AN ABSTRACT OF THE THESIS OF

Ariadne T. DeMarco for the degree of Master of Science in Sustainable Forest Management presented on March 21, 2014.

Title: Pine Butterfly (*Neophasia menapia*) Outbreak in the Malheur National Forest, Blue Mountains, Oregon: Examining Patterns of Defoliation

Abstract approved:

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The pine butterfly (*Neophasia menapia* C. Felder & R. Felder) (Lepidoptera: Pieridae) is a relatively host-specific defoliator of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws). From 2008 to 2012, the Malheur National Forest was subject to an outbreak of pine butterfly in ponderosa pine, peaking at ~100,000 ha of forest visibly defoliated in 2011. Silvicultural- based management guidelines have been used to manage stand resilience to other insect defoliators, but guidelines specific to the pine butterfly are currently lacking. The goal of this study is to examine pine butterfly defoliation patterns to relate stand and tree structure characteristics to inform management guidelines. I randomly sampled 25 stands within ponderosa pine forests delineated as heavily defoliated in 2011 by annual forest health aerial surveys. Within each stand I randomly located three transect plots, 10 x 40m, and measured diameter at breast height (DBH), height, and estimated defoliation for the entirety of all trees > 5cm DBH. Data was analyzed using linear mixed effects models to account for all other determinants of defoliation before measuring variables under study. Defoliation averaged

67% for all trees. Stand density index, stand structure, tree crown class, and level within a tree canopy demonstrated no meaningful effects on mean defoliation. I infer from these results that defoliation levels during pine butterfly outbreaks are not influenced by structural or crown characteristics; virtually all available foliage is consumed in these single host-species stands (though note that ~10% of trees studied showed <50% defoliation levels). This suggests that the most relevant factor to managers interested in reducing tree mortality and growth loss may prove to be individual tree health prior to an outbreak. Therefore, standard silvicultural recommendations of thinning ponderosa pine to reduce competition and increase tree vigor and resilience is likely to be a good course in areas that are prone to pine butterfly outbreaks, although the best available information suggests that thinning should not be conducted during an outbreak.

Pine Butterfly (*Neophasia menapia*) Outbreak in the Malheur National Forest, Blue

Mountains, Oregon: Examining Patterns of Defoliation

by

Ariadne T. DeMarco

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

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Ariadne T. DeMarco, Author

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CONTRIBUTION OF AUTHORS

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Chapter 1: General Introduction

"...instantly the air was alive with butterflies, flitting round the pines in countless numbers, and glistening against the dark green of the young timber, like the most delicate snowflakes."

(Stretch, 1882).

Insect pests can cause significant changes to forest landscapes and resources throughout the word. The United Nations Food and Agriculture Organization (FAO) report (2009) included 72 different species of forest insect pests causing damage in 25 different countries. One of the most prevalent insect groups reported throughout the majority of these areas were Lepidopteran defoliators. Some of the most damaging Lepidoptera species exist at low population levels for years, then unpredictably outbreak and cause massive damage to forest resources (FAO 2009, Barbosa et al. 2012). Defoliation during an outbreak period of any of these species can affect tree growth and mortality, nutrient allocation and cycling throughout the ecosystem, tree seed production, light penetration to the understory or forest floor, and populations of predators, in ways that other types of forest disturbances (such as fire and logging) do not (Kolb et al. 1999, Lovett et al. 2002). Because insect outbreaks can occur suddenly and somewhat unpredictably, there is a sense of urgency regarding quantifying the effects of a particular outbreak and mitigating any damage that is caused (Western North American Defoliator Working Group, 2013). Moreover, climate change is certain to continue to influence the biology and range of many forest defoliators, making information on these pests even more valuable, as managers attempt to anticipate likely future forest health conditions (Roualt et al. 2006, Vanhanen et al. 2007, Jepsen et al. 2013, and others).

The causes of insect outbreaks are generally poorly understood. Climate, predators, parasites, and diseases, tree physiology, and other factors have been explored as influencing the outbreak cycles of insect pests (Barbosa et al. 2012), to no general conclusions. However, silvicultural management guidelines use an understanding of a pest species' ecology to create and manage forests that are resilient to outbreaks. Silvicultural treatments focus on controlling stand structure, forest species composition, and habitat for naturally occurring predators, and have been used successfully for some of the most prevalent defoliators (Brookes et al. 1985, Brookes et al. 1978, McManus 1989, Gottschalk 1995). This type of management is a desirable alternative to treatments using insecticides or biocontrols, which can be expensive, difficult, or ineffective. However, silvicultural guidelines are still lacking for many pest species that affect large regions of the world.

The forests of western North America are vital to the ecosystem processes and economic health of the region. Currently, many of these forests are experiencing characteristics that are very different from historical conditions. Many stands are overstocked, dense, and even-aged, due to historically poor management, including fire suppression efforts throughout the state. Understanding the relationships between defoliator populations and stand structure may be especially relevant to managers in these stands which have been heavily altered from their historical state. Insect defoliators that evolved to a historical stand type (defined by characteristics such as a greater percentage of larger trees, frequent and mild surface fires, and more open stands) may interact with

current stand structures in unexpected ways.

In the ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forests of eastern Oregon, common defoliating insects include the pandora moth (*Coloradia pandora* Blake) (Lepidoptera: Saturniidae), pine sawflies (Hymenoptera: Diprionidae), sugar pine tortrix (*Choristoneura lambertiana* Obraztsov) (Lepidoptera: Tortricidae), and the pine butterfly (*Neophasia menapia* C. & R. Felder) (Lepidoptera: Pieridae). Of these, only the pandora moth and pine butterfly exhibit outbreaks that last several years and can defoliate many thousands of hectares of ponderosa pine (Speer et al. 2001). The pandora moth is cyclic, and its two-year life cycle allows trees to recover between defoliation events. However, the pine butterfly may be a much more aggressive defoliator which can cause tree mortality and growth loss.

The family Pieridae is spread worldwide; the subfamily Pierinae contains the only two species within the genus *Neophasia,* which feed on conifers. Unlike the pine butterfly, *Neophasia terlootii* Behr does not exhibit outbreaks, and causes little damage on its host of ponderosa pine within its range in the American southwest and Mexico (Scott 1986).

At endemic levels, the pine butterfly causes little noticeable damage to foliage, though adults may be casually observed in the canopy (Scott 2012). Yet during outbreak years, larval feeding reduces tree fitness and resiliency, and can cause cumulative growth loss over many years (Evenden 1940, Cole 1954, Cole 1966, Dewey et al. 1973). These outbreak periods typically last for three to five years (Scott 2010). In severe areas of an

outbreak, pine butterfly larvae may consume all green needles on a single tree. However, they prefer older foliage, and do not eat the live buds. A tree that has been completely defoliated will usually be able to produce a complete crop of needles the following year (Dewey et al. 1973). Thus, defoliation alone is regarded as a factor that weakens trees, and does not usually cause mortality, although growth may be affected.

Growth impacts of the pine butterfly appear to vary by outbreak event, from more limited growth reduction (40%, Cole 1966) to zero basal growth for an average of 2.6 years after defoliation (Evenden 1940). Tree mortality following a defoliation event depends upon the severity and duration of defoliation, drought conditions, and local abundance and activity of bark beetles (*Dendroctonus* spp.). Evenden (1940) reported 14% of trees died after defoliation due to the severity of defoliation alone, but many other outbreaks have occurred with no reports of tree mortality following severe defoliation (Dewey et al. 1974, Scott 2010). Bark beetles have been responsible for some of the mortality reported in pine butterfly- defoliated areas (Webb 1906, Furniss & Carolin 1977). However, this association appears to occur in less than 25% of reported pine butterfly outbreaks (Scott 2010). Reports vary from <1% of trees killed by bark beetles (Helzner & Thier 1993), which likely represents endemic bark beetle population levels, to 17% of highly defoliated trees (Evenden 1940). The most dramatic example of tree loss occurred after the 1893-1895 defoliation event, which killed an estimated 20-90% of trees in Yakima area of eastern Cascades in south central Washington due to a mixture of defoliation and bark beetle attacks (Furniss & Carolin 1977).

Little is known about factors that control pine butterfly outbreaks, and silvicultural management guidelines are lacking. A recent (2008-2012) outbreak of pine butterfly in the Malheur National Forest defoliated over 100,000 hectares of ponderosa pine, and provided an opportunity to study the relationships of stand structure to defoliation.

Factors influencing tree stress and susceptibility to defoliation by the pine butterfly have not been studied in depth, though numerous Forest Service reports have suggested ideas. Tree age and canopy position have been noted as potential factors in defoliation and damage levels, but conclusions are mixed. Although it was not directly studied, Cleator (1910) noted in an annual report that mature trees were more defoliated by pine butterfly than seedlings and saplings, and that eggs seemed to be laid almost exclusively on mature trees. Numerous reports have noted that females may prefer to lay eggs in tops of mature trees (Cleator 1910, Evenden 1926, Evenden 1940, Helzner & Thier 1993), but none of the above studies have sought to quantify or directly address this behavior during an outbreak period. During their study on prescribed fire and pine butterfly, Kerns and Westlind (2013) found a small difference in defoliation based on tree height at some of their study sites, though this conclusion is uncertain. But Cole (1956) reports that during outbreaks, eggs are laid uniformly throughout the crown.

Records of pine butterfly outbreaks in eastern Oregon date back to 1908 and 1940 (Scott 2010), none lasting longer than three years. A dendrochronology of the pine butterfly is not available, although data from a historical record of pandora moth

outbreaks (Speer et al. 2001), which share the ponderosa pine host, might contain information on pine butterfly outbreaks, as well. In 2011, at the peak of the outbreak period observed here, pine butterfly defoliation centered in the Malheur National Forest caused noticeable defoliation in over ~100,000 ha of ponderosa pine forest (USDA, 2011). The prior outbreak in that area may have occurred during 1982 – 1984, on the Prairie City Ranger District, Malheur National Forest, Blue Mountains, but due to simultaneous pine needle sheathminer (*Zelleria haimbachi* Busck) (Lepidoptera: Yponomeutidae) activity, it was not well documented (Scott 2010). The area defoliated from 2008-2012 was primarily pure ponderosa pine, with marginal defoliation in the mixed conifer type at higher elevations.

I took the opportunity that this outbreak provided to investigate application-based questions regarding management for resilience to these outbreaks. I quantified tree defoliation using ground-based observation and investigated relationships between defoliation intensity, stand density index (SDI), stand structure, crown class, and crown position. These four aspects of stand structure have been previously hypothesized to have a relationship to defoliation by pine butterfly, or are influential in defoliation severity from other, similar defoliators.

The questions I sought to answer were: 1) After accounting for all other legitimate determinants of defoliation, is there an effect of stand density index on defoliation?; 2) Do even, uneven, and mixed- structure stands exhibit different levels of defoliation?; 3) How does tree dominance in the crown affect defoliation patterns?; and 4) are there

patterns or differences to defoliation throughout vertical thirds of the crown? Answers to

these questions will be used to suggest management guidelines.

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Chapter 2: Pine Butterfly (*Neophasia menapia*) Outbreak in the Malheur National Forest, Blue Mountains, Oregon: Examining Patterns of Defoliation

Introduction

The pine butterfly (*Neophasia menapia* C. & R. Felder) (Lepidoptera: Pieridae) is a defoliator of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Scott 2010). This insect is endemic to the Pacific Northwest, and usually causes little noticeable damage to foliage (Scott 2012). However, approximately every 20-30 years in a given area (Scott 2012), the pine butterfly population may dramatically expand to outbreak proportions, defoliating many thousands of hectares, reducing tree fitness and resiliency, and causing cumulative growth loss over many years (Evenden 1940, Cole 1954, Cole 1966, Dewey et al. 1973). These periods of population expansion typically last for three to five years before falling back under the control of predators, parasitoids and diseases, tree physiology, or other factors (Scott 2010). In general, the factors affecting timing and severity of insect outbreaks are not well understood.

Ponderosa pine is host to relatively few serious defoliators; of these, the pine butterfly is perhaps the most damaging (Furniss & Carolin 1977). The pandora moth (*Coloradia pandora* Blake) (Lepidoptera: Saturniidae) is another important defoliator that also reduces tree growth (Cochran 1998) and exhibits periodic outbreaks. Evidence

of pandora moth outbreaks indicates that at regional and decadal levels, these occur at a mean interval of 27 years, though within-stand variation in intervals can be very large (9 - 156 years) (Speer et al. 2001). The pine sawflies (Hymenoptera: Diprionidae) and the sugar pine tortrix (*Choristoneura lambertiana* Obraztsov) (Lepidoptera: Tortricidae) also defoliate ponderosa, and but are not considered to be as damaging as the pine butterfly and pandora moth (Furniss and Carolin 1977, Ciesla et al. 2010).

The pine butterfly has one generation per year; eggs are laid in late August and overwinter on host tree foliage. Larvae emerge in spring, and selectively feed on older foliage. Several researchers have hypothesized that gregarious feeding might help to overcome the host tree's resin defenses, which otherwise may overwhelm early-instar individual larvae (Evenden 1926, Cole 1956, Dewey et al. 1974). In mid-June, larvae lower themselves to the ground on silk threads from branches where they have been feeding. Larvae then crawl up tree boles or nearby shrubs to pupate in sheltered locations. In early August, the adults emerge and nectar on understory and meadow flowers such as goldenrod (*Solidago sp.*), rabbitbrush (*Ericameria* sp.) and bitterbrush (*Purshia tridentata* (Pursh) DC.). Females lay eggs on host tree needles, then senesce by late summer.

At outbreak population levels, pine butterfly larvae may consume all green needles on a single tree. However, they do not eat the live buds, and a tree that has been completely defoliated will usually be able to produce a complete complement of needles the following year (Dewey et al. 1973). Thus, defoliation alone is regarded as a factor

that usually weakens trees, and does not commonly cause mortality, although growth may be affected. Growth impacts appear to vary widely; Evenden (1940) reported that the majority of trees that survived severe defoliation exhibited no basal growth for an average of 2.6 years after defoliation, but during a different outbreak, Cole (1966) reported only 40% reduction in growth. Any mortality following a defoliation event may be dependent upon the severity and duration of defoliation, drought conditions, and abundance of bark beetles. The most dramatic example of tree loss was the 1893-1895 defoliation, which killed an estimated 20-90% of trees in eastern Washington (Furniss & Carolin 1977). Several decades later, Evenden (1940) reported that 14% of trees died after defoliation due to the severity of defoliation alone. However, Dewey et al. (1974) reported only 3% tree mortality in heavily defoliated stands, and many other outbreaks have occurred with no reports of tree mortality following severe defoliation (Scott 2010).

Bark beetles, especially the western pine beetle (*Dendroctonus brevicomis* LeConte) (Coleoptera: Curculionidae: Scolytinae) are attracted to stressed trees (Furniss & Carolin 1977) and have been responsible for much of the mortality reported in pine-butterfly defoliated areas (Webb 1906, Furniss & Carolin 1977). However, this association is not very common, only occurring in less than 25% of reported cases (Scott 2010). Of these, reports vary from <1% of trees killed by bark beetles (Helzner & Thier 1993), to 17% of highly defoliated trees (Evenden 1940).

Tree age and canopy position have been noted as potential factors in defoliation and damage levels for the pine butterfly, but conclusions are mixed. Although it was not

directly studied, Cleator (1910) noted in an annual report that mature trees were more defoliated by pine butterfly than seedlings and saplings, and that eggs seemed to be laid almost exclusively on mature trees. Numerous reports have stated that females prefer to lay eggs in tops of mature trees (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden 1940), but none of the above studies sought to quantify or directly address this behavior. During their study on prescribed fire and pine butterfly, Kerns and Westlind (2013) found a small difference in defoliation based on tree height at some of their study sites, though they this conclusion is uncertain. But Evenden (1940) concluded that crown dominance plays no part in tree recovery and Cole (1956) reported that during outbreaks, eggs are laid uniformly throughout the crown.

Understanding the relationship between stand structure dynamics and pest insect biology is an important step in developing management guidelines that may reduce stand susceptibility to outbreaks, and minimize tree injury when outbreaks do occur. Silvicultural-based management guidelines have been used to manage stand resilience to many other insect defoliators, both in western conifer forests (Brookes et al. 1985, Brookes et al. 1978) and in eastern forests (Gottschalk 1995).

The pine butterfly shares with the western spruce budworm (*Choristoneura freemani* Razowski 2008 (Lepidoptera: Tortricidae) the trait of larvae lowering through the canopy on silk threads. In western spruce budworm, multistoried stands promote survivability in these larvae, and if intermediate trees and understory hosts are not available, larvae fall to the ground and perish. Therefore, management guidelines for the

western spruce budworm involve thinning to achieve open, even-aged stands. Structural-based management could also affect availability of pupation and egg laying sites for pine butterfly (Cole 1956b), and predator or parasitoid habitat and alternative food sources (Dickson et al. 1979, Jervis et al. 1993).

Some forest defoliators such as Eastern budworm (*Choristoneura fumiferana* Clemens) (Lepidoptera: Tortricidae) appear to prefer mature trees, or trees with more availability to sunlight (Brookes et al. 1985, Brookes et al. 1987). Recommendations for mitigating white pine weevil damage is to use shelterwood cutting to regenerate stands in shade cover, since damage is most severe in open-grown stands (Gottschalk 1995). Cochran (1998) found that defoliation by pandora moth increased as basal area decreased from 40.1 m^2/ha to 21.5 m^2/ha, then declined as basal area further decreased from 21.5 m^2/ha to 16.3 m^2/ha. Correlations between stand density and tree dominance have been tested as predictors of defoliation by *Diprion pini* L. (Hymenoptera: Diprionidae) in Scots pine *(Pinus sylvestris* L.) stands, with varying conclusions (Saarenmaa 2003, De Somviele 2004, Augustiatis 2006).

Studies designed specifically to test the effects of tree and stand structural attributes on defoliation levels have not been conducted for the pine butterfly, and management guidelines specific to the pine butterfly currently do not exist. As in other pest systems, results of such studies could be helpful in developing management regimes that increase tree resistance or decrease tree mortality.

From 2008 to 2012, the Malheur National Forest was subject to an outbreak of pine butterfly in ponderosa pine. In 2011, at the peak of the epidemic, aerial surveys estimated ~100,000 ha of ponderosa pine defoliated. An estimated ~97,000 ha of this area was qualified as showing >50% crown loss (USDA 2011). The area defoliated was primarily pure ponderosa pine, with marginal defoliation in the mixed conifer type at higher elevations. This recent epidemic of the pine butterfly provided an opportunity to investigate application-focused questions regarding management for resilience to these outbreaks.

I took this opportunity to quantify tree defoliation and investigate relationships between defoliation intensity, stand density index (SDI), stand structure, crown class, and crown position. These four aspects of stand structure have been previously hypothesized to have a relationship to defoliation by pine butterfly, and are influential in defoliation levels from other defoliators. My intention is to determine the need for management guidelines specific to the pine butterfly, if applicable.

The questions I sought to answer were: 1) Is there a relationship between stand density index and defoliation? 2) Do even, uneven, and mixed- structure stands exhibit different levels of defoliation? 3) How does tree dominance in crown position relate to defoliation patterns? and 4) Are there patterns or differences to defoliation throughout vertical thirds of the crown?

Methods

Study area

This study was conducted in central Oregon in the Malheur National Forest (Emigrant Creek and Blue Mountain Ranger Districts) (Table 1.1, Figure 2.1). The Malheur National Forest is located in the Blue Mountains, Oregon, an area characterized by dry forests, with ponderosa pine at lower elevations and dry mixed conifer at higher elevations consisting of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), grand fir (*Abies grandis* [Douglas ex. D. Don] Lind.), and western larch (*Larix occidentalis* Nutt.). Current stand conditions in the Malheur National Forest are affected by past logging, fire suppression, and intensive grazing. Common management regimes for the ponderosa pine forests in this area involve thinning, prescribed fire, and grazing (Malheur National Forest, 1990).

In the Blue Mountains region of Oregon, ponderosa pine grows in sites with annual precipitation ranging on average from 36cm – 76cm, most of which falls as snow during the winter (Emmingham et al. 2005). Associated vegetation includes western juniper (*Juniperus occidentalis* Hook.) at lower elevations and on rocky sites, Douglas-fir at higher elevations, and mountain mahogany (*Cercocarpus ledifolius* Nutt.) and associated vegetation at drier sites. The fire regime of these ponderosa pine types was historically low-severity fires with frequent return intervals (Agee 1993, Heyerdahl et al. 2001). However, fire suppression is practiced in the region today and grazing influences understory vegetation fuel characteristics (Kerns et al. 2001). This is an area that historically has been intensely managed for timber by the Hines Lumber Company,

Seneca, Oregon (USDA 2014), with second-growth stands predominantly aged from 60 –

150 years (Lia Spiegel, 2014, personal communication).

My study was conducted in stands defoliated by the pine butterfly, and dominated

by ponderosa pine. The Rock Spring SNOTEL station, (44°1′N/118°50′W, 1602 m

elevation), located slightly southeast of my study sites, reports average annual

precipitation as 46.0 cm (20-year average), with 68% of this falling as snow during the

winter. In 2012, the growing season under study, annual precipitation at Rock Springs

SNOTEL was 35.6cm, 77% of average for that site. Monthly mean temperatures range

between -6° and 31 °C, with a January mean of 1° and a June mean of 16 °C (20-year

average). Daily temperature fluctuations can be large (Carlson 1974). Bedrock

composition includes rhyolite, rhyolitic ejects and tuffaceous sediments, altered tuffs, and

breccia (Carlson 1974).

The potential vegetation group of my study sites is defined as either warm dry or

hot dry upland ponderosa pine forests (Powell et al. 2007); these forests are categorized

as demonstrating a fire regime of 0-35 year fire frequency, with low fire severity on

dominant overstory vegetation (Schmidt et al. 2002, Powell et al 2007).

Stand selection

I sampled stands within the area of "high" (>50% visible crown loss) defoliation

estimated by USFS/ODF cooperative aerial detection survey (ADS) data for 2011

(USDA 2011, Flowers et al. 2012), in plant association groups dominated by ponderosa

pine. Ground-truthing of stands was used to verify that pine butterfly, and not pine

sawfly, was responsible for the majority of reported defoliation. Stand polygons were delineated by data on management history, and I excluded areas with very recent logging activity.

Twenty-five stands were randomly selected using ArcGIS 10.0 (ESRI 2010). These ponderosa pine stands met criteria described above. Stands were typically characterized by open understories, small amounts of coarse woody debris, and evidence of cattle grazing. Elevation of study stands ranged from 1500m - 1700m. Within each stand, the three 10m x 40m transects were delineated from random starting points and random azimuths (total of 75 transects). Transects that fell outside the boundary of the stand or that overlapped previous transects were discarded, and new transects randomly chosen. A total of 25 stands and 75 belt transects were measured, representing a total of 750 live ponderosa pines >5cm DBH.

Sampling protocol

Defoliation was estimated for all ponderosa pine trees in each 10m x 40m belt transect. Percent defoliation was visually estimated to the nearest 5% by ground observation, using binoculars when needed. Defoliation was estimated for the entire tree, and for each third of a tree crown. A photographic guide to defoliation was developed prior to taking measurements, and referenced in the field (Figure 1.1). All defoliation estimates were conducted by the same observer. All defoliation was measured in April 2013, before bud break on ponderosa pine, and represented 2012 defoliation.

Other tree structural characteristics at study sites were measured for 15 stands in summer 2012 and 10 stands in April 2013. Trees were measured for species, diameter at breast height (DBH), crown class (following Helms 1998, see Table 2.1), vigor rating, and height. Trees <5cm DBH were not measured. Trees measured for these characteristics in different years were treated identically in the analysis, since they were measured within the same growing season.

GPS coordinates were recorded at each end of a transect, and slope, aspect, elevation, and a physiographic categorization (see Table 1.2) of each transect was recorded.

Indices of stand structure

I defined two variables as indices of stand structure. Stand density index (Equation 1, Reineke 1933) was determined from the measurements of trees within transects. A qualitative description of stand structure, as even, uneven, or mixed, was developed by examining diameter distribution plots (Figure 2.2a, 2.2b, 2.2c).

[1] $$\text{SDI} = TPA \left(\frac{Dq}{10}\right)^{1.605}$$

where TPA is the number of trees per acre, and Dq is quadratic mean diameter in inches.

Data analysis

I used three different linear mixed effects models to describe the response of defoliation to structural variables, crown class, and vertical position within a tree crown. Random effects of stand, transect, and tree location were incorporated as nested effects

into the models as needed. Covariates were assessed for collinearity prior to analysis.

Assumptions of equal variance and normality were tested using graphical tools, and tree

diameter was transformed logarithmically to correct for a violation of equal variance.

Evidence of interactions was tested graphically.

In addition to analyzing the data all together, I also described patterns for stands

and trees with <50% defoliation. Descriptive statistics of these groups are briefly

discussed and presented in tables and figures. All other results presented and discussed

included these <50% stands and trees in the analysis.

I developed sets of models *a priori* that included all measured variables that could

have an effect on the response, except for the variables whose influence I wanted to

judge. I developed three different sets of variables, and thus, three different sets of

models, to answer my questions at three different scales (stand-level, tree-level, and

crown third-level). These models were used as a base upon which to add the variables of

interest. Stands were assigned a defoliation severity rating based on ADS data, where the

sum of severity depended upon number of years of defoliation, and level of defoliation

for each of those years. I used this variable in all of the models, since I considered it to be

a very likely explanation of other patterns in the data that I wanted to account for before

examining relationships of other variables. In this way, I determined the effects of the

variables under study on the fit of the model, after having accounted for all other

legitimate determinants of defoliation. From each set of models, I used second-order

Akaike Information Criterion (AICc) to select a base model. Second-order AIC provides

an estimate of how well a model explains the data, balancing goodness of fit with model complexity, while taking sample size into account. The selection of terms in the base models did not infer any particular value to those terms. The AICc best-ranking model was then refit, with the variable under study added as a term. The effect of that study variable on the fit of the model was determined by examining its associated degrees of freedom, F-statistic at the $\alpha = 0.05$ level, and p-values.

If I found evidence of a significant ($\alpha \leq 0.05$) difference in effect from a study variable, *post hoc* pairwise comparisons of least-squares means were used to estimate differences between levels of that variable. P-values and confidence limits were adjusted for multiple comparisons using general linear hypothesis testing that preserved a 95% family-wise error rate. Least-squares means for each level of the variable were also estimated. All analyses were performed using the program R, version 3.0.2 (R Development Core Team 2013).

Results

Mean tree defoliation was 67% (standard deviation = 14%) and most of the mean stand defoliation values ranged from 45% to 75%, with only a few outliers. Of the three stands with mean defoliation <50%, one was uneven-structured, and the other two were mixed-structured (Table 2.1). Two of those stands were located relatively close to one another (36 and 38), but there are no other apparent similarities between these three less-defoliated stands.

Of the 785 trees measured, 72 trees were <50% defoliated, spread throughout seven different stands (Table 2.1, Figure 2.3). Differences in means within stand structure groups (even, mixed, uneven) were within 12%. Differences in means within crown class groups were within 7%. Crown class did not have a significant relationship to defoliation ($F_{3, 53}$= 0.97, p=0.41) for this group.

SDI and Stand Structural Relationships to Defoliation

I found no evidence of a relationship between stand density index and mean defoliation ($F_{1, 47}$= 0.18, p=0.67). The tested values for SDI covered a range of 1400 (Table 2.1).

I categorized nine stands as even-structured; the mean defoliation of this group was 71.2%. Mixed-structure stands showed a mean defoliation value 62.2%; I sampled seven. Uneven-structure stands had a mean defoliation value of 66.1% and a sample size of nine (Table 2.2). However, when I added the structure variable to the base model, no significant relationship was found between structure and mean defoliation ($F_{2, 22} = 2.23$, p = 0.13) and marginal means demonstrated no significant difference in values (all 95% confidence intervals included zero). In this case, marginal means preserved a familywise error rate necessary for accurately estimating significant differences between group means, and arithmetic means were not appropriate for assessing group differences.

I used the same base model to assess the effects of both SDI and stand structure, since other relevant explanatory variables were the same for both of these stand-level attributes. Variables considered for inclusion in this base model included sum of severity,

aspect, physiographic type, and log of tree diameter. I did not include crown class

because it was highly correlated with log of tree diameter, and I considered tree diameter

to provide more detailed information on tree size, vigor, and crown position than crown

class. The AICc preferred model included only sum of severity and log of tree diameter

(Table 1.1).

Crown Class Relationships to Defoliation

Arithmetic means of crown class groups are given in Figure 2.4. The marginal

mean of defoliation for dominant trees was 67.6%; for codominant trees, 65.0%; for

intermediate trees, 66.2%; and for suppressed trees, 63.7% (Table 2.3). My analysis

reported strong evidence that crown class had some relationship to defoliation ($F_{3, 708}$ =

3.17, p = 0.02); however, upon further examination the estimate of the difference in

means between the two differing groups (codominant and intermediate) was only

significant at the $\alpha = 0.1$ level. There is no evidence of any difference in mean defoliation

among any of the other crown class comparisons (pairwise comparison of means, 95%

adjusted family-wise confidence interval).

Variables considered for inclusion in this base model were sum of severity,

aspect, physiographic type, log of tree diameter, structure, stand density index, and an

interaction between structure and mean tree diameter. I included the stand-level attributes

because their lack of significance in the previous model did not imply that they had zero

effect. Although log of tree diameter was correlated with crown class, the AICc preferred

candidate model included sum of severity and stand structure (Table 1.2); any potential

effects of the correlation between log of tree diameter and crown class were irrelevant.

Vertical Patterns of Defoliation

Means of crown thirds are presented in Figure 2.5; all mean defoliation values

were within 3.3%. The marginal means of defoliation in the upper third of the crown was

64.0%; in the middle third, 66.4%; and in the lower third, 67.2%. Standard error for all of

these marginal means was 2.2%. I found strong evidence that crown third had some

influence on mean percent defoliation ($F_{2, 2279} = 38.08$, p-value = <0.001). Variables

included for consideration in this base model included sum of severity, aspect, log of tree

diameter, and stand density index. I did not include physiographic code or structure to

avoid oversaturating the models. I included log of tree diameter instead of height because

diameter more reliably connotes tree size, vigor, and crown position. The AICc preferred

base model included only sum of severity (Table 1.3).

The results of the analysis indicate that the upper third of the crown was, on

average, 2.4% less defoliated than the middle third (p-value <.001, 95% confidence levels

1.5%, 3.4%). There was also strong evidence that the lower third was 3.3% more

defoliated than the upper third (p<0.001, 95% confidence levels 2.3%, 4.1%). I found

some evidence that mean difference in defoliation between the middle and lower third

was 0.8% (p = .057) but the 95% confidence intervals included zero (-1.8, 0.02) (Table

2.4).

Discussion

Given the amount of speculation that structural factors have received in relationship to pine butterfly defoliation (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden 1940) and other defoliators (i.e., western spruce budworm, eastern spruce budworm, Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) (Lepidoptera: Lymantriidae) (Brookes et al. 1978, Brookes et al. 1985, Brookes et al. 1987, Torgerson 2011)) and sawflies in Scots pine (Saarenmaa 2003, De Somviele 2004, Augustiatis 2006), I expected to see a strong pattern or large differences in relation to my studied variables. However, in these highly defoliated areas, the pine butterfly appeared to feed uniformly throughout the extent of stand structure and SDI attributes that I measured, and my results demonstrated only slight differences between crown class groups and crown third groups.

Ground-based observation is commonly used in estimations of tree damage by defoliation (Maclean and Lidstone 1982, Batzer et al. 1995, De Somviele et al 2004, Jacquet 2013, Kerns and Westlind 2013, for example). A study on defoliation estimation techniques for the eastern spruce budworm concluded that ground observers may overestimate defoliation values, with most error occurring at low (<40%) levels of defoliation (Maclean & Lidstone 1982), and <10% error occurring at levels between 60% and 80% defoliation. Since I measured only 72 trees with defoliation values <50%, I am confident that the majority of my estimates are very likely to be nearly as accurate as an estimate based on branches sampled from an individual tree and quantified by closer

analysis methods (Fettes 1950, Maclean & Lidstone 1982); however, I was mainly

interested in patterns and differences at the stand-level. During their survey in 2012,

which took place in the same area as my study, Kerns and Westlind (2013) also used

ground-based observation and found overall defoliation in their sites to average 71%,

approximately the same amount that I estimated (67%).

SDI and Stand Structural Relationships With Defoliation

Neither stand structure nor SDI demonstrated a relationship to overall tree

defoliation. I hypothesized that stands with an uneven structure would have higher levels

of defoliation, via the mechanism of multi-storied canopies promoting larval survival as

they move to pupating sites (Brookes et al. 1985, Brookes et al. 1987). I also expected

larvae to move more easily to new food sources through an uneven-structured, more

multi-storied canopy.

I hypothesized that stands with higher SDI would demonstrate associated higher

defoliation values for two reasons. I expected that larvae would more easily move to new

food sources among a dense canopy. I also expected that trees in stands with higher SDI

would be less able to defend against feeding larvae. It has been speculated that resin

production (a defense mechanism) is required to kill early-instar pine butterfly larvae

(Evenden 1926, Cole 1956, Dewey et al. 1974). The tree resistance hypothesis (Berryman

1976) argues that trees with more competition for resources have fewer resources to

allocate to defend against insects. Although I did not measure this directly, I assumed that

my stands with higher SDI are under more competitive pressure for resources (Ford and

Sorrenson 1992). Kolb (1998) tested the tree resistance idea in ponderosa pine in Arizona (var. *scopulorum* Engelm.) and concluded that lower basal area resulted in thicker phloem, greater resin production, and more days of resin production.

Cochran (1998) studied pandora moth defoliation during an outbreak that occurred in a spacing study of ponderosa pine, and concluded that defoliation increased as basal area decreased from 40.1 m^2/ha to 21.5 m^2/ha, then declined as basal area further decreased from 21.5 m^2/ha to 16.3 m^2/ha. However, in their recent study during the same outbreak, on four half-acre sized-plots, Kerns and Westlind (2013) also found no relationship between SDI and defoliation. And in a Scots pine-sawfly system in Europe, De Somviele (2004) found no relationship between stand density and defoliation by *Diprion pini* L. (Hymenoptera: Diprionidae).

Since I found no relationship of either stand structure or SDI on defoliation, I conclude that in highly defoliated areas, availability of understory canopy levels does not affect larvae survival, stands with more tree cover are not more likely to facilitate pine butterfly movement between trees, and resource stress does not affect defoliation level.

Crown Class Relationships with Defoliation

I hypothesized that more dominant trees, with presumed greater light levels and older ages (dominant > codominant > intermediate > suppressed) would be more defoliated. Tree dominance has been discussed as a potential factor affecting defoliation levels of the pine butterfly (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden

1940, Kerns & Westlind 2013) and appears to be the case for the western spruce budworm (Brookes et al. 1985, Brookes et al. 1987).

Studies of *Diprion pini* defoliation of Scots pine also generally agree that dominant trees are more heavily defoliated (Saarenmaa 2003) though this may be true only when mean stand defoliation is >60% (Augustiatis 2006) or in young stands, and may in fact be reversed in older stands (De Somviele et al. 2004). Augustiatis (2006) also reported quicker recovery in dominant trees, which were more heavily defoliated; this is attributed to increased light availability. It has been proposed that this defoliator may prefer trees above a certain diameter (De Somviele et al. 2004).

I found a very small difference (1.2% at the alpha = 0.1 level) in defoliation means between two crown classes. Since I found no large patterns in the relationship of crown class on defoliation, and since this single difference was very small, I conclude that at high levels of defoliation, tree dominance does not strongly affect pine butterfly feeding behavior. This is in contrast to several observational reports on the pine butterfly (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden 1940, Kerns & Westlind 2013); however, no research has directly studied this relationship. My results corroborate Cole's (1956) observation that during outbreak periods, defoliation is uniform throughout the canopy.

Vertical Crown Patterns of Defoliation

In other studies of the pine butterfly, higher defoliation was observed in the tops of mature trees, suggesting that light availability to foliage may play a part in egg site

choice or larval survival (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden 1940). Therefore, I hypothesized that I would find a large and significant difference between the thirds of the crown, predicting that foliar availability to light, egg-laying site preference, and larvae distribution throughout the crown would influence defoliation. Estimated differences in mean defoliation between crown thirds were very small (within 3.3% of each other). It should be noted that these slight differences did follow a pattern of increasing defoliation towards lower levels; however, estimations of defoliation within a crown may be less accurate than for whole-tree estimates (MacLean and Lidstone 1982).

Related patterns have been shown to exist in other defoliators, though the mechanism behind the pattern is often unknown. For instance, the hemlock looper (*Lambdina fiscellaria* Guenée 1858) (Lepidoptera: Geometridae) pupates on lower parts of the tree during outbreak periods (Hebert et al 2001), and the forest tent caterpillar (*Malacosoma disstria* Hbn.) (Lepidoptera: Lasiocampidae) moves throughout the aspen canopy during its larval stage, changing horizontal patterns as population density changes (Batzer et al. 1995). *Neodiprion sertifer* Geoffroy (Hymentopera: Diprionidae) has been shown to avoid sun needles (Niemela et al. 1982, cited in De Somviele 2004); however, this defoliator may have different chemical tolerances than other defoliators (De Somviele 2004). Because of the small observed differences in defoliation, and the higher likelihood of error, I conclude that during severe outbreaks, pine butterfly larvae are not greatly limited by foliar characteristics, and feed similarly throughout the entire canopy. Given the small trends that I observed, this is an area that may warrant further study.

Management Implications

The variables that I studied showed minimal relationships to defoliation during this outbreak. Tree crown class and canopy third demonstrated some differences, but these were neither patterned nor large enough to consider biologically relevant. Stand density index and stand structure showed no relationship to defoliation. My results indicated that during an outbreak period, in stands with high levels of crown loss, pine butterfly appeared to feed throughout broad differences in stand structure during its outbreak phase. These conclusions are only applicable to areas generally highly defoliated, and medium to low-severity defoliation areas may demonstrate different patterns. I hypothesize that the most relevant factor to managers interested in reducing tree mortality and growth loss will prove to be individual tree health prior to an outbreak. In particular, stands that have historically experienced less competition throughout their growth may include more vigorous trees (Lorimer 1983) that are tolerant to defoliation. The majority of my stands had SDI values higher than the recommended SDI of ~365 (for resistance to mountain pine beetle [*D. ponderosae* Hopkins] attacks, and depending on site type) (Cochran 1992); 22 out of 25 of my stands were above this recommended SDI value.

However, stand thinning treatments have been found to increase defoliator survival and reproductive success in sawflies. This appears to be facilitated by the increase in available nitrogen in host foliage (Moreau and Quiring 2011) or increased host foliage growth and decreasing monoterpenes (Bauce 1996), which are an important

part of plant defense (Langenheim 1994, and others). It is also reasonable that any growth loss due to defoliation may be offset by direct effects of thinning on tree growth (Bauce 1996), but thinning during an outbreak may increase defoliation on remaining trees, and any potential gains in productivity or tree health may be lost (De Somviele 2004). Thinning of ponderosa has been demonstrated to have no apparent nutritional effect on larvae of pandora moth (Ross 1995). Ross also demonstrated that thinning hastened egg hatch and adult emergence of pandora moth; this is likely due to solar radiation and increased temperatures in the stand. It is unclear if these effects are also applicable to the pine butterfly, which may have different biological responses to these factors than the pandora moth.

Although I did not observe unusual numbers of bark beetles for the time period of this study, bark beetles have caused significant mortality in defoliated trees during some past outbreaks (Webb 1906, Evenden 1940, Helzner & Thier 1993, Furniss & Carolin 1977). Therefore, stand resistance to bark beetles is an important consideration for managers during a pine butterfly outbreak.

In summary, no stand treatments are known to directly affect pine butterfly defoliation. Thinning during an outbreak is not recommended (Oregon Department of Forestry 2010), as reductions in tree health may not become apparent until the recovery period. Early thinning and maintaining recommended stocking levels is likely to enhance tree survival. Since specific effects on the pine butterfly population are unknown,

thinning to achieve generally healthy, beetle-resistant, drought-tolerant stands is likely to

be the best use of resources.

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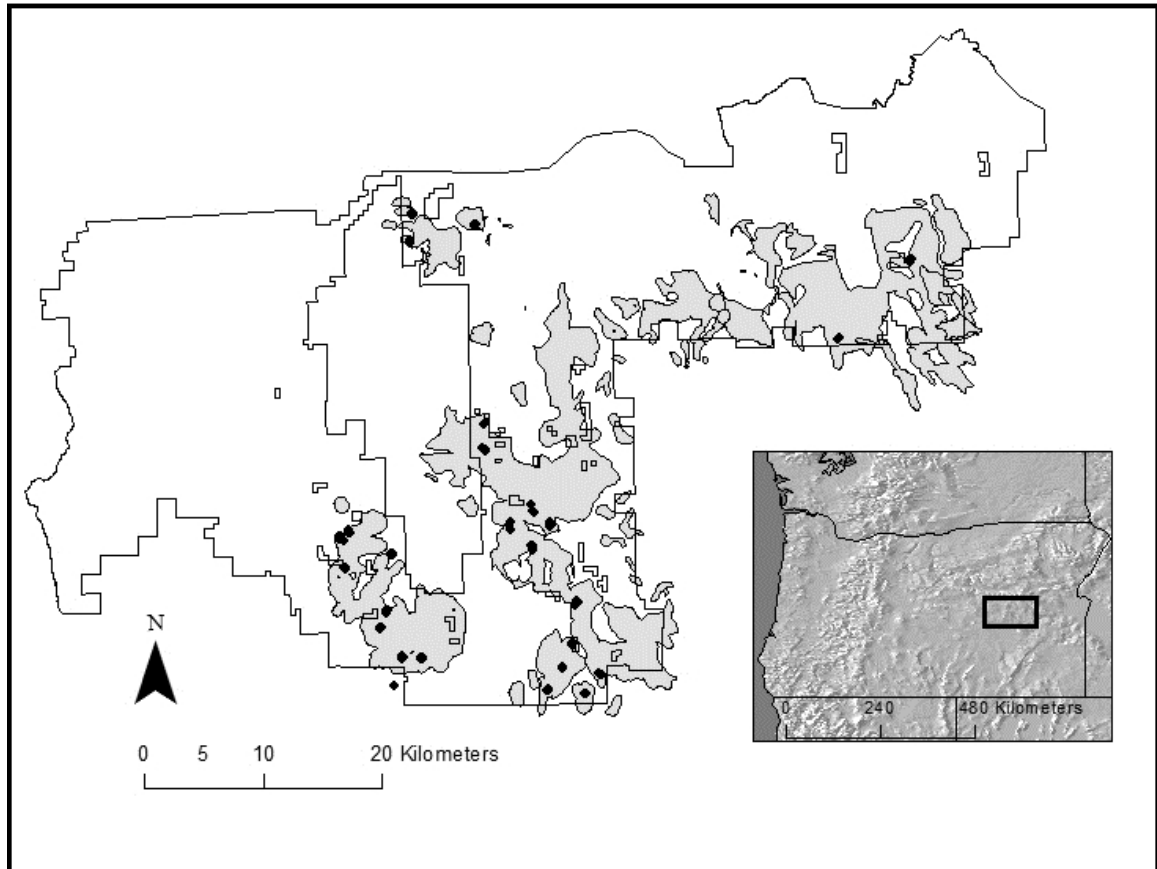
Figures

Figure 2.1. Study area map. Boundary of Malheur National Forest. Grey shading represents area of high defoliation by pine butterfly in 2011. Points represent study stands.
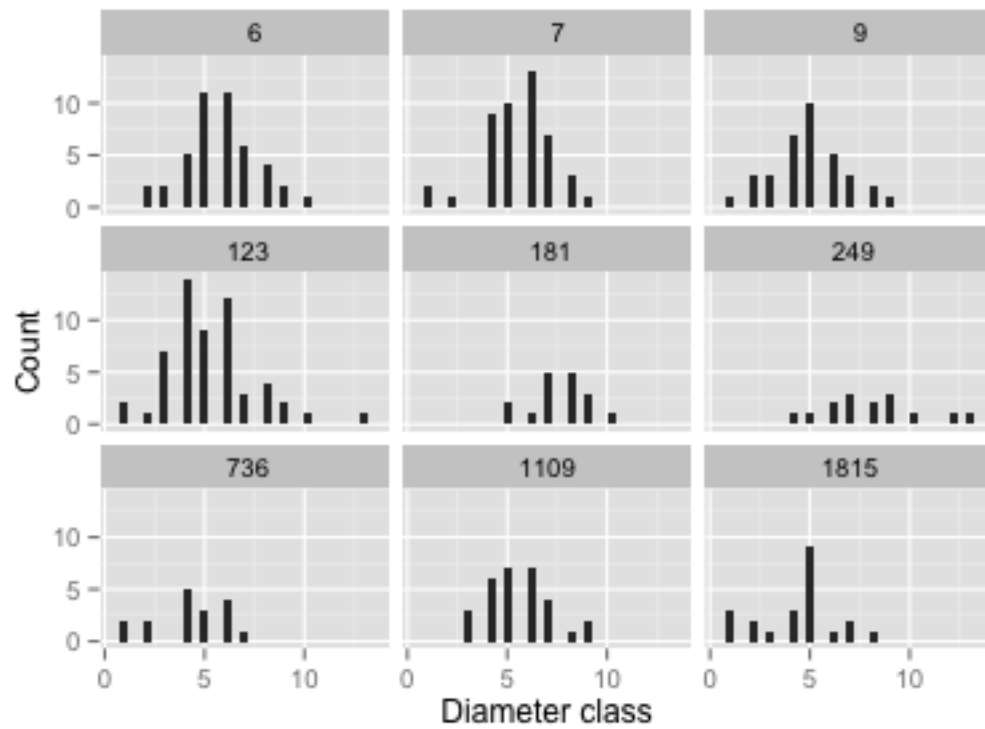
Figure 2.2a. Diameter distribution plots of even-structured stands. Heading numbers represent individual stands. Diameter classes represent each 5cm class measured; i.e., diameter class 1 = 5-10cm, diameter class 2 = 10-15cm, etc.
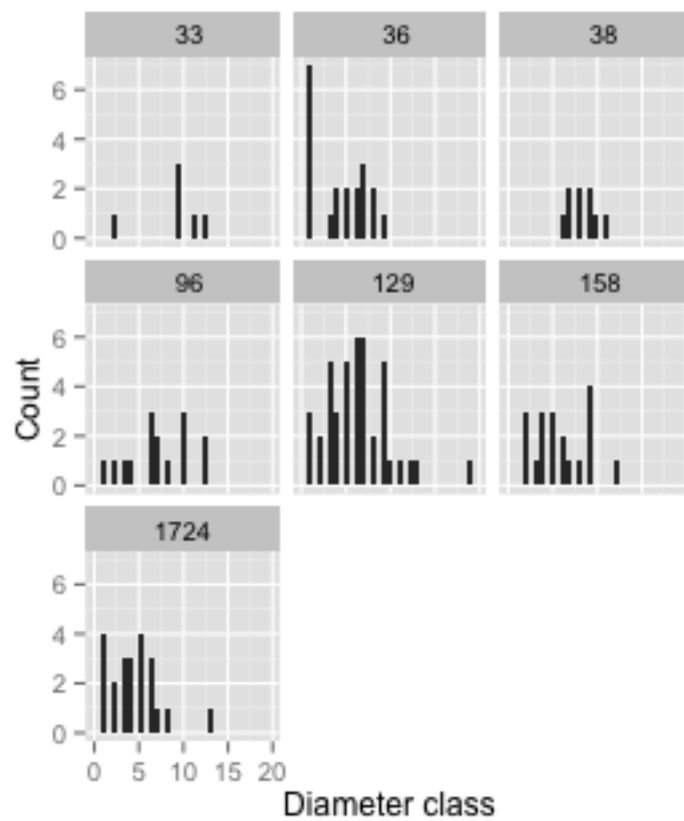
Figure 2.2b. Diameter distribution plots of mixed-structure stands. These stands were neither clearly even-structured nor clearly uneven-structured.
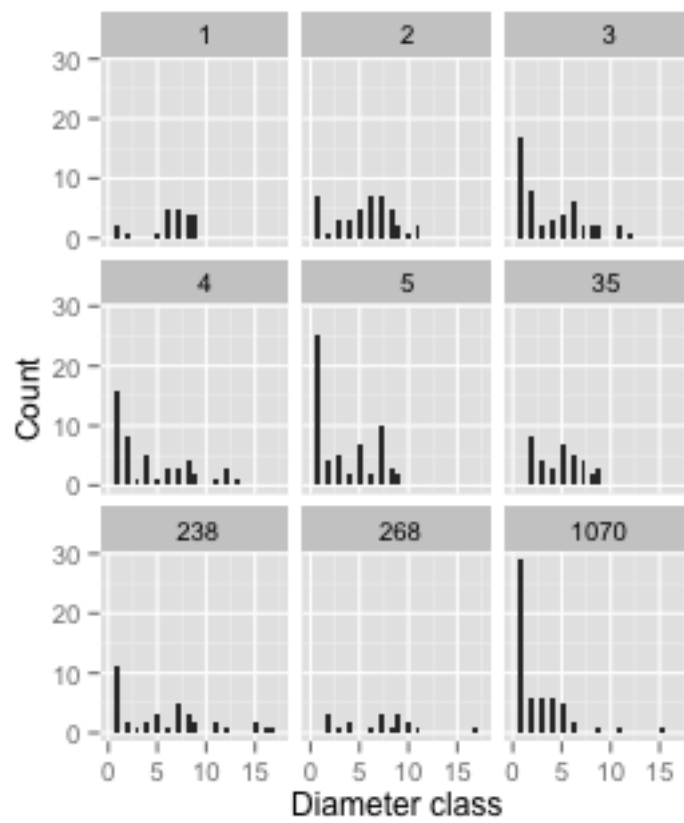
Figure 2.2c. Diameter distribution plots of uneven-structured stands.
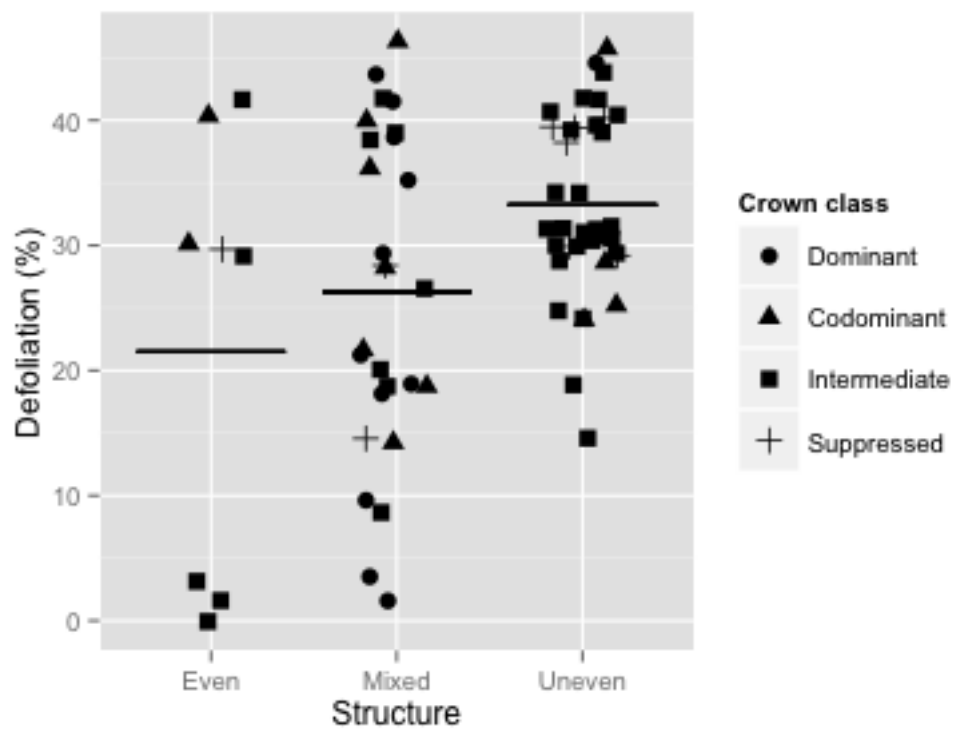
Figure 2.3. Seventy-two trees with defoliation values <50%. Horizontal lines represent structure group means.
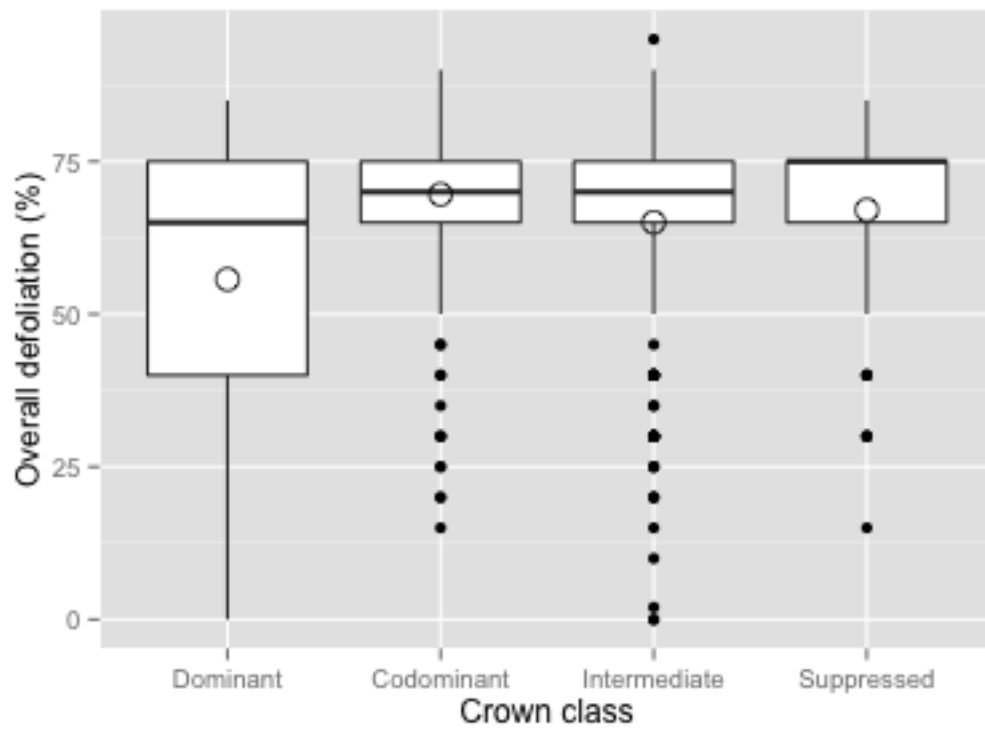
Figure 2.4. Defoliation by crown class group for all trees. Horizontal lines indicate median. Open circles indicate arithmetic means (for marginal means, see Table 2.3). Boxes represent first and third quartiles, whiskers represent 1.5*inter quartile range. Points represent outliers.
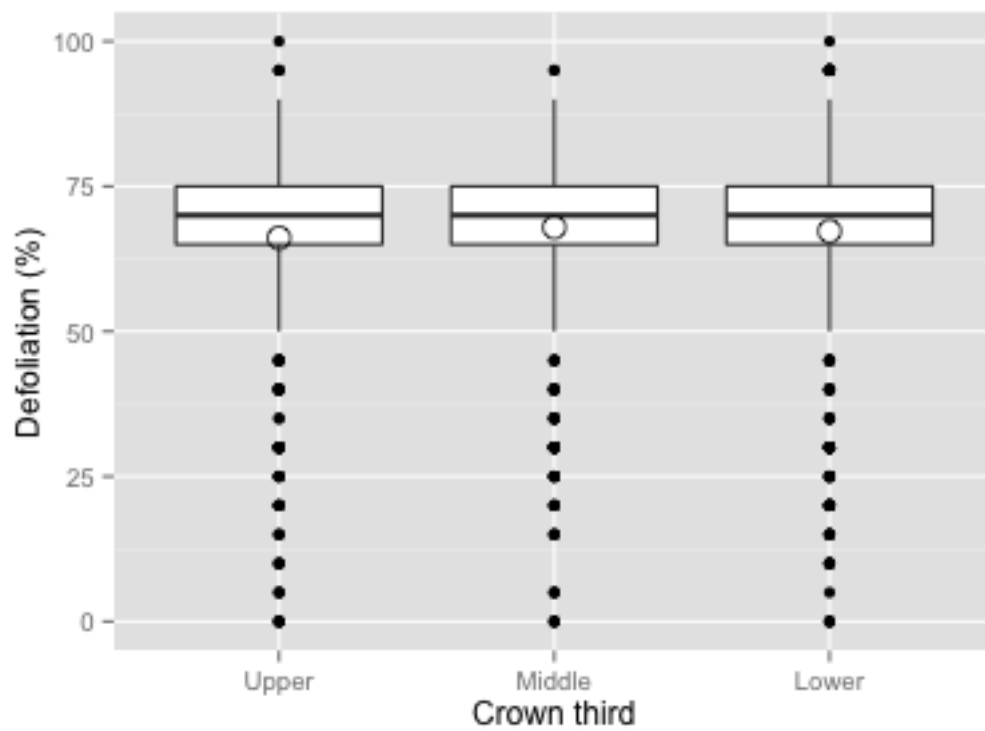
Figure 2.5. Defoliation by crown thirds for all trees. Horizontal lines indicate median. Open circles indicate means. Boxes represent first and third quartiles, whiskers represent 1.5*inter quartile range. Points represent outliers.

Tables

Table 2.1. Characteristics of 25 stands sampled in Malheur National Forest, Oregon. Stands are ordered first by increasing elevation, then by structure. DBH is diameter at breast height. SDI is stand density index. CI is confidence interval. * = stands containing trees <50% defoliated. ** = stands with <50% overall defoliation.

| Stand	elevation (m)	Structure	SDI	trees per ha	basal area per ha	mean DBH (cm) ± 95% CI	standard deviation of mean DBH (cm)	mean defoliation (%) ± 95% CI	standard deviation of mean defoliation (%)
*1815	1562	Even	252	150	2.8	23.9 ± 4.3	9.6	62.7± 5.1	11.4
*736	1640	Even	260	367	4.9	23.9 ± 5.0	9.6	52.2± 15.6	30.3
33	1585	Mixed	340	200	1.6	45.6 ± 18.0	17.2	65.± 7.4	7.1
*1724	1713	Mixed	377	300	2.9	23.8 ± 6.3	14.2	50.7± 8.2	18.5
158	1740	Mixed	470	308	3.9	31.9 ± 6.6	13.7	75.3± 1.0	2.0
96	1646	Mixed	485	150	3.4	37.0 ± 9.1	16.5	77.0± 3.3	5.9
249	1605	Even	549	408	5.0	42.5 ± 6.8	12.3	67.0± 4.2	7.5
181	1587	Even	554	192	1.9	40.5 ± 3.7	7.2	68.5± 2.0	3.9
*38	1573	Mixed	565	142	3.2	44.2 ± 5.8	7.6	23.3± 12.6**	16.4
1	1611	Uneven	586	208	4.0	34.4 ± 5.1	11.5	71.6± 1.3	2.8
1070	1677	Uneven	599	400	4.8	15.5 ± 3.5	13.2	73.3± 1.4	5.2
9	1651	Even	602	142	3.1	26.2 ± 3.0	8.8	72.3± 1.3	3.7
268	1674	Uneven	613	525	3.9	37.7 ± 9.8	19.6	71.7± 2.6	5.1
1109	1665	Even	618	142	1.2	29.9 ± 2.9	7.9	72.2± 0.9	2.5
35	1541	Uneven	789	367	4.9	26.7 ± 3.8	11.2	72.2± 1.4	4.2
3	1680	Uneven	803	275	3.6	21.6 ± 4.6	15.0	67.7± 1.7	5.9
5	1608	Uneven	847	392	7.0	20.1 ± 3.6	13.9	68.2± 1.2	4.5
7	1559	Even	944	208	2.2	29.7 ± 2.5	8.3	76.7± 1.5	5.1
*4	1562	Uneven	960	508	5.7	24.2 ± 5.3	18.4	46.4± 3.9**	13.3
2	1559	Uneven	967	475	2.5	29.6 ± 4.3	13.9	76.2± 1.0	3.2
6	1626	Even	979	208	2.7	31.2 ± 2.6	8.6	75.5± 1.8	5.9
123	1704	Even	1123	442	3.8	28.6 ± 2.8	10.4	73.0± 1.4	5.2
*36	1585	Mixed	1139	308	6.3	24.2 ± 7.2	15.3	45.5± 10.2**	21.7
*238	1635	Uneven	1146	75	1.9	32.1 ± 7.9	23.8	51.9± 5.9	17.6
129	1715	Mixed	1200	58	2.0	33.7 ± 5.5	17.5	73.0± 2.1	6.8

Table 2.2**.** Structure groups: sample sizes, mean defoliation, and 95% confidence intervals on the mean.

Structure	number of stands	mean defoliation (%) and 95%CI
Even	9	71.2 (69.9, 72.5)
Mixed	7	62.2 (58.7, 65.7)
Uneven	9	66.1 (64.8, 67.4)

Table 2.3. Crown class: sample sizes, marginal mean defoliation values, and standard error on the marginal mean. Marginal means represent group means after having controlled for other covariates (in this case, sum of severity and structure).

Crown class	number of trees	marginal mean defoliation (%)	Standard error (%)
Dominant	36	67.6	2.4
Codominant	433	65.0	2.0
Intermediate	253	66.2	2.1
Suppressed	63	63.7	2.3

Table 2.4. Linear hypotheses of group means by crown thirds and 95% confidence intervals. Asterisks (*) represent p values <0.001 on the estimate of difference.

Comparison	Estimate of difference (%)	95% CI
Upper - Middle	-2.4*	-3.3, -1.5
Upper - Lower	-3.2*	-4.1, -2.3
Middle - Lower	0.8	-1.8, 0.02

Chapter 3. General Conclusions

Pine butterfly defoliation levels during an outbreak showed minimal relationships to structural characteristics. Tree crown class and canopy third demonstrated some differences, but these were neither patterned nor large enough to consider biologically relevant. Stand density index and stand structure showed no relationship to defoliation (Chapter 2). My results indicate that during an outbreak period, in stands with high levels of crown loss, structural effects on pine butterfly defoliation are small or nonexistent.

In the highly defoliated areas that I studied, the pine butterfly appeared to feed throughout broad differences in stand structure during its outbreak phase (Evenden 1940). Given the amount of speculation and study that structural factors have received in relationship to pine butterfly defoliation (Helzner & Thier 1993, Cleator 1910, Evenden 1926, Evenden 1940) and other defoliators (i.e., western spruce budworm, eastern spruce budworm, Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) (Lepidoptera: Lymantriidae) (Brookes et al. 1978, Brookes et al. 1985, Brookes et al. 1987, Torgerson 2011)) and sawfly in Scots pine (Saarenmaa 2003, De Somviele 2004, Augustiatis 2006), I expected to see a strong pattern or biologically relevant difference in relation to my studied variables. However, given the results of this study, I hypothesize that the most relevant factor to managers interested in reducing tree mortality and growth loss will prove to be individual tree health prior to an outbreak, as has been suggested for other insect pests in the West.

Future research

Structural patterns are not always observed during insect outbreaks, but given the small trends observed in my data, I suggest that future studies focus on differences between crown class groups, and crown thirds. Furthermore, it may be useful to purposefully incorporate areas with lower levels of defoliation (i.e., entire stands with estimated crown loss $\leq 50\%$), which may display different patterns of defoliation.

Fifteen of the stands used in this study are also part of a long-term monitoring project. Each tree in these 15 stands is tagged; data on these are available through Dr. Dave Shaw's Forest Health Lab at Oregon State University. Planned future research by the Forest Health Lab on these stands includes monitoring for bark beetle activity and tree mortality in 2014, 2015, and 2016, and coring a subset of trees in 2022 (Flowers and Shaw 2011). Future studies could combine information from this monitoring project with the data collected in the study reported here to develop estimates of growth loss directly relating to defoliation amounts. Results from my analysis suggested that coring a sample of trees that includes different crown classes may give the most accurate estimates of stand-level growth loss, since trees in different crown classes may undergo different intensities of defoliation.

Broader impacts

Disturbances shape the landscapes that we are familiar with, and widespread defoliation by the pine butterfly has likely played a historical role in these processes. A majority of current forest conditions are the products of centuries of manipulation by

humans, much of which has occurred only relatively recently. Studying the relationship of anthropogenic forest attributes to the biology of a native disturbance force is an important part of understanding the effects that we have on the ecosystem. Such understanding will be relevant as we continue to learn about the effects of management decisions and climate change on local and global scales.

Beyond the chance to further our technical understanding of an ecological process, these outbreaks provide opportunities for the public to encounter insect disturbance effects that are dramatic, intriguing, and often beautiful. The effects of such encounters may be difficult to quantify, but increased ecological interest and literacy can only promote more curiosity and support of exploratory research.

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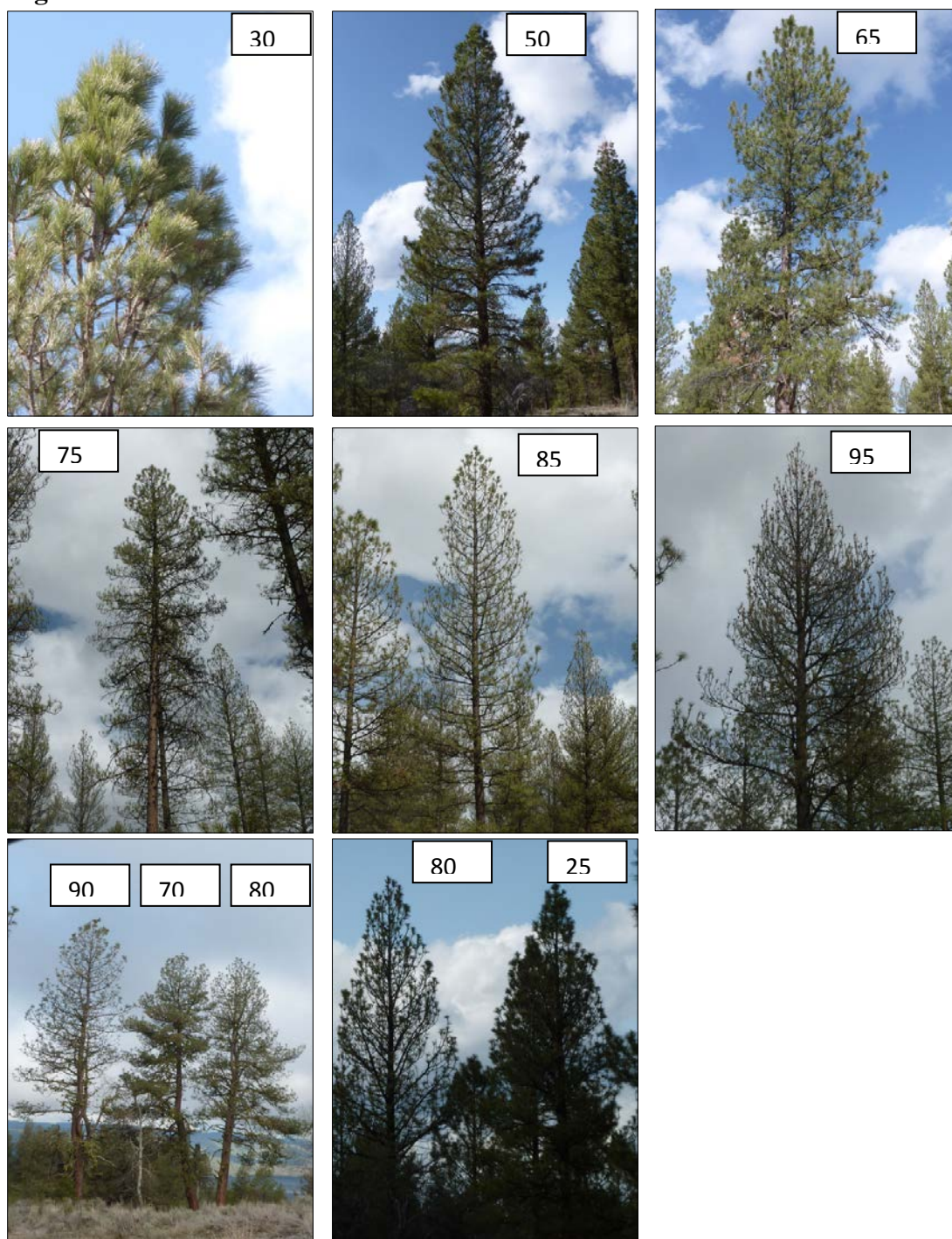
Appendix

Figures

Figure 1.1. Defoliation guide developed within the study area and referenced in the field.

Tables

Table 1.1. Crown classes for live trees (Helms 1998).

Class	Description	Definition
1	Dominant	Trees with crown extending above the general level of the crown cover and receiving full light from above and partly from the sides. These trees are taller than the average trees in the stand and their crowns are well developed. Also, trees whose crowns have received full light from above and from all sides during early development and most of their life. Their crown form or shape appears to be free of influence from neighboring trees.
2	Co-dominant	Trees with crowns at the general level of the crown canopy. Crowns receive full light from above but little direct sunlight penetrates their sides. Usually they have medium-sized crowns and are somewhat crowded from the sides. In stagnated stands, co-dominant trees have small-sized crowns and are crowded on the sides.
3	Intermediate	Trees that are shorter than dominants and co-dominant, but their crowns extend into the canopy of co-dominant and dominant trees. They receive little direct light from above and none from the sides. As a result, intermediates usually have small crowns and are very crowded from the sides.
4	Suppressed	Trees with crowns entirely below the general level of the crown canopy that receive no direct sunlight either from above or the sides.

Table 1.2. Physiography codes (Natural Resource Inventory, USDA 2002).

Code	Definition
1	Ridgetop or mountain peak over 40 m wide, flat
2	Narrow ridgetop or peak less than 40 m wide, convex
3	Sidehill - upper 1/3, convex
4	Sidehill - middle 1/3, no rounding
5	Sidehill - lower 1/3, concave
6	Canyon bottom less than 200 m wide, concave
7	Bench, terrace or dry flat; flat
8	Broad alluvial flat over 200 m wide, flat
9	Swamp or wet flat; flat

Table 1.3. AICc table for SDI and stand structure base model selection. Codes used to describe covariates: SS = sum of severity, A = aspect, P = physiographic type.

Model	number of estimated parameters	AICc	ΔAICc	Relative likelihood	AICc weight	Log likelihood	Cumulative AIC weight
SS + logDBH	7	5075.21	0.00	1.00	0.39	-2530.53	0.39
SS + A	10	5076.52	1.30	0.52	0.20	-2528.11	0.59
SS + logDBH + P	8	5077.07	1.86	0.40	0.15	-2530.44	0.74
SS + A + logDBH	11	5078.27	3.05	0.22	0.08	-2527.95	0.83
SS + A + P	11	5078.45	3.24	0.20	0.08	-2528.05	0.90
P	6	5080.05	4.84	0.09	0.03	-2533.97	0.94
SS + A + logDBH + P	12	5080.20	4.98	0.08	0.03	-2527.89	0.97
logDBH + P	7	5081.76	6.55	0.04	0.01	-2533.81	0.99
logDBH	6	5083.00	7.79	0.02	0.01	-2535.44	0.99
A + P	10	5084.82	9.60	0.01	0.00	-2532.26	1.00
A	9	5086.24	11.02	0.00	0.00	-2534.00	1.00
A + logDBH + P	11	5086.56	11.35	0.00	0.00	-2532.10	1.00
A + logDBH	10	5088.00	12.78	0.00	0.00	-2533.85	1.00

Table 1.4 AICc table for crown class base model selection. Codes used to describe covariates: SS = sum of severity, STRUCT = stand structure, A = aspect, P = physiographic type, meanDBH = mean DBH at stand level.

Model	number of estimated parameters	AICc	ΔAICc	Relative likelihood	AICc weight	Log likelihood	Cumulative AIC weight
SS + STRUCT	8	5450.38	0.00	1.00	0.26	-2717.10	0.26
SS	6	5451.07	0.69	0.71	0.18	-2719.48	0.44
SS + P+ STRUCT	9	5452.41	2.03	0.36	0.09	-2717.09	0.53
SS + A + STRUCT	12	5452.83	2.46	0.29	0.08	-2714.21	0.61
SS + SDI	7	5452.89	2.52	0.28	0.07	-2719.37	0.68
SS + logDBH	7	5453.00	2.62	0.27	0.07	-2719.43	0.75
SS+ P	7	5453.06	2.68	0.26	0.07	-2719.46	0.82
SS + A + STRUCT + SDI	13	5454.25	3.87	0.14	0.04	-2713.89	0.85
SS + A	10	5454.55	4.18	0.12	0.03	-2717.13	0.88
SS + P+ A + STRUCT	13	5454.58	4.20	0.12	0.03	-2714.05	0.92
SS + P+ SDI	8	5454.86	4.49	0.11	0.03	-2719.34	0.94
SS + P+ logDBH	8	5454.99	4.61	0.10	0.03	-2719.40	0.97
SS + P+ A + STRUCT + SDI	14	5456.03	5.65	0.06	0.02	-2713.74	0.98
SS + P+ A	11	5456.61	6.23	0.04	0.01	-2717.13	1.00
SS + A + STRUCT + logDBH + STRUCT : meanDBH	16	5460.10	9.73	0.01	0.00	-2713.70	1.00
SS + P+ A + STRUCT + logDBH + STRUCT : meanDBH	17	5461.39	11.01	0.00	0.00	-2713.30	1.00
SS + A + STRUCT + logDBH + SDI + STRUCT : meanDBH	17	5461.80	11.43	0.00	0.00	-2713.50	1.00
SS + P + A + STRUCT + logDBH + SDI + STRUCT : meanDBH	18	5463.17	12.80	0.00	0.00	-2713.14	1.00

Table 1.5 AICc table for crown thirds base model selection. Codes used to describe covariates: SS = sum of severity, A = aspect, P = physiographic type.

Model	number of estimated parameters	AICc	ΔAICc	Relative likelihood	AICc weight	Log likelihood	Cumulative AIC weight
SS	6	17019.86	0.00	1.00	0.34	-8503.91	0.34
SS + P	7	17021.85	1.99	0.37	0.13	-8503.90	0.46
SS + A	10	17022.00	2.14	0.34	0.12	-8500.95	0.58
SS + SDI + P	8	17023.55	3.68	0.16	0.05	-8503.74	0.63
SS + logDBH + P	8	17023.68	3.82	0.15	0.05	-8503.81	0.68
SS + SDI + A	11	17023.71	3.85	0.15	0.05	-8500.80	0.73
SS + logDBH + A	11	17023.88	4.02	0.13	0.05	-8500.88	0.78
SS + P + A	11	17024.02	4.15	0.13	0.04	-8500.95	0.82
P	6	17024.34	4.48	0.11	0.04	-8506.15	0.86
SS + logDBH + SDI + P	9	17025.39	5.53	0.06	0.02	-8503.66	0.88
A	9	17025.46	5.60	0.06	0.02	-8503.69	0.90
logDBH	6	17025.48	5.62	0.06	0.02	-8506.72	0.92
SDI	6	17025.49	5.63	0.06	0.02	-8506.73	0.94
SS + logDBH + SDI + A	12	17025.60	5.74	0.06	0.02	-8500.73	0.96
SS + SDI + P + A	12	17025.73	5.87	0.05	0.02	-8500.80	0.98
SS + logDBH + P + A	12	17025.90	6.04	0.05	0.02	-8500.88	0.99
SS + logDBH + SDI + P + A	13	17027.62	7.76	0.02	0.01	-8500.73	1.00