otherwise), CL is tree crown, length (m), SLA_i is specific leaf area ($cm^2\ g^{-1}$) for age class i, and FOL_i is an indicator variable for foliage age class i. MAX.LAI was included in the equation because branch samples were taken both before and after loss of the older foliage age classes in the fall. Branch surface area was predicted using equation 4 of Weiskittel and Maguire (2006).

Branch-level estimates of foliage biomass and leaf area by age class were summed to the individual tree- and plot-levels. Estimates of aboveground biomass at the plot-level were used to estimate belowground biomass with an equation presented in Figure 1 of Ranger and Gelhaye (2001), which was:

[5] $$BB_{stand} = 0.208 * AB_{stand} - 1.405$$

where BB_{stand} is stand belowground biomass ($kg\ ha^{-1}$) and AB_{stand} is stand aboveground biomass ($kg\ ha^{-1}$). The parameters were estimated from 38 case studies on Douglas-fir published in the literature. Plot percent canopy cover was estimated as suggested by Crookston and Stage (1999):

[6] $$1 - \exp(-0.01 * (100 * \sum \frac{\text{MAX.TCRD}^2 * \pi * \text{EXPF}}{10000}))$$

where MAX.TCRD is maximum tree crown radius (m) and EXPF is tree expansion factor.

Net primary production (NPP)

Bud burst and flush was assumed to occur linearly for 30 days after the degree-days exceed 578 (Thomson and Moncrieff, 1982). Recent evidence has suggested this type of model is inaccurate and more complex models that incorporate chilling hours, heat forcing, photoperiod and the occurrence of freeze events in the spring are needed (e.g. Bailey and Harrington, 2006). Standard functions to predict solar zenith angle, day length, and time of sunrise for a given latitude are presented on pages 115 – 118 in Gates (1980). Soil water holding capacity (kg H_2O m^2) and plant available water were calculated similar to equations 73 – 81 in Schwalm and Ek (2004). Soil water holding capacity is based on soil texture, depth, and rock content and estimated using empirical soil physics equations (Cosby *et al.*, 1984; Rawls *et al.*, 1992). Daily plant available water is taken as the minimum of soil water holding capacity and previous day's residual plant available water minus evapotranspiration. Daily canopy transpiration and soil evaporation were simulated with modified Penman-Monteith equations as presented in Waring and Schlesinger (1985) and Kirschbaum (1999), respectively. Net precipitation is added to the plant available water after accounting for incomplete canopy closure and the storage capacity of the canopy:

[7] NET_PRCP = (1 – CAN_COV)*PRCP + CAN_COV*exp(-0.5*LAI + BAI)*PRCP

where NET_PRCP is net precipitation (mm), PRCP is total precipitation (mm), CAN_COV is percent canopy cover, LAI is leaf area index, and BAI is branch area index. Incoming shortwave radiation was separated into direct and diffuse with the equation of Bristow and Campbell (1985):

$$[8] \qquad \%\mathrm{RAD}_{\mathrm{DIR}} = 1 - \left(\frac{\mathrm{SW.RAD}_{\mathrm{day}}}{\mathrm{PSR}} * \left(1 - \exp\left(0.6 * \frac{\left(1 - \frac{0.74}{\mathrm{SW.RAD}_{\mathrm{day}}/\mathrm{PSR}} \right)}{0.7} \right) \right) \right)$$

where $\%\mathrm{RAD}_{\mathrm{DIR}}$ is the percent direct radiation, $\mathrm{SW.RAD}_{\mathrm{day}}$ is daily total of shortwave radiation (MJ), and PSR is potential short wave radiation calculated from solar latitude, solar declination, and half daylength (Gates, 1980). Soil water potential was estimated from soil texture and plant available water as presented in equations 82-84 in Schwalm and Ek (2004). Daily mean leaf water potential was calculated similar to equation 3 in Manter *et al* (2003a):

$$[9] \qquad \psi_{\mathrm{leaf}} = \psi_{\mathrm{soil}} - \left(\frac{\mathrm{gs} * \mathrm{VPD}}{0.11} \right)$$

where ψ_{leaf} is leaf water potential (MPa), ψ_{soil} is soil water potential, gs is daily mean canopy conductance (mmol m^{-2} s^{-1}), and VPD is the vapor pressure deficit (Pa). Daylight was divided into five normalized Gaussian distance (i.e. 0.0469101, 0.2307534, 0.5, 0.7692465, 0.9530899), converted to local time, and air temperature and vapor pressure deficit were estimated with standard equations of Goudriaan and van Laar (1994):

[10] $$\mathrm{Temp} = (\mathrm{T}_{\max} - \mathrm{T}_{\min}) * \sin\left(\frac{\pi * \mathrm{TIME\text{ - }0.5}}{\mathrm{DAYLEN} + 4.5}\right) + \mathrm{T}_{\min}$$

where Temp is instantaneous temperature (°C), T_{max} is daily maximum temperature (°C), T_{min} is daily minimum temperature (°C), TIME is local apparent time, and DAYLEN is day length (s). Instantaneous direct and diffuse shortwave radiation are calculated using a cosine-approach of Wang *et al.* (2002):

[11] $$\mathrm{SW.RAD}_{\mathrm{DIR}} = \mathrm{SW.RAD.NOON}_{\mathrm{DIR}} * \cos\left(\frac{\mathrm{SZA\text{ - }SZA}_{\mathrm{noon}}}{\frac{\pi}{2} - \mathrm{SZA}_{\mathrm{noon}}} * \frac{\pi}{2}\right) * \frac{\cos(\mathrm{SZA})}{\cos(\mathrm{SZA}_{\mathrm{noon}})}$$

[12] $$\mathrm{SW.RAD}_{\mathrm{DIF}} = \mathrm{SW.RAD.NOON}_{\mathrm{DIF}} * \cos\left(\frac{\mathrm{SZA\text{ - }SZA}_{\mathrm{noon}}}{\frac{\pi}{2} - \mathrm{SZA}_{\mathrm{noon}}} * \frac{\pi}{2}\right)$$

[13] $$\mathrm{SW.RAD.NOON}_{\mathrm{DIR}} = (2.28 - 1.1 * \mathrm{SZA}_{\mathrm{noon}} + 0.8 * \mathrm{SZA}_{\mathrm{noon}}{}^{2} - 0.23 * \mathrm{SZA}_{\mathrm{noon}}{}^{3}) * \frac{\mathrm{SW.RAD.DAY}_{\mathrm{DIR}}}{\mathrm{DAYLEN}}$$

[14] $$\mathrm{SW.RAD.NOON}_{\mathrm{DIF}} = (1.73 - 0.81 * \mathrm{SZA}_{\mathrm{noon}} + 0.58 * \mathrm{SZA}_{\mathrm{noon}}{}^{2} - 0.16 * \mathrm{SZA}_{\mathrm{noon}}{}^{3}) * \frac{\mathrm{SW.RAD.DAY}_{\mathrm{DIF}}}{\mathrm{DAYLEN}}$$

where $\mathrm{SW.RAD}_{\mathrm{DIR}}$ is instantaneous shortwave direct radiation (W m^{-2}), $\mathrm{SW.RAD}_{\mathrm{DIF}}$ is instantaneous shortwave diffuse radiation (W m^{-2}), $\mathrm{SW.RAD.NOON}_{\mathrm{DIR}}$ is shortwave direct radiation at noon (W m^{-2}), $\mathrm{SW.RAD.NOON}_{\mathrm{DIF}}$ is shortwave diffuse radiation at noon (W m^{-2}), $\mathrm{SW.RAD.DAY}_{\mathrm{DIR}}$ is the daily total shortwave direct radiation (W m^{-2}), $\mathrm{SW.RAD.DAY}_{\mathrm{DIF}}$ is the total shortwave diffuse radiation (W m^{-2}), SZA is solar zenith angle estimated from latitude and solar declination and hour angle (Gates, 1980), and $\mathrm{SZA}_{\mathrm{noon}}$ is solar zenith angle at noon. Shortwave radiation (W m^{-2}) was converted to photosynthetically active radiation (μmol m^{-2} s^{-1}) by multiplying by 4.55.

The effective radiation canopy extinction coefficient was estimated from an equation in Smith (1993) and converted to the direct radiation extinction coefficient using as assumption presented in Goudriaan (1988):

[15] $$k_{\mathrm{dir}} = \frac{0.3024 * \mathrm{RD}_{\mathrm{DF}}{}^{0.4575} * \frac{\mathrm{LAI}}{\cos(\mathrm{SZA})}^{-0.4607}}{\sqrt{0.8}}$$

where k_{dir} is the direction radiation extinction coefficient, $\mathrm{RD}_{\mathrm{DF}}$ is relative stand density (Curtis, 1982), and all other variables have been defined above. The diffuse radiation extinction coefficient was calculated from a linear relationship with LAI based on a spherical distribution of foliage (Campbell and Norman, 1998):

[16] $$k_{dif} = 0.806 - 0.075 * \ln(LAI)$$

where k_{dif} is the diffuse radiation extinction coefficient. Canopy absorbance was calculated separately for direct and diffuse radiation and corrected for incomplete canopy closure:

[17] $$\begin{aligned} Q &= Q_{dir} + Q_{dif} \\ Q_{dif} &= PAR_{dir} * (1 - CAN\_COV * 0.06 + (1 - CAN\_COV) * 0.04) \\ &\quad - \exp(\sqrt{0.8} * k_{dif} * LAI) \\ Q_{dir} &= PAR_{dir} * (1 - CAN\_COV * 0.06 + (1 - CAN\_COV) * 0.04) \\ &\quad - \exp(\sqrt{0.8} * k_{dir} * LAI) \end{aligned}$$

where Q is total amount of absorbed PAR (µmol m^{-2} s^{-1}), Q_{dir} is the total amount of absorbed direct PAR (µmol m^{-2} s^{-1}), Q_{dif} is the total amount of absorbed diffuse PAR (µmol m^{-2} s^{-1}), PAR_{dir} is total direct incoming PAR (µmol m^{-2} s^{-1}), and PAR_{dif} is total incoming diffuse PAR (µmol m^{-2} s^{-1}). Canopy and soil reflectance were assumed to be 0.06 and 0.04, respectively. The canopy was divided into sunlit and shaded LAI based on the approach of Wang *et al.* (2002):

$$
\begin{aligned}
\mathrm{LAI}_{\mathrm{sun}} &= 1-\exp\left(\frac{-\mathrm{k}*\mathrm{LAI}_{\mathrm{slope}}}{\cos(\mathrm{SZA}_{\mathrm{adjusted}})}\right)*\frac{\cos(\mathrm{SZA}_{\mathrm{adjusted}})}{\mathrm{k}}\\
\mathrm{LAI}_{\mathrm{shade}} &= \mathrm{LAI}_{\mathrm{slope}}\ \text{-}\ \mathrm{LAI}_{\mathrm{sun}}\\
\mathrm{LAI}_{\mathrm{slope}} &= \mathrm{LAI}*\cos(\mathrm{atan}(\frac{\%\mathrm{SLOPE}}{100}))
\end{aligned}
$$

$$
\text{[18]}\qquad
\begin{aligned}
\mathrm{SZA} = {} & a\cos(\cos(\mathrm{SZA})*\cos(\mathrm{atan}(\frac{\%\mathrm{SLOPE}}{100}))\\
& +\sin(\mathrm{SZA})*\sin(\mathrm{atan}(\frac{\%\mathrm{SLOPE}}{100})*\\
& \cos(\mathrm{SOLAZM}\ \text{-}\ \mathrm{ASPECT}_{\mathrm{rad}}))
\end{aligned}
$$

$$
\mathrm{ASPECT}_{\mathrm{rad}} = (180-\mathrm{ASPECT})*\frac{\pi}{180}
$$

where $\mathrm{LAI}_{\mathrm{sun}}$ is the amount of leaf area index in full sunlight, $\mathrm{LAI}_{\mathrm{shade}}$ is the amount of leaf area index in the shade, $\mathrm{LAI}_{\mathrm{slope}}$ is the horizontal LAI adjusted for percent slope (%SLOPE), SOLAZM is the solar azimuth, ASPECT is site aspect (0° north, 180° south), and $\mathrm{ASPECT}_{\mathrm{rad}}$ is site aspect in radians (north positive, south negative).

Net photosynthesis was estimated with the Farquhar *et al.* (1980) biochemical equation. The necessary parameters for this model were estimated from equations presented in Manter *et al.* (2005) at an optimal level of foliar nitrogen and modified from a function in Brix (1993) to adjust net photosynthesis to the level of foliar nitrogen in the canopy:

$$A1_n = \left(\min\left(\frac{V*(C_i - \Gamma)}{C_i + K}, \frac{J*(C_i - \Gamma)}{4.5*C_i + 10.5*\Gamma} \right) - R_{dark} \right)$$

$$* \frac{-8.3 + 124.7*CAN\_N - 35.9*CAN\_N^2}{100}$$

$$\Gamma = 1.92*10^{-4}*21000*1.75^{\frac{Temp-25}{10}}$$

$$C_i = \frac{-k.2 - \sqrt{k.2^2 - 4*k.1*k.3}}{2*k.1}*0.1$$

$$k.1 = -\frac{g_s}{1000}$$

$$k.2 = \frac{g_s}{1000}*((C_a*10) - K) - V$$

$$k.3 = K*(C_a*10)*\frac{g_s}{1000} + V*36.9 + (1.88*(Temp-25)$$

$$+ 0.036*(Temp-25)^2)$$

$$K = 30*2.1^{\frac{Temp-25}{10}}*\frac{21001}{30000*1.2^{\frac{Temp-25}{10}}}$$

[19]

$$R_{dark} = 1.57*\exp\left(\frac{66.4*1000*(Temp-25)}{298*8.314*(Temp+273)} \right)$$

$$J_t = 58.13*\frac{\exp\left(29.443 - \frac{72.188}{0.00831*(Temp+273.16)}\right)}{1+\exp\left(\frac{0.65*(Temp+273.16) - 196.555}{0.00831*(Temp+273.16)}\right)}$$

[20]

$$J = \frac{J_t*Q}{Q + 2.1*J_t}$$

$$V = 44.82*\frac{\exp\left(37.469 - \frac{91.708}{0.00831*(Temp+273.16)}\right)}{1+\exp\left(\frac{0.65*(Temp+273.16) - 195.261}{0.00831*(Temp+273.16)}\right)}$$

where $A1_n$ is the net photosynthesis rate for the 1-yr old foliage age class (μmol m^{-2} s^{-1}), C_i is the intercellular CO_2 pressure (Pa), R_{dark} is the temperature adjusted dark respiration rate (μmol m^{-2} s^{-1}), V is the temperature adjusted rate of maximum rubisco carboxylation (V_{cmax}; μmol m^{-2} s^{-1}), J is the temperature and radiation adjusted value of maximum rate of electron transport (J_{max}; μmol m^{-2} s^{-1}), K is enzyme kinetics (a function of Michaelis constant for CO_2 and the inhibition constant for O_2), and Γ is the partial pressure of O_2 (Pa). Stomatal conductance (g_s; μmol m^{-2} s^{-1}) was calculated as:

$$[21] \qquad g_s = \min\left(\begin{array}{l} 150 * \dfrac{.1 * \psi_{soil} - \psi_{leaf}}{\mathrm{VPD}}, 150 * (1 - \exp\left(-0.003 * \dfrac{Q * 2}{4.55}\right), \\ 150 * (1 - 0.066 * (\mathrm{TIME - SUNRISE})) \end{array}\right)$$

where SUNRISE the local time of sunrise and all other variables have been defined above. The estimated net photosynthesis rate for the 1-yr old foliage was reduced for the each of the subsequent foliage age classes, weighted by the amount of leaf area in each age class, and multiplied by the corresponding Gaussian weight for each relative time (i.e. 0.1184635, 0.2393144, 0.2844444, 0.2393144, 0.1184635). This mean value was multiplied by the day length (s), converted to biomass, and summed for an entire year to estimate gross primary production (GPP; kg ha^{-1}). Respiration was estimated in several different ways, but assuming net primary production is one-half of GPP was the most correlated with actual growth.

Annual foliage litterfall was predicted using equation [4] in Weiskittel and Maguire (2007). Nitrogen mineralization was assumed to occur in the upper 80% of the soil to a maximum of 1 m and was estimated with the approach of Paul *et al.* (2002):

$$[22]\quad \begin{aligned} N_{\min} &= k_n * \exp\left(\frac{3.36*(\mathrm{Temp}_{\mathrm{soil}}-40)}{\mathrm{Temp}_{\mathrm{soil}}+31.79}\right) * \frac{1}{1+6.63*\exp\left(-5.69*\frac{\mathrm{PAW}}{\mathrm{WHC}}\right)} \\ k_n &= \exp\left(\begin{array}{l} 32.22216 - 2.48502*\mathrm{LFALL}_{\mathrm{FOL}} + 0.01931 \\ *\,\mathrm{WHC} - 3.28905*\log(\mathrm{WHC}) \end{array}\right) \end{aligned}$$

where N_{min} is nitrogen mineralization rate (mg N kg^{-1}), $Temp_{soil}$ is the soil temperature (°C) estimated with the approach of Paul *et al.* (2004), PAW is the daily plant available water (kg H_2O m^{-2}), WHC is the soil water holding capacity (kg H_2O m^{-2}), k_n is the optimum nitrogen mineralization rate based on data presented in Chappell *et al.* (1999), and $LFALL_{FOL}$ is annual foliage litterfall (kg ha^{-1}). To upscale this value to the plot-level, soil bulk density was estimated an equation presented in Kaur *et al.* (2002):

$$[23]\quad \mathrm{BD}_{\mathrm{soil}} = \exp\left(\begin{array}{l} 0.313 - 0.191*\frac{\mathrm{SOIL\_C}}{100} + 2.102*10^{-2}*\mathrm{SOIL\_CLAY} \\ -4.76*10^{-4} - 4.32*10^{-3}*\mathrm{SOIL\_SILT} \end{array}\right)$$

where BD_{soil} is the soil bulk density (kg m^{-3}), SOIL_C is the soil carbon content estimated from the data of Perakis *et al.* (2006) (13.66*CAN_N – 9.99), SOIL_CLAY is the soil clay percentage, and SOIL_SILT is the soil silt percentage. Nitrogen uptake by the canopy was estimated from a modified function in Thornley (1991):

$$[24]\qquad \begin{aligned} \mathrm{N}_{\mathrm{uptake}} &= \frac{\mathrm{ROOT}_{\mathrm{fine}} * \mathrm{ROOT}_{\mathrm{act}} * \mathrm{N}_{\mathrm{aval}}}{\left(1 + \dfrac{0.5}{\mathrm{ROOT.C}_{\mathrm{fine}}}\right) * \left(1 + \dfrac{\mathrm{ROOT.N}_{\mathrm{fine}}}{0.05}\right)} \\ \mathrm{ROOT}_{\mathrm{act}} &= 0.00001 * \mathrm{TEMP}_{\mathrm{soil}} \end{aligned}$$

where $\mathrm{N}_{\mathrm{uptake}}$ is nitrogen uptake (kg N day^{-1}), $\mathrm{ROOT}_{\mathrm{fine}}$ is fine root biomass (kg ha^{-1}), $\mathrm{ROOT}_{\mathrm{act}}$ is root activity that is dependent on soil temperature, $\mathrm{N}_{\mathrm{aval}}$ is soil available nitrogen (kg ha^{-1}), $\mathrm{ROOT.C}_{\mathrm{fine}}$ is the fine root carbon concentration (assumed to be 0.5), and $\mathrm{ROOT.N}_{\mathrm{fine}}$ is the fine root nitrogen concentration (assumed to be equal to CAN_N). $\mathrm{N}_{\mathrm{min}}$ and $\mathrm{N}_{\mathrm{uptake}}$ were summed to estimate annual values.

Allocation and Growth (ALOGRO)

The amount of net primary production (NPP; kg ha^{-1}) allocated to the stem was estimated with the approach of Landsberg and Waring (1997) corrected for inherent bias (Duursma and Robinson, 2003):

$$[25]\qquad \mathrm{pNPP}_{\mathrm{stem}} = \left(1.770196 * \mathrm{DBH}_{\mathrm{mean}}{}^{-0.82391}\right) * \begin{pmatrix} 1 + 0.5 * (-0.82391 \\ * (-0.82391 - 1)) * \dfrac{\mathrm{DBH}_{\mathrm{stdev}}}{\mathrm{DBH}_{\mathrm{mean}}}^{2} \end{pmatrix}$$

where $pNPP_{stem}$ is the proportion of NPP allocated to the stem, DBH_{mean} is the stand mean diameter at breast height (cm), and DBH_{stdev} is the stand standard deviation of diameter at breast height (cm). This value was multiplied by NPP, converted to volume using a regional average of wood density, and disaggregated to individual trees based on their proportion of stand weighted leaf area (Brunner and Nigh, 2003):

$$[26] \qquad \mathrm{pVGR}_{\mathrm{tree}} = \frac{\mathrm{TLA} * \exp - \begin{pmatrix} 1.89554 + 0.04612 * \mathrm{HCM} \\ + 0.00019199 * \mathrm{TPH} - 0.01461 * \mathrm{CCH} \end{pmatrix}}{\sum \left(\mathrm{TLA} * \exp \begin{pmatrix} -1.89554 + 0.04612 * \mathrm{HCM} \\ + 0.00019199 * \mathrm{TPH} - 0.01461 * \mathrm{CCH} \end{pmatrix} \right)}$$

where $pVGR_{tree}$ is the individual tree's proportion of stand volume growth, TLA is tree leaf area (m^2), HCM is the height to crown midpoint (m), TPH is the trees per ha, and CCH is crown closure in trees higher than the subject tree. Diameter and height growth were predicted with a differentiated allometric equation as presented in Kirschbaum (1999):

$$DGR = \left(DBH * \frac{STEM.1}{STEM.2}^{\frac{1}{a3*a5+a4}} \right) - DBH$$

$$HGR = \left(HT * \frac{STEM.1}{STEM.2}^{\frac{1}{\left(\frac{a5+a4}{a3}\right)}} \right) - HT$$

$$\begin{aligned} &[27] \qquad a3 = -3.17310 + 0.013284 * SBA - 0.02139 * DQ_{DF} - 0.00064 * SDI_{DF} \\ &a4 = 2.710265 + 0.254454 * a3 + 0.011907 * DBH_{cv} \\ &a5 = 0.554703 - 0.60151 * a3 - 0.96379 * a4 + 0.000808 * DBH_{cv} \end{aligned}$$

where DGR is diameter growth rate (mm yr^{-1}), HGR is height growth rate (m yr^{-1}), DBH is initial diameter at breast height (cm), HT is initial total tree height (HT), STEM.1 is initial stem biomass (kg), STEM.2 is initial stem biomass plus stem biomass increment (kg), SBA is stand basal area (m^{2} ha^{-1}), DQ_{DF} is Douglas-fir stand quadratic diameter (cm), SDI_{DF} is Douglas-fir stand density index (Reineke, 1933), and DBH_{cv} is the stand diameter at breast height coefficient of variation. This approach performed better than other equations (Thornley, 1999; Valentine and Mäkelä, 2005), but had a level of precision below the empirical and hybrid approaches. The hybrid equations were developed by using the DGR and HGR models of Weiskittel *et al.* (2007) to estimate individual tree growth on an independent subsample of plots with predicted stand-level NPP. Using the fixed parameters of Weiskittel *et al.* (2007), the equation was refitted with a multiplier that was linear function of NPP and annualized with the technique of Cao (2000). Future refinements could easily be made by collecting annual growth estimates from tree cores and descriptively sampled stems so the assumption that NPP stayed constant during the remeasurement period of 2 to 4 years would not be necessary. Individual branch growth and mortality were estimated from empirical equations. Height to crown base (HCB) was defined as the lowest live branch. Equations from BCACS were then used to predict branch-, tree-, and stand-level biomass and leaf area from the updated values of DBH, HT, and HCB. Canopy foliage nitrogen was updated assuming that 35% of the nitrogen uptake was allocated to the new foliage (see Fig. 12 of Kirschbaum, 1999) and retranslocated nitrogen from the litterfall, which was predicted as a function of canopy nitrogen concentration from data in Reid (1983):

[28] $$N_{trans} = (CAN\_N - (0.6507 * \ln(CAN\_N) + 0.6474)) * LFALL_{FOL}$$

where N_{trans} is retranslocated nitrogen (kg ha^{-1}) and all other variables have been defined above.

Finally, stem taper along the bole was predicted with an equation of the form presented in Ikonen *et al.* (2006):

$$\text{DGR}_{\text{dib}} = \text{-0.0421} * \Delta\text{STEM}^{\text{-0.5390}} * \text{DIB} + \tag{29}$$

$$\left(\frac{0.9235}{1 - 0.7162 * \dfrac{\dfrac{\text{STEM}_{\text{abv}}}{\text{STEM.1}}}{\dfrac{\text{STEM}_{\text{abv}}}{\text{STEM.1}} + 1}} \right) * \text{STEM.1}^{0.4544} * \Delta\text{STEM}^{0.6343}$$

where DGR_{dib} is the diameter inside bark growth at (cm), ΔSTEM is the stem biomass increment (kg), DIB is the diameter inside bark (cm), and STEM_{abv} is the stem mass above the location where DGR_{dib} is being predicted.

The final model was coded and implemented in R v2.4.0 (http://www.r-project.org). Use of the model in R requires the installation of several libraries including Hmisc, nlme, and RODBC. The complied R library, model manual, and example inputfiles are available online (http://www.holoros.com/DF.HGS.htm).

APPENDIX B

LIST OF SYMBOLS USED IN THE TEXT

Symbol	**Definition**	**Units**
Γ	partial pressure of O_2	Pa
ψ_{leaf}	leaf water potential	MPa
ψ_{soil}	soil water potential	MPa
%SLOPE	percent slope	%
%RAD$_{DIR}$	percent direct radiation	%
%ROCK.B	percent rock content in the B horizon of the soil profile	%
$A1_n$	net photosynthesis rate in 1-yr old foliage	μmol m^{-2} s^{-1}
AB_{stand}	aboveground stand biomass	kg ha^{-1}
AIC	Akaike's information criteria	-
ALOGRO	Allocation and Growth model	-
ASP1	percent slope multiplied by COSA	-
ASP12	cosine transformation of slope and aspect	-

	[%SLOPE* cos(4*π*(aspect/360))]	
ASP22	sine transformation of slope and aspect [%SLOPE* sin(4*π*(aspect/360))]	-
ASPECT	site aspect (0 is north, 180 is south)	°
$\text{ASPECT}_{\text{rad}}$	site aspect in radians (north positive, south negative)	-
BA	branch angle from vertical	°
BAI	branch area index	$m^2\ m^{-2}$
BAL	basal area in larger trees	$m^2\ ha^{-1}$
BB_{stand}	belowground stand biomass	$kg\ ha^{-1}$
BCACS	Branch, Crown, And Canopy Simulator	-
BD	branch diameter	mm
BD_{max}	maximum branch diameter in an annual segment	mm
BD_{soil}	soil bulk density	$kg\ m^{-3}$
BDA	summation of branch diameters above the subject branch	mm

BDG	branch diameter growth	mm yr^{-1}
BHAGE	mean breast-height age	yrs.
BHT	branch height above ground	m
BHSAP	constant amount of foliage per unit of sapwood area at breast height	-
BHT_{rel}	relative branch height above ground	-
C_a	ambient atmospheric CO_2	Pa
C_i	intercellular CO_2	Pa
CAI	stand current annual increment	m^3 ha^{-1}
CAN_COV	percent canopy cover	%
CBSAP	constant amount of foliage per unit of sapwood area at crown base	-
CCH	crown closure in higher trees	-
CCR	compacted crown ratio	-
CF_i	cumulative foliage biomass in age class i	-

CL	crown length	m
$CLSA_{mean}$	stand mean crown sparseness	cm cm^{-2}
COSA	cosine transformation of aspect [cos(2*π*(aspect/360))]	-
CR	crown ratio	-
CRD_{TOT}	total crown radius	m
CRD_{NFOL}	non-foliated crown radius	m
DAYLEN	day length	s
DBH	tree diameter at breast height	cm
DBH_{cv}	stand DBH coefficient of variation	cm
DBH_{mean}	mean stand DBH	cm
DBH_{stdev}	standard deviation of DBH in the stand	cm
DGR	tree diameter growth rate	cm yr^{-1}
DGR_{dib}	diameter inside bark growth rate	cm
DIB	diameter inside bark	cm

DIN_CAN	depth into canopy (maximum tree height in stand – branch height)	m
DINC	depth into crown (tree height – branch height)	m
DQ_{DF}	Douglas-fir quadratic mean diameter	cm
ELEV	elevation	m
EXPF	tree expansion factor	# ha^{-1}
FERT	indicator variable for fertilization (1 if fertilized, 0 otherwise)	-
FOL_i	indicator variable for foliage age class i	-
FOL_{BRNCH}	branch foliage biomass	g
FOLRET	foliage retention (measure of SNC severity, inverse relationship with disease)	-
g_s	stomatal conductance	μmol m^{-2} s^{-1}
GE	growth efficiency	kg m^{-2}
GEA	growth effective age	-
GPP	gross primary production	kg ha^{-1}

HT	tree total height	m
HCB	tree height to crown base (lowest live branch)	m
HCM	tree height to crown midpoint	m
HGR	tree height growth rate	m yr^{-1}
HMOD	height growth modifier	-
HRB	complete control of herbaceous vegetation	-
HSC	Hardwood Silviculture Cooperative	-
J	temperature and radiation adjusted electron transport capacity	µmol m^{-2} s^{-1}
J_{max}	electron transport capacity	µmol m^{-2} s^{-1}
K	enzyme kinetics	-
k_{dir}	direct light extinction coefficient	-
k_{dif}	diffuse light extinction coefficient	-
LAI	leaf area index	m^2 m^{-2}
LAI_{shade}	leaf area index in the shade	m^2 m^{-2}

LAI_{slope}	leaf area index horizontal to the slope	$m^2\ m^{-2}$
LAI_{sun}	sunlight leaf area index	$m^2\ m^{-2}$
$LFALL_{FOL}$	annual foliage litterfall	$kg\ ha^{-1}$
MAX.LAI	indicator variable for maximum leaf area	-
MAX.TCRD	maximum tree crown radius	m
ML	maximum likelihood	-
MLME	multilevel mixed effects	-
MSE	mean square error	-
N_{aval}	soil available nitrogen	$kg\ ha^{-1}$
N_{min}	nitrogen mineralization rate	$mg\ kg^{-1}$
N_{uptake}	plant nitrogen uptake from soil	$kg\ ha^{-1}$
N_{trans}	nitrogen retranslocated by the foliage	$kg\ ha^{-1}$
NB_W	total number of whorl branches per annual segment	-
NB_I	total number of interwhorl branches per annual	-

	segment	
NET_PRCP	net precipitation	mm
NFBL	non-foliated branch length	m
NPP	net primary production	kg ha^{-1}
P_{MORT}	probability of individual branch mortality	-
PAR	photosynthetically active radiation	µmol m^{-2} s^{-1}
PAR_{dir}	direct photosynthetically active radiation	µmol m^{-2} s^{-1}
PAR_{dif}	diffuse photosynthetically active radiation	µmol m^{-2} s^{-1}
PAW	soil plant available water	kg H_2O m^{-2}
PCT	precommercial thinning	-
PHT	potential height growth	m
PNW	Pacific Northwest	-
$pNPP_{stem}$	percent NPP allocated to the stem	%
$pVGR_{tree}$	percent of stand volume growth allocated to an individual tree	%

PRCP	precipitation	cm
PSR	potential solar radiation	$W\ m^{-2}$
Q	canopy absorbed radiation	$\mu mol\ m^{-2}\ s^{-1}$
Q_{dir}	canopy absorbed direct radiation	$\mu mol\ m^{-2}\ s^{-1}$
Q_{dif}	canopy absorbed diffuse radiation	$\mu mol\ m^{-2}\ s^{-1}$
R_{dark}	dark respiration rate	-
RHACB	relative height above crown base	-
RD_{DF}	Douglas-fir relative stand density	-
$ROOT_{fine}$	fine root biomass	$kg\ ha^{-1}$
$ROOT.C_{fine}$	fine root carbon concentration	%
$ROOT.N_{fine}$	fine root nitrogen concentration	%
$ROOT_{act}$	fine root activity	-
RMSE	root mean square error	-
RUE	radiation use efficiency	-

SBA	stand basal area	m^2 ha^{-1}
SDI_{DF}	Douglas-fir stand density	
SEGAGE	annual segment age	yrs
SEGDINC	annual segment depth into crown	m
SEGHT	annual segment height above ground	m
$SEGHT_{rel}$	annual segment relative height	-
SEGLEN	annual segment length	m
SI	site index	m
SLA	specific leaf area	cm^2 g^{-1}
SMC	Stand Management Cooperative	-
SNC	Swiss needle cast	-
SNCC	Swiss Needle Cast Cooperative	-
SOIL_C	soil carbon concentration	%
SOIL_CLAY	soil clay content	%

SOIL_SILT	soil silt content	%
SOIL_SAND	soil sand content	%
SOLAZM	solar azimuth	°
STEM	stem biomass	kg
$STEM_{abv}$	stem biomass above a given location in the stem	kg
STEM.1	initial stem biomass	kg
STEM.2	initial stem biomass plus stem biomass increment	kg
SUNRISE	local apparent time of sunrise	-
$SW.RAD_{DIR}$	shortwave direct radiation at a given local apparent time	$W\ m^{-2}$
$SW.RAD_{DIF}$	shortwave diffuse radiation at a given local apparent time	$W\ m^{-2}$
$SW.RAD.NOON_{DIR}$	shortwave direct radiation at noon	$W\ m^{-2}$
$SW.RAD.NOON_{DIF}$	shortwave diffuse radiation at noon	$W\ m^{-2}$

$SW.RAD_{day}$	total daily shortwave radiation	MJ
SWP	soil water potential	-
SZA	solar zenith angle	°
SZA_{noon}	solar zenith angle at noon	°
T_{max}	maximum daily temperature	°C
T_{min}	minimum daily temperature	°C
Temp	temperature at give local area time	°C
$Temp_{soil}$	soil temperature	°C
THIN	indicator for commercial thinning	-
TIME	local apparent time	-
TLA	tree leaf area	m^2
TPH	trees per ha	-
TST	time since treatment	-
TVC	total vegetation control	-

UCR	uncompacted crown ratio	-
V	temperature adjusted Rubisco activity	μmol m^{-2} s^{-1}
V_{cmax}	maximum Rubisco activity	μmol m^{-2} s^{-1}
VMRC	Vegetation Management Research Cooperative	-
W	indicator variable for whorl branches (1 if whorl branch, 0 otherwise)	-
WDY	complete control of woody vegetation	-
WHC	soil water holding capacity	kg H_2O m^{-2}