AN ABSTRACT OF THE THESIS OF

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Abstract approved ______________________________

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Plants respond to defoliation in many different and complex ways, depending on their growth habit and form as well as the extent and duration of the defoliation. Tree crowns have been shown to be quite sensitive to disturbances such as defoliation, however quantitative relationships have rarely been developed, making the true biological meaning of crown condition assessments quite difficult to decipher. The sudden emergence of Swiss needle cast (SNC) in the Oregon Coast Range prompted investigation of the response of Douglas-fir crown structure, crown morphology, and foliage dynamics to extended defoliation. Using data from permanent plots and 82 destructively sampled trees, hypotheses regarding the response of trees to defoliation were tested with linear and nonlinear models. Responses of crowns were investigated at multiple levels including the needle, branch, tree, and stand scales.

At the individual-needle level, SNC has resulted in foliage that is smaller in length, width, and projected area; lower in dry mass; and higher in specific leaf area. The disease has influenced the foliage age structure by increasing the proportion in the younger age classes with greater SNC severity. The disease has also resulted in crowns that have a greater proportion of their current and 1-year-old needles located higher in the crown than

normal, while the 2-, 3- and 4-year-old needles are shifted towards the crown base relative to healthy trees.

At the branch-level, the disease has modified growth patterns as well as dry matter production and allocation. The number of secondary lateral branches on a primary branch declined in response to the disease, as did the foliated branch length and diameter for a given position in the crown. The ratio of branch length to branch diameter, however, increased with disease severity, which suggests altered elongation patterns. Branches in the lower portion of the heavily diseased crowns were elongating faster than normal, while elongation of branches in the mid-crown was slower. Elongation of branches in the upper crown was unaffected. The disease significantly reduced branch foliage dry matter and area for a given position in the crown and diameter. Branches, however, allocated more dry matter to higher order branches, but less dry matter to primary branch elongation.

At the tree-level, the disease has led to crowns that are shorter than normal, while the largest measured standing width remains unaffected. Crown radii and maximum branch diameter profiles suggested that changes within the crown might be occurring at different levels due to variations in SNC damage within the crown. The number of primary interwhorl branches decreased with greater disease severity. SNC also significantly reduced total foliage and branchwood dry matter. Overall, the vertical distribution of foliage dry matter was less skewed and more uniform with increased disease severity.

At the stand-level, SNC has significantly increased crown recession rates, woody litterfall, the specific leaf area of the litter, and growth efficiency. The disease caused a decline in foliage litterfall rates as well as leaf area index. In addition, the seasonal

distribution of foliage litterfall was altered, with a greater amount occurring in the summer than normal. Crown condition, as assessed by foliage retention and the crown sparseness index, varied with SNC and other site factors. Within-tree variability of foliage retention was significantly higher than between-tree or between-plot variability. Although assessments of foliage retention were found to be highly variable, the sample size required to attain a sufficiently precise estimate for a given tree and stand are lower than the sample sizes currently being collected. The crown sparseness index was found to be significantly less variable than foliage retention and was primarily influenced by stand factors such as age and stand density.

Defoliation caused significant changes at the individual needle, branch, tree, and stand levels, complicating efforts to accurately predict growth responses to defoliation. This detailed analysis of crown and foliage dynamics helps to establish links among current SNC studies. For example, growth losses associated with SNC are due to the reduction of foliage area, but also to changes in the size and vertical distribution of the needles. In addition, crown assessment indices such as foliage retention and crown length to sapwood area ratio represent different aspects of crown condition. Crown attributes are sensitive to the direct and indirect effects of SNC, which have important implications for tree growth and stand management. Important direct effects include the premature loss of foliage, while important indirect effects of SNC include changes in the within-crown light environment. Integrating measures of crown condition into forest models, therefore, represents an important step towards incorporating physiological-mechanisms into models for predicting growth

responses to environmental changes such as tree disease and for understanding the complex responses of tree morphology and growth.

Alterations in Douglas-fir Crown Structure, Morphology, and Dynamics Imposed by the Swiss Needle Cast Disease in the Oregon Coast Range

by

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

Aaron R. Weiskittel, Author

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ALTERATIONS IN DOUGLAS-FIR CROWN STRUCTURE, MORPHOLOGY, AND DYNAMICS IMPOSED BY SWISS NEEDLE CAST IN THE OREGON COAST RANGE

CHAPTER ONE: INTRODUCTION

INTRODUCTION

To fully understand a regional forest health problem, research must be concentrated at a variety of different levels (LeBlanc 1990). Research on the Swiss needle cast epidemic (SNC) in the Oregon Coast Range conforms to this approach because the disease has been intensively studied at several different scales, including molecular genetics, needle morphology and physiology, stand growth, and landscape patterns of occurrence and risk. The SNC-causing fungus, *Phaeocrytopus gaeumannii*, is thought to now comprise two reproductively isolated sympatric lineages (Winton et al. 2001). Fruiting bodies of the fungus significantly reduce needle gas exchange (Manter 2001). Annual volume growth losses attributable to the disease are between 23-52% (Maguire et al. 2002), and a variety of environmental factors such as November minimum temperature, June degree days, July precipitation, and aspect are good indicators of the disease risk severity (Rosso 2002). Little work, however, has been done at the individual tree crown level, which is fundamental for understanding the physiological impact of the disease as well as for establishing appropriate techniques for rating its severity. Moreover, Douglas-fir is generally regarded as an excellent tolerator of environmental stresses, which means that it should exhibit slow and relatively small morphological changes to stress (Grime 2002). The study described in the following chapters serves as a link between disease impacts and growth responses and as a test of general theories regarding plant response to stress.

The growth form (shape, arrangement, and size of foliage) and pattern (maximum height, width) of the tree crown plays an essential role in stand productivity. The crown is the center of physiological activity, particularly gas exchange, which drives growth and development. Tree crowns also directly influence stand ecology (Tanabe et al. 2001), fire susceptibility (Keyes and O'Hara 2002), physical stability (Wilson and Oliver 2000), and microclimate (Grace et al. 1987). Furthermore, crown attributes such as density, color, and foliage retention serve as basis for qualitative assessments of stand health and condition. The most important aspects of crown architecture are generally regarded to include crown shape, branch and foliage distribution, dry matter production and allocation, and the condition and dynamics of foliage.

Several studies have noted crown architecture and foliage attributes to be quite plastic (Fisher and Hibbs 1982), particularly in relatively shade tolerant species such as Douglas-fir (Chen et al. 1996). Crown structure and morphology has been shown to be influenced by age (Ishii et al. 2000), crown class (Gilmore and Seymour 1997), stand density (Mäkinen 1999), species composition (Bartelink 2000, Garber 2002), and management activities such as fertilization (Brix 1981), thinning (Medhurst and Beadle 2001), and vegetative control (Newton et al. 1992). Some attention has been given to the influence of insects as natural disturbances on crown structure and dynamics, but relatively little work has been done on crown response to fungal diseases.

In order to accurately predict stand productivity and many other ecosystem processes, more physiologically-based models must be developed. These models should account for the variability caused by diverse stand structures resulting from site quality, age, and disturbance differences. Quantifying the change in crown shape, vertical distribution of foliage within the crown, and foliage to sapwood area relationships relative to stand density, age, and health can lead to better predictions for any forest structure.

Existing permanent plots in the Oregon Coast Range provided an opportunity to assess and quantify regional changes in crown structure and dynamics attributable to alterations in stand condition due to SNC. Since Douglas-fir is the dominant tree species in this region and SNC severity is stable or slightly increasing (Kanaskie et al. 2002), a better understanding of disease impacts on crown structure and dynamics is needed, particularly for developing a meaningful index of disease severity and, in turn, predicting future growth. Results of this study add new information to the current state of knowledge on crown architecture, tree biomass, and foliage dynamics as well as on tree response to stress. The results also offer researchers a future approach for developing more precise models and for practicing foresters and silviculturists, better rating of disease severity, and improved management decisions.

OBJECTIVES

The overall objective of this study was to quantitatively describe changes in crown structure and tree morphology resulting from SNC in the Oregon Coast Range. The primary goal of this research was to establish the best procedure for rating SNC severity and for linking changes in crown structure to important processes such as such as stand growth, fire behavior, and wind stability. To puruse this comprehensive objective and goal, the study addressed four specific questions: (a) Is crown size, shape, and morphology altered by SNC severity? (b) How does SNC severity influence crown dry mass production, allocation, and vertical distribution? (c) What is the relationship between SNC severity and needle condition, size, and age distribution? and (d) Does SNC severity influence crown dynamics at the stand-level? It is hypothesized that SNC results in more light filtering through the defoliated crown, allowing lower foliage and branches to remain on trees longer, slowing the rate of crown recession. These changes in the within-crown light environment may result in greater dry matter production, increased carbon allocation to foliage, and a less skewed vertical distribution of foliage. In addition, increased light availability may lead to larger needles and a greater retention of the older foliage age classes in the lower crown. At the stand-level, changes in crown size and foliage dynamics may increase litterfall rates, alter its seasonal distribution, and decrease growth efficiency.

Chapter Two synthesizes the pertinent literature regarding crown structure and foliage dynamics and assessments of crown health. Chapter Three analyzes the impact of

SNC on overall crown size, structure, and morphology. Chapter Four presents relationships between SNC and dry matter production, allocation, and vertical distribution. Chapter Five assesses the impact of SNC on needle size and age distribution, while Chapter Six describes changes in stand crown recession rates, litterfall, and growth efficiency due to SNC. Chapter Seven integrates these findings and makes recommendations for future research and crown assessments.

CHAPTER TWO: LITERATURE REVIEW

INTRODUCTION

An extensive literature describes tree crown architecture and dry mass as well as tree disease and forest health rating systems. Most of this work has concentrated on even-aged, pure stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), loblolly pine (*Pinus taeda*), radiata pine (*Pinus radiata* D. Don), Scots pine (*Pinus sylvestris* L.), and a few deciduous trees in Europe and North America. This review will focus on five aspects of past research on crown architecture and health, namely crown structure and morphology; crown dry mass production, allocation, and vertical distribution; needle size and foliage dynamics; impact of tree disease on crowns; and use of crown indicators for forest health assessments. This review synthesizes the current state of knowledge regarding these topics and relates them to various aspects of SNC in the Oregon Coast Range.

CROWN STRUCTURE AND MORPHOLOGY

Crown morphology is here defined as the size, shape, and location of a tree crown, while crown structure refers to branching habit (number, size, and distribution). At the stand level, crown morphology influences production efficiency (Jack & Long 1992; Gilmore et al. 1996), ecology (Tanabe et al. 2001), fire susceptibility (Keyes & O'Hara 2002), mechanical stability (Wilson & Oliver 2000), understory diversity (Alaback 1982), wildlife habitat (Brokaw

& Lent 1999), and microclimate (Grace et al. 1987). At the individual tree-level, crown morphology has an effect on physiological processes (Jahnke & Lawrence 1965) throughfall (Tiktak & Bouten 1994), stem form (Larson 1963), and behavior under wind stress (Moore 2002). Crown structure, on the other hand, is directly related to crown morphology as branch location and size determines the shape of the crown. Crown structure also influences wood quality (Maguire et al. 1991; 1994), wildlife use potential (Clement & Shaw 1999), and ecopysiological processes (Maguire et al. 1991).

Several factors influence the size and shape of tree crowns including individual tree characteristics, site factors, and environmental conditions. Many researchers, however, have concluded that light availability is the single most important factor (Hashimoto 1991). While light might be the ultimate determinant of crown morphology and structure, tree crowns respond to many other conditions and processes that modify their structure and morphology at multiple scales. This review will focus on the interactions that occur at the individual crown, canopy (aggregation of crowns), and landscape levels (combination of distinct canopies).

At the individual crown level, tree genetics appears to exert strong control over crown structure and morphology. Several recent studies have found significant differences in crown size and shape between families of the same species (St. Clair 1994b; Xiao et al. 2003). For example, in a genetic test of 18-year-old Douglas-fir in the Coast Range of Oregon, considerable genetic variation was found for relative crown width, stem increment per crown projection area, branch diameter and length adjusted for stem size, and cross-sectional area of branches per crown length (St. Clair 1994b). Little genetic variation, however, was found for branch numbers per whorl and branch angle (St. Clair 1994b). McCrady and Jokela (1996) found significant family differences in live crown length, live crown ratio, and crown shape ratio (crown length/crown width) but no difference in shoot and branch characteristics in a variety of loblolly pine families. Similarly, Sheppard and Ford (1986) found significant differences between the crown development of four clones of Sitka spruce (*Picea sitchensis*) but could not distinguish whether genetics, site factors, or their interaction ultimately controlled the resulting tree crown form. Santini and Camussi (2000) concluded that the locations in which trees have grown have a greater discriminating effect on crown shape than genetics. While it is difficult to assess the relative importance of genetics in comparison to environmental factors, it is interesting to note the high diversity of forms that a tree can display simply by adjusting a few characteristics. Using a computer model, Honda (1971) showed that slight changes in branch angles, which may appear to be trivial, can in fact result in major changes in crown shape after being repeated over many orders of branching. This finding, however, depends heavily on species. The growth habit of some trees is so rigidly controlled genetically that they always possess a characteristic shape and form, particularly in shade-intolerant conifers. Thus, it is best to conclude that a tree's crown structure and morphology is the consequence of the interaction between deterministic (inherited) and opportunistic factors (Fisher & Hibbs 1982).

One important opportunistic factor that strongly influences crown structure and morphology is the tree's social position within the stand, which is often reflected in its height to diameter ratio (HT/DBH; Hann 1999). For example, a dominant Douglas-fir (HT/DBH near 0.5) has a more conic shape and an understory tree (HT/DBH near 1.5) has a more parabolic shape (Oliver & Larson 1996; Hann 1999). Canopy position has also been shown to affect branch angle, branch diameter, branch length, crown radius, and the number of living branches per whorl (Gilmore and Seymour 1997). Chen et al. (1996) found that with decreasing light availability, Douglas-fir tended to increase the ratio of mean lateral to terminal increment. Consequently, it is generally observed that tolerant conifers modify their crown architecture in response to light conditions by rounding their crown profiles (becoming shorter and wider) when they suffer competition from surrounding individuals (Raulier et al. 1996). In contrast, some broad-leaved species in a Bornean lowland rain forest did not change their crown shape and relative length with decreasing tree height or previous diameter growth (Sterck et al. 2001), highlighting an important difference between shade-tolerant conifers and angiosperms. It might, therefore, be better to conclude that for a given level of light, species that are less shade-tolerant produce foliage, branches, and stem length at a higher rate than more shade tolerant species (Shukla & Ramakrishnan 1986), implying high rates of foliage and branch shedding at the base of the crown and resulting in a shallow crown with few leaf layers (Sterck et al. 2001). Relative crown and stem growth rates may have been selected to maintain their stability at small safety margins in relation to the light environment (Sterck et al. 2001). Moreover, most species, regardless of shade tolerance, tend to direct their crowns and show asymmetric development in response to the direction of incoming solar radiation (Rouvinen & Kuuluvainen 1997; Schoettle & Smith 1991; Skatter & Kucera 1998). Thus, a tree's past and current light environment can explain most of the variation in its crown asymmetry and profile. Because initial branch dispersion is generally invariant throughout the stand's development (that is, the distribution around the main stem is regular, irrespective of numbers produced) it is largely suppression mortality of needles and branches that induces asymmetry (Cochrane & Ford 1978).

At the stand level, tree crown structure and morphology is strongly affected by the mean tree spacing, age, and fertility of the site, as well as by silvicultural practices that modify stand density and nutrient availability. Stand density is essentially a measure of the amount of competition that crowns experience in a stand, and is widely applied to find the desired compromise between maximizing growing space occupancy and minimizing losses due to suppression mortality. Crown competition factor is one measure of stand density that reflects the very plastic response of crown width to availability of growing space (Krajicek et al. 1961). Likewise, crown profile has been shown to respond to level of competition in black spruce (*Picea mariana*; Raulier et al. 1996), Scots pine (Rouvinen and Kuuluvainen 1997), and sugar maple (*Acer saccharum*; Brisson 2001). Generally, increasing stand density reduces crown diameter and crown projection area (Kellomäki 1986), primarily by influencing both the rate of crown recession (Curtis & Reukema 1970) and average attainable branch size (Grah 1961). Fully open-grown trees of many western conifers have crowns roughly twice as wide as normal, stand-grown trees (Smith 1958). While crown widths tend to be greater in the direction of lesser competitive pressure from neighboring trees (Brisson 2001), the direction of local competition could not adequately explain the direction of crown asymmetry in Scots pine due to the complicating effects of relatively low solar angles (Rouvinen & Kuuluvainen 1997). Increasing competition for light also shifts allocation of new foliage to a higher position in the crown, accelerates crown lift, and causes crown thinning (Mäkelä & Vanninen 1998). These effects are exacerbated by direct mechanical contact between competitors, in turn, influencing branch spread and inclination (Deleuze et al. 1996).

Crown structure and morphology show distinct changes with age as a result of the combined effects of branch growth and death (Ishii & McDowell 2002). In general, larger trees tend to use their growing space less efficiently than smaller trees at all stages of stand development (Larocque & Marshall 1994a). Contributing factors probably include the shift in vertical distribution of branch volume toward the upper-crown with increasing tree age (Ishii & McDowell 2002), which results in the crown becoming more cylindrical and not as effective at capturing light (Ishii et al. 2000). Furthermore, in some species, such as Douglas-fir, epicormic branching increases with age as a response to damage, defoliation, and changing light conditions, thereby enhancing the branch-size variability in the crown (Ishii & Wilson 2001). Reduced efficiency of the crown is also due to hydraulic limitations, increased respiration, greater belowground carbon allocation, and maturation of tissue. Ishii et al. (2000) identified three different crown forms in old Douglas-fir trees resulting from these processes, namely: mature (increasingly wide range of branch diameters found toward the lower crown, while the diameter distribution of the dead branches remains relatively constant); old (few large diameter live branches and many dead ones); and stressed (branch diameters are relatively small and there are very few if any live branches in the lower crown). These modifications of crown form with age are particularly important to recognize in models that describe the inner defoliated and outer foliated regions of the crown (Baldwin & Peterson 1997; Mitchell 1975). Thus, models predicting crown structure and morphology become more difficult to develop for older trees due to the increasing role that disturbance plays in forming their crown shape.

Site fertility influences crown structure and morphology by altering both branching characteristics (Mäkinen et al. 2001) and needle longevity (Pensa & Sellin 2002). Research has generally indicated that fertilization tends increase the number of new branches, but has little effect on branch angle and branch mortality (Brix 1981; Mäkinen et al. 2001). Fertilization tends to increase not only the diameter of the branches that were formed after the initiation of the treatment, but also the diameter of the branches that were formed before fertilization commenced (Mäkinen et al. 2001). Without cultural addition of nutrient amendments, branch diameter likewise tends to increase with increasing site fertility (Mäkinen 1999). However, Madgwick et al. (1986), found that fertilized trees have a more rapid decrease in branch extension with increasing depth in crown, resulting in a narrower relative crown profile. Perhaps consistent with these patterns, Zeide and Gresham (1991) found that crowns were denser on better quality sites. Needle longevity, on the other hand, tends to decrease with increasing site fertility (Pensa & Sellin 2002).

Water deficiency may also influence crown expansion given that grass competition can have a negative effect (Deleuze et al. 1996). Tasissa and Burkhart (1998) found that stand factors, particularly stand density, failed to significantly enter stem profile models, largely because they were reflected in the combination of tree attributes like DBH, height, and crown ratio. However, crown attributes are directly affected by stand density (Ritchie & Hann 1987; Zumrawi & Hann 1989; Larocque & Marshall 1994).

At the landscape scale, the most important factors influencing crown structure and morphology are elevation (Kuuluvainen & Sprugel 1996), latitude (Kuuluvainen 1992), slope position (Umeki 1995), and wind (Whitehead 1968; Moore 2002). Narrow crown forms are usually associated with sites having low resource supply rates (for example, high altitudes), while broad crown shapes are often found where supply rates are higher and competition for resources plays a more important role (Kuuluvainen & Sprugel 1996). Needle density per unit of crown volume tends to increase with altitude, increasing the proportion of interior crown volume occupied by branches carrying little or no needles (Kuuluvainen & Sprugel 1996). At higher latitudes, crowns are typically much deeper and narrower, perhaps because the light comes more from the side than from directly above (Kuuluvainen 1992). Wind usually causes crowns to be asymmetrical in the direction of the prevalent wind direction (Whitehead 1968) and wind exposure can also cause maximum branch diameter on a tree to increase substantially (Watt et al. in review). Similarly, steep slopes tend to cause crown asymmetry with longer crowns towards the downhill side of the tree (Umeki 1995). For this reason, the thickest branches are typically located on the downhill side of the tree (Colin & Houllier 1991). The structure and morphology of a tree crown is not only a product of individual tree and stand features but also landscape factors.

Complexity of the crown structure and morphology increases significantly with age, species composition, and the spatial distribution of stems. Climatic and physiographic features of the landscape, particularly wind and elevation, also govern crown complexity, partly through the latter two factors. However, in young, pure even-aged stands, the challenge is to simplify the complex interactions between genetics and environmental factors, which ultimately determine crown structure and morphology.

CROWN DRY MATTER PRODUCTION, ALLOCATION, AND VERTICAL DISTRIBUTION

There is considerable interest in estimating the above-ground dry matter of trees and forests for both practical forestry issues and scientific purposes (Parresol 1999). In particular, crown dry matter amount, allocation, and vertical distribution are primary determinants of tree productivity. They also influence many different physiological processes and are sensitive to a variety of environmental factors. This review will focus on the factors that influence production, allocation, and vertical distribution of crown mass at multiple scales including the individual branch, tree, and stand.

Production

Light plays a critical role in determining the amount of dry matter production at the branch, tree, and stand levels. This is indicated by the fact that dry matter amount is often predicted using depth into crown for branches, relative size for trees, and total leaf area index for stands, all of which are surrogates for light availability and absorption. Production is also governed by several other factors, which can be classified into three general categories, namely individual tree attributes, stand-level attributes, and environmental factors.

Individual tree attributes

Total crown mass, particularly foliage, has often been found related to the sapwood area. This relationship is explained by the pipe model theory, which states that a unit of water conducting tissue (sapwood) should service a fixed amount of leaf mass (Shinozaki et al. 1964; Shinozaki et al. 1964). Like entire trees, branches, contain conducting tubes so foliage amount can be effectively predicted from branch diameter. While several studies have found branch diameter to be an important predictor of dry matter, branch position in the crown is also important as it integrates both branch size and light availability. Branch dry matter generally decreases gradually as shading increases, growth ceases, and as the branch approaches mortality, highlighting the importance of branch position. This reduction in dry matter production with increasing depth in the crown may be due to water stress in lower branches (Waring & Silvester 1994; Portz et al. 2000) and insufficient light intensities above the light compensation point (Perry 1994). Thus, although branch diameter tends to be the overall best predictor of branch dry matter, it cannot account for the decline in foliage mass near the base of the crown. Ishii et al. (2002) recently indicated that branch length was a better predictor of foliage area in mature Douglas-fir than diameter because of the increasing importance of disturbance and branch dieback with age. Therefore, individual tree factors, particularly crown length, are also primary determinants of dry matter production at the branch-level as they influence branch characteristics and light availability.

Important tree attributes influencing tree dry matter accumulation include crown size and relative tree height in the stand. Crown size, particularly length and surface area, reflect the photosynthetic potential of tree as well as its vigor and local competitive environment. Maguire and Hann (1989) found that crown surface area was a good predictor of sapwood area at crown base, and presumably, leaf area. The close relationship between sapwood in many species confirms the pipe model theory (Parresol 1999). However, since sapwood area is not commonly measured in routine forest inventories, attempts have been made to develop surrogates for it. One of the important surrogates in addition to crown surface area has been the tree basal area times modified crown ratio (BACR; Valentine et al. 1994; Kenefic & Seymour 1999; Garber 2002). Crown length, however, has been found to be superior to BACR-based model in some species (Gilmore et al. 1996; Maguire & Bennett 1996). Regardless, crown size and tree social position within stand largely reflect a tree's ability to capture light. Mäkelä and Vanninen (1998) indicated that trees react to competition by growing sparser crowns. Thus, tree growth tends to increase with improved social position in the stand, and variables integrating sapwood area with tree social position are therefore strong growth predictors. Although difficult to measure, tree genetics may also influence dry matter production (St. Clair 1993; St. Clair 1994b).

For a given set of environmental conditions, dry matter production at the stand-level depends on tree crown interactions and resulting interception of solar radiation. Thus, characteristics associated with a good crop ideotype for conifers frequently include tall, narrow crowns with less carbon partitioning to branches and greater partitioning to the stem; a large needle or dry weight per unit crown volume, crown projection area or branch width; and a large amount of stem growth per unit leaf area or crown projection area (St. Clair 1994b). This ideotype is based on the idea that tall, narrow crowns reduce self-shading and between-tree shading (Kuuluvainen & Pukkala 1987), which increases light penetration to the inner and lower canopy regions. Thus, the influence of crown characteristics on dry matter production extends to the stand as well as tree-level.

Stand-level factors

Of particular importance at the stand level are the influences of site quality, density, and age on dry matter production. In general, dry matter production tends to increase with site quality, stand density, and stand age (Satoo & Madgwick 1982). Important aspects of site quality that influence dry matter production are water balance (Grier & Running 1977) and nutrient availability (Waring et al. 1981). Gower et al. (1992) found that with an irrigation treatment aboveground net primary production (ANPP) was increased by nearly 25% when compared to a control treatment. With improved nutrition, Brix (1981) indicated that Douglas-fir needle size, needle number per shoot, and the number of shoots produced significantly increased, which all helped to amplify dry matter production in these stands. Fertilization has also been shown to increase the diameter of the branches formed after the initiation of the treatment, but also the diameter of the branches that were formed before the fertilization commenced (Mäkinen et al. 2001), partly through increased branch longevity. Crown dry matter production tends to increase with density up to a certain point and then decrease (Satoo & Madgwick 1982). Baskerville (1965), however, indicated that in immature balsam fir stands dry matter production increased with increasing stand density throughout the density range examined (1,750 to 12,500 stems per ha). Dry matter production generally tends to decrease with density because maximum sustainable foliage dry matter increases with decreasing plant density (Blake et al. 1991). Similar to density, crown dry matter tends to increase with age up to a certain point and then decrease. Turner and Long (1975) indicated that foliar and total crown dry matter reached a steady state of 1,000 kg ha^{-1} at between 40 and 50 years, depending on stand density. In contrast, Acker et al. (2002) found bole dry matter to be positive and increasing in a young stand; positive and constant in a mature stands; and fluctuating between positive and negative in the old-growth stand. Thus, site index, density, and age all influence dry matter production because they affect the amount of foliage within the stand. Composition may also be an important factor as well as Binkley et al. (1984) indicated that Douglas-fir stem dry matter increment was 40 percent greater in a stand with Sitka alder (*Alnus sinuata*) present.

Environmental factors

Climate plays a very important role in determining dry matter production as it influences growth rate and the amount of leaf area that can be attained (Waring et al. 1982). Extreme climatic conditions such as low temperatures limit the growing season, and thereby, constrain dry matter production. Changes in climate may, therefore, induce changes in biomass production; for example, DeLucia et al. (2000) found that pines (*Pinus spp.*) may carry less leaf area as the climate warms. Coble et al (2001) found that all measures of productivity, both above- and below-ground were higher on a north aspect when compared to a southern one. Although elevation may influence dry matter production, Kuuluvainen and Sprugel (1996) indicated that altitude had a weaker effect on crown dry matter amount, particularly foliage, when compared to tree age. The effects of climate are particularly apparent in the work of Gholz (1982) as he found that Pacific Northwest forests have about twice the basal area and dry matter, on average, when compared to other forested regions of the temperate zone, due to their moderate temperatures and high annual precipitation.

Allocation

Allocation of dry matter follows certain allometric relationships, allowing it to be readily modeled and effectively predicted. Although these relationships may vary by species, region, and stands, the fundamental aspects of the relationship remain unchanged. Trees, in particular, follow a predictable pattern of allocation, as foliage tends to be considered a fairly high priority and stem growth is commonly thought of as a low priority (Waring and Pitman (Waring & Pitman 1985; Waring & Schlesinger 1985). Allocation not only determines ecological success and productivity (Perry 1997), it has also been shown to contribute as much to species shade tolerance as leaf-level photosynthetic acclimation (Kull & Tulva 2002). Similar to total production, allocation of dry matter appears to be influenced by site index, stand density, and age.

With increasing site index, the allocation of dry matter to stems increases, while allocation to foliage and branch dry matter decreases, although exceptions have been noted (Satoo & Madgwick 1982). With fertilization, there has been shown to be a relative shift from foliage to branches (Madgwick et al. 1975) and from stem to branches (Will & Hodgkiss 1977). Furthermore, Kurz (1989) indicated that with increasing site index, a decreasing proportion of the dry matter production was allocated to the belowground stand components. These shifts in allocation may due to the improved efficiency of the foliage with increased tree nutrition (Brix 1971) as well as the declining need to invest in fine and coarse roots (Kurz 1989).

Allocation to stems, at the expense of branches, tends to increase with increasing stand densities (Burkes et al. 2003). At the tree-level, larger trees allocate a greater proportion of their stem dry matter to diameter rather than height growth, while smaller trees tend to avoid suppression by allocating stem dry matter to height growth at the expense of diameter (St. Clair 1994a). Xiao (2003) indicated that as crown width increased or stand density decreased, a greater production of dry matter was allocated to the production and maintenance of branches in the central portion of the crown, at the expense of stem wood production. Thus, stand density controls dry matter allocation by influencing the amount of light available for individual crown development.

Changes in allocation patterns have been shown to vary significantly with age, although the effect is not clear (Satoo & Madgwick 1982). Pensa et al. (2001) predicted that allocation is expected to shift from foliage to transport tissues, most notably fine roots, with increasing tree age. The proportion of woody dry matter tends to increase with stand age as branch growth slows and foliage is lost due to disturbances (Ponette et al. 2001). Bartelink (1998), however, concluded that dry matter partitioning is more or less constant, especially after the juvenile phase provided that growth conditions do not change. Mäkelä and Vanninen (1998) indicated that an increase in the proportion of the stem at the cost foliage and branch with tree size demonstrated that the ratio of aboveground to belowground dry matter remains largely the same throughout the lifetime of a tree.

Although site index, stand density, and tree age have been shown influence dry matter allocation on a given site, there are several other factors that have been shown to influence it. Genetics has been shown to be important factor for several species, including Douglas-fir (St. Clair 1994a). DeLucia et al. (2000) also indicated that pines may shift their dry allocation from foliage to stems as the climate warms. Relative tree height plays a role as suppressed trees tended to allocate more in the stem at the expense of branches (Bartelink 1998). While allocation of dry matter is influenced by a variety of factors, dry matter allocation is primarily determined by crown characteristics, particularly height growth (Bartelink 1998). Thus, the factors determining dry matter allocation are essentially those that influence the shape and size of tree crowns.

Vertical distribution

The distribution of foliage within a crown influences light interception (Larsen & Kershaw 1996) and thus, several physiological processes such as gas exchange and photosynthesis (Grace et al. 1987; Russell et al. 1989; Baldwin & Peterson 1997). The vertical distribution of foliage dry matter has been extensively studied with a variety of probability density functions. Distributions that have been experimented with include: the normal (Beadle et al. 1982), chi-square (Massman 1982), lognormal (Schreuder & Swank 1974), gamma (Schreuder & Swank 1974; Massman 1982) and Weibull (Schreuder & Swank 1974). The beta distribution, however, has been preferred when compared to many other distribution due to its flexibility and constraint between 0 and 1 (Massman 1982; Wang et al. 1990; Maguire & Bennett 1996; Garber 2002). In addition to the vertical distribution, the horizontal distribution of foliage dry matter has been studied as well (Wang et al. 1990; Kershaw and Maguire 1996; Temesgen 1998). These studies indicate that the distribution of foliage is influenced by branch-, tree-, and stand-variables as well as environmental factors (Xu & Harrington 1998).

Important tree factors include tree size, relative tree height, shade tolerance, and age. Shade tolerant species have a lower light compensation point and can maintain longer crowns with more foliage than shade intolerant species, elongating their vertical distribution (Garber 2002). The mode of foliage distribution shifted downward and the distribution became more normal with increasing diameter at breast height in a hinoki (*Chamaecparis obtusa*) stand (Mori & Hagihara 1991). Less dominant trees have been shown to shift their relative foliage peak upward, most likely as a response of the reduced light availability and associated loss of apical control (Maguire & Bennett 1996; Xu & Harrington 1998). With increasing age, patterns observed in a Scots pine indicate a downward shift in the foliage peak (van Hees & Bartelink 1993).

At the stand-level, vertical distribution of foliage dry matter appears to be influenced by density, canopy depth, stand top height, and to some extent, composition. Increased spacing or decreased density often results in a greater canopy depth and consequently, proportionately more foliage at greater depth into the crown (Maguire & Bennett 1996; Garber 2002). Similarly, thinning has been shown to result in a more normal vertical distribution of foliage dry matter as lower branches are retained longer than normal (Gary 1978; Medhurst & Beadle 2001). Hashimoto (1991) found that the mode of vertical foliage distribution in the canopy moved upward with stand age, which was accompanied by increases in canopy depth and foliage mass. Garber (2002) indicted that species composition did not significantly influence relative foliage distributions directly, but profiles of absolute distributions showed slight differences between pure and mixed stands. Vertical distribution of dry matter is also determined by stand successional stage; for example, Yang et al. (1999) indicated that early successional stands had more foliage near the upper canopy and later successional stands were more symmetric in distribution.

Foliage distribution on individual trees is sensitive to tree and stand variables as well stand manipulation. Foliage distribution tends to change with time and even stand development, but little quantitative work has been done on this assumption. The distribution of foliage in the tree as well as a stand essentially correspond to light availability.

Conclusion

Dry matter production, allocation, and vertical distribution are sensitive to a variety of factors at multiple scales. Changes in dry matter production, allocation, and vertical distribution, however, are often accompanied by modifications in the size and shape of tree crowns. Although extensive work has been done on dry matter, there is relatively little understanding about the response of production, allocation, and vertical distribution to disturbances, particularly defoliation.

FOLIAGE SIZE AND DYNAMICS

Needle size and foliage dynamics are quite sensitive to changes in the within-crown light environment, and have received a great deal of attention in the scientific literature. Despite the commercial importance of Douglas-fir, relatively little is known about regional variability in its needle size and foliage dynamics.

Size

Needle size is influenced primarily by light but a variety of other factors influence it. Most studies have used specific leaf area as a measure of needle allocation as it represents the efficiency with which the leaf captures light relative to the dry matter invested in the leaf (Marshall & Monserud 2003). Thus, it essentially integrates needle length, width, and dry matter content, which are each further discussed below.

Length and width

Needle length and width represent the cumulative growth of the foliage and are largely influenced by light. Niinemets (1997b) indicated that relative irradiance was the major determinant of Norway spruce (*Picea abies*) needle morphology; i.e., greater irradiance caused needle width, thickness, and length all to increase. However, Youngblood and Ferguson (2003) found that needle width and length differed by year in shade tolerant advance regeneration, but not by light environment. Similarly, Morgan et al. (1983) as well as Smith (1972) found that needle length and presumably width significantly differed by foliage age for balsam fir (*Abies balsamea*) and Douglas-fir, respectively. Morgan et al.

(1983) attributed these differences to climatic conditions in a given year. Significant positive correlations between needle length and the mean temperature of the current growing season, particularly June-August temperature have been shown for Scots pine (Juttila & Heide 1981). Annual variability in cone production has likewise been shown to cause age-class differences in needle length (Morris 1951; Tappeiner 1969). Although needle length and width can be influenced by light, needle length in balsam fir showed no pattern with respect to crown position. Change in needle width with increasing relative irradiance is the major light-related modification in needle structure for most conifers (Niinemets 1997b). Sprugel et al. (1996), however, indicated that shade needles in Pacific silver fir (*Abies amabilis*) are generally as long as or longer than sun needles. Morgan et al. (1983) indicated that differences in needle length between balsam fir trees were not related to tree characteristics such as diameter, height, or crown dimensions, while Niinemets (1997b) found needle length to significantly increase with total height of Norway spruce. Although total height did not affect needle thickness or width in Norway spruce (Niinemets 1997b), needle length and width are both influenced by the tree's position in the stand or light availability. Needle dimensions also change with tree age as needle length, thickness, and width appear maximal in 40-year-old Douglas-fir trees (Apple et al. 2002). Needle dimensions are also sensitive to tree nutrition. Application of nitrogen fertilizer increased both needle length and width in a young Douglas-fir stand (Brix & Ebell 1969), underscoring the fact that needle length and width are sensitive to light but also to other tree and site factors such as age and site index.

Dry matter content

Dry matter content of a needle is influenced largely by light, but shows more variation than needle length or width. Needle dry weight increases linearly with relative irradiance (Niinemets 1997b), which is primarily due to changes in leaf thickness (Sprugel et al. 1996). The increase in needle thickness is mostly due to the thicker palisade parenchyma in sun foliage (Lambers et al. 1998). Needle dry weight tends to decrease with depth in the crown (Smith 1972; Hager & Sterba 1985). However, Kay (1978) indicated that needles tended to be the heaviest in the central crown region. Needle dry weight has been shown to increase with foliage age (Smith 1972; Kay 1978; Gilmore et al. 1995), although Hager and Sterba (1985) found no difference in the dry matter content of older and current-year needles. Needle dry weight content tends to increase with foliage age because of the accumulation of nonstructural carbohydrates and other secondary substances over time (Niinemets 1997). Needle dry weight content is also influenced by several tree-level factors including relative tree height in the stand as well as size. Relative tree height in the stand influences light availability and thus, needle dry weight content tends to increase with improved social status (Gilmore & Seymour 1997). Similarly, needle dry weight also increases with both diameter (Hager & Sterba 1985) and total tree height (Niinemets 1997b). Needle dry weight increases with tree age and size because of increased investment in lignified hypodermal cells and in astrosclereids. The greater proportion of these supporting structures in the needles of larger trees may function to protect from damage by abiotic and biotic factors (Apple et al. 2002). Needle dry matter content has also been shown to vary with thinning as well as regionally. Both Brix (1981) and Smith (1981) reported an increase in needle dry matter content with thinning. Smith (1981), however, indicated that needles from trees grown in the Oregon Coat Range maintained a nearly constant weight throughout the year, regardless of whether stands were thinned or left unthinned. In contrast, the needle mass of Douglas-fir of Douglas-fir in the Cascades increased by more than 50% during the summer (Smith et al. 1981). Thus, leaf dry matter content is sensitive not only to tree and site factors but also to leaf water status and the time of day and season at which leaves are sampled (Garnier et al. 2001).

Specific leaf area

Due to the changes in needle size and dry matter content described above, specific leaf area tends to increase from tree top to crown base and decrease with needle age (Bartelink 1996). Alternative explanations for the decrease in specific leaf area with foliage age and needle size include the accumulation of nonstructural carbohydrates and other secondary substances over time mentioned above (Niiemets 1997), and/or the selective retention of needles with lower specific leaf area (Hager & Sterba 1985). Ishii et al. (2002) found that rates of accumulation of secondary substances were greater (needles with greater specific leaf area were shed more rapidly) in needles on lower-crown branches than on upper-crown branches in mature Douglas-fir, and Ishii et al. (2002) also found there was no statistical difference in specific leaf area between regular and epicormic shoots, while it decreased with increasing distance from branch base, particularly in the upper portion of the crown. In addition to light, Marshall and Monserud (2003) concluded that water potential is an important factor as specific leaf area was only significantly related to branch height and not branch length or canopy elevation.

Specific leaf area is also influenced by other factors such as tree size. Specific leaf area was correlated with tree height (Niinemets & Kull 1995) and diameter (Hager & Sterba 1985) in Norway spruce. Similarly, St. Clair (1994b) indicated that tree size was negatively correlated with specific leaf area, as larger trees tended to have heavier, stouter needles. St Clair (1994b) also indicated that there was little genetic variation in specific leaf area. Chen et al. (1996), however, found that Douglas-fir had more plastic specific leaf area than the shade intolerant shore pine (*Pinus contorta* var. *contorta*). With decreasing light availability, specific leaf area significantly increased. Specific leaf area also significantly varies with sampling date and fertilizer treatment (Nippert & Marhsall 2003). Thus, specific leaf area has been shown to vary within- (Bartelink 1996) and between-trees (Gilmore & Seymour 1997) for a variety of reasons.

Dynamics

Although foliage dynamics have been modeled (Fleming 2001), the age distribution and senescence rates of foliage are highly variable within- and between-trees. Foliage dynamics have particular importance on tree productivity because photosynthetic efficiency declines drastically with foliage age (Clark 1961; Woodman 1971).

Age

Conifers generally hold their needles between 2 to 10 years (Kikuzawa & Ackerly 1999), although needle retention of up to 45 years has been reported (Ewers & Schmid 1981). Cost-benefit models of foliage lifespan suggest that leaves with high construction costs should be retained longer to maximize carbon gain (Kikuzawa 1991). These construction costs must also include the costs of supporting structures (Kikuzawa & Ackerly 1999). Supporting structures, particularly branches, can have high maintenance respiration costs associated with them (Sprugel 1990).

Within individual trees, needle lifespan has been shown to vary with crown position. Niinemets (1997a) found, irrespective of irradiance, needles with maximum longevity were situated in the middle rather than the bottom of the canopy. This was interpreted as evidence that needle lifespan is determined by the irradiance levels to which needles are exposed during their primary growth (Niinemets 1997a). Fleming and Piene (1992), on the other hand, found that crown level did little to improve predictions of needle lifespan, but when they were significant the trend was shorter needle lifespan in the lower crown (Piene & Fleming 1996). Kohyama (1980) and Balster and Marhsall (2000) indicated that needles on branches with a lower growth rate had a longer lifespan than those on branches with a higher growth rate. Maillette (1982) suggested that needles located on the leader had a much lower survivorship than all other needles. Schoettle and Smith (1991) found that leaf longevity did not vary by crown aspect. Piene and Fleming (1996) indicated that age-specific rates of needlefall tended to increase with needle age throughout the observed crown.

The variability of needle lifespan within crowns is controlled by several tree-level factors. Maillette (1982) concluded that tree age, apical dominance, and growth pattern appeared to be the most important factors influencing needle survivorship. Maximum needle life span, therefore, tends to be greater in shaded trees than in sun-exposed trees (Niinemets 1997a). Xiao (2003), on the other hand, found needle longevity to be negatively associated with total tree height. Fleming and Piene (1992) as well as Xiao (2003) found that needle longevity increased with tree age. Apple et al. (2002) indicated that this longer retention is due to the metabolically expensive needles that mature trees invest in to help protect against damage. This may also be related back to growth as Balster and Marshall (2000) hypothesized that greater growth would caused faster self-shading and lower needle longevity. Although needle longevity has been shown to be primarily a phenotypic response (Reich et al. 1996), McCrady and Jokela (1996) suggested there was significant genotype variation in foliage longevity. Thus, between-tree variability can be high, but it is relatively minor compared to between-stand variability of needle longevity.

The longevity of needles is influenced by several site factors including density (Piene & Fleming 1996), nutrition (Balster & Marshall 2000), altitude (Reich et al. 1996), latitude (Xiao 2003), and climatic factors (Maillette 1982). Although Brix (1981) found no difference between spaced and unspaced trees, Piene and Fleming (1996) found that needle lifespan was significantly greater in a spaced stand when compared to an unspaced one. Generally, needle lifespans increase with decrease nutrient and water availability (Pensa et al. 2001). The response of Douglas-fir needle retention to fertilization, however, has varied from an increase (Turner & Olson 1975), decrease (Balster & Marshall 2000), and to no effect (Brix & Ebell 1969). Needle longevity has been shown to increase with altitude (Reich et al. 1996) and latitude (Xiao 2003), primarily because of their influence on climate (Pensa et al. 2001) and growth rate. Pensa and Jalkanen (1999) indicated that summer temperatures were particularly important in determining needle longevity, while Xiao (2003) indicated that longevity decreased with mean January temperature. Needle longevity, therefore, can be considered a complex interaction with light, genetics, tree size, and site conditions.

Seasonal

Studies have examined the seasonality of foliage primarily through patterns in litterfall timing (Bray & Gorham 1964). These studies have suggested that needle death tends to occur between mid-August and mid-September (Maillette 1982), with foliage litterfall generally peaking in the late fall with the onset of the winter storms (Gessel & Turner 1976). Will (1959), on the other hand, found that the rate of needlefall under Douglas-fir in New Zealand did not vary greatly with season. Furthermore, Dimock (1958) noted that extremely low temperatures can influence the seasonal distribution of foliage litterfall, and increased rates of needlefall have been caused by drought (Bray & Gorham 1964) or severe winter conditions (Reukema 1964b; Grier 1988). Thus, rates of needlefall are not constant over the year and controlled largely by tree and environmental factors.

Conclusion

The distribution of foliage among various age classes is highly dynamic within-crowns as well as between trees and stands. Light availability plays a particularly important role in determining the variability within a crown and between trees. Climate, especially temperature, becomes an increasingly influential factor in determining the variability of needle longevity between stands. Genetics can have an influence, but observed phenotypic responses are largely a result of tree size and environmental factors. While there is great variability in the longevity of foliage, needlefall tends to follow a distinctly seasonal pattern with a peak in the early to late fall. This seasonal pattern is controlled, however, by tree and environmental factors as well.

TREE CROWNS AND DISEASE

Disease and disease organisms are one component of forest ecosystems. Disease has led to the recent decline of several important tree species in the United States such as sugar maple in the northeast, oak (*Quercus spp.*) in the southeast, and red spruce in the east (Houston 1992). Diseases affect many parts of the tree including the crown, foliage, and roots. The impacts of tree disease on the crown and foliage are discussed below.

Crown condition

Numerous factors influence crown architecture and condition, including genetics, competition, and site quality. Klap et al. (2000) found crown condition to vary naturally with tree age, altitude, and drought stress. Tree age was determined to be the most important factor influencing the condition of the crown (Klap et al. 2000). Solberg (1999) estimated the annual reduction of crown density due to age was 0.12% for Norway spruce in Norway. Crown density appears to be independent of tree height and crown length (Innes 1991). Horntvedt (1993) found that the number of live branches per tree, needle retention, and shoot length for Norway spruce all were positively correlated with increasing crown density. Crown density and long-term growth increment are positively correlated (Innes and Neumann 1991). Emergent trees have thinner crowns than trees situated within the interior of the stand (Innes 1991). As a slightly different crown index, crown transparency was found to be positively correlated with site elevation (Kandler 1992). Crown closure also strongly influences crown transparency as it tends to increase in more open stands (Innes 1993). Crown transparency has also been found to increase with age in Norway spruce and Scots pine (Innes 1993).

Disease generally influences the condition of the crown by decreasing density and the live crown ratio, while increasing dieback and transparency. This generally leads to the tufted appearance of the crown, which is one of the most defining features of a diseased tree (Innes 1993). This increased transparency of the crown can also lead to a greater proportion of secondary branches on the tree (Innes 1993). Diseases also tend to affect the condition of the tree tip, which leads to further crown malformations.

Foliage condition

The same factors that influence crown architecture also affect the condition of the foliage. Needle morphology varies significantly in response to the light conditions under which it develops as more exposed needles are thicker, denser, and have a greater projected area than unexposed needles (Kuuluvainen & Sprugel 1996). Needle length mainly depends on age and the amount of water and nitrogen stress experienced by the tree during the growing season (Raison et al. 1992). Needle size has been shown to be directly related to climatic condition, particularly drought (Roloff 1988; Innes 1992). Needle retention is significantly influenced by genetics, crown position, altitude, and latitude (Kurkela & Jalkanen 1990; Innes 1993; Merrill & Wenner 1996; Pouttu & Dobbertin 2000). Specific leaf area is genetically encoded but can differ significantly within and between individuals (Pierce et al. 1994). The density of the needle is strongly affected by the degree of competition a tree has undergone (Mäkelä & Vanninen 1998). Eckmullner and Sterba (2000) found specific needle area to increase with decreasing light, while only crown-condition class and cross-sectional area had an effect on needle mass in Norway spruce.

Rate of litterfall may be a diagnostic for foliar diseases as Albrektson (1988) found needle litterfall in stands of Scots pine to increase with site quality and decrease with increasing stand age and latitude. Kouki and Hokkanen (1992) observed a strong correlation between needle litterfall and mean July temperature with high temperatures implying high needle litterfall. Some studies, however, have found no correlation between defoliation and litterfall (Bille-Hansen & Hansen 2001; Poikolainen & Kubin 1997), while other studies have documented a positive correlation (Jukola-Sulonen et al. 1995; Arkley & Glauser 1980). On the other hand, litterfall is sensitive to silvicultural treatments such as thinning (Trofymow et al. 1991; Dimock 1958) and fertilization (Gessel & Turner 1976), both of which influence crown recession and branch structure. Needle litterfall helps to assess the influence of climate and air pollution on crown condition (Innes 1993), but the primary limitation of this measure is that it does not reveal the amount of needles remaining on the tree (Kurkela & Jalkanen 1990).

Tree diseases tend to affect foliage condition through discoloration, premature loss, reduction in leaf size and density, and nutritional loss (Innes 1993). Discoloration is one of the main symptoms associated with tree decline (Innes 1993). Foliage on diseased trees tends to turn yellow or brown (Innes 1993). Dramatic increases in foliage loss are one of the most influential impacts of disease on tree growth and vigor. Tree physiological response to defoliation is complex and dependent on the timing of the damage, fraction of crown affected, and the impacted needle age class (Honkanen et al. 1994; Långström et al. 2001). Some studies suggest that severely defoliated trees, which are usually defined as trees with more than 60% foliage loss, are incapable of recovery (Innes 1993). Furthermore, it has been noted in several studies that Scots pine normally survives one year of severe defoliation, while two years of defoliation may cause substantial mortality (Långström et al. 2001). Diseased trees often produce smaller and less dense foliage due to the reallocation of their available resources (Innes 1993). Masuch et al. (1989) found that the average length of three-year-old Norway spruce needles was 10 mm and dropped to 8 mm in trees exposed to acidic fog. The reduction of leaf size and density has significant implications for tree growth as thicker foliage usually has markedly higher maximum photosynthetic rates than thinner leaves of the same species (Sprugel et al. 1996).

Innes (1993) summarized that nutrient concentrations of coniferous foliage vary according to the nutrient content of the soil, with needle and tree age, with needle position in the crown, and with the annual physiological cycle. Roelofs et al. (1985) observed that needles of Scot pine that were infected by *Gremmeniella abietina* and *Sphaeropsis sapinea* had higher nitrogen concentrations and lower magnesium concentrations than unaffected needles. Mohren et al. (1986) found nitrogen: phosphorous ratios were higher in defoliated Douglas-fir. Calcium and zinc were observed to be higher in chlorotic Scots pine (Innes 1993). Finally, Clancy et al. (1993) found the Douglas-fir most susceptible to western spruce budworm (*Choristoneura occidentalis*) defoliation to have lower levels of nitrogen and sugars than resistant trees.

Influence of SNC on Douglas-fir

SNC is a foliar disease so its primary impact has been on the foliage condition of coastal Douglas-fir. The disease causes yellowing, premature needle loss, decreased needle retention, abundant fungal pseudothecia on needles, smaller average needle size, and reductions in height and basal area growth (Hansen et al. 2000; Maguire et al. 2002). Premature needle loss has been observed to be greater in the upper crowns of trees (Hansen et al. 2000). In severely diseased forest plantations in Washington, many trees retained only 1 or 2 years of needles (Hansen et al. 2000). In a Douglas-fir Christmas tree plantation, Chastagner (1984) found that infected trees usually retained 2-3 age classes of needles. Pseudothecial density is correlated with needle age and level of defoliation (Hansen et al. 2000). The disease has translated into an estimated average volume growth loss for 1996 in young plantations of 23%, with the loss being as high as 52% for the most severely impacted plantations (Maguire et al. 2002).

CROWN INDICATORS AND FOREST HEALTH

Assessment of forest health is a subjective evaluation that is strongly influenced by the frame of reference chosen to examine forest conditions (McLaughlin & Percy 1999). This means that comparisons between regions and time may or may not be valid, depending on how the survey was conducted (Innes 1988). A healthy forest has commonly been defined as one that is balancing growth with mortality (Manion & Griffin 2001). Most surveys have assessed health by rating a fixed number of individual trees, which are then extrapolated to the stand level (McLaughlin et al. 1992). Most forest health surveys assess two general types of tree characteristics, attributes of the crown and the condition of the tree foliage.

Measures of Crown Condition

Important indicators of crown condition that have been used in previous studies include density, dieback, and transparency (California Department of Forestry and Fire Protection (CDFF) 2000). These measures have been used because visible crown features during the normal growing season can provide an assessment of overall forest condition at a variety of spatial levels including the individual tree, stand, and watershed levels (Lewis & Conkling 1994). Also, crowns influence many important stand attributes such as organic matter accumulation, forest microclimate, and habitat properties (Maguire & Bennett 1996). Finally, several studies have reported the strong influence of crown condition on tree growth and vigor (Anderson & Belanger 1987; Oak & Tainter 1988; Millers et al. 1991; Smith et al. 1997).

Crown density

Crown density is the most widely used measure of crown condition, particularly in Europe (Innes & Boswell 1990). This indicator measures the two-dimensional crown fullness by estimating the amount of sky blocked by the upper tree bole, live branches, foliage, and reproductive structures (CDFF 2000). Density scores range from 0 to 100% and are usually measured in 5% classes (CDFF 2000). Crown density is determined in a variety of ways, but usually the crown of a target tree is compared with that of a reference tree in the near vicinity or on a photograph (Innes 1988). Horntvedt (1993) found that visual assessment of crown density on slightly defoliated tree tended to underestimate the actual reduction in foliage biomass. Furthermore, he found that branch geometry in older Norway spruce trees tends to become increasingly complex, making assessments of crown density difficult. Steinman (2000) found that trees with crown densities less than 30 percent were the ones most likely to die. Innes and Boswell (1990) noted that crown density is a nonspecific symptom, which means the absence of any qualification about the measure is an important shortcoming of any survey. Solberg and Moshaug (1999) found that when crown density changes for a plot, most of the trees were generally affected, which indicates that any effects from competition between trees were sufficiently removed in assessments of crown density.

Crown dieback

Crown dieback has been found to be the most significant indicator of tree mortality (Steinman 2000). This indicator measures the mortality percentage of relatively new branches in the upper part of the crown (Stolte et al. 1994; CDFF 2000). Dieback values range from 0 to 100% and are again measured in 5% classes (CDFF 2000). Softwoods with more than 20 percent dieback are the most likely to die within one year (Steinman 2000). Innes (1993) concluded that dieback and shoot death plus other estimates of crown architecture were better indices of forest health than were crown discoloration and transparency.

Crown transparency

Crown transparency measures the amount of light passing through the foliated portion of the crown ranging from 0 to 100% (CDFF 2000). The measure estimates how dense the foliage is on branches, which is indicative of a loss of vigor or stress (Metzger & Oren 2001). This measure has been used in forest health surveys in Europe, especially Great Britain, the Forest Health Monitoring Program in the United States, and the Sugar Maple Decline Project (Innes 1993; Burkman et al. 1998; Millers et al. 1991). Gertner and Köhl (1995) found that error in estimating crown transparency can be as much as ±15%. A recent study found crown transparency to be even more biased as trees with large crowns are rarely classified as unhealthy (Metzger & Oren 2001). Steinman (2000) also found crown transparency to be a weaker indicator of tree mortality when compared to other crown measures. Another measure similar to crown transparency is crown sparseness. Recently, Maguire and Kanaskie (2002) have proposed the ratio of live crown length to sapwood area as a measure of crown sparseness.

Studies have shown that the relationship between growth, crown appearance, and tree health is not explicit (Innes 1993; Oren et al. 1993; Metzger & Oren 2001). It is assumed that trees with high density, low transparency, and wide crowns have a greater potential for carbon fixation and nutrient storage (Stolte et al. 1994). In general, trees with 30% crown transparency), 50% crown density, and 20% dieback are considered healthy (Bechtold et al. 1992). However, visual monitoring of crown conditions can be strongly influenced by observer training (Gertner & Köhl 1995), perception (Innes 1990), crown dimensions (Metzger & Oren 2001), and by weather and lighting conditions (Barnett et al. 1995). One relatively objective measure of crown condition is the crown length to sapwood area ratio (Maguire & Kanaskie 2002).

Assessment of Foliage

Because plant leaf area is considered to be the most important single determinant of plant productivity, several different indices are used to assess the condition of the foliage on a tree (Monserud & Marshall 1999; Innes 1993). Some of the most important indices include foliage discoloration, needle retention, leaf size, and needle litterfall (Innes 1993).

Discoloartion

Discoloration is often the main symptom associated with tree decline (Innes 1993). It is the key factor in diagnosing several types of pollution and oxidant injuries (Innes 1993). Like crown density, discoloration is a subjective measurement because there are a variety of ways of measuring it (Innes 1988). Generally, the extent of discoloration is recorded and no distinction is made between browning and yellowing, which effectively limits the usefulness of the measure (Innes 1988). It has been found that discoloration is correlated with the extent of older needle browning and not correlated with crown density (Innes & Boswell 1990).

Needle retention

Needle retention can be a better index of crown condition than crown density if an accurate count can be made (Innes & Boswell 1990). This measure provides an index of the number of years that needles are retained (1993). The measure is only a useful estimate of needle loss if loss occurs progressively from the oldest to the youngest needles (Innes 1993). Usually, this index is estimated with the use of binoculars, which increases the subjectivity of the measure (Innes 1993). The measure is particularly difficult when more than seven years of needles are present on the branch (Innes 1993). However, a more objective technique, the needle trace method, has been effectively utilized in many studies (Pouttu & Dobbertin 2000; Jalkanen et al. 1994; Kurkela & Jalkanen 1990).

Two indirect measures of foliage condition that have been used in studies are needle litterfall and the sapwood cross-sectional area to estimate foliage area (Jalkanen et al. 1994; Waring et al. 1980). Needle litterfall has mainly been used to assess the influence of climate and air pollution on crown condition. The primary limitation of this measure is that it does not reveal the amount of needles remaining on the tree (Kurkela & Jalkanen 1990). Furthermore, some studies have found no correlation between defoliation and litterfall, while other studies have (Bille-Hansen & Hansen 2001). Growth per unit of sapwood cross-sectional area or per unit estimated leaf area has been used to detect the impact of disease (Waring et al. 1980; Oren et al. 1985) and to estimate tree susceptibility to insect attack (Waring & Pitman 1985). Limitations of this index are the need for a standard measurement point on the tree due to the sapwood taper from breast height to the base of live crown and the possibility that leaf area to sapwood area ratios may vary with ring width and sapwood permeability (Albrektson 1984; Whitehead et al. 1984).

Foliage deterioration and loss is often the end-result of a series of changes in the tree's condition (Innes 1993). This means that changes in the foliage condition of a tree may take time to develop and reflect the effects of an event that occurred several years previous (Innes 1988). Despite these limitations, assessment of foliage still remains an effective measure of tree health.

SNC Indices

Both aerial and ground-based surveys have been used to assess the impact of SNC in the Oregon Coast Range. The aerial surveys are flown in early spring and rate stands on the degree of discoloration (Kanaskie et al. 2002). Ground checks use permanent monitoring plots, and health ratings are based on visual assessments of average needle retention by crown thirds and other crown characteristics such as discoloration and density. The stands are rated on a scale of 1 to 6, with 1 being a healthy, normal-appearing Douglas-fir stand with 3.5 years of needle retention at the middle crown, and a 6 being a stand with extremely yellow foliage and low needle retention. These measurements are subjective and can consequently be biased, which limits spatial and temporal comparisons. They do, however, establish zones where forest management needs to take into account the effects of the disease (Kanaskie et al. 2002). Maguire et al. (2002) recently found that the mean needle retention was the most effective SNC index in explaining both basal area and top height growth. The crown length to sapwood area ratio has been found to increase with increasing

SNC severity, highlighting the ability of the index to objectively assess tree condition (Maguire & Kanaskie 2002).

CONCLUSION

Crown structure and morphology, dry matter production, and needle size are all influenced by a variety of factors including crown condition. Therefore, as forest health has become an important topic in recent years, crowns are the focal point of forest health assessments. Current diagnostic techniques, however, have not been effective due to their subjective nature. Crown density and transparency are the most common methods used to assess the condition of a tree. Foliage is usually examined with respect to discoloration and needle retention. All of these measures are subjective and can be highly biased by observer's training, perception, crown dimensions, and by weather and lighting conditions. Currently, SNC surveys in the Oregon Coast Range use crown density, discoloration, and needle retention to rate stand health, which limits temporal and spatial comparisons due to the inherent biases of the measures. Tree disease can significantly alter the crown and foliage condition of a tree. Some of the common influences of tree diseases are decreased crown density, lower needle retention, and premature foliar loss, which tend to result in a loss of diameter and height growth. SNC primarily affects the foliage condition of coastal Douglas-fir by causing yellowing, smaller needles, and premature needle loss. Development of an effective crown health index, therefore, requires knowledge of how disease changes tree crowns and what the index represents biologically.

CHAPTER THREE: SWISS NEEDLE CAST AND DOUGLAS-FIR CROWN STRUCTURE AND MORPHOLOGY IN THE OREGON COAST RANGE

ABSTRACT

Plant diseases are known to influence crown structure and morphology but this has rarely been quantified. Swiss needle cast (SNC), an endemic foliar disease, may be modifying Douglas-fir crown structure and morphology in the Oregon Coast Range by increasing epicormic branching and slowing the rate of crown recession. This study was initiated to better understand SNC's influence on Douglas-fir crown dynamics and foliage density within this region. In the spring and fall of 2002, 82 trees from 23 different plantations were destructively sampled. Various linear and nonlinear equations were used to examine the relationship between several crown characteristics and SNC. Significant relationships existed between Douglas-fir crown size, shape, location, branching habit and SNC. The disease has led to crowns that are shorter and receding faster than normal, while their largest measured width remains unaffected. The number of primary interwhorl and secondary lateral branches decreased with lower foliage retention, while foliated branch length decreased. Crown radii and maximum branch diameter profiles suggested that changes within the crown might be occurring at different levels due to variations in SNC damage within the crown. Some of these findings can be supported by the indication that

branches in the lower portion of the heavily diseased crowns may be elongating faster than normal and attaining higher length to diameter ratios. This study provides a foundation for understanding the changes that can occur in crowns with extended defoliation and a framework for assessing alterations in carbon allocation patterns due to the disease.

INTRODUCTION

Crown shape and size are two of a tree's most defining characteristics. At the stand level, crown shape and size influence production efficiency (Jack & Long 1992; Gilmore et al. 1996), biological diversity (Tanabe et al. 2001) fire susceptibility (Keyes & O'Hara 2002), mechanical stability (Wilson & Oliver 2000), and microclimate (Grace et al. 1987). At the individual tree-level, crown dimensions have an effect on physiological processes (Jahnke & Lawrence 1965), stem form (Larson 1963), wildlife use potential (Clement & Shaw 1999), behavior under wind stress (Moore 2002), and wood quality (Maguire et al. 1991). Thus, crown structure is fundamental to a long list of resource professionals, including: forest ecologists, wildlife biologists, silviculturalists, biometerologists, and forest biometricians (Gill & Biging 2002). Several computer models rely on accurate descriptions of crown shape and size to represent competitive interactions and growth potential. For example, the growth and yield model ORGANON depends on crown dimensions to compute crown closure, rate of height growth, and the probability of death for a given tree (Hann 1997; Dubrasich et al. 1997). Therefore, understanding the factors that influence crown structure and development is critical for accurate forecasting of stand dynamics, growth, and yield.

Crown shape and size are often expressed in relative measures, such as crown slenderness ratio (crown width/crown length) and live crown ratio (crown length/total tree height) (Larocque & Marshall 1994). Although these ratios are similar in concept and indicative of individual tree stem growth potential, they express different measures of space occupancy and tree allometry. Crown slenderness ratio indicates the ability of crowns to intercept solar radiation (Horn 1971), which has a direct impact on stand competition and self-thinning (Kuuluvainen & Pukkala 1987). Live crown ratio is an index of tree vigor since it can be estimated as the proportion of potential photosynthetic surface area (Oliver & Larson 1996). In a practical sense, live crown ratio also relates directly to proportions of tree biomass components (Mäkelä & Vanninen 1998).

Several studies have noted crown shape and size to be quite plastic (Fisher & Hibbs 1982; Raulier et al. 1996; Santini & Camussi 2000), particularly in fairly shade tolerant species such as Douglas-fir (Chen et al. 1996). This plasticity is primarily related to the high degree of autonomy that individual branches have within a tree (Sprugel et al. 1991; Kull & Tulva 2000). Branching is often related to spatially heterogeneous radiation within a stand and tends to depend strongly on the photosynthetic production of the tree (Kull & Tulva 2002). Branches have multiple functions in a tree including mechanical support of foliage, water transport, and storage of photosynthate (Ishii et al. 2000). They also directly influence wood quality given that lumber grade recovery is a function of knot size (Fahey et al. 1991) and distribution (Maguire et al. 1994). Since crown morphology is the net results of the number, size, and vertical distribution of branches, understanding variation in branching patterns leads to better insight into the causes of variation in crown morphology.

Crown morphology and branching patterns change with age (Kuuluvainen & Sprugel 1996; Ishii et al. 2000), stand density (Kellomäki 1986; Kurttio & Kellomäki 1990; Mäkinen 1999), composition (Bartelink 2000; Garber 2002) and silvicultural regime (Brix 1981; Medhurst & Beadle 2001). However, the causes of variation in crown and branch structure are poorly understood, because they are the result of complex interactions of genetic and environmental factors (Kuuluvainen & Sprugel 1996). One aspect of the environment that has received relatively little attention is the impact of foliar diseases. Although general indices of foliage loss are common, more comprehensive analyses of total foliage loss, shifts in needle age class distributions, and net effects on crown structure are rare.

Swiss needle cast (SNC) is an increasingly important foliar disease of Douglas-fir (*Psedotsuga menziesii* (Mirb.) Franco) in the Oregon Coast Range and is thought to be changing crown shape, size, and structure by inducing premature needle loss and reduced tree growth. This disease, which is caused by the endemic pathogen *Phaeocryptopus gauemannii*, has been noted to reduce foliage retention to as little as one year and volume growth by as much as 52% (Maguire et al. 2002). Over 157,000 ha in the Oregon Coast Range are showing SNC symptoms detectable by aerial survey, reflecting the dramatic increase in this disease in recent years (Kanaskie et al. 2002).

The overall objective of this study was to examine the impact of SNC on crown structure in the Oregon Coast Range. Specific objectives were to: (1) describe changes in the crown height, size, and shape; (2) examine the disease impact on overall crown profile and vertical trends in maximum branch diameter; and (3) assess the influence of the disease on branching. It is hypothesized that as a result of increased crown sparseness caused by SNC, light now penetrates deeper into the crown, stimulating epicormic branching and slowing the rate of branch suppression mortality (crown recession). This deeper penetration of light may be one of several mechanisms responsible for the observed increase in crown length to sapwood ratio under increasingly severe SNC (Maguire and Kanaskie 2002). The scope of inference for the study is young (10-30 year old), managed Douglas-fir plantations in the northwestern portion of the Oregon Coast Range.

METHODS

Study area

The twenty-two relatively young Douglas-fir plantations used in this study were selected from 76 permanent plots being monitored as part of the SNC Growth Impact Study sponsored by the SNC Cooperative at Oregon State University (Figure 3.1). The plots were located in the Oregon Coast Range within 32 km of the Pacific coast, north of Newport and south of Astoria, Oregon. The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall in this area varies from approximately 180 to 300 cm/yr, and January mean minimum and July mean maximum temperatures range from –2 to

2°C and from 20 to 28°C, respectively (Maguire et al. 2002). Variations in precipitation and temperature for this area are strongly correlated with elevation and proximity to the coast. Elevation of the study plots ranged from 337 to 1,312 m, all aspects were represented, and proximity to the coast varied from 0.97 to 31.8 km.

Species composition of the plots was ≥90% Douglas-fir by basal area with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla*) and other conifer and hardwood species. The plots had similar stand attributes but varied in SNC intensity as estimated by average stand foliage retention (Table 3.1).

Data collection

Sampling occurred both prior to bud break in the spring and after the end of the growing season in fall of 2002. Fifty-nine trees were sampled near 10 different permanent plots in the spring and 39 trees were sampled near 13 different permanent plots in the fall. Within approximately 30 m of each permanent monitoring plot, trees were sampled with diameters at breast height (DBH) and foliage retentions similar to those on the permanent plot. All sample trees were subjectively chosen, surrounded by other Douglas-fir trees, and located away from any gaps or landings. The number of sample trees per plot ranged from 3 to 6. Sample tree characteristics are shown in Table 3.2. Before felling, DBH was measured with a diameter tape to the nearest 0.1 cm. In the fall, two perpendicular measurements of the largest crown width (LCW) were made. Each sample tree was then felled in a manner that minimized foliage loss and breakage. Total height (HT) from the base of the stump to the tip of the tree as well height to the crown base (HCB=lowest live branch) was recorded using a metric tape stretched along the bole. Basal diameters and height of each live branch were measured to the nearest millimeter and centimeter, respectively. A total of six whorl branches, two from each third of the crown, and three interwhorl branches, one from each third of the crown, were selected at random. Sample branches were cut at the base and measured for total length along the stem; sample branches collected in the fall were measured for foliated length. Mean branch characteristics are shown in Table 3.3. Average foliage retention to the nearest 0.5 yr for the branch was recorded as well as the number of whorl and interwhorl secondary branches for the last five growing seasons. The remaining portion of the branch was clipped into segments and placed in a plastic bag. After branch sampling, thin disks were removed from the tree at breast height (1.37 m) and crown base. In the fall, one-year old foliage samples were also randomly taken from branches located in the top crown third for PCR assessment of *Phaeocryptopus gauemannii* biomass (Manter et al. 2001).

The two stem disks from each tree were measured for sapwood area on the two radii forming the long axis of the disk and on the two radii perpendicular to the longest. Sapwood cross sectional area (cm^2) was computed assuming that the total cross-sections and heartwood cross sections were elliptical in shape. Current and five-year growth increments were also measured on the four perpendicular radii.

Data on each of the study sites have been collected every year since 1996 by the Oregon Department of Forestry. Square, 0.08 ha permanent plots were established by the SNC Cooperative in 1998. On each measurement plot, all trees were tagged at breast height and measured for DBH (nearest 0.1 cm). In addition, a subsample of at least 40 Douglas-fir were measured for total height and height to crown base. Plots are remeasured every two years; however, ten trees on each plot have been scored for SNC every year since 1998. On these trees, the crown is divided vertically into thirds and the average number of years that foliage was retained in each third was estimated visually to the nearest 0.1 year. Overall crown discoloration was also recorded on a 1 to 4 scale, with 4 represented by the most severe discoloration. On branches in the fifth whorl from the top of the tree, the percentage of the full complement of needles remaining on the branch is recorded. Plot ratings were computed as the average from all ten trees.

Data analysis

Various linear and nonlinear regression models were fit to the data to assess the relationship between SNC, crown morphology, and crown structure. All-subsets regression analyses were run to screen for the potentially most powerful explanatory variables. Predictor variables included various stand and site values such as Douglas-fir basal area, basal area of competing species, site index, elevation, and distance from the coast. Final models were chosen on the basis of biological appeal, residual analysis, Furnival's index (FI) (Furnival 1961), and Akaike's information criterion (AIC). SNC impact was then assessed by adding various SNC indices such as foliage retention as well as crown color and crown density to the model. Final predictor variables were all significant at the $\alpha=0.05$. For nonlinear models the generalized coefficient of multiple determination (R_g^2) (Kvålseth 1985) was calculated as 1 – (residual sum of squares/ total corrected sum of squares). It was assumed that there is no plot effect besides SNC, and each individual tree was, therefore, treated as if it were drawn at random from all possible trees. All analyses were done in SAS v8.2 (SAS Institute, Cary, NC) and SPLUS 2000 (Mathsoft, Seattle, WA).

Crown size, shape, and height

For each sample tree and measured plot tree, crown length (CL) was calculated by subtracting the height to crown base from the total height, and crown ratio (CR) as the proportion of total tree height occupied by live branches. Quadratic mean of LCW of each sample tree was computed as the square root of the two perpendicular LCWs.

Various linear regression models were fitted to the data to assess the relationship between SNC and crown size and shape. The relationship between SNC, CL, and LCW was examined using the following models:

$$[3.1] \quad \mathrm{LCW} = \beta_{10}\mathrm{MCW}^{\beta_{11}} \times \mathrm{CR}^{\beta_{12}\mathrm{BADF}\times\mathrm{FOLRET}^{\beta_{13}}} + \varepsilon_1$$

$$[3.2] \quad \mathrm{CL} = \frac{\mathrm{HT}}{1+\exp(\beta_{20}+\beta_{21}\mathrm{DBHHT}+\beta_{22}\mathrm{RHT}+\beta_{23}\mathrm{BAPH}+\beta_{24}\mathrm{AGE}+\beta_{25}\mathrm{FOLRET})} + \varepsilon_2$$

where maximum crown width (MCW) = 1.4081 + 0.22111 x DBH – 0.00053438 x DBH^2 (Paine and Hann 1982), BAPH is total stand basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), BADF is total Douglas-fir basal area in the stand ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), AGE is average stand breast height age, FOLRET is the stand's average foliage retention in 2002, DBHHT is the ratio of diameter to tree height, RHT is the relative tree height in the stand (HT/maximum HT on the plot), ß$_i$'s are parameters to be estimated from the data, $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$, $\varepsilon_2 \overset{iid}{\sim} N(0, \sigma_2^2)$, and all other variables are defined above. Since cross-equation correlations were expected, the models were fit by system-of-equation algorithms (Borders 1989). Specifically, the nonlinear three-stage least squares technique was utilized with the MODEL procedure in SAS. First, an equation to predict crown ratio was developed by modifying equation 3.2. The initial equation was fit to the data and some variables were insignificant. These variables were dropped from the equation and the model refitted. The resulting equation was:

[3.3] $$\mathrm{CR} = \frac{1}{1 + \exp(\beta_{30}\mathrm{DBHHT} + \beta_{31}\mathrm{RHT} + \beta_{33}\mathrm{FOLRET})} + \varepsilon_3$$

where CR is the crown ratio, the β$_i$'s are parameters to be estimated from the data, $\varepsilon_3 \overset{iid}{\sim} N(0, \sigma_3^2)$, and all other variables are defined above. The system of equations that was used for the final model analysis, therefore, was:

$$\mathrm{LCW} = \beta_{40}\mathrm{MCW}^{\beta_{41}} \times \hat{\mathrm{C}}\mathrm{R}^{\beta_{42}\mathrm{BADF}} + \varepsilon_{41}$$

[3.4] $$\hat{\mathrm{C}}\mathrm{R} = \frac{1}{1 + \exp(\beta_{43}\mathrm{DBHHT} + \beta_{44}\mathrm{RHT} + \beta_{45}\mathrm{FOLRET})} + \varepsilon_{42}$$

where ß$_i$'s are parameters estimated from the data, $\varepsilon_{41} \overset{iid}{\sim} N(0, \sigma_{41}^2)$, $\varepsilon_{42} \overset{iid}{\sim} N(0, \sigma_{42}^2)$,

$\begin{bmatrix} \varepsilon_{41} \\ \varepsilon_{42} \end{bmatrix} = N(0, \Sigma)$, and all other variables are defined above.

Crown shape in this study was defined as the ratio of crown width to crown length (Larocque & Marshall 1994a). Various linear regression models were fitted to the data to assess the relationship between SNC and crown shape. The general form of the model was:

$$[3.5] \quad \begin{aligned} \mathrm{CSR} = \beta_{50} &+ \beta_{51}\mathrm{DBHHT} + \beta_{52}\mathrm{CR} + \beta_{53}\mathrm{RHT} + \beta_{54}\mathrm{AGE} + \beta_{55}\mathrm{FOLRET} \\ &+ \beta_{56}(\mathrm{CR} * \mathrm{FOLRET}) + \varepsilon_5 \end{aligned}$$

where CSR is the crown shape ratio, the β_i's are parameters to be estimated from the data, $\varepsilon_5 \overset{\mathrm{iid}}{\sim} N(0, \sigma_5^2)$, and all other variables are defined above.

The relationship between foliage retention and height to crown base was examined with the following nonlinear model:

$$[3.6] \quad \mathrm{HCB} = \frac{\mathrm{HT}}{1 + \exp(\beta_{60}\mathrm{RHT} + \beta_{61}\mathrm{AGE} + \beta_{62}\ln(\mathrm{BAPH}) + \beta_{63}\mathrm{DBHHT} + \beta_{64}\mathrm{FOLRET})} + \varepsilon_6$$

where HCB is the height to crown base, the β_i's are parameters estimated from the data, $\varepsilon_6 \overset{\mathrm{iid}}{\sim} N(0, \sigma_6^2)$, and all other variables are defined above.

Crown profile

Crown profile was defined as the curve connecting the tips of the average branch within each whorl, when viewed on a plane longitudinally bisecting the stem and crown. Total branch length was estimated as a function of branch diameter, depth of branch in the crown and height of the tree as follows:

$$[3.7] \quad \mathrm{BL} = e^{\beta_{70}} \times \mathrm{DINC}^{\beta_{71}} \times e^{\beta_{72} \bullet \mathrm{DINC}} \times \mathrm{BD}^{\beta_{73}} \times \mathrm{HT}^{\beta_{74}} + \varepsilon_7$$

where BL is total branch length (m), DINC is depth in crown (total tree height – branch height), BD is branch basal diameter, HT is total tree height, the β_i's are parameters to be estimated from the data for each plot, and $\varepsilon_7 \overset{iid}{\sim} N(0, \sigma_7^2)$.

Crown radius was then estimated for each whorl branch using the following equations from Roeh and Maguire (1997):

$$[3.8] \quad VA = [87.31 - 1.167 \times HT] \times [1 - \exp(-0.3906 \times DINC - 0.01583 \times SI)]^{0.0989 \times BD}$$

$$[3.9] \quad CRD = BL_i \times [\pi \times \sin(VA_i / 180)]$$

where VA is branch angle, SI is King (1966) site index, and CRD is crown radius. The average crown radius for each whorl was then computed as the mean of predictions for all branches within that whorl.

A function developed by Kozak (1988) for describing stem taper was modified for application to the trend in crown profile (trend in crown radius over height within the crown). The model form was developed by assuming that the crown radius was a nonlinear function of predicted maximum crown width, branch position, and tree descriptors, resulting in the following model:

$$[3.10] \quad CRD = \beta_{100} MCW \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\beta_{110} CR}} \right)^{C} + \varepsilon_{10}$$

where Z is relative height above crown base (1.0-(DINC/CL)), C is a function of various transformations of branch position and tree descriptors such as DBH, HT, CL, CR, HCB and

DBHHT, the ßi's are parameters to be estimated from the data, $\varepsilon_{10} \overset{iid}{\sim} N(0, \sigma_{10}^2)$, and all other variables are defined above.

Since multiple observations of crown radius were estimated for each of the 82 sample trees (average of 15 observations per tree), the data violated the assumption of independence or zero covariance among observations (Neter et al. 1998; Rawlings et al. 1998). Moreover, preliminary residual analysis and a Durbin-Watson test indicated the presence of positive autocorrelation. This autocorrelation may largely be an artifact of poor model fits for individual trees. A mixed-effects model containing a random tree effect may help account for subtle differences in crown profile among different trees. The general form of this model is:

$$\mathrm{CRD_i} = f(\mathrm{V}_i, \lambda, \mathrm{D_i}, \delta_i) + \varepsilon_i$$

where CRD is a n x 1 vector of crown radii observed on tree i; f_i can be any nonlinear function; V_i is a n x k matrix of fixed-effect covariates; λ is a p x 1 vector of fixed parameters; D_i is a n x j matrix of random-effect covariates; δ_i is an r x 1 vector of random parameters with $\delta_i \sim N(0, M_i)$; and ε_i is an n x 1 vector of random errors with ε_i.~ $N(0, R_i)$. Since the sample trees were taken from different plots, a random effect was introduced for both trees and plots (Fang & Bailey 2001). In this case, r = 2 so δ_i is a vector and it is assumed that $\delta_i \sim N(0, \sigma^2 I)$. Moreover, it was assumed that $\varepsilon_i \sim N(0, \sigma_e^2\, I)$.

All-subsets regression was used to assess the relative performance of different predictor variables. The best subests, with and without SNC, were then refitted in nonlinear form with mixed effects using maximum likelihood in the SPLUS nlme function. Models with alternative sets of fixed covariates and with alternative formulations of random tree effects were compared by AIC, and nested models were compared by likelihood ratio tests (LRT). All models were also evaluated on the basis of residual plots, bias, standard error of estimates, and biological behavior.

Preliminary analysis indicated that introduction of the random tree and plot effects partially reduced autocorrelation, but they were not sufficient to completely eliminate it. A second-order autoregressive (AR(2)) error process was, therefore, incorporated to model the autocorrelation and provide valid tests of significance on model parameter estimates.

Branching structure

Two attributes of branch structure were examined, branch number and size. An equation modified from Maguire et al. (1994) was used to assess the relationship between branch number and SNC:

$$[3.11] \quad \sqrt{\mathrm{NB}+0.5} = \beta_{110}\mathrm{NL}^{\beta_{111}} * \exp(\beta_{112}\mathrm{DINC}) + \beta_{113}\mathrm{RDBH} + \beta_{114}\mathrm{BAPH} + \beta_{115}\mathrm{SIB} + \beta_{116}\mathrm{FOLRET} + \beta_{117}(\mathrm{SIB} * \mathrm{FOLRET}) + \varepsilon_{11}$$

where NB is the number of branches, NL is interwhorl length, RDBH is relative diameter at breast height in the stand, SIB is Bruce's (1981) site index, the β_i's are parameters to be estimated from the data, $\varepsilon_{11}^{\mathrm{iid}} \sim \mathrm{N}(0, \sigma_{11}^2)$, and all other variables are defined above. The $\sqrt{\mathrm{NB}+0.5}$ transformation was made to improve the normality of count data as suggested by Steel and Torrie (1980). Preliminary analysis suggested the presence of autocorrelation, therefore a first-order autoregressive (AR(1)) error process was incorporated into the final model to provide valid estimates of variance and tests on parameters.

Branch size was examined by modeling the trend in maximum branch diameter (MBD) over depth into the crown with a modified variable exponent function developed by Kozak (1988). Since multiple observations of branch diameter were collected from each of the samples trees, which were selected from a wide variety of plot locations, a multilevel nonlinear mixed-effects model with a random plot and tree effect to account for within-plot and between-plot variation was selected (Fang & Bailey 2001). Preliminary analysis indicated that introduction of a random plot and tree effect partially reduced autocorrelation, but they were not sufficient to completely eliminate it. A mixed autoregressive moving average (ARMA(1,1)) error process was, therefore, incorporated into the final model to provide valid tests of significance on model parameter estimates.

Branch structure and elongation

Four attributes of branch structure were examined in this study: foliated branch length, the number of secondary lateral branches, mean branch elongation rate, and the branch length to branch diameter ratio for whorl branches. The relationship between SNC and foliated branch length was examined with the following nonlinear regression model:

$$[3.12] \quad \mathrm{FBL} = \frac{\mathrm{BL}}{1+\exp(\beta_{121}\mathrm{RDINC} + \beta_{122}\mathrm{BD} + \beta_{123}\mathrm{HTDBH} + \beta_{124}\mathrm{FOLRET})} + \varepsilon_{12}$$

where FBL is the foliated branch length, RDINC is relative depth in the crown, BD is branch diameter, the ßᵢ's are parameters estimated from the data, $\varepsilon_{12} \overset{iid}{\sim} N(0, \sigma_{12}^2)$, and all other variables are defined above. Preliminary analysis suggested that whorl and interwhorl branches were not significantly different in their proportional foliated branch lengths so they were pooled together, resulting in a total of 351 branches available for analysis. Preliminary analysis also suggested the presence of significant autocorrelation, so a first-order autoregressive (AR(1)) error process was incorporated into the final model.

The number of secondary branches was analyzed using the following nonlinear model:

$$\text{[3.13]} \quad \sqrt{\mathrm{NSLB}+0.5} = \beta_{130}\mathrm{BD}^{\beta_{131}}\mathrm{CL}^{\beta_{132}}\mathrm{SIB}^{\beta_{133}}\mathrm{FOLRET}^{\beta_{134}} + \varepsilon_{13}$$

where NSLB is the number of secondary lateral branches, the ßi's are parameters estimated from the data, $\varepsilon_{13} \overset{\text{iid}}{\sim} \mathrm{N}(0, \sigma_{13}^2)$, and all other variables are defined above. Again, the $\sqrt{\mathrm{NB}+0.5}$ transformation was made to improve the normality of count data as suggested by Steel and Torrie (1980). Whorl and interwhorl branches were pooled together, resulting in a total of 739 branches available for analysis. Preliminary analysis also suggested the presence of significant autocorrelation, therefore a first-order autoregressive (AR(1)) error process was incorporated into the final model.

Mean branch elongation for each sample branch was calculated as the total branch length divided by its age. The relationship between mean branch elongation and foliage retention was assessed with the following multiple linear regression model:

$$\text{[3.14]} \quad \begin{aligned} \mathrm{BI} = {} & \beta_{140} + \beta_{141}\mathrm{DINC} + \beta_{142}\mathrm{BD} + \beta_{143}\mathrm{RHT} + \beta_{144}\mathrm{SIB} + \beta_{145}\mathrm{FOLRET} \\ & + \beta_{146}(\mathrm{SIB} * \mathrm{FOLRET}) + \beta_{147}\mathrm{W} + \varepsilon_{14} \end{aligned}$$

where BI is mean branch increment (cm/year), W is an indicator variable for branch type (1 if whorl, 0 if interwhorl), the ßi's are parameters to be estimated from the data, $\varepsilon_{14} \overset{iid}{\sim} N(0, \sigma_{14}^2)$, and all other variables are defined above. Preliminary analysis suggested the presence of significant autocorrelation, therefore a first-order autoregressive (AR(1)) error process was incorporated into the final model.

The relationship between foliage retention and whorl branch length to diameter ratio was examined with the following linear model:

$$\begin{aligned} \text{BLBD} = {} & \beta_{150} + \beta_{151}\text{DINC} + \beta_{152}\text{CV} + \beta_{153}\text{CLSA}_{\text{CB}} + \beta_{154}\text{FOLRET} \\ & + \beta_{155}(\text{CV} * \text{FOLRET}) + \varepsilon_{15} \end{aligned} \tag{3.15}$$

where BLBD is the ratio of branch length to diameter, CV is the crown volume estimated by numerically integrating equation 3.10, CLSA_{CB} is the crown length to sapwood area ratio, the ßi's are parameters to be estimated from the data, $\varepsilon_{15} \overset{iid}{\sim} N(0, \sigma_{15}^2)$, and all other variables are defined above. Preliminary analysis suggested the presence of significant autocorrelation, therefore a first-order autoregressive (AR(1)) error process was incorporated into the final model.

RESULTS

Crown size, shape, and location

Measured crown widths ranged from 2.79 to 7.22 m, with the length of the live crown between 5.46 and 25.13 m (Figure 3.2). Foliage retention did not have a significant relationship with the largest crown width at α=0.05 (Table 3.4) and was dropped from the final model. In general, crown width tended to increase with maximum crown width and crown ratio, while it decreased with increasing Douglas-fir basal area. Crown length increased with the diameter to height ratio, relative tree height in the stand, and foliage retention, while it declined with age and Douglas-fir basal area (Table 3.5; Figure 3.3). A likelihood ratio test also indicated that the fit of the model was significantly improved ($p<0.0001$) with the inclusion of foliage retention. A tree on a plot with one year of foliage retention is associated with a crown that is 14% shorter than a tree on a plot with four years of foliage retention all else being equal. Similarly, foliage retention had a significant effect on crown ratio. In general, crown ratio tended to decrease with relative height, but increased with the diameter to height ratio and foliage retention. Parameter estimates and standard errors were similar using both nonlinear and nonlinear 3-stage least squares techniques (Table 3.6). The root mean squared error (RMSE) and R_g^2 values for the final models are presented in Table 3.7.

Crown shape ratios varied from 0.23 to 0.56 and decreased with crown ratio, stand age, relative height in the stand, and increased with greater diameter to height ratios. The ratio was significantly related to foliage retention and decreased with higher retention scores (Table 3.8). Foliage retention, however, has a negative effect up until a crown ratio of 0.70. The model had a R^2 of 0.52 and a RMSE of 0.0715. A tree on a plot with one year of foliage retention is associated with a crown shape ratio that is 42.5% greater than a tree on a plot with four years of retention after accounting for stand age, relative height in the stand, crown ratio, and the height to diameter ratio.

Height to crown base tended to increase with stand age and Douglas-fir basal area, but decrease with increasing relative height, diameter to height ratio, and foliage retention (Table 3.9). A tree on a plot with one year of foliage retention is associated with a height to crown base that is 21.4% higher than a tree on a plot with four years of retention after accounting for relative height in the stand, the diameter to height ratio, stand age and basal area (Figure 3.4). The model explained 68% of the original variation and had a RMSE of 1.74.

Crown profile

The following model was selected as the best equation for predicting crown profile:

$$[3.16]\quad \mathrm{CRD} = (\beta_{161} + \delta + \alpha)\mathrm{MCW}\left(\frac{1-\sqrt{\mathrm{Z}}}{1-\sqrt{\beta_{162}\mathrm{CR}^{\beta_{163}}}}\right)^{\beta_{164}\mathrm{HTDBH}+\beta_{165}\mathrm{Z}+\beta_{166}\mathrm{FOLRET}+\beta_{167}(\sqrt{\mathrm{Z}}*\mathrm{HTDBH})} + \varepsilon_{16}$$

where HTDBH is the height to diameter ratio, the β_i's are parameters to be estimated from the data, δ is the random tree effect parameter, α is the random plot effect parameter, $\varepsilon_{16}{}^{iid} \sim N(0, \sigma_{16}{}^{2})$, and all other variables are defined above. The final model was weighted by DINC^{-1} to correct for heteroskedasticity (Figure 3.5). AIC, likelihood ratio tests, and autocorrelation plots indicated that a model with random plot and tree effects on MCW and an AR(2) structure was the best (Table 3.10). The R_g^2 for the model was 0.48. All parameters were significantly different from zero (α = 0.05; Table 3.11). A likelihood ratio test further indicated that modles with FOLRET were significantly improved with the variable ($p<0.001$). A tree on a plot with one year of foliage retention is associated with a whorl crown radius that is on average 13.7% smaller than a tree on a plot with four years of retention after accounting for relative height above crown base, maximum crown width, crown ratio, the height to diameter ratio, and stand basal area. The vertical profile of average sample trees with different foliage retentions indicate that trees with higher foliage retentions have a more curvilinear shape, while trees with lower retention are more linear. Regardless of foliage retention, crown radius tended to peak near the crown base (0.1-0.55 RHACB; Figure 3.7).

Branching structure

Number of branches

The total number of primary branches on an individual tree ranged from 108 to 401, with interwhorl branches accounting for a large percentage of the total. The total number of branches tended to increase with increasing shoot length, site index, and foliage retention, but decreased with node height and the interaction between site index and foliage retention (Table 3.12). When analyzed separately, a significant relationship between foliage retention and the number of branches was only significant for interwhorl but not whorl branches. A shoot on a plot with one year of foliage retention is associated with 12.5% fewer interwhorl branches than a shoot on a plot with four years of retention, all else being equal. RDBH as well as BAPH, except for the number of whorl branches model, was not significant in any of the models and was dropped from the final models. The number of whorl branches tended to increase with node length, but decrease with depth into crown and stand basal area. The final equations were weighted by NL^{-1} and explained between 21 to 38% of the original variation, with RMSE values ranging from 0.44 to 1.13.

Maximum branch diameter

The following model was selected as the best equation for predicting maximum branch diameter:

$$[3.17] \quad MBD = (\beta_{170} + \delta_1) MCW \left(\frac{1 - \sqrt{Z}}{1 - \sqrt{\beta_{171} CR}} \right)^{(\beta_{172} + \delta_2)*(Z*DBHHT) + \beta_{173} Z + (\beta_{174} + \alpha)*FOLRET} + \varepsilon_{17}$$

where the β_i's are fixed effects parameters to be estimated from the data, the δ_i's are random tree effect parameters, α is the random plot effect parameter, $\varepsilon_{17} \overset{iid}{\sim} N(0, \sigma_{17}^2)$, and all other variables are defined above. The final model was weighted by $DINC^{-1}$ to reduce heteroskedasticity (Figure 3.8). A likelihood ratio test and autocorrelation plots indicated that autocorrelation was largely reduced by the random plot and tree effects and incorporation of the ARMA(1,1) error structure (Table 3.13). The R_g^2 for the final model was 0.48. All parameters were significantly different from zero ($\alpha = 0.05$; Table 3.14). A likelihood ratio test, however, indicated that models with FOLRET were only moderately improved with the inclusion of that variable ($p<0.1$). All parameters were positive, which indicates that relative maximum branch diameter increases with a greater diameter to height ratio and foliage retention. A tree on a plot with one year of foliage retention is associated with a maximum branch diameter that is on average 10.2% smaller than a tree on a plot with four years of retention, all else being equal. The model was curvilinear, peaking just above the base of the live crown regardless of the foliage retention level (Figure 3.9). On the 82 sample trees, maximum branch diameters were observed at relative depth into crown between approximately 0.40 and 1.0 (Figure 3.10). The smallest bias was generally at the base of the live crown and the largest near the middle (Table 3.15), but both bias and standard error of the estimate tended to be small regardless of foliage retention.

Branch structure and elongation

Foliated length

Foliated branch length tended to increase with greater diameter to height ratios, branch diameter, and foliage retention, but decrease with relative depth in the crown (Table 3.16). The foliated branch length model performed well with R_g^2 near 0.93 and the RMSE equal to 0.3648. The equation was weighted by $DINC^{-2}$ to correct for nonconstant variance. A likelihood ratio test indicated that foliage retention significantly improved model fit ($p<0.001$). A branch on a plot with one year of foliage retention is associated with 13.4% less foliated branch length than a branch on a plot with four years of foliage retention, after accounting for depth into the crown, branch diameter, and the tree diameter to height ratio.

Secondary branches

The number of secondary lateral branches tended to increase with branch length, site index, and foliage retention, but decreased with crown length (Table 3.17). The secondary lateral branch model explained 27% of the original variation and had a RMSE of 1.62. A branch on a plot with one year of foliage retention is associated with 20.4% fewer secondary branches than a branch on a plot with four years of retention, all else being equal.

Branch elongation

Branch increment increased with branch diameter, site index, and foliage retention, and was significantly greater for whorl branches. Increment decreased with increasing depth in crown, and relative height (Table 3.18). There was a positive effect of foliage retention up to a site index of 42.3 m. A branch on a plot with one year of foliage retention is associated a mean elongation rate that is 34.2% less than a branch on a plot with four years of retention after accounting for depth into crown, branch diameter, relative height, site index, branch type, and the interaction between site index and foliage retention. The model explained 55% of the original variation and had a RMSE value of 0.1138.

When branches were analyzed separately by crown third (upper, mid, lower), a slightly different pattern emerged. Branches in the mid and lower crown third were still significantly related to foliage retention ($p<0.05$), while growth of branches in the upper crown was not. However, branches in the lower crown third showed a negative relationship with increasing foliage retention and branches in the upper and middle portions of the crown showed a positive one (Table 3.19). In all the models, mean branch increment still increased with branch diameter and site index, but decreased with increasing depth in crown and relative height. No significant autocorrelation was detected in these models. A branch in the lower portion of the crown and on a plot with one year of foliage retention is associated a mean elongation rate that is 15.3% greater than a similar branch on a plot with four years of retention after accounting for depth into crown, branch diameter, relative height, and site index. R^2 for the three models varied from 0.46 to 0.74, while RMSEs ranged from 0.0553 to 0.1152.

Branch length to branch diameter ratio

The branch length to branch diameter ratio showed a significant relationship with foliage retention ($p<0.001$) and with the crown length to sapwood area at crown base ($p<0.05$). The ratio increased with depth into crown, the crown length to sapwood area at crown base ratio, but decreased with crown volume and foliage retention (Table 3.20). Foliage retention, however, had a negative effect up until a crown volume of 217 m^2. The model explained 33% of the original variation and had a RMSE of 18.58.

DISCUSSION

Crowns are considered to be the most sensitive and plastic component of a tree (Johansson 1992). Crown structure and morphology are the results of complex dynamic processes, which include genetics, site conditions, stand developmental stage, stand density, and tree social status (Meredieu et al. 1998). The present study indicates that foliar diseases such as SNC are an important factor influencing crown structure and morphology. With increasing SNC defoliation, Douglas-fir crowns were shorter in length with a greater crown shape ratio and a higher height to crown base (Figure 3.11). This leads to a crown that is more conical than the typical parabolic shape of a healthy tree. Consistent with this crown shape is the fact that maximum branch diameters and elongation rates were smaller for trees with increasing SNC severity, except in the lower crown. Trees with lower foliage retention also had fewer interwhorl branches on the mainstem, secondary lateral shoots on primary branches, and shorter foliated lengths on primary branches. These results do not support the hypothesis that trees with lower foliage retention have a slower rate of crown recession or that they are compensating the foliage loss by higher branch density. Trees experiencing extended defoliation are simply growing less with regard to branch diameter, branch length, and interwhorl branch number.

Crown size, shape, and location

Crown length, width, and the height to crown base are strongly controlled by stand density (Dean et al. 2002; Garber 2002; Makinen & Colin 1999) and to a lesser extent by genetics (Xiao et al. 2003). Both crown length and width tend to decrease with increasing stand density, while height to crown base usually increases (Curtis & Reukema 1970). The rate at which crown length and width increase usually slows as the spacing narrows (Larocque & Marshall 1994). After canopy closure, crown recession rates are roughly proportional to the height growth rates as the entire canopy of approximately constant leaf area rises (Deleuze et al. 1996). Moreover, crown spread in trees with strong apical control such as Douglas-fir also occurs only in proportion to height growth. Thus, potential rates of increase in crown length and width tend to decrease as height growth potential declines with age (Hashimoto 1991). St. Clair (1994) found significant genetic variation in relative crown width and length for coastal Douglas-fir, indicating that carbon allocation traits are highly heritable.

Despite this inherent high variation, consistent allometric relationships among stem and crown dimensions provide a high level of predictability of some dimensions. For example, Hann (1997) found that 73% of the variation in the largest crown width in Douglas-fir can be explained by crown length and tree diameter to height ratio. In these models, explicit representation of stand density is usually achieved through the addition of basal area and age as explanatory variables (Ritchie & Hann 1987); however, in even-aged, single-species stands, a large portion of the variation in crown size can be explained implicitly by tree-level variables. These stands are relatively simple and homogeneous, so variables representing tree size can adequately represent the effects of stand density and site quality on tree allometrics (Tasissa & Burkhart 1998). Height to diameter ratio can serve as an indicator of relative tree height within the canopy, while crown length reflects local stand density and spacing. Hanus et al. (2000) found that local competition measures such as crown competition factor only slightly improved the prediction of height to crown base in Douglas-fir. Thus, the finding that crown length increases and height to crown base decreases with increasing values of diameter to height ratio agrees with the findings of other studies (Ritchie & Hann 1987; Hanus et al. 2000).

Crowns can respond directly to silvicultural treatments, particularly thinning. Crown length increases after stand reduction because the lower branches of the released Douglas-fir remain alive due to the improved light environment (Aussenac et al. 1982; Reukema 1964). Brix (1981) concluded nitrogen nutrition was also an important factor. Thus, crown recession generally slows or ceases after thinning and possibly fertilization until the stand density and tree height have increased enough to offset the effects of the treatment (Oliver & Larson 1996). Crown recession rates were consistent with Ritchie and Hann's (1987) observation in that the height to crown base was lower where site index was higher, all else being equal. Maguire and Kanaskie (2002) hypothesized that reduced foliage retention in the upper and middle portion of the crown due to SNC could promote longer retention of branches in the bottom of the crown, since more foliage would be illuminated above the light compensation point. The findings of this study, however, do not support this hypothesis as crown length was found to decrease and the height to crown base increase for trees with lower foliage retention. Although Hanus et al. (2000) reported that the height to crown base was higher and the crown ratio smaller for damaged vs. undamaged trees, damage in this study referred to suppression and natural mechanical injury.

The loss of crown found in this study can be attributed both to the reduced height growth caused by SNC and the accelerated rate of crown recession due to increased branch mortality in the lower crown. Although the defoliation caused by this disease affects diameter growth before height, increasing SNC severity can cause significant losses of height growth.

Maguire et al. (2002) estimated the past top height growth losses in Douglas-fir plantations with the most severe SNC in 1997 were as high as 25%.

Branches, on the other hand, are in different states of vigor depending on their relative position in crown and on the position of the tree relative to its neighbors (Mäkinen 1996). Upper crown branches have numerous large buds that act as strong carbon sinks, importing stored carbon for elongation and growth (Sprugel et al. 1991). In contrast, lower shaded branches may fail to form annual growth rings at their base (Kershaw et al. 1990) and contribute very little carbon to the rest of the tree (Kozlowski & Pallardy 1997). These lower branches are autonomous for carbon, having insufficient sink strength to draw on carbon reserves from the rest of the tree and fixing just enough carbon to meet their own needs (Sprugel et al. 1991). Eventually, the negative cumulative carbon budget of a lower branch leads to mortality (Witowski 1996). The self-pruning of these dead branches, however, is often an extremely slow process in Douglas-fir (Maguire et al. 1999). SNC, by causing premature needle loss, has essentially sped this process up. While it has been hypothesized that the improved light conditions in the bottom part of the crown could stimulate additional production of current-year foliage (Maguire & Kanaskie 2002), most studies have shown that foliage recovery is a slow process (Långström et al. 2001).

Reukema (1964) argued that the retention of lower branches is unimportant for stem growth. Although Brix (1981) found that an increase in crown length due to thinning significantly contributed to total tree needle mass, the increase in total needle mass was due to rapid expansion of crowns into newly available growing space. A review of Douglas-fir pruning studies concluded that pruning does not significantly reduce tree growth if one-third or less of the lower live crown length is removed (Maguire & Petruncio 1995), which supports the theory that the functional crown is composed of approximately the upper two-thirds of the live crown (Assmann 1970). While research has shown that the loss of older needle age classes may be compensated by higher photosynthetic rates of the remaining younger foliage age classes (Beyschlag et al. 1994), this research indicates that premature loss of older age classes of needles coupled with reductions in foliage density, can lead to significant volume growth losses (Maguire et al. 2002). With increasing SNC severity, however, physiological disruption of surviving needles intensifies (Manter 2001), inhibiting any compensatory photosynthesis.

The crown shape ratio in this study decreased with age in a manner consistent with other studies (Larocque & Marshall 1994), which Hashimoto (1991) attributed this change to increased competition. The increase of the crown shape ratio with declining relative tree height in the stand, on the other hand, is caused by the tendency of crowns to shorten and widen under severe suppression (Raulier et al. 1996). Likewise, Larocque and Marshall (1994) found the crown shape ratio decreased with an increase in diameter in the absence of severe competition and decreased with increasing diameter under severe competitive stress. Although intensive silvicultural treatments such as thinning and fertilization have been documented to produce no effect on the crown shape ratio (Xiao et al. 2003), prolonged defoliation by SNC can lead to crowns that are relatively wider than normal for a given relative height. Since crown size and shape are the result of the relationship between branch and height growth (Ottorini 1991), SNC may be modifying this relationship. The relative lack of cross-equation correlation in the crown ratio and crown width systems of equations model, may suggest that Douglas-fir is losing some of its apical control over lower branches.

Crown profile

Modeling crown profile in this study relies on two critical assumptions, namely that branch length can be predicted accurately from site-specific equations and SNC does not influence branch angle. Most studies have found branch length to be readily predicted by depth in the crown and branch diameter (Monserud & Marshall 1999; Meredieu et al. 1998). As was found in these Douglas-fir, R^2 values were generally high (0.93 – 0.99) and residual standard errors low (20 – 55 cm) (Monserud & Marshall 1999; Meredieu et al. 1998). Branch angle, on the other hand, appears to have little genetic variation (St. Clair 1994) and isn't influenced by stand manipulations such as fertilization (Mäkinen et al. 2001) or thinning (Medhurst & Beadle 2001). Gilmore and Seymour (1997) did, however, find that branch angle was influenced by tree canopy position in balsam fir (*Abies balsamea*) as branches tended to become flatter with decreasing relative tree height in the stand. Relatively little within-whorl variation of branch angle, makes it easily predicted when branch depth into the crown is known (Roeh & Maguire 1997; Kuuluvainen et al. 1988).

A variety of approaches have been employed for modeling crown profile including flexible polynomial models (Baldwin & Peterson 1997; Hann 1999), fractal geometry (Zeide 1998), systems of equations (Roeh & Maguire 1997), and stochastic techniques (Nepal et al. 1996; Biging & Gill 1997). Recently, Gill and Biging (2002 a,b) have shown first-order autoregressive models to be an effective means for modeling crown profile. The Douglas-fir models presented here combined a number of approaches including published equations for branch length, angle, and crown radius, a flexible variable exponent model (Kozak 1988) for crown profile, a mixed-effects model to account for within- and between-plot variation, and an autoregressive error structure to account for within-subject autocorrelation. Kozak (1997) demonstrated that prediction in the variable exponent model is not seriously affected by the presence of either multicollinearity or autocorrelation, and statistical theory establishes that predictions are unbiased in the presence of autocorrelation. However, tests on specific covariates are not valid unless the autocorrelation is addressed. The modeling approach used in this study met the assumptions of regression and therefore provided valid tests on factors accounting for the inherent variability of crown profiles without requiring a large number of observations per tree. For example, Gill and Biging (2002a) generally used 35 to 50 measures of crown radii in each tree crown simulated.

Numerous tree attributes, such as depth into crown, largest crown width, crown ratio, and height to diameter ratio have proved effective for predicting aspects of crown profile (Mitchell 1975; Biging & Wensel 1990; Baldwin & Peterson 1997; Ottorini 1991;

Raulier et al. 1996; Hann 1999). All four of these variables as well as the interaction between the height to diameter ratio and relative height above crown base were relevant to crown profile of SNC-impacted Douglas-fir. Garber and Maguire (2003) similarly concluded that the effect of relative height above crown base depends on the tree's height to diameter ratio and that this interaction term gave the model even greater flexibility.

Hann (1999) found that dominant Douglas-fir have a conic crown shape and that understory trees have a parabolic shape. Furthermore, he separated the upper "light" crown and the lower portion of the "shade" crown in his model by the location of largest crown width (Hann 1999). When the largest crown width occurred above the crown base, which was generally the case in this study, the shade crown was best described as having a cylindrical shape (Hann 1999). Healthy Douglas-fir in this study similarly had a curvilinear profile. Trees with low foliage retention, on the other hand, show both a smaller crown radius for a given relative height in the crown and a conic profile. This finding is primarily a result of the loss of the lower 20% of the crown and more subtle change in crown shape above. On healthy Douglas-fir with 4-5 years of foliage retention, branches in the lower part of crown become increasingly shaded by younger branches in upper whorls as well as by neighboring tree crowns, which creates a gradient in branch vigor with relative depth into a tree's crown (Labyak & Schumacher 1954). In a defoliated crown, more light filters through, which can increase the photosynthetic productivity per unit leaf area (Beyschlag et al. 1994) as well as allow foliage to remain on branches longer in the lower portion of the crown than they might otherwise (Pensa et al. 2001). The slightly greater longitudinal growth of these lower branches on trees with severe SNC (Figure 3.6), leads to a more linear crown profile.

Number of branches

The number and size of branches within the crown are an important attribute of a tree as they support and conduct the water and nutrients needed for a tree to photosynthesize. For example, King et al. (1992) showed that the total number of branches located on the tree could account for 42% of the variation in volume accumulation among Douglas-fir families. Also, Ter-Mikaelian and Lautenschlager recently (2001) concluded that the total number of branches per tree to be an excellent predictor of total tree foliage biomass.

The number of branches on a shoot is affected by site fertility, stand density, and genetic factors, allowing the variation in branch number to be captured mainly in the annual height increment of the stem (Mäkinen & Colin 1999). This relationship can become modified by the height to diameter ratio, a surrogate for the competitive status of the tree, given that a higher density of branches per meter of shoot have been observed for trees at the upper end of the diameter distribution due to increased levels of light (Ilonen et al. 1979; Maguire et al. 1994). This also explains why the number of branches per node slowly decreases with depth in the crown (Maguire et al. 1994; Björklund 1997). Relative diameter or height to diameter ratio probably did not enter the final model for SNC-impacted Douglas-fir because the sample trees were primarily dominants or codominants and light was less of a factor.

Both thinning (Maguire 1983) and fertilization have been shown to increase the number of branches on a tree (Brix & Ebell 1969; Mäkinen et al. 2001), indicating that light as well nutrient availability influence the branching structure of a tree. Lämmä (1990) found that the number of branches was positively correlated with foliar nitrogen concentration and fine soil fraction, similar perhaps to the significance of site index on SNC-impacted Douglas-fir. Mäkinen and Colin (1999) found that site index was not significant in their model for predicting the number of whorl branches in Scots pine. Site index is a difficult variable to define because it is as much a genetic response as it is an attribute of the site (Rehfeldt & Hamiltion 1999). Although Curt et al. (2001) found Douglas-fir site index to be correlated with soil nutrient status and moisture regime, these differences in branching habits underscore the importance of genetics (St. Clair 1994) and differences between relative shade-tolerance of conifer species (Woollons et al. 2002) in terms of branching habits.

One of the primary differences between shade-tolerant and intolerant species is the ability of shade-tolerant conifers to form interwhorl branches. For example, species such as Scots pine form one or more distinct nodes per year with no internodal branches, whereas *Chamaecyparis* produces branches regularly along the stem (Woollons et al. 2002). Douglas-fir is intermediate between these two patterns (Woollons et al. 2002). Generally, there are more interwhorl than whorl branches on shade-tolerant species (Sheppard & Ford 1986), which helps to redistribute foliage biomass more evenly throughout the crown (Ishii & McDowell 2002) as well as renew foliage quality (Ishii et al. 2002). Cochrane and Ford

(1978) found that at year 11, interwhorl branches contributed 57% of the total shoot extension produced from the leading shoot, while the whorl branches and new leader only produced 33% and 10%, respectively. Gilmore and Seymour (1997) found that average percentage of oven-dry foliage mass in interwhorl branches was 33% for open-grown trees, 33% for codominant, 16% for intermediates, and 13% for suppressed. Jensen and Long (1983) found that internodal branches can support up to 50% of the foliage biomass on only 10% of the branch biomass. Thus, interwhorl branches are important structural components of these trees. The fact that the number of branches on Douglas-fir can respond positively to thinning and fertilization is primarily due to the significant increase in interwhorl bud density (Maguire 1983). Significant amounts of epicormic branching can occur also after pruning Douglas-fir, which tends to become more severe as more live crown is removed irrespective of stand density (Collier & Turnblom 2001). However, Collier and Turnbolm (2001) concluded that a genetic or other site factor not accounted for might control the amount of epicormic sprouting since this trend was not observed on all sites. The model for SNC-impacted Douglas-fir explained little of the variation in the number of branches per node. Doruska and Burkhart (1994) concluded that efforts to model branching structure are frustrated by the tremendous variation occurring among trees. Kurttio and Kellomäki (1990) likewise found that the variability of branching can vary substantially even within a fairly homogeneous tree stand, depending on site conditions.

Despite anecdotal evidence suggesting that the increased defoliation caused by SNC has lead to greater epicormic sprouting, trees with poorer foliage retention had fewer interwhorl branches per annual shoot. This is most likely a reflection of the diminishing net assimilation rates caused by extended defoliation, leaving the tree with little or no resources to maintain or enhance its branching habit. Other studies have found that trees severely defoliated temporarily by insects increase shoot production because of the prolific production of epicormic buds (Piene & Eveleigh 1996; Piene & MacLean 1999). There, however, appears to be a lag time of 2 to 3 years in stem growth after the insect infestation as the trees put higher priority on needle production rather than stem or root growth (Piene & MacLean 1999). Since the Douglas-fir trees in this study continue to lose foliage prematurely, it seems probable that needle production would be given even higher priority than branch construction and growth. Bartelink (1998) found that Douglas-fir invested more dry matter into foliage, especially at the cost of branch and stem components, when compared to beech (*Fagus sylvatica*). It is also significant to note that branches tend to have higher respiration rates than boles for a given amount of living tissue (Kinerson 1975; Sprugel 1990), especially at higher crown positions (Ryan 1996), suggesting that a greater amount of fixed carbon is needed to construct and maintain branches. The greater number of branches per shoot on trees with more foliage retention further supports the idea that branches are not independent of tree condition when light is not the primary factor limiting photosynthesis and growth (Sprugel 2002).

The significance of the interaction between site index and foliage retention indicates that other factors besides SNC influence Douglas-fir foliage retention. Turner and Olson (1976) observed greater needle retention in fertilized vs. unfertilized Douglas-fir stand growing under extreme nitrogen deficiencies. In contrast, Brix (1981) found that fertilization decreased the retention of 5- and 6-year-old needles. Work in Europe with Scots pine and Norway spruce suggested that variation in needle retention is largely a phenotypic acclimation strongly regulated by the environment rather than a genotypic adaptation (Reich et al. 1996). With respect to site fertility, these studies have generally found that needle retention decreases with increased resource availability (Pensa & Sellin 2002). Balster and Marshall (2000) hypothesized that this may be caused by faster self-shading. In SNC-impacted Douglas-fir, foliage retention increased with site index, most likely a byproduct of several other factors and emphasizing the lack of understanding regarding Douglas-fir needle retention. However, in general site index tends to influence both branch longevity and crown recession rates (Maguire 1994). The increase in the number of branches with site index supports the hypothesis that conditions that increase branch length also increases the accumulation of branches (Kellomäki & Kurttio 1991).

Branch size

The size of a branch directly influences tree foliage photosynthetic capabilities (Walcroft et al. 1996) as well as the quality of the stem wood (Mäkinen 1996). Maguire et al. (1999) noted that even a small increase in average branch-size has a deleterious effect on the quality of lumber recovered from trees. The diameter growth of a branch depends on the branch position within the crown, tree social position, and stand structure (Makinen 1999), particularly density (Colin & Houllier 1991; Maguire et al. 1994; Makinen 1999) and species composition (Garber 2002). In general, branch diameter growth begins rapidly, then decreases markedly as a negative exponential function of branch age (Kershaw et al. 1990). Branch diameter growth in the upper crown is more influenced by regional conditions, whereas local stand conditions have an increasing effect in the lower portion of the crown (Mäkinen 1996). Nearly half or more of the life of a branch can be spent without perceivable increment (Kershaw et al. 1990; Makinen & Colin 1999) due to self-shading (Brooks et al. 1991; Sampson & Smith 1993) and competition (Mäkinen 1996). Senescent branches are assumed to satisfy their own maintenance costs, but do not contribute to net tree production (Sprugel et al. 1991). Branch size increased at a decelerating rate with depth into crown in both healthy and severely infected Douglas-fir trees. However, the shape of the profile varied with crown condition, as there was little difference in branch diameter between healthy and severely infected trees in top third of the crown, an increased difference in the mid-crown, and again, little difference in the lower crown. SNC seemed to alter branch growth allocation patterns by increasing relative growth in the lower part of the crown, reflecting changes in crown condition caused by the disease.

Manter (2001) suggested that within individual trees, SNC fungal colonization is consistently higher in the upper portions of the crown and on the south-side, so defoliation is greater in the upper rather than the lower crown (Hansen et al. 2000). This trend implies that branches in mid-crown of trees with low foliage retention are less vigorous because they have been infected the longest and have lost a substantial amount of their photosynthetic capacity. Branches in the upper canopy, on the other hand, rely on stored carbohydrates and greater net photosynthetic rates in current-year needles (Woodman 1971) prior to infection by the fungus. Branches in the lower portion of the crown maintain growth better than usual due to the increased light conditions and relatively lower loss of foliage. This trend likely intensifies as the infection of the trees continues.

Branch diameter growth of both newly initiated and older branches can be significantly increased with fertilization (Mäkinen et al. 2001). Thinning, on the other hand, doesn't appear to directly influence branch growth when assessed by total biomass, except thinning does allow branches in the lower crown to continue growing for a longer period of time (Brix 1981). Thirty years after thinning, Gary (1978) noted that the largest branch diameter for a whorl of a similar age was nearly 1.6 times greater on the thinned trees when compared to the unthinned trees. In this case the branches were measured in 20 year-old whorls, so were in the lower part of the crowns, where thinning was expected to have its greatest effects. Besides light available for carbon fixation, branch diameter growth may also be influenced by growth hormones, water transport, and respiratory load (Kozlowski & Pallardy 1997). Light, however, has consistently been found to be the primary driving factor (Mäkinen 2002). Recent work indicates that Douglas-fir branches may have a partially autonomous behavior in terms of water (Brooks et al. 2003). Thus, older branches might be able to respond positively to increased light conditions within the crown, similar to mature Douglas-fir trees to thinning (Latham & Tappeiner 2002).

Branch structure

Foliated length

Broadleaved species generally avoid self-shading by distributing their foliage towards the crown periphery (Sterck et al. 2001). In conifers, suppression mortality of shaded foliage on the interior of crowns, leads to the development of a non-foliated, bare inner core (Assmann 1970), and this core increases as the crown size expands with stand development (Jack & Long 1992). Stand density, therefore, has a strong influence on the foliated length of branches. Trees with small bare cores or high foliated branch lengths for a given total leaf area are generally more efficient producers of stemwood volume (Jack & Long 1992). Thus, foliated branch length would be expected to increase with social position and branch vigor and decrease with depth in the crown, as the model in this study indicated. However, despite the increased light conditions in the lower crown caused by SNC, branches on sites with low foliage retention usually have a larger bare branch length, which is similar to its impact on overall tree crown length. This may be due to the inability of the foliage near the stem to adjust to the new light conditions, as needle physical characteristics are unlikely to change from intial characteristics regardless of modifications in the local environment (Sprugel et al. 1996). Thus, branches are more likely allocating more resources towards diameter growth and elongation rather than renewing of its bare length with epicormic shoots. This trend may differ with branch aspect as Schoettle and Smith (1991) found that foliated length was 7% greater on shoots with a southern aspect when compared to shoots with a more northern aspect.

Number of secondary shoots

The number of secondary shoots on a branch has been shown to increase with improved light conditions (Kohyama 1980; Suzuki 2003), fertilization (Brix & Ebell 1969), branch age (Ishii & Ford 2001), and annual shoot length (Suzuki 2003). Thus, most studies have predicted the number of secondary shoots on a branch as a simple linear function of branch length (Hailemariam 1999). A nonlinear model performed better for the number of secondary branches on SNC-impacted Douglas-fir. The number of lateral branches increased with branch diameter, site index, and foliage retention, but decreased with greater crown length. These findings agreed with other studies as the number of secondary lateral branches increased with branch size and site fertility, while decreasing with canopy social position. The finding that crown condition also influenced the number of secondary shoots indicated a shift in allocation patterns. While a similar finding hasn't been reported in the literature, Kozlov et al. (2001) indicated that the size of secondary shoots in Norway spruce (*Picea abies*) branches was influenced by pollution.

Branch increment

Restricted crown expansion is a universal response to competition (Deleuze et al. 1996). When it is not hampered by neighboring trees, crown expansion depends heavily on height growth (Ottorini 1991) but to a large extent, shoot growth is predetermined in the bud (Mao-Yi & Tamm 1985). In general, the rate of shoot elongation declines toward the base of the crown (Schoettle & Smith 1991), which is why crown shape more closely resembles a paraboloid rather than a cone (Mitchell 1975). Branch growth also tends to decrease along the branch from 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). Shoot elongation rates are also influenced by fertilization (Brix & Ebell 1969), thinning (Reukema 1964), water and nutrient stress (Cannell & Morgan 1990), defoliation (Kulman 1965), aspect (Schoettle & Smith 1991), slope (Colin & Houllier 1991; Umeki 1995), and canopy social position (Gilmore & Seymour 1997). Branch increment increased with branch vigor and site fertility in the SNC-impacted Douglas-fir, but decreased with greater relative height in the stand and depth in the crown. Similar to foliated branch length, light intensity and apical control are considered the primary factors influencing elongation rates (Schoettle & Smith 1991; Chen et al. 1996; Duchesneau et al. 2001). Thus, branch increment tends to decrease with increasing relative height because trees in this social position tend to increase faster in height rather than width. Extended defoliation in the upper crown by SNC, however, might be changing this relationship.

While the method used to calculate mean branch elongation in this study can not detect growth patterns prior to and after SNC damage, it does give some indication of the general branch elongation patterns. The finding that branch elongation is not affected or slower in the upper and mid-crowns on plots with less retention is consistent with Kulman's (1965) observation that one year after artificial defoliation, shoot elongation was reduced 10 to 40%. The higher branch elongation rates in the lower crown of trees on plots with low foliage retention, however, was not expected. This again might be due to the gradient of increasing light and decreasing SNC, as foliage retention tends to be the highest near the base of the live crown. It is important to note that branch elongation varies greatly even within a whorl (Mäkinen 1999) as well as among years due to the fluctuations in the climate (Pensa & Jalkanen 1999). Furthermore, the higher observed elongation rates in the lower crown is not necessarily an advantage because greater lengths increase susceptibility to wind damage (Moore 2002) as well as lower the water potential of foliage (Walcroft et al. 1996).

Branch length to diameter ratio

The tree height to diameter ratio has been widely used as a relative measure of tree stability under wind and snow loads as gives a reasonable estimation of stem taper (Wilson and Oliver 2000). Trees generally become unstable when their height to diameter ratios increase beyond 80. Little work, however, has examined the stability of individual branches. Watt et al. (in review) indicated that mean branch diameter was nearly 26% greater in New

Zealand grown *Pinus radiata* (Monterrey pine) located on more exposed sites when compared to more sheltered areas. Thus, similar to tree stems (Telewski 1995), primary branches tend to counteract wind-induced deflection by increasing flexural stiffness through allocating more of their mass to diameter and less to length. This present study indicates that primary branches on trees with greater defoliation caused by SNC allocate more of their mass to length rather than diameter. This increases branch taper and leads to branches that are more instable than normal, which makes them more susceptible to damage. This might explain why primary branches in the lower portion of heavily SNC-infested trees are expanding faster than normal, while also receding faster than normal.

CONCLUSION

Disturbances such as plant disease can greatly modify crown structure and morphology. In stands with poor crown condition due to SNC, Douglas-fir tended to have a smaller live crown and higher rate of crown recession, while its largest width remained similar to healthy sites. Crown radii and maximum branch diameter profiles suggest that changes within the crown may be specific to different heights, consistent with the fact that SNC damage tended to be worse in the upper two-thirds of the crown. Morphologically, the disease has led to a lower number of branches, with a smaller foliated length and a smaller number of secondary shoots than normal. Branches in the lower portion of the heavily diseased crowns may be elongating faster than normal due to the increased light intensity and altered patterns of carbon allocation, and may be causing higher branch length to diameter ratios. Foliage density may be higher on sites with less severe SNC not only because they retain more age-classes of needles, but also because they form and retain a larger number of interwhorl and secondary branches. The results support the hypothesis that stress tolerant species such as Douglas-fir respond to stress with slow and often small changes in morphology (Grime 2002).

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Table 3.1. Attributes of the 23 plots sampled in 2002.

Attribute	**Mean**	**SD**	**Min**	**Max**
Douglas-fir basal area (m^2/ha)	26.44	8.44	9.97	45.44
Douglas-fir trees per ha	624	272	259	1223
Douglas-fir quadratic mean diameter (cm)	24.56	6.73	11.41	36.45
Douglas-fir relative density (Curtis (1982))	5.31	1.32	2.95	7.91
Douglas-fir stand density index (Reineke (1933), trees/ha at mean DBH of 25.4 cm)	526.6	1.3	2.9	7.9
Basal area in other conifers (m^2/ha)	0.45	0.76	0	2.21
% basal area in other conifer	1.2	2.1	0	6.7
Basal area in hardwoods (m^2/ha)	0.59	0.77	0	2.86
% basal area in hardwoods	1.8	2.3	0	9.3
Total basal area (m^2/ha)	33.37	12.84	10.44	69.65
Average breast-height age (yr)	21.1	4.8	11.1	27.8
Average foliage retention (yr)	2.36	0.71	1.2	4.3
Site index (Bruce (1981); height at 50 yr, in m)	39.6	2.6	34.8	43.9

Table 3.2. Attributes of the 82 Douglas-fir trees sampled in 2002.

Attribute	**Mean**	**SD**	**Min**	**Max**
DBH (cm)	25.3	5.2	12.5	43.2
Height (m)	19.41	5.33	5.88	33.6
Height to live crown (m)	7.21	3.77	0.1	22.5
5-yr height increment (m)	0.70	0.23	0.31	1.18
Crown length (m)	12.20	3.38	3.40	23.30

Table 3.3. Attributes of the 739 sample branches.

Attribute	**Mean**	**SD**	**Min**	**Max**
Diameter (cm)	17.9	9.6	1.30	56.00
Length (m)	1.11	1.21	0.09	6.79
Foliated length (m) (n=352)	1.51	0.87	0.08	4.25
Depth in crown (m)	6.14	3.64	0.17	16.40
Number of secondary branches	24.26	18.18	0.00	84.00
Foliage mass (g)	114.04	139.69	0.01	898.49
Woody mass (g)	283.29	349.66	0.06	36841.44

Table 3.4. Parameter estimates, standard errors, and p-values of model [3.1] relating largest crown width to SNC (n=125).

Model parameter	**Value**	**Standard error**	**P-value**
β_{10}	0.8523	0.1534	<0.001
β_{11}	0.9267	0.0923	<0.001
β_{12}	0.0061	0.0020	0.0037

Table 3.5. Parameter estimates, standard errors, and p-values of model [3.2] relating length of live crown to SNC (n=845).

Model parameter	**Value**	**Standard error**	**P-value**
β_{20}	0.8174	0.2075	0.001
β_{21}	-0.9863	0.0628	<0.001
β_{22}	-1.0747	0.1342	<0.001
β_{23}	0.0089	0.0017	<0.001
β_{24}	0.0365	0.0043	<0.001
β_{25}	-0.1221	0.0340	0.0004

Table 3.6. Parameter estimates and standard errors for nonlinear least-squares (NL) and nonlinear 3-stage least squares (N3SLS) (n=125).

		NL		N3SLS	
Model	**Variable**	**Estimate**	**SE**	**Estimate**	**SE**
LCW	β_{40}	0.8523	0.1534	0.8759	0.1243
	β_{41}	0.9267	0.0923	0.9077	0.0045
	β_{42}	0.0061	0.0020	0.0044	0.0029
CR	β_{43}	-1.7354	0.2565	-1.7002	0.2713
	β_{44}	2.8791	0.3962	2.8353	0.4227
	β_{45}	-0.3554	0.0862	-0.3566	0.0920

Table 3.7. Final model fit statistics for NL and N3SLS methods.

	NL		N3SLS	
Model	**RMSE**	R_g^2	**RMSE**	R_g^2
CL	1.7629	0.7821	-	-
CR	0.1166	0.4063	0.1159	0.4062
LCW	0.6215	0.5494	0.5904	0.5611

Table 3.8. Parameter estimates, standard errors, and p-values for the crown shape ratio model (equation 3.5).

Parameter	**Estimate**	**SE**	**P-values**
β_{50}	1.0786	0.1511	<0.0001
β_{51}	0.2189	0.0406	<0.0001
β_{52}	-1.0466	0.2020	<0.0001
β_{53}	-0.1385	0.0474	0.0045
β_{54}	-0.0069	0.0020	0.0009
β_{55}	-0.1240	0.0562	0.0299
β_{56}	0.1759	0.0772	0.0252

Table 3.9. Parameter estimates, standard errors, and p-values for model [3.6] for height to crown base.

Model parameter	Value	Standard error	P-values
β_{60}	1.0348	0.1269	<0.0001
β_{61}	-0.0344	0.0043	<0.0001
β_{62}	-0.3274	0.0389	<0.0001
β_{63}	0.9949	0.0625	<0.0001
β_{64}	0.1196	0.0246	<0.0001

Table 3.10. Akaike's information criterion (AIC; smaller is better) and –2 log likelihood for various maximum branch diameter model forms. GNLS refers to the generalized nonlinear least square run (no random effect or correlation structure), MNLME(2) is the multilevel nonlinear mixed effects model run with three random effects, and MNLME(2) + AR(2) is the multilevel nonlinear mixed effects model run with three random effects and a correlation structure.

Model	AIC	-2 log likelihood
GNLS	962.75	-473.37
MNLME(2)	994.44	-486.22
MNLME(2) + AR(2)	632.62	-303.31

Table 3.11. Parameter estimates and asymptotic standard errors of the best variable exponent crown profile model.

Parameter	Estimated value	SE
β_{161}	0.5037	0.01545
β_{162}	0.4295	0.13654
β_{163}	5.1330	2.58086
β_{164}	0.3072	0.08258
β_{165}	0.7509	0.07557
β_{166}	-0.0289	0.01619
β_{167}	-0.4625	0.12598
SD(δ)	0.0463	-
SD(α)	0.0289	-
SD(ε)	0.2836	-
Φ_1	0.5337	-
Φ_2	0.1557	-

Table 3.12. Parameter estimates, standard errors, generalized coefficient of determination (R_g^2), and root mean square errors (RMSE) for number of whorl (NWB), interwhorl (NIB), and total branches (NB).

Model	**Parameter**	**Estimated value**	**SE**	R_g^2	**RMSE**
NB				0.2486	0.9419
	β_{110}	1.7965	0.2438		
	β_{111}	0.8216	0.2203		
	β_{112}	-0.0492	0.0140		
	β_{113}	-	-		
	β_{114}	-	-		
	β_{115}	0.0562	0.0081		
	β_{116}	1.5567	0.3796		
	β_{117}	-0.0362	0.0086		
	Φ	0.5124			
NIB				0.2128	1.1287
	β_{110}	1.2902	0.1953		
	β_{111}	1.5342	0.3155		
	β_{112}	-0.0595	0.0177		
	β_{113}	-	-		
	β_{114}	-	-		
	β_{115}	0.0479	0.0069		
	β_{116}	1.6573	0.4379		
	β_{117}	-0.0384	0.0098		
	Φ	0.5149			
NWB				0.3784	0.4422
	β_{110}	2.5034	0.0617		
	β_{111}	0.0885	0.0174		
	β_{112}	-0.0103	0.0018		
	β_{113}	-	-		
	β_{114}	-0.0038	0.0015		
	β_{115}	-	-		
	β_{116}	-	-		
	β_{117}	-	-		
	Φ	0.2790			

Table 3.13. Akaike's information criterion (AIC; smaller is better) and –2 log likelihood for various maximum branch diameter model forms. GNLS refers to the generalized nonlinear least square run (no random effect or correlation structure), MNLME(3) is the multilevel nonlinear mixed effects model run with three random effects, and MNLME(3) + ARMA(1,1) is the multilevel nonlinear mixed effects model run with three random effects and a correlation structure.

Model	AIC	-2 log likelihood
GNLS	6854.1	-3421.1
MNLME(3)	6337.8	-3158.9
MNLME(3) + ARMA(1,1)	6221.8	-3096.9

Table 3.14. Parameter estimates and asymptotic standard errors of the best variable exponent maximum branch diameter model.

Parameter	Estimated value	SE
$ß_{170}$	4.2165	0.09769
$ß_{171}$	0.7323	0.03649
$ß_{172}$	0.2173	0.05831
$ß_{173}$	0.1909	0.07893
$ß_{174}$	0.0322	0.00833
$SD(\delta_1)$	0.3889	-
$SD(\delta_2)$	0.0494	-
$SD(\alpha)$	0.0118	-
$SD(\varepsilon)$	2.5942	-
Φ	0.7745	-
θ	-0.4575	-

Table 3.15. Bias and standard error of estimate (SEE) of maximum branch diameter from crown base to top for various foliage retention classes.

Relative height above crown	**Foliage retention (years)**															
	1.0 – 1.9				2.0 – 2.9				3.0 – 3.9				4.0 – 4.9			
	n	Bias (mm)	Bias (%)	SEE (mm)	n	Bias (mm)	Bias (%)	SEE (mm)	n	Bias (mm)	Bias (%)	SEE (mm)	n	Bias (mm)	Bias (%)	SEE (mm)
0.0 – 0.1	3	1.63	6.70	1.53	76	0.10	-1.28	4.35	28	0.19	-2.13	5.98	15	-1.53	-7.15	6.07
0.1 – 0.2	3	-0.63	-6.12	2.47	60	0.04	-2.25	4.57	27	0.69	0.09	4.52	12	0.69	-0.16	8.34
0.2 – 0.3	4	-3.91	-25.76	4.63	60	-0.11	-1.28	3.06	27	1.78	2.46	6.76	11	1.02	3.14	6.26
0.3 – 0.4	4	-2.91	-15.50	3.20	62	-0.24	-2.70	3.22	23	-0.31	-2.84	5.06	11	-0.20	-1.25	5.37
0.4 – 0.5	1	-6.03	-45.33	2.28	71	0.59	0,22	3.77	27	0.70	1.76	3.51	12	2.54	8.39	6.57
0.5 – 0.6	4	-2.24	-14.45	3.38	72	0.54	-0.52	4.04	31	0.03	-0.75	3.47	12	3.84	12.15	8.10
0.6 – 0.7	4	-2.93	-24.54	3.20	67	0.02	-1.91	3.24	30	-0.51	-4.13	3.43	11	1.46	3.52	7.23
0.8 – 0.9	4	-1.98	-21.35	3.81	82	-0.27	-4.00	3.08	34	-1.02	-6.70	3.32	11	1.63	7.48	4.85
0.9 – 1.0	5	-2.73	-31.93	2.27	96	0.04	-5.30	3.32	31	-0.78	-7.45	2.71	13	2.51	9.87	8.31
All	6	-0.34	-5.72	3.56	96	-0.22	-9.30	2.50	32	0.43	4.70	2.19	10	0.97	6.81	6.03

Table 3.16. Parameter estimates, standard errors, and p-values for the foliated branch length equation.

Parameter	**Estimated value**	**SE**	**P-value**
ß$_{121}$	1.9753	0.2549	<0.0001
ß$_{122}$	-0.0201	0.0071	0.0055
ß$_{123}$	-1.3459	0.1833	<0.0001
ß$_{124}$	-0.4297	0.0936	<0.0001
Φ	0.1947		

Table 3.17. Parameter estimates, standard errors, and p-values for the number of secondary branches equation.

Parameter	**Estimated value**	**SE**	**P-value**
ß$_{130}$	0.3998	0.4589	0.3853
ß$_{131}$	0.3349	0.0198	<0.0001
ß$_{132}$	-0.2589	0.0922	0.0051
ß$_{133}$	0.7649	0.3106	0.0140
ß$_{134}$	0.1385	0.0710	0.0515
Φ	0.1344		

Table 3.18. Parameter estimates, standard errors, and p-values for the branch elongation equation.

Parameter	**Estimated value**	**SE**	**P-value**
ß$_{140}$	-1.6252	0.4091	0.0001
ß$_{141}$	-0.0119	0.0015	<0.0001
ß$_{142}$	0.0069	0.0007	<0.0001
ß$_{143}$	-0.1183	0.0348	0.0008
ß$_{144}$	0.0465	0.0099	<0.0001
ß$_{145}$	0.4994	0.1640	0.0025
ß$_{146}$	-0.0118	0.0039	0.0001
ß$_{147}$	0.0414	0.0108	0.0029
Φ_1	0.1788	-	
Φ_2	-0.0390	-	

Table 3.19. Parameter estimates and standard errors as well as model fit statistics for branch elongation rates by crown third.

Model	Parameter	Estimated value	SE	P-value	R_g^2	RMSE
Upper					0.4592	0.1152
	$ß_{140}$	-1.3109	0.2539	0.0001		
	$ß_{141}$	-0.0329	0.0120	0.0021		
	$ß_{142}$	0.0122	0.0028	<0.0001		
	$ß_{143}$	-	-	-		
	$ß_{144}$	0.0.375	0.0633	0.0001		
	$ß_{145}$	-	-	-		
	$ß_{146}$	-	-	-		
	$ß_{147}$	0.0569	0.0286	0.0005		
Middle					0.7368	0.0553
	$ß_{140}$	-0.3394	0.1345	<0.0001		
	$ß_{141}$	-0.0101	0.0031	0.0053		
	$ß_{142}$	0.0092	0.0006	<0.0001		
	$ß_{143}$	-0.1134	0.0379	<0.0001		
	$ß_{144}$	0.0134	0.0033	<0.0001		
	$ß_{145}$	0.0195	0.0097	<0.0001		
	$ß_{146}$	-	-	-		
	$ß_{147}$	-	-	-		
Lower					0.5825	0.0664
	$ß_{140}$	-0.0232	0.1617	0.0001		
	$ß_{141}$	-0.0057	0.0029	0.0021		
	$ß_{142}$	0.0074	0.0007	<0.0001		
	$ß_{143}$	-0.1554	0.0455	0.0001		
	$ß_{144}$	0.0142	0.0380	0.0053		
	$ß_{145}$	-0.0243	0.0116	0.0119		
	$ß_{146}$	-	-			
	$ß_{147}$	-	-			

Table 3.20. Parameter estimates, standard errors, and p-values for equation 3.15

Parameter	Estimated value	SE	P-value
β_{150}	100.8876	6.9701	<0.0001
β_{151}	3.3939	0.2288	<0.0001
β_{152}	-0.1522	0.0359	<0.0001
β_{153}	0.8295	0.2451	0.0008
β_{154}	-8.6907	2.5241	0.0006
β_{155}	0.0432	0.0133	0.0013

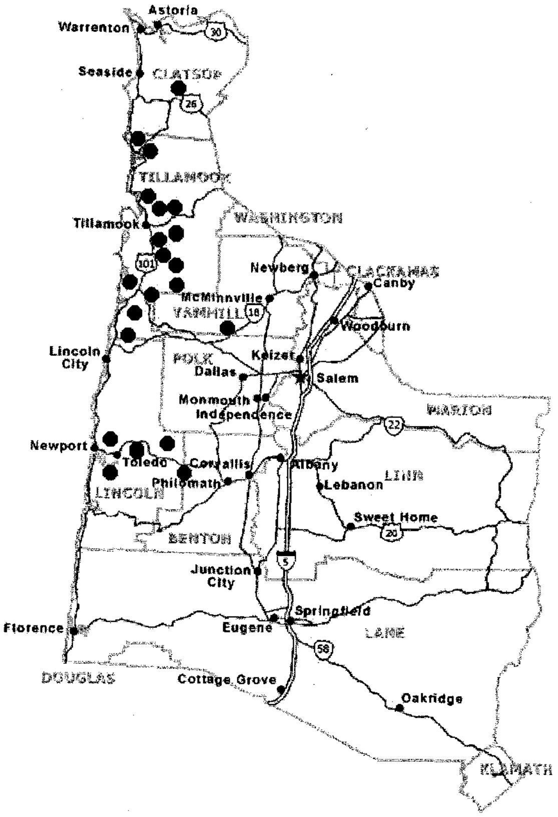

Figure 3.1. Location of the 23 study plots in the Oregon Coast Range that were intensively sampled in 2002. The plots are part of the Swiss Needle Cast Cooperative permanent growth impact analysis network.

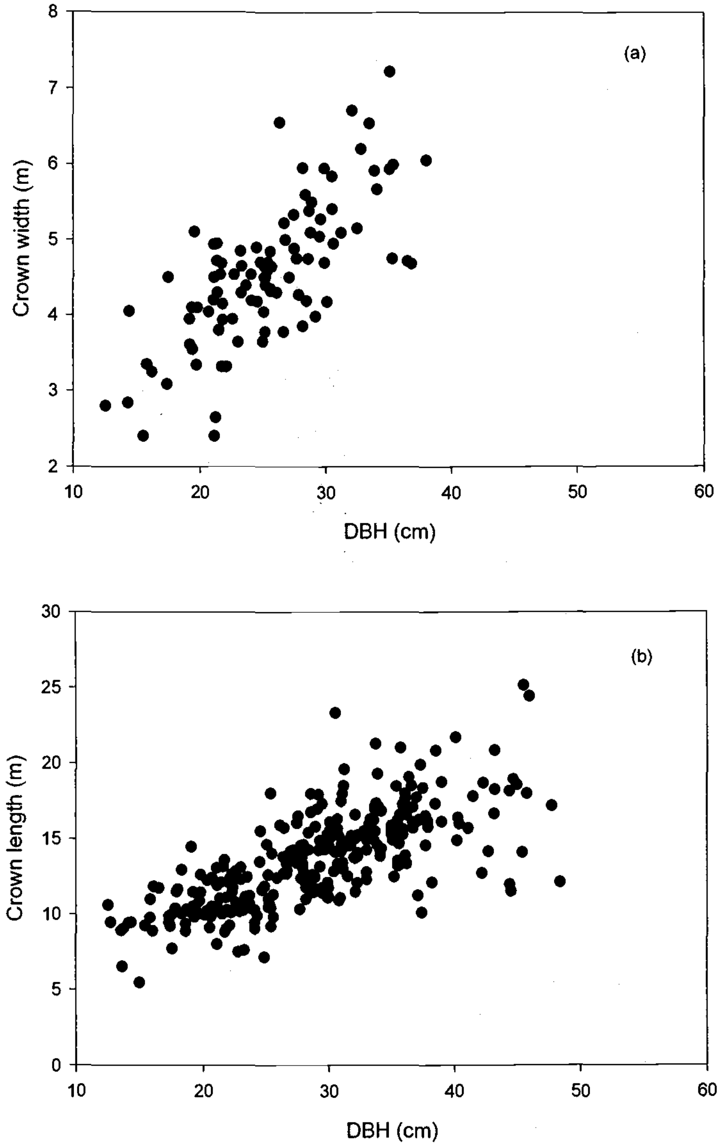

Figure 3.2. Sample and permanent plot tree distribution by crown width (a) and length of live crown (b) over diameter.

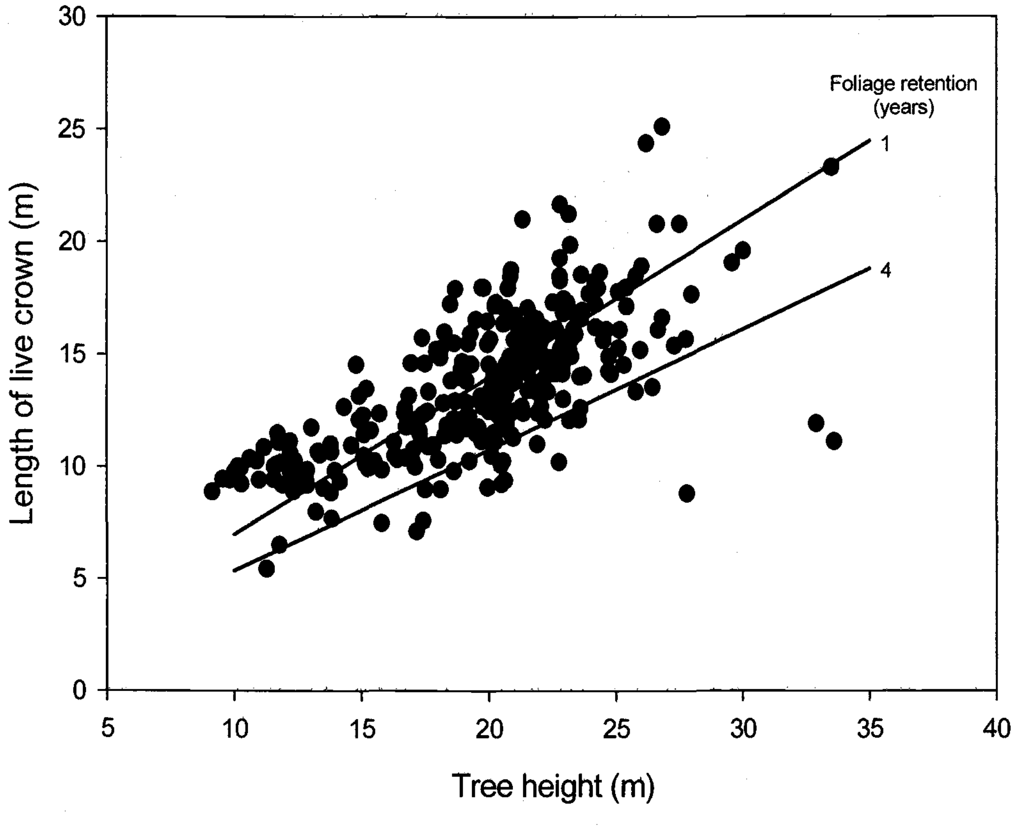

Figure 3.3 Trends in length of live crown over tree height and foliage retention. Trends are the results from fitting equation 3.2 to the data. The diameter to height ratio and relative tree height in stand were set equal to the sample mean, which were 1.42 and 0.86, respectively.

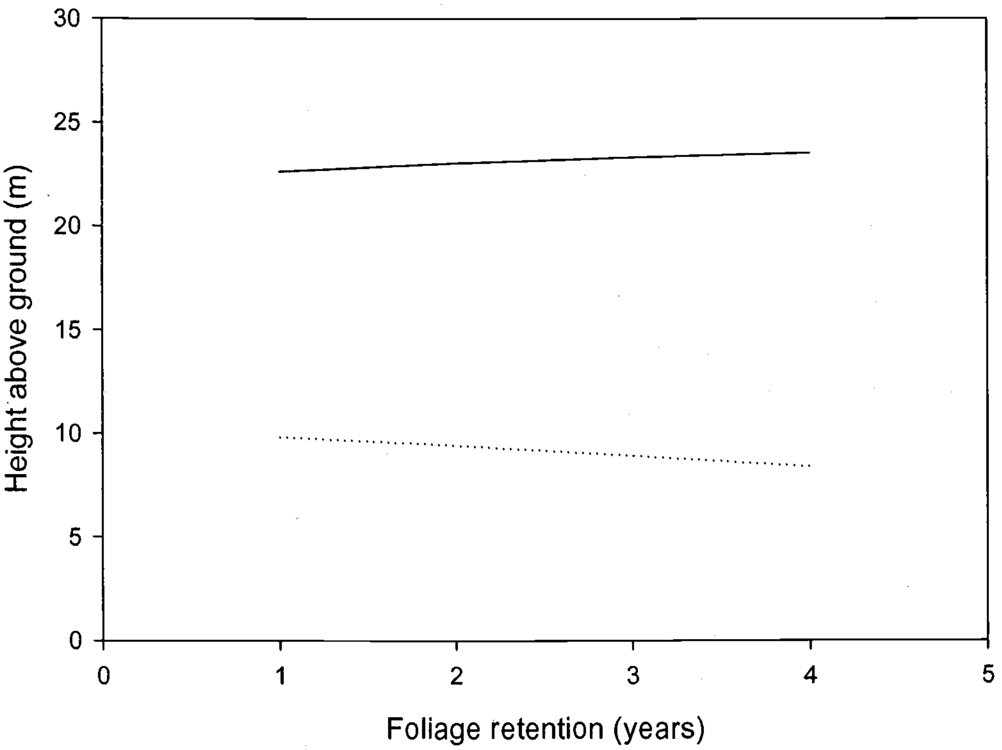

Figure 3.4. Trends in total height (solid line) and height to crown base (dashed line) suggested by equation 3.6 and Maguire et al. (2002) after five years of growth.

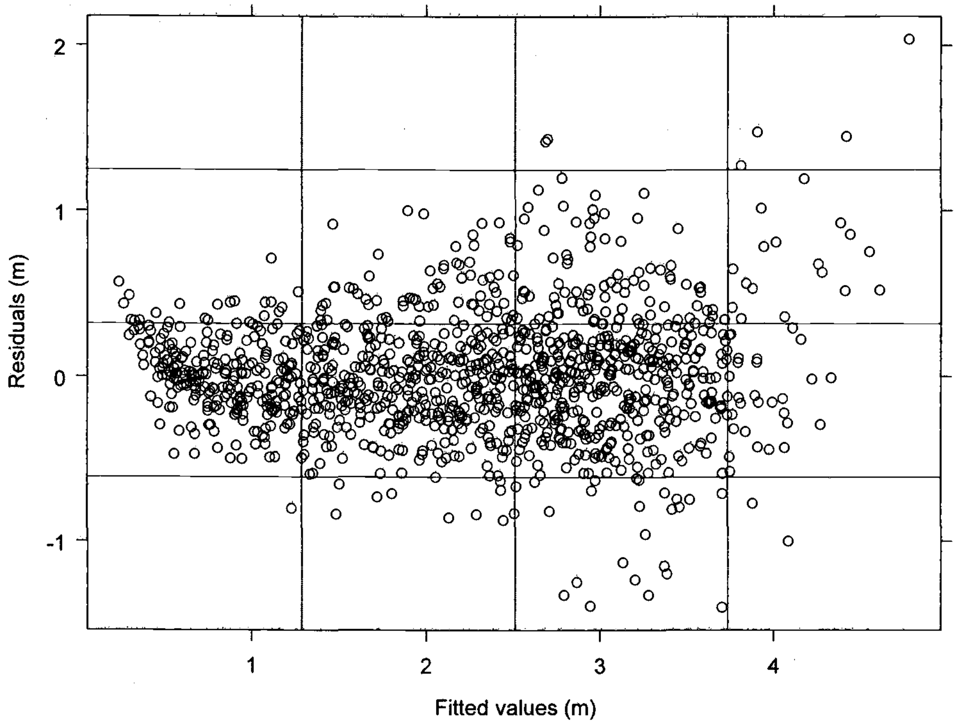

Figure 3.5. Plot of residual on fitted values for equation 3.16.

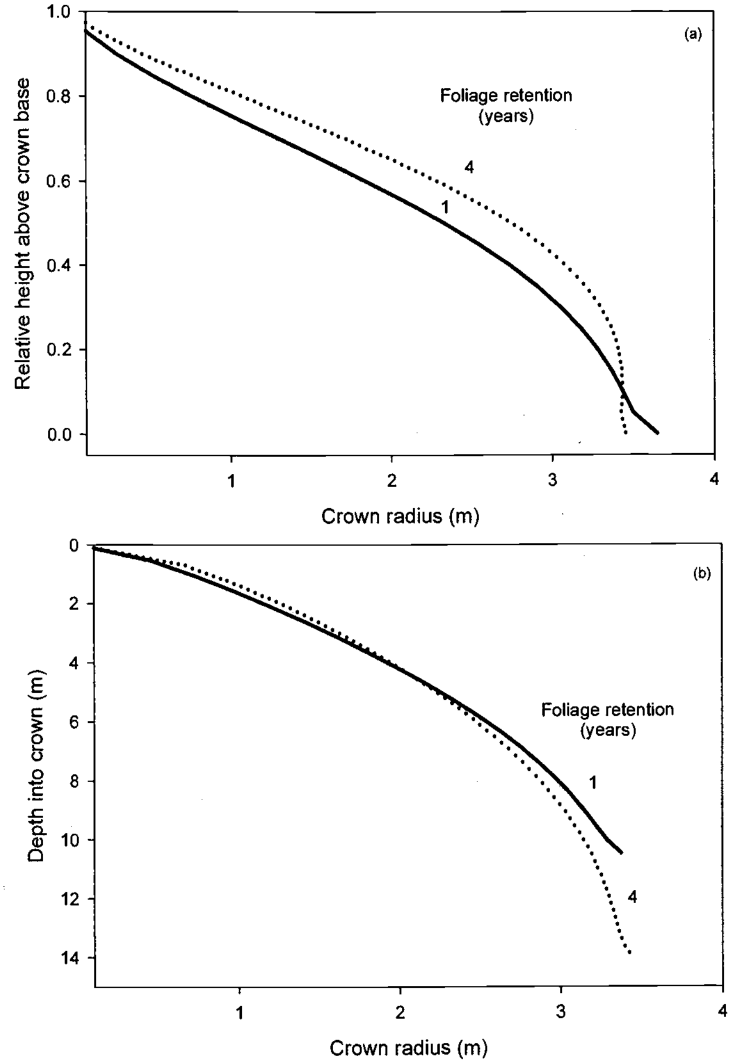

Figure 3.6. Profiles of crown radius with relative height above the crown base (a) and depth into the crown (b) for average-sized trees. The trends are result of fitting equation 3.16 to the data. The solid line represents a tree with only 1 year of foliage retention and the dashed line is a tree with 4 years of foliage retention. The height to diameter ratio was set equal to the sample mean of 79.0 cm/cm and the crown ratios were adjusted using Equation 3.3. The crown ratio for the tree with 1 year of foliage retention is 0.55, while the crown ratio for the tree with 4 years of foliage retention is 0.73.

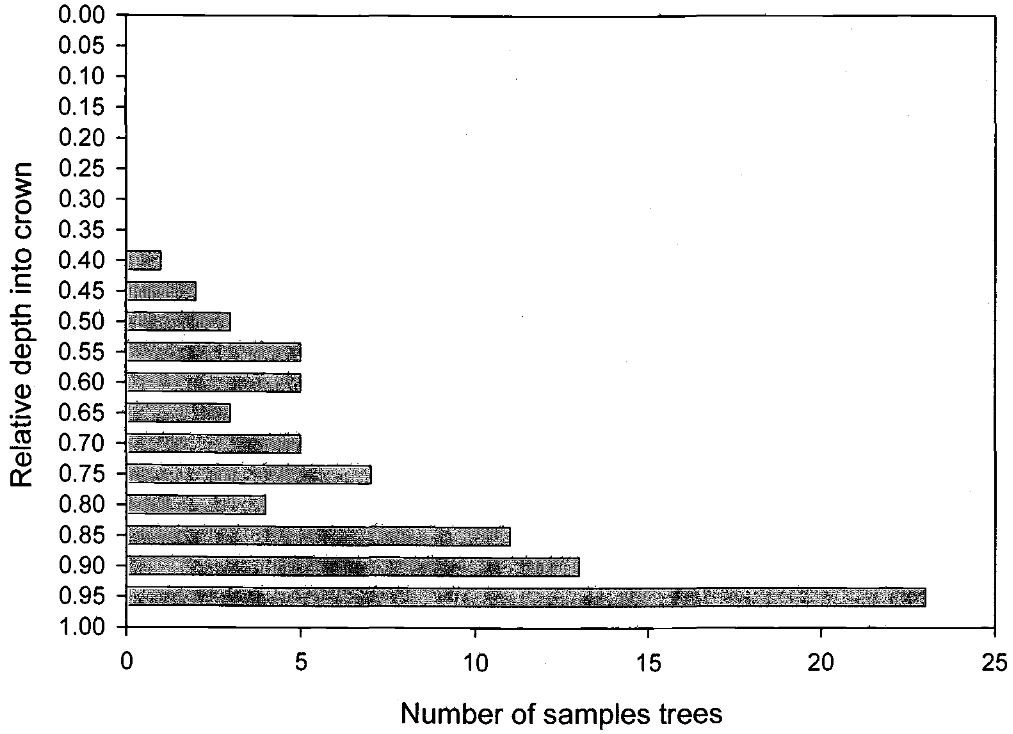

Figure 3.7. Histogram showing the relative depth into crown at which maximum crown radius occurred for individual sample trees (mean relative depth =0.83).

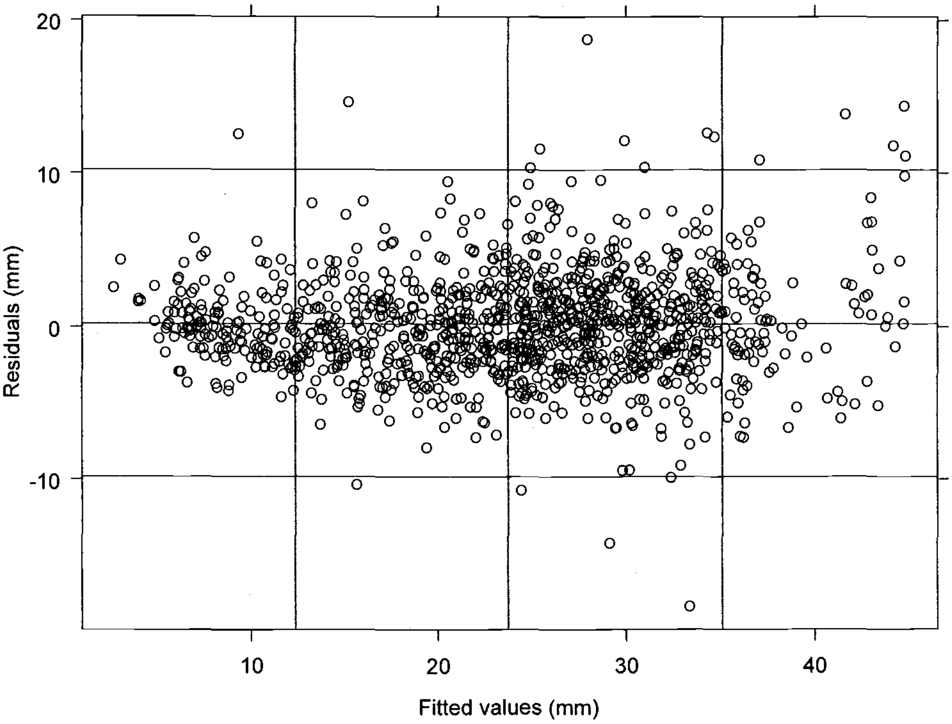

Figure 3.8. Plots of residuals on fitted values for equation 3.17.

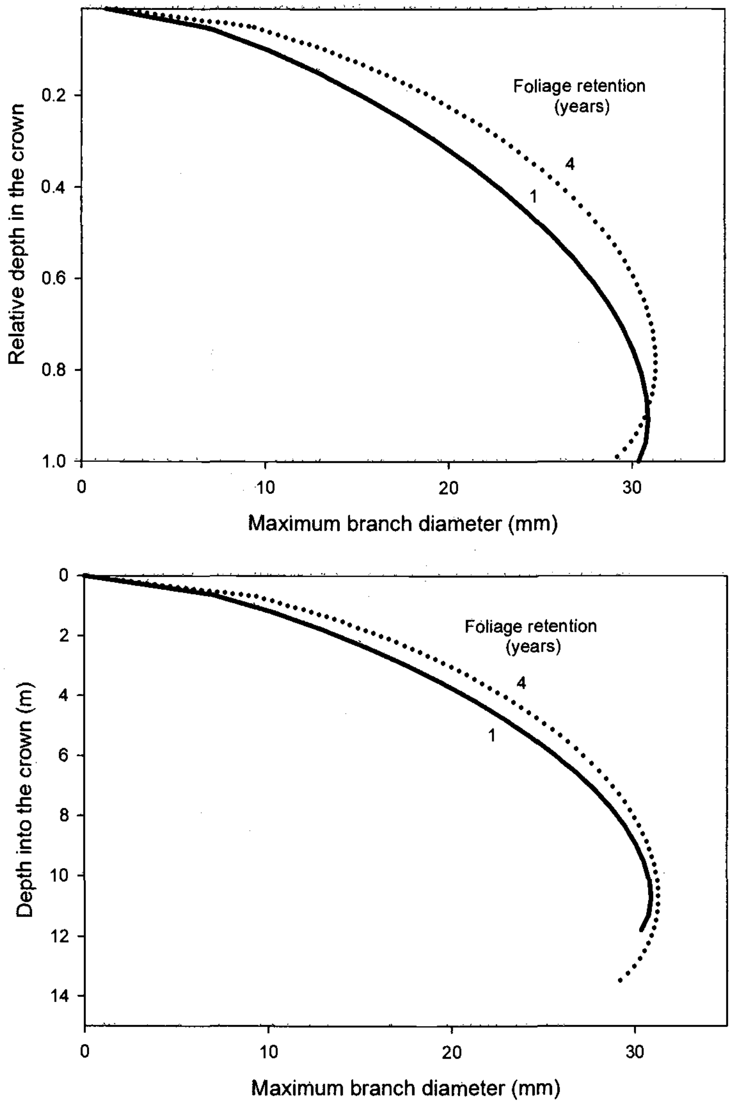

Figure 3.9. Profiles of maximum branch diameter with relative height above the crown base (a) and depth in the crown (b) for average-sized trees. The trends are predicted from equation 3.17. The solid line represents a tree with only 1 year of foliage retention and the dashed line is a tree with 4 years of foliage retention. The diameter to height ratio was set equal to the sample mean of 1.26 cm/m and the crown ratios were adjusted using equation 3.3. The resulting crown ratio for the tree with 1 year of foliage retention is 0.55, while the crown ratio for the tree with 4 years of foliage retention is 0.73.

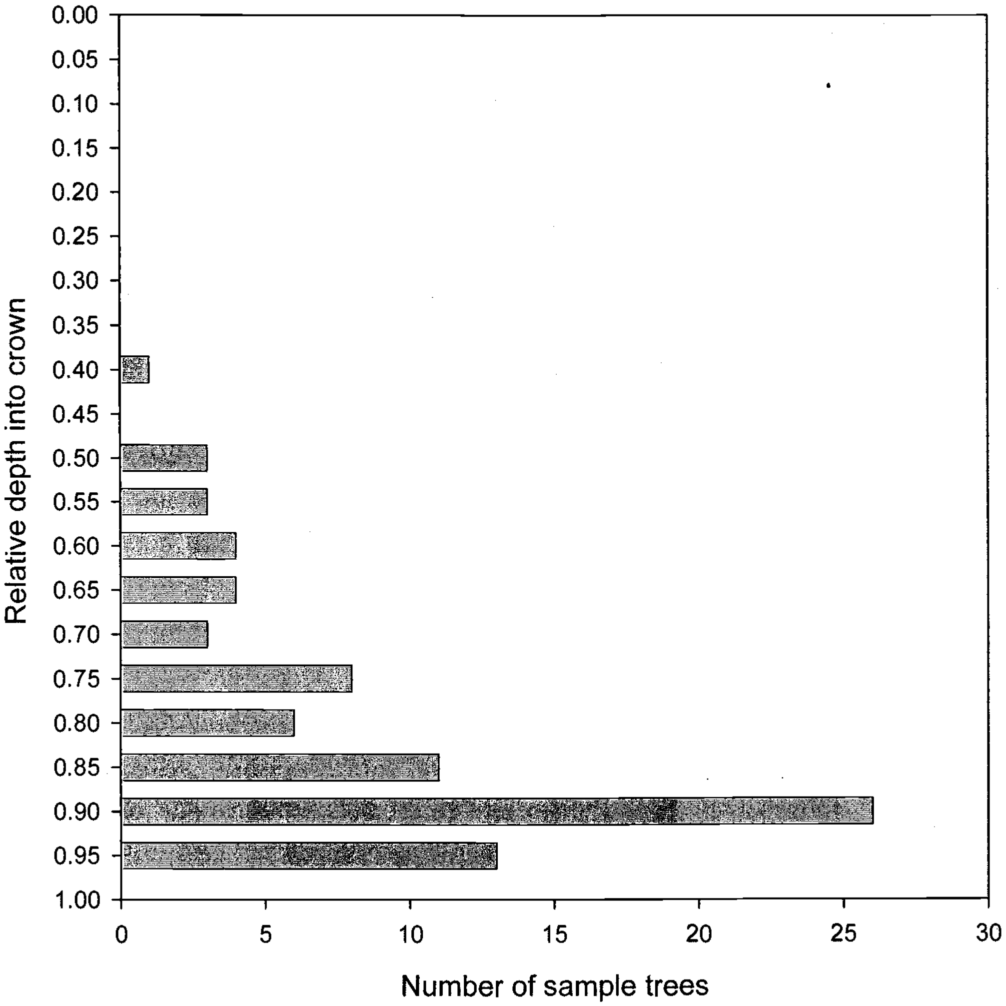

Figure 3.10. Histogram showing the relative depth into crown at which maximum branch diameter occurred for individual sample trees (mean relative depth =0.81).

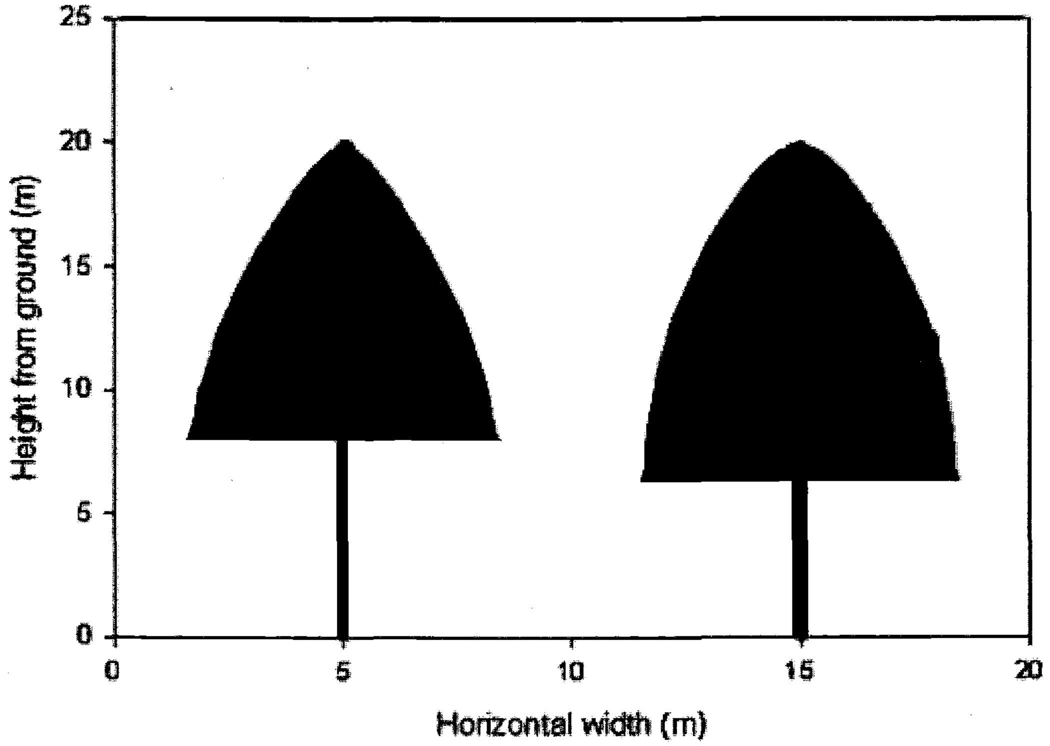

Figure 3.11. Depiction of an average-sized tree on plots with one year of foliage retention (left) and four years of retention (right). Height to crown base was predicted using equation 3.6, while crown profile was estimated using equation 3.16.

CHAPTER FOUR: IMPACTS OF SWISS NEEDLE CAST ON THE PRODUCTION, ALLOCATION, AND DISTRIBUTION OF DOUGLAS-FIR CROWN MASS IN THE OREGON COAST RANGE

ABSTRACT

Defoliation can drastically alter production, allocation, and distribution of crown mass in coniferous tree species. Swiss needle cast (SNC), which causes premature needle loss in Douglas-fir throughout the Oregon Coast Range, provided an opportunity to assess changes in branch and foliage mass under varying severity of defoliation. Seventy-nine trees from a variety of stand structures and SNC severity classes were destructively sampled to develop allometric relationships for examining production, allocation, and distribution of crown mass. At the branch-level, SNC significantly reduced foliage mass in the lower two-thirds of upper crown, but did not influence the amount of live branch mass. With increasing SNC severity, branches allocated more to higher order branches, but less to primary branch elongation. At the tree- and plot-levels, SNC significantly reduced both foliage and woody crown mass, including current-year foliage. The vertical distribution of foliage mass became less skewed and more uniform with increasing SNC. Production, allocation, and distribution of crown mass were highly sensitive to crown condition. Patterns in these attributes help define their quantitative relationship to various indices of SNC severity.

INTRODUCTION

Many practical forestry issues and scientific applications require accurate estimates of mass production, allocation, and distribution (Parresol 1999). Forest mass research has steadily grown in importance over the last four decades and has facilitated some hybridization of ecophysiological models with traditional growth and yield models (e.g. Waring & McDowell 2002). Mass production and allocation directly influence ecosystem attributes such as energy and nutrient flows (Johnson et al. 1996; Kellomaki et al. 1980), as well as susceptibility to disturbances, such as fire (Graham 1999; Scott & Reinhardt 2002). At the tree-level, crown mass, particularly foliage, directly controls transpiration-respiration processes and total carbon uptake (Zhang 1997), in turn influencing the amount of stemwood production (St. Clair 1994). Crown mass has also been found to be an excellent indicator of environmental and stand stress (Johnson et al. 1996). Extensive work has been done on the impacts of short-term defoliation caused by insects (Långström et al. 2001) and air pollution (Reich & Lassoie 1985) on crown mass. Relatively little work has been done on the effects of foliar disease on crown mass. More generally, the majority of work on defoliation effects has imposed treatments on tree seedlings in controlled experimental settings (Långström et al. 2001). Spruce budworm (*Choristoneura occidentalis*) research in eastern and western North America is one notable exception.

The Swiss needle cast (SNC) epidemic of Douglas-fir (*Psedotsuga menziesii* Mirb. Franco) in the Oregon Coast Range (Hansen et al. 2000) provided an excellent opportunity to assess the impact of a foliar disease on production, allocation, and distribution of foliage mass. SNC may be changing primary production patterns in this region by decreasing foliage retention and tree growth. This disease, which is caused by the endemic fungus, *Phaeocryptopus gauemannii*, reduces foliage retention to as little as one year and average volume growth as much as 52% (Maguire et al. 2002). In the late 1990s, over 157,000 ha in the Oregon Coast Range showed symptoms detectable by aerial survey, reflecting the dramatic increase in this disease since the early 1990s (Kanaskie et al. 2002).

Mass production, allocation, and distribution are very sensitive to climatic patterns and silvicultural treatments (Yang 1998). Stand mass production is also influenced by stand age (Turner & Long 1975), site quality (Kurz 1989), species composition (Bartelink 2000; Garber 2002), and stand density (Blake et al. 1991). Production of an individual tree crown mass is influenced by its social position within the stand (Xu & Harrington 1998), the competition it experiences (Mäkelä & Vanninen 1998), and its genetic constitution (St. Clair 1994). Generally, mass production increases with enhanced water and nutrient availability and allocation shifts towards foliage at the expense of below-ground portions, branches and stem (Gower et al. 1992).

Production, allocation, and distribution of mass have been studied extensively in Douglas-fir (Bartelink 1996). Dice (1970) estimated that an average Douglas-fir at 36 years old contained 82 kg of biomass, with 4% in foliage, 6% in live branches, 3% in dead branches, 9% in bole bark, 63% in bole wood, and 15% in roots. Bartelink (1998) found mass partitioning and production more or less constant after age 20. However, Turner and Long (1975) concluded that it didn't reach a steady state until age 40-50 in sites of low quality, highlighting the suggestion that height growth has the most influence on mass allocation patterns in Douglas-fir (Bartelink 1998).

Patterns in vertical distribution of Douglas-fir foliage have also been characterized. Maguire and Bennett (1996) found that as the relative height of a tree within a stand increases, the mode of relative foliage distribution shifts down the stem and the distribution becomes more skewed upward, perhaps as an adaptation to better light environment. In short, mass production, allocation, and distribution follow predictable patterns in Douglas-fir and many other species in the absence of severe stress (Bazzaz & Grace 1997). Changes in these relationships are expected when plant stress is high, and these changes in turn may indicate the level of stress being experienced.

The overall objective of this study was to examine the impact of SNC on the production, allocation, and distribution of Douglas-fir crown mass in the Oregon Coast Range. Several hypotheses were tested: (1) total foliage mass is reduced by the disease (i.e., premature loss of older foliage was not compensated for by greater production of new foliage; (2) for a given basal diameter, allocation to foliage mass in higher order vs. first order branches increases and elongation is reduced by SNC; (3) crown bulk density of both foliage and branchwood is reduced by SNC; and (4) SNC imposes a more uniform vertical distribution of foliage (due to deeper penetration of light). The scope of inference for the study is young (10-30 year old), managed Douglas-fir plantations in the Oregon Coast Range.

METHODS

Study area

The twenty-two relatively young Douglas-fir plantations used in this study were selected from 76 permanent plots being monitored as part of the Growth Impact Study sponsored by the Swiss Needle Cast Cooperative at Oregon State University (Figure 4.1). The plots were located in the Oregon Coast Range within 32 km of the Pacific coast, north of Newport and south of Astoria, Oregon. The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 180 to 300 cm/yr, and January mean minimum and July mean maximum temperatures range from –2 to 2°C and from 20 to 28°C, respectively (Maguire et al. 2002). Variations in precipitation and temperature for this area are strongly correlated with elevation and proximity to the coast. Elevation of the study plots ranged from 337 to 1,312 m, all aspects were represented, and proximity to the coast varied from 0.97 to 31.8 km.

Species composition of the plots was ≥90% Douglas-fir by basal area with varying amounts of naturally regenerated western hemlock and other conifer and broadleaved trees. The plots had similar stand attributes but varied in SNC intensity as estimated by average stand foliage retention (Table 4.1).

Data collection

Sampling occurred prior to bud break in spring and after the end of the growing season in the fall of 2002. Fifty-nine trees were sampled adjacent to thirteen different permanent plots in the spring, and 39 trees adjacent to nine additional permanent plots were sampled in the fall. Within approximately 30 m of each permanent plot, trees with diameter at breast height (DBH) and foliage retention similar to those on the permanent plot were sampled. All sample trees were surrounded by other Douglas-fir trees, and were away from any gaps or landings. A set of 3-6 sample trees was chosen at each plot. Sample trees ranged from 12 to 43 cm in DBH (Table 4.2). Before felling, DBH (to the nearest 0.1 cm) and crown width (LCW; to the nearest 0.1 m) were measured. Each sample tree was then felled in a manner that minimized foliage loss and breakage. Total height (HT) from the base of the stump to the tip of the tree and height to the crown base (HCB=lowest live branch) were measured using a metric tape stretched along the bole. Basal diameters and height of each live branch were also measured (to the nearest mm and cm, respectively). A total of six whorl branches, two from each third of the crown, and three interwhorl branches, one from each third of the crown, were selected at random. Sample branches were cut at the base and measured for total length along the stem. Sample branches ranged from 1 to 56 mm in basal diameter (Table 4.3). Average foliage retention (to the nearest 0.5 yr) was recorded for each branch, as was the number of secondary branches formed during each of the last five growing seasons. Approximately 50 fresh needles were randomly removed from each branch in rough proportion to the number of needles present in each age class. This subsample was placed in a plastic bag and stored in a cooler for transport to the laboratory. The remaining portion of the branch was clipped into segments and placed in a plastic bag. After branch sampling, thin disks were removed from the tree at breast height (1.37 m) and crown base. In the fall sampling, one-year old foliage samples were also randomly taken from branches located in the top crown third for PCR assessment of Phaeocryptopus gauemannii biomass (Manter et al. 2001).

In the lab, sample branches were placed into smaller paper bags and dried. Branches in the spring were separated into foliage, primary branchwood, and higher order branchwood and branches sampled in the fall were separated by 1-yr age class. The samples were air-dried for at least 1 month and placed into an oven at a temperature of 85°C for three days. The needles were removed from the branch, separated, and weighed to the nearest 0.01 g. The two stem disks from each tree were measured for sapwood area on the two radii forming the long axis of the disk and on the two radii perpendicular to the longest. Sapwood cross sectional area (cm^2) was computed assuming that the total cross-sections and heartwood cross sections were elliptical in shape. Current and five-year growth increments were also measured on the four perpendicular radii.

SNC severity on each of the study sites has been recorded every year since 1996 by the Oregon Department of Forestry. Square, 0.08-ha permanent plots were established by the Swiss Needle Cast Cooperative in 1998. On each measurement plot, all trees were tagged at breast height and measured for DBH (nearest 0.1 cm). In addition, a subsample of at least 40 Douglas-fir were measured for total height and height to crown base. Plots were remeasured every two years, but ten trees on each plot have been scored for SNC every year since 1998. On these trees, the crown was divided vertically into thirds and the average number of years that foliage was retained in each third was estimated visually to the nearest 0.1 year. Overall crown discoloration was also recorded on a 1 to 4 scale, with 4 represented the most severe discoloration. On branches in the fifth whorl from the top of the tree, the percentage of each age class of needles remaining on the branch was recorded. Plot ratings were computed as the average from all ten trees.

Data analysis

Missing heights on the permanent plots were predicted with a nonlinear regression fit to measured trees on the same plot and for the same measurement year:

$$[4.1] \qquad \mathrm{HT} = 1.37 + \beta_1 \exp\left(\frac{\beta_2}{\mathrm{DBH}}\right) + \varepsilon_1$$

where the β_i's are parameters to be estimated from the data, $\varepsilon_1 \overset{iid}{\sim} \mathrm{N}(0, \sigma_1^2)$, and all other variables are defined above. Any missing heights to crown base were predicted using the following model, again fitted to data for the specific plot and year:

$$[4.2] \qquad \mathrm{HCB} = \mathrm{HT}\left[1 + \exp\left(\gamma_0 + \gamma_1 \mathrm{RHT} + \gamma_2 \frac{\mathrm{DBH}}{\mathrm{HT}}\right)\right]^{-1} + \varepsilon_2$$

where the γ_i's are parameters to be estimated from the data, $\varepsilon_2 \overset{iid}{\sim} \mathrm{N}(0, \sigma_2^2)$, RHT is relative height in the stand, and all other variables are defined above.

Various linear and nonlinear regression models were fit to the data to develop predictive branch-, tree-, and plot-level equations applicable to the sampled populations. Final models were chosen on the basis of biological appeal, residual analysis, Furnival's index (FI) (Furnival 1961), and Akaike's information criterion (AIC). When predictive equations were based on a logarithmic scale, arithmetic transformations were corrected for log bias (Baskerville 1972). Although alternative correction factors for log bias may perform better under certain conditions (Flewelling & Pienaar 1981), MSE/p, where MSE is the mean square error and p is the number of parameters in the model, was chosen for simplicity (Sprugel 1983). All analyses were done in SAS v8.2 (SAS Institute, Cary, NC) and SPLUS 2000 (Mathsoft, Seattle, WA).

Branch-level

Foliage and woody mass

A series of weighted and unweighted, linear and nonlinear models were screened to develop branch-level equations for predicting foliage mass and branch mass from branch diameter and depth in the crown. Both published and unpublished model forms were tested (Table 4.4). The general model can be written as:

[4.3] $\mathrm{DM} = \mathrm{f}(\mathrm{X};\theta) + \varepsilon_3$

where DM is total branch foliage or woody mass, X are explanatory variables, θ are the parameters and $\varepsilon_3^{\mathrm{iid}} \sim \mathrm{N}(0, \mathrm{X}^{\mathrm{W}} \sigma_3^{\,2})$, where W = 0 (unweighted case), -0.5, -1.0, ..., -6.0 in the case of increasing variance. Parameter estimates were obtained separately for each plot.

The amount of current foliage (or woody) mass on branches was predicted as a percentage of the total foliage (or woody) mass using the following generalized linear model (McCullagh and Nelder 1989) previously applied by Kershaw and Maguire (1995):

[4.4] $M = \beta_{40} + \beta_{41}\mathrm{RHACB} + \varepsilon_4$

where M=ln[%C/(1 - %C)], %C is percentage of either current foliage or woody mass, RHACB is relative height above crown base (1-(DINC/CL)), and the β_i's are parameters to be estimated from the data for each sample plot. The parameter estimates were obtained using PROC GENMOD in SAS assuming normally distributed errors.

Effect of SNC on foliage and woody mass

The relationship between total branch mass (foliage or wood) and SNC was assessed with the following nonlinear equations:

[4.5] $\mathrm{DM} = \beta_{50}\mathrm{BD}^{\beta_{51}}\mathrm{RHACB}^{\beta_{52}}\mathrm{DINC}^{\beta_{53}}\mathrm{FOLRET}^{\beta_{54}} + \varepsilon_5$

where BD is branch diameter (mm), DINC is depth into the crown (tree height – branch height), all other variables are defined above, the β_i's are parameters to be estimated from the data, and $\varepsilon_5 \overset{\mathrm{iid}}{\sim} N(0, \sigma_5^2)$. Significant autocorrelation within trees and plots was detected in preliminary analysis, which resulted in the final model being fitted with a first-order autoregressive error structure (AR(1)). No statistically significant difference was detected for branch type (interwhorl vs. whorl) or season (spring vs. fall) so the sample branches were pooled together, which resulted in a total of 694 branches available for analysis.

Foliage ratio for each branch was estimated by dividing of foliage mass by woody mass. The relationship between foliage ratio and SNC was assessed with the following nonlinear regression model:

$$[4.6] \quad \mathrm{FR} = \beta_{60}\mathrm{DINC}^{\beta_{61}}\mathrm{RHACB}^{\beta_{62}}\mathrm{BD}^{\beta_{63}}\mathrm{AGE}^{\beta_{64}}\mathrm{FOLRET}^{\beta_{65}} + \varepsilon_6$$

where FR is the foliage ratio, AGE is the average stand breast height age, all other variables are defined above, the β_i's are parameters to be estimated from the data and $\varepsilon_6 \overset{iid}{\sim} N(0, \sigma_6^2)$. The final model was fitted with an AR(1) error structure.

The mass of higher order branches on primary branches was assessed with the following linear model:

$$[4.7] \quad \begin{aligned} \ln(\mathrm{HOWDM}) = {} & \beta_{70} + \beta_{71}\mathrm{BD} + \beta_{72}\frac{\mathrm{FDM}}{\mathrm{BBA}} + \beta_{73}\mathrm{SIB} + \beta_{74}\mathrm{FOLRET} + \\ & \beta_{75}(\mathrm{SIB} * \mathrm{FOLRET}) + \varepsilon_7 \end{aligned}$$

where HOWDM is the mass of higher order branches (g), BBA is the branch basal area, the β_i's are parameters to be estimated from the data, $\varepsilon_7 \overset{iid}{\sim} N(0, \sigma_7^2)$, and all other variables are defined above. The relationship between the mass in the 2001 primary branch axis and foliage retention was analyzed with the following linear model:

$$[4.8] \quad \ln(\mathrm{PBP}) = \beta_0 + \beta_1\mathrm{DINC} + \beta_2\mathrm{RHACB} + \beta_3\mathrm{BD} + \beta_4\mathrm{RHT} + \beta_5\mathrm{FOLRET}$$

where PBP is mass in the 2001 primary branch axis, DINC is depth into the crown, the β_i's are parameters to be estimated from the data, $\varepsilon_8 \overset{iid}{\sim} N(0, \sigma_8^2)$, and all other variables are defined above.

Mass allocation

The amount of current foliage or wood in current shoots was examined with the following linear model:

$$[4.9] \quad \ln(CDM) = \beta_{90} + \beta_{91}BD + \beta_{92}DINC + \beta_{93}RHACB + \beta_{94}DBH + \beta_{95}BAPH + \beta_{96}PBADF + \beta_{97}FOLRET + \varepsilon_9$$

where CDM is the amount of current-year mass, DBH is the diameter at breast height, BAPH is the stand basal area per ha, PBADF is the percent basal area of Douglas-fir, the β_i's are parameters to be estimated from the data, $\varepsilon_9 \overset{iid}{\sim} N(0, \sigma_9^2)$, and all other variables are defined above.

The amounts of mass allocated to higher order branches and to 2001 primary branch axis mass were analyzed as a proportion of the total branch mass. Parameter estimates were obtained from generalized linear models assuming a normal distribution and a logit link function in SAS PROC GENMOD. Final models were selected on the basis of reduction in deviance, significance of parameter estimates, and plots of residual deviances. The final model forms were:

$$[4.10] \quad M_{HOBDM} = \beta_{100} + \beta_{101}01BD + \beta_{102}\frac{FDM}{BBA} + \beta_{103}SIB + \beta_{104}FOLRET + \beta_{105}(SIB * FOLRET) + \varepsilon_{10}$$

[4.11] $$M_{PBDMP} = \beta_{110} + \beta_{111}DINC + \beta_{112}RHACB + \beta_{113}BD + \beta_{114}RHT + \beta_{115}FOLRET + \varepsilon_{11}$$

where M_{DM} is equal to ln[%DM/(1-%DM)], %DM is either proportion higher order branches (HOBDM) or the proportion of mass on the 2001 primary branch axis (PBDMP), the β_i's are parameters to be estimated from the data, $\varepsilon_{10} \overset{iid}{\sim} N(0, \sigma_{10}^2)$, $\varepsilon_{11} \overset{iid}{\sim} N(0, \sigma_{11}^2)$, and all other variables are defined above.

Finally, the foliage ratio of current-year shoots was examined with the following linear model:

[4.12] $$CFD = \beta_{120} + \beta_{121}RHACB + \beta_{122}BD + \beta_{123}FOLRET + \beta_{124}W + \varepsilon_{12}$$

where CFD is the foliage ratio of current-year shoots, W is an indicator variable for branch type (1 if whorl branch, 0 otherwise), the β_i's are parameters to be estimated from the data, $\varepsilon_{12} \overset{iid}{\sim} N(0, \sigma_{12}^2)$, and all other variables are defined above.

Tree-level

Foliage and branchwood mass

Branch-level equations were applied to sample trees to estimate tree-level foliage and branchwood mass. A number of weighted and unweighted, linear and nonlinear, published and unpublished model forms were tested (Table 4.5). The response variables were tree foliage mass and tree branchwood mass, while explanatory variables included: DBH, HT, crown length (CL), basal area times crown ratio above breast height (BACR), height to crown midpoint (HCM), lateral crown surface area (CSA), crown volume (CV), and diameter to height ratio (DBHHT).

The amount of current-year foliage was predicted with the following nonlinear equation:

$$[4.13] \quad \text{PCFDM} = \beta_{130}\text{CSA}^{\beta_{131}} + \varepsilon_{13}$$

where PCFDM is the proportion of current-year foliage mass, CSA is crown surface area (m^2), the ß$_i$'s are parameters estimated from the data for each plot, and $\varepsilon_{13} \overset{iid}{\sim} N(0, \sigma_{13}^2)$. The predicted proportions were multiplied by the estimated total foliage mass on individual trees and summed to obtain an estimate of plot-level annual foliage production.

Mass amount

The following linear model was used to assess the relationship between mass amount and foliage retention:

$$[4.14] \quad \begin{aligned} \ln(\text{DM}_{\text{tree}}) = {} & \beta_{140} + \beta_{141}\text{BACR} + \beta_{142}\text{CBSAP} + \beta_{143}\text{RHT} + \beta_{144}\text{SIB} + \\ & \beta_{145}\text{FOLRET} + \beta_{146}(\text{SIB} * \text{FOLRET}) + \beta_{147}(\text{BACR} * \text{CBSAP}) + \varepsilon_{14} \end{aligned}$$

where DM$_{\text{tree}}$ is tree foliage or branchwood mass, BACR is basal area (m^2) times crown ratio above breast height (BA * CL /(HT-1.37)), CBSAP is the sapwood area at crown base, RHT is relative tree height in the stand, SIB is Bruce's (1981) site index, the β$_i$'s are parameters to be estimated from the data, $\varepsilon_{14} \overset{iid}{\sim} N(0, \sigma_{14}^2)$, and all other variables are defined above.

The following linear regression model was used to assess the relationship between foliage ratio (FR_{tree}=tree foliage mass/tree branchwood mass) and SNC at the individual tree-level:

[4.15] $$FR_{tree} = \beta_{150} + \beta_{151}AGE + \beta_{152}SIB + \beta_{153}FOLRET + \beta_{154}(SIB * FOLRET) + \beta_{15}$$

where the β_i's are parameters to be estimated from the data, $\varepsilon_{14} \overset{iid}{\sim} N(0, \sigma_{14}^2)$, and all other variables are defined above.

The relationship between the amount of foliage mass per unit of sapwood and foliage retention was analyzed with the following linear model:

[4.16] $$\begin{aligned} LMSA = {} & \beta_{160} + \beta_{161}CL + \beta_{162}BALT + \beta_{163}TOPHT + \beta_{164}SIB + \beta_{165}BAPH \\ & + \beta_{166}FOLRET + \beta_{167}CLSA_{CB} + \varepsilon_{16} \end{aligned}$$

where LMSA is the amount of foliage mass per unit of sapwood area (g cm^{-2}), BALT is basal area in larger trees (m^2), TOPHT is stand top height in 2002 (m), the β_i's are parameters to be estimated from the data, $\varepsilon_{16} \overset{iid}{\sim} N(0, \sigma_{16}^2)$, and all other variables are defined above.

The relationship between crown bulk density and SNC was assessed with the following linear model:

[4.17] $$\begin{aligned} \ln(CBD_{FOL}) = {} & \beta_{170} + \beta_{171}\ln(TPH) + \beta_{172}RD + \beta_{173}SIB \\ & + \beta_{174}RHT + \beta_{175}CLSA_{CB} + \varepsilon_{17} \end{aligned}$$

[4.18] $$\begin{aligned} \ln(CBD_{BWOD}) = {} & \beta_{180} + \beta_{181}CL + \beta_{182}CSA + \beta_{183}DQDF + \beta_{184}DQ + \beta_{185} \\ & \ln(ELEV) + \beta_{186}SINA + \beta_{187}ASP22 + \beta_{188}CLSA_{CB} + \varepsilon_{18} \end{aligned}$$

where CBD_{FOL} is foliage crown bulk density (g m^{-3}), CBD_{BWOD} is branchwood crown bulk density (g m^{-3}), TPH is trees per ha, RD is Curtis' (1982) stand relative density, DQ is stand quadratic mean diameter (cm), ELEV is plot elevation (m), SINA is the sine-transformation of aspect, ASP22 is the sine transformation of aspect and slope (Stage 1976; % SLOPE * sin[(2*π*ASPECT)/360)]), $\varepsilon_{17} \overset{iid}{\sim} N(0, \sigma_{17}^2)$, $\varepsilon_{18} \overset{iid}{\sim} N(0, \sigma_{18}^2)$, the ßi's are parameter to estimated from the data and all other variables are defined above.

Mass allocation

The changes in the amount of current-year foliage and woody mass with foliage retention was assessed with the following linear models:

$$[4.19] \quad \ln(CDFM) = \beta_{190} + \beta_{191}CSA + \beta_{192}SIB + \beta_{193}ASP1 + \beta_{194}FOLRET + \beta_{195}CLSA_{CB} + \beta_{196}(SIB * FOLRET) + \varepsilon_{19}$$

$$[4.20] \quad \ln(CDWM) = \beta_{200} + \beta_{201}DBH + \beta_{202}BALT + \beta_{203}TOPHT + \varepsilon_{20}$$

where CDFM is current-year foliage mass, CDWM is current-year woody mass, $\varepsilon_{19} \overset{iid}{\sim} N(0, \sigma_{19}^2)$, $\varepsilon_{20} \overset{iid}{\sim} N(0, \sigma_{20}^2)$, the βi's are parameters to be estimated from the data, and all other variables are defined above. The parameters were estimated using seemingly unrelated regression because the correlations between the error terms were expected.

The amount of foliage and woody mass in whorl and interwhorl branches was examined with the following models:

$$[4.21] \quad \ln(WFDM) = \beta_{210} + \beta_{211}CL + \beta_{212}BALT + \beta_{213}SIB + \beta_{214}BAPH + \beta_{215}CLSA_{CB} + \varepsilon_{21}$$

$$[4.22] \quad \ln(IFDM) = \beta_{220} + \beta_{221}CL + \beta_{222}BALT + \beta_{223}SIB + \beta_{224}BAPH + \beta_{225}CLSA_{CB} + \varepsilon_{22}$$

$$[4.23] \quad \ln(WWDM) = \beta_{230} + \beta_{231}DBH + \beta_{232}CL + \beta_{233}SINA + \beta_{234}CLSA_{CB} + \varepsilon_{23}$$

[4.24] $\ln(\mathrm{IWDM}) = \beta_{240} + \beta_{241}\mathrm{DBH} + \beta_{242}\mathrm{CL} + \beta_{243}\mathrm{SINA} + \beta_{244}\mathrm{CLSA}_{\mathrm{CB}} + \varepsilon_{24}$

where WFDM is foliage mass in whorl branches, IFDM is foliage mass in interwhorl branches, WWDM is woody mass in whorl branches, IWDM is woody mass in interwhorl branches, the ßi's are parameters to be estimated from the data, $\varepsilon_k \overset{iid}{\sim} N(0, \sigma_k^2)$, and all other variables are defined above. The equations were fitted using seemingly unrelated regression because of the expected correlation of error terms.

Vertical foliage distribution

Observed vertical foliage distribution was characterized on the felled plot trees by dividing the crown into ten segments of equal length and summing the foliage within that segment using the branch-level equations developed separately for each plot. The proportion of total tree foliage in each of the ten segments was then determined. A standard two-parameter beta distribution (Johnson & Kotz 1970) was fitted to the empirical distribution for each tree:

$$f(x;a,b) = \frac{1}{B(a,b)} x^{a-1}(1-x)^{b-1}, 0 \le x \le 1$$

where

$$B(a,b) = \frac{\Gamma(a)\Gamma(b)}{\Gamma(a+b)},$$

$\Gamma(a) = \int_0^\infty e^{-x} x^{a-1} dx$ for all $a > 0$, a and b are shape parameters (0<α, β<∞) and x is a beta random variable.

The beta distribution was chosen because it has the desirable properties of being extremely flexible and logically defined on an interval with fixed endpoints. Other distributions that have been fit to vertical foliage distribution include the normal (Beadle et al. 1982), chi-square (Massman 1982), lognormal (Schreuder & Swank 1974), gamma (Schreuder & Swank 1974; Massman 1982) and Weibull (Schreuder & Swank 1974; Mori & Hagihara 1991; Gillespie et al. 1994); however, all lack two fixed endpoints. The interval (0,1) was rescaled to crown length making the tree tip and lowest live branch the respective endpoints. Estimates of the parameters *a* and *b* were determined using maximum likelihood estimation.

Parameters estimates from the beta distribution were regressed on tree (DBH, HT HLB, and CL) and SNC (FOLRET, CLSA, CC, CD) variables to determine the effects of SNC. Because a and b are correlated, seemingly unrelated regression was applied to obtain unbiased and consistent estimators (Kmenta 1997). Vertical foliage distributions were then predicted for the average-sized trees found on plots across the range of stand density and SNC to graphically depict effects of the disease.

Plot-level

At the plot-level, the following linear model was used to assess the relationship between total foliage mass and SNC severity as measured by foliage retention:

$$[4.25] \quad \begin{aligned} \ln(\mathrm{FDM}_{\mathrm{plot}}) = \beta_{250} + \beta_{251}\ln(\mathrm{BAPH}) + \beta_{252}(\mathrm{SIB}) + \beta_{253}\mathrm{FOLRET} \\ + \beta_{254}(\mathrm{SIB} * \mathrm{FOLRET}) + \beta_{255}\mathrm{I} + \varepsilon_{25} \end{aligned}$$

where $\mathrm{FDM}_{\mathrm{plot}}$ is total foliage mass on the plot (kg ha^{-1}), BAPH is stand basal area, I is an indicator variable for time of sampling (1 if fall, 0 otherwise), $\varepsilon_{25} \overset{\mathrm{iid}}{\sim} \mathrm{N}(0, \sigma_{25}^2)$, the β_i's are parameters to be estimated from the data, and all other variables are defined above. The following linear model was used to assess the relationship between plot woody mass amount and retention:

$$[4.26]\quad \ln(\mathrm{WDM}_{\mathrm{plot}}) = \beta_{260} + \beta_{261}\ln(\mathrm{TPH}) + \beta_{262}\mathrm{SIB} + \beta_{263}\mathrm{COAST} + \beta_{264}\mathrm{PCLSA}_{\mathrm{CB}} + \varepsilon_{26}$$

where WDM is woody mass (kg ha^{-1}), COAST is distance from the coast (km), $\mathrm{PCLSA}_{\mathrm{CB}}$ is plot mean crown length to sapwood area ratio, $\varepsilon_{26} \overset{iid}{\sim} N(0, \sigma_{26}^2)$, the β_i's are parameters to be estimated from the data, and all other variables are defined above.

The relationship between the plot foliage ratio (FR) and SNC was examined with the following linear model:

$$[4.27]\quad \mathrm{FR}_{\mathrm{plot}} = \beta_{270} + \beta_{271}\mathrm{AGE} + \beta_{272}\mathrm{TPH} + \beta_{273}\mathrm{BAPH} + \beta_{274}\mathrm{SIB} + \beta_{275}\mathrm{FOLRET} + \beta_{276}(\mathrm{SIB} * \mathrm{FOLRET}) + \beta_{277}\mathrm{I} + \varepsilon_{27}$$

where the β_i's are parameters to be estimated from the data, $\varepsilon_{27} \overset{iid}{\sim} N(0, \sigma_{27}^2)$, and all other variables are defined above.

The relationship between plot current-year foliage production and SNC severity was examined with the following linear model:

$$[4.28]\quad \mathrm{CDFM}_{\mathrm{plot}} = \beta_{280} + \beta_{281}\mathrm{RD} + \beta_{282}\mathrm{SIB} + \beta_{283}\ln(\mathrm{TPHDF}) + \beta_{284}\ln(\mathrm{ELEV}) + \beta_{285}\mathrm{PBADF} + \beta_{286}\mathrm{COAST} + \beta_{287}\mathrm{PCLSA}_{\mathrm{CB}} + \varepsilon_{28}$$

where TPHDF is the number of Douglas-fir trees per ha, the β_i's are parameters to be estimated from the data, $\varepsilon_{28} \overset{iid}{\sim} N(0, \sigma_{28}^2)$, and all other variables are defined above.

RESULTS

Branch-level

Foliage and woody mass

The best model, defined by FI, for estimating both foliage and woody mass was the model introduced by Kershaw and Maguire (1995):

$$[4.29] \quad \ln(\hat{DM})_k = b_{0k} + b_{1k}\ln(BD) + b_{2k}\ln(DINC) + b_{3k}\ln(RHACB)$$

where $\ln(\hat{DM})_k$ is the estimated foliage or woody mass for branches on plot k, the b_{ik}'s are parameter estimates for plot k, and all other variables are defined above. Significant differences were found among plots, underscoring the need for site-specific parameter estimates (Figure 4.2). The models fit well with R^2 values between 0.68 and 0.98 and root mean square errors (RMSE) varying from 0.25 to 1.21 (Tables 4.6 and 4.7).

Effect of SNC on foliage and woody mass

The amount of foliage mass on a branch ranged from 0.01 to 898.49 g, while woody mass varied from 0.06 to 3,681.44 g (Table 4.3). Parameter estimates for equation 4.5 indicated that foliage retention accounted for a significant amount of the residual variation in total foliage mass after accounting for branch diameter and position (Table 4.8). However, foliage retention added no predictive power to woody mass (Table 4.8). In general, foliage mass increases with branch diameter, depth into the crown, relative height above crown base, and foliage retention in the foliage mass model. An average branch on a site with 1 year of foliage retention is expected to have 46% less foliage mass than a branch on site with 4 years of retention with the same diameter and position in the crown. The foliage mass model explained 56% of the variation and had a RMSE of 0.38, while the woody mass model had an R^2 of 0.81 and a RMSE of 0.82.

The ratio of foliage to woody mass had a significant relationship with foliage retention ($p<0.05$ for β_{65} in equation 4.6). In general, this ratio increased with depth into the crown, relative height above crown base, and foliage retention, but decreased with increasing branch diameter and stand average breast height age (Table 4.9). An average branch on site with 1 year of foliage retention was expected to have a foliage ratio that is 26.6% less than a branch on site with 4 years of retention with all else being equal. The final model was weighted by BD^{-1}, explained 17.2% of the original variation, and had a RMSE of 1.5856.

The mass of higher order branches on the primary branch was significantly related to foliage retention ($p<0.02$ for β_{74} in equation 4.7) for whorl branches but not interwhorl branches ($p>0.08$). Higher order branch mass in whorl branches increased with branch diameter, the ratio of foliage mass to branch basal area, and the interaction between site index and foliage retention, but decreased with greater site index and foliage retention (Table 4.10). A branch on a plot with one year of foliage retention was estimated to have 68.7% more mass in higher order branches than a branch in a similar location on a plot with four years of retention. The model explained 78% of the original variation and had a RMSE of 0.6469.

The amount of mass in the 2001 portion of the main axis of primary branches was also significantly related to foliage retention ($p<0.01$ for β_{85} in equation 4.8). Mass in the 2001 portion of the primary branch main axis increased with relative height above crown base, branch diameter, and foliage retention, but decreased with depth into the crown and relative tree height in the stand (Table 4.11). A branch in the upper crown third on a plot with one year of foliage retention was expected to have 60.3% less primary branch production than a similar branch on a plot with four years of retention. The overall model explained 56% of the original variation and had a RMSE of 1.302.

Effect of SNC on allocation

The amount of foliage and branchwood mass in current shoots showed no relationship with foliage retention ($p>0.05$ for β_{97} for equation 4.9). Current mass tended to increase with branch diameter, basal area per ha, and percent basal area in Douglas-fir, but decreased with depth into crown and diameter at breast height. When analyzed by crown thirds, the amount of branchwood mass in the current shoots of the top third of the crown showed a significant positive relationship with foliage retention ($p<0.05$). The models generally explained around 55% of the original variation and RMSEs tended to be near 1.2.

Neither the proportion of mass allocated to higher order branches on the primary branch nor the proportion of mass in the 2001 primary branch axis were related to foliage retention ($p>0.05$ for β_{104} in equation 4.10 and for β_{115} in equation 4.11). When analyzed by crown third, a significant relationship between foliage retention and the proportion of mass allocated to higher order branches in the upper crown third existed ($p<0.04$). Branches in the upper crown also increased their allocation to higher order branches with greater diameter, foliage mass to branch basal area ratio, and the interaction between site index, and foliage retention, but decreased allocation with increasing site index and foliage retention.

Overall, the foliage ratio on current-year shoots showed no relationship with foliage retention ($p>0.05$ for β_{123} in equation 4.12). In general, the foliage ratio tended to decrease with relative height above crown base and increase with branch diameter. When the relationship is examined at the different levels in the crown, foliage retention shows a significant relationship with foliage density on current-year shoots. In the upper crown third, foliage ratio of current-year shoots significantly decreased with relative height above crown base, and foliage retention, and was significantly lower on whorl branches. In the middle and lower portions of the crown, foliage ratio of current-year shoots tended to increase with foliage retention. In the middle third of the crown, foliage ratio of current-year shoots likewise decreased with relative height above crown base. However, foliage ratio of current-year shoots in the lower crown third, only was significantly related to foliage retention and branch type and tended to increase on whorl branches. The overall model explained 38% of the original variation and had a RMSE of 1.7859, while the models for each crown third had R^2 values between 0.09 and 0.29 and RMSEs varying from 1.2087 to 2.1821.

Tree level

Foliage and branchwood mass

For predicting total tree foliage and woody mass mass, the best model was a linear model of the following form (Tables 4.12, 4.13):

[4.30] $\ln(DM_{tree}) = \beta_{290} + \beta_{291}\ln(CSA) + \varepsilon_{29}$

where DM_{tree} and CSA are defined above, $\varepsilon_{29} \overset{iid}{\sim} N(0, \sigma_{29}^2)$, and the β_i's are parameters to be estimated from the data by plot. When fitted to each plot, R^2 values ranged from 0.52 to 0.99 for foliage mass, while R^2 values varied between 0.44 and 0.99 for branchwood mass.

Effect of SNC on crown mass

Tree foliage mass varied between 1.54 to 52.12 kg, while woody mass ranged from 5.00 to 114.02 kg (Table 4.2). Foliage retention showed a significant linear relationship with both foliage mass ($p<0.01$ for β_{145} in equation 4.14) as well as woody mass ($p<0.05$). In general, foliage mass increased with the basal area live crown ratio, sapwood area at crown base, relative height in the stand, site index, and foliage retention, but decreased with the interaction between site index and foliage retention as well as the interaction between sapwood area at crown base and the basal area times modified live crown ratio (Table 4.14; Figure 4.3). Foliage retention, however, has a positive effect that declines with increasing site index. A tree on a plot with one year of foliage retention was estimated to have 54.3% less foliage mass than a tree on a plot with four years of retention. Branchwood mass at the tree-level also increased with the product of basal area and modified live crown ratio, relative height in the stand, site index, and foliage retention, but decreased with the interaction between site index and foliage retention (Table 4.15). Foliage retention, however, has a positive effect except at the highest site indices. A tree on a plot with one year of foliage retention was estimated to have 37.6% less woody branch mass than a tree on a plot with four years of retention.

Although foliage retention was significant in all the models examined and explained a fair portion of the original variation (≈ 15%), the ratio of crown length to sapwood area at crown base ($CLSA_{CB}$) as indicated by AIC and FI tended to perform the best when compared to other SNC indices (crown color, crown density, foliage retention, and crown length to sapwood area at breast height ratio($CLSA_{BH}$)) (Table 4.16). A tree with a $CLSA_{CB}$ of 15 was estimated to have 46.0% less foliage mass than a tree with a $CLSA_{CB}$ of 2 at fixed levels of the other covariates. Again, the $CLSA_{CB}$ tended to perform better in the branchwood mass models as indicated by AIC and FI (Table 4.17). A tree with a $CLSA_{CB}$ of 15 was estimated to have 60.9% less woody branch mass than a tree with a $CLSA_{CB}$ of 2 at fixed levels of the other covariates. Overall, the models performed well as R^2 was generally near 0.7 and RMSEs tended towards 0.4.

The amount of foliage mass per unit of branchwood mass varied from 0.15 to 0.75 and showed a significant relationship with foliage retention ($p<0.05$ for β_{153} in equation 4.15). The ratio increased with site index and foliage retention, but decreased with average stand breast height age and the interaction between site index and foliage retention. A tree on a plot with one year of foliage retention was expected to have a foliage to branchwood mass ratio that is 16.2% less than a tree on a plot with an average of four years of retention. The model explained 56.8% of the original variation and had a RMSE of 0.1010.

The amount of foliage mass to unit of sapwood area varied from 18.59 to 133.48 g cm^{-2} and showed a significant relationship with foliage retention ($p<0.005$ for $ß_{166}$ in equation 4.16) and the crown sparseness index (the crown length to sapwood area ratio) ($p<0.0001$ for $ß_{167}$ in equation 4.16). The ratio increased with crown length, site index, and the crown length to sapwood area ratio, but decreased with basal area in larger trees, stand top height, basal area, and foliage retention (Table 4.19). There was a positive effect of foliage retention up to a site index of 41.5. The model explained 65% of the original variation and had a RMSE of 0.3204.

Foliage crown bulk density ranged from 15.97 to 243.71 g m^{-3} and showed a significant relationship with the crown sparseness index ($p<0.0001$ for $ß_{175}$ for equation 4.17). Foliage crown bulk density increased with the number of trees per ha, site index, and relative tree height, but decreased with increasing relative stand density and crown sparseness index (Table 4.20). A tree with a crown sparseness index of 15 is expected to have a crown bulk density that 42.1% less than a tree with a crown sparseness index of 2. The model explained 53% of the original variation and had a RMSE of 0.3403.

Branchwood crown bulk density ranged from 70.82 to 428.38 g m^{-3} and also showed a significant relationship with the crown length to sapwood area ratio ($p<0.0001$ for β_{188} in equation 4.18). Branchwood crown bulk density increased with crown length, and stand quadratic mean diameter, but decreased with crown surface area, Douglas-fir quadratic mean diameter, elevation, the sine-transformation of aspect, the sine-transformation of aspect and slope, and the crown length to sapwood area ratio (Table 4.21). A tree with a crown sparseness index of 15 is expected to have a crown bulk density that 52.4% less than a tree with a crown sparseness index of 2. The model explained 55% of the original variation and had a RMSE of 0.2378.

Effects of SNC on allocation to foliage and branchwood

The amount of current-year foliage was related to foliage retention ($p<0.05$ for β_{194} in equation 4.19), while branchwood mass in current-year shoots was not. Current-year foliage mass increased with crown surface area, site index, cosine transformation of slope and aspect, and foliage retention, but decreased with crown length to sapwood area ratio and the interaction between site index and foliage retention (Table 4.22). Branchwood mass in current shoots increased with DBH and stand top height, but decreased with basal area in larger trees. The system explained 76% of the original variation had a RMSE of 0.9979.

The proportion of foliage mass in whorl branches ranged from 39.4 to 93.9%, while the proportion of branchwood mass in whorl branches varied from 38.9 to 95.7%. The crown sparseness index was significantly related to foliage and branchwood mass in interwhorl branches (p<0.0001 for ß$_{215}$ in equation 4.21 and ß$_{225}$ in equation 4.22), as well as the amount foliage and branchwood mass in whorl branches (p=0.0011 for ß$_{234}$ in equation 4.23 and p=0.0016 for ß$_{244}$ in equation 4.24). Foliage mass in whorl and interwhorl branches increased with crown length and site index, but decreased with basal area in larger trees, stand basal area, and the crown sparseness index (Table 4.23). Branchwood mass in whorl and interwhorl branches increased with DBH and crown length, but decreased with the sine-transformation of aspect and the crown sparseness index. A tree with a crown sparseness index of 15 is expected to have 66.8 and 71.2% less foliage mass in whorl and interwhorl branches, respectively, than a tree with a crown sparseness index of 2. Furthermore, a tree with a crown sparseness index of 15 is expected to have 56.0 and 63.0% less branchwood mass in whorl and interwhorl branches, respectively, than a tree with a crown sparseness index of 2. The models explained between 36 to 70% of the original variation and had RMSEs between 0.3942 and 0.7091.

Vertical foliage distribution

Both individual tree and stand variables performed poorly in predicting parameters of the beta distribution as most predictive equations accounted for less than 50% of the original variation. Foliage retention showed a significant relationship with the *a*-parameter (p<0.0001) but not the *b*. The best models for predicting the *a*- and *b*-parameters were the following linear models:

$$[4.31] \quad a = \beta_{310} + \beta_{311}\mathrm{DBH} + \beta_{312}\mathrm{RDBH} + \beta_{313}\mathrm{SIB} + \beta_{314}\mathrm{FOLRET} + \beta_{315}(\mathrm{SIB} * \mathrm{FOLRET}) + \varepsilon_{31}$$

[4.32] $b = \beta_{320} + \beta_{321}\mathrm{CL} + \beta_{322}\mathrm{CBSAP} + \beta_{323}\mathrm{RD} + \varepsilon_{32}$

where RDBH is relative tree diameter in the stand, $\varepsilon_{31}^{\mathrm{iid}} \sim \mathrm{N}(0, \sigma_{31}^{2})$, $\varepsilon_{32}^{\mathrm{iid}} \sim \mathrm{N}(0, \sigma_{32}^{2})$, ß$_i$'s are parameters to be estimated from the data, and all other variables area defined above. The *a*-parameter significantly increased with relative diameter in the stand, site index, and foliage retention, but decreased with tree diameter and the interaction between site index and foliage retention (Table 4.24). The model explained 40.2% of the original variation and had a RMSE of 0.5213 (Table 4.24). The *b*-parameter significantly increased with crown length and relative density, but decreased with sapwood area at crown base. The model explained 20.3% of the original variation and had a RMSE of 0.5608. Together, the systems of equations explained 46.5% of the original variation in the parameters and had a RMSE of 0.9863. In the systems of equations, sapwood area at crown base was no longer significantly related to the *b*-parameter. With decreasing foliage retention, the mode of foliage relative distribution shifted down and became more uniform (Figure 4.4).

Plot level

On plots sampled in the fall, plot foliage mass ranged from 2.32 to 15.26 t ha^{-1}, and branchwood mass varied from 4.51 to 24.61 t ha^{-1} (Table 4.25). On plots sampled in the spring, plot foliage mass ranged from 2.39 to 17.37 t ha^{-1}and branchwood mass varied from 9.84 to 31.97 t ha^{-1}. The amount of foliage was significantly related to foliage retention ($p<0.01$ for ß$_{253}$ in equation 4.25) and the amount of branchwood mass was significantly related to the crown sparseness index ($p=0.0166$ for ß$_{264}$ in equation 4.26). Foliage mass increased with basal area, site index, and foliage retention, and was higher for plots sampled in the fall (Table 4.26). However, the positive effect of foliage retention declined to zero at site index of 42 m. Plot branchwood mass increased with site index and decreased with trees per ha, distance from the coast, and plot mean crown sparseness index (Table 4.27). A plot with an average of one year of foliage retention and a crown sparseness index of 10 was expected to have 82.4% and 51.8% less foliage and branchwood mass, respectively, than a plot with an average of four years of retention and a crown sparseness index of 3. The foliage mass model explained 56% of the original variation and had a RMSE of 0.4744, while the woody mass model had an R^2 of 0.71 and a RMSE of 0.2999.

The plot-level foliage ratio ranged from 0.17 to 0.61 on plots sampled in the spring and varied between 0.43 and 0.76 on plots sampled in the fall. Foliage ratio significantly increased with site index, the number of trees per ha and stand age, and was greater for plots sampled in the fall (Table 4.28). Conversely, plot-level foliage ratio decreased with stand basal area and the interaction between foliage retention and site index. A plot with one year of foliage retention was expected to have a foliage ratio that was on average 70.5% lower than a plot with four years of retention. The plot foliage ratio model explained 86% of the original variation and had a RMSE of 0.0672.

Current-year foliage production ranged from 0.95 to 4.38 kg ha^{-1} and was significantly related to the crown sparseness index ($p<0.0005$ for β_{287} in equation 4.28). Foliage production increased with stand relative density, site index, elevation, and percent basal area in Douglas-fir, but decreased with the number of Douglas-fir tree per ha, distance from the coast, and plot mean crown sparseness index (Table 4.29). A plot with a crown sparseness index of 10 was expected to have a current-year foliage production that is 41.5% less than a plot with a crown sparseness index of 3. The model had a R^2 value of 0.99 and a RMSE of 0.0253.

DISCUSSION

The amount, allocation, and vertical distribution of dry mass in a tree crown are partly controlled by crown shape and its effect on light attenuation within the crown. SNC significantly modifies Douglas-fir crown shape (Chapter 3), and has a significant impact on the density of dry mass within the crown. At the individual branch-level, branches on sites with lower retention (higher SNC) have less foliage and lower mass in the 2001 primary branch axis. However, more dry mass is allocated to high order branches, negating any significant relationship between foliage retention and branchwood mass for a given branch diameter and crown position. Also at this level, there is no relationship between SNC and current-year mass production, but current-year shoots had a higher foliage ratio in the upper crown and a lower foliage ratio in the middle and lower portions of the crown. Trees on sites with lower foliage retention had significantly less total crown dry mass, including current-year foliage production. The vertical distribution of foliage on a tree is also modified by SNC as it tends to be a more uniform distribution and less skewed upward with decreasing foliage retention. At the plot-level, SNC reduced total foliage and branchwood mass by as much as 82% and 52%, respectively.

Branch-level

Amount

Similar to several other studies that have developed branch-level equations, variables representing position within the crown were important components of the predictive model (Ek 1979; Kershaw 1995; Baldwin et al. 1997). In addition, incorporating a relative branch height measure significantly improved prediction, which has been observed in other studies as well (Madgwick & Jackson 1974; Brooks 1987; Kershaw & Maguire 1995). In general, allometric relationships are considered to be site independent (Gholz et al. 1979; Waring et al. 1978; Gower et al. 1987), but significant variation in predictive equations have been noted among regions (Whitehead 1978), among stands (Albrektson 1984; Dean & Long 1986), and among individual trees within stands (Dean et al. 1988). This study reaffirms the importance of using site-specific equations, particularly under insect and disease conditions that impact foliage mass directly.

While branches generally tend to reach a maximum size near two-thirds depth into crown on Douglas-fir (Maguire et al. 1994), substantial amounts of foliage are lost in this portion of the crown due to self-shading (Ford 1982; Maillette 1982). Below two-thirds depth into the crown, the shade foliage produced generally has greater annual retention than sun foliage that subsequently becomes shaded (Maillette 1982), resulting in slightly greater foliage densities than might otherwise be expected near the base of the crown (Kershaw & Maguire 1995). Thus, the combination of depth in the crown and relative height above the crown base in an equation can accommodate a decline in foliage mass for a given branch diameter at crown base. These patterns still hold for SNC-infested Douglas-fir, but become modified with increasing disease severity. Regardless of SNC, woody mass continues to accumulate with depth into the live crown.

The lack of a significant relationship between foliage amount and SNC in the upper canopy may be due to changes in allocation and SNC disease biology. Using a physiologically-based model, Kaitaniemi (2000) predicted that trees allocate more resources to the upper canopy and foliage maintenance after defoliation. Thus, branches in the upper crown of severely infested trees may be better able to renew their foliage because of the greater availability of resources when compared to the lower two-thirds of the crown. Furthermore, while SNC symptoms and fungal colonization are usually the worse in the upper two-thirds of the crown (Manter 2001), needles are usually not shed until 50% of their stomata are clogged by the fungal fruiting bodies (Hansen et al. 2000). The rates at which this can happen vary significantly between years due to changes in climatic conditions, minimizing differences between severity classes as only 1 to 2 foliage age classes are generally present in the upper crown.

Allocation

Allocation to current-year growth on branches is mostly dependent on the resources accumulated during the previous year (Haukioja et al. 1985) and the within-crown light environment (Schoettle & Smith 1991). Branches are generally considered autonomous (Sprugel et al. 1991), even with respect to water (Brooks et al. 2003). Thus, branches tend to allocate resources to satisfy their own maintenance costs rather than importing carbon from elsewhere in the tree (Sprugel et al. 1991). Branches on sites with high SNC severity have altered their allocation by investing greater mass in secondary and higher order shoots and less in elongation of the primary branch axis, while production of current-year mass was unaffected.

Ishii et al. (2002) indicated that basal reiteration of epicormic shoots maintained a constant rate of production and occurred over a wide range of axis ages (5-58 years), highlighting the importance of this process for renewing foliage in mature Douglas-fir. While the number of secondary branches appeared to decrease on a branch with increasing SNC (Chapter 3), increased epicormic shoots on these shoots may be increasing their mass. This pattern most likely reflects the improved within-crown light environment caused by defoliation (Beyschlag et al. 1994) and the idea that costs of supporting tissue shared by one leaf must be incorporated into the construction costs of the leaf (Kikuzawa & Ackerly 1999). These improved light conditions may increase mass production further down in the crown than normal (Maguire & Kanaskie 2002). Since shoots on an individual Douglas-fir branch appear to be fairly autonomous with respect to water (Brooks et al. 2003), it may be more cost-effective for the branch to increase production of third- and higher-order shoots rather than increasing the number of secondary shoots.

Although branchwood mass in a branch of a given diameter was not greater on branches on sites with high SNC severity, the foliage ratio on current-year shoots was greater in the upper canopy. Yagi (2000) found that the ratio of foliage to branch mass was greater in shorter current-year shoots than in longer current-year shoots. Needle primordia are formed in the previous season, and their density is controlled by both the previous environmental conditions influencing primordia formation and current season conditions influencing shoot elongation (Oliver & Larson 1996). Thus, for a given number of primordia, greater shoot growth leads to a lower density of needles, which implies that current-year shoots in severely SNC infested trees are most likely shorter than a healthy tree. Yagi (2000) concluded that shorter current-year shoots represent a strategy to maximize efficiency of light interception, while longer current-year shoots facilitate crown-expansion and capture of site resources. Thus, shoots in the upper crown of severely infected trees may be more orientated towards light capture, while shoots in the lower two-thirds of the crown are more oriented towards expansion of the crown.

Tree-level

Amount

Although sapwood area at crown base has been the preferred variable for predicting tree foliage mass and area (Waring et al. 1977; Waring et al. 1982; Marchand 1984; Coyea & Margolis 1992), it is relatively difficult to measure in the field so it is often replaced by surrogates (Dean & Long 1986; Valentine et al. 1994). These surrogates, however, did not perform as well as lateral crown surface area in this study. This result agrees with previous findings that conic surface area performs quite well in predicting sapwood area at crown base in Douglas-fir, with R^2 values as high as 0.95 (Maguire & Hann 1989). Similarly, studies have shown that crown projection area alone can explain more than 97% of the variation in total seedling or sapling dry mass, a large portion of which is foliage and branchwood (Suh & Miles 1988; Norgren et al. 1995).

Both foliage and woody mass in this study showed a significant relationship with the product of basal area and modified live crown ratio (BACR), sapwood area at crown base, relative height in the stand, site index, and foliage retention. Valentine et al. (1994) suggested the proportion of tree basal area at crown base that is sapwood should be related to the percentage of the tree height above breast height covered by the live crown. Thus, sapwood area at breast height (without taper) would be equal to the cross-sectional area of the bole at breast height times a modified live crown ratio (CL/(HT –1.37)). On the other hand, BACR may serve as a surrogate for taper to crown base (Maguire & Bennett 1996) as suggested by the fact that in this study sapwood area at crown base was accounted for in the model. Furthermore, BACR may also serve as an indicator of crown size. Crown base sapwood tends to work well in predicting crown dry mass because of the theory that a unit of foliage requires a corresponding unit of sapwood for support (Shinozaki et al. 1964). Crown base sapwood also tends to work well because sapwood area increases below crown base to breast height, probably because of differences in permeability (Whitehead 1984). Bormann (1990) found that within stands, trees with a thick sapwood consistently had 2 to 3 times more foliage and branchwood mass than paired trees with a thin sapwood but nearly equal diameter. Relative height in the stand represents a tree's social position, which is a surrogate for crown competition and the amount of light received. As trees become taller relative to their neighbors, they are typically less shaded (Kuroiwa 1960; Caldwell 1987; Russell et al. 1989) and presumably, have less contact with other crowns. Both foliage and branchwood mass have been shown to decrease with increased competition (Mäkinen 1996) and reduced light availability (Gilmore & Seymour 1997; Mäkelä & Vanninen 1998). Foliage and branchwood mass have also been shown to increase with site quality (Satoo & Madgwick 1982; Albrektson 1988; Kurz 1989). However, Satoo (1971) found that foliage mass did not show any systematic trend with site index for Norway spruce (*Picea abies*) planted in Japan. Although not accounted for in this study, Douglas-fir crown dry mass amounts are also strongly influenced by genetics (St. Clair 1993; 1994)

Mass amounts are sensitive to cultural treatments such as fertilization and thinning. Brix (1981) found that thinning and heavy fertilization separately increased needle mass per tree after 7 years by 90% and when combined, by 271%. Needle production increased 2 to 3 years after fertilization and resulted from an increase in needle size, needle number per shoot, and number of shoots produced, while thinning increased needle dry weight and crown volume (Brix 1981). Madgwick (1970) found that in red pine (*Pinus resinosa*) the increase in total biomass caused by fertilization was primarily due to an increase in needle longevity, but Brix (1981) showed that with nitrogen fertilization of Douglas-fir, needle longevity varied greatly within the tree crowns, making comparisons difficult. Conversely, Balster and Marshall (2000) found a decline in Douglas-fir needle longevity with fertilization. The long-term impacts of premature needle lost from foliar diseases have rarely been reported. The strong correlation between SNC indices and tree foliage mass reflect the premature needle loss, shorter crown lengths, and reduced number of primary and secondary branches, as well as the lack of compensatory new foliage production caused by the disease.

Foliage retention indicated the average number of years that needles remain on a sample branch. However, its correlation with the total amount of foliage has been questioned by several authors (Innes 1993; Maguire & Kanaskie 2002; Johnson 2002). This study indicated that foliage retention, as well as crown color and crown density do provide a reasonable estimate of foliage mass after accounting for other variables; however, $CLSA_{CB}$

provided a better indication of foliage mass, perhaps due to its ability to integrate numerous complex responses to defoliation (Maguire & Kanaskie 2002). Thus, $CLSA_{CB}$ may represent an alternative to the ratio of needle mass to branch basal area (Horntvedt 1993); an alternative that is easier to apply, particularly in the field. Both should control the probable long-term drift in visual assessments that Horntvedt (1993) was concerned about.

Leaf mass to sapwood area ratios can vary significantly within a species, particularly across gradients in site moisture regime (Waring et al. 1982; White et al. 1998), vapor pressure deficit and maximum summer temperatures (Mencuccini and Grace 1995; Mencuccini and Bonosit 2001), site quality (Dean and Long 1986), fertilization and thinning (Brix and Mitchell 1983), stand density (Keane and Weetman 1987; Long and Smith 1988), canopy position (O'Hara and Valappil 1995), and absolute tree height (McDowell et al. 2002). Thus, leaf mass to sapwood area ratios are sensitive to growth rates (Whitehead et al. 1984; Pothier et al. 1989) as smaller leaf area to sapwood area ratios are expected on slower growing sites due to the lower saturated sapwood permeability (Pothier et al. 1989). Exceptions to this general rule, however, have been found as Dean and Long (1986) found suppressed trees to have more leaf area per unit sapwood area; Whitehead et al. (1984) found no difference in leaf area to sapwood area ratios between control and fertilized Sitka spruce (*Picea sitchensis*); and Garber (2002) found higher leaf area to sapwood ratios on a more xeric site in the Oregon Cascades. Similarly, this study found a higher leaf mass to sapwood area ratio on trees severely infested by SNC, which may be due to the lag time between foliage loss and subsequent re-adjustment of sapwood area. Although some pruning experiments indicate that sapwood adjustment is rapid (Margolis et al. 1988), other experiments suggest a lag time of at least four years (Långstrom and Hellqvist 1991). Thus, re-adjustment of sapwood area is influenced by the rate of foliage loss and the age distribution of both the lost and retained foliage (Maguire & Kanaskie 2002). In the case of SNC, foliage loss proceeds gradually over many years and older, less physiologically active foliage is lost, which may slow sapwood area re-adjustment. Thus, SNC may lead to a temporarily higher leaf mass to sapwood area ratios as indicated by this study.

Crown bulk density is the amount of foliage and branchwood mass per unit of crown volume. Crown bulk density has been shown to be sensitive to tree age (Kuuluvainen and Sprugel 1996), genetics (St. Clair 1994), tree social position (Mäkelä and Vanninen 1998), stand density (Larocque and Marshall 1994), and elevation (Kuuluvainen and Sprugel 1996). The most important factors in this study appeared to be crown size, stand density, aspect, elevation and SNC severity. Branchwood bulk density, in particular, was sensitive to environmental factors such as elevation and aspect as it decreased as sites became more northerly and higher in elevation. This is most likely a result of the differences in site conditions created by these two factors. As hypothesized, SNC resulted in reduced foliage and branchwood crown bulk densities. Furthermore, the crown sparseness index proved to a better predictor of crown bulk density than foliage retention, which supports Maguire and

Kanaskie's (2002) assertion that the crown sparseness index has the potential to be an indicator of crown bulk density.

Allocation

Allocation of carbon to different tree compartments is largely influenced by stand density and site index. Burkes et al. (2003) found that partitioning to stem growth increased relative to foliage or fine roots as stand density increased. Similarly, Kellomäki (1986) concluded that the total amount of branch and stem wood increases with increasing stand density but eventually leveled off at greater stand densities, depending on crown shape. With increasing site index, Kurz (1989) found a decreasing proportion of total production was allocated to belowground stand components, while coarse roots and branches showed no significant change in allocation across a range in site index. Increasing site index tends to increase allocation to foliage (Blake et al. 1991). In Douglas-fir from the Oregon Coast Range, foliar density within the crown increased with site index, in turn causing an increase in the foliage ratio. Stand age, on the other hand, causes the foliage ratio to decrease as branchwood continues to increase (Satoo & Madgwick 1982).

Yagi (2000) suggested that allocation to current-year dry mass is primarily controlled by light. At the tree-level, light availability is primarily determined by stand density and tree social position. Greater canopy coverage results in shallower penetration of direct light into the stand (Sampson & Smith 1993). Because tighter spacing can accelerate differentiation and magnify the influence of canopy stratification (Roberts et al. 1993), taller trees in a stand exert a greater influence on shading with increasing stand density (Ford & Diggle 1981; Cannell & Dewar 1994). One result of this process is that current-year production of dry mass is largely dependent on a tree's relative height in a stand and vigor, particularly at higher densities. The decrease of current-year production with SNC severity, however, reflects the impacts of this disease on Douglas-fir's ability to compensate for the premature loss of its foliage. Renewing foliage after defoliation is a survival strategy that has apparently been selected for, since this response confers priority on the photosynthetic factory (Kaitaniemi 2000). This finding differs from the one reported by Piene and Eveleigh (1996) in that they observed young balsam fir (*Abies balsamea*) remained green and rapidly recovered from defoliation caused by the spruce budworm due to their prolific epicormic shoot production and the development of new foliage at the expense of volume growth. This latter effect explains why there is generally a lag of 2 to 6 years after defoliation before there are significant increases in stem volume (Piene 1989). Prolific shoot development has also been credited for rapid recovery rates in Douglas-fir after defoliation by insects (Wickman 1978), but this study indicates that SNC has reduced the species' ability to compensate for premature foliage loss.

The allocation of dry mass between interwhorl and whorl branches is an important process for species such as Douglas-fir (Ishii & Ford 2001), particularly as tree age increases. Jensen and Long (1983) found that these short-lived interwhorl branches provided much of the photosynthetic capacity for the tree as these branches can support up to 50% of the foliage mass on only 10% of the branch mass. An important factor that influences allocation to interwhorl and whorl branches is tree size and social position within a stand. Gilmore and Seymour (1997) found that the average percentage of oven-dry foliage mass in interwhorl branches was 33% for open-grown trees, 33% for codominant, 16% for intermediates, and 13% for suppressed ones. Thus, the development of interwhorl branches in Douglas-fir is not necessarily a response to exogenous stimuli such as light and nutrient availability, but a natural part of tree growth and development (Ishii & Ford 2001). The reduction of foliage and woody mass in interwhorl branches with increasing SNC severity, however, reflects a shift in allocation patterns. These results support the finding that increased SNC reduces the number of interwhorl branches on a tree (Chapter 3). Reduction of woody mass in Douglas-fir tree crowns with increasing SNC is due to the reduction of mass in both interwhorl and whorl branches.

Vertical foliage distribution

The vertical distribution of foliage mass within a crown varies with both tree social position, stand structure, and site factors such as site quality (Xu & Harrington 1998). Suppressed trees, particularly shade-intolerant ones, tend to shift the mode of foliage mass upwards (Kellomaki et al. 1980). On the other hand, Mäkelä and Vanninen (2001) indicated that the relative vertical distribution of foliage in shade-intolerant species peaked at approximately the midpoint of the live crown regardless of age or social position, similar to the findings of Stephens (1969) and Simeon et al. (1980). Trees, however, generally react to competition for light by allocating new foliage higher up and forming sparser crowns (Mäkelä & Vanninen 1998). Variation in vertical foliage distribution due to stand factors is generally controlled by differences in stand top height, canopy depth, and stand density (Maguire & Bennett 1996) as well as by species composition (Garber 2002). Generally an upward shift of crown foliage occurs with increasing density (Maguire & Bennett 1996; Xu and Harrington 1998). Vertical distribution of foliage also tends to move upward with stand age (Hashimoto 1991), commensurate with changes in stand height and canopy depth. Generally, foliage mass is skewed upward (Xu & Harrington 1998; Maguire & Bennett 1996), due to light availability (Brix 1981) and self-shading (Xu & Harrington 1998). This is also due to constraints of crown form in conifers.

While Gillespie et al. (1994) argued that the vertical distribution of foliage mass remained unchanged after thinning and fertilization treatments, Brix (1981) reported that foliage vertical distribution responded to thinning and fertilization. Fertilization influences the distribution of foliage in the top half of the crown (Brix 1981; Kershaw & Maguire 1995), presumably resulting in a more skewed distribution and a longer upwards tail. Vose (1988) concluded that fertilization in loblolly pine (*Pinus taeda*) increased foliage in the lower crown positions, causing a shift of the foliage modes closer to the crown base (Wang et al. 1990). In contrast, thinning has been shown to lead to a more uniform and less skewed vertical distribution of foliage mass (Gary 1978; Medhurst & Beadle 2001). Despite the tremendous variability in the vertical distribution of foliage, Ishii et al. (2000) indicated that stressed, mature trees have a significantly different foliage distribution than mature, unstressed trees. Similar to thinning treatments, SNC led to a less skewed and more uniform vertical distribution of foliage mass, most likely a result of defoliation modifying the within-crown light environment and reducing self-shading. Reduced foliage retention in the upper and middle portions of the crown may promote longer retention in the bottom of the crown as a result of more foliage being illuminated above the light compensation point (Maguire & Kanaskie 2002). However, increased uniformity also seems to result from a dramatic reduction in the height of the mode in the distribution (Figure 4.4).

Plot-level

Amount

Crown mass in this study ranged from 6.8 to 49.3 t ha^{-1}, with percent woody mass varying from 56.3 to 85.7%. In other studies of Douglas-fir stands of a similar age and density, crown mass ranged from 3.4 to 51.4 t ha^{-1} (Heilman 1961; Turner & Long 1975; Webber 1977; 1982; Binkley 1983; Binkley et al. 1984; Espinosa-Bancalari & Perry 1987; Ranger et al. 1995; Mitchell et al. 1996; Bartelink 1996; Ponette et al. 2001). For the same studies, the foliage ratios ranged from 0.32 to 1.32 (Figure 4.5). Stand dry mass tends to increase with age (Turner & Long 1975), site fertility (Binkley 1983), and higher early growth rates (Espinosa-Bancalari & Perry 1987), but decreases with greater stocking levels (Madgwick et al. 1970). On the other hand, there is a “cross-over” effect with initial spacing and age as wider spacings have a lower initial dry mass but tend to attain a greater dry mass with increasing age. Foliage ratios, however, decline with increasing age and basal area due to accumulation of branchwood, while foliage mass remains constant or declines slightly (Gower et al. 1996).

In the Pacific Northwest, annual foliage production of Douglas-fir has been estimated at about 2 to 2.2 t ha^{-1} (Dice 1970; Turner and Long 1975), while Kay (1978) estimated it to be about 2.6 t ha^{-1} for Douglas-fir plantations in New Zealand. Similarly, the mean annual foliage production for Douglas-fir in the Oregon Coast Range was 2.2 t ha^{-1}, but several plots showed production values above 3.0 t ha^{-1}, which may be related to the younger age and better site quality of plots in this study when compared to other studies. In addition to crown condition, foliage production was influenced by a variety of other stand and site factors, indicating that annual foliage production is a highly complex response to growing conditions, even within a similar geographic region.

Stand dry mass amount and allocation has also been shown to be sensitive to silvicultural treatments (Mitchell et al. 1996), climate change (DeLucia et al. 2000), and disturbance (Campbell & Grime 1992). Relatively little work has investigated the impacts of foliar disease as a disturbance. With respect to defoliation caused by insects, Piene et al. (2003) reported that six years into a spruce budworm outbreak, foliage dry mass in the defoliated plots reached its minimum levels, representing a reduction of 83.3 and 84.3% for spaced and unspaced stand, respectively, when compared with a protected stand. These losses are similar to those reported in this study. After three years of recovery, however, reductions in foliage mass were only 37.5% and 68.5% for the spaced and unspaced plots (Piene et al. 2003), respectively, which are even closer to the values found in this study. The number of years that defoliation occurred is an important factor influencing dry mass recovery because a longer period of severe defoliation reduces stored reserve energy (Webb 1980). In Piene et al.'s (2003) study, trees had been defoliated for 6 years, with defoliation concentrated on current and young age classes needles. In contrast, plots with severe SNC in this study have experienced premature loss of the old foliage for nearly 8 years, and seems to be altering their ability to recover.

CONCLUSION

Defoliation caused by plant foliar diseases such as SNC can significantly alter the production, allocation, and vertical distribution of foliage and branchwood mass. SNC in the Oregon Coast Range has led to greatly reduced amounts of foliage and branchwood dry mass in both individual-trees and entire stands. In addition, severely diseased trees show a decreased production of current-year foliage and a more uniform vertical distribution of the foliage mass. These changes in total mass are accompanied by an alteration of allocation patterns. At the branch-level, SNC has led to a greater allocation to higher order branches, but a decreased allocation to the elongation of the primary branch axis. Current-year shoots show a higher foliage density in the upper crown, but a lower density in the middle and lower portions of the crown. Although Douglas-fir has been shown to recover rapidly after severe defoliation, SNC in the Oregon Coast Range may limit this recovery due to the duration of the current epidemic. The limitation to recovery has important implications for stand structure, productivity, and susceptibility to further disturbance.

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Table 4.1. Attributes of the 22 plots sampled in 2002 for crown mass determination.

Attribute	**Mean**	**SD**	**Min**	**Max**
Douglas-fir basal area (m^2/ha)	26.54	8.62	9.97	45.44
Douglas-fir trees per ha	634	275	260	1223
Douglas-fir quadratic mean diameter (cm)	24.43	6.85	11.41	36.45
Douglas-fir relative density [Curtis (1982); (m^2 ha/$\sqrt{}$cm)]	5.35	1.34	2.95	7.91
Douglas-fir stand density index (Reineke (1933), trees/ha at mean DBH of 25.4 cm)	529.54	139.23	270.04	808.99
Basal area in other conifers (m^2/ha)	0.48	0.77	0	2.21
% basal area in other conifer	0.60	0.79	0	2.85
Basal area in hardwoods (m^2/ha)	0.59	0.77	0	2.86
% basal area in hardwoods	1.8	2.3	0	9.3
Total basal area (m^2/ha)	33.53	13.12	10.44	69.65
Average breast-height age in 2002 (yr)	21.28	4.87	11.00	27.80
Average foliage retention in 2002 (yr)	2.39	0.71	1.20	4.30
Site index (Bruce (1981); height at 50 yr, in m)	39.45	2.57	34.80	43.90

Table 4.2. Attributes of the 79 Douglas-fir trees sampled in 2002 for crown mass determination.

Attribute	**Mean**	**SD**	**Min**	**Max**
DBH (cm)	25.3	5.2	12.5	43.2
Height (m)	19.41	5.33	5.88	33.6
Height to live crown (m)	7.21	3.77	0.1	22.5
5-yr height increment (m)	0.70	0.23	0.31	1.18
Crown length (m)	12.20	3.38	3.40	23.30
Foliage mass (kg)	13.05	8.46	1.55	52.12
Branchwood mass (kg)	31.81	20.96	5.00	114.02

Table 4.3. Attributes of the 700 sample branches used for crown mass determination.

Attribute	Mean	SD	Min	Max
Diameter (mm)	17.9	9.6	1.3	56.0
Length (m)	1.11	1.21	0.09	6.79
Depth in crown (m)	6.14	3.64	0.17	16.4
Foliage mass (g)	114.04	139.69	0.01	898.49
Woody mass (g)	283.29	349.66	0.06	36841.44

Table 4.4. Various published model forms for estimating branch-level foliage and woody mass.

Model	Model form	Source
1	$\beta_0 BD^{\beta 1} DINC^{\beta 2}$	Monserud and Marshall 1999
2	$\beta_0 + \beta_1 \ln(BD) + \beta_2 DINC$	Kershaw and Maguire 1995
3	$\beta_0 + \beta_1 \ln(BD) + \beta_2 \ln(DINC) + \beta_3 \ln(RHACB)$	Kershaw and Maguire 1995
4	$\beta_0 BD^2 + \beta_1 BD^2 * RHT * (1-RHT)$	Bartelink 1996
5	$\beta_0 BD^{\beta 1} RDINC^{\beta 3-1} * \exp(-(\beta_2 RDINC)^{\beta 3}$	Maguire and Bennett 1996

Table 4.5. Various published model forms for estimating tree-level foliage and woody mass.

Model	Model form	Source
6	$\beta_0 CL^{\beta 1} \exp(\beta_2 DBHHT)$	Maguire and Bennett 1996
7	$\beta_0 BACR^{\beta 1}$	Kenefic and Seymour 1999
8	$\beta_0 SBHCR^{\beta 1}$	Kenefic and Seymour 1999
9	$\beta_0 + \beta_1 \ln(DBH) - \beta_2 \ln(HT)$	Bartelink 1996
10	$\beta_0 DBH^{\beta 1}$	Garber 2002
11	$\beta_0 + \beta_1 \ln(CSA)$	

Table 4.6. Model forms, weighting factors, and fit statistics for linear and nonlinear branch-level models screened for prediction of total foliage mass. Model numbers correspond to Table 4.4. The statistics are a result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
1	BD^{-3}	0.49	0.92	53.2	Monserud and Marshall 1999
2	-	0.73	0.94	37.6	Kershaw and Maguire 1995
3	-	0.73	0.86	34.5	Kershaw and Maguire 1995
4	-	0.60	1.22	49.1	Bartelink 1996
5	BD^{-3}	0.61	0.71	41.3	Maguire and Bennett 1996

Table 4.7. Model forms, weighting factors, and fit statistics for linear and nonlinear branch-level models screened for prediction of total woody mass. Model numbers correspond to Table 4.4. The statistics are a result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
1	BD^{-3}	0.80	1.62	94.1	Monserud and Marshall 1999
2	-	0.89	0.68	59.2	Kershaw and Maguire 1995
3	-	0.89	0.68	57.6	Kershaw and Maguire 1995
4	-	0.79	1.32	115.9	Bartelink 1996
5	BD^{-3}	0.81	1.64	94.2	Maguire and Bennett 1996

Table 4.8. Parameter estimates and standard errors as well as model fit statistics for branch-level foliage (FDM) and woody (WDM) mass.

Model	Parameter	Parameter estimates	SE	P-values	R_g^2	RMSE
FDM					0.5630	0.3809
	β_{50}	0.0961	0.0190	<0.0001		
	β_{51}	2.0600	0.0563	<0.0001		
	β_{52}	0.8452	0.1204	<0.0001		
	β_{53}	0.5691	0.0956	<0.0001		
	β_{54}	0.4414	0.1164	<0.0001		
	Φ	0.2356	-	-		
WDM					0.8137	0.8229
	β_{50}	0.1529	0.0286	<0.0001		
	β_{51}	2.1987	0.0653	<0.0001		
	β_{52}	0.1840	0.0745	0.0080		
	β_{53}	0.4967	0.0893	<0.0001		
	β_{54}	-	-	-		
	Φ	0.0207	-	-		

Table 4.9. Parameter estimates, standard errors, and p-values for branch-level foliage ratios (equation 4.6).

Parameter	Estimate	SE	P-value
β_{60}	7.3484	3.8957	0.0597
β_{61}	-0.5364	0.0479	<0.0001
β_{62}	0.2717	0.0812	0.0009
β_{63}	0.5371	0.1305	<0.0001
β_{64}	-0.4460	0.1581	0.0049
β_{65}	0.2374	0.1033	0.045
Φ	0.2099		

Table 4.10. Model fit and parameter estimates, standard errors, p-values for branch-level higher order branch mass (equation 4.7).

Parameter	Parameter estimates	SE	P-values	R^2	RMSE
				0.7828	0.6469
β_{70}	16.1552	4.8639	0.0019		
β_{71}	0.1389	0.0057	<0.0001		
β_{72}	0.0191	0.0019	<0.0001		
β_{73}	-0.3738	0.1191	0.0020		
β_{74}	-5.5269	1.9763	0.0057		
β_{75}	0.1300	0.0476	0.0069		
Φ	0.3021	-	-		

Table 4.11. Model fit and parameter estimates, standard errors, p-values for branch-level mass in 2001 primary branch axis (equation 4.8).

Parameter	Parameter estimates	SE	P-values	R^2	RMSE
				0.5575	1.3029
β_{80}	-4.2025	0.8380	<0.0001		
β_{81}	-0.1897	0.0575	0.0011		
β_{82}	4.2097	0.7693	<0.0001		
β_{83}	0.1134	0.0088	<0.0001		
β_{84}	-1.0504	0.5182	0.0434		
β_{85}	0.3083	0.1333	0.0213		
Φ	0.2024	-	-		

Table 4.12. Model forms, weighting factors, and fit statistics for linear and nonlinear tree-level models screened for prediction of total foliage mass. Model numbers correspond to Table 4.5. Fit statistics are a result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
6	$CL^{-1.0}$	0.43	1.71	6.03	Maguire and Bennett 1996
7	$BACR^{-0.5}$	0.38	13.13	5.59	Kenefic and Seymour 1999
8	$SBHCR^{-0.5}$	0.12	1.94	7.43	Kenefic and Seymour 1999
9	-	0.25	0.60	6.21	Bartelink 1996
10	$DBH^{-1.0}$	0.24	1.40	6.98	Garber 2002
11	-	0.53	0.48	5.07	

Table 4.13. Model forms, weighting factors, and fit statistics for linear and nonlinear tree-level models screened for prediction of total woody mass. Model numbers correspond to Table 4.5. Fit statistics are a result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
6	-	0.43	14.99	14.99	Maguire and Bennett 1996
7	$BACR^{-1.0}$	0.53	69.67	12.68	Kenefic and Seymour 1999
8	-	0.10	19.74	19.74	Kenefic and Seymour 1999
9	-	0.44	0.45	12.26	Bartelink 1996
10	$DBH^{-1.0}$	0.54	2.73	13.58	Garber 2002
11	-	0.70	0.33	8.93	

Table 4.14. Parameter estimates and standard errors for the tree-level foliage mass model (equation 4.14).

Parameter	Estimate	SE	p-value
$ß_{140}$	-8.6264	2.8478	0.0034
$ß_{141}$	32.0459	6.5213	<0.0001
$ß_{142}$	0.0032	0.0009	0.0008
$ß_{143}$	0.9893	0.3670	0.0088
$ß_{144}$	0.2046	0.0704	0.0049
$ß_{145}$	2.6172	1.1676	0.0281
$ß_{146}$	-0.0596	0.0284	0.0394
$ß_{147}$	-0.0492	0.0209	0.0212

Table 4.15. Parameter estimates and standard error for the tree-level branchwood mass model (equation 4.14)

Parameter	Estimate	SE	p-value
$ß_{140}$	-4.0107i	2.6182	0.1299
$ß_{141}$	23.2898	2.9189	<0.0001
$ß_{142}$	0.0007	0.0003	0.0206
$ß_{143}$	0.8680	0.3387	0.0125
$ß_{144}$	0.1333	0.0639	0.0405
$ß_{145}$	2.2399	1.0642	0.0388
$ß_{146}$	-0.0537	0.0258	0.0412
$ß_{147}$	-	-	-

Table 4.16. Akaike information criterion (AIC) and Furnival's index (FI) values for the tree-level foliage mass model with alternative SNC indices (equation 4.14).

SNC variable	AIC	FI
foliage retention	46.2216	4.4669
crown color	55.1127	5.1091
crown density	51.1607	4.8362
CLSA_{CB}	42.3302	4.3269
CLSA_{BH}	55.9193	5.2258

Table 4.17. Akaike information criterion (AIC) and Furnival's index (FI) values for the tree-level branchwood mass model with alternative SNC indices (equation 4.14).

SNC variable	AIC	FI
foliage retention	46.8092	4.5526
crown color	44.8447	4.6549
crown density	48.5430	4.7169
CLSA$_{CB}$	28.0615	3.5491
CLSA$_{BH}$	44.8473	4.4808

Table 4.18. Parameter estimates, standard errors, and p-values for the tree-level foliage to woody mass ratio model (equation 4.15).

Parameter	Estimate	SE	P-value
ß$_{150}$	-1.8791	0.6932	0.0083
ß$_{151}$	-0.0161	0.0029	<0.0001
ß$_{152}$	0.0656	0.0178	0.0004
ß$_{153}$	0.6560	0.2914	0.0273
ß$_{154}$	-0.0158	0.0072	0.0299

Table 4.19. Parameter estimates, standard errors, and p-values for the tree-level foliage mass to sapwood area ratio model (equation 4.16).

Parameter	Estimate	SE	P-value
ß$_{160}$	1.4577	0.7163	0.0456
ß$_{161}$	0.1012	0.0197	<0.0001
ß$_{162}$	-0.1499	0.0501	0.0038
ß$_{163}$	-0.0453	0.0164	0.0075
ß$_{164}$	0.0820	0.0195	<0.0001
ß$_{165}$	-0.0163	0.0041	0.0002
ß$_{166}$	0.0549	0.0108	<0.0001
ß$_{167}$	-0.2868	0.0865	0.0014

Table 4.20. Parameter estimates, standard errors, and p-values for tree-level foliage crown bulk density model (equation 4.17).

Parameter	**Estimate**	**SE**	**P-value**
β_{170}	-0.8794	0.8944	0.3288
β_{171}	0.4552	0.1052	<0.0001
β_{172}	-0.0981	0.0217	<0.0001
β_{173}	0.0508	0.0169	0.0037
β_{174}	1.1019	0.3091	0.0006
β_{175}	-0.0419	0.0111	0.0003

Table 4.21. Parameter estimates, standard errors, and p-values for branchwood crown bulk density model (equation 4.18).

Parameter	**Estimate**	**SE**	**P-value**
β_{180}	6.7584	0.3659	<0.0001
β_{181}	0.0968	0.0282	0.0010
β_{182}	-0.0034	0.0012	0.0067
β_{183}	-0.0992	0.0185	<0.0001
β_{184}	0.0972	0.0185	<0.0001
β_{185}	-0.3029	0.0519	<0.0001
β_{186}	-0.2847	0.0522	<0.0001
β_{187}	-0.0034	0.0010	0.0015
β_{188}	-0.0519	0.0083	<0.0001

Table 4.22. Parameter estimates, standard errors, and p-values for current-year foliage and branchwood mass models (equations 4.19 and 4.20) fitted using seemingly unrelated regression.

Model	**Parameter**	**Estimate**	**SE**	**P-value**	**R^2**	**RMSE**
CDFM (4.19)					0.7629	0.2812
	β_{190}	-4.5527	2.5510	0.0838		
	β_{191}	0.0045	0.0009	<0.0001		
	β_{192}	0.1428	0.0654	0.0366		
	β_{193}	0.0054	0.0019	0.0068		
	β_{194}	2.0549	1.0125	0.0500		
	β_{195}	-0.0552	0.0123	<0.0001		
	β_{196}	-0.0534	0.0249	0.0398		
CDWM (4.20)					0.7846	0.1012
	β_{200}	0.5019	0.0995	<0.0001		
	β_{201}	0.0262	0.0045	<0.0001		
	β_{202}	-0.1249	0.0257	<0.0001		
	β_{203}	0.0253	0.0085	0.0051		
System					0.7629	0.9983

Table 4.23. Model fit statistics, parameter estimates, standard errors, and p-values for foliage and branchwood mass in whorl and interwhorl branches models (equations 4.21, 4.22, 4.23,4.24) fitted using seemingly unrelated regression.

Model	Parameter	Estimate	SE	P-value	R^2	RMSE
WFDM (4.21)					0.6962	0.3942
	β_{210}	-1.4393	0.6301	0.0253		
	β_{211}	0.1663	0.0192	<0.0001		
	β_{212}	-0.1567	0.0408	0.0003		
	β_{213}	0.0563	0.0134	<0.0001		
	β_{214}	-0.0074	0.0029	0.0129		
	β_{215}	-0.0585	0.0127	<0.0001		
IWDM (4.22)					0.6486	0.5119
	β_{220}	-2.0470	0.8398	0.0172		
	β_{221}	0.1339	0.0249	<0.0001		
	β_{222}	-0.2343	0.0546	<0.0001		
	β_{223}	0.0613	0.0180	0.0011		
	β_{224}	-0.0076	0.0039	0.0500		
	β_{225}	-0.0745	0.0165	<0.0001		
WWDM (4.23)					0.3602	0.7091
	β_{230}	0.6368	0.2519	0.0136		
	β_{231}	0.0285	0.0071	0.0001		
	β_{232}	0.1513	0.0193	<0.0001		
	β_{233}	-0.1414	0.0499	0.0060		
	β_{234}	-0.0392	0.0116	0.0011		
IWDM (4.24)					0.4861	0.5656
	β_{240}	-0.2915	0.3961	0.4641		
	β_{241}	0.0394	0.0113	0.0009		
	β_{242}	0.1082	0.0304	0.0007		
	β_{243}	-0.1645	0.0799	0.0430		
	β_{244}	-0.0594	0.0181	0.0016		
System					0.5745	0.8544

Table 4.24. Model fit statistics, parameter estimates, standard errors, and p-values for models predicting *a*- and *b*-parameters from fitting the beta distribution to the vertical foliage distribution using seemingly unrelated regression.

Model	Parameter	Estimated value	SE	P-value	R^2	RMSE
a (4.31)					0.4024	0.5212
	ß$_{311}$	-16.3798	3.7925	<0.0001		
	ß$_{312}$	-0.05547	0.0132	<0.0001		
	ß$_{313}$	2.2084	0.5219	<0.0001		
	ß$_{314}$	0.4682	0.0947	<0.0001		
	ß$_{315}$	6.9482	1.5571	<0.0001		
	ß$_{316}$	-0.1685	0.0381	<0.0001		
b (4.32)					0.2031	0.5608
	ß$_{321}$	0.8292	0.3596	0.0238		
	ß$_{322}$	0.0632	0.0239	0.0098		
	ß$_{323}$	-	-	-		
	ß$_{324}$	0.0853	0.0194	<0.0001		
System					0.4462	0.9905

Table 4.25. Total crown mass(t ha^{-1}) in the various components of the plots by season of sampling.

Plot	Age	No. of trees (# ha^{-1})	Foliage retention (years)	Foliage	Woody	Total	Season
Jensen	11	1025	4.3	5.93	7.64	13.57	Fall
Juno Hill	16	4409	1.2	2.32	4.51	6.82	Fall
Smith Creek	15	1791	2.4	3.90	8.01	11.91	Fall
4	16	605	2.1	14.66	24.61	39.27	Fall
5	22	408	3.0	13.31	24.74	38.05	Spring
5	22	408	3.0	15.26	25.69	40.96	Fall
6	25	383	2.1	6.46	16.46	22.91	Fall
7	21	679	3.9	6.55	10.77	17.33	Spring
7	21	679	3.9	7.49	15.82	23.30	Fall
16	16	1173	1.9	7.80	18.18	25.98	Fall
20	27	902	2.0	6.65	14.41	21.05	Fall
36	22	642	2.4	10.52	24.26	34.78	Spring
41	21	580	2.7	4.36	10.35	14.71	Spring
41	21	580	2.7	7.18	15.00	22.18	Fall
55	24	618	2.4	9.72	18.83	28.55	Spring
57	22	543	2.1	2.95	9.84	12.80	Spring
58	14	618	2.9	16.60	23.84	40.44	Fall
63	25	543	1.9	5.50	23.21	28.71	Fall
77	19	1309	3.0	17.37	31.97	49.34	Spring
81	24	556	2.4	2.39	14.17	16.57	Spring
83	28	1013	1.7	4.44	16.19	20.63	Spring
85	28	259	2.0	5.97	18.89	24.86	Fall
85	28	259	2.0	3.92	18.00	21.92	Spring
105	25	815	2.0	8.81	17.53	26.34	Spring
124	24	445	2.5	3.46	20.67	24.13	Spring
139	27	1383	1.7	9.88	16.44	26.32	Spring

Table 4.26. Parameter estimates, standard errors, and p-values for plot-level foliage mass model (equation 4.25).

Parameter	Estimate	SE	P-value
β_{250}	-20.2923	4.4878	0.0003
β_{251}	0.4427	0.2267	0.0437
β_{252}	0.6012	0.1005	<0.0001
β_{253}	9.3075	1.8288	<0.0001
β_{254}	-0.2203	0.0434	<0.0001
β_{255}	0.5955	0.1592	0.0016

Table 4.27. Parameter estimates, standard errors, and p-values for plot-level woody mass model (equation 4.26).

Parameter	Estimate	SE	P-value
ß$_{260}$	6.9061	1.6219	0.0005
ß$_{261}$	-0.4891	0.1217	0.0008
ß$_{262}$	0.1916	0.0438	0.0004
ß$_{263}$	-0.0993	0.0241	0.0006
ß$_{264}$	-0.1042	0.0394	0.0166

Table 4.28. Parameter estimates, standard errors, and p-values for plot-level foliage ratio model (equation 4.27).

Parameter	Estimate	SE	P-value
ß$_{270}$	-6.7995	1.4516	0.0002
ß$_{271}$	0.0279	0.0095	0.0093
ß$_{272}$	0.0003	0.0001	<0.0001
ß$_{273}$	-0.0106	0.0028	0.0018
ß$_{274}$	0.1578	0.0323	0.0002
ß$_{275}$	2.3212	0.5407	0.0006
ß$_{276}$	-0.0537	0.0128	0.0007
ß$_{277}$	0.2053	0.0526	0.0013

Table 4.29. Parameter estimates, standard errors, and p-values for plot-level current-year foliage mass production (equation 4.28).

Parameter	Estimate	SE	P-value
ß$_{280}$	-7.0921	0.3303	0.0002
ß$_{281}$	0.1489	0.0071	0.0002
ß$_{282}$	0.1483	0.0093	0.0005
ß$_{283}$	-0.2887	0.0229	0.0011
ß$_{284}$	0.2329	0.0209	0.0016
ß$_{285}$	3.4032	0.1511	0.0002
ß$_{286}$	-0.1199	0.0057	0.0002
ß$_{287}$	-0.0765	0.0046	0.0005

Table 4.30. Summary of the impact of SNC on dry mass production, allocation, and vertical distribution at the branch-, tree-, and stand-levels. A blank space indicates that the variable was not tested at that level. A plus sign indicates a positive effect, a negative sign indicates a negative effect, and a zero is represents a non-significant relationship.

	Impact of increased SNC		
Variable	**Branch-level**	**Tree-level**	**Stand-level**
Foliage mass	-	-	-
Branchwood mass	0	-	-
Foliage ratio	+	+	+
Higher order shoot mass	+		
2001 primary branch axis	-		
Current-year foliage	0	-	-
Current-year branchwood	0	0	
Foliage dry mass per unit sapwood area		+	
Foliage bulk density		-	
Branchwood bulk density		-	
Foliage in whorl branches		-	
Foliage in interwhorl branches		-	
Branchwood in whorl branches		-	
Branchwood in interwhorl branches		-	
Vertical foliage distribution		shifted downwards and more uniform	

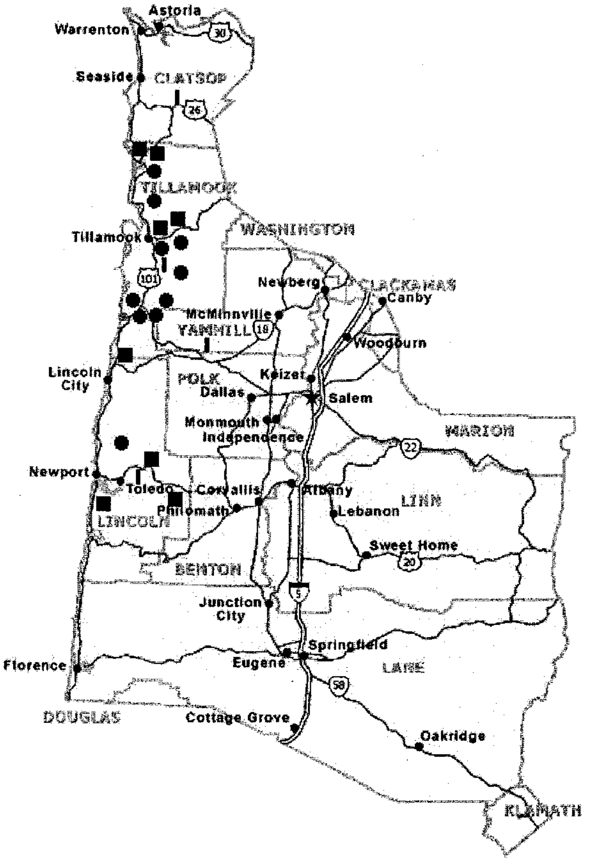

Figure 4.1. Location of the 22 permanent monitoring plots used in this study. Plots marked with a circle were sampled in the spring, plots marked with a square were sampled in the fall, and plots marked with the vertical lines were sampled in both the fall and spring.

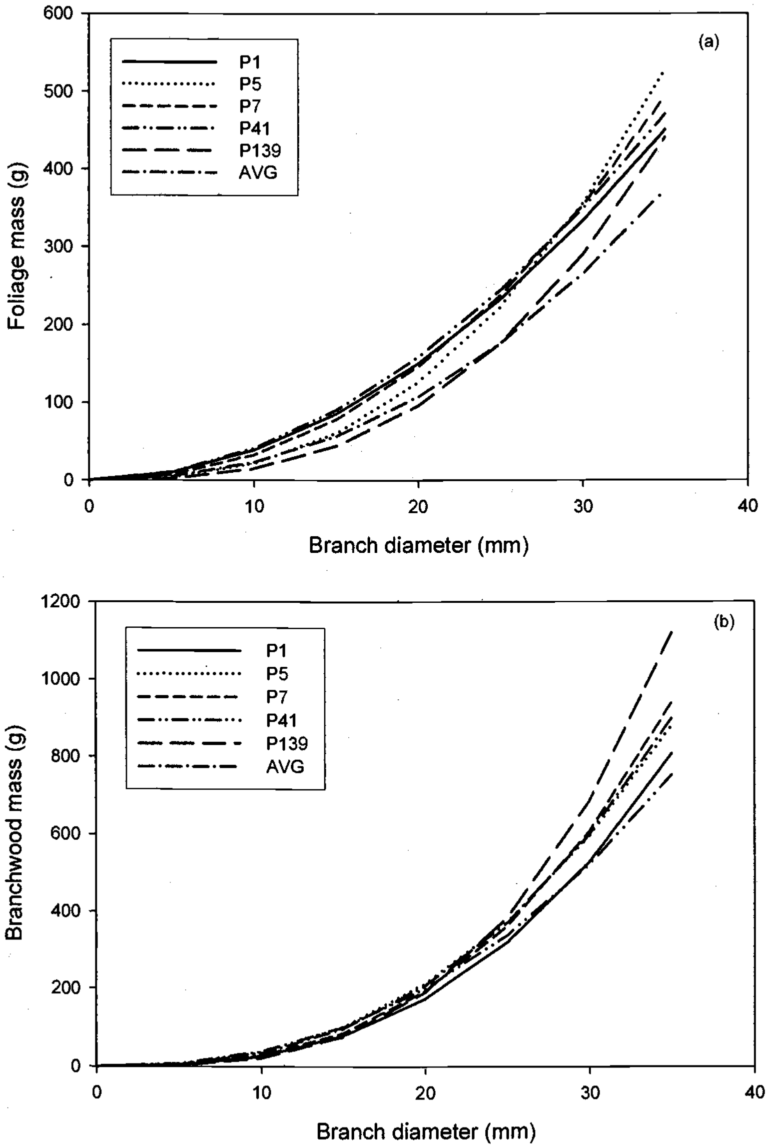

Figure 4.2. Behavior of branch-level equations for total foliage (a) and branchwood (b) mass branch diameter assuming a DINC of 5.25 m and RHACB of 0.70.

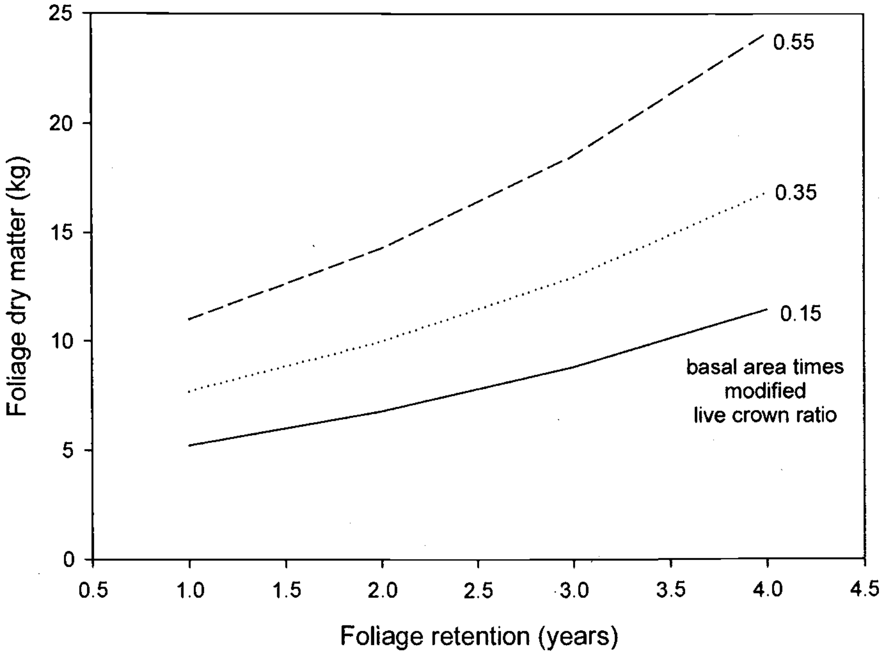

Figure 4.3. Total foliage mass for an individual tree over foliage retention and product of tree basal area and live crown ratio (BACR). The predictions are from equation 4.14.

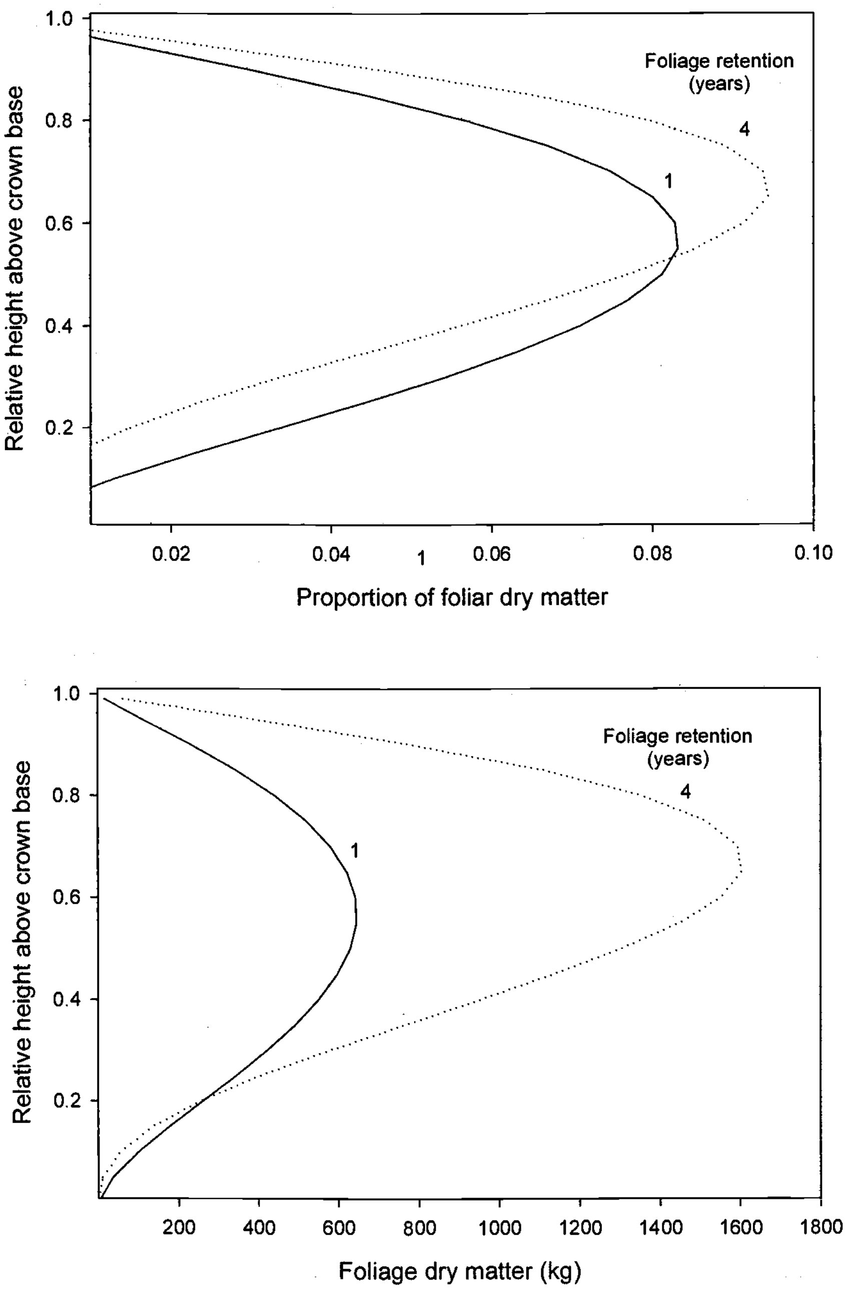

Figure 4.4. Profile of foliage distribution for an average-size tree on a plot with one year of foliage retention (solid line) and four years of retention (dashed line) in terms of relative (top) and absolute (bottom) foliage mass.

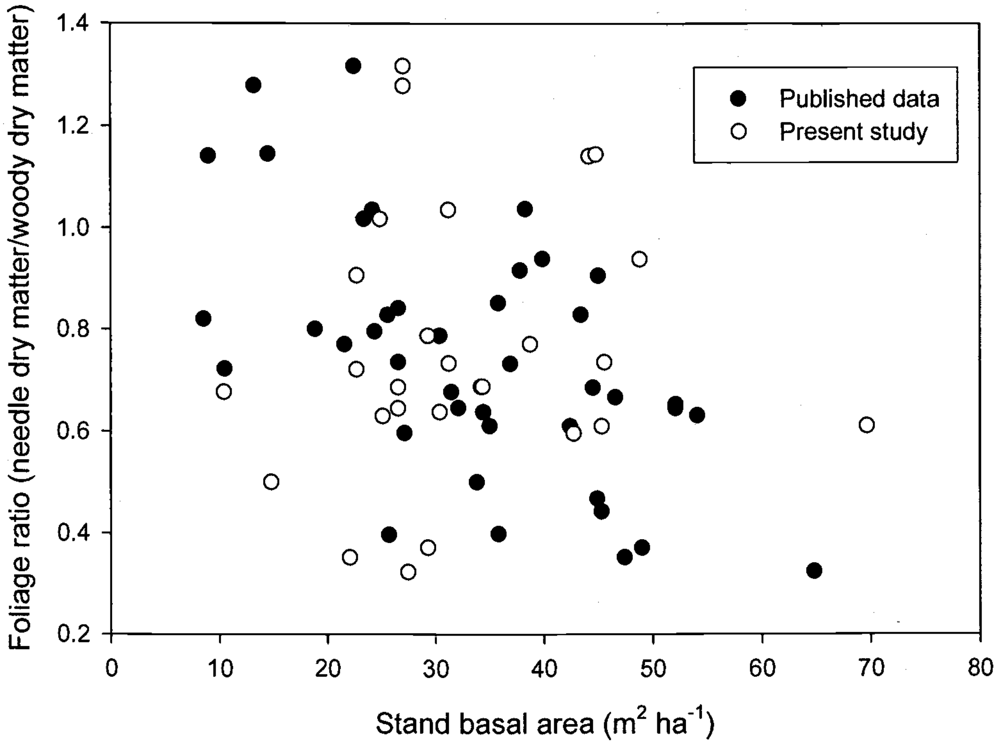

Figure 4.5. Relationship between stand basal area and foliage ratio for Douglas-fir stands in previously published studies and the present one.

CHAPTER FIVE: CHANGES IN DOUGLAS-FIR FOLIAGE AGE DISTRIBUTION AND SIZE CAUSED BY SWISS NEEDLE CAST IN THE OREGON COAST RANGE

ABSTRACT

Foliage size has been previously shown to be significantly, slightly, and insignificantly influenced by defoliation. In conifers, however, defoliation can drastically alter the foliage age distribution on an individual tree. This study was designed to examine the impacts of defoliation caused by a plant disease on needle size and age distribution. Swiss needle cast (SNC), which causes premature needle loss in Douglas-fir, has significantly increased in importance in the Oregon Coast Range over the last decade, creating a gradient of crown conditions in the region. In the fall of 2002, thirty-six trees from twelve different plantations, varying in density, age, and SNC severity, were destructively sampled to examine the impacts of the disease on foliage characteristics. Results indicate that SNC led to needles that are shorter in length and narrower in width as well as lighter in mass. Specific leaf area (SLA) of the foliage, however, increased with disease severity. At both the individual branch- and tree-levels, SNC significantly reduced foliage area. In addition, SNC drastically altered the age distribution of the foliage as well as its location within the crown. SNC resulted in a foliage age distribution skewed more towards the younger age classes. Foliage age distribution, however, was shown to be influenced by several other tree- and

stand-level variables such as tree relative height, site index, and stand density, which makes it difficult to decipher the impacts of SNC. Also, with greater SNC, the vertical distribution of the current and 1-year old foliage shifted upwards, while the vertical distribution of the 2-, 3- and 4-year-old and older foliage age classes shifted downwards. The results of this study indicate that the growth losses associated with SNC in the Oregon Coast Range are not only due to the loss of foliage, but the impacts of the disease on foliage size and age distribution.

INTRODUCTION

Tree growth is influenced to a large extent by the amount, condition, and distribution of its foliage. While total foliage area is considered to be the single most important determinant of plant productivity (Korner 1991), other foliage characteristics reflect physiological conditions and environmental influences. Forest health assessments have relied heavily on indices that include various foliage characteristics. Some of the most important of these indices are foliage discoloration, needle retention, leaf size, and needle litterfall (Innes 1993). These indices give a coarse measure of foliage condition and density within the crown but deciphering their biological meaning and implications for tree growth is more difficult and has rarely been examined thoroughly.

In general, needle morphology varies in response to the light conditions under which it develops; for example, more exposed needles are thicker, denser, and have greater area than needles formed in deep shade (Sprugel et al. 1996). Needle length mainly depends on tree age and the degree of water and nitrogen stress experienced during the period of needle growth (Raison et al. 1992). This dependence is verified by the response of needle size to drought (Roloff 1988; Innes 1992). Specific leaf area is genetically encoded but can differ significantly within and between individuals as a plastic response to environmental conditions (Pierce et al. 1994). The density of needles is also strongly affected by the degree of competition a tree has undergone (Mäkelä & Vanninen 1998). In Norway spruce (*Picea abies*), Eckmullner and Sterba (2000) found that specific needle area increased with decreasing light, while only crown-condition class and sapwood cross-sectional area had an effect on needle mass in Norway spruce.

Needle retention, on the other hand, is significantly influenced by genetics, crown position, altitude, and latitude (Kurkela & Jalkanen 1990; Innes 1993; Merrill & Wenner 1996; Pouttu & Dobbertin 2000). Xiao (2003) also indicated that needle longevity was positively correlated with tree age and stand density. Thus, the environmental and individual tree factors that influence foliage characteristics have been documented for some species. Few studies, however, examined how these characteristics change in response to repeated defoliation by insects (Piene et al. 2003) or foliage diseases.

Tree and needle physiological response to defoliation is complex, but depends on the timing of the damage, fraction of the crown removed, and the needle age classes impacted (Långström et al. 2001; Honkanen et al. 1994). Diseased trees often produce smaller and less dense foliage due to the loss or reallocation of their available resources

(Innes 1993). Masuch et al. (1989) found that the average length of three-year-old Norway spruce needles was 10 mm and dropped to 8 mm in trees exposed to acidic fog. This reduction of leaf size and density has significant implications for tree growth as thicker foliage usually has markedly higher maximum photosynthetic rates per unit surface area than thinner leaves of the same species (Sprugel et al. 1996).

Needle retention has been used for rating young conifer plantations in Europe (Innes 1993) and is the primary means for assessing the severity of Swiss needle cast (SNC) in the Oregon Coast Range (Maguire & Kanaskie 2002). Other indices such as crown color and density have been used in the region with varying degrees of success. SNC is caused by the endemic pathogen, *Phaeocryptopus gauemannii*, and has been noted to reduce foliage retention to as little as one year and volume growth by as much as 52% (Maguire et al. 2002). Currently, over 157,000 ha in the Oregon Coast Range are showing symptoms detectable by aerial survey, reflecting the dramatic increase in this disease in recent years (Kanaskie et al. 2002).

Needle retention has been shown to be highly correlated with the proportion of stomates occluded by fungal pseudothecia as well as with relative and absolute foliage mass of various age classes on sample branches (Maguire et al. 2002). Needle retention, however, may not well represent total foliage on an individual tree basis; for example Johnson (2002) found crown density and color to be more strongly correlated with growth. The crown length to sapwood area ratio, on the other hand, has been shown to highly correlated with the mass of 1-year-old foliage and the proportion of 2-year-old foliage on 5-year-old sample branches (Maguire & Kanaskie 2002). Again, there is little understanding, however, of how these indices relate to the foliage age distribution on an entire tree.

The overall objective of this study was to examine the impact of SNC on Douglas-fir needle size and foliage age distribution in the Oregon Coast Range. Specific objectives were to: (1) quantify changes in needle length, width, mass, and specific leaf area due to SNC; (2) examine branch and tree foliage area in relation to several SNC indices; and (3) describe patterns in age distribution of foliage across a gradient from severely infected to healthy Douglas-fir. It is hypothesized that SNC results in needles that are smaller and less dense than normal, and that the disease modifies the foliage age class distribution as well as the vertical distribution of the age classes. The scope of inference for the study is young (10-30 year old), managed Douglas-fir plantations in the northern half of the Oregon Coast Range.

METHODS

Study area

Twenty-two relatively young Douglas-fir plantations that are part of SNC Growth Impact Study permanent monitoring program sponsored by the Swiss Needle Cast Cooperative in the Oregon Coast Range were used in this study (Figure 5.1). The plots were located within 32 km of the Pacific coast and between Newport, Oregon, in the south and Astoria, Oregon, in the north. The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall in this area varies from approximately 180 to 300 cm/yr, and January mean minimum and July mean maximum temperatures range from –2 to 2°C and from 20 to 28°C, respectively (Maguire et al. 2002). Variations in precipitation and temperature for this area are strongly correlated with elevation and proximity to the coast. Elevations of the study plots ranged from 337 to 1,312 m and all aspects were represented.

Plots contained ≥90% Douglas-fir by basal area, with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla*) and other conifer and hardwood species (Table 5.1). The plots were similar in structure and composition, but varied in SNC intensity as measured by average stand foliage retention.

Data collection

Trees were sampled in the fall of 2002 after the cessation of growth. Thirty-nine trees from 12 different plots were sampled, with 3 sample trees were chosen from each plot. At each plot, sample trees adjacent to the permanent monitoring plots were selected for sampling based on their similarity to plot tree with regard to diameter at breast height (DBH) and foliage retention. All sample trees were surrounded by other Douglas-fir trees and were located away from gaps or landings. Before felling, diameter at breast height (DBH) (to the nearest 0.1 cm) and crown width (to the nearest 0.1 m) were measured. Each sample tree was then felled in a manner that minimized foliage loss and breakage. Total height from the base of the stump to the tip of the tree was recorded using a metric tape stretched along the bole. Basal diameters and height of each live branch were measured to the nearest millimeter and centimeter, respectively. Sample trees ranged in DBH from 12 to 36 cm (Table 5.2). A total of six whorl branches, two from each third of the crown, and three interwhorl branches, one from each third of the crown, were selected at random. The cardinal aspect of the selected branches depended on the position of the tree after felling and was essentially random. Sample branches were cut at the base and measured for total length along the stem. Sample branches ranged in basal diameter from 1 to 42 cm (Table 5.3). Average foliage retention to the nearest 0.5 yr for the branch was recorded as well as the number of whorl and interwhorl branchlets for the last five growing seasons. A subsample of approximately 100 fresh needles were randomly removed from each of the ages classes on the branch, placed in a plastic bag, and stored in a cooler for transport to the laboratory. The remaining portion of the branch was clipped into segments and placed in a plastic bag. After branch sampling, thin disks were removed from the tree at breast height (1.37 m) and crown base. One-year old foliage samples were also randomly taken from branches located in the top crown third for PCR assessment of *Phaeocryptopus gauemannii* biomass (Manter et al. 2001).

The sample branches were sectioned by age class, placed into smaller paper bags, and dried in an oven at a temperature of 85°C for three days. The needles were separated from the branch, and weighed to the nearest 0.01 g. The two stem disks from each tree were measured for sapwood area on the two radii forming the long axis of the disk and on the two radii perpendicular to the longest. Current and five-year growth increments were also measured on four perpendicular radii.

The fresh needle subsamples were analyzed for length (NL; to the nearest 0.001 mm), width (NW; to the nearest 0.001 mm), and projected leaf area (PLA; to the nearest 0.001 cm^2) using a computer image analysis system (CID corporation; Longview, WA). After measurement, the needles were dried at 80°C for 48 hours and weighed to the nearest 0.001 g. Specific leaf area (SLA) was calculated as the ratio of total PLA to total dry weight of the sample.

SNC severity on each of the study sites has been recorded every year since 1996 by the Oregon Department of Forestry. The square 0.08 ha permanent plots were established in 1998 and on each plot, all trees were tagged at breast height and measured for DBH, total height and height to crown base. These measurements were repeated in 2000 and 2002. Ten trees on each plot have been scored for SNC every year. On these trees, the crown was divided vertically into thirds and the average number of years that foliage was retained in each third was estimated visually to the nearest 0.1 year. On branches in the fifth whorl from the top of the tree, the percentage of the each age class of needles remaining on the branch was recorded. Finally, overall crown discoloration on a 1 to 4 scale was determined. Plot ratings were computed as the average from all ten trees.

Data analysis

Various linear and nonlinear regression models were fit to the data to examine relationships between SNC, needle size, and foliage age distribution. Final models were chosen on the basis of biological appeal, residual analysis, Furnival's index (FI) (Furnival 1961), and Akaike's information criterion (AIC). All analyses were done in SAS v8.2 (SAS Institute, Cary, NC) and SPLUS 2000 (Mathsoft, Seattle, WA).

Needle size

Since multiple measurements were made on an individual branch, tree, and plot, the data violated the assumption of independence or zero covariance among observations (Neter et al. 1998). Moreover, preliminary residual analysis and Durbin-Watson tests indicated the presence of positive autocorrelation. Autoregressive error structures were therefore, incorporated into the final models to account for this autocorrelation.

The relationship between 100-needle dry weight and SNC was assessed with the following linear model:

$$[5.1] \quad \begin{aligned} \ln(\mathrm{NDW}) = {} & \beta_{10} + \beta_{11}\mathrm{FAGE} + \beta_{12}\mathrm{DINC} + \beta_{13}\mathrm{CR} + \beta_{14}\mathrm{SIB} + \beta_{15}\mathrm{FOLRET} \\ & + \beta_{16}(\mathrm{FOLRET} * \mathrm{SIB}) + \varepsilon_1 \end{aligned}$$

where NDW is 100-needle dry weight, DINC is depth into the crown, CR is crown ratio, SIB is Bruce's (1981) site index, FOLRET is plot foliage retention in 2002, FAGE is an indicator variable for foliage age, the ßi's are parameters to be estimated from the data, and $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$.

The relationship between average PLA and SNC was examined with the following linear model:

[5.2] $$\ln(\mathrm{MPLA}) = \beta_{20} + \beta_{21}\mathrm{FAGE} + \beta_{22}\ln(\mathrm{CBSAP}) + \beta_{23}\mathrm{RHT} + \beta_{24}\mathrm{FOLRET} + \varepsilon_2$$

where MPLA is mean projected leaf area of the sample, RHT is relative height in the stand, the ßi's are parameters to be estimated from the data, $\varepsilon_2 \overset{iid}{\sim} N(0, \sigma_2^2)$, and all other variables are defined above..

The relationship between mean needle length and SNC was examined with the following linear model:

[5.3] $$\ln(\mathrm{MNL}) = \beta_{30} + \beta_{31}\mathrm{FAGE} + \beta_{32}\mathrm{BL} + \beta_{33}\mathrm{RHT} + \beta_{34}\ln(\mathrm{CBSAP}) + \beta_{35}\mathrm{FOLRET} + \varepsilon_3$$

where MNL is mean needle length, BL is branch length, the ßi's are parameters to be estimated from the data, $\varepsilon_3 \overset{iid}{\sim} N(0, \sigma_3^2)$, and all other variables are defined above.

The relationship between mean needle width and SNC was assessed with the following linear model:

[5.4] $$\ln(\mathrm{MNW}) = \beta_{40} + \beta_{41}\mathrm{FAGE} + \beta_{42}\mathrm{BL} + \beta_{43}\mathrm{CL} + \beta_{44}\mathrm{SIB} + \beta_{45}\mathrm{FOLRET} + \beta_{46}(\mathrm{CL} * \mathrm{FOLRET}) + \varepsilon_4$$

where MNW is mean needle width, the ßi's are parameters to be estimated from the data, $\varepsilon_4 \overset{iid}{\sim} N(0, \sigma_4^2)$, and all other variables are defined above.

The relationship between SLA and SNC was assessed with the following linear model:

[5.5] $$\mathrm{SLA} = \beta_{50} + \beta_{51}\mathrm{FAGE} + \beta_{52}\mathrm{DINC} + \beta_{53}\mathrm{TPH} + \beta_{54}\mathrm{TPHDF} + \beta_{55}\mathrm{CLSA}_{CB} + \varepsilon_5$$

where TPH is the number of trees/ha, TPHDF is the number of Douglas-fir trees/ha, $CLSA_{CB}$ is the crown length to sapwood area at crown base ratio, the β_i's are parameters to be estimated from the data, $\varepsilon_5 \overset{iid}{\sim} N(0, \sigma_5^2)$, and all other variables are defined above.

Branch needle area

Predictive model

Total branch needle area was determined by multiplying the SLA of each age class by the total needle dry weight in that age class and summing these values. Branch SLA was then calculated as the ratio of branch leaf area to total needle weight.

A series of weighted and unweighted, linear and nonlinear models were screened to develop branch-level equations for predicting leaf area from branch diameter and depth in the crown. Both published and unpublished model forms were tested (Table 5.4). The general model can be written as:

$$\text{BLA} = f(X;\theta) + \varepsilon$$

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

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

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

SNC effects

The relationship between the amount of leaf area on a branch and foliage retention was assessed with the following linear model:

[5.6] $$\ln(BLA) = \beta_{60} + \beta_{61}\ln(BD) + \beta_{62}\ln(DINC) + \beta_{63}\ln(RHACB) + \beta_{64}W + \beta_{65}SINA + \beta_{66}CLSA_{CB} + \varepsilon_6$$

where W is an indicator variable for branch type (1 if whorl, 0 otherwise), SINA is a transformation of aspect (ASP; $\sin[(2 * \pi * ASP)/360]$; Stage (1976)), the ß$_i$'s are parameters to be estimated from the data, $\varepsilon_6 \overset{iid}{\sim} N(0, \sigma_6^2)$, and all other variables are defined above. A first-order autoregressive (AR(1)) error structure was added to the final model to account for the significant autocorrelation between observations.

Tree needle area

Prediction

Plot-specific branch-level equations were applied to sampled trees to estimate tree-level needle area. A number of weighted and unweighted, linear and nonlinear, published and unpublished model forms were tested (Table 5.5). The response variable was tree foliage needle area, while explanatory variables included: DBH, HT, CL, basal area times crown ratio above breast height (BACR), height to crown midpoint (HCM), and height to diameter ratio (HTDBH).

Amount

The relationship between total tree leaf area amount and foliage retention was assessed with the following linear model:

[5.7] $$\ln(TLA) = \beta_{70} + \beta_{71}CSA + \beta_{72}\ln(TPHDF) + \beta_{73}\ln(TPH) + \beta_{74}SIB + \beta_{75}PBARA + \beta_{76}SINA + \beta_{77}CLSA_{CB} + \varepsilon_7$$

where TLA is tree leaf area (m^2), CSA is crown surface area (m^2) estimated by numerically integrating equation 3.16, PBARA is percent basal area in red alder (*Alnus rubra*), β_i 's are parameters to be estimated from the data, $\varepsilon_7 \overset{iid}{\sim} N(0, \sigma_7^2)$, and all other variables are defined above.

Needle age distribution

Amount

Needle age distribution for trees was estimated by first estimating branch-level mass by age class, specific to a plot. Then these branch-level equations were applied to the trees on the same site to estimate tree-level foliage mass by age class.

Similar to the approach outlined in Kleinschmidt et al. (1980), a three-step procedure was used to predict foliage dry matter on a branch by age. First, the total foliage dry matter was predicted with the following equation developed in Chapter Four:

$$[5.8] \qquad \ln(\text{FDM}) = \beta_{80} + \beta_{81}\ln(\text{BD}) + \beta_{82}\ln(\text{DINC}) + \beta_{83}\ln(\text{RHACB}) + \varepsilon_8$$

where FDM is foliage dry matter (g), the β_i's are parameters to be estimated from the data for each plot, $\varepsilon_8 \overset{iid}{\sim} N(0, \sigma_8^2)$, and all other variables are defined above. Second, the proportions of each age class of foliage on a branch were determined with the following system of equations:

$$
\begin{aligned}
&\mathrm{PF1} = \beta_{90}\mathrm{DINC}^{\beta_{91}} + \varepsilon_{91}\\
&\mathrm{PF2} = \beta_{92}\mathrm{DINC}^{\beta_{93}}\mathrm{RHACB}^{\beta_{94}} + \varepsilon_{92}\\
&\mathrm{PF3} = \beta_{95}\mathrm{DINC}^{\beta_{96}} + \varepsilon_{93}\\
5.9 \qquad &\mathrm{PF4} = \beta_{97}\mathrm{DINC}^{\beta_{98}} + \varepsilon_{94}\\
&\mathrm{PF5} = \beta_{99}\mathrm{DINC}^{\beta_{100}}\mathrm{RHACB}^{\beta_{101}} + \varepsilon_{95}\\
&\quad 1 = \beta_{90}\mathrm{DINC}^{\beta_{91}} + \beta_{92}\mathrm{DINC}^{\beta_{93}}\mathrm{RHACB}^{\beta_{94}} + \beta_{95}\mathrm{DINC}^{\beta_{96}} + \beta_{97}\mathrm{DINC}^{\beta_{98}}\\
&\qquad + \beta_{99}\mathrm{DINC}^{\beta_{100}}\mathrm{RHACB}^{\beta_{101}} + \varepsilon_{96}
\end{aligned}
$$

where PF_i is the proportion of dry matter in each foliage age class (1 is current-year, 2 is one-year old, etc.), RHACB and DINC are defined above, the $ß_i$'s are parameters to be estimated from the data for each plot, and $\varepsilon_k \overset{iid}{\sim} N(0, \sigma_k^2)$, where $\varepsilon_K = [\varepsilon_{91}, \varepsilon_{92}, \ldots, \varepsilon_{96}]$. The model was fit using seemingly unrelated regression in SAS PROC MODEL. Finally the estimates of total dry matter and the estimated proportions were combined to estimate the weight of foliage on each branch of the sample trees. The amount of foliage in current, 1-, 2-, 3-, and 4-year and older age class were then summed for each tree.

The tree-level analysis of the relationship between SNC and foliage age class distribution started by identification of a best model for each age class by all-subsets regression and selection of a model based on biological appeal and statistical performance. Parameters for the final models were estimated by a seemingly unrelated regression system, with the following form:

$$
\begin{aligned}
\ln(\text{F1}) = {} & \beta_{100} + \beta_{101}\text{CSA} + \beta_{102}\text{RHT} + \beta_{103}\text{SIB} + \beta_{104}\text{AGE} + \beta_{105}\text{ASP1} + \beta_{106}\text{FOLRET} \\
& + \beta_{107}\text{CLSA}_{\text{CB}} + \beta_{108}(\text{SIB} * \text{FOLRET}) + \varepsilon_{101} \\
\ln(\text{F2}) = {} & \beta_{109} + \beta_{110}\text{CSA} + \beta_{111}\text{RHT} + \beta_{112}\text{SIB} + \beta_{113}\text{AGE} + \beta_{114}\text{FOLRET} \\
& + \beta_{115}\text{CLSA}_{\text{CB}} + \beta_{116}(\text{SIB} * \text{FOLRET}) + \varepsilon_{102} \\
\ln(\text{F3}) = {} & \beta_{117} + \beta_{118}\text{CSA} + \beta_{119}\text{RHT} + \beta_{120}\text{SIB} + \beta_{121}\text{AGE} + \beta_{122}\text{FOLRET} + \beta_{123}\text{CLSA}_{\text{CB}} \\
& + \beta_{124}(\text{SIB} * \text{FOLRET}) + \varepsilon_{103} \\
\ln(\text{F4}) = {} & \beta_{125} + \beta_{126}\text{CSA} + \beta_{127}\text{RHT} + \beta_{128}\text{SIB} + \beta_{129}\text{AGE} + \beta_{130}\text{FOLRET} + \beta_{131}\text{CLSA}_{\text{CB}} \\
& + \beta_{132}(\text{SIB} * \text{FOLRET}) + \varepsilon_{104} \\
\ln(\text{F5}) = {} & \beta_{133} + \beta_{134}\text{CSA} + \beta_{135}\text{RHT} + \beta_{136}\text{CR} + \beta_{137}\text{TOPHT} + \beta_{138}\text{FOLRET} + \beta_{139}(\text{RHT} * \text{CR}) \\
& + \beta_{140}(\text{CR} * \text{FOLRET}) + \varepsilon_{105} \\
\text{F} = {} & \exp[\beta_{100} + \beta_{101}\text{CSA} + \beta_{102}\text{RHT} + \beta_{103}\text{SIB} + \beta_{104}\text{AGE} + \beta_{105}\text{ASP1} + \beta_{106}\text{FOLRET} \\
& + \beta_{107}\text{CLSA}_{\text{CB}} + \beta_{108}(\text{SIB} * \text{FOLRET})] + \exp[\beta_{109} + \beta_{110}\text{CSA} + \beta_{111}\text{RHT} + \beta_{112}\text{SIB} \\
& + \beta_{113}\text{AGE} + \beta_{114}\text{FOLRET} + \beta_{115}\text{CLSA}_{\text{CB}} + \beta_{116}(\text{SIB} * \text{FOLRET})] + \exp[\beta_{117} + {} \\
& \beta_{118}\text{CSA} + \beta_{119}\text{RHT} + \beta_{120}\text{SIB} + \beta_{121}\text{AGE} + \beta_{122}\text{FOLRET} + \beta_{123}\text{CLSA}_{\text{CB}} + {} \\
& \beta_{124}(\text{SIB} * \text{FOLRET})] + \exp[\beta_{125} + \beta_{126}\text{CSA} + \beta_{127}\text{RHT} + \beta_{128}\text{SIB} + \beta_{129}\text{AGE} + {} \\
& \beta_{130}\text{FOLRET} + \beta_{131}\text{CLSA}_{\text{CB}} + \beta_{132}(\text{SIB} * \text{FOLRET})] + \exp[\beta_{133} + \beta_{134}\text{CSA} + \beta_{135}\text{RHT} \\
& + \beta_{136}\text{CR} + \beta_{137}\text{TOPHT} + \beta_{138}\text{FOLRET} + \beta_{139}(\text{RHT} * \text{CR}) + \beta_{140}(\text{CR} * \text{FOLRET})] + \varepsilon_{106}
\end{aligned}
$$

[5.10]

where F_I is the amount of foliage dry matter (kg) in each age class (F1 is current-year, F2 is one-year, F3 is two-year, F4 is three-year, and F5 is four-year and older), AGE is average stand breast height age in 2002 (years), ASP1 is cosine transformation of aspect and slope ($\%\text{SLOPE} * \cos[(2 * \pi * \text{ASP})/360 *]$; Stage (1976)), TOPHT is stand top height in 2002 (m), F is the total amount of foliage on the tree (kg), the β_i's are parameters to be estimated from the data, $\varepsilon_k{}^{\text{iid}} \sim \text{N}(0, \sigma_k{}^2)$, where $\varepsilon_K = [\varepsilon_{101}, \varepsilon_{102}, \ldots, \varepsilon_{103}]$, and all other variables are defined above.

Vertical distribution

Observed vertical foliage distribution was characterized on the measured plot trees by dividing the crown into ten segments of equal length and summing the foliage within that segment using the developed branch-level equations. The proportion of tree foliage in each of the foliage age classes in each of the ten segments was then determined. A standard two-parameter beta distribution (Johnson & Kotz 1970) was fit to the empirical distribution for each tree. The beta distribution has the desirable properties of being extremely flexible and logically defined on an interval with fixed endpoints. Other distributions that have been experimented with, which include the normal (Beadle et al. 1982), chi-square (Massman 1982), lognormal (Schreuder & Swank 1974), gamma (Schreuder & Swank 1974; Massman 1982) and Weibull (Schreuder & Swank 1974; Mori & Hagihara 1991; Gillespie et al. 1994) distributions; but none of these has fixed endpoints. The interval (0,1) was rescaled to crown length making the tree tip and lowest live branch the respective endpoints. Estimates of the parameters *a* and *b* were determined using maximum likelihood estimation.

Parameters estimates from the beta distribution were modeled as a linear function of tree variables (DBH, HT HLB, and CL) and SNC variables (FOLRET, CLSA, CC, CD) using seemingly unrelated regression for the purposes of determining effects of other variables on foliage distribution and prediction. Vertical foliage distributions were predicted from the developed equations for the average-sized trees found on plots across the range of stand density and SNC to provide a graphical assessment of the effects of SNC on the vertical distribution of foliage by age class.

RESULTS

Needle size

Needle characteristics varied greatly between plots (Table 5.6). Foliage retention showed a significant relationship with 100-needle dry weight (p=0.0003 for ß$_{15}$ in equation 5.1), projected leaf area (p=0.0176 for ß$_{24}$ in equation 5.2), needle length (p<0.0001 for ß$_{35}$ in equation 5.3), and needle width (p=0.0021 for ß$_{45}$ in equation 5.4), but not specific leaf area. The crown sparseness index (CLSA$_{\mathrm{CB}}$), on the other hand, showed a significant relationship with specific leaf area (p=0.0003 for ß$_{55}$ in equation 5.5) Needle dry weight increased with foliage age, site index, and foliage retention, but decreased with depth in the crown (Table 5.7). Foliage retention, however, has a positive effect up to site index of 41.4 m. Mean needle length increased with foliage age, sapwood area at crown base, and foliage retention, but decreased with branch length, and relative height (Table 5.8). The difference in needle length between 2- and 3-year-old foliage, however, was not statistically significant (p=0.2365). Mean needle width increased with foliage age, site index, and foliage retention but decreased with branch length (Table 5.9). Foliage retention, however, only had a positive effect up to site index of 41.4 m. Mean projected leaf area increased with age, foliage retention, and sapwood area at crown base, but decreased with relative height in the stand (Table 5.10). Specific leaf area increased with depth into the crown, the crown sparseness index, and the number of trees/ha but decreased with foliage age and the number of Douglas-fir trees/ha (Table 5.11). The models explained between 0.22 to 0.53% of the original variation and had RMSEs from 0.1041 to 0.3748 (Table 5.12).

When analyzed by crown thirds, the relationship between mean projected leaf area and foliage retention is only significant ($p<0.001$) for the upper portion of the crown. Similarly, the relationship between mean needle length and foliage retention was only significant for the upper portion of the crown. For mean needle width, only needles located in the lower portion of the crown were significantly ($p<0.0001$) related to foliage retention. The relationship between foliage retention and needle dry weight as well as foliage retention and specific leaf area was consistent throughout the crown.

Branch leaf area

Predictive model

The best model for estimating branch leaf area contained both branch diameter and crown position variables as predictors; (Kershaw and Maguire 1995; Table 5.13):

[5.11] $\ln(\mathrm{BLA}) = \beta_{110} + \beta_{111}\ln(\mathrm{BD}) + \beta_{112}\ln(\mathrm{DINC}) + \beta_{113}\ln(\mathrm{RHACB}) + \beta_{114}\mathrm{W} + \varepsilon_{11}$

where the β_i's are parameters to be estimated from the data for each plot, $\varepsilon_{11} \overset{iid}{\sim} N(0, \sigma_{11}^2)$, and all other variables are defined above. When fit to the data by site, the models fit well with R^2 values between 0.69 and 0.98 and root mean square errors varying from 0.25 to 0.84.

SNC effects

Branch leaf area ranged from 0.21 to 2,441.24 cm^2 and was significantly related to foliage retention ($p<0.01$ for β_{66} in equation 5.6). Branch leaf area increased with relative height above crown base, depth into the crown, branch diameter, and was greater in whorl branches, but decreased with the crown sparseness index (Table 5.14). Branch leaf area also tended to peak on the northerly aspects. The combination of relative height above crown base and depth into the crown in the model allowed for a decline in branch leaf area for a given branch size near the crown base (Figure 5.2). An average branch on a site with a crown sparseness index of 15 has 34.9% less leaf area than an average branch on a site with a crown sparseness index of 2, all other covariates being equal. The model explained 79% of the original variation and had a RMSE of 0.7503.

Tree leaf area

Prediction

For predicting total tree leaf area, the best model was a linear model of the following form (Table 15):

$$[5.12] \quad \ln(\text{TLA}) = \beta_{120} + \beta_{121}\ln(\text{CSA}) + \varepsilon_{12}$$

where CSA and TLA are defined above, the β_i's are parameters to be estimated from the data by plot, and $\varepsilon_{12} \overset{iid}{\sim} N(0, \sigma_{12}^2)$. Significant differences were found among plots, underscoring the need for site specific parameter estimates (Figure 5.3). When fit to each plot, R^2 values ranged from 0.61 to 0.99, while root mean square errors varied between 0.0094 and 0.8373.

Amount

Tree leaf area ranged from 14.13 to 574.29 m² and showed a significant relationship with the crown sparseness index (p=0.0007 for β_{77} in equation 5.7). Tree leaf area increased with crown surface area, Douglas-fir trees per ha, site index, and percent basal area in alder, but decreased with trees per ha and the crown (Table 5.16). Tree leaf area also tended to peak in the more northerly aspects. A tree with a crown sparseness index of 15 is expected to have 42.3% less leaf area than a tree with a crown sparseness index of 2. The model explained 83.3% of the original variation and had a RMSE of 0.3158.

Needle age distribution

Amount

Needles as old as eight years were found at one site, while most other sites only had needles as old as six or seven years. The models had R^2 values ranging from 0.83 to 0.85, while the RMSEs varied between 0.2281 and 0.9093 (Table 5.17). In general, the foliage amount in each age class increased with crown surface area, relative height of the tree, site index, and foliage retention, but decreased with age, and crown length to sapwood area at crown base (Table 5.18). Foliage retention showed a significant relationship with all foliage age classes, while crown length to sapwood area only had a significant relationship with the first three age classes. The positive effect of foliage retention, however, decreased with increasing site index. Foliage retention had a positive effect up to a site index of 39.1, 40.0, 41.4, and 43.9 m for current-, 1-, 2-, and 3-year-old foliage, respectively. Similarly, foliage retention had a positive effect up to a crown ratio of 0.87 for the 4-year-old and older foliage. The mass of current-year foliage also tended to peak on the more northerly aspects. A tree on a plot with mean foliage retention of one year was estimated to have 50.4, 30.3, 16.6, 2.6, 0.2% of its foliage in current, 1-, 2-, 3-, 4-year-old, and older age classes, respectively. On average, a tree on a plot with a foliage retention of four years was estimated to have 29.2, 26.8, 22.9, 15.6, and 5.5% of its foliage in current, 1-, 2-, 3-, 4-year-old and older age classes, respectively. The younger age classes became proportionally more dominant with increasing SNC, lower relative social position in the stand, decreasing site index, and greater stand basal area (Figure 5.4).

Vertical distribution

Variables representing crown size (CL, CR, CSA), stand structure (BAPH, PBADF, AGE, TPH), site location (SLOPE, COAST, ASP12), and SNC severity (FOLRET) had a statistically significantly effect on the beta distribution parameters, and, hence, foliage distribution (Table 5.19). In general, the beta distribution parameters increased with distance from the coast, slope, stand age, percent slope, crown ratio, the transformation of slope and aspect, and the number of trees per ha. An increase in the *a*-parameter causes the distribution to shift downward, while an increase in the *b*-parameter causes the distribution to shift upward. The beta distribution parameters decreased with stand basal area, Douglas-fir percent basal area, and crown length (Table 5.20, 5.21). A decrease in the *a*-parameter causes the distribution to shift upward, while a decrease in the *b*-parameter causes the distribution to shift downward. Foliage retention increased the *b*-parameter and reduced the *a*-parameter, while just the opposite occurred for the plot mean of the crown sparseness index. With greater SNC, the mode of the vertical distribution of current and 1-year old foliage shifted upwards, while the mode of the 2-, 3- and 4-year-old and older foliage age classes shifted downwards (Figure 5.5). The models explained between 40 to 71% of the original variation in the beta parameters and had RMSEs that ranged from 0.4260 to 1.7609.

DISCUSSION

Extended defoliation by a foliar disease can drastically influence both needle size and foliage age distribution. SNC in the Oregon Coast Range has resulted in Douglas-fir foliage of lesser length, width, and mass, although SLA has increased with disease severity. At the individual branch- and tree-levels, SNC has significantly reduced total leaf area for branches and trees of a given set of dimensions. The disease has also resulted in a needle age distribution that has heavier representation of the younger age classes. SNC has also modified the vertical distribution of this foliage as a greater proportion of the current- and 1-year old foliage occurs higher in the crown, while the of majority the 2-, 3-, and 4-year and older foliage is located lower in the crown. Thus, SNC has significantly influenced both the size and age distribution of foliage as well as its distribution within the crown.

Needle size

The needle characteristics found in this study are similar to ones reported in the literature for Douglas-fir (Brix & Ebell 1969; Smith 1972; Del Rio & Berg 1979; Borghetti et al. 1986; Apple et al. 2002). Smith (1972) reported that one-hundred needle dry mass ranged from 0.31 to 0.72 g for both open- and forest-grown trees. Needle length tended to be between 1.88 and 2.54 cm, while widths generally ranged from 1.22 to 1.70 mm (Brix & Ebell 1969; Smith 1972; Apple et al. 2002). SLA has been shown to vary from 55.3 to 94.5 $cm^2 g^{-1}$ for current-year needles and from 50.7 to 75.8 $cm^2 g^{-1}$ for older needles (Del Rio & Berg 1979; Borghetti et al. 1986).

Conifers develop sun- or shade-adapted needles depending on the amount of irradiance received when buds are expanding (Tucker et al. 1987). In general, needles fully exposed to sunlight are heavier, with a thicker palisade mesophyll but have less chlorophyll than needles developed under more shaded conditions (Del Rio & Berg 1979). Needle size tends to increase and SLA decrease with age, while needle size generally decreases and SLA increases from tree top to crown base (Bartelink 1996). Needle dry weight tends to decrease from tree top to crown base because the needles become thinner (Smith 1972). Leaf thinning or greater SLA is generally interpreted as reallocation of carbon to increase light interception (Chen et al. 1996; Stenberg et al. 1999; Evans & Poorter 2001). SLA is affected by both cross-sectional shape (flatness) and by density (mass per unit volume). This study found that needle length and width were not only influenced by the vertical light gradient in the crown but a horizontal one as indicated by the significance of branch length. Both needle length and width decreased with increasing branch length, which may be reflective of the tendency of needle size to decrease from tree top to crown base. Ishii et al. (2002) found SLA to decrease with increasing distance from the branch base, which was attributed to the increasing light gradient from inner to outer branches and hydraulic limitations. However, Marshall and Monserud (2003) found that branch length had no influence on SLA. Sprugel et al. (1996) concluded that needle morphology and structure are essentially irreversible after it has formed. Needle length has been reported to increase 0.7% (-27.3 to 23.1%) for each age class (Smith 1972; Morgan et al. 1983; Gilmore et al. 1995), while in this study, needle length tended to increase 3.7% (-67.4 to 40.5%). The differences in SLA and mean needle length due to foliage age found in this study may, therefore, represent the cumulative effects of SNC on the needles.

In addition to light, needle characteristics may also be influenced by other environmental factors such as temperature, vapor pressure difference, water potential, and CO_2 concentrations (Nagel & O'Hara 2001). Marshall and Monserud (2003) concluded that water potential at the point of leaf display modified SLA rather than light being the sole environmental control. SLA also varies seasonally. Nippert and Marshall (2003) found that the SLA of the 1-year-old foliage increased nearly 26% by the end of the summer. Smith et al. (1981) found that foliage from trees grown in the Oregon Coast Range maintained a nearly constant weight per unit of leaf area, while foliage weight per unit of leaf area in trees of the Oregon Cascades increased by more than 50% during the summer. They concluded that these seasonal changes in leaf weight were a reflection of the annual growing condition as trees in the Coast Range can maintain a relatively high level of photosynthesis throughout the year (Smith et al. 1981).

Needle characteristics possibly change with foliage age for a variety of reasons including the accumulation of nonstructural carbohydrates and other secondary substances with time (Niinemets 1997b) and the selective retention of needles with a lower SLA (Hager & Sterba 1985). Ishii et al. (2002) in mature Douglas-fir found that the rate of accumulation of secondary substances were greater in lower-crown branches and needles with a higher SLA were shed more rapidly. Gilmore et al. (1995), however, indicated that SLA decreased with needle age because of growth of secondary phloem and the absence of carbon sinks in the needle. Needle length (Smith 1972; Morgan et al. 1983; Gilmore et al. 1995), width (Smith 1972), and dry mass (Borghetti et al. 1986; Gilmore et al. 1995) have also been shown to increase with foliage age. On the other hand, Gilmore et al. (1995) found foliage age and needle width to be significantly related, but there was no consistent change with age. Needle length and width are strongly controlled by the climatic conditions in the year of formation (Morgan et al. 1983). Junttila and Heide (1981) found a positive correlation between needle length and the mean temperature of the current growth season in Scots pine (*Pinus sylvestris*). Similarly, Youngblood and Ferguson (2003) found that needle width and length differed by year, but not by light environment for shade-tolerant seedlings. Even after foliage has fully expanded in length and width, it continues to thicken and increase in dry mass (Kozlowski & Pallardy 1997). Hager and Sterba (1985), however, found no significant difference between the dry weight of older and current-year needles. SLA has been reported to decline on average 13.2% (2.8 – 19.7%) from current- and 1-year-old foliage and 7.4% (5 – 15.3%) from 1-year-old and older foliage for Douglas-fir and balsam fir (Del Rio and Berg 1979; Hager and Sterba 1985; Borghetti et al. 1986; Gilmore et al. 1995). In this study, the difference between current- and 1-year-old foliage SLA averaged 17.3% (0.1 – 66.1%) and the difference between 1-year-old and older foliage SLA averaged 14.5 (0.3 – 48.3%), which are significantly higher than those reported in the literature. These differences may, therefore, indicate the marginal effect of SNC on SLA.

Bartelink (1996) found SLA to strongly vary within a Douglas-fir tree, but not between trees. However, Gilmore et al. (1995) found that between-tree variation in SLA was greater than within-tree variation in balsam fir (*Abies balsamea*). Regardless of where the greatest variation occurs, needle characteristics are influenced by several tree- and stand-level variables. St. Clair (1994) found tree size to be moderately positively correlated with Douglas-fir needle size and negatively correlated with specific leaf area in open-grown genetic trials; large trees tended to have larger, more cylindrical needles. In stand-grown Norway spruce trees, Hager and Sterba (1985) similarly found SLA to decrease with increasing DBH, while needle dry mass tended to increase with DBH. On the other hand, Morgan et al. (1983) found differences in needle length were not related to tree characteristics such as DBH, height, or crown dimensions in balsam fir. In this study, needle length was found to be positively correlated with tree size as indicated by sapwood area at crown base. In addition to tree size, another important tree-level factor influencing needle characteristics is the tree's social position in the stand. Chen et al. (1996) indicated that with decreasing light availability, SLA increased in Douglas-fir saplings. In this study, needle length was found to increase with decreasing relative height in the stand. Presumably this is a result of a greater proportion of the needles on lower status trees receiving less intense sunlight. Sprugel et al. (1996) found that shade needles in Pacific silver fir (*Abies amabilis*) were generally as long as or longer than sun needles. Needle characteristics also change with tree age. Upper-canopy needles on younger trees in comparison to mature trees are longer and have proportionately smaller vascular cylinders, larger resin canals, and fewer hypodermal cells (Apple et al. 2002). Needle length, thickness, width, cross-sectional area, and perimeter, however, were maximal in 40-year-old trees (Apple et al. 2002). Some of the values found in this study are relatively high perhaps because a majority of the stands in this study are approaching 40 years. St. Clair (1994) found considerable genetic variation in Douglas-fir needle size, but little genetic variation in SLA.

At the stand-level, SLA appears to be influenced largely by density and site fertility. Lower stand densities as a result of thinning have been shown to increase (Smith et al. 1981; Brix 1981) or have no influence (Moir & Francis 1972; Smith et al. 1981; Hager & Sterba 1985) on needle dry weight. These findings, however, may be confounded by the fact that changes in needle morphology may require more than 4 years to respond to increases in light availability created by thinning (e.g. response of shade-tolerant advance regeneration reported by Youngblood and Ferguson (2003)). Adjustments in needle morphology to light, however, are the result of two processes, namely adjustments of shade foliage to increased light and replacement of old shade needles by newer sun needles. In general, leaf area and leaf weight increase with stand density up to a certain point and then decrease (Temesgen 1999). Similar to the results of Smith (1981), SLA in this study was found to increase with density. Fertilization studies indicate that site fertility can significantly influence needle characteristics as needle length and width, increasing in response to nitrogen fertilization in Douglas-fir (Brix & Ebell 1969; Brix 1981). Both needle length and dry mass were shown to increase with site index in this study. The influence of fertilization on SLA has been shown to vary by crown position in Douglas-fir and grand fir (*Abies grandis*). Nippert and Marshall (2003) indicated that in shade foliage, SLA was lower in potassium-treated trees than in the nitrogen plus potassium treated trees. However, for the sun foliage, SLA was lower in nitrogen treated trees than in nitrogen plus potassium treated trees (Nippert & Marhsall 2003).

Defoliation has been shown to significantly influence needle characteristics. Piene and MacLean (1999) reported that trees defoliated by spruce budworm (*Choristoneura fumiferana)* showed much more year-to-year variation in needle lengths than protected trees, resulting in longer needles one year and shorter needles in three other years.

Similarly, Kulman (1965) reported a 14 to 32% reduction of needle length after artificial defoliation in red pine (*Pinus resinosa*), while Jokela et al. (1996) found that root reduction induced shorter needles in Scots pine. Piene (1980) indicated that needles from balsam fir trees that had been almost completely defoliated by spruce budworm in the previous year had significantly higher weights than needles from protected trees. However, in artificially defoliated Japanese red pine (*Pinus densiflora*; Furuno 1965), red pine (Kulman 1965), and tamarack (*Larix larcinia*; Ives & Nairn 1966), needles weights significantly declined. Similar to Tucker and Emmingham's (1977) conclusion for western hemlock, this study indicated that with increasing SNC stress, Douglas-fir needles tend to decrease in size. However, with increasing SNC severity, Douglas-fir foliage has a lower dry weight and a net increase in SLA. While net assimilation rate per unit leaf area is greater in foliage with a low SLA (Oren et al. 1986), high SLA foliage tends to be relatively productive (Poorter & Van der Werf 1998; Van der Werf et al. 1998), but is necessarily short-lived and vulnerable to infection and herbivores (Coley et al. 1985; Grime et al. 1996). This indicates that Douglas-fir may be responding to defoliation by investing in foliage that maximizes light capture and has faster payback on the investment rather than one that maximizes longevity and robustness (Poorter 1994). On the other hand, stress caused by SNC may be depleting biochemicals in the needles and hence, decreasing mass and effectively increasing SLA.

Leaf area

Branch-level

Branch leaf area generally decreases gradually as shading increases, branch growth ceases as net photosynthesis and growth of the branch declines, and as the branch succumbs to suppression. With the decline in branch elongation and loss of older foliage near the main stem, there is less carbon available for the growth of new foliage (Kershaw & Maguire 1995). The mode of foliage area distribution tends to be shifted downwards relative to foliage mass because specific leaf area increases with depth into the crown (Maguire & Bennett 1996). In this study, branch leaf area was found to increase as the plot aspect become more northerly. While the photosynthetic capability of Douglas-fir varies significantly at different vertical and horizontal locations among the four cardinal directions (Woodman 1971), aspect in this study most likely reflects its interaction with SNC by reducing branch leaf area. Manter (2001) found that trees on south slopes of coastal sites had higher fungal colonization and more severe symptoms (poorer foliage retention) when compared to north slopes. Although whorl branches may have a higher leaf area than interwhorl branches, this study and others (Ishii et al. 2002) indicate that the size of needles seems to be unaffected by branch type.

Tree-level

A simple linear model with crown surface area as the predictor proved to be the best model for estimating individual tree leaf area within a study site. Although more complex models have been used (e.g. Maguire & Bennett 1996), Woods et al. (1991) concluded that more sophisticated models had little effect on the error of estimating leaf area and that the only way to improve precision was to sample more trees. Similarly, Meadows and Hodges (2003) found that there was little difference in accuracy among simple linear, multiple linear, and nonlinear models for predicting leaf area. Results from this study are corroborated by the previous conclusion that crown surface area is closely correlated with sapwood area at crown base, a surrogate for leaf area, (Maguire and Hann 1989). In addition, Temesgen (2003) noted that stratified random sampling, similar to the sampling strategy implemented in this study, resulted in the lowest mean square error when compared to other sampling alternatives.

Previous work has shown that crown length is an effective predictor of tree foliage area (Gilmore et al. 1996; Maguire & Bennett 1996). Likewise, crown ratio has repeatedly emerged as an important predictor of tree growth in individual tree models (Wykoff 1990) Crown length and crown ratio reflect the total size of the crown, local stand density, and spacing. Because foliage area is expected to increase with crown length, a more dominant social position and lower stand density, Smith (1993) found that Douglas-fir leaf area could be estimated using only stem size and stand density. Height to diameter ratio can also be a strong predictor given its close correlation with crown ratio, stand density, and social position. Kurz (1989) similarly found that foliage dry matter was primarily influenced by stem size and individual-tree competition indices.

Foliage age distribution

Modeling

Although relatively little work has been done on modeling foliage age distribution in conifers, a variety of approaches have been used in the few studies that have examined it. These approaches include using Leslie matrices (Hayslett & Solomon 1983), average age-class percentages from sample branches (Silver 1962; Kay 1978; Piene et al. 2003), and an iterative algorithm (Baskerville & Kleinschmidt 1981). This study utilized a system of equations approach (nonlinear seemingly unrelated regression) with parameter restrictions to estimate parameters. This type of approach forces additivity, accounts for cross-equation correlation, and gives more efficient predictions (Kmenta 1997). Parresol (1999; 2001) found this approach superior to other procedures for guaranteeing the property of additivity among components of dry matter and total tree dry matter. Although R^2 values for the models varied significantly by plot (0.51 – 0.96), the predictions are unbiased and highlight the high variability of foliage age distribution within an individual tree.

Amount

Anecdotal evidence suggests that healthy Douglas-fir in the Oregon Coast Range typically retain 3 to 4 annual cohorts of needles, and sometimes more (Filip et al. 2000; Maguire et al. 2002). Silver (1962) suggested that the rule of thumb in British Columbia was that Douglas-fir retained its needles for five years. On four 80-year-old Douglas-fir trees on Vancouver Island, Silver (1962) found that the average percentage of foliage in the youngest five years was 28, 23, 17, 13, and 10%. He suggested that 90% of the foliage consisted of five-year-old or younger needles, although there were considerable amounts of six and seven-year old foliage. On eight sites in the Oregon Coast Range and Cascade foothills, Mitchell (1974) only rarely found young, open-grown Douglas-fir with more than five years of needles, yet frequently observed 7 years of needles on older trees. Brix (1981) found at least six years of foliage on 24-year-old Douglas-fir in British Columbia, while Dice (1970) and Silver (1962) found foliage up to 8- and 10-years old, respectively. Most research, however, has found that Douglas-fir retains most of its needles over the first 3 to 4 years (Mitchell 1974; Ishii et al. 2002).

In other species, foliage retention has been found to be correlated with nutritional status (Balster & Marshall 2000), water availability (Raison et al. 1992), elevation (Reich et al. 1996), and other environmental factors such as light (Niinemets 1997a), temperature (Kajimoto 1993), and annual evaporation (Xiao 2003). Generally, needle life span follows a cost-benefit model as foliage with high construction costs tends to be retained longer in order to maximize carbon gain (Kikuzawa 1995a). The photosynthetic rate of the foliage, as well the construction and maintenance costs of both the foliage and supporting structure, significantly influence foliage leaf span (Kikuzawa & Ackerly 1999). Thus, foliage retention is influenced by several tree and stand variables. At the tree-level, foliage life span is correlated with tree growth status (Xiao 2003), size (Niinemets 1997c), social position (Niinemets 1997a), and age (Fleming & Piene 1992). At the stand-level, needle retention has been shown to be influenced by spacing (Kellomaki et al. 1980; Piene & Fleming 1996), site fertility (Gower et al. 1993), and exposure (Kajimoto 1993).

Foliage age distribution on Douglas-fir in the Northern Coast Range of Oregon was also influenced by both tree- and stand-level factors. For a given crown surface area, relative height, site index, and average stand breast height age all influenced the age distribution. Crown surface area has been shown to be a good predictor of sapwood area at crown base (Maguire & Hann 1989) and tree volume increment (Hamiliton 1969) so by inference should be an effective surrogate for foliage mass or area. In addition, crown size is sensitive to competition (Mäkelä & Vanninen 1998) so it reflects stand conditions such as stand density (Krajicek et al. 1961). Relative height in the stand is an indication of tree position and the amount of available light. Most studies have shown extended needle longevity to be associated with relatively shaded conditions (Lowman 1992; Suehiro & Kameyama 1992; Ackerly & Bazzaz 1995; Miyaji et al. 1997; Niinemets 1997a; Xiao 2003). Likewise, Douglas-fir with a greater relative height in this study held a higher proportion of the younger age classes. Seiwa (1999) reported that leaf longevity was greater on both seedling and adults grown in the sun vs. shade, although the differences were larger in seedlings than in adults. This result was attributed to seedling leaves that were adapted to high irradiances prior to canopy closure, and were therefore unable to adapt to the low irradiances after canopy closure. According to one model relating leaf growth and senescence to acclimation, leaf longevity increased with improved irradiance, although leaves grown continuously in high light generally had a shorter life than leaves grown continuously in low light (Thornley 1991).

The difference between the findings of these studies and the apparent behavior of Douglas-fir in the Oregon Coast Range is most likely attributable to the experimental design. Trees sampled in this study were primarily dominants and codominants from an even-aged stand, while other studies have concentrated on a wide range of tree size within stands. Seedlings may show a longer duration of leaf longevity in response to the greater spatial and temporal heterogeneity of the environmental resources available in the forest understory (Lechowicz & Bell 1991; Seiwa 1998). Conversely, adults may have lower plasticity because of the relatively stable environmental conditions (Seiwa 1999). Maguire and Kanaskie (2002) reported that Douglas-fir situated lower in the canopy have greater crown sparseness due to lower light intensity. Canopy trees of a lower social status may, therefore, have lower leaf longevity because of competition, slower growth rates, and reduced light availability. In other studies, leaf longevity increased with resource-poor conditions (Kikuzawa 1991; Kikuzawa 1995b; Pensa & Sellin 2002), probably to compensate for reduced photosynthetic rates (Chabot & Hicks 1982). The response of Douglas-fir foliage retention to fertilization, however, ranged from an increase (Turner & Olson 1976), decrease (Brix 1981; Balster & Marshall 2000), to no effect (Brix & Ebell 1969). In Douglas-fir of the Oregon Coast Range, the amount of foliage dry matter in each age class increased with improved site quality, but the distribution contained a greater proportion of older age classes than trees on sites with lower site index. This observation may due to the confounding influence of site index on SNC and tree genetics. Rehfeldt and Hamiliton (1999) indicated that site index is as much a genetic response as an attribute of the site. Although research has indicated that foliage retention is largely a phenotypic response (Reich et al. 1996), there may be some genetic component to it as well (McCrady and Jokela 1996). The significance of age on foliage age class distribution may also indicate the influence of stand structural features such as stand density.

Needle longevity generally increases with tree age (Fleming & Piene 1992; Pensa et al. 2001; Xiao 2003). The tendency for foliage amount in each foliage age class to decrease with tree age may reflect the limited tree age range (10 to 30 years) examined in this study. Turner and Long (1975) concluded that rapid turnover of foliage and shorter needle retention in 22- and 30-year-old stands of Douglas-fir, is attributable to the young, highly competitive status of these stands. However, the percentage of foliage dry matter in current foliage increased as stand density increased, a result similar to that observed by Piene et al. (2003) in balsam fir. The distribution of foliage on a Douglas-fir is apparently controlled by several different factors and their interactions. Manipulative experiments are needed to determine the complex causal relationships involed in foliage retention and age class distribution (e.g. Balster and Marshall 2000).

Piene et al. (2003) showed that defoliation can drastically alter the foliage age structure in trees. On balsam fir severely defoliated by spruce budworm, there were essentially three foliage age classes present, compared with about 11 age classes on protected trees (Fleming & Piene 1992). On defoliated trees, current and 1-year-old foliage comprised on average 58 and 72% of the foliage weight for spaced and unspaced plots, respectively, which was significantly greater than protected plots that had 41 and 49% of foliage weight in the two youngest age classes. On New Zealand Douglas-fir impacted by SNC and lepidopterous defoliators, needle retention was reduced to the point that 67-82% of the total foliage was current and one-year-old needles (Kay 1978). Four of the five trees sampled also held a greater dry weight of one-year-old than current-year needles (Kay 1978). In the Oregon Coast Range, Douglas-fir held between 37 and 87% of its foliage as current and one-year-old needles, a range containing the values reported by Kay (1978) and Piene et al. (2003). An average-sized Douglas-fir tree held 81% of its foliage as current and 1-year-old needles on a plot rated to have one year of retention, while a tree on a plot rated as four years for foliage retention had 56% of its needles in the two youngest age classes. These trends are not surprising given that SNC causes pre-mature loss of older needles. For a relatively healthy Douglas-fir in the Oregon Coast Range was similar, but slightly higher than, those reported both for other Douglas-fir in the Pacific Northwest (Silver 1962; Dice 1970) and for balsam fir in eastern North America (Baskerville 1965; Clark 1961).

Both mean foliage retention on a plot and crown length to sapwood area ratio for an indiviual tree provide an effective index of the amount of foliage dry matter in each age class. While plot foliage retention is correlated with relative and absolute foliage mass by age class (Maguire et al. 2002), crown length to sapwood ratio had a greater correlation with the foliage mass in 2-year-old needles on an individual sample branch than any other SNC indices (Maguire & Kanaskie 2002). The failure of crown length to sapwood area ratio to predict four-year-old and older foliage indicates that foliage retention may be a slightly better index of relative foliage mass by age class. Conversely, crown length to sapwood area gives a more useful index of absolute foliage mass (Chapter Four).

Vertical distribution

The distribution of current-year foliage has been regarded as influenced by prevailing light conditions, while environmental factors other than light (e.g. water supply) become more important as the foliage ages (Kellomaki et al. 1980; Piene & MacLean 1999). This generalization by the greater production of new foliage in the upper third of a tree's crown, and the predominance of older foliage in the lower crown (Silver 1962; Dice 1970). On SNC-impacted Douglas-fir in New Zealand, Kay (1978) found that younger foliage still predominated in the upper crown and older foliage predominated in the lower crown, but a well-defined maximum mass for each age class was found in the mid-crown region. On healthy Douglas-fir in the Pacific Northwest, Dice (1970) found the maximum foliage dry matter relatively high in the crown, and Woodman (1971) found the maximum amount often located at a height approximately equal to 80% of the tree height. Maximum foliage dry matter of current and 1-year-old foliage on trees severely impacted by SNC was shifted upwards in comparison to a relatively healthy Douglas-fir, while the maximum of the 2-, 3-

and 4-year-old and older foliage age classes are shifted downwards (Figure 4.5). This pattern is most likely reflected in the infection biology of SNC. Manter (2001) indicated that within individual trees, fungal colonization was consistently higher in the upper portions of the crown, reducing needle retention nearly 15% when compared to a healthy tree. Rather than refoliating its lower branches with epicormic shoots, SNC-infested Douglas-fir shifted their production of current-year foliage towards the top of the crown. Although the construction costs of shoots increase with relative irradiance, construction costs of needles are independent of relative irradiance (Niinemets 1997c). Douglas-fir with severe SNC formed their new foliage where it can capture the greatest light, thereby shifting the distribution upwards. In contrast, foliage in healthy Douglas-fir place is generally near the crown periphery presumably to avoid self-shading. The higher specific leaf area and greater density of current-year foliage in the upper crown in SNC-impacted Douglas-fir may predispose the trees to continual reinfestation by the fungus. Furthermore, the deeper penetration of light appeared to promote longer retention in the bottom of the crown, as suggested by Maguire and Kanaskie (2002) and indicated by the models of Thornley (1991). This alteration in the spatial distribution of the needle area within the crown and canopy may have pronounced effects on light interception, canopy assimilation, and total dry matter production (Mohren & Bartelink 1990; Larsen & Kershaw 1996).

Vertical distribution of total foliage dry matter is influenced by relative tree height (Maguire & Bennett 1996; Gilmore & Seymour 1997; Garber 2002), tree size (Maguire &

Bennett 1996; Xu & Harrington 1998) and stand density (Kellomaki et al. 1980; Maguire & Bennett 1996). Relatively little work has been done on the vertical distribution of foliage by age class. In Scots pine, Kellomaki (1980) indicated that stand top height and stand density influenced the vertical distribution of each needle age class. However, very little of the variance was explained and the explanatory power of stand density decreased with increasing needle age (Kellomaki et al. 1980). In Douglas-fir of the Oregon Coast Range, most of the variation in the vertical distribution of needle age classes was explained by stand and site factors rather than individual tree attributes. However, crown length, crown ratio, and crown surface area were significant in several of the equations, probably related to both light distribution within the crown and the social position of the tree or competition for light and other resources among trees. Overall, crown condition was the most important variable influencing vertical foliage distribution given distance from the coast, aspect, and foliage retention are all factors influencing the presence and severity of SNC.

The effects of premature needle loss, changes in the age-class structure, and shifts in vertical distribution are strongly dependent on the stand's initial leaf area index (Mohren & Bartelink 1990). Baskerville and Kleinschmidt (1981) suggested that modifications in foliage age structure and its spatial distribution can influence the canopy productive structure for at least eight more years even after cessation of budworm defoliation. The effects of prolonged defoliation, by insects has received considerable attention (e.g. Brookes et al. 1978;

Brookes et al. 1987; Piene et al. 2003), but long-term fluctuations in and effects of premature foliage loss induced by foliar diseases have rarely been documented.

CONCLUSION

Indices of crown condition represent many different aspects of crown structure and health. Crown density is correlated with the amount of foliage dry matter on a tree, while crown color is associated with the physiological condition of the foliage, including photosynthetic ability. Most of these indices attempt to describe the condition and size of needles because they have a profound influence on tree growth. Little is known, however, about how well these indices, particularly foliage retention, relate to detailed aspects of crown structure that are difficult to measure. In addition, the size of the foliage is highly sensitive to crown condition, which has important implications for the connection between these crown indices and their biological meaning. Douglas-fir needles in the Oregon Coast Range appear to be significantly influenced by the presence of SNC. Needle dry weight, length, width, and projected leaf area all showed a significant positive relationship with foliage retention. Specific leaf area, on the other hand, was positively related to crown sparseness, but not foliage retention. Both foliage retention and crown length to sapwood area ratio showed a significant relationship with the absolute amount of foliage in each age class. Foliage retention had slightly more predictive power, primarily because the crown length to sapwood area ratio was not significantly related to the amount of 4-year-old and older foliage on a tree. SNC altered foliage dynamics in a way that increased representation of the younger age classes, mostly due to the premature loss of the older age classes. SNC has also modified the vertical distribution of each foliage age class. With more severe SNC, current and 1-year-old foliage was shifted higher in the crown, while 2-, 3-, and 4-year-old and older foliage were shifted lower in the crown. These shifts reflected the infection biology of the disease and the light conditions imposed by premature loss of older needles. Growth losses associated with SNC in the Oregon Coast Range were imposed not only by the loss of foliage area, but also by the impacts of SNC on the size and age-class distribution of the needles.

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Table 5.1. Attributes of the 12 plots sampled in 2002 for determination of needle size, leaf area, and foliage age distribution.

Attribute	Mean	SD	Min	Max
Douglas-fir basal area (m^2/ha)	23.29	7.86	9.97	36.62
Douglas-fir trees per ha	707.04	327.86	259.35	1222.65
Douglas-fir quadratic mean diameter (cm)	22.39	8.06	11.41	36.45
Douglas-fir relative density (Curtis (1982); (m^2 ha^{-1}/$\sqrt{}$)	4.91	1.19	2.95	6.56
Douglas-fir stand density index (Reineke (1933), trees/ha at mean DBH of 25.4 cm)	481.89	124.04	270.04	667.41
Basal area in other conifers (m^2/ha)	0.63	0.85	0.00	2.21
% basal area in other conifer	0.10	0.21	0.00	0.76
Basal area in hardwoods (m^2/ha)	0.50	0.60	0.00	2.13
% basal area in hardwoods	0.06	0.06	0.00	0.16
Total basal area (m^2/ha)	30.97	14.95	10.44	69.64
Average breast-height age (yr)	18.67	4.96	11.00	27.80
Average foliage retention (yr)	2.61	0.84	1.20	4.30
Site index (Bruce (1981); height at 50 yr, in m)	39.53	3.21	34.80	43.90

Table 5.2. Attributes of the 36 Douglas-fir trees sampled in 2002 for determination of needle size, leaf area, and foliage age distribution.

Attribute	Mean	SD	Min	Max
DBH (cm)	23.88	5.34	12.50	35.10
Height (m)	17.74	5.37	9.14	33.5
Height to live crown (m)	5.62	3.03	0.10	10.90
5-yr height increment (m)	0.74	0.22	0.33	1.18
Crown width (m)	4.44	0.97	2.79	7.22
Crown length (m)	11.28	2.22	6.59	15.71
Sapwood area at crown base (cm^2)	286.15	199.34	30.19	847.29
Relative height in the stand	0.92	0.11	0.63	0.99

Table 5.3. Attributes of the 328 sample branches used for determination of needle size, leaf area, and foliage age distribution.

Attribute	Mean	SD	Min	Max
Diameter (cm)	17.01	9.19	1.30	41.60
Length (m)	1.74	1.00	0.09	4.63
Depth in crown (m)	5.68	3.40	0.27	14.80
Current-year foliage mass (g)	31.33	40.46	0.00	211.74
One-year foliage mass (g)	35.17	44.63	0.00	226.30
Two-year foliage mass (g)	30.68	35.14	0.00	205.48
Three-year foliage mass (g)	20.17	29.63	0.00	161.98
Four-year and older foliage mass(g)	4.86	17.01	0.00	156.65
Total foliage mass (g)	116.67	146.14	0.36	794.96
Woody mass (g)	226.81	284.92	0.16	1766.86

Table 5.4. Linear and nonlinear model forms for predicting leaf area at the branch-level.

Model	Model form	Source
1	$\beta_0 BD^{\beta_1} DINC^{\beta_2}$	Monserud and Marshall 1999
2	$\beta_0 + \beta_1 \ln(BD) + \beta_2 DINC$	Kershaw and Maguire 1995
3	$\beta_0 + \beta_1 \ln(BD) + \beta_2 \ln(DINC) + \beta_3 \ln(RHACB)$	Kershaw and Maguire 1995
4	$\beta_0 BD^2 + \beta_1 BD^2 * RHT * (1-RHT)$	Bartelink 1996
5	$\beta_0 BD^{\beta_1} RDINC^{\beta_3 - 1} * \exp(-(\beta_2 RDINC)^{\beta_3}$	Maguire and Bennett 1996

Table 5.5. Linear and nonlinear model forms screened for prediction of total leaf area at the tree-level.

Model	Model form	Source
6	$\beta_0 CL^{\beta_1} \exp(\beta_2 DBHHT)$	Maguire and Bennett 1996
7	$\beta_0 BACR^{\beta_1}$	Kenefic and Seymour 1999
8	$\beta_0 SBHCR^{\beta_1}$	Kenefic and Seymour 1999
9	$\beta_0 + \beta_1 \ln(DBH) - \beta_2 \ln(HT)$	Bartelink 1996
10	$\beta_0 DBH^{\beta_1}$	Garber 2002
11	$\beta_0 + \beta_1 \ln(CSA)$	

Table 5.6. Attributes of the 100-needle subsamples including total dry weight (DW; g), mean needle length (NL; mm), mean needle width (NW; mm), and mean specific leaf area (SLA; cm^2/g).

Foliage age class	Measurement	# of samples	Mean	SD	Min	Max
1	DW	155	0.37	0.18	0.07	0.89
	NL	146	19.84	4.12	9.49	34.44
	NW	141	1.24	0.15	0.83	2.04
	SLA	103	81.09	28.31	45.45	180.44
2	DW	138	0.42	0.16	0.07	1.00
	NL	128	20.57	3.51	14.23	32.91
	NW	125	1.22	0.14	0.93	1.52
	SLA	89	72.09	23.76	34.33	103.88
3	DW	111	0.45	0.15	0.15	0.92
	NL	101	21.64	3.87	14.85	33.07
	NW	99	1.24	0.14	0.96	1.29
	SLA	70	64.98	12.55	35.66	95.61
4	DW	81	0.51	0.14	0.18	0.94
	NL	72	22.32	3.37	15.49	31.29
	NW	72	1.28	0.12	0.97	1.63
	SLA	45	59.69	9.05	29.94	77.94

Table 5.7. Parameter estimates, standard errors, and p-values for needle dry weight model (equation 5.1).

Parameter	Estimate	Standard error	P-value
β_{10}	-6.9595	1.0978	<0.0001
β_{11} Current	-0.5267	0.0424	<0.0001
1-yr-old	-0.3044	0.0350	<0.0001
2-yr-old	-0.1236	0.0288	<0.0001
β_{12}	-0.0540	0.0071	<0.0001
β_{13}	1.2874	0.2496	<0.0001
β_{14}	0.1424	0.0260	<0.0001
β_{15}	1.7021	0.4587	0.0003
β_{16}	-0.0411	0.0111	0.0003

Table 5.8. Parameter estimates, standard errors, and p-values for mean projected leaf area (equation 5.2).

Parameter	Estimate	Standard error	P-value
β_{20}	3.7237	0.1095	<0.0001
β_{21} Current	-0.1106	0.0181	<0.0001
1-yr-old	-0.0748	0.0156	<0.0001
2-yr-old	-0.0159	0.0134	0.2365
β_{22}	-0.03416	0.0116	0.0037
β_{23}	-0.4314	0.0805	<0.0001
β_{24}	0.1129	0.0168	<0.0001
β_{25}	0.0421	0.0126	0.0011

Table 5.9. Parameter estimates, standard errors, and p-values for mean needle length (equation 5.3).

Parameter	Estimate	Standard error	P-value
β_{30}	0.4359	0.1283	0.0009
β_{31} Current	-0.0594	0.0133	0.0133
1-yr-old	-0.0535	0.0118	<0.0001
2-yr-old	-0.0275	0.0102	0.0072
β_{32}	-0.0347	0.0081	<0.0001
β_{33}	0.0377	0.0092	<0.0001
β_{34}	0.0085	0.0026	0.0013
β_{35}	0.1266	0.04045	0.0021
β_{36}	-0.0114	0.0035	0.0013

Table 5.10. Parameter estimates, standard errors, and p-values for mean needle width (equation 5.4).

Parameter	Estimate	Standard error	P-value
β_{40}	-1.5413	0.1374	<0.0001
β_{41} Current	-0.1534	0.0217	<0.0001
1-yr-old	-0.0942	0.0178	<0.0001
2-yr-old	-0.0386	0.0146	0.0085
β_{42}	0.1363	0.0212	<0.0001
β_{43}	-0.5108	0.0978	<0.0001
β_{44}	0.0347	0.0144	0.0176

Table 5.11. Parameter estimates, standard errors, and p-values for specific leaf area (equation 5.5).

Parameter	Estimate	Standard error	P-value
β_{50}	3.7234	0.0609	<0.0001
β_{51} Current	0.3794	0.0341	<0.0001
1-yr-old	0.2219	0.0308	<0.0001
2-yr-old	0.0981	0.0273	<0.0001
β_{52}	0.0524	0.0048	<0.0001
β_{53}	0.00007	0.0001	<0.0001
β_{54}	-0.0003	0.0001	<0.0001
β_{55}	0.0105	0.0039	0.0003

Table 5.12. Model fit statistics for models describing 100-needle subsamples equations 5.1 to 5.5.

Model	RMSE	R^2
NDW	0.3748	0.3215
MPLA	0.1986	0.3226
MNL	0.1505	0.3619
MNW	0.1041	0.2203
SLA	0.1912	0.5343

Table 5.13. Weighting factors and fit statistics for linear and nonlinear models screened for prediction of leaf area at the branch-level. Model numbers correspond to Table 5.4. The fit statistics are the result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
1	BD^{-2}	0.6983	4.4488	76.1369	Monserud and Marshall 1999
2	-	0.6922	0.9059	55.2277	Kershaw and Maguire 1995
3	-	0.7720	0.7720	47.0633	Kershaw and Maguire 1995
4	-	0.5960	1.0378	63.2669	Bartelink 1996
5	BD^{-2}	0.7041	4.9999	77.0125	Maguire and Bennett 1996

Table 5.14. Parameter estimates, standard errors, and p-values for the model predicting total between branch leaf area (equation 5.6).

Parameter	Estimate	Standard error	P-value
β_{60}	-1.8713	0.2112	<0.0001
β_{61}	1.6502	0.1040	<0.0001
β_{62}	1.2996	0.0966	<0.0001
β_{63}	1.2546	0.0941	<0.0001
β_{64}	0.5140	0.1148	<0.0001
β_{65}	0.2492	0.0622	<0.0001
β_{66}	-0.0329	0.0108	0.0024

Table 5.15. Weighting factors and fit statistics for linear and nonlinear models screened for prediction of leaf area at the tree-level. Model numbers correspond to Table 5.5. The fit statistics are a result of fitting the models to the pooled data set.

Model	Weight	R_g^2	$\sqrt{MSE}$	FI	Source
6	$CL^{-4.0}$	0.7234	0.0378	5.3883	Maguire and Bennett 1996
7	$BACR^{-1.0}$	0.6083	32.7395	5.8912	Kenefic and Seymour 1999
8	$SBHCR^{-1.0}$	0.3409	8.3999	8.2132	Kenefic and Seymour 1999
9	-	0.3397	0.6070	7.6643	Bartelink 1996
10	$DBH^{-1.5}$	0.3543	0.7014	7.7624	Garber 2002
11	-	0.6978	0.4161	5.2545	

Table 5.16. Parameter estimates, standard errors, and p-values for the model predicting total tree leaf area (equation 5.7).

Parameter	Estimate	Standard error	P-value
β_{70}	0.4597	0.8833	0.6046
β_{71}	0.0088	0.0008	<0.0001
β_{72}	0.6471	0.2053	0.0024
β_{73}	-0.7119	0.1505	<0.0001
β_{74}	0.0392	0.0174	0.0273
β_{75}	4.1518	1.2502	0.0015
β_{76}	0.2158	0.0692	0.0027
β_{77}	-0.0424	0.0119	0.0007

Table 5.17. Root mean square error and R^2 for models in the systems of equation used to predict the amount of foliage in each age class at the tree-level (equation 5.10).

	Ordinary least squares		Seemingly unrelated regression	
Model	Root mean square error	R^2	Root mean square error	R^2
F1	0.2333	0.8592	0.2281	0.8429
F2	0.3126	0.8322	0.2985	0.8251
F3	0.3502	0.8611	0.3371	0.8530
F4	0.7315	0.8382	0.7030	0.8292
F5	0.9089	0.8466	0.9093	0.8245
F	-	-	6270.0	0.6847

Table 5.18. Parameter estimates, standard errors, and p-values for models predicting total tree foliage mass by age class (equation 5.10).

Parameter	Estimate	Standard error	P-value
β_{100}	-1.717	1.6195	0.2999
β_{101}	0.010	0.0011	<0.0001
β_{102}	1.495	0.3136	<0.0001
β_{103}	0.220	0.0402	<0.0001
β_{104}	-0.056	0.0084	<0.0001
β_{105}	0.004	0.0009	0.0003
β_{106}	3.518	0.6429	<0.0001
β_{107}	-0.039	0.0078	<0.0001
β_{108}	-0.090	0.0159	<0.0001
β_{109}	-3.281	2.0431	0.1214
β_{110}	0.010	0.0014	<0.0001
β_{111}	1.969	0.4046	<0.0001
β_{112}	0.241	0.0506	<0.0001
β_{113}	-0.059	0.0107	<0.0001
β_{114}	3.357	0.8101	0.0004
β_{115}	-0.050	0.0098	<0.0001
β_{116}	-0.084	0.0200	0.0003
β_{117}	-5.496	2.3426	0.0276
β_{118}	0.012	0.0014	<0.0001
β_{119}	2.144	0.4564	<0.0001
β_{120}	0.279	0.0581	<0.0001
β_{121}	-0.075	0.0120	<0.0001
β_{122}	3.852	0.9199	0.0003
β_{123}	-0.055	0.0117	<0.0001
β_{124}	-0.093	0.0227	0.0004
β_{125}	-17.973	5.1206	0.0018
β_{126}	0.018	0.0032	<0.0001
β_{127}	5.139	0.9768	<0.0001
β_{128}	0.463	0.1264	0.0012
β_{129}	-0.104	0.0258	0.0005
β_{130}	7.501	2.0113	0.0010
β_{131}	-0.089	6.0420	0.0197
β_{132}	-0.171	0.0047	<0.0001
β_{133}	15.102	6.2983	0.0028
β_{134}	0.032	0.0581	<0.0001
β_{135}	-20.951	7.3912	0.0088
β_{136}	-0.334	0.9464	<0.0001
β_{137}	-21.094	8.0972	<0.0001
β_{138}	5.530	1.2583	<0.0001
β_{139}	37.188	0.0263	0.0023
β_{140}	-6.338	0.0495	0.0021

Table 5.19. Model forms and fit statistics for ordinary least squares models predicting beta-distribution parameters describing vertical distribution of foliage by age class.

Age class	**Model form**	**R^2**	**RMSE**
Current	$a_1 = \eta_{11} + \eta_{12}AGE + \eta_{13}BAPH + \eta_{14}PBADF + \eta_{15}SLOPE + \eta_{16}COAST + \eta_{17}FOLRET$	0.6819	0.4260
Current	$b_1 = \eta_{21} + \eta_{22}\ PBADF + \eta_{23}\ COAST + \eta_{24}ASP12$	0.6457	0.6996
1	$a_2 = \eta_{31} + \eta_{32}CL + \eta_{33}BAPH + \eta_{34}\ FOLRET + \eta_{35}(CL*FOLRET)$	0.4448	0.6402
1	$b_2 = \eta_{41} + \eta_{42}AGE + \eta_{43}BAPH + \eta_{44}PBADF + \eta_{45}SLOPE + \eta_{46}COAST + \eta_{47}FOLRET + \eta_{48}(COAST*FOLRET)$	0.7145	0.4991
2	$a_3 = \eta_{51} + \eta_{52}CL + \eta_{53}AGE + \eta_{54}BAPH + \eta_{55}COAST + \eta_{56}FOLRET$	0.6108	0.6231
2	$b_3 = \eta_{61} + \eta_{62}CR + \eta_{63}AGE + \eta_{64}BAPH + \eta_{65}PBADF + \eta_{66}COAST + \eta_{67}\ FOLRET + \eta_{68}(CR*FOLRET)$	0.7149	0.3828
3	$a_4 = \eta_{71} + \eta_{72}BAPH + \eta_{73}PBADF + \eta_{74}COAST + \eta_{75}FOLRET + \eta_{76}(COAST*FOLRET)$	0.5115	1.5234
3	$b_4 = \eta_{81} + \eta_{82}CR + \eta_{83}AGE + \eta_{64}BAPH + \eta_{85}PBADF + \eta_{86}COAST$	0.4547	0.3796
4+	$a_5 = \eta_{91} + \eta_{92}AGE + \eta_{93}CSA + \eta_{94}TPH + \eta_{95}PBADF$	0.4019	1.7609
4+	$b_5 = \eta_{101} + \eta_{102}CR + \eta_{103}BAPH + \eta_{105}PBADF + \eta_{106}FOLRET + \eta_{106}(CR*FOLRET)$	0.5218	0.4276
System		0.7094	0.8594

AGE, stand average breast height age (years); BAPH, stand basal area ($m^2\ ha^{-1}$); PBADF, Douglas-fir percent basal area; SLOPE, slope (%); COAST, stand distance from coast (km); FOLRET, stand foliage retention in 2002; ASP12, cosine transformation of aspect and slope; CL, tree crown length (m); CR, tree crown ratio; CSA, crown surface area (m^2); TPH, number of trees in stand (# ha^{-1})

Table 5.20. Parameter estimates, standard errors, and p-values for predicting the *a*-parameter of the beta-distribution for vertical distribution of foliage by age class. Estimates were obtained using seemingly unrelated regression.

Parameter	**Estimate**	**Standard error**	**P-value**
η_{11}	7.0926	1.1215	<0.0001
η_{12}	-0.0698	0.0142	<0.0001
η_{13}	-0.0281	0.01278	0.0361
η_{14}	-2.0726	0.7913	0.0139
η_{15}	0.01762	0.0038	<0.0001
η_{16}	0.1287	0.0265	<0.0001
η_{17}	-0.8401	0.1929	0.0002
η_{31}	7.4111	1.3650	<0.0001
η_{32}	-0.3464	0.09872	0.0014
η_{33}	-0.0206	0.0096	0.0405
η_{34}	-0.5732	0.4662	0.2282
η_{35}	0.0741	0.3666	0.0490
η_{51}	9.3283	0.9294	<0.0001
η_{52}	-0.1236	0.05699	0.0382
η_{53}	-0.0804	0.0267	0.0052
η_{53}	-0.0444	0.0089	<0.0001
η_{54}	0.1204	0.0299	0.0004
η_{55}	-0.8677	0.2501	0.0016
η_{71}	25.7706	4.6156	<0.0001
η_{72}	-0.2495	0.04962	<0.0001
η_{73}	-18.4953	2.9497	<0.0001
η_{74}	1.0675	0.2215	<0.0001
η_{75}	0.0609	1.1126	0.9566
η_{76}	-0.2548	0.0772	0.0025
η_{91}	-14.5024	5.2715	0.0098
η_{92}	0.2737	0.0859	0.0033
η_{93}	-0.0336	0.0083	0.0004
η_{94}	0.0031	0.0008	0.0010
η_{95}	18.9400	4.0099	<0.0001

Table 5.21. Parameter estimates, standard errors, and p-values for *b*-parameter of the beta-distribution for vertical distribution of foliage by age class. Estimates were obtained using seemingly unrelated regression.

Parameter	**Estimate**	**Standard error**	**P-value**
η_{21}	4.7179	0.4578	<0.0001
η_{22}	-3.7181	0.5888	<0.0001
η_{23}	0.1078	0.0229	<0.0001
η_{24}	0.0288	0.0047	<0.0001
η_{41}	7.6202	1.0689	<0.0001
η_{42}	0.0975	0.0141	<0.0001
η_{43}	-0.0823	0.0123	<0.0001
η_{41}	0.0244	0.0028	<0.0001
η_{42}	0.3739	0.0506	<0.0001
η_{43}	0.1948	0.2232	<0.0001
η_{44}	-0.0739	0.0151	<0.0001
η_{61}	6.2319	1.0492	<0.0001
η_{62}	1.0847	0.8875	0.2318
η_{63}	0.0249	0.0115	0.0380
η_{64}	-0.0509	0.0101	<0.0001
η_{65}	-4.8753	0.6224	<0.0001
η_{66}	0.0577	0.0201	0.0074
η_{66}	0.4452	0.2993	0.1481
η_{67}	-0.7297	0.3377	0.0394
η_{81}	4.4186	0.6256	<0.0001
η_{82}	-0.6745	0.2803	0.0225
η_{83}	0.0330	0.0110	0.0054
η_{84}	-0.0245	0.0078	0.0040
η_{85}	-2.5214	0.5359	<0.0001
η_{86}	0.0256	0.0120	0.0410
η_{111}	3.1209	1.1061	0.0084
η_{112}	1.1010	1.3314	0.4148
η_{113}	-0.0233	0.0086	0.0110
η_{114}	-2.5769	0.5266	<0.0001
η_{115}	1.0629	0.3877	0.0102
η_{116}	-1.0870	0.4981	0.0370

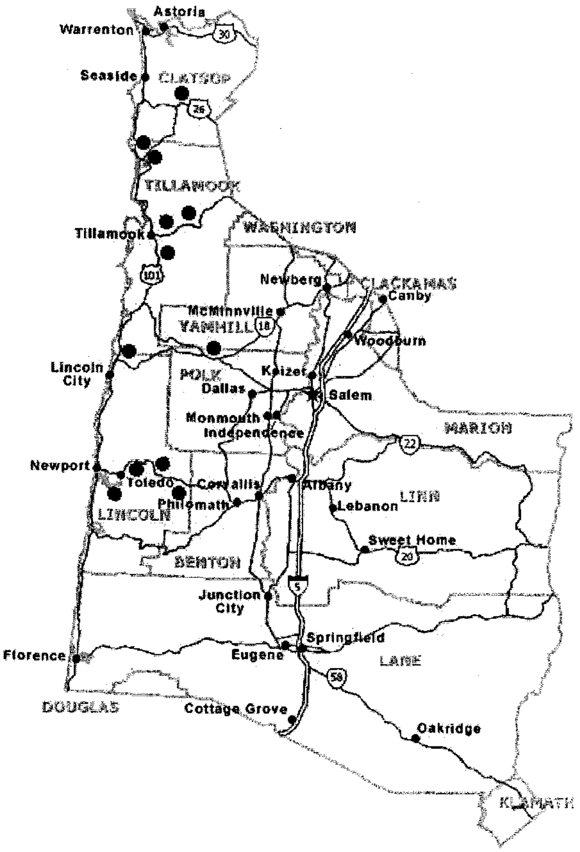

Figure 5.1. Location of the twelve plots used in this study.

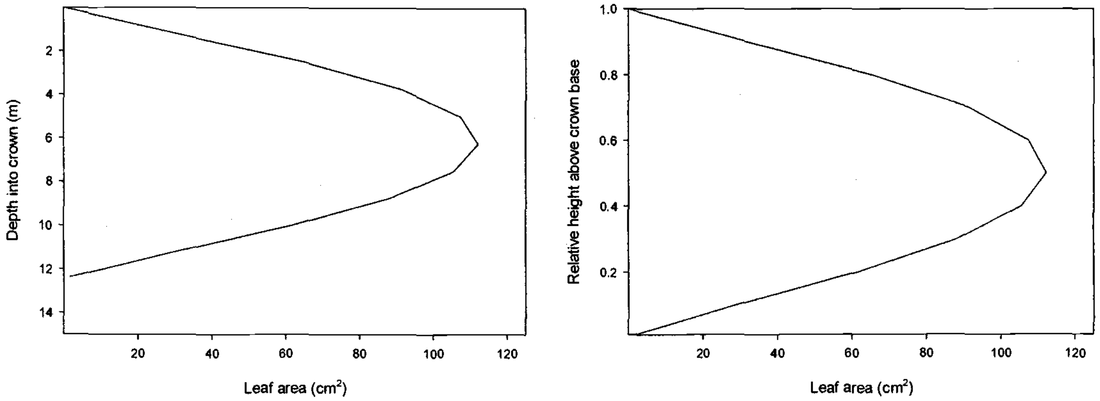

Figure 5.2. Behavior of branch leaf area model (equation 5.6) over depth into crown (left) and relative height above crown base (right) for an average-sized branch on a tree with a crown sparseness index of 6.5.

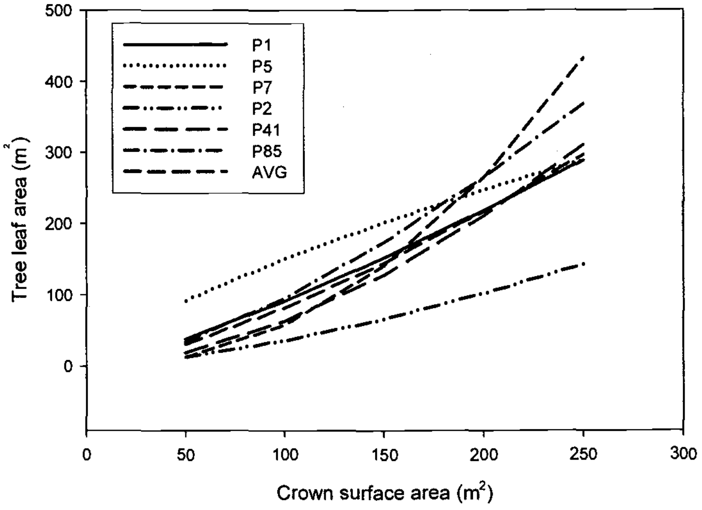

Figure 5.3. Behavior of the tree leaf area model (equation 5.12) for a few selected plots and the pooled data set.

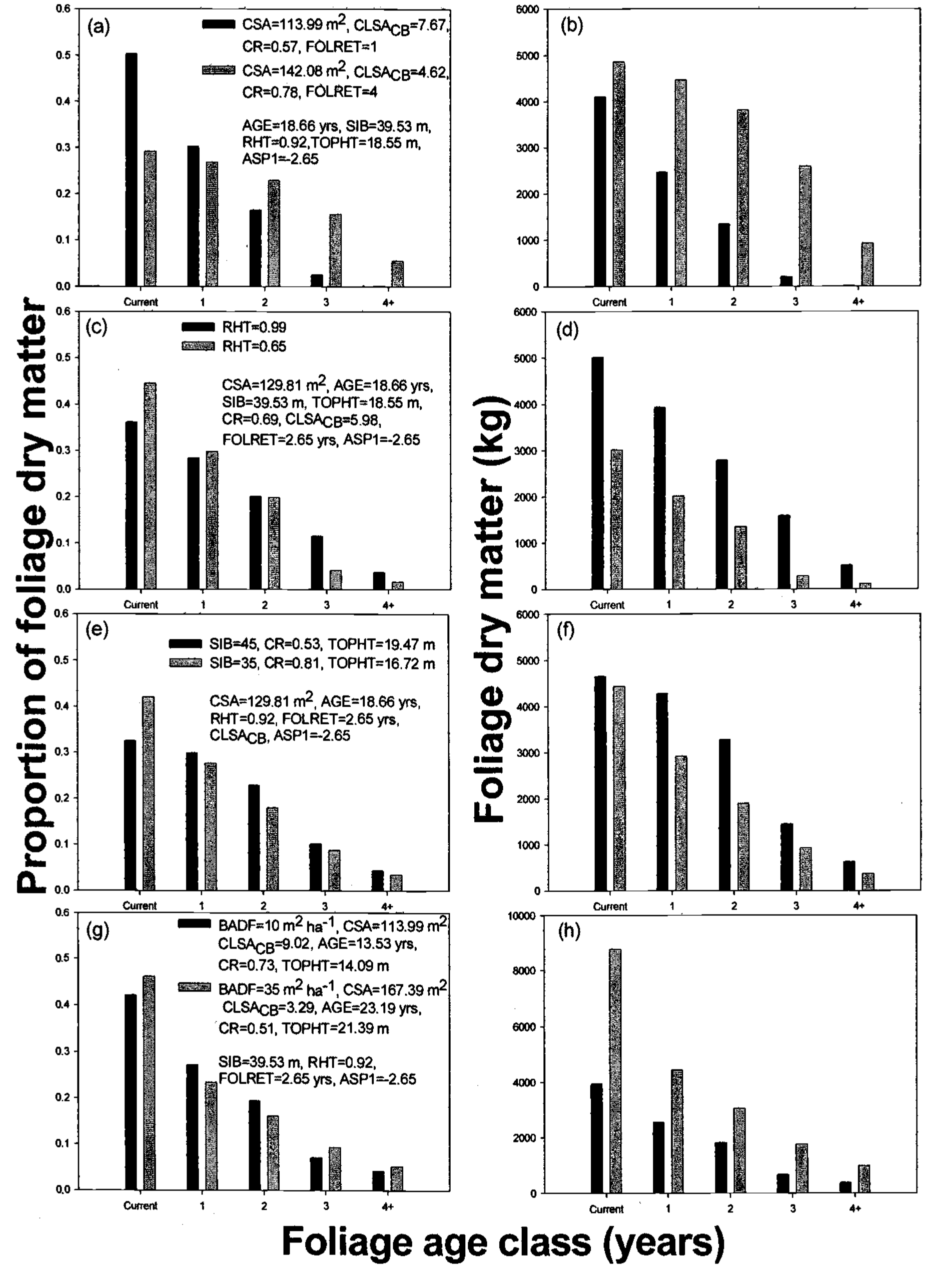

Figure 5.4. Influence of SNC (a, b); tree social position within stand (c, d); site index (e, f); and basal area (g, h) on the proportion (left panel) and total amount (right panel) of foliage dry matter on an average-sized tree.

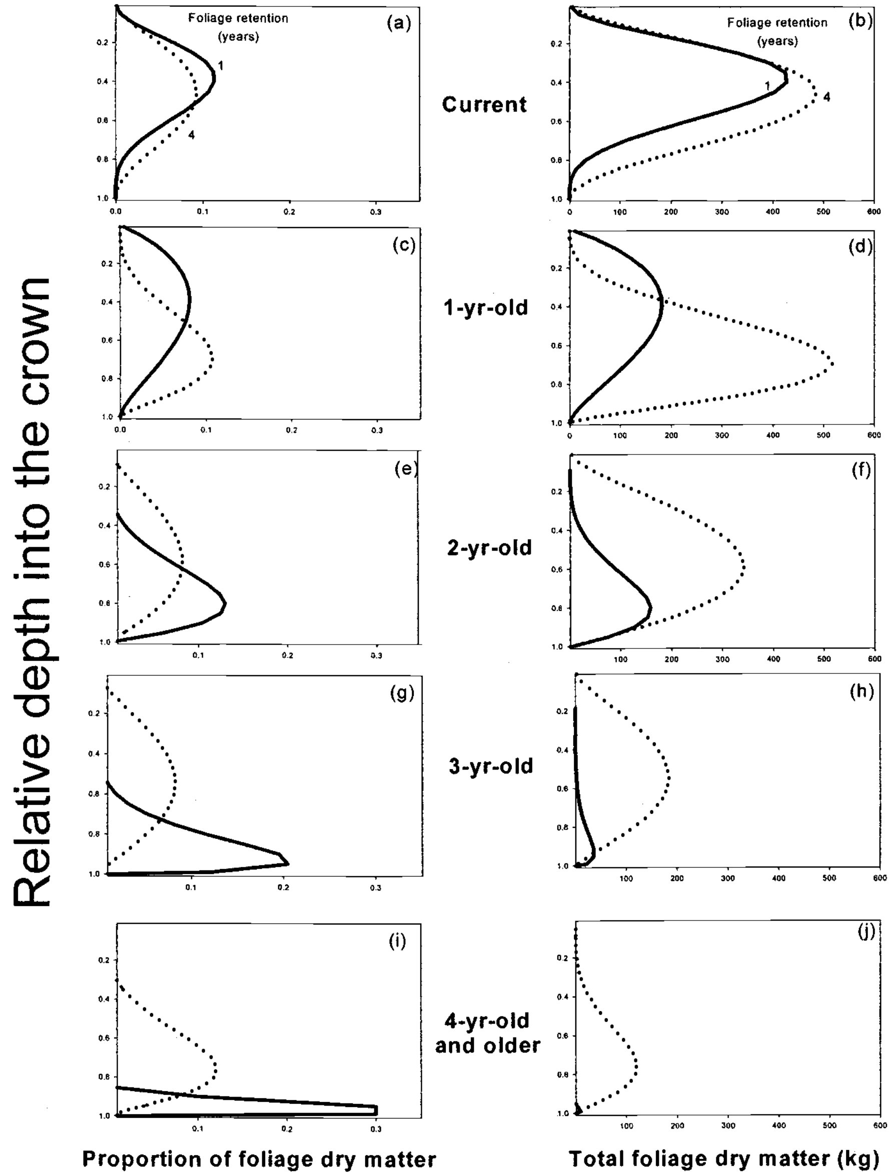

Figure 5.5. Relative (left) and absolute (right) vertical distribution by current (a, b); 1- (c, d); 2- (e, f); 3- (g, h); and 4-year-old and older (i j) foliage age classes for an average size tree on a plot with one (solid line) and four (dashed line) years of foliage retention.

CHAPTER SIX: INFLUENCES OF SWISS NEEDLE CAST ON DOUGLAS-FIR STAND DYNAMICS IN THE OREGON COAST RANGE

ABSTRACT

The effects of tree defoliation caused by an endemic plant disease on stand-level attributes were examined to understand how ecosystem processes might be altered by extended defoliation. This study was conducted in permanent monitoring plots located in Oregon Coast Range Douglas-fir plantations, which varied in density, age, composition, and Swiss needle cast (SNC) severity. The stand dynamic variables examined in this study included: crown recession rates; the amount, seasonal distribution, and size of litterfall; leaf area index (LAI); growth efficiency (GE); and crown condition variability. Results indicate that crown recession rates increase with more severe SNC, associated with a significantly higher rate of fine woody litterfall. Foliage litterfall, however, declined with greater SNC and most tended to occur in the fall, while a large portion fell in the summer as well. Under the influence of SNC, the specific leaf area (SLA) of foliage litterfall was higher than normal, implying changes in decomposition rates. The disease significantly reduced stand LAI, but overall growth efficiency increased. Variability of crown condition, as assessed by foliage retention and the crown sparseness index, showed a relationship with SNC as well as other site factors. Within-tree variability of foliage retention was significantly higher than within- or between-plot variability. The crown sparseness index was significantly less variable than foliage retention. Defoliation by SNC can significantly alter stand-level attributes as well as

ecosystem and landscape processes. Measurement of tree crown condition is difficult but has important implications for ecosystem dynamics.

INTRODUCTION

Extensive tree defoliation can significantly alter stand (Orwig et al. 2002) and ecosystem dynamics (Kizlinski et al. 2002), particularly volume growth (Piene et al. 2003). Other important stand and ecosystem attributes influenced by defoliation include litterfall (Bille-Hansen & Hansen 2001), decomposition (Cobb & Orwig 2003), soil temperature and moisture, nutrient-cycling (Kizlinski et al. 2002) and susceptibility to further disturbance (Mitchell 2000). Understanding the effects of defoliation at the landscape-scale, therefore, requires knowledge of its influence on stand-level attributes. Furthermore, in order to accurately understand the ecological implications of specific measures of defoliation intensity, annual variation in these measures between and within stands must be quantified.

Canopy structure strongly influences ecosystem processes by modifying the microclimatic conditions (Baldwin & Peterson 1997; Nagel & O'Hara 2001). In relatively simple single-cohort stands, canopy structure is largely determined by the geometry of individual tree crowns and their spatial aggregation. An important canopy attribute in these types of stands, therefore, is the depth of individual crowns and the entire canopy. Crown and canopy depth are primarily controlled by the crown recession rate relative to height growth rate. Generally after crown closure, crown recession rates are roughly proportional to height growth (Deleuze et al. 1996), but the proportion depends largely on stand density. Extensive defoliation may alter these rates by influencing height growth as well as the within-crown light environment. Litterfall rates resulting from accelerated needle loss and greater light and moisture at the forest floor may in turn increase decomposition, providing a feedback to growth and productivity

Litterfall rates have been documented for many forest types (Bray & Gorham 1964), but the influence of crown condition has not been clearly defined. Needle litterfall helps to assess the influence of climate and air pollution on crown condition (Innes 1993), but the primary limitation of this measure is that it does not reveal the amount of needles remaining on the tree (Kurkela & Jalkanen 1990). Some studies have found no correlation between defoliation and litterfall (Bille-Hansen & Hansen 2001; Poikolainen & Kubin 1997), while other studies have documented a positive correlation (Jukola-Sulonen et al. 1995; Arkley & Glauser 1980). On the other hand, Douglas-fir litterfall is sensitive to silvicultural treatments such as thinning (Trofymow et al. 1991; Dimock 1958) and fertilization (Gessel & Turner 1976), both of which influence crown recession and branch structure. Changes in the amount, composition, and size of litterfall have important implications for fire susceptibility (Bilgili 2003), tree regeneration (Molofsky & Augspurger 1992), decomposition (Piene 1981), soil microenvironment (Facelli & Pickett 1991), and nutrient-cycling (Trofymow et al. 1991).

Leaf area index (LAI) can explain 85-96% of the variation in the aboveground net primary production (ANPP) of forests in the western United States (Gholz 1982; Gower et al.

1992). LAI is strongly influenced by site conditions (Grier & Running 1977), stand species composition (Garber 2002), age (Woodward 1995), and other factors that influence the number and size of leaves such as climate (Margolis et al. 1995). The relatively slow growth, long leaf life spans, and late development of maximum LAI in conifer stands (Kozlowski and Pallardy 1997) allows them to develop higher LAI values (up to 20) than deciduous forest stands (3 to 6) (Waring & Schlesinger 1985). While LAI has been recognized as important stand attribute, relatively little is known about the degree of LAI change in response to fluctuations in stand health.

LAI is not perfectly correlated with annual net primary production (ANPP), in one sense because production per unit of leaf area can vary. Growth efficiency (GE; stemwood volume per unit leaf area) has received a significant amount of attention as a good measure of tree vigor (Waring et al. 1980) and biomass allocation (Waring 1983). Growth efficiency varies with site quality as well as stand spacing, age, and species composition (Oliver & Larson 1996). Tree crown shape strongly influences growth efficiency, in part because trees with smaller crowns have higher foliage mass to crown mass ratios and lower sapwood volumes, and therefore lower respiratory losses (Smith & Long 1989). While growth efficiency has been used to estimate the susceptibility to insect attack (Waring & Pitman 1985), relatively few studies have examined how stand disturbances such as extended defoliation caused by fungal diseases may modify stand growth efficiency.

A fundamental aspect of forest health assessments is the need for accurate and reliable stand-level indices. Crown indices such as discoloration, density, and transparency have been widely used (Innes 1993), but each has shortcomings resulting from the highly subjective nature of these ratings (Innes 1990). When needle loss occurs progressively from the oldest to the youngest needles, foliage retention is an excellent indicator of tree vigor (Innes & Boswell 1990; Innes 1993). This index, however, does not provide the relative amount of foliage by age class or the total amount of foliage (Maguire & Kanaskie 2002). Furthermore, little has been published on the variation of crown condition, particularly foliage retention and the crown sparseness index, within and between stands, nor on the relative degree of variation as stand health indicators fluctuate annually (Innes & Boswell 1990). While the mean foliage retention value for a stand is significantly correlated with SNC fungal pseduothecia counts (Maguire et al. 2002) and the crown sparseness index is significantly correlated with the mass in 2-year-old needles (Maguire & Kanaskie 2002), understanding and modeling their variability facilitates interpretation of their biological implications.

Swiss needle cast (SNC) is an increasingly important foliar disease of Douglas-fir (*Psedotsuga menziesii* (Mirb.) Franco) in the Oregon Coast Range and is thought to be changing important ecosystem processes by inducing premature needle loss and reduced tree growth. This disease, which is caused by the endemic pathogen, *Phaeocryptopus gauemannii*, has been noted to reduce foliage retention to as little as one year and volume growth by as much as 52% (Maguire et al. 2002). Currently, over 157,000 ha in the Oregon

Coast Range are currently showing SNC symptoms detectable by aerial survey, reflecting the dramatic increase in this disease in recent years (Kanaskie et al. 2002).

The overall objective of this study was to examine the impact of SNC on important stand attributes in the Oregon Coast Range. Specific objectives were to: (1) describe changes in the amount, composition, needle size, and timing of litterfall; (2) examine the disease impact on LAI and its implications for plot growth efficiency; and (3) assess the variability of foliage retention between years as well as within and between stands. The scope of inference for the study is young (10-30 year old), managed Douglas-fir plantations in the northwestern portion of the Oregon Coast Range.

METHODS

Study area

A sample of 22 young Douglas-fir plantations was selected from 76 permanent plots being monitored as part of the SNC Growth Impact Study sponsored by the SNC Cooperative at Oregon State University (Figure 6.1). The plots were located in the Oregon Coast Range within 32 km of the Pacific coast, north of Newport and south of Astoria, Oregon. The climate in this study area is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall in this area varies from approximately 180 to 300 cm/yr, and January mean minimum and July mean maximum temperatures range from –2 to 2°C and from 20 to 28°C, respectively (Maguire et al. 2002). Variations in precipitation and temperature for this area are strongly correlated with elevation and proximity to the coast. Elevation of the study plots ranged from 337 to 1,312 m, all aspects were represented, and proximity to the coast varied from 0.97 to 31.8 km.

Species composition of the plots was ≥90% Douglas-fir by basal area with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla*) and other conifer and hardwood species. The plots had similar stand attributes but varied in SNC intensity as estimated by average stand foliage retention (Table 1).

Data collection

Ratings of SNC intensity at each of the study sites has been collected every year since 1996 by the Oregon Department of Forestry. Square, 0.08 ha permanent plots were established by the SNC Cooperative (Oregon State University) in 1998. On each measurement plot, all trees were tagged at breast height and measured for DBH (nearest 0.1 cm). In addition, a subsample of at least 40 Douglas-fir were measured for total height and height to crown base. Plots were remeasured in 2000 and 2002, but, ten trees on each plot have been scored for SNC every year since 1998. On these trees, the crown is divided vertically into thirds and the average number of years that foliage was retained in each third was estimated visually to the nearest 0.1 year. Overall crown discoloration was also recorded on a 1 to 4 scale, with 4 representing the most severe discoloration. On branches in the fifth whorl from the top of the tree, the percentage retention by needle age class was recorded. Plot ratings were computed as the average from all ten trees.

Litterfall traps were placed in 15 of the sampled permanent plots in April, 2002 and were collected monthly for one year. Ten square 0.18 m^2 traps were systematically placed in the center of each of the plots, with at least 3 m from the plot edge and 3 m between traps. The litterfall was dried at 70°C for 48 h and separated into several different components including: (1) Douglas-fir foliage; (2) Douglas-fir woody material; (3) hardwood foliage; (4) hemlock foliage; and (5) other materials such as fruits, bud scales, and cones. A subsample from each month's litterfall was taken for specific leaf area (SLA) determination and nutrient analysis.

Data analysis

Various linear and nonlinear regression models were fitted to the data to assess the relationship between SNC and stand attributes. All-subsets regression analyses were run to screen for the potentially most powerful explanatory variables. Predictor variables included various stand and site values such as Douglas-fir basal area, basal area of competing species, site index, elevation, and distance from the coast. Final models were chosen on the basis of biological appeal, residual analysis, Furnival's index (FI) (Furnival 1961), and Akaike's information criterion (AIC). SNC impact was then assessed by adding various SNC indices such as foliage retention, crown sparseness index (crown length to sapwood area ratio), crown color, and crown density to the model. Final predictor variables were all significant at the $\alpha=0.05$. For nonlinear models the generalized coefficient of multiple determination (R_g^2) (Kvålseth 1985) was calculated as 1 – (residual sum of squares/ total corrected sum of squares). It was assumed that there is no plot effect besides SNC. All analyses were done in SAS v8.2 (SAS Institute, Cary, NC) and SPLUS 2000 (Mathsoft, Seattle, WA).

Crown recession

Mean crown recession rates for each stand were calculated by subtracting individual tree estimates of the height to crown base in 2002 from height to crown base made in 1998 and averaging for all trees on the plot. The relationship between crown recession rate and foliage retention was assessed with the following linear model:

$$\text{[6.1]} \quad \begin{aligned} \text{CRESS} = {} & \beta_{10} + \beta_{11}\ln(\text{PAGE}) + \beta_{12}\text{TOPHT} + \beta_{13}\text{ASP1} + \beta_{14}\ln(\text{BADF}) \\ & + \beta_{15}\text{FOLRET} + \beta_{16}(\text{ASP1} * \text{FOLRET}) + \varepsilon_1 \end{aligned}$$

where CRESS is mean stand crown recession rate (cm yr^{-1}), PAGE is plantation age in 2002, TOPHT is top height in 2002, ASP1 is a cosine transformation of aspect and slope (Stage 1976; % SLOPE * cos[(2*π*ASPECT)/360)]), BADF is Douglas-fir basal area (m^2 ha^{-1}) in 2002, FOLRET is mean plot foliage retention in 2002, ßi's are parameters to be estimated from the data, and $\varepsilon_1 \overset{iid}{\sim} N(0, \sigma_1^2)$.

Litterfall

Amount

The relationship between SNC and the amount of Douglas-fir foliage litterfall was examined with the following linear model:

$$\text{[6.2]} \quad \begin{aligned} \ln(\text{FLF}) = {} & \beta_{20} + \beta_{21}\text{CRESS} + \beta_{22}\text{COSA} + \beta_{23}\text{SIB} + \beta_{24}\text{FOLRET} \\ & + \beta_{25}(\text{CRESS} * \text{SIB}) + \varepsilon_2 \end{aligned}$$

where FLF is Douglas-fir litterfall (kg/ha), SIB is Bruce's (Bruce 1981) site index, COSA is the cosine-transformation of aspect (ASP; cos[(2*π*ASP)/360]), FOLRET is plot foliage retention in 2002, the β_i's are parameters to be estimated from the data, and $\varepsilon_2 \overset{iid}{\sim} N(0, \sigma_2^2)$.

The relationship between SNC and the amount of Douglas-fir fine woody litterfall was examined with the following linear model:

$$[6.3] \quad \ln(WLF) = \beta_{30} + \beta_{31}CRESS + \beta_{32}SIB + \beta_{33}COSA + \beta_{34}FOLRET + \varepsilon_3$$

where WLF is fine woody litterfall (kg,ha), the β_i's are parameters to be estimated from the data, $\varepsilon_3 \overset{iid}{\sim} N(0, \sigma_3^2)$, and all other variables are defined above.

Timing

To examine the influence of SNC on the seasonal trends of litterfall, four separate seasons were investigated: spring (Mar., Apr., and May.), summer (Jun, Jul., Aug), fall (Sept., Oct. and Nov.), and winter (Dec., Jan., and Feb.). The seasonal trend in foliage litterfall was then assessed with the following linear model:

$$[6.4] \quad \begin{aligned} \ln(FLF_{SEA}) = {} & \beta_{40} + \beta_{41}I_{SPR} + \beta_{42}I_{SUM} + \beta_{43}I_{FALL} + \beta_{44}COSA + \beta_{45}SIB + \beta_{46}FOLRET \\ & + \beta_{47}(SIB * FOLRET) + \varepsilon_4 \end{aligned}$$

where FLF_{SEA} is the total amount of foliage litterfall (kg ha^{-1}) in the season, I_{SPR} is an indicator variable for spring (1 if spring, 0 otherwise), I_{SUM} is an indicator variable for summer (1 if summer, 0 otherwise), I_{FALL} is an indicator variable for fall (1 if fall, 0 otherwise), the β_i's are parameters to be estimated from the data, $\varepsilon_4 \overset{iid}{\sim} N(0, \sigma_4^2)$, and all other variables are defined above.

The seasonal trend in fine woody litterfall was examined with the following linear model:

$$[6.5]\quad \ln(WLF_{SEA}) = \beta_{50} + \beta_{51}I_{SPR} + \beta_{52}I_{SUM} + \beta_{53}I_{FALL} + \beta_{54}\ln(ELEV) + \beta_{55}PCLSA_{CB} + \varepsilon_5$$

where WLF_{SEA} is the total amount of woody litterfall (kg ha^{-1}) in each season, ELEV is plot elevation (m), $PCLSA_{CB}$ is the plot mean crown length to sapwood area ratio at crown base ratio (a measure of crown sparseness) the β_i's are parameters to be estimated from the data, $\varepsilon_5 \overset{iid}{\sim} N(0, \sigma_5^2)$, and all other variables are defined above.

Litter specific leaf area

Similar to the seasonal distribution of litterfall, the SLA of each month's litterfall was separated into four seasons and compared using the following linear model:

$$[6.6]\quad \begin{aligned} SLA = {} & \beta_{60} + \beta_{61}I_{SPR} + \beta_{62}I_{SUM} + \beta_{63}I_{FALL} + \beta_{64}PAGE + \beta_{65}BADF + \beta_{66}SNC \\ & + \beta_{67}I_{SPR} * SNC + \beta_{68}I_{SUM} * SNC + \beta_{69}I_{FALL} * SNC + \varepsilon_6 \end{aligned}$$

where SLA is the specific leaf area (cm^2 g^{-1}), BADF is Douglas-fir basal area (m^2 ha^{-1}), SNC is a stand rating on 1 to 6 scale with 1 being healthy and 6 being a heavily infested plantation, the β_i's are parameters to be estimated from the data, $\varepsilon_6 \overset{iid}{\sim} N(0, \sigma_6^2)$, and all other variables are defined above.

Leaf area index

An equation to predict tree-level leaf area was developed (Chapter 5) and applied to trees within the permanent monitoring plot. The equation was of the following form:

[6.7] $\ln(\mathrm{TLA}) = \beta_{70} + \beta_{71}\mathrm{CSA} + \varepsilon_7$

where TLA is tree leaf area (m^2), CSA is crown surface area (m^2) estimated by numerically integrated equation 3.15, the β_i's are parameters to be estimated from the data for each plot, and $\varepsilon_7 \overset{\mathrm{iid}}{\sim} N(0, \sigma_7^2)$. LAI was then calculated by summing the tree leaf areas within the plot and dividing by plot area. The relationship between LAI and SNC was then assessed with the following model:

[6.8] $\ln(\mathrm{LAI}) = \beta_{80} + \beta_{81}\mathrm{SIB} + \beta_{82}\mathrm{AGE} + \beta_{83}\mathrm{PCLSA}_{\mathrm{CB}} + \beta_{84}\mathrm{FOLRET} + \varepsilon_8$

where AGE is mean stand breast height age in 2002, the β_i's are parameters to be estimated from the data, $\varepsilon_8 \overset{\mathrm{iid}}{\sim} N(0, \sigma_8^2)$, and all other variables are defined above.

Plot growth efficiency

Plot growth efficiency was defined in this study as stand stemwood volume increment per unit of leaf area. Stemwood volume was computed using Bruce and DeMars's (1974) volume equations. The relationship between foliage retention and plot growth efficiency was assessed with the following linear model:

[6.9]
$$\begin{aligned}\mathrm{GE} = {} & \beta_{90} + \beta_{91}\mathrm{SDIDF} + \beta_{92}\mathrm{ELEV} + \beta_{93}\mathrm{PCLSA}_{\mathrm{CB}} + \beta_{94}\mathrm{SIB} + \beta_{95}\mathrm{FOLRET} \\ & + \beta_{96}(\mathrm{SIB} * \mathrm{FOLRET}) + \varepsilon_9\end{aligned}$$

where GE is plot growth efficiency (cm^3 m^{-2} yr^{-1}), SDIDF is Reineke's (1933) stand density for Douglas-fir, the ß$_i$'s are parameters to be estimated from the data, $\varepsilon_9 \overset{iid}{\sim} N(0, \sigma_9^2)$, and all other variables are defined above.

Crown condition variability

Two methods were used to examine the variability of crown condition. First, the number of trees per plot and branches per tree in the case of foliage retention needed to detect a biologically meaningful change in crown condition was estimated. Equations presented in Maguire (2002) and Maguire and Kanaskie (2002) were used to determine biologically reasonable differences to detect for foliage retention as well as the crown length to sapwood area ratio. Since reductions of 0.2 years and 2.0 in foliage retention and the crown length to sapwood area ratio, respectively, were associated with 10% volume losses, these values were assumed to indicate biologically meaningful values. The sample-size formula for sampling without replacement from finite populations was calculated to determine the number of sample trees needed to have a 95% confidence interval with 0.2-yr and 2.0 half width for foliage retention and crown length to sapwood area ratio, respectively. The formula is of the following form:

[6.10] $$n = \frac{1}{(\frac{E}{2 * s})^2 + \frac{1}{N}}$$

where n is the number of sample units that should be measured to obtain the desired standard of precision, E is the desired half-width of the confidence interval, s is the standard deviation obtained from sampling the same population, and N is the number of sampling units in the population.

A similar approach was used to determine the number of samples needed from an individual tree to obtain a 95% confidence interval within 0.1-yr half width. Although some values within the sample-size formula depend on sample size, an iterative solution generally does not improve precision enough to justify its use (Avery et al. 2002). These values were then used in all-subset regression analysis to determine the effects of individual tree, stand, site and SNC variables. Finally, SAS PROC VARCOMP was used to see how the variability partitioned among years, within-tree, within-stand, and between stands.

RESULTS

Crown recession rates

Crown recession rates varied from 1.07 to 78.78 cm yr^{-1} and were significantly related to foliage retention ($p<0.001$ for β_{15} in equation 6.1). These rates increased with stand top height, Douglas-fir basal area, but decreased with plantation age and foliage retention (Table 6.2). Crown recession rates also peaked on more southerly sites. Foliage retention, however, had a decreasing effect as plots became more northerly. A one year decrease in foliage retention was associated with a 34 cm yr^{-1} increase in crown recession rate. The model explained 77% of the original variation and had a root mean square error (RMSE) of 9.5525.

Litterfall

Amount

Douglas-fir foliage accounted for, on average, 78% (54 – 92%) of the total annual litterfall, while Douglas-fir fine woody material comprised 13% (8 – 22%). Douglas-fir annual foliage litterfall ranged from 2,201.71 to 5,200.43 kg ha^{-1}, while Douglas-fir annual woody litterfall varied between 263.73 and 1,111.95 kg ha^{-1} (Table 6.3). Both the annual amount of Douglas-fir foliage ($p<0.0001$ for $ß_{24}$ in equation 6.3) and fine woody litterfall ($p<0.01$ for $ß_{33}$ in equation 6.4) were related to foliage retention. Douglas-fir foliage litterfall increased with mean stand crown recession rate, site index, and foliage retention (Table 6.4). Foliage litterfall peaked as sites became more northerly. The crown recession rate had a positive effect up until a site index of 39.5 m. Douglas-fir fine woody litterfall increased with crown recession rate, but decreased with both site index and foliage retention (Table 6.5). Woody litterfall also peaked as sites became more northerly. A stand with one year of foliage retention is expected to have 76.0% more annual foliage litterfall but 45.6% less fine woody litterfall than a stand with four years of foliage retention. The foliage litterfall model explained 91% of the original variation and had a root mean square error (RMSE) of 333.65, while the woody litterfall model had a R^2 of 0.91 and a RMSE of 83.41.

Timing

In general, nearly 52% (27 – 68%) of the foliage litterfall fell during the months of October, November, and December, regardless of foliage retention. On the other hand, nearly 52% (17 – 87%) of the fine woody litterfall fell during December, January, and February, regardless of foliage retention. The amount of foliage litterfall in each season increased with both site index and foliage retention (Table 6.6). The amount of foliage litterfall in each season also peaked as sites became more northerly. Foliage retention had a positive effect up until a site index of 40.2 m. Regardless of foliage retention, foliage litterfall rates were the highest in the fall, followed by the summer, winter, and spring (Figure 6.2). Woody litterfall increased with elevation and plot crown sparseness index. Woody litterfall rates were the highest in the winter, followed by the fall, spring, and summer. The foliage litterfall by season model explained 79.1% of the original variation and had a RMSE of 0.3683, while the woody litterfall by season model had a R^2 of 0.30 and a RMSE of 1.4266.

Size

Seasonal litterfall SLA ranged from 47.4 to 77.6 $cm^2 g^{-1}$ and was significantly related to SNC intensity ($p<0.05$ for $ß_{65}$ in equation 6.6). Litterfall SLA increased with plantation age and SNC intensity, but decreased with Douglas-fir basal area. Between seasons, litterfall SLA was the highest in the winter, but was only significantly greater than summer litterfall SLA ($p=0.0006$ for $ß_{62}$). Litterfall SLA was also significantly influenced by the interaction between SNC and season ($p<0.05$), indicating that the seasonal pattern in litterfall SLA differs between SNC intensities (Figure 6.3). The model explained 34.5% of the original variation and had a RMSE of 4.3933.

Leaf area index

The estimated LAI of these plots ranged from 0.59 to 16.71 (Figure 6.4) and had a significant relationship with foliage retention ($p<0.05$ for $ß_{84}$ in equation 6.9). LAI increased with site index, age, and foliage retention, but decreased with plot mean crown sparseness index (Table 6.9). A plot with one year of foliage retention is estimated to have a LAI that was 64.5% less than a plot with four years of foliage retention. The model explained 83% of the original variation and had a RMSE of 0.3323.

Plot growth efficiency

Plot growth efficiency ranged from 86.8 to 452.7 $cm^3\ m^{-2}\ yr^{-1}$ and was significantly related to foliage retention ($p=0.0055$ for $ß_{95}$ in equation 6.9). Growth efficiency increased with Douglas-fir stand density index, elevation, and plot mean crown sparseness index, but decreased with site index and foliage retention. Foliage retention had a positive effect on growth efficiency until a site index of 40.4 m. A plot with one year of foliage retention was estimated to have a growth efficiency that is 49.3% greater than a plot with four years of foliage retention. The model explained 80% of the original variation and had a RMSE of 59.8183.

Crown condition variability

The best model for predicting the number of sample trees needed to obtain a confidence interval for a plot-level foliage retention that has a 0.2-yr half width:

$$[6.11] \quad \begin{aligned} \mathrm{NFST} = {} & \beta_{110} + \beta_{111}\mathrm{YEAR} + \beta_{112}\mathrm{AGE} + \beta_{113}\mathrm{SIB} + \beta_{114}\mathrm{MFOLRET} \\ & + \beta_{115}(\mathrm{AGE} * \mathrm{MFOLRET}) + \beta_{116}(\mathrm{SIB} * \mathrm{MFOLRET}) + \varepsilon_{11} \end{aligned}$$

where NFST is the number of sample trees needed to determine plot mean foliage retention, YEAR is a set of indicator variables for year (2002, 2001, 2000, 1999, 1998, 1997), MFOLRET is six-year mean plot foliage retention, the ßi's are parameters to be estimated from the data, $\varepsilon_{11} \overset{iid}{\sim} N(0, \sigma_{11}{}^{2})$, and all other variables are defined above. The model explained 16% of the original variation and had a RMSE of 1.8445. The number of sample trees needed to obtain a confidence interval of a plot-level foliage retention value that has a half width of 0.2-yr increased with age, site index, mean plot foliage retention and each successive year since 1997, however sample size decreased with interactions between foliage retention, site index, and age (Table 6.11; Figure 6.5). The mean number of sample trees needed to obtain a confidence interval for a foliage retention value of 2.3 ± 0.2 yrs was 2.9, but ranged from 2 to 9 sample trees.

The best model for predicting the number of sample branches needed to obtain a confidence interval for tree-level foliage retention value with a half-with of 0.1-yr was:

$$[6.12] \quad \text{NBS} = \beta_{120} + \beta_{121}\text{YEAR} + \beta_{122}\text{DBHHT} + \beta_{123}\text{BAPH} + \beta_{124}\text{SDIDF} + \beta_{125}\text{SNC} + \varepsilon_{12}$$

where NBS is the number sample branches per tree, DBHHT is the diameter to height ratio, BAPH is the stand basal area (m^2 ha^{-1}), the ßi's are parameters to be estimated from the data, $\varepsilon_{12} \overset{iid}{\sim} N(0, \sigma_{12}{}^{2})$, and all other variables are defined above . The model only explained 7% of the original variation and had a RMSE of 0.6007. The number of sample branches needed to obtain a confidence interval for tree-level foliage retention value that has a half width of 0.1-yr increased with the tree diameter to height ratio and Douglas-fir stand density index, but decreased with stand basal area, SNC severity, and successive years from 1997 to 2002 (Table 6.12; Figure 6.6). The mean the number of sample branches needed to obtain a confidence interval for tree-level foliage retention value that has a half-width of 0.1-yr was 2.66, but varied from 2 to 5.

The best model for predicting the number of sample trees needled to obtain a confidence interval of a plot mean crown length to sapwood area ratio that has a half width of 2.0 was:

[6.13] $\mathrm{NCST} = \beta_{130} + \beta_{131}\mathrm{TPH} + \beta_{132}\mathrm{AGE} + \beta_{133}\mathrm{BADF} + \beta_{134}\mathrm{ASP12} + \beta_{135}\mathrm{FOLRET} + \varepsilon_{13}$

where NCST is the number of sample trees required to estimate the plot mean crown length to sapwood area ratio within the desired level of precision, TPH is the number of stems per ha, ASP12 is sine-transformation of slope and aspect (Stage 1976; % SLOPE * sin[(2*π*ASPECT)/360)]), the ßi's are parameters to be estimated from the data, $\varepsilon_{13} \overset{iid}{\sim} \mathrm{N}(0, \sigma_{13}^2)$, and all other variables are defined above. The number of sample trees required to obtain a confidence interval for a plot mean crown length to sapwood area ratio that has a half width of 2.0 increased with the number of trees per ha, age, and foliage retention, but decreased with Douglas-fir basal area (Table 6.13; Figure 6.7). The number of sample trees also peaked with southerly aspects. The model explained 78% of the original variation and had a RMSE of 0.6668. The mean number of sample trees needed to obtain a confidence interval for a plot mean crown sparseness index with a half width of 2 was 4.93 and varied from 2 to 9.

Most of the variation (39.0%) in foliage retention was influenced by within-tree variability (Table 6.14). A significant portion of the variation in foliage retention, however, was due to unaccounted for random variation (26.7%). On the other hand, the variance attributable to within- and between-plots variability was 6.5 and 19.4%, respectively, while SNC accounted for 7.2% of the variance. The variance attributable to year-to-year variation was small, comprising only 1.2% of the total variability in foliage retention. Most of the variation (87.3%) in the crown sparseness index was influenced by within-plot variability. Variation attributed to between-plot only comprised 9.9%, while variation due to SNC only made up 2.8%.

DISCUSSION

Litterfall, LAI, growth efficiency, and crown condition variability have a significant influence on several ecosystem processes. SNC in the Oregon Coast Range significantly altered these stand features in several ways. SNC induced higher rates of fine woody litterfall, but lower rates of foliage litterfall. In addition, SNC has modified the timing by causing a larger amount of foliage to fall in the summer and early fall. The SLA of the needles falling from trees is also greater under severe SNC. As would be implied by the nature of this needle cast disease, stand LAI declined with increasing SNC severity. However SNC has unexpectedly led to a higher stand growth efficiency. The variability of foliage retention changes with stand variables such as age and site index, but also with greater SNC. Variability of foliage retention, however, was greatest within individual-trees opposed to within- or between-stand variability. Variability of the crown sparseness index, on the other hand, was largely influenced by within-stand variability. Similar to foliage retention, the variability changed with stand variables such as age and basal area, but also with greater SNC. Foliage retention, however, was significantly more variable than the crown sparseness index.

Crown recession rates

Self-pruning and the resultant lifting of the live canopy significantly accelerates following crown closure due to the reduction of light availability (Beekhuis 1965; Assman 1970). However, Protz et al. (2000) recently found that crown recession rates were not controlled solely by light; rather branch death was also influenced by reduced stomatal conductance and lower net photosynthesis due to reductions in hydraulic conductivity. In general, the rate of crown recession tends to be proportional to height growth after canopy closure (Deleuze et al. 1996), causing crown recession rates to have a sigmoid pattern of development similar to height growth curves. Crown recession rates are therefore expected to decrease with age as height growth decelerates. Maguire (1986) estimated that crown recession peaked at approximately 6 years breast height age for southwestern Oregon Douglas-fir, but the location of the peak depended on tree, stand, and site variables.

Important stand and site influences on crown recession include density, site index, and habitat type (Wykoff et al. 1982). Increases in stand density tend to accelerate crown recession by preventing lower branches from receiving side light and by limiting the amount of aerial growing space (Ritchie & Hann 1987). Heterogeneity in stand density, however, can produce large differences in crown recession rates (Stiell 1978). Cultural treatments that influence stand density such as thinning (Peterson et al. 1997) tend to temporarily arrest or slow crown recession. Site index, as reflected in the crown recession model by the combination of age and stand top height, influences crown recession primarily through its impact on height growth. Crown recession increased with greater slope and on more southerly sites, perhaps reflecting water limitations. Although Monserud et al. (1990) found slope and aspect to be unrelated to site index, some studies have found that site index is significantly higher on southerly sites (Carmean 1954; Dunbar et al. 2002). The interaction between aspect and foliage retention, however, suggested that these variables partly represent the effect of SNC. Manter (2001) found that trees on south slopes had higher SNC fungal colonization and more severe symptoms when compared to north slopes of the same ridge.

Crown recession is also affected by the social position of the tree within the stand (Petersson 1997), as well as the amount and vertical distribution of dry matter (Kinerson et al. 1974; Schreuder & Swank 1974). Crown recession tends to increase as tree social position improves since it is directly related to height growth (Petersson 1997). Maguire and Hann (1989) estimated that maximum rates of crown recession occurred when crown ratios approached 29% in Douglas-fir. Although SNC can reduce top height growth up to 25% (Maguire et al. 2002), crown recession rates apparently increased due to premature shedding of foliage. In addition to reducing foliage dry mass, SNC causes the vertical distribution of foliage dry mass to be shifted downwards on trees with low retention (Chapter Four). The positive relationship between crown recession rate and SNC intensity suggests that trees place high priority on renewing their foliage in the upper portion of the crown. Although branches in the lower third of the crown continue to increase in length (Chapter Three), they most likely do not have enough foliage to meet their own maintenance respiration costs and have high length to diameter ratios, which may leave them more vulnerable to mechanical breakage. Higher crown recession rates on southerly aspects may also be related to greater exposure to the generally southerly, winter winds (MacMillan 1991). Regardless of causal mechanisms, accelerated canopy lifting has important implications for litterfall rates and decomposition, as well as stand susceptibility to fire.

Litterfall

Amount

Total litter production increases with age due to the increasing input of woody material, while foliage litterfall remains constant after age 40 (Gessel & Turner 1976). Several factors beside age influence litterfall rates including stand spacing (Piene & Fleming 1996), site quality (Maguire 1994), species composition, and latitude (Albrektson 1988). Climate plays a particularly important role; for example Kouki and Hokkanen (1992) observed a strong positive correlation between needle litterfall and mean July temperature with high temperatures. Conversely, Dimock (1958) found that unseasonably low fall temperature nearly tripled the amount of litter that was dropped during the ensuing year. Thus, even within a stand, litterfall rates can vary substantially year to year.

This study on Douglas-fir found that site index and crown recession are important variables influencing litterfall rates (Maguire 1994). Site quality influences foliage litterfall through its effect on height growth, crown recession, and branch litterfall. Litterfall also increased with Douglas-fir stand density index in this study, probably due to its correlation with LAI and/or its effect on crown recession and lateral shading. Piene and Fleming (1996) noted that spacing affects many aspects of needlefall including timing and annual variation. In their work, the unspaced or higher density plots had a significantly lower needle lifespan, implying that greater needlefall rates are expected at greater stand densities. Trofymow et al. (1991) and Turnbull and Madden (1983) similarly found a positive correlation between litterfall rates and stand basal area, although Trofymow et al. (1991) noted that litterfall rates correlated poorly with stand density index. Not surprisingly, Edmonds and Murray (2002) found no relationship between litter inputs and total tree basal area in an old-growth hemlock forest. The influence of aspect on litterfall rates has not been previously described. The cosine transformation of aspect shifts the minimum to the southwest quadrant and the maximum to the northeast quadrant (Stage 1976). Thus, needle litterfall rates in this study decreased as aspect became more northeasterly. This may be related to the greater basal area growth on southerly aspects (Stage 1976), water stress on northerly aspects, or both. Previous studies have noted a positive correlation between stemwood increment and litterfall rates (Trofymow et al. 1991; Turnbull & Madden 1983). In this study, however, aspect likely indicated the additional effects of SNC on litterfall rates. Manter (2001) found that trees on south slopes had higher SNC fungal colonization and more severe symptoms when compared to north slopes.

Bray and Gorham (1964) noted that, in general, leaf material contributes 60-76% of the annual litter, while branches comprise 12-15%. For the most part, the litterfall composition of the plots examined in this study fell within these ranges. However, plots with greater retention tended to have a greater proportion of needlefall because of crown recession being relatively slower on these plots. Green needle litterfall was similar to the 3% reported in Edmonds and Murrary (2002) and supported their theory that sites closer to the ocean experience greater green needle litterfall due to the commonality of winter storms with high winds near the coast.

In Pacific Northwest Douglas-fir stands, varying in age from 22 to 450 years, Gessel and Turner (1976) found that total annual litterfall ranged from 1,300 to 6,138 kg ha^{-1}. For a 43-year-old Douglas-fir stand located in the eastern Oregon Coast Range, Fogel and Hunt (1979) reported that total litterfall was 2,680 kg/ha and that almost 90% was foliage. Thinning has been shown to dramatically decrease litterfall rates for 8 to 15 years (Trofymow et al. 1991; Dimock 1958), but fertilization significantly increase the rate (Trofymow et al. 1991; Heilman & Gessel 1963). Regardless of foliage retention, the litterfall rates found in this study (3763.62 ± 914.05 kg ha^{-1}) are significantly greater than expected from previous reports (Figure 6.8). This may be due to site conditions, litterfall collector size and number, and duration of this study. The litterfall, however, approached rates that Binkley et al. (1984) reported for a 22-year-old Douglas-fir plantation with natural, seeded Sitka alder (*Alnus sinuate*; 5,210 kg ha^{-1}) as well as the 55-year-old Douglas-fir stand with and without red alder (*Alnus rubura*; 5,800 kg/ha and 4,000 kg ha^{-1}, respectively) reported in Binkley et al. (1992).

Most of studies on Douglas-fir litterfall in the Pacific Northwest have been conducted on sites of relatively low quality, which strongly influences foliage retention and hence, litterfall rates. For example, the sites examined by Gessel and Turner (1976) were mainly in the range of low to high Site Class IV (King 1966), while the sites monitored in the Oregon Coast Range were primarily low Site Class I and high Site Class II. The higher litterfall rates in this study can therefore be partly attributed to the more rapid turnover of needles (Albrektson 1988). Douglas-fir litterfall studies in the Pacific Northwest have also concentrated primarily on inland sites. The greater proximity to the Pacific Ocean, may have increased exposure to stronger winds from winter storms and again causing a greater turnover rate for foliage.

The litterfall traps in this study were smaller than have typically been used in this type of research. For example, Trofymow et al. (1991) used traps that were 0.372 m^2, while Binkley et al. (1992) used ones that were 1 m^2. This may explain why the standard errors of the estimate in this study (9.4 - 38.4%) are also much higher than those reported by Binkley et al. (1992) and Will (1959). Furthermore, Satoo and Madgwick (1982) noted that square litterfall traps tended to give slightly higher values than round ones. However, McShane et al. (1983) found that estimates of annual needlefall were very similar for collector sizes ranging from 0.010 to 0.933 m^2. Variation in total litterfall from year to year may be quite large. Bray and Gorham (1964) report maximum to minimum ratios ranging from 1.1 to 5.1 with an average of 2.6 for evergreen and 1.4 for deciduous species. Thus, the significantly higher litterfall rates reported in this study may be due to its limited time frame (1 year). On the other hand, Olson (1971) was unable to detect any year to year variation in 11 tulip-poplar (*Liriodendron tulipifera*) stands studied for three consecutive years.

Timing

Both foliage and woody litterfall rates peak in the fall and early winter with the onset of strong, windy rain storms in the Pacific Northwest (Gessel & Turner 1976). Douglas-fir foliage litterfall generally peaks in October, with minimal litterfall occurring during the late winter and early spring (Dimock 1958; Gessel & Turner 1976; Fogel 1979). Litterfall of fine woody material shows a less definite pattern but, like foliage litterfall, the majority of it tends to occur after winter storms with heavy wet snows or strong winds (Trofymow et al. 1991). While the general pattern observed in this study was similar to other studies, SNC, however, modified the seasonal distribution of foliage litterfall. Although a most of the foliage litterfall occurred in the fall, a significant amount of foliage fell in the summer, which follows the biological lifecycle of the SNC-causing fungus, *Phaeocryptopus gauemannii*. The SNC disease cycle begins in the spring when spores are released from the pseudothecia on the older diseased needles and are carried by the wind and rain to newly emerged needles (Hansen et al. 2000). The spores germinate on the new needles, enter the needles through the stomates, and reside in the intercellular spaces of the leaf tissue until pseudothecia ramify through the needle and appear in the fall (Hansen et al. 2000). Needles are then shed, regardless of age, when about 50% of stomata are occupied. This generally occurs in the late spring and early summer. This may create a seasonal distribution similar to the one found by Will (1959) for Douglas-fir in New Zealand, where the rate of foliage litterfall does not vary greatly with season. Fine woody material litterfall, however, still tended to occur primarily in the winter.

Size

Few studies have reported the SLA of needles in foliage litter, nor its seasonal variation (Roberts et al. 1999), despite the fact that litter SLA is a good predictor of the rate of decomposition (Lambers et al. 1998). Litter SLA is usually very similar in many respects to living foliage (Roberts et al. 1999), but has a definite seasonal pattern because of foliage dynamics and translocation patterns within the canopy (Piene & Fleming 1996). Roberts et al. (1999) and Bouriaud et al. (2003) found a wide range of SLA occurs in the litter throughout the year, but SLA was generally highest in the early fall due to the larger contribution of foliage from the bottom of the canopy to the litter. As the year progresses, foliage with smaller SLA from the upper canopy contributed substantially more to the litter

(Roberts et al. 1999). Piene and Fleming (1996) found that age-specific rates of needlefall tend to increase with needle age, particularly in the lower crown. Litter SLA, therefore, should increase with stand age because a greater proportion of the litterfall comes from the lower crown, where SLA is usually the highest (Bartelink 1996). SNC has modified the litterfall SLA and its seasonal distribution by altering foliage age distribution and age class dynamics. SNC has resulted in a higher foliage turnover rate, a greater proportion of the younger age classes, and on average, a greater SLA (Chapter Five). This higher SLA is due to the fact that the needles are flatter and less dense. This effect led to a greater litter SLA because on sites with severe SNC, relatively younger needles with a higher SLA tend to be lost. SNC altered the seasonal trend in litter SLA by altering where the needle loss is occurring. Manter (2001) found consistently higher fungal colonization and more severe symptoms in the upper portions of the crown, implying that a greater proportion of the litter in a severe SNC site comes from the upper canopy. The positive correlation between rate of litter decomposition and litter SLA (Lambers et al. 1998) suggests that decomposition may increase with greater SNC, especially when considering the compounding SNC effects on forest floor temperate and moisture. SNC and the responses it stimulates therefore have important implications for nutrient-cycling within these stands.

Leaf area index

LAI is currently the most common and useful measure of total stand foliage quantity (Thomas and Winner 2000). LAI controls the amount of photosynthetically active radiation that is intercepted, the exchange rate of carbon dioxide and water vapor, and the potential amount of growth of tree components such as stemwood (Gholz 1982; Pierce & Running 1988; Margolis et al. 1995). LAI is often shown to increase with enhanced nutrition (Kaufmann & Ryan 1986; McCrady & Jokela 1998; Balster & Marshall 2000b), greater water availability (Grier & Running 1977) (Gholz 1982; Fassnacht & Gower 1997), increased age up to a steady-state at 5 to 20 yrs (Kull & Tulva 2000), and more stand basal area (Gholz 1982). Turner and Long (1975), however, report that Douglas-fir stands do not reach an LAI plateau until age 40-60 yrs. Thus, LAI increased with site index and plantation age in the Oregon Coast Range Douglas-fir from this study. The significance of the crown length to sapwood area ratio (CL:SA) and foliage retention in predicting LAI indicated that crown condition is a particularly important factor influencing leaf area density within crowns and canopies. CL:SA functions largely as an index of crown sparseness and has been shown to increase with greater SNC severity (Maguire & Kanaskie 2002). Similar, but less drastic, reductions in stand LAI have also been reported in response to climatic disturbances such as drought and ice storms (Thomas & Winner 2000; Olthof et al. 2003).

Mean LAI was 7.4 in this study, but several values were higher than previously published values for Douglas-fir. Although Gholz (1982) contended that Pacific Northwest ecosystems can attain maximum of LAIs near 18 because of the region's high annual precipitation, most studies have found LAIs between 4.2 to 14.0 (Marshall & Waring 1986; Thomas & Winner 2000; Turner et al. 2000; McDowell et al. 2002). These differences may be attributable to site conditions and methodology. Most of these studies have taken place in the Cascades rather than near the coast, where potential LAIs are higher (Gholz 1982). Secondly, most of the Pacific Northwest studies have estimated LAI using optical techniques, which consistently underestimate LAI because of the aggregation of needles within crowns and canopies (Marshall & Waring 1986). Allometric techniques, similar to the approach used in this study, tend to produce the highest estimates of LAI (Marshall & Waring 1986; Hall et al. 2003). Estimated LAIs, however, were close to levels reported in young Douglas-fir plantations that had been thinned, pruned, and fertilized (Velazquez-Martinez et al. 1992).

Growth efficiency

Stand-level growth efficiency (stem volume growth per unit leaf area) is primarily controlled by stand structure and the resource-use efficiencies of individual trees (Binkley et al. 2002). Of particular importance are canopy depth and foliar density within the canopy (Smith & Long 1989). O'Hara (1988) found that tall trees with medium-sized crowns were most efficient in thinned Douglas-fir, while tall trees with relatively large crowns were most efficient in unthinned stands. GE has been shown to decrease with increasing leaf area at both the individual tree- (Maguire et al. 1998) and stand-level (Waring et al. 1981; Mitchell et al. 1983; Oren et al. 1987). Growth efficiency declines with increasing tree size because of several factors including: increasing respiration load associated with live cells in the sapwood of stems or branches (Ryan 1989; Ryan & Waring 1992; Roberts & Long 1992);

relative allocation to stemwood production (Kuuluvainen 1988); hydraulic limitations (Ryan & Yoder 1997), tissue maturation (Greenwood & Hutchinson 1993) or the combination of all four. Although GE has been reported to increase with decreasing stand density (Velazquez-Martinez et al. 1992), GE tends to increase with density, as in this study, because crowns become shorter and more compact. GE has also been reported to increase with fertilization (Velazquez-Martinez et al. 1992; Balster & Marshall 2000b) as result of shifts in allocation patterns and increased photosynthetic rates (Brix 1971). In Coast Range Douglas-fir from this study, growth efficiency tends to decrease with site index, probably due to the higher leaf area held on higher sites. With each additional unit of leaf area, average growth declines due to the less intense light the additional unit receives. Site index tends to be the highest on southerly aspects (Dunbar et al. 2002), but Kaufmann and Ryan (1986) found lower growth efficiencies on southern exposures, possibly due to higher temperature and reduced water supply. Site index also reduces needle retention, consistent with a general decline in retention with increased resource availability (Pensa & Sellin 2002). Balster and Marshall (2000a) hypothesized that this may be caused by more rapid self-shading under faster needle production. This leads to a relatively smaller foliage ratio (needle dry mass per unit of branchwood mass) and a greater LAI, which directly influences growth efficiency by causing a low photosynthetic efficiency of middle and lower canopy leaves (Oren et al. 1986). Elevation, on the other hand, has been shown to be an important predictor of site index (Monserud & Rehfeldt 1990), given its link to exposure (Dunbar et al. 2002). Research has shown GE to both increase (Kaufmann & Ryan 1986) and decrease (Kuuluvainen 1988) at higher elevations. The tendency for GE to increase with elevation in this study may reflect site conditions and their influence on both crown form and absolute growth. For example, Fujimori et al. (1976) found foliage to be retained a year longer than similar stands at lower elevations. This supports the idea that GE is primarily controlled by physiographic and stand variables that control crown structure and dynamics.

SNC increases GE possibly because it leads to a decreased canopy depth, greater concentration of foliage in the upper crown, a greater relative distribution of foliage in the upper crown, sparser crown, deeper penetration of light, and a higher proportion of current-year foliage, which perhaps has higher photosynthetic rates that are typical of younger foliage age classes in healthy trees (Woodman 1971). Furthermore, trees with severe SNC may have lower maintenance respiration costs with the reduced number of branches (Chapter Three) and total branchwood mass (Chapter Four), particularly since branches tend to have higher respiration rates than boles for a given amount of living tissue (Kinerson 1975; Sprugel 1990). Smith and Long (1989) found growth efficiency declined with increasing canopy depth. SNC has resulted in greater crown recession rates and a higher height to crown base, which effectively decreases canopy depth. Tadaki (1986) suggested that leaf efficiency is highest for canopies with foliage concentrated near the top. SNC has caused a relatively greater proportion of current and 1-year-old foliage to be located towards the upper canopy when compared to healthy Douglas-fir (Chapter Five). Net photosynthetic rates tend to decrease with foliage age and in Douglas-fir; specifically Woodman (1971) found 1-, 2-, 3- and 4-yr-old needles to be 72, 50, 30, and 12% of the rates per unit of mass observed for current foliage. Furthermore, older needles maintain relatively high transpiration rates, which significantly increases their cost to a tree (Lange et al. 1989). The photosynthetic water use efficiency of the tree may improve by casting the costly older needles and producing a significant amount of the more efficient younger-needles (Beyschlag et al. 1994). Beyschlag (1994) showed that the loss of older needle age classes may be compensated by higher photosynthetic rates of the remaining younger foliage age class due to higher levels of photosynthetically active radiation within the thinned tree crown and perhaps greater water availability. Hood (1977), however, found that infected current- and 1-year-old foliage photosynthesized at a lower mean rate than uninfected needles of the same age on Douglas-fir seedlings inoculated with SNC in New Zealand. SNC results in needles that have a higher SLA (Chapter Five). High-SLA leaves are productive (Poorter & Van der Werf 1998; Van der Werf et al. 1998), but are necessarily short-lived and vulnerable to infection and herbivores (Coley et al. 1985; Grime et al. 1996). The level of productivity, however, depends on whether the needles have a high SLA because they are flatter or less dense. Although SNC can reduce volume growth as high as 52% (Maguire et al. 2002), Douglas-fir in the Oregon Coast Range are partly compensating the loss of foliage by growing more efficiently. This result may support Smith and Long's (1989) conclusion that vigorous stands (ones with deep, full canopies and high absolute growth rates) are not as efficient as those that have a vertically restricted, compact canopy.

Crown condition variability

Foliage retention

Analysis indicated that samples sizes required to estimate 95% confidence intervals that are within ±0.2 and ±0.1 at the stand and tree-levels, respectively ranged from 2 to 8 tree per stand and 2 to 4 branches per tree. The analysis also indicated that there is significant variation in these values from year to year, but a fair portion of its variability can be attributed to within-tree factors. A large portion of the variation in foliage retention can not be accounted for as indicated by the high percentage of variation attributed to random variation and the low R^2 values of the sample size models. Most importantly, they are within the sample sizes recommended by Filip et al. (2000) for rating SNC and similar to the ones put forth by MacLean and MacKinnon (1998) for estimating defoliation caused by the spruce budworm (*Choristoneura fumiferana*).

Research on spruce budworm indicates that the variance in mean defoliation between plots was low relative to intertree or intratree variance (MacLean & Lidstone 1982). Insect defoliation of the new foliage differs little between crown levels (MacLean & Lidstone 1982; Piene 1996), but estimates of foliage retention increase significantly with depth into the crown. In addition, this study found that the variability of foliage retention within in a tree was related to the diameter to height ratio, density of Douglas-fir, stand basal area, years into the epidemic, and SNC-intensity. The diameter to height ratio is an indication of tree's relative social position within the stand. The increase in the number of sample branches with greater diameter to height ratios most likely reflects the high variability of needle retention generally associated with trees of lower social positions (Niinemets 1997; Xiao et al. 2003). The significance of stand density and basal area may relate to microclimatic variation or interaction of SNC with competitive stress. The significant increase in variability over time most likely represents an intensification of SNC severity on susceptible genotypes. Pensa et al. (2001) suggested that needle longevity increases slightly with tree age, although it was very variable from tree to tree. Both summer (Pensa & Jalkanen 1999) and winter (Xiao et al. 2003) temperatures have been associated with foliage retention at a regional-level. Assessment of tree health is a subjective evaluation that is strongly influenced by the frame of reference chosen to examine forest conditions (McLaughlin & Percy 1999). On individual shoots, MacLean and Morgan (1981) found that average estimation error ranged from 0.9% on shoots with 81-99% defoliation to 16% on shoots with less than 20% defoliation. Observer bias has been found to be correlated with observer's training, perception, crown dimensions, and weather and lighting conditions (Innes 1993). The increase in the number of sample branches need to accurately estimate tree foliage retention with decreasing SNC reflects the high variability of foliage retention even in healthy Douglas-fir. Similarly, MacLean and MacKinnon (1998) found that samples sizes were the largest at moderate defoliation levels.

The high within-tree variability of foliage retention reflects the dynamic nature of foliage and variability of microclimate within the crown. Although a greater number of age classes are present in the lower portion of the crown, Piene and Fleming (1996) found that needle lifespans were shorter when compared to the upper crown due to decreased light availability and increased competition. While the distribution of current-year needles is mainly determined by prevailing light condition, stochastic environmental factors are of increasing importance as the foliage ages (Piene & MacLean 1999), creating a high variability even within a crown. In addition, Manter (2001) found than SNC fungal colonization was consistently higher in the upper portions of the canopy and in south-facing foliage, which adds to within-tree variability. Therefore, it is recommended to estimate foliage retention on at least 3 levels within the crown to help reduce this large within-tree variability.

The number of sample trees required to precisely estimate foliage retention at the stand-level was related to age, site index, SNC severity, and the number of years into the epidemic. The significance of years into the epidemic may again reflect differential responses of genotypes. Age also influences both ease of observation and observer bias. Xiao (2003) found that needle longevity was positively correlated with stand age and density. Fleming and Piene (1992) found a similar relationship between needle longevity and stand age for balsam fir (*Abies balsamea* L.). Turner and Long (1975) noted a rapid turnover of foliage in young Douglas-fir stands and attributed it to short foliage retention under highly competitive status. Furthermore, Horntvedt (1993) concluded that determining needle retention in older stands can be difficult because of the increased complexity of the branch geometry, which has important implications for observation error through time. Site index, on the other hand, influences the variability in foliage retention by creating a wide gradient in stand growth and vigor. Douglas-fir needle retention has been shown to increase (Turner & Olson 1976), decrease (Brix 1981), and not be influenced by fertilization (Brix & Ebell 1969). Soil nutrient and water availability, however, have a particularly important influence on needle retention (Pensa & Sellin 2002), perhaps due to the influence of site fertility on photosynthetic rate (Brix 1971) and leaf construction cost (Pensa & Sellin 2002) or self-shading (Balster & Marshall 2000a). Similar to the sample size required for estimating tree-level foliage retention, a smaller number of trees were needed to accurately estimate foliage retention when SNC severity is high. This decrease again reflects the high variability in Douglas-fir foliage retention, even without the influence of disease. Defoliation caused by SNC is fairly uniform within a stand and its variability is relatively small when compared to the variability within an individual crown. Assessment of SNC using foliage retention should, therefore, concentrate on sampling more intensively within an individual crown rather increasing the number of sample trees. However, foliage retention, even after accounting for stand structure, site location, and SNC severity, was found to be highly variable, which may indicate the importance of genetics and climatic factors on its annual variability. Therefore, estimates of foliage retention on at least 5 trees within a stand may help to reduce this large variability.

Crown sparseness index

Variability associated with the crown sparseness index was significantly less than the variability associated with foliage retention. This may due to limited size of the data available for analysis, but is most likely a reflection of the more objective nature of the index when compared to foliage retention. Although there is some error associated with measuring sapwood area in the field (Maguire & Kanaskie 2002), it can be significantly reduced by using two cores taken at a 45° angle (Maguie et al. in review). Furthermore, the relatively small amount of variability in the ratio due to between-stand factors emphasizes Maguire and Kanaskie's (2002) conclusion that the ratio has a strong potential for discriminating effectively among stands with varying degrees of foliage loss. Although the number of samples needed to have a confidence interval with a half width of 2.0 was significantly related to several stand variables, the absolute change in the number of samples is actually quite small. Thus, estimating the crown length to sapwood area ratio on 3 to 5 dominant or codominant samples trees should be sufficient for detecting a biologically meaningful value across a range of stand densities, ages, and SNC severity classes.

CONCLUSION

This study highlights the drastic changes that can occur in several important stand-level attributes due to defoliation caused by an endemic foliar disease. These changes have a strong influence on ecosystem processes such as decomposition and nutrient-cycling, and have implications for accurately assessing the stand's health. SNC in the Oregon Coast Range has led to a greater woody material but lower foliage litterfall rate. Most of the foliage litterfall tends to occur in the fall, but a greater proportion now falls in the summer rather than in the winter with the needles having a higher SLA with more severe SNC. Stand LAI is greatly reduced by the disease, but growth efficiency was improved. Foliage retention was found to vary significantly among trees and stands and by year into the epidemic. The variability of foliage retention, however, was greater within an individual crown rather than among trees or stands. A large portion of this variability could not be accounted for, suggesting the importance of genetic and climate factors on foliage retention. The crown sparseness index, on the other hand, is much less variable than foliage retention. Regardless, 3 to 5 trees within these young plantations should be assessed for crown condition estimates. Defoliation caused by SNC is leading to the stands that are restricted in canopy depth, have a higher component of woody material in the litter layer, a lower LAI, a higher GE, and a more uniform crown condition, with important implications for many ecosystem attributes.

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Table 6.1. Attributes of the 22 plots sampled in 2002.

Attribute	Mean	SD	Min	Max
Douglas-fir basal area (m^2/ha)	26.44	8.44	9.97	45.44
Douglas-fir trees per ha	624	272	259	1223
Douglas-fir quadratic mean diameter (cm)	24.56	6.73	11.41	36.45
Douglas-fir relative density (Curtis (1982))	5.31	1.32	2.95	7.91
Douglas-fir stand density index (Reineke (1933), trees/ha at mean DBH of 25.4 cm)	526.6	1.3	2.9	7.9
Basal area in other conifers (m^2/ha)	0.45	0.76	0	2.21
% basal area in other conifer	1.2	2.1	0	6.7
Basal area in hardwoods (m^2/ha)	0.59	0.77	0	2.86
% basal area in hardwoods	1.8	2.3	0	9.3
Total basal area (m^2/ha)	33.37	12.84	10.44	69.65
Average breast-height age (yr)	21.1	4.8	11.1	27.8
Average foliage retention (yr)	2.36	0.71	1.2	4.3
Site index (Bruce (1981); height at 50 yr, in m)	39.6	2.6	34.8	43.9

Table 6.2. Parameter estimates, standard errors, and p-values for plot mean crown recession rate (equation 6.1).

Parameter	Estimate	Standard error	P-value
ß$_{10}$	81.2721	30.8215	0.0720
ß$_{11}$	-45.1567	14.5975	0.0377
ß$_{12}$	2.5125	1.0275	0.0440
ß$_{13}$	24.7092	8.4085	0.0002
ß$_{14}$	-0.2779	0.2818	0.0435
ß$_{15}$	-33.8101	8.5529	0.0060
ß$_{16}$	0.2965	0.1134	0.0188

Table 6.3. Attributes of the foliage and woody litterfall by season.

Type/Season	Mean	SD	Min	Max
Foliage litterfall	3763.62	914.05	2201.71	5200.43
Spring	321.11	147.54	96.71	705.46
Summer	1052.83	380.23	470.12	2037.73
Fall	1689.08	644.95	818.76	3048.97
Winter	700.69	390.00	247.96	1853.93
Woody litterfall	625.61	236.91	263.73	1111.95
Spring	125.13	165.86	20.51	700.14
Summer	52.88	73.25	3.52	288.14
Fall	125.60	91.64	16.25	325.27
Winter	322.01	161.98	45.22	658.95

Table 6.4. Parameter estimates, standard errors, and p-values for total foliage litterfall amount (equation 6.2).

Parameter	Estimate	Standard error	P-value
β_{20}	-92125.0	12697.0	<0.0001
β_{21}	1686.6917	233.6503	<0.0001
β_{22}	2325.6879	307.0699	<0.0001
β_{23}	-679.3925	153.5796	0.0017
β_{24}	1801.9733	303.8574	0.0002
β_{25}	-42.6979	5.8637	<0.0001

Table 6.5. Parameter estimates, standard errors, and p-values for total woody litterfall amount (equation 6.3).

Parameter	Estimate	Standard error	P-value
β_{30}	3910.9665	547.2065	<0.0001
β_{31}	11.6028	1.9732	0.0002
β_{32}	-92.3797	14.8218	<0.0001
β_{33}	-118.8064	46.0465	0.0274
β_{34}	-123.2304	38.3072	0.0092

Table 6.6. Parameter estimates, standard errors, and p-values for foliage litterfall amount by season (equation 6.4).

Parameter	Estimate	Standard error	P-value
β_{40}	-8.4930	4.1881	0.0477
β_{41}	-0.7600	0.1345	<0.0001
β_{42}	0.4686	0.1345	0.0010
β_{43}	0.9307	0.1345	<0.0001
β_{44}	-0.1799	0.0808	0.0303
β_{45}	0.3086	0.1031	0.0042
β_{46}	4.9757	1.7452	0.0062
β_{47}	-0.1237	0.0424	0.0052

Table 6.7. Parameter estimates, standard errors, and p-values for woody litterfall amount by season (equation 6.5).

Parameter	Estimate	Standard error	P-value
β_{50}	-3.5687	1.9931	0.0752
β_{51}	-1.2385	0.3044	<0.0001
β_{52}	-2.4631	0.3080	<0.0001
β_{53}	-1.1904	0.3007	0.0001
β_{54}	0.3587	0.1812	0.0494
β_{55}	1.6461	0.7871	0.0380

Table 6.8. Parameter estimates, standard errors, and p-values for litter specific leaf area by season (equation 6.6).

Parameter	Estimate	Standard error	P-value
β_{60}	67.4647	3.0012	<0.0001
β_{61}	-4.9275	3.3555	0.1442
β_{62}	-13.3111	3.8048	0.0006
β_{63}	-5.4321	3.8048	0.1555
β_{64}	0.3413	0.0917	0.0003
β_{65}	-0.3318	0.0622	<0.0001
β_{66} (SNC 2)	-9.4626	3.1377	0.0030
(SNC 3)	-8.0015	3.1093	0.0111
(SNC 4)	-9.5054	2.3348	<0.0001
β_{67} (I_{SPR} * SNC 2)	5.0137	5.0730	0.3247
(I_{SPR} * SNC 3)	2.6158	4.5727	0.5682
(I_{SPR} * SNC 4)	2.7858	3.5458	0.4334
β_{68} (I_{SUM} * SNC 2)	9.6517	5.0730	0.0591
(I_{SUM} * SNC 3)	10.1423	4.7454	0.0343
(I_{SUM} * SNC 4)	13.4826	3.9657	0.0009
β_{69} (I_{FALL} * SNC 2)	1.6589	6.2131	0.7899
(I_{FALL} * SNC 3)	8.9480	4.7454	0.0614
(I_{FALL} * SNC 4)	7.0523	3.9652	0.0774

Table 6.9. Parameter estimates, standard errors, and p-values for stand leaf area index model (equation 6.8).

Parameter	Estimate	Standard error	P-value
β_{80}	-2.8223	1.3639	0.0562
β_{81}	0.0987	0.0368	0.0173
β_{82}	-0.2119	0.0418	0.0001
β_{83}	0.0618	0.0177	0.0033
β_{84}	0.7477	0.3519	0.0500

Table 6.10. Parameter estimates, standard errors, and p-values for stand growth efficiency model (equation 6.9).

Parameter	Estimate	Standard error	P-value
ß$_{90}$	3816.6915	954.0469	0.0015
ß$_{91}$	0.3771	0.1268	0.0108
ß$_{92}$	0.1162	0.04725	0.0287
ß$_{93}$	20.7076	8.86002	0.0361
ß$_{94}$	-100.5334	23.6713	0.0010
ß$_{95}$	-1261.1012	385.6826	0.0061
ß$_{96}$	31.2209	9.3981	0.0055

Table 6.11. Parameter estimates, standard errors, and p-values for estimating sample size needed to obtain a confidence interval for a plot-level foliage retention value that has a half-width of 0.2-yr (equation 6.11).

Parameter	Estimate	Standard error	P-value
ß$_{110}$	-4.0739	1.1663	0.0001
ß$_{111}$ (1997)	-0.1496	0.1045	0.0997
(1998)	-0.4888	0.0888	<0.0001
(1999)	-0.2148	0.0988	0.0227
(2000)	-0.0302	0.0846	0.7252
(2001)	-0.3372	0.0774	0.0008
ß$_{112}$	0.0907	0.0216	0.0002
ß$_{113}$	0.0799	0.0273	0.0142
ß$_{114}$	2.4335	0.4916	<0.001
ß$_{115}$	-0.0405	0.0112	0.0013
ß$_{116}$	-0.0334	0.0092	0.0013

Table 6.12. Parameter estimates, standard errors, and p-values for estimating sample size needed to obtain a confidence interval for a tree-level foliage retention value that has a half-width of 0.1-yr (equation 6.12).

Parameter	Estimate	Standard error	P-value
ß$_{120}$	0.4386	0.0434	<0.0001
ß$_{121}$ (1998)	0.0631	0.0186	0.0007
(1999)	0.0123	0.0180	0.4938
(2000)	0.0330	0.0163	0.0436
(2001)	0.0288	0.0135	0.0355
ß$_{121}$	0.0800	0.0242	0.0010
ß$_{123}$	-0.0035	0.0007	<0.0001
ß$_{124}$	0.0002	0.0001	<0.0001
ß$_{125}$ (SNC 2)	0.3441	0.0337	<0.0001
(SNC 3)	0.3884	0.0224	<0.0001
(SNC 4)	0.3819	0.0203	<0.0001
(SNC 5)	0.3573	0.0343	<0.0001

Table 6.13. Parameter estimates, standard errors, and p-values for estimating the number of samples needed to obtain a confidence interval for a plot mean crown sparseness index that has a half width of 2.0 (equation 6.13).

Parameter	Estimate	Standard error	P-value
ß$_{130}$	-3.9026	1.6325	0.0287
ß$_{131}$	0.0013	0.0002	<0.0001
ß$_{132}$	0.1898	0.0454	0.0006
ß$_{133}$	-0.0681	0.0233	0.0095
ß$_{134}$	-0.0209	0.0077	0.0151
ß$_{135}$	1.0688	0.2869	0.0017

Table 6.14. Sources of variation for foliage retention and the crown sparseness index.

	Foliage retention	Crown sparseness index
Within-tree	0.3506 (39.0%)	-
Between-tree	0.0587 (6.5%)	5.9910 (10.0%)
Between-plot	0.1745 (19.4%)	0.6836 (87.3%)
SNC	0.0647 (7.2%)	0.1900 (2.8%)
Annual variation	0.0106 (1.2%)	-
Random variation	0.2396 (26.7%)	0.0000 (0.0%)

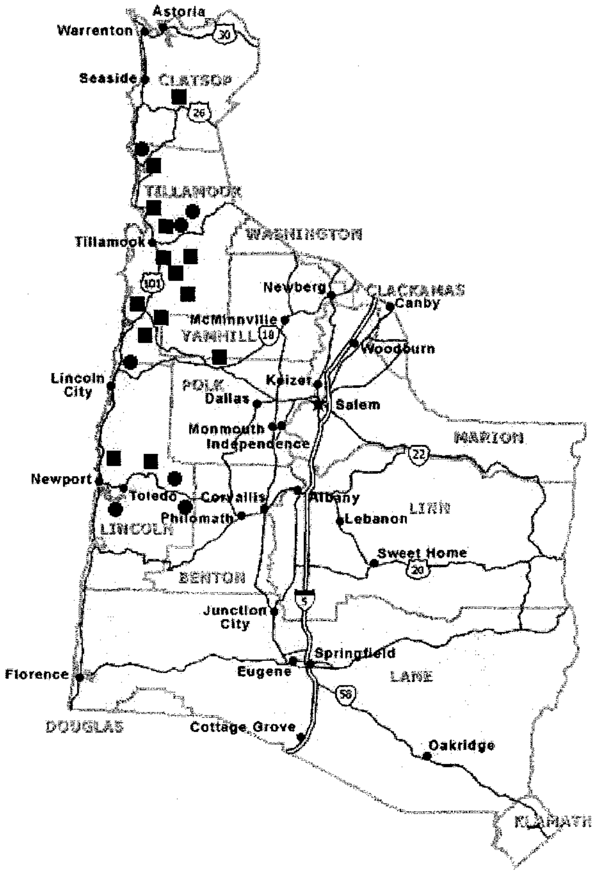

Figure 6.1. Location of the 22 plot used in this study. Plots marked with a square are locations where litterfall traps were placed and a collected monthly for one year.

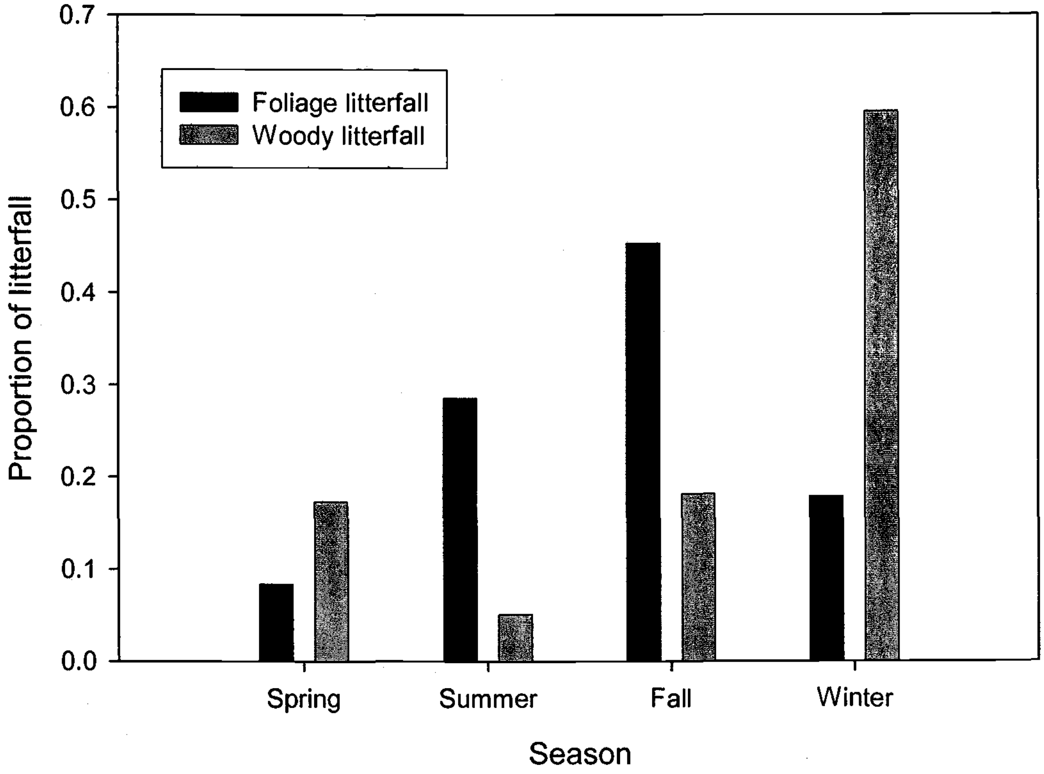

Figure 6.2. Distribution of foliage and woody litterfall by season for an average plantation in this study.

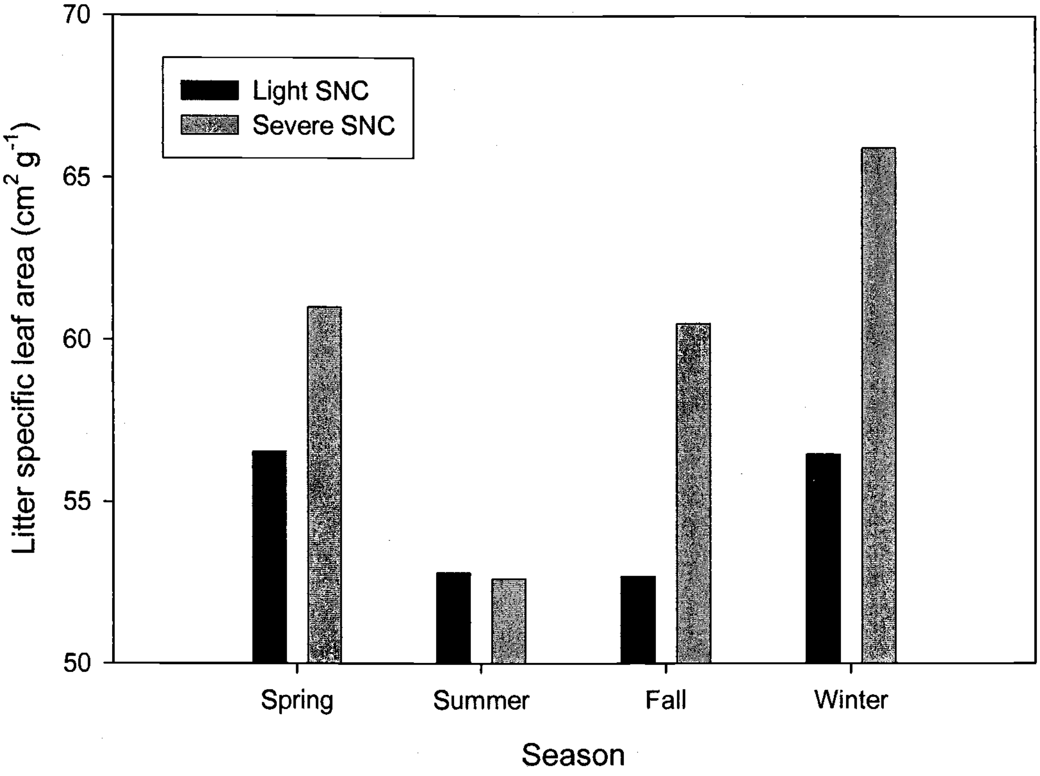

Figure 6.3. Litter specific leaf area by season and SNC severity.

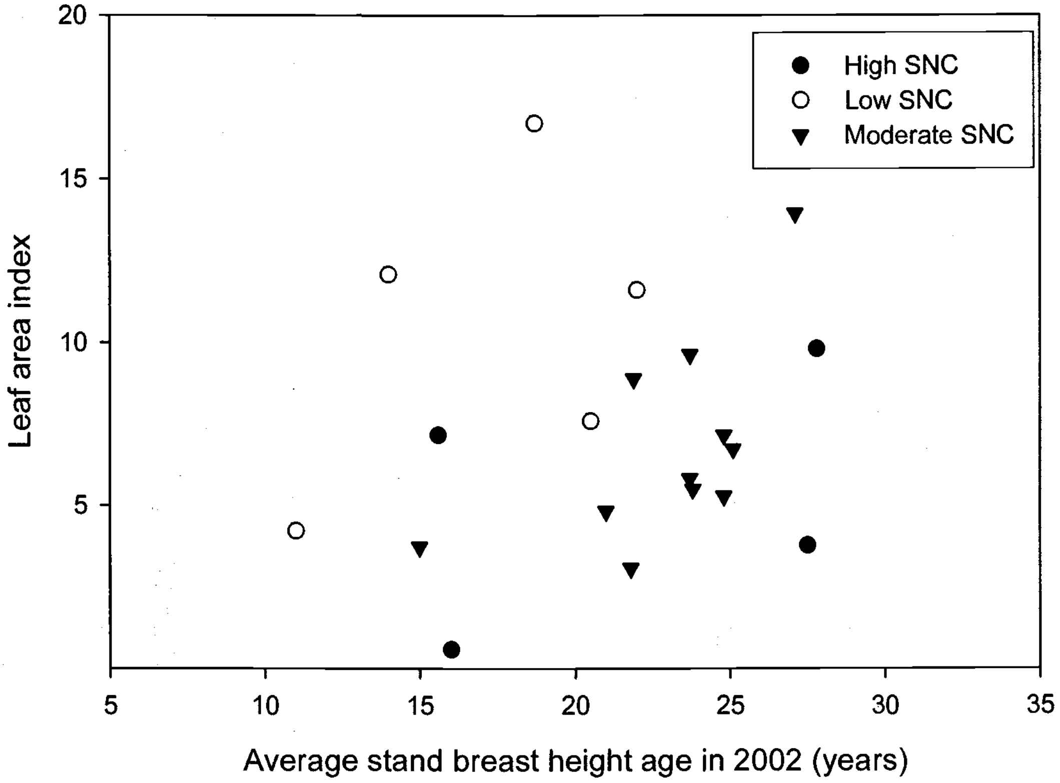

Figure 6.4. Leaf area index over average stand breast height age in 2002 and SNC severities.

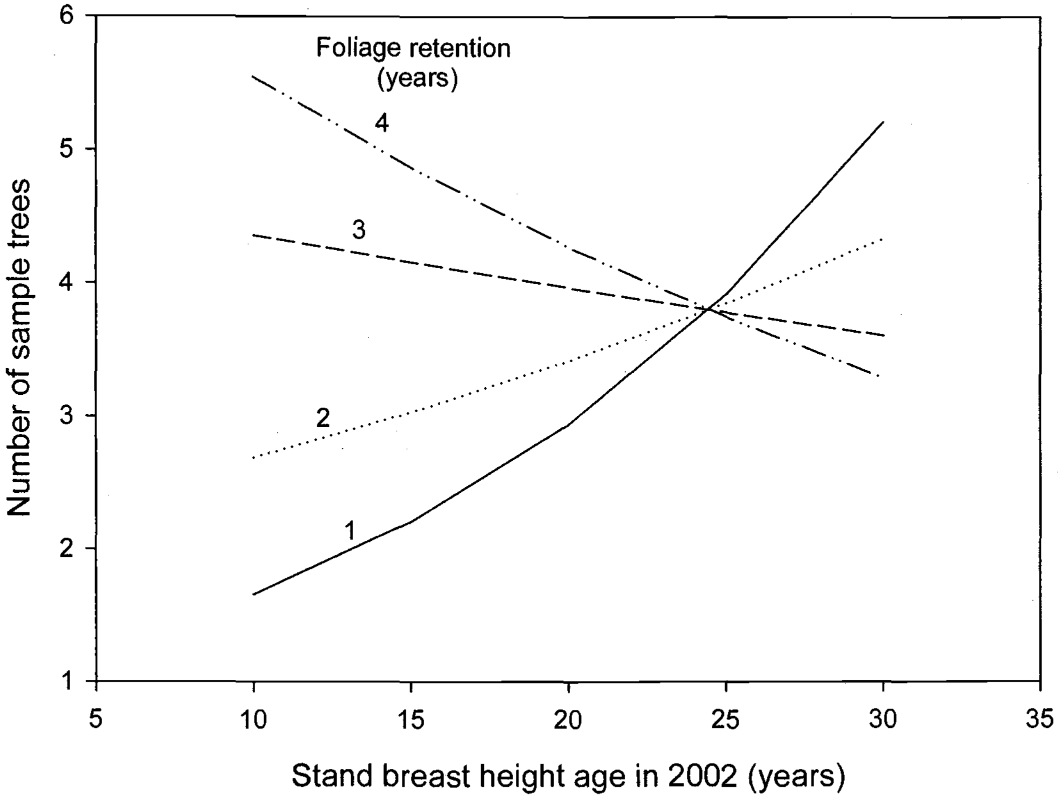

Figure 6.5. The number of sample trees needed to obtain a 95% confidence interval for a plot estimate of foliage retention with a half width of 0.2-yr for a given stand age and mean foliage retention.

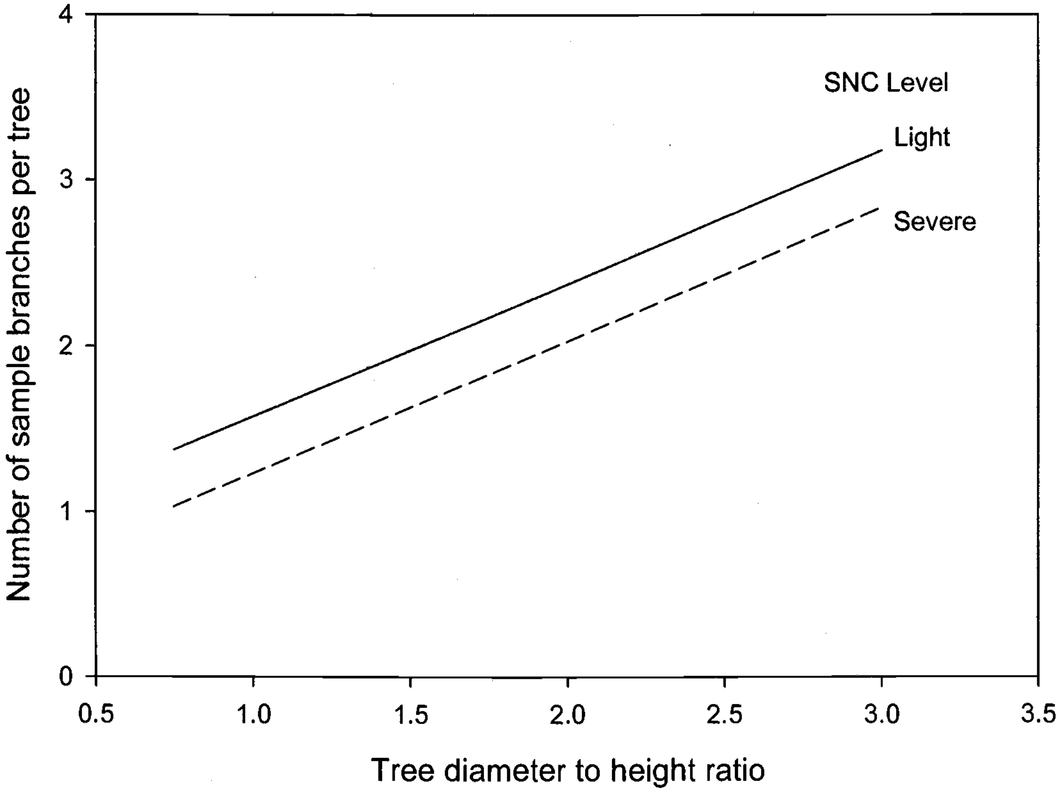

Figure 12.6. The number of sample branches per tree needed to obtain a 95% confidence interval for a tree estimate of foliage retention with a half width of 0.1-yr for a given tree diameter to height ratio and SNC severity.

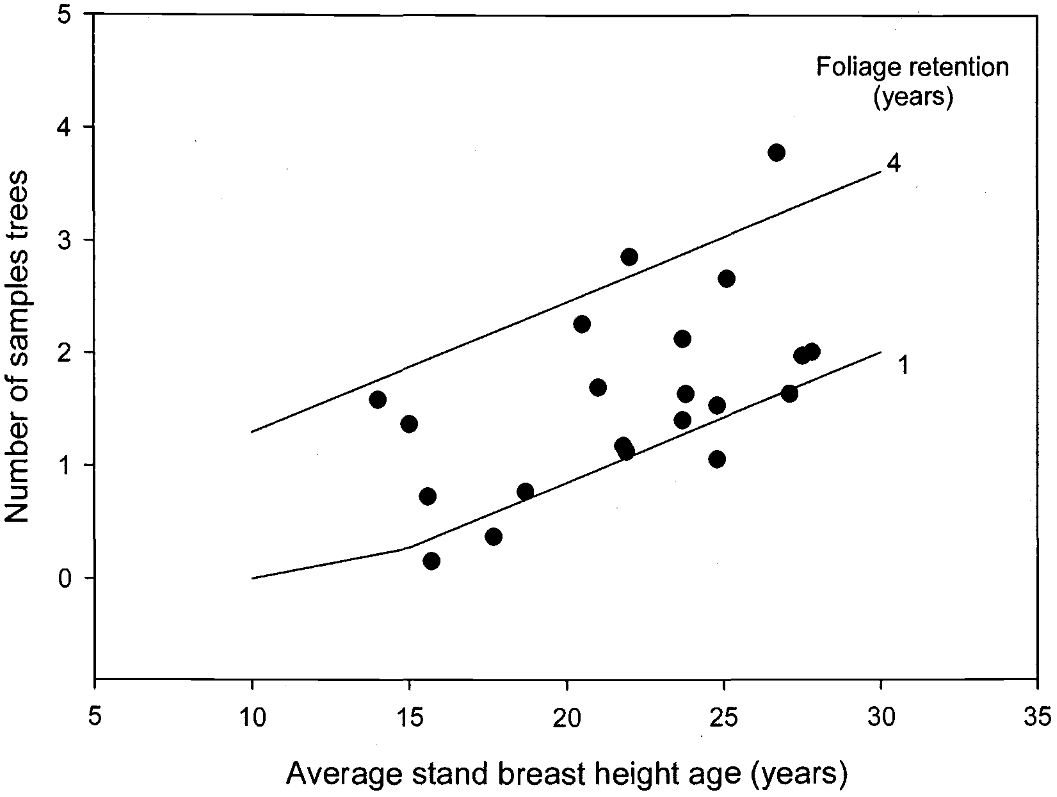

Figure 6.7. Number of samples tree needed to obtain a 95% confidence interval for plot estimate of the crown sparseness index with a half width of 2.0 for a given stand age and SNC severity.

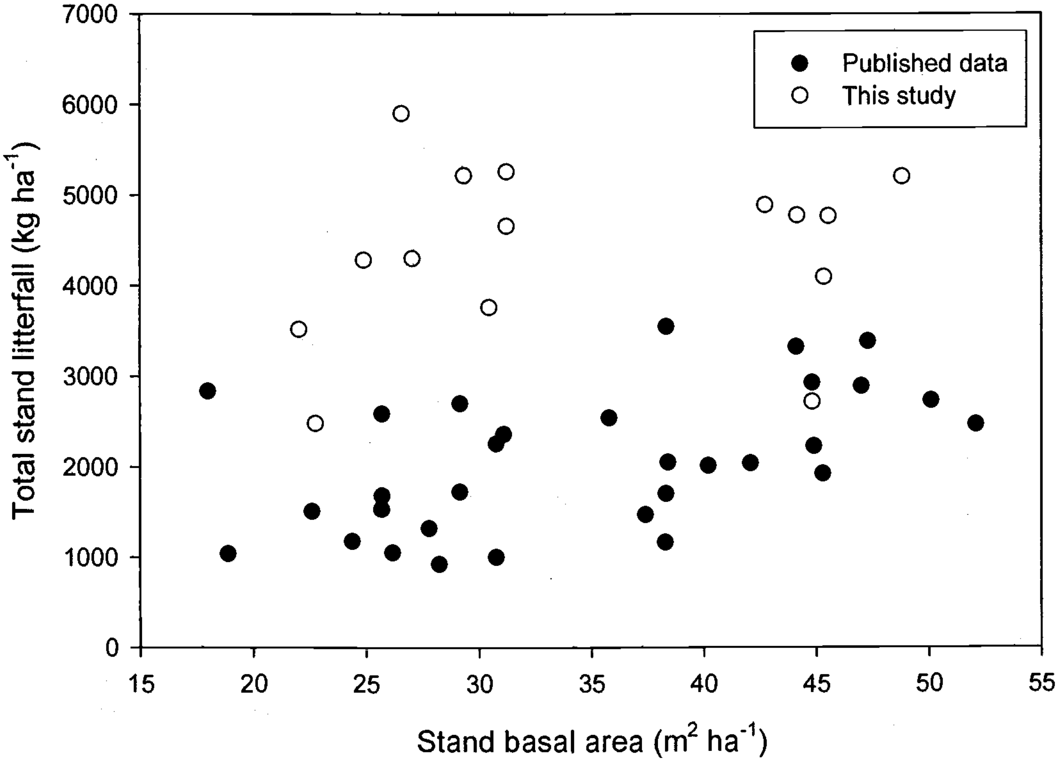

Figure 6.8. Total litterfall (kg ha^{-1}) over stand basal area (m^2 ha^{-1}) for this study (open dots) and other published data (filled dots).

CHAPTER SEVEN: CONCLUSIONS

Crown condition is a difficult concept to define and to quantify. Understanding reactions of crowns to environmental change, particularly disturbance, is an important step towards modeling ecophysiological processes and managing forest stands. Although disturbances vary in their form and intensity, they all essentially involve the destruction of plant parts. Extended defoliation, in particular, is an important form of disturbance because it directly affects the photosynthetic capability of the crown and often creates conditions conducive for other forms of disturbance. The Swiss needle cast endemic central in the northern Oregon Coast Range provided an opportunity to develop quantitative relationships between degree of defoliation, resulting crown structure, and changes in tree and stand growth. This disease has created a wide gradient in crown health over a large geographic area. In this case, premature loss of foliage was the impact and several other aspects of crown structure were the response, along with tree growth. Specifically, this thesis examined the effects of SNC at the individual needle, branch, tree, and stand levels to better understand the impact of defoliation on tree crowns and to develop biological meaningful indices of tree crown health.

Chapter Three describes how the disease has greatly modified the overall structure of the crown. Under severe SNC, crowns were shorter and had fewer primary interwhorl branches than healthy trees, while crown width was unaffected. Crown shape and maximum branch diameter profile responded to the disease in a variety of ways. First, the maximum branch diameter profile differed between severely impacted and healthy Douglas-fir, more so than crown shape. Thus, branch length to diameter ratios significantly increased with disease severity, which may have important implications for mechanical strength of the branches. Second, the difference in crown shape of healthy and unhealthy trees indicated that there was little difference in branch lengths in the upper and lower crown, while mid-crown branches were shorter. Branches in the lower crown of trees with severe SNC were elongating faster than those on healthy trees, while elongation of upper crown branches was unaffected and elongation of mid-crown branches was slower than on healthy trees. Finally, branches on sites with severe SNC have smaller foliated lengths and a reduced number of secondary interwhorl shoots. Disturbances such as SNC and other needle casts can significantly alter the overall structure and morphology of tree crowns by influencing branch growth, morphology, and longevity.

Chapter Four explored the impacts of SNC on the production, allocation, and vertical distribution of crown mass. SNC influenced production and allocation at three different levels, the branch, tree, and stand. Foliage dry mass declined at all three levels under increasing SNC severity, while woody mass declined only at the individual tree and stand levels. Thus, foliage ratios (the amount of foliage dry mass per unit of woody dry mass) decreased at all three levels with increasing SNC. Branches, however, allocated a greater proportion of dry mass to higher order branches, and less to primary branch axis elongation. The vertical distribution of foliage dry mass in individual trees was less skewed and more uniform under more severe SNC. The crown sparseness index (crown length to sapwood area at crown base) proved to be the best index for predicting tree foliage dry mass for a given tree size, relative height in the stand, and site index. The production, allocation, and vertical distribution of crown mass changed in response to SNC.

Chapter Five examined changes in Douglas-fir needle size and foliage age class distribution. Understanding of Douglas-fir foliage dynamics is currently limited, including the response of individual needles to changes in the within-crown light environment. Furthermore, functional links between SNC indices such as foliage retention and the relative distribution of foliage by age class are lacking. Results of this study indicated that needle weight, length, width, and projected leaf area were smaller with increasing disease severity. Specific leaf area of the foliage, however, increased under more severe SNC when the latter was measured by crown sparseness, but not by foliage retention. Younger age classes comprise a greater proportion of the foliage age distribution with increasing SNC severity. Very little foliage greater than two-years of age survived on heavily diseased trees. In addition, a greater proportion of current and 1-year-old foliage occurred higher in the crown than normal, while 2-, 3-, and 4-year-old and older foliage were concentrated lower in the crown. These responses have important implications for light interception and gas exchange. Finally, foliage retention was a better index than the crown sparseness index for predicting relative foliage age class distribution. Growth losses associated with SNC in the

Oregon Coast Range are due to the loss of foliage area, but also to changes in the needle size, age structure, and vertical distribution.

Chapter Six assessed the affects of SNC on stand-level crown and growth dynamics. The disease has induced an increase in crown recession rate, woody litterfall, and the litter specific leaf area, implying corresponding changes in decomposition rates and nutrient-cycling within these plantations. The leaf area index and foliage litterfall rates of the stands have decreased. Most of the foliage litterfall occurred in the fall, while an increased proportion fell in the summer months in comparison to similar litterfall studies. Growth efficiency of the stands improved possibly due to deeper penetration of light, reductions in the amount of respiring tissue, and greater proportion of younger, more efficient foliage. Variability of crown condition, as assessed by foliage retention and the crown sparseness, was related to both SNC as well as other individual tree and site factors. Variabiliy of within-tree foliage retention, however, was significantly greater than between-tree or between–stand variability. The number of samples required to detect a biologically reasonable confidence interval width was between 2 to 8 trees per stand and 2 to 4 branches per tree, similar to values previously recommended in the literature. The crown sparseness index, on the other hand, was found to be significantly less variable than foliage retention. SNC may induce changes in stand-level functions such as habitat availability, susceptibility to further disturbance, nutrient-cycling, and ecological processes related to heterogeneity.

The quantitative relationships explored and developed in this work highlight the plasticity of tree crowns and the modifications that can occur due to defoliation. While crown condition can be difficult to assess, it is an important measure that needs to be to be continually examined and incorporated into current forest surveys and models given its significant ecophysiological implications.

Recommendations

A primary objective of this research project was to examine the biological mechanisms behind the efficacy of several SNC indices, particularly foliage retention and the crown sparseness index. While assessments of crown color and crown density give coarse but integrative estimates of tree vigor, more intensive assessments like foliage retention and the crown sparseness index provide a more objective and biologically justifiable representation of crown condition. Foliage retention was significantly related to total tree foliage dry mass, as well as the distribution of foliage across age classes. The crown sparseness index, however, was a better predictor of the total amount of foliage dry mass on a tree, for a given tree size, relative height in the stand, and site index. The crown sparseness index, on the other hand, was not significantly related to the amount of foliage in the 4-year-old and older age class. The crown sparseness index may therefore give a better estimate of absolute foliage dry matter on a tree, while foliage retention most likely gives a slightly better estimate of the relative distribution of this foliage among the age classes.

Estimation of foliage retention, however, has several drawbacks, particularly its high subjectivity and the difficulty of estimates in older stands with higher crowns. The crown sparseness index, on the other hand, is much less variable and relatively easier to apply in the field. Regardless of the crown assessment index used, estimates on 3 to 5 five tree within each stand should be made in order to reduce variability associated with the measures. Incorporating measurements of the crown sparseness index and foliage retention when possible may prove to be the best means for rating SNC severity and tree vigor in the Oregon Coast Range.

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APPENDIX