Factors Influencing Understory Douglas-fir Vigor in Multi-Cohort Prairie Colonization Stands at Fort Lewis, Washington

Derek John Churchill

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

University of Washington

2005

Program Authorized to Offer Degree:
College of Forest Resources

University of Washington

Abstract

Factors Influencing Understory Douglas-fir Vigor in
Multi-Cohort Prairie Colonization Stands at Fort Lewis, Washington

Derek John Churchill

Co-Chairs of the Supervisory Committee:
Professor Thomas M. Hinckley
Professor Bruce R. Lippke
College of Forest Resources

Forest stands on Fort Lewis, Washington are being managed for multiple values under an uneven-age silvicultural system that relies on natural regeneration. In stands that were former prairies and have well drained, outwash soils, Douglas-fir (*Pseudotsuga menziesii*) is the only understory conifer present and the principal regeneration species. Factors influencing the vigor of Douglas-fir advanced regeneration were investigated in thirteen stands at both the individual tree and stand levels. Live crown ratio, height growth, height-to-diameter ratio, and crown density were used to produce two methods of quantifying vigor: a regression model that predicts volume growth as a percent of maximum site potential (relative volume growth) and a simple vigor classification system. Overstory recruitment potential and release potential were estimated for different level of vigor. At the individual tree level, understory Douglas-fir with low levels of understory competition was found to require an average 45% full sunlight or overstory stocking of less than 150 SDI (30% full site occupancy (Long 1985)) to achieve vigor levels where recruitment into the overstory without further release is likely. Between 10-35% full sunlight or 150-275 SDI (30-55% full site occupancy), regeneration was found to be growing slowly but able to maintain its ability to respond to release and regain growth rates comparable with trees that were not suppressed, especially if less than 5m in height at time of release. Below 10% full sunlight or above 275 SDI (55% full site occupancy), regeneration was scarce and of very poor vigor. Regeneration with high levels of understory competition was found to require more light to achieve the same growth rates, and this effect increased in hig light environments. A stand level model was developed and demonstrated that while overstory density is the dominant factor influencing understory vigor, understory stocking, shrub cover, spatial arrangement of the cohorts are also important. A three stage progression of overstory treatment types is recommended to balance the tradeoffs between stand volume growth, structural and habitat goals, and understory vigor. By combining elements of shelterwood, group selection, and single tree selection systems, multi-cohort, structurally complex stands can be created and maintained in a shifting mosaic of patches. Results suggest that uneven-age management is possible with Douglas-fir on dry sites, although stands will be structurally different from west-side, late-successional forests that contain shade tolerant conifers and will require periodic stand entries to maintain.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would first like to acknowledge and thank Jeff Foster and Gary McCausland of the Fort Lewis Forestry Program for funding this project and giving me the opportunity to work and do research at Ft. Lewis. Jim Rhode and numerous members of the Fort Lewis Forestry field crew also provided valuable assistance along the way. I am also grateful to: Bruce Lippke and Larry Mason of the Rural Technology Initiative at the College of Forest Resources for their support throughout my 3 years at the CFR; members of my graduate advising committee, Drs. Tom Hinckley, Bruce Lippke, Eric Turnblom, Kristina Vogt, and Tim Harrington for their guidance, ideas, encouragement, and feedback throughout the project; Drs. Tim Harrington, Dave Marshall, Connie Harrington, and the summer field crew of the U.S.F.S. Pacific Northwest Research Station in Olympia, for being key partners in the project and offering invaluable advice and field assistance; Amy Miller for her help in the field and partnership in the analysis; fellow grad students at the CFR who were a vital part of both this project and my overall graduate experience, Andrew Larson, Michael Andreau, Cara Nelson, Elaine Oneil, Ann Andreau; Bianca Perla, Mitchell Almaguer-Bay, Mariano Amoroso, Jeff Comnick, and many others; Dr. Gabe Tucker for his mentorship early on in this project; Dr. Rolf Gersonde for his helpful ideas and critical review; and Dr. Charlie Halpern for the use of field equipment. Finally, I would like to thank my father Jack Churchill for his help in the field and encouragement, and most of all my wife, Wendy Finkleman for her tremendous support and understanding during this project.

Introduction

In recent years, changing social values and increasing scientific understanding of forest ecosystems have led to greater consideration of alternatives to traditional even-aged management in forests west of the Cascade Mountains in the Pacific Northwest, especially where economic returns are not the driving management objective (Gordon 1994, Kohm and Franklin 1997, Curtis et al. 1998). After research into “partial cutting” was largely abandoned in the 1950’s (Munger 1950, Issac 1956), it was re-established in the mid 1990’s (Curtis et al. 1998, Ruel et al. 2000, Hunter 2001). Much of this research has been aimed at developing the knowledge and tools to grow conifer species under partial overstories, whether in silvicultural prescriptions designed to retain or accelerate the development of late seral structures (Franklin et al. 1997, Carey 2003), restore riparian function (Emmingham et al. 2000, Tappeiner et al. 2002), or establish successful regeneration in uneven-age management systems (Tappeiner et al. 1997, Miller and Emmingham 2001, Coates et al. 2003). Managers and landowners have been reluctant to implement alternatives to traditional even-aged management on a wider level, however, due in large part to the lack of proven management strategies to grow Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the understory, and the perception of an inevitable shift in overstory composition towards more shade tolerant species (Becker 1995, Emmingham 2002).

Considerable debate exists in the scientific literature and among foresters whether uneven-age management of Douglas-fir, which is moderately shade tolerant (Issac and Dimock 1958, Herman and Lavender 1990), is possible using single tree selection or whether group selection is necessary (Curtis 1998, Malcolm et al. 2001). Single tree selection typically involves removing individual mature and low-vigor trees dispersed throughout the stand in relatively frequent light thinnings with the goal of creating and maintaining multiple cohorts over time (Smith et al. 1997). While establishment of Douglas-fir seedlings in the understory is not uncommon after light thinning entries (Bailey and Tappeiner 1998, Harrington et al. 2003), growth rates generally decline substantially as the sapling stage is reached (1-3m, 3-10ft), virtually eliminating recruitment into the mid- and upper-canopy (Herman and Lavender 1990, Williams et al. 1999). To maintain adequate vigor and recruit into the mid- and upper- canopy, understory Douglas-fir saplings require a substantial amount of growing space (Oliver 1995).

Thus for single tree selection to work, it is recommended that the overstory be heavily thinned early in a stand's development and then kept open through successive light thinnings (Bailey 1996, Emmingham et al. 2000, Brandeis et al. 2001b, Tappeiner et al. 2002).

In group selection, trees are removed in patches of varying sizes in multiple thinning entries over time. This creates a mosaic of even-aged groups of differing ages within a stand (Smith et al. 1997). As group selection creates larger openings than single tree selection, it is often proposed as a more viable method for regenerating and growing shade-intolerant species (Coates and Burton 1997, Smith et al. 1997). Minimum gap size suggested for Douglas-fir is approximately 0.25-0.5ha (approximately 0.5 -1 ac) (Ketchum 1994, Mailly and Kimmins 1997) or a gap diameter of 1.5 times the height of the surrounding overstory trees (Malcolm et al. 2001).

The critical question in making either approach work is the amount of growing space Douglas-fir needs to maintain adequate vigor in the understory, and thus at what densities and spatial arrangements to maintain the overstory. Numerous investigators have addressed this question by correlating measures of overstory density and/or light availability with understory Douglas-fir growth, both at the stand and individual tree level (Table 1). From these studies, a very general conclusion can be drawn that a maximum of 40% of full stocking or 30-40% of full sunlight is necessary to maintain adequate vigor. However, conclusions from different studies have been variable and can be difficult to develop into comprehensive silvicultural guidelines for several reasons.

First, the definition of adequate vigor is often not well defined or consistent among studies. Many authors directly or indirectly define adequate vigor as growth rates that are close enough to open grown, maximum site potential for a tree to recruit into the overstory without any release in the future (Wampler 1994, Bailey 1996, Brandeis et al. 2001b, Drever and Lertzman 2001) Yet, in uneven-age management systems with periodic overstory removals, understory trees need only to maintain sufficient leaf area, stem stability, and root system to avoid mortality and be able to respond to release in the future (O'Hara 1996, Ruel et al. 2000). Thus growth rates that are far below open grown, maximum site potential can be considered adequate for understory trees. Clearly defining vigor in terms of a tree's ability to grow into the overstory without further release, maintain its release potential, or merely survive is a critical step in translating the variable results created by the different definitions of adequate vigor (Table 1) into guidelines for uneven-age management.

Table 1: Suggested levels of overstory density for understory Douglas-fir to maintain vigor

Author	Overstory density or light level	Region
Bailey (1996)	<= 16 trees per ha max to grow[a]	W. Oregon
Brandeis (2001)	< 20 m^2/ha BA to grow[a]	W. Cascades, OR
Carter & Klinka (1992)	>30-40% PACL: other factors have greater influence on relative height growth than light.	Coastal B.C.
Deisenhofer (2000)	7% indirect light: Lowest level to maintain DF	W. Oregon
Del Rio & Berg (1979)	27-41m^2/ha BA; 5-12% full sun to maintain[b]	E. Coast Range, OR
Drever & Lertzman (2001)	40% full sun to grow[a]	Coastal B.C.
Emmingham & Waring (1973)	7% RL: No DF advanced regeneration survival under this level	Southwest OR
Mailly & Kimmins (1997)	>40% RLI to grow[a]; 20-40% RLI to survive	Coastal B.C.
Miller & Emmingham (2001)	18-28 m^2/ha BA to grow[a]	Willamette Valley, OR
Wampler (1993)	<= 12 trees per ha max to grow[a]	W. Washington
Williams et al. (1999)	5% of PPFD to survive 50 years and reach 3m	Interior B.C.

Note: [a] : Grow is defined as achieving growth rates for trees to be able recruit into the mid and upper canopy without further overstory removal.
[b] : Maintain is defined as achieving sufficient growth rates, live crown, and stem stability to maintain release potential for future overstory removal.
BA: Basal Area; RLI: Relative Light Intensity; PACL: Percent above canopy light; PPFD: Photosynthetic photon flux density; RL: relative light.
BA in English units = Metric BA*4.36; Acres= ha * 2.47

Defining vigor in terms of maintaining release potential requires an understanding of response to release. Results from studies on release of Douglas-fir, as well as inference from release studies of other western conifers, suggest that Douglas-fir can respond to release after even severe suppression and that risk of mortality, lag time before response, and post-release growth are strongly related to duration of suppression, and pre-release growth rates and live crown ratio (LC ratio) (Helms and Standiford 1985, Carlson and Schmidt 1989, Tesch and Korpela 1993, Kobe and Coates 1997, Deisenhofer 2000, Wright et al. 2000). Thus, acceptable levels of risk and desired post-release growth rates should guide definitions of pre-release vigor in terms of thresholds for pre-release growth rates or live crown ratio (Helms and Standiford 1985, Tesch and Korpela 1993, Ruel et al. 2000).

Several investigators have designed vigor classification systems that have set such thresholds for Douglas-fir (Carter and Klinka 1992, Emmingham et al. 2000, Miller and Emmingham 2001). However, these systems are based on different growth metrics, involve qualitative criteria that can be difficult to replicate, or were designed for different size classes of trees. As rates of height and radial growth are affected by tree size, vigor thresholds set for seedlings based on absolute, and not relative, growth metrics may not be appropriate for saplings. The same is true for height to diameter ratio (HD ratio). Although an HD ratio of 60 is a commonly used threshold of adequate vigor (Newton and Comeau 1990), this number is questionable as the stem height of diameter measurements and the total height of the tree influence the value and implication of the ratio (Mustard and Harper 1998, Wilson and Oliver 2000). More research is needed to develop thresholds for multiple growth metrics that can be applied across different size classes and correspond to definitions of vigor that have clearly defined management implications.

The second reason for the lack of comprehensive guidelines for uneven-age management of Douglas-fir is the difficulty in accounting for the large number of factors that affect growing space in complex stands, often with methods that were designed for even-aged management systems. Traditional, distant-independent stem measurements such as basal area or Stand Density Index (SDI) (Reineke 1933) are often poorly correlated at the plot level to light levels reaching the understory (Chan et al. 1997, Brandeis et al. 2001a, Aukema and Carey 2003) and thus are typically weak predictors of understory growth for individual trees (Wampler 1994, Deisenhofer 2000, Brandeis et al. 2001a). Light or canopy closure measurements have shown greater predictive power (Carter and Klinka 1992, Chen and Klinka 1997, Drever and Lertzman 2001), but are time consuming and hard to translate into stand level management prescriptions.

Accounting for side shading (Oliver and Larson 1996) from intra-cohort and shrub competition is also essential to better explain what controls the growth of advance regeneration (Brandeis et al. 2001b, Duchesneau et al. 2001, Canham et al. 2004). Adding further complexity is research that suggests that Douglas-fir may be more shade tolerant on drier sites (Carter and Klinka 1992, Wampler 1994, Bailey 1996, Chen et al. 1996, Williams et al. 1999). A final factor is tree size. There is evidence that as Douglas-fir get older and taller, its light requirements to maintain growth also increase (Carter and Klinka 1992, Messier et al. 1999).

Growth models have been developed for multi-cohort stands in other forest types that factor in some or all of the complex set of variables listed above to help managers determine stocking guidelines for different stand structures and management objectives. These models include: stand-level, distant-independent models based on crown competition (Biging and Dobbertin 1995, Hasenauer and Kindermann 2002), leaf area (O'Hara and Valappil 1999), or SDI (Long 1995, Ralston et al. 2003); and spatially explicit crown and light models (Biging and Dobbertin 1995, Coates et al. 2003, Gersonde 2003). Many of these models show promise for uneven-age management of Douglas-fir. However, spatially explicit models in particular require more inventory information and technical resources than most management agencies, who are accustomed to models designed for even-age stands such as Forest Vegetation Simulator (FVS) or Organon, typically have. There is a clear need for stand level growth models that do not require spatially explicit inventory information but can account for the vertical and horizontal heterogeneity of multi-cohort stands (Monserud and Robinson 2003).

In this study, I inventoried vigor and stand structure of naturally regenerated Douglas-fir advanced regeneration in dry-site conifer forests in the southern Puget Lowlands of Washington State. Methods were developed to quantitatively assess and classify vigor using metrics that can be integrated with existing inventory datasets. I sought to clearly define the implications of different levels of vigor by linking quantitative classifications of vigor with estimates of release potential and the likelihood of recruitment into the overstory without further release. These estimates were made from some data gathered in this study, but primarily from results from other investigators. I then used these vigor assessment methods to investigate and model the factors influencing vigor of understory regeneration at the individual tree and stand levels. Finally, results were combined into silvicultural recommendations for uneven-age management in dry site Douglas-fir forests.

Methods

Study area

The study was conducted at the Fort Lewis Military Reservation, which is a 35,000ha (77,000ac) U.S. Army installation located between Tacoma and Olympia, Washington. Sites were restricted to forests that have colonized former prairies and have somewhat excessively drained, glacial outwash soils of the Spanaway and Fitch series (Typic Melanoxerands) (Anderson et al. 1955, Foster and Shaff 2003) These forests established over the last 150 years after burning by Native Americans to maintain prairie landscapes subsided (Perdue 1997). Elevation within the study area is 60-150m (200-500ft) and the terrain is generally flat with few, gentle topographic features. The climate is temperate and xeric, with mild, wet winters, and warm, dry summers. The mean summer temperature is 15^{o}C (59^{o} F), the mean winter temperature is 3.5^{o}C (38^{o} F) and annual precipitation is 800-1200mm (32-48in.), with less than 25% falling between March – September. The coarse texture and droughty nature of the outwash soils make these forests drier than most Douglas-fir - western hemlock (*Tsuga heterophylla)* forests in lowland Puget Sound. Douglas-fir dominates both the overstory and understory, and occasional Oregon white oak (*Quercus garryana* Dougl. ex Hook.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and big leaf maple (*Acer macrophyllum)* are found. Shade tolerant conifers are almost entirely absent. Ft. Lewis has been managing 6,600ha (14,740ac) of these forests for the past several decades with light thinning entries that remove 15-20% of standing volume at roughly 10 year intervals (Foster and Shaff 2003).

Field sampling

Sampling was conducted in two phases from May through October of 2004. First, 13 stands were inventoried to broadly characterize overall stand structure and vigor of advanced regeneration and to generate an extensive data set of understory trees for analysis. The sampling protocol for this phase was designed so that it could be integrated into the forest inventory system currently used by Ft Lewis managers. The second phase consisted of more detailed measurements and analysis on a smaller sub-sample of trees from the first phase to investigate the factors influencing understory vigor in greater depth, develop regression models that could be extrapolated to the larger phase I dataset, and to test and calibrate visual estimation techniques used in the phase I stand inventory with instrument based measurements.

More intensive sampling techniques were used in phase II that are not practical for a typical forest inventory.

The 13 stands in the phase I stand inventory, totaling approximately 680 ha (1500ac), were selected using a proportional, stratified random sample. First, the total population of prairie colonization stands was divided into 3 overstory basal area (BA) classes: 18-29m^2/ha (90-142ft^2/ac), 30-39 m^2/ha (143-190 ft^2/ac), and 40+ m^2/ha (190+ ft^2/ac). Stands that had been thinned in the last five years or had access restrictions were excluded. Stands were then randomly selected from the three BA classes in proportion to the number of stands in each BA class in the total population. This process produced a set of stands that were a good representation of the range of structural conditions found in the total population of prairie colonization stands (Foster, pers comm.). All stands had had at least two thinning entries. Site index (King 1966) ranged from 34-38 (metric) (110-125, English) (Foster, unpublished data) and was assumed to be 35 (metric) (115; English) for all stands given that within stand variation is as great as among stands due to the heterogeneity of the glacial soils.
In each stand, systematic sampling with a random start was used to locate a pre-determined number of plot centers. The number of plots was based on the size and density of the stand. Three sets of measurements with different plot configurations were taken at each plot center: (1) shrub cover and dead understory trees, (2) overstory trees, and (3) live understory Douglas-fir trees. Percent cover of shrubs taller than 1.37m (4.5ft) and less than 1.37m was estimated using a 0.008ha (0.02ac) fixed area, circular plot. The number of dead understory trees was also tallied in this plot.

The overstory was sampled in two ways. First, trees over 15cm (6in.) diameter at breast height (dbh; diameter at 1.37m above ground level) were sampled using point sampling (variable radius plots) (Bitterlich 1947). Basal area factors used were 28, 34, or 40 (English scale) depending on the basal area class of the stand. Height, crown length, and crown width were measured on two randomly selected trees per plot. Second, a visual estimate of the percent of open sky (VOS), excluding shrubs or trees under 15cm (6in.) dbh, was made from each plot center. The same person estimated VOS in all 13 plots. This VOS measure was modified from Brandeis et al. (2001a) and Deisenhofer (2000) and consisted of estimating the percent openness of the canopy in both the northern and southern halves of the sky and averaging them. Where VOS was at least 20% higher in the southern half, the average was weighted to adjust for edge effects (Hasenauer and Kindermann 2002) using the equation below. It is treated as a unitless, relative measure, instead of an absolute measure of percent of open sky.

Eq. 1: *Weighted VOS = (3VOS,South + VOS,North)/4* .

Understory trees, defined as less than 15cm (6in) dbh and taller than 1.37m (4.5ft), were sampled within a circular fixed area plot of either 0.04 or 0.008ha (0.1 or 0.02ac), depending on the BA class of the stand. For all understory trees, dbh was measured and crown class determined based on the height of trees within a cohort: dominant, co-dominant, intermediate, or overtopped. Crown class for open grown trees not near clumps was determined by comparing the height of the tree to nearby trees in the same cohort. The following additional measurements were taken for all understory trees, or a sub-sample, depending on the number trees in the plot: diameter at 15cm (6in) above ground; total height; height to live crown, measured at the lowest whorl with two live branches with new growth; annual height increment for each of the past six years; total age determined from whorls and bud scars, crown density, and degree of crown crowding from intra-cohort competition (neighboring understory trees) and shrubs. Crown density was measured with a 1-5 rating that combined visual estimates of average branch length and diameter, number of internodal buds and branches, and number of branches and each whorl; all in the last 3 years of growth. Ranges of these variables used to rate trees are provided in Appendix A. Carter and Klinka (1992) and Miller and Emmingham (2001) developed similar systems to rate vigor based on visual crown ratings. Crown crowding, defined as any infringement on the live crown of the sample tree from neighboring understory trees in the same cohort or shrubs, was measured using a combination of methods from Howard and Newton (1984) and Wagner and Radosevich (1991, 1998). At the base of the live crown, a horizontal, two dimension circle was visualized around the tree using the longest live branch as the radius. The proportion of this two dimensional circle (projected crown area) overlapped by foliage of neighboring trees or shrubs from the base of the live crown to the top was estimated to the nearest 10 percent. This combined measure of intra-cohort and shrub competition was termed percent crown overlap. A diagram of this method is provided in Appendix B.

Data from the phase I stand inventory were generated from 13 stands, 212 plots, and 637 understory Douglas-fir trees and used to broadly characterize structure of the overstory, understory, and shrub layers. After this analysis, a sub-sample of 25 plots from the 212 phase I plots was selected for further intensive analysis. A stratified random sample was used to ensure that the phase II sub-sample of 25 plots came from a balanced distribution of light environments.

At each phase II plot, two understory trees were selected for destructive sampling: the tallest tree within the cohort and the tree closest to the average height. For each tree, dbh of all overstory trees were recorded in a 0.09ha (0.2ac) fixed area plot as well as in a variable radius plot, both centered on the sample tree. Before each tree was cut down, two methods were used to measure crown crowding from intra-cohort competition and shrubs. First, the percent crown overlap method from phase I was expanded to include a vertical dimension. For each competitor, the two dimensional horizontal overlap and the percent overlap along the vertical live crown of the sample tree were estimated. By adding all the competitors together, an estimate was made of the percent occupancy of competing understory trees and shrubs within a three dimensional cylinder projected from the base of the live crown to the top of the tree with the radius being the longest live branch. The second method consisted of measuring the dbh of, and azimuth and distance from the stem of the sample tree to, the stem of each competitor within a radius set by the farthest competitor that overlapped the crown of the sample tree. Competitors had to be as high as the live crown of the sample tree. This variable radius method was chosen based on Wagner and Radosevich (1991, 1998), who found that "The optimum radius appeared to be defined by those neighbors whose crowns intermingled with that of the Douglas-fir." A neighborhood competition index (NCI) was calculated for each tree based on the following equation from Canham et al. (2004), where DBH_i is the diameter at 1.37m of *i*th competitor, $Dist_i$ is the distance to the *i*th competitor, and α and β are model parameters:

Eq 2: $$NCI = \sum_{i=1}^{n} \frac{(DBH_i)^{\alpha}}{(Dist_i)^{\beta}}$$

As competition from shrubs and other tree species was minimal compared to intraspecific competition, the same parameters were used for all competitors. Parameter estimates for these equations were iteratively tested to determine the most powerful values used in later analysis.

After each tree was cut down, percent open sky was estimated using the VOS procedure described above and a hemispherical photograph was taken as close to 66% of tree height as could be safely reached with a 5m (16.4ft) orchard ladder using a digital Nikon camera with a 2.5 F-Stop fisheye lens mounted on a monopod with a level. Gap Light Analyzer/C, version 2.0 light modeling software (Frazer et al. 1999) was used to analyze these photographs and determine site openness and an index of total solar radiation (TSR) (Canham et al. 1990, Frazer et al. 1997). TSR combines the seasonal distribution of the sun's path with the distribution of canopy openness to calculate a single index of available light in units of percentage of full sun for a specified growing season which was set at April 1 – Oct 15th for the Ft Lewis area.

All tree measurements from phase I were also re-measured on each phase II tree. In addition, branch length and number of internodal buds were measured for the last 3 years. Percent cover of shrubs by species was estimated in a 0.008ha (0.02ac) fixed area plot around each tree. Height growth increments were measured from the top of the tree to breast height and checked against rings counted on a disc cut at dbh. Discs were also cut at ground level and at the base of the live crown. These discs were later oven dried for 48 hours, sanded, and analyzed using a high resolution computer scanner and WinDENDRO v2001a (Regent Instruments, Inc.) tree ring analysis software, which calculated age and annual radial growth along 4 radii for each disc. These radial growth measurements were combined with height growth data to calculate annual volume increment using a tapered rocket formula where the three discs were used to create two tapered cylinders and a cone at the top. Inside bark diameters were used. Height to diameter ratio history was also calculated using the ground level disc, but diameters were adjusted for bark thickness, drying, and the discrepancy between field measurements with a dbh tape and radial measurements on a disc. This was done by multiplying all inside bark diameters by the ratio of the 2004 field measured diameter to the 2004 inside bark diameter obtained from WinDENDRO.

Assessing vigor

Two methods were developed to assess vigor of understory trees. For the first method, volume growth was chosen as the primary measure of vigor as it is a more robust measure of current biomass accumulation than height or radial growth. Both height and radial growth are not always well correlated with volume growth, especially in stressed trees where allocation of carbon to height growth is prioritized over radial growth and wood deposition can be uneven along the length of the bole. (Tucker and Foster unpublished, Oliver and Larson 1996). Volume growth is also highly correlated with post release growth (Tesch and Korpela 1993) and leaf area (Waring 1983, O'Hara 1996, Kollenberg and O'Hara 1999). A system was then designed to compare volume growth across the wide range of understory trees sampled in this study: 1.4 – 16 m (4.5 – 53ft). Annual volume growth increment for a tree of a given height was divided by maximum site potential growth for a tree of that height to generate a percent of maximum potential growth or relative volume growth (RVG). Height and volume growth data from 19 naturally-regenerated, open-grown, “best” trees with long, full crowns that were located near the sample stands on the same soil type (Tucker and Foster unpublished), were used to generate the following model to determine maximum potential annual volume growth increment (*y*) in cm^3 per year for a tree of a given height (*x*).

Eq 3: $y = 0 .018x^2 - 0.27x - 466.74$

This quadratic equation was the best fit for the maximum site potential tree data ($R^2 = 0.96$, $p<0.0001$) until tree heights approached 1.4 meters, below which it underestimated maximum potential growth. A graph of this regression model is provided in Appendix C.

For the 54 trees that were intensively analyzed in phase II, actual RVG was calculated for every year from when the tree was 1.37m to its current height. The last 5 years were averaged to create the primary vigor metric for further analysis: actual 5yr RVG. For the 637 understory trees in the stand inventory, however, coring trees to measure diameter and volume growth was intentionally not done to keep the sampling design within what could be practically integrated into the existing Fort Lewis inventory system. Exploratory analysis was thus done with the 54 tree data set to test which variables that were measured in the stand inventory best correlated with actual RVG. These variables were: past 5yr mean annual height growth increment (HG), 2004 live crown ratio (LC Ratio), 2004 height to diameter ratio (HD Ratio), and visual crown density rating (CDR). Single variables, as well as biologically meaningful products of these variables, were tested using simple linear regression. Stepwise, linear regression was then used to test multiple variables and derive a best fit model using SPSS, version 12.0 (SPSS 2003). This model was used to predict 5yr RVG for the 637 understory trees from the stand inventory.

The second method of assessing vigor was a simple four class classification system. This additional method was developed to provide a more efficient and sufficiently accurate means for managers to assess vigor of understory cohorts, conceptualize vigor, and design silvicultural prescriptions. Classes were based on thresholds of HD ratio, HG, and LC Ratio that are listed in Table 2. Trees must meet the thresholds for all three metrics to be placed in a certain class or else they are placed in the next lowest class. Crown density rating was not included to allow for this vigor assessment method to be easily used with existing data sets. Also, crown density rating is a qualitative measure that requires consistency, which can be hard to achieve with multiple observers.

A HD ratio of 70, measured at 15cm above ground, was chosen as the HD threshold for high vigor (class 4) (Table 2). This correlates with an HD ratio of 60 at the root collar. This threshold value is based on observations from: Newton and Comeau (1990) who suggest that HD ratios over 60, measured at the root collar, threaten the long term growth potential of young plantation trees; Wonn and O'Hara (2001) who showed that an HD ratio of 80, measured at dbh, is a critical threshold for stem stability in interior Douglas-fir; Cole and Newton (1987) who found that decreases in height growth occurred at HD ratios above 70 in plantation trees; and Emmingham et al. (2000) who specified 60 as a threshold for a vigorous understory tree, 80 for a stable tree, and 100 for a weak tree. Height growth thresholds were based on approximately 66%, 33%, and 15% of the site index potential height growth for the average tree height found in the study (King 1966). Live crown ratio thresholds (Table 2) were based on the positive relationships of live crown ratio to post-release growth observed by Helms and Standiford (1985), Seidel (1983a), Oliver (1985), and Tesch and Korpela (1993); as well as recommendations by Emmingham et al. (2000).

Table 2: Summary data for vigor classification system for understory trees. Trees must meet thresholds for all three growth metrics to be in a class, otherwise they are placed in the next lowest class.

		Vigor Class			
		1	2	3	4
Classification Thresholds	Height:Diameter Ratio	90+	80-89	70-79	<70
	Height Growth (cm)	<10	10-30	30-49	50+
	Live Crown Ratio (%)	<40	40-54	55-64	65+
Average Growth Rates	Relative Vol. Gr. (%) [a]	10	20	35	50
	Radial Growth (mm) [b]	0.9	1.6	3.6	5.0
	Yrs to reach overstory	222	174	93	62

Note:
[a]: Rounded average of mean RVG of phase I and phase II data sets for each vigor category Relative volume growth is the past 5 year, mean annual percent of maximum site potential growth based on tree height; radial growth is the past 5 year mean annual radial growth; and years to reach overstory is the projected time it would take to reach the current stand average overstory height of 45m (148ft) based on a current tree height of 5m (16.4ft) and maintaining current average height growth rates.
[b] From phase II dataset

The two methods of assessing vigor were compared to evaluate whether the simpler vigor classification system could estimate 5yr RVG within a reasonable range. Analysis of variance (ANOVA) and a Scheffe’s post hoc test was used to test for significant differences between the mean RVG values for each vigor category, for both the phase 1 and phase 2 datasets (α = 0.05 for this test and all subsequent analysis) (Zar 1999). To derive an overall, target mean RVG for each vigor class, the means from phase I and phase II trees were averaged together and rounded to the nearest 5% increment. Scatterplots and boxplots were also generated to examine the spread of the RVG values for each vigor class.

Overstory recruitment and release potential

In order to translate the vigor assessment methods developed above into meaningful tools for managers, it was necessary to make an attempt to define the release potential and likelihood of recruitment into the overstory without further release for each vigor class. As much research examining release potential, predicting response after response, and risk of mortality from suppression has already been done, the methods used for this part of the study were exploratory and descriptive and done for comparison with conclusions found in the literature.

Similar to Tucker and Foster (unpublished), the number of years needed to reach the average overstory height of the 13 stands, 45m (148ft), was used as an indicator of the likelihood of reaching the overstory without further release, assuming that current height growth rates are maintained and that trees are currently 5m (16.4ft) in height. This indicator was a simple thought exercise used to compared vigor classes and purposely ignored the dynamic nature of forest stands and the fact that Douglas-fir height growth begins to slow as trees reach approximately 25m (80ft) on site class III sites (King 1966).

As a biological limit exists regarding how slow trees can grow and remain alive (Oliver and Larson 1996, Kobe and Coates 1997), risk of mortality from suppression was then examined. As the 54 tree sub-sample was a representative sample of the total population of understory trees, the slowest radial growth rates found from analysis of lifetime radial growth rates were assumed to be close to the threshold of mortality. These minimum growth rates were compared with mortality threshold rates from other studies. Estimates of mortality risk for each vigor class were based on how close the past 5yr mean radial growth increment were to these mortality thresholds. HD ratio thresholds for each vigor class were also considered as high HD ratios are associated with a higher risk of stem failure and suppression mortality (Wilson and Oliver 2000, Wonn and O'Hara 2001). Hemispherical photographs were then used to evaluate whether trees from different classes had enough space directly above them to recruit into the overstory, assuming that existing overstory trees would expand their crowns. Percent of total solar radiation and visual examination of the photos were used.

Release potential was defined in terms of a released tree’s ability to regain comparable growth rates, for a given light environment, to trees that did not undergo suppression. To assess release potential, lifetime RVG histories of the 54 intensively analyzed trees were examined for patterns of suppression and release. Trees that showed patterns of release were compared to trees growing in similar light environments that had not undergone suppression. Lifetime HD ratios were also examined to see the extent to which trees recovered from high ratios. Although the exact history of overstory removal around each tree could not be confidently determined, it was assumed that at least some of the trees currently growing in open conditions had been released in the past and should therefore show a growth response. Trees growing in open conditions that were growing at low RVG rates were closely examined to determine why they had not responded to release. Finally, the live crown ratio thresholds for each vigor class were also considered.

Factors influencing vigor: individual tree and stand level

Stepwise linear regression was used to characterize the response of 5yr RVG for individual trees to measures of overstory and understory density, light, crown crowding from neighboring trees and shrubs, percent shrub cover around the tree, and understory tree height. Crown crowding, measured by crown overlap, was also classified into high and low categories and used as an indicator variable in regression models. Analysis of co-variance (ANCOVA) was used to test for differences among slopes and intercepts. Various thresholds that defined high and low crown overlap were iteratively tested to determine which would create the greatest difference in slopes and intercepts and highest R^2 values for the overall model. Analysis was done for both the phase I stand inventory and phase II intensive analysis datasets. For the stand inventory dataset, only dominant and co-dominant understory trees were used as these were considered the future “crop” trees and for comparison with other studies where dominant trees where selected (Carter and Klinka 1992, Deisenhofer 2000, Drever and Lertzman 2001). LC ratio and HD ratio were also tested individually in place of RVG as dependent variables.

At the stand level, two methods were used to compare the overall vigor of the understory between stands. First, the number of understory trees per acre in each vigor class was tabulated for each stand. Second, the stand level, mean tree 5yr RVG was calculated for all trees, and then separately for crop trees, by averaging the mean RVG of each plot with understory trees. A non-linear model was developed to explain variations in stand mean RVG and test which factors influence understory vigor at the stand level. The model was based on the concept that average growth of an understory cohort is determined by growing space available to the cohort divided by the number of trees in the cohort (O'Hara 1996, Oliver and Larson 1996). Although multiple understory cohorts did exist in some stands, all understory trees were lumped into one cohort to simplify the analysis. Stand density index (SDI) was chosen to measure growing space occupancy for both the overstory and understory, as it has been shown to be a good indicator of leaf area index (Long 1995, O'Hara 1996) and is commonly used to measure site occupancy (Long 1985, Long and Daniel 1990). Percent shrub cover was tested in the model to account for its potential effect on resource availability. The average crown overlap for the stand was also tested to account for the spatial distribution of understory trees; whether they are clumped or more evenly distributed. A final variable was tested to account for the distribution of understory trees in relation to the heterogeneity of overstory density. This variable was the ratio of average overstory SDI for plots with understory trees to the average overstory SDI of all the plots. Stands with understory trees in more open plots thus have a lower value than stands where more trees are in plots with higher levels of overstory or where gaps are occupied with shrubs instead of trees. Several model forms were tested and the best combination of variables was chosen through iterative trials. SPSS, version 12.0 (SPSS 2003) was used for this analysis.

Results

Stand inventory

The 13 stands inventoried had a wide range of stand structures and understory vigor levels. Some were very open with large, evenly distributed overstory trees and dense understories and resembled shelterwood cuts. Others had large gaps and dense patches and were the result of ongoing prairie colonization and possibly some group selection harvesting. Yet others were fairly dense with small gaps. Most of the stands had high levels of spatial heterogeneity. Overstory stocking ranged from very open (91 SDI, 20% of full site occupancy) to somewhat dense (298 SDI, 60% of full site occupancy), with 510 SDI being full site occupancy (Long 1985). Understory densities had an even greater range: 10-842 trees per acre. Structural attributes for all 13 stands are presented in Table 3. The percentage of understory trees in each vigor class is also included in Table 3.

Assessing vigor

Results from exploratory analysis to find the best predictors of RVG using the 54 tree intensive analysis data set are presented in Figure 1. HD ratio was the weakest individual predictor (R^2= 0.50) of RVG, followed by past 5yr mean annual height growth increment (HG) (R^2= 0.55). LC ratio was the best individual predictor (R^2= 0.64), although variance increases below 30% RVG. The product of LCR^2 and visual crown density rating (CDR) was even better, however. (R^2= 0.76). The increase in variance at 30% RVG in still evident, but is lessened. This product was created to provide a relative measure of total leaf area as the visual crown density rating estimates crown fullness and showed a strong relationship to mean branch length and number of internodal branches (Figure 2).

Stepwise linear regression produced the following best fit model to predict 5 yr mean RVG using all the above variables and total height (Ht) (R^2= 0.89. $p<.0001$, Standard Error of Estimate (SEE) =0.058, All coefficients are significant $p<.005$).

Eq 4: $\textit{Predicted RVG} = 1.337 + 0.076\,LCR^2CDR - 0.009\,Ht(m) - 0.028\,ln(\textit{HD Ratio}) + .003\,HG(cm)$

Table 3: Summary data for all 13 stands. Standard errors are in ( ) for selected variables. Values are stand level means unless otherwise stated.

		Stand Code[a]												
		Bw	Jp	Wn	Et	Sm	Kp	Rd	Ww	Sh	Ch	Tw	Rj	Jm
Overstory	# of acres	84	54	150	50	50	80	153	117	112	110	74	55	45
	# of plots	28	19	16	15	16	16	17	15	14	15	15	12	13
	SDI	298 (23)	298 (32)	260 (24)	256 (41)	252 (35)	242 (30)	226 (21)	223 (27)	209 (28)	163 (28)	152 (31)	141 (22)	91 (13)
	Rel. Density (Curtis)	48	47	41	42	41	39	35	35	33	26	25	22	14
	Basal Area (ft^2/acre)	224	229	195	176	183	181	188	179	166	134	110	114	82
	Trees per Acre	87	80	79	106	98	88	44	50	52	39	70	31	13
	Visual Open Sky	25(2)	19 (1)	22 (1)	27 (4)	26 (2)	36 (3)	23 (1)	27 (3)	24 (1)	35 (3)	37 (4)	39 (3)	45 (3)
	Tall Shrubs (% cov)	8 (2)	29 (5)	26 (7)	14 (6)	5 (2)	4 (2)	37 (7)	32 (7)	16 (4)	24 (7)	25 (5)	40(10)	34 (7)
	Low Shrubs (% cov)	26 (5)	71 (5)	66 (8)	20 (5)	27 (6)	30 (6)	61 (7)	74 (5)	62 (6)	70 (8)	37 (6)	64(10)	39 (9)
	SDI Plot Ratio	0.94	0.92	1.00	0.91	0.79	0.70	0.93	0.87	0.85	0.98	0.84	0.94	0.97
Understory	% of plots w/regen	39%	53%	69%	80%	56%	38%	88%	80%	79%	66%	46%	75%	85%
	SDI	.3(.2)	3.1(1)	3.2(1)	7.1(2)	3.1(1)	4.8(3)	8.4(2)	7.2(5)	7.9(3)	12 (3)	15 (7)	59(18)	42(8)
	Trees per acre	10	18	47	45	30	33	43	83	80	317	147	842	265
	Crop Tree TPA	6	8	21	15	15	9	19	14	19	53	50	138	119
	Crop Trs: Vig Cat 1	47%	31%	47%	36%	29%	7%	41%	17%	37%	19%	13%	33%	13%
	Crop Trs: Vig Cat 2	53%	56%	50%	50%	54%	33%	44%	67%	41%	50%	47%	39%	16%
	Crop Trs: Vig Cat 3	0%	13%	3%	14%	8%	27%	16%	5%	19%	19%	20%	24%	29%
	Crop Trs: Vig Cat 4	0%	0%	0%	0%	8%	33%	0%	10%	4%	13%	20%	3%	42%
	RVG (%) (All trees)	17 (2)	13 (2)	16 (2)	12 (3)	16 (3)	23 (3)	16 (1)	17 (2)	16 (2)	24 (3)	19 (2)	20 (2)	28 (3)
	Crop Tree RVG (%)	18 (2)	17 (3)	17 (2)	12 (3)	23 (3)	30 (3)	16 (2)	23 (3)	18 (2)	29 (3)	28 (2)	26 (2)	37 (2)
	Dbh (mm)	17	76	52	69	52	59	80	38	41	44	60	47	89
	Height (m)	2.1	6.6	5.4	6.7	5.4	5.7	7.4	4.1	4.7	4.3	6.0	5.2	7.5
	Crown Overlap (%)	20 (4)	43 (5)	29 (4)	49 (7)	32 (9)	52 (6)	30 (5)	39 (5)	32 (4)	48 (6)	47 (9)	72 (4)	49 (7)
	Crop Tree HD Ratio	85 (5)	75 (4)	76 (4)	85 (4)	74 (3)	71 (3)	78 (3)	74 (2)	82 (4)	76 (3)	65 (2)	75 (5)	68 (2)
	Crop Tree LCR (%)	54 (3)	53 (2)	50 (2)	54 (3)	57 (3)	65 (2)	55 (3)	57 (3)	49 (3)	61 (3)	55 (4)	55 (2)	67 (3)
	Dead Trees per acre	0	24	106	97	247	228	62	7	150	127	470	1608	165

(Table 3 continued)

Note: SDI is stand density index; Visual Open Sky is a visual estimate of percent open sky; SDI Plot Ratio is the ratio of SDI of plots with understory trees divided by the SDI of all plots; Crop trees are dominant and co-dominant crown classes; Vig Cat is Vigor Category; RVG is relative volume growth : the past 5 year, mean annual percent of maximum site potential growth based on tree height; Crown overlap is the percentage of the projected crown area occupied by competing understory trees and shrubs.

[a] Stand names are as follows: Bw: Badacre West; Jp: Jaypee: Wn: West Needloh; Et: North Eastom; Sm: Somemore; Kp: Kalipso; Rd: Redomsky; Ww: West Weir; Sh: Shaver; Ch: Cherry Hill; Tw: Thorpe Woods; Rj: Recondo Johnson; Jm: Jaypee M.C.

Without height, HG drops out of the model due to collinearity with LCR^2*CDR. In the full model, however, the variance inflation factor (VIF) is below 10 for each variable indicating the collinearity is not significant. Height is a not a significant predictor of RVG on its own, but affects the interaction of the other variables. Residual and QxQ plots indicated a relatively constant variance and approach to normality for the overall model. A second, slightly weaker model to predict RVG that does not include crown density rating is listed in Appendix D for use with data sets where crown density rating is not available.

The model in equation 4 produces negative RVG values for trees with very high height to diameter ratios and/or very low live crown ratios. Few of these low vigor trees were part of the 54 tree, phase II sub-sample used to create the model only the average and tallest trees were selected for sampling. While the model is adequate for intermediate, co-dominant, and dominants trees, it is likely to be less accurate for trees from the overtopped crown class. Although negative values do not make biological sense, they were included in subsequent analysis as indicative of RVG close to zero.

The second method of assessing vigor, vigor classes based on thresholds, is compared with RVG in Figure 3. The extreme upper values in each category are due to high height to diameter ratios. For the 54 phase II trees, the means of actual RVG and radial growth for the 4 vigor categories are all significantly different from each other ($p<0.05$). The means of RVG from 637 trees from the phase I data set, which are also significantly different from one another ($p<0.001$)., all fall within the 95% confidence intervals of the phase II dataset displayed as the solid horizontal lines in figure 3a. There is also a clear separation of the 50th percentile boxes of each class within the boxplots in figure 3b. Finally, the combined phase I and II average RVG values (rounded to the nearest 5%) for each vigor class are presented in Table 2.

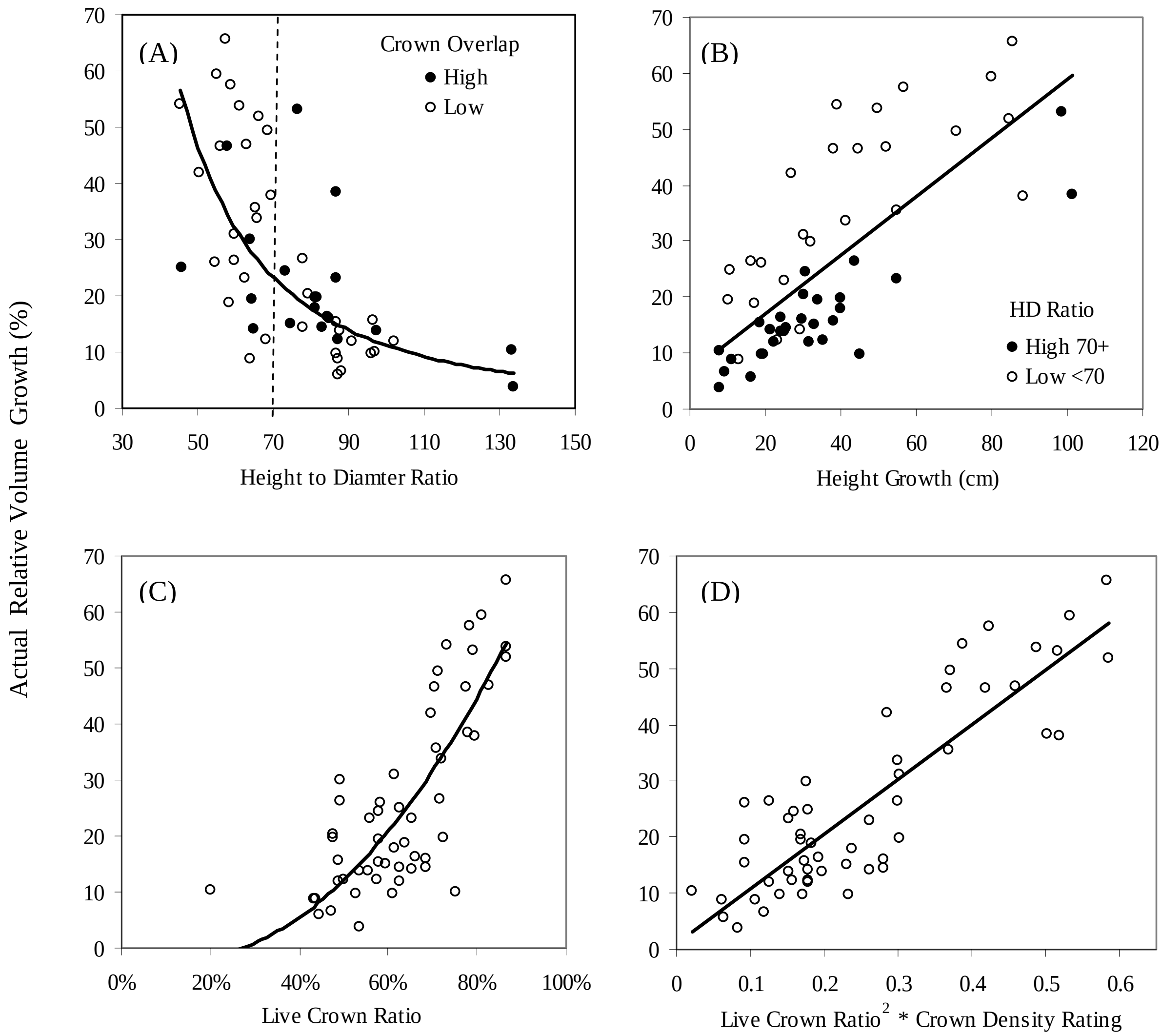


Figure 1: Scatterplots and fitted regression models of average of past 5yr relative volume growth to: (A) Height to diameter ratio: the threshold of 70 is included for reference (y=1481.950 $x^{-2.016}$, R^2= 0 .50 , SEE=0.476, p<.0001). (B) Height growth annual increment, past 5yr average (y=0 .005x + 0.066 , R^2= 0 .55 , SEE=0.110, p<.0001). (C) Live crown ratio (y=1.054x^2 – 0.284x, R^2= 0.64 SEE=0.100, p<.0001). (D) LCR^2 * Visual Crown Density Rating (y=0 .145x + 0.068 , R^2= 0 .76 , SEE=0.084, p<.0001). N = 54 for all models.

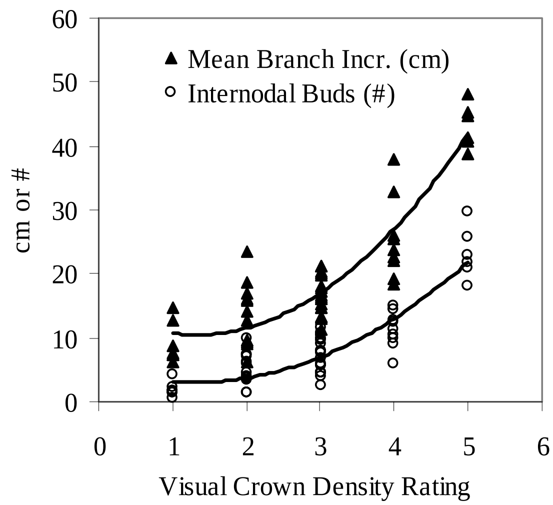


Figure 2: Scatterplot and fitted regression models of visual rating of crown density rating vs. mean branch increment (N=54, y=2.202x^2 - 5.648x + 14.660, R^2= 0.830, *SEE*=4.490 , p<.0001), and number of internodal buds and branches (N=54, y=1.305 x^2 – 3.303x + 5.474, R^2= 0 .79 ,*SEE*=3.014 , p<.0001). Both measures are for last 3 years of growth.

Overstory recruitment and release potential

The length of time trees in each vigor class would take to reach the height of the current overstory, assuming current height growth rates are maintained, is presented in Table 2. The slowest radial growth rate observed that was maintained for 4 consecutive years was 0.3mm (0.01in.) for trees less than 5m in height and 1.3mm (0.05in.) for trees above 5m. The average 5yr mean annual radial growth rates for each vigor class are presented in Table 2. In general, vigor class one and two trees had little canopy space directly above them and class 3 trees had a moderate amount. Only class 4 trees had what appeared to be enough canopy space above them to grow into the overstory without further overstory removal. Percent total solar radiation (TSR) averages and examples of hemispherical photos for each vigor class are shown in Appendix E.

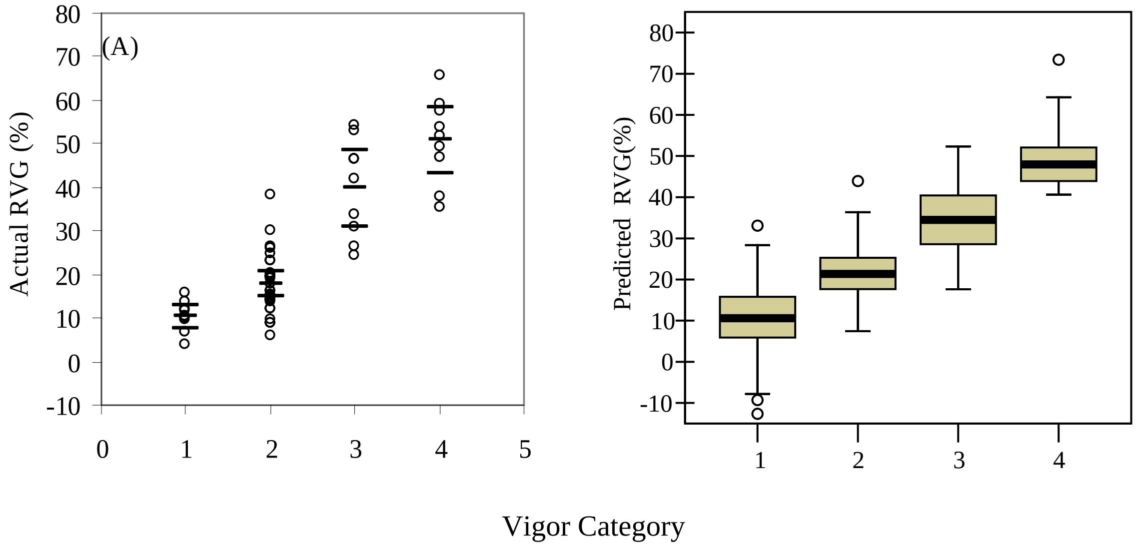
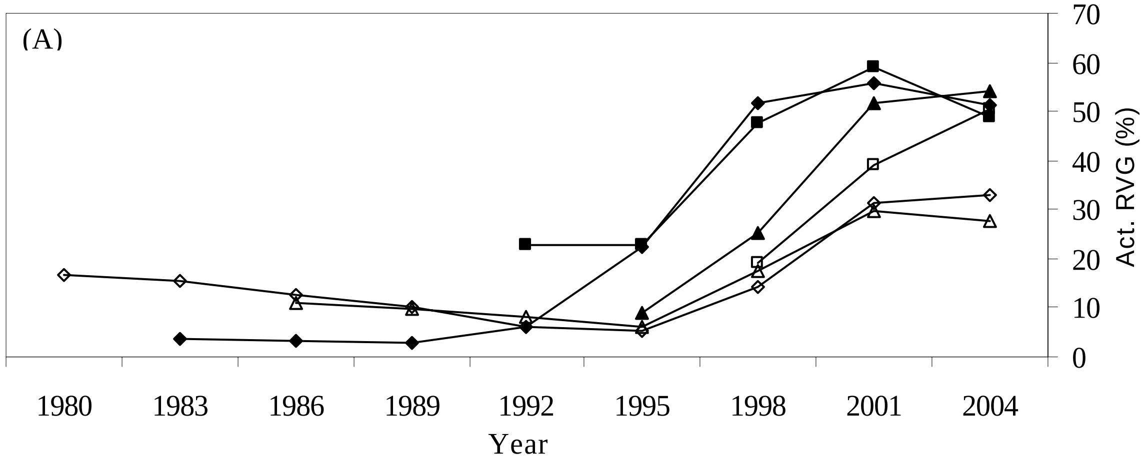


Figure 3: Vigor classes displayed against percent of maximum volume growth. Definitions of vigor classes are listed in table 2. (A) Scatterplot of 54 trees from phase 2. Means and 95% confidence intervals are displayed by hash marks. Means for all classes are significantly different from one another, Scheffe's post hoc test, ($p<.05$). (B): Boxplot of 637 trees from phase 1. Means for all classes are significantly different from one other ($p<.0001$).

Of the 54 phase II trees, six were found to have strongly responded to release (Figure 4a). Pre-release RVG rates were under 20% and radial growth rates were less than 2mm (0.08in.) per year. Trees maintained these slow growth rates for up to 15 years and were all less than 5m (16.4 ft) in height at time of release. Their height to diameter ratios all declined to values below 65 and in some cases were over 100 prior to release (Figure 4b). These six trees had RVG rates similar to trees in the same light environment that had not undergone suppression and were all above the regression lines in models relating RVG to open sky (Figure 5a). Two trees were found that did not respond strongly to release and were growing at levels below their potential. They both showed some response and had high levels of crown overlap from neighboring understory trees and shrubs.



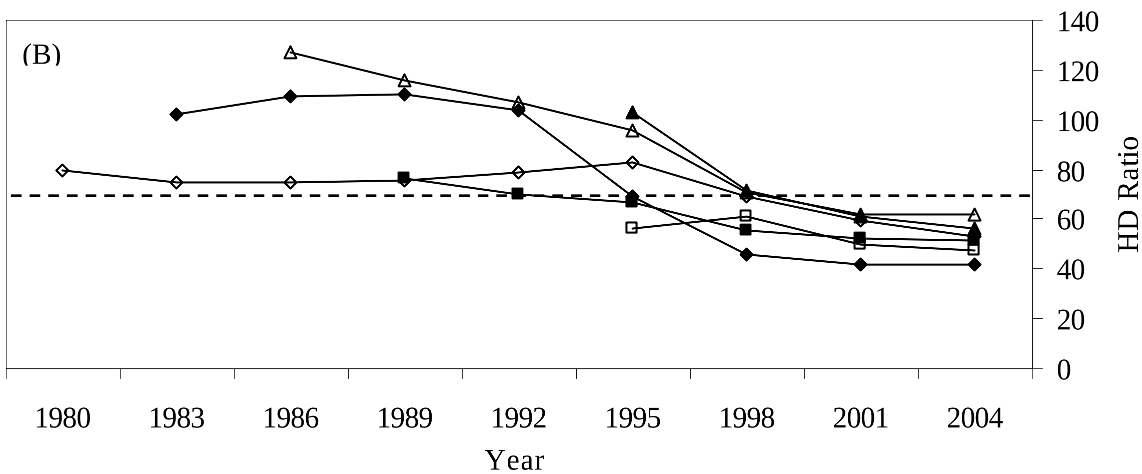


Figure 4: Relative volume growth and height to diameter ratio histories for 6 release trees. Increments are 3 year averages. Histories begin at breast height. The HD threshold of 70 is included for reference (dashed line).

Factors influencing vigor: individual tree level

Light and overstory density were the dominant drivers in predicting RVG of understory trees (Figures 5, 6, & 7). Both the visual estimate of open sky (VOS) and percent total solar radiation derived from analysis of hemispherical photos (TSR) were used as measures of light. Stand density index (SDI) was selected as the primary measure of overstory density as it performed as well or better than basal area, relative density (Curtis 1986), crown competition factor, or basal area of all trees taller than the subject tree (Biging and Dobbertin 1995). Adding in measures of crown crowding (infringement on the live crown of the sample tree from neighboring trees as well as competing shrubs) increased R^2 values by only 5-10%. The 3-dimensional crown overlap method of quantifying crown crowding performed as well in multiple regression models as the distance dependent neighborhood competition index (NCI) and better than measures of understory density, such as understory trees per acre, basal area, or SDI. Percent of shrub cover around the tree, as well as tree height, had no significant effect in the models.

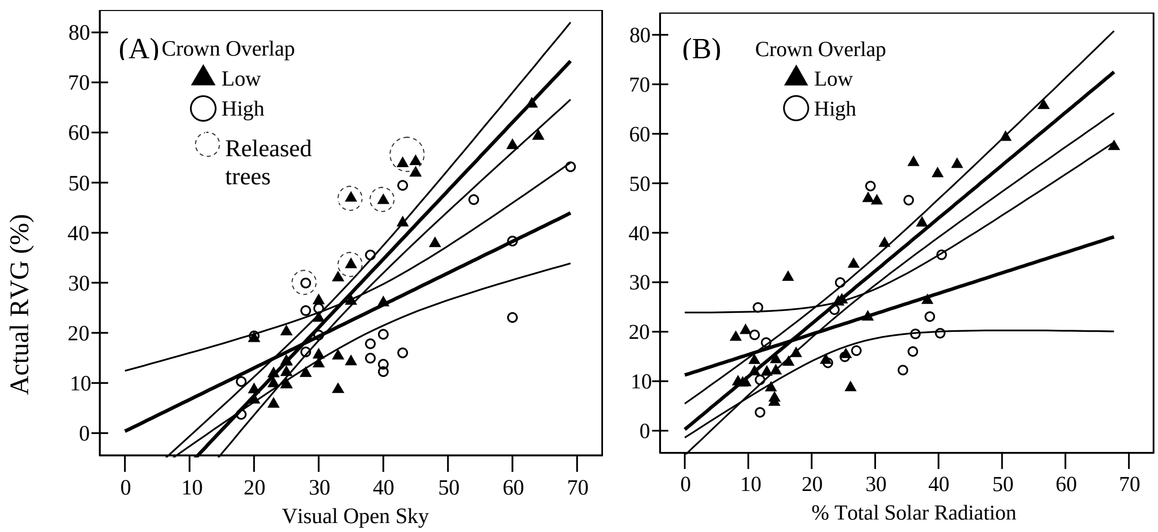


Figure 5: Fitted regression lines and 95% confidence intervals of actual RVG to measures of light for phase 2 trees. Three-dimensional crown overlap is included as a indicator (*d)* variable in regression models: low (<30%,3d) = 0, high (30%+,3d) = 1. (A) Visual estimate of open sky (N=54, y=0.014x - 0.199 - 0.008dx + 0.207d, R^2= 0.71, *SEE*=0.092 , p<.0001, all coefficients are significant p<.01. R^2= 0.79 for low crown overlap regression and R^2= 0.43 for high crown overlap) (B) Percent of total solar radiation (N=52, y=0.011x + 0.003 - 0.007dx + 0.110d, R^2= 0.65 ,*SEE*=0.099 , p<.0001, only slope coefficients are significant , p<.01. R^2= 0.75 for low crown overlap regression and R^2= 0.18 for high crown overlap.

Dividing crown overlap into two classes (high and low) and including it as an indicator variable generated the best regression models to predict RVG (Figures 5 & 6). The breakpoint for the two classes that produced the best models was 30% for the 3-dimensional crown overlap measured on the 54 phase II trees, and 50% for the 2-dimensional crown overlap measured on the 637 trees in the phase I dataset. Regression models are constrained to the range of the data and caution should be used making any extrapolations. The boxplots in Figure 7 were included as a secondary method of showing the relationships between RVG and VOS, SDI, and crown overlap and to better display the distribution of the data.

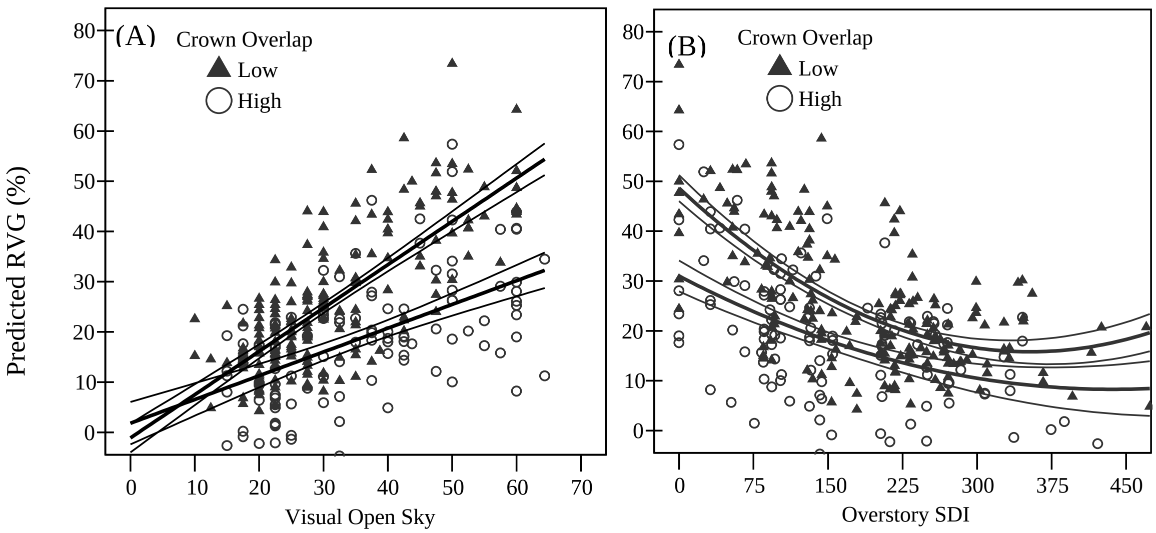


Figure 6: Fitted regression lines and 95% confidence intervals of predicted RVG to overstory measures for phase 1 crop trees (N=312). Crown overlap is included as an indicator (*d*) variable in regression models: low (<50%,2d) = 0, high (50%+,2d) = 1.(A) Visual open sky (y=.009x - 0.011 - 0.004dx + 0.027d, R^2= 0.53, *SEE*=0.090 , p<.0001, only slope coefficients are significant p<.0001. R^2= 0.57 for low crown overlap regression and R^2= 0.32 for high crown overlap) (B) Stand density index (y= 0.0000027x^2 - 0.0000015dx^2 - 0.0019x + 0.000842dx + 0.487 - 0.179d, R^2= 0.41, *SEE=0.103* , p<.0001, all co-efficients are significant except for dx^2, R^2= 0.42 for low crown overlap regression and R^2= 0.26 for high crown overlap)

In the phase I VOS (Figure 6a), phase II VOS (Figure 5a), and phase II TSR (Figure 5b) regression models, ANCOVA showed statistically significantly steeper slopes and higher R^2 values for trees with low crown overlap than trees with high crown overlap. Intercepts were not significant for either high or low crown overlap. The effect of crown overlap was not significant at the lowest light levels but became significant at the point where the 95% CI of the regression lines diverged, and had an increasing effect as open sky increased and overstory density decreased. The divergence in the 95% CI intervals is due to increasing differences between means, as well as a drop in variance, as light levels increased.

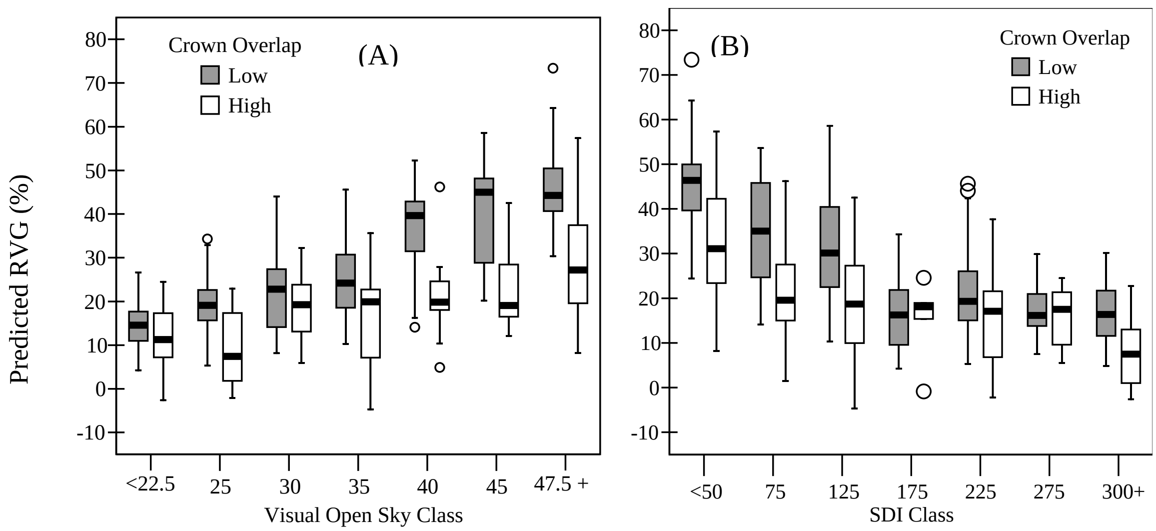


Figure 7: Boxplots of predicted relative volume growth of phase 1 crop trees for visual open sky and overstory stand density index classes. N=312. Values displayed for classes are midpoints, except for lower and upper classes. Classes for (A) visual open sky are: <22.5, 22.6-27.5 , 27.6-32.5, 32.6-37.5, 37.6-42.5, 42.5-47.5, 47.5+. Classes for (B) SDI are: <50, 50-99, 100-149, 150-199, 200-249,250-299,300+. Low crown overlap is <50% (2-dimensional), high crown overlap is 50%+ (2-dimensional).

The phase II VOS model (Figure 5a) has a higher R^2 value and lower intercept and slope than the phase I VOS model (figure 6a). The drop in R^2 values is most likely due to increased variance introduced by the RVG prediction model and increased measurement error as VOS was measured at plot center in phase I and not for each individual tree as in phase II.

Phase I and II regression models for SDI had similar slopes, intercepts and R^2 values and so only the results for the phase I, larger data set are presented in Figure 6b. Low crown overlap had a higher R^2 value and a significantly different intercept than high crown overlap, but the slope and curvature were not significantly different. Similar to the VOS models, a pattern of an increasing effect of crown overlap as SDI decreased was found. Between 200 and 250 SDI (Figure 6b), there is a clump of 6 trees above 35% RVG that were all on the edges of gaps and so were receiving more light for their SDI value than trees that were underneath a more continuous canopy. Accounting for this clump of outliers, there is a clear jump in the response of RVG at 150 SDI, which is very evident in the boxplot shown in Figure 7b. It should be noted that 0 SDI does not mean that the tree is open grown, only that no overstory trees are within the plot radius measured. The upward lip in the quadratic model beginning at 350 SDI is due to the lack of data above this level and the nature of the quadratic function. A quadratic model form was chose over an exponential form as it had a much higher R^2 value. The model should be constrained to SDI values less than 350.

The second vigor assessment method, the 4 vigor classes, was also related to VOS, SDI, and crown overlap using boxplots (Figure 8). These were derived to clearly show the ranges of VOS and SDI values that trees from the 4 vigor classes were found in.

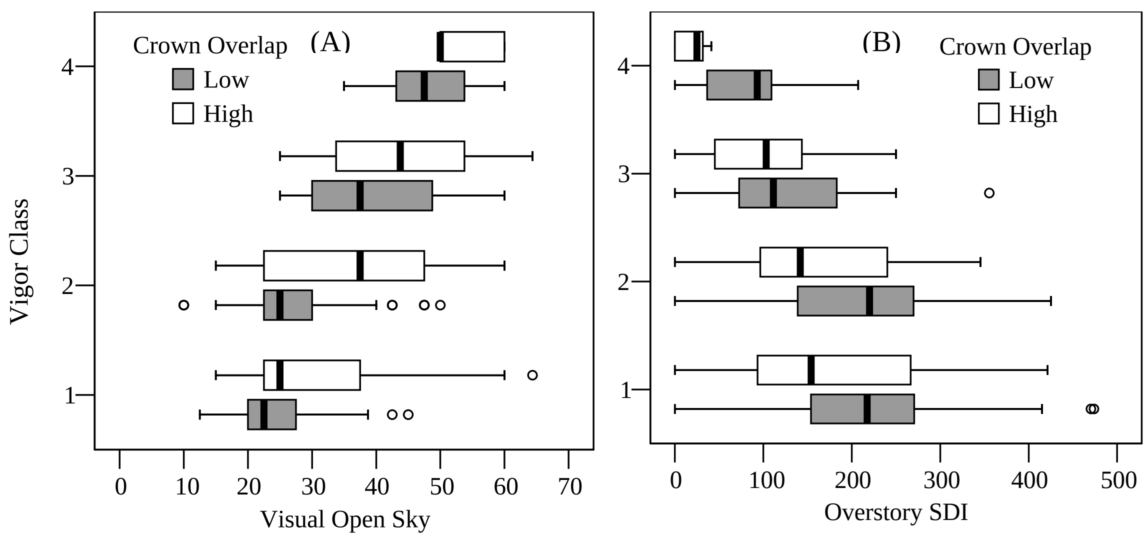


Figure 8: Boxplots of high and low crown overlap for 4 vigor classes displayed against (A) visual open sky (VOS) and (B) overstory SDI. Data are from dominant and co-dominant trees from phase I stand inventory (N=312). Low crown overlap is <50% (2-dimensional), high crown overlap is 50%+ (2-dimensional).

VOS showed a strong relationship to TSR (Figure 9), especially for trees with lower crown overlap (R^2=0.86). This was expected as VOS measured openness of just the overstory trees, while TSR measured all trees affecting the light environment of the subject tree. The relationship is not a 1:1 relationship as VOS over-predicts TSR at lower levels and under-predicts it at higher levels. This indicates that VOS is a relative and not absolute measure of actual solar radiation and should not be interpreted or applied as an absolute percent of open sky. The regression equation in Figure 9 can be used to convert the relative, visually estimated VOS into TSR in order to compare light levels with other studies.

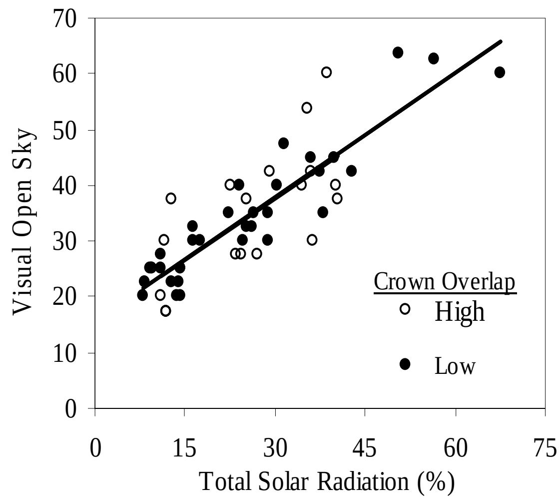


Figure 9: Scatterplot and fitted regression mdoel of visual estimation of percent open sky (VOS) vs. total solar radiation (TSR) index from analysis of hemispherical photographs (N=52: y=0 .739x + 15.601 , R^2= 0.73 , *SEE*=5.899, p<.0001). For trees with low crown overlap (<30%,3d) R^2=0.86, with high crown overlap (30%+,3d) R^2=0.48. Slope and constant are not significantly different between low and high crown overlap regressions.

In addition to the main vigor metric, RVG, regression models predicting live crown ratio and HD ratio were developed from the same set of explanatory variables as RVG. LC ratio and HD ratio showed the same basic relationships to VOS, SDI and crown overlap. Regression models were consistently weaker than models for RVG and so are not presented here. Instead, boxplots are shown in Figure 10 to display the distribution of LCR and HD ratio data by VOS and SDI class and crown overlap.

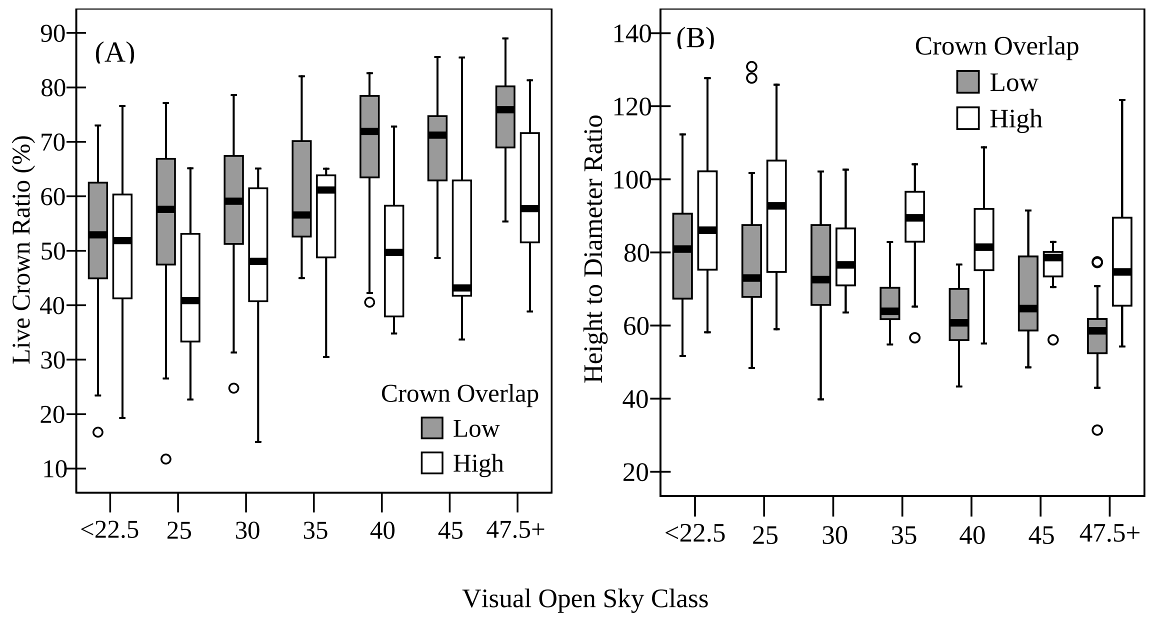


Figure 10: Boxplots of live crown ratio and height to diameter ratio for visual open sky classes for dominant and co-dominant trees in stand inventory (N=312). Classes are: <22.5, 22.6-27.5 , 27.6-32.5, 32.6-37.5, 37.6-42.5, 42.5-47.5, 47.5+. Low crown overlap is <50% (2-dimensional), high crown overlap is 50%+ (2-dimensional).

Factors influencing vigor: stand level

At the stand level, overstory SDI was the dominant factor influencing stand level, average RVG (Figure 11a). It also was a strong predictor of understory TPA (Figure 11b), and understory SDI ($understory\ SDI = 340.1\ e^{-.018Overs.SDI}$, $R^2 = 0.76$, p<.0001). Adding in other stand parameters to more fully quantify growing space into a non-linear models produced an excellent predictor of average RVG of all understory trees, as well as dominant and co-dominant understory trees (figure 11c). Variables included are: oSDI: Overstory SDI, uSDI: SDI of understory trees, ShT: percent cover of tall shrubs (>1.37m in height), ShL: percent cover of low shrubs, CMP: average crown overlap of understory trees, SPR: SDI plot ratio (ratio of average SDI for plots with understory trees and average SDI of all plots). The following models were derived:

Eq. 5*:* *RVG(all trees)* = $33.995 \times \mathrm{oSDI}^{-1.162} \times \mathrm{uSDI}^{-0.195} \times \mathrm{ShT}^{-0.245} \times \mathrm{ShL}^{0.355} \times \mathrm{CMP}^{0.318}$

R^2= 0.93. all coefficients are significant, except for constant and CMP)

Eq. 6: *RVG(crop trees)=*

$$120.121 \times \mathrm{oSDI}^{-1.45} \times \mathrm{uSDI}^{-0.298} \times \mathrm{ShT}^{-0.134} \times \mathrm{ShL}^{0.358} \times \mathrm{CMP}^{.521} \times \mathrm{SPR}^{-1.046}$$

(R^2= 0.94, only coefficients for oSDI, uSDI, and ShL are significant)

Between 85-90% of the variation in RVG was explained with only overstory SDI, understory SDI, and tall shrubs or low shrubs in each model. Non-significant coefficients were included to add predictive power. As only 13 data points were used, the asymptotic confidence intervals of the non-linear regression method are large. With more data points, they may in fact be skewed in a negative or positive direction and be significant.

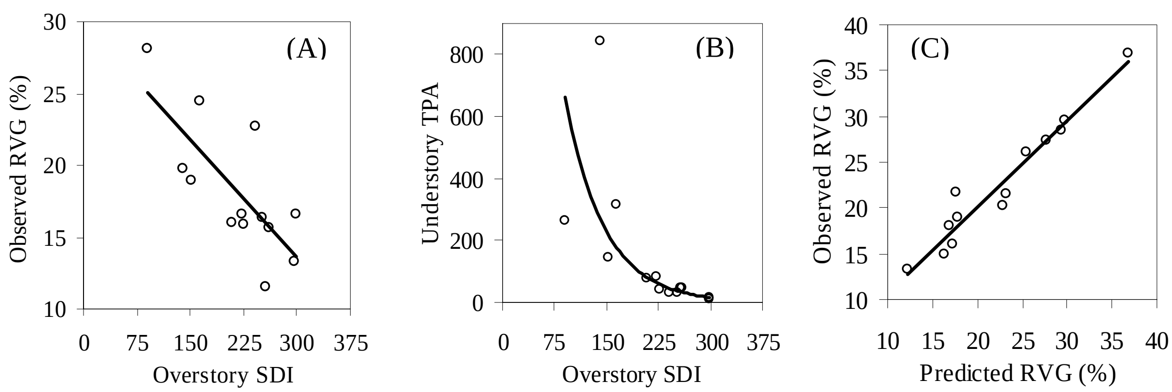


Figure 11: Stand level scatter plots and models for (A) overtstory (trees >150mm dbh) vs. understory (tree <150 mm dbh) SDI (y=3361.5 $e^{-.018x}$, R^2= 0 .82 , *SEE*=0.56, p<.0001).
(B) Stand average of relative volume growth (RVG) for all understory trees vs. overstory Stand Density Index (y=-0.006x + 0.303, R^2= 0.66, *SEE*=0.027, p<.001). (C) Goodness of fit of the stand level, non-linear RVG model. Line is 1:1 relationship between predicted and observed stand averages of RVG for crop trees (R^2= 0.94). N=13 for all 3 models.

Discussion

Assessing vigor

The considerable scatter in the relationships of height growth, HD ratio, and LC ratio to relative volume growth suggests that these metrics, used alone, are not strong indicators of relative volume growth for understory Douglas-fir (Figure 1). Of the 36 trees that had a RVG of less than 30%, 9 had a HD ratio less than the threshold of 70, and 14 had a live crown ratio of greater than 60%. A low HD ratio or high live crown ratio is thus not a certain indication of faster growth. The almost perfect split in Figure 1b of trees with HD ratios of less than 70 above the regression line and trees with HD ratios greater than 70 below confirms that trees with low HD ratios put on more volume growth per unit of height growth than trees with higher HD ratios. It also shows that factoring in HD ratio with height growth is a more powerful method of predicting volume growth than using height growth alone. The increase in predictive power achieved by combining live crown ratio with crown density, which was derived from and highly correlated with the number and length of internodal and whorl branches (Figure 2), shows the importance of considering more than live crown ratio when assessing a tree's carbon production capacity (Figure 1d). This concurs with Maquire and Kanaskie (2002) who developed a vigor assessment method for Douglas-fir plantations based on live crown ratio and sapwood area. They conclude: "consideration of both the total amount of leaf area and the volume or length over which it is distributed can provide an objective measure of tree condition during silvicultural stand examination, operational forest inventory, or forest health monitoring."

Combining all four of these metrics into a single model based on relative volume growth proved to be a more powerful approach to both predicting current volume growth and measuring response to overstory stocking and crown crowding than using individual, absolute metrics. All of the coefficients have signs that make biological sense. The significance and negative sign of total height in the model, as well as its affect on the significance of height growth, reflects the change in maximum potential height and radial growth and exponential increase in volume growth with increasing tree size (King 1966). Other investigators examining growth of understory Douglas-fir in relation to environmental variables have generally used two or more vigor metrics in their analysis (Carter and Klinka 1992, Mailly and Kimmins 1997, Williams et al. 1999, Deisenhofer 2000, Drever and Lertzman 2001). However, combining multiple crown and growth metrics into a single, relative metric that is strongly correlated with volume growth is advantageous in situations where coring large numbers of trees is not feasible and investigators want a single, continuous, and comprehensive vigor metric to assess and compare advanced regeneration across a wide range of tree sizes. In situations where a more detailed understanding of understory vigor is needed, the model may be less appropriate as multiple metrics provide more complete information and variance is likely increased by using a predicted instead of a directly measured metric.

The second method of assessing vigor suggests that understory trees can be separated out into four ranges of RVG using the height growth, HD ratio, and live crown ratio thresholds with a degree of accuracy that is appropriate when general and rapid stand assessments are desired and a continuous variable is not needed (Figure 3). The height growth, LC ratio, and HD ratio thresholds (Table 2) used to classify trees are generally supported by results from the RVG scatterplots in Figure 1. For the 18 trees growing at more than 35% RVG, all had live crown ratios greater than 65%, only one had height growth less than 30cm, and only two had HD ratios above 70. These two trees both had high crown overlap, suggesting that trees growing above 35% RVG will maintain HD ratios less than 70 if they have less than 30% crown overlap (3-dimensional).

Overstory recruitment and release potential

Based on the projected number of years to reach the overstory calculated for each vigor class (Table 2), it is unlikely that vigor class one and two trees could survive growing beneath the overstory canopy for 222 and 174 years, respectively. Without further overstory thinning, the overstory will close, reduce available growing space, and further suppress the growth of understory trees. Additionally, as trees get taller they theoretically need more growing space due to the increased carbon demand from the higher proportion of non-photosynthetic tissues required for structural support (Givnish 1988, Messier et al. 1999). In un-thinned interior forests of British Columbia, Williams et al. (1999) found the oldest understory Douglas-fir to be 55 years old. Deisenhofer (2000), working in Douglas-fir stands managed with a selection system, found the oldest mid-story trees to be 46-52 years old. In a survey of Douglas-fir stands in western Oregon 10-15 years after thinning, Bailey and Tappeiner (1998), observed that high mortality of understory Douglas-fir saplings was likely without further thinning.

There is a biological limit to how slow trees can grow and survive. Models from Kobe and Coates (1997) for western conifers in interior boreal forests show an exponential increase in probability of mortality as annual radial growth declines below a species specific, threshold level for a period of 4 years. If coastal Douglas-fir is assumed to have a shade tolerance in between lodgepole pine and hybrid spruce (Coates, pers comm.), these models suggest that probability of mortality in the next 3 years is approximately 30% at an annual radial growth rate of 0.5 mm per year. Although this extrapolation is clearly problematic, it approximates the slowest growth rates observed in this study (0.3mm) and by Deisenhofer (2000), who slowest rates were 0.2-0.5 mm. While further research is needed to better quantify the risk of mortality associated with slow growth rates for coastal Douglas-fir and adjust for tree size, a rate of 0.5mm per year sustained for at least four consecutive years was considered the most reasonable estimate of a threshold of mortality risk. Vigor class one trees are at or close to this threshold and class two trees are not far away, while class three and four trees appear to have a low risk of mortality from suppression (Table 2). This is further evidence that class one and two trees will not recruit into the overstory without release.

Results from this study (Figure 4), and all other studies reviewed on the release of Douglas-fir advanced regeneration and other western conifers less shade tolerant than Douglas-fir, indicate that response to release, from even severe suppression, is highly likely and risk of mortality from thinning shock is low (Seidel 1983a, Helms and Standiford 1985, Oliver 1985, McCaughey and Ferguson 1988, Carlson and Schmidt 1989, Tesch and Korpela 1993, Deisenhofer 2000, Wright et al. 2000, Miller and Emmingham 2001, Kneeshaw et al. 2002). Furthermore, evidence from this study supports the conclusion reached by Tesch and Korpela (1993) and Wright et al (2000) that, for a given light environment, released trees are capable of attaining growth rates comparable to trees that did not undergo suppression. Wright et al (2000) also found that the time it takes to attain comparable growth rates tends to increase with length and severity of suppression, some trees may never attain such rates in cases of severe suppression, and trees can undergo multiple episodes of suppression and release.

The fact that roughly 75% of trees growing in low light environments (the lowest two VOS classes in Figure 10) had LC ratios greater than 40% and HD ratios less than 90, suggests that the vast majority of trees surveyed in this study have sufficient live crown to respond to release and low enough current HD ratios to regain acceptable HD ratios (between 60-70) in a reasonable period of time. Seidel (1983), Oliver (1985), McCaughey and Ferguson (1988) and Deisenhofer (2000) all recommend a LC threshold between 40-50% for selecting future crop trees from advanced regeneration. Chen and Klinka (1997) found that Douglas-fir can shift from growing shade needles to sun needles on the same branch. Low vigor trees with long but sparse crowns can thus add sun foliage to the existing live branches to take advantage of increased sunlight after release, in addition to building new crown through height growth.

After release, height growth often declines for a short period while trees build up the root capacity and stem conductive tissue needed for increased growth (Helms and Standiford 1985, Kneeshaw et al. 2002). The result can be a rapid decline in height to diameter ratios as was observed in this study and in other data collected from 103 understory Douglas-fir saplings at Fort Lewis (Foster, unpublished data). Foster (unpublished data) observed that mean HD ratios declined from 92 to 72 in 3 years after partial release. Emmingham et al. (2000) used an HD ratio of 60 at ground level, which corresponds to 70 at 15cm above ground, as a threshold for acceptable vigor of understory trees. This threshold, which is a common threshold for young plantations (Newton and Comeau 1990), does appear to be a reasonable guide for assessing overstory recruitment potential without release for understory Douglas-fir in this forest type. However, trees with higher HD ratios can recover if released and become viable replacement overstory trees. Furthermore, risks of stem failure associated with high HD ratios (Wonn and O'Hara 2001) are likely to be lower in understory environments where the overstory ameliorates the effects of heavy snow loads and high winds.

While it is highly probable that most of the understory trees surveyed in this study are capable of release, the lag time before response to release, the degree of response, and decline in HD ratio after release will depend on the level of overstory removal, the degree of crown crowding after release; and pre-release growth rates, live crown ratio, and length of suppression. In a study of response to release after shelterwood removals in Douglas-fir stands, Tesch and Korpela (1993) showed that pre-release volume growth was strongly correlated with post release volume growth. In addition, height growth and live crown ratio have also been shown to be strong predictors of post-release growth for Douglas-fir and other western conifers (Seidel 1983a, Oliver 1985, McCaughey and Ferguson 1988). Tesch and Korpela (1993) and Helms and Standiford (1985) both used discriminant anaylsis to predict post release height growth. They found that pre-release LC ratio and height growth were the most powerful variables selected, and that the discriminant functions correctly classified post release height growth 63-84% of the time. In a summary of vigor metrics that predict release potential, Ruel et al. (2000) recommends HD ratio and crown metrics such as number of buds and branches for intermediate shade tolerant species such as Douglas-fir. As RVG combines all of these metrics, it is reasonable to assume that RVG is a strong predictor of response to release. For a given post-release light environment, trees with higher pre-release RVG are likely to achieve higher post-release RVG and thus have a greater probability of attaining rates comparable to trees that did not undergo release and do so in a shorter period of time. Results from this study are not sufficient to statistically verify this conclusion, however, and further investigation is needed to confirm the value of RVG as a predictor of magnitude of, and lag time before, response to release.

Tree height should also be factored into release potential. Trees observed in studies of release have generally been less 5m in height at time of release. Risk of stem failure from high HD ratios is greater in taller trees due to greater physical stress loads on the stem (Wilson and Oliver 2000, Wonn and O'Hara 2001). Rebuilding live crown and rebalancing HD ratios after release takes longer in taller trees as new growth is a smaller proportion of total tree size. While no height cutoff exists at which response to release is possible (Deisenhofer 2000, Wright et al. 2000), the window of risk of stem failure from high HD ratios and the lag time before response to release is likely to be longer for taller trees. Kneeshaw et al (2002) and Deisenhofer (2000) found some evidence of an negative effect of increasing tree height on the degree of response to release. In open grown plantations trees, Wilson and Oliver (2000) found that 10m was a critical height for trees to be able to recover from high HD ratios and reach full growth potential.

Based on these findings regarding overstory recruitment and release potential, the following assessments were made regarding each vigor class. Class four trees are "free to grow" in that they have enough growing space projected into the future to have a high likelihood of reaching the overstory without further release. If they are released, either from overstory removal or pre-commercial thinning of neighboring competitors, they will respond quickly and attain growth rates close to or at the maximum potential for that light environment, if they are not already there. Class three trees can likely maintain their current growth rates for some time, but will probably need release from overstory removal or pre-commercial thinning of neighboring competitors at some point to recruit into the overstory. If released, they will quickly attain growth rates close to or at the maximum potential for that light environment.

It is highly unlikely that class two trees will reach the overstory without release. They will need release from overstory removal, and possibly also from pre-commercial thinning of neighboring competitors, in the next 1-2 thinning cycles to avoid severe suppression and substantial risk of mortality. If thinned within this time period, they should attain post-release growth rates comparable to trees that were not suppressed, after a period of time. Class one trees are currently at some risk of mortality from suppression and will not reach the overstory without release. Although it is likely they will respond to release, they may take a long time to attain post-release growth rates comparable to trees that were not suppressed and some trees may never do so. Trees taller than 5m in both class one and two should be carefully evaluated to determine if they are worth releasing. A LC ratio of at least of 50% and an HD ratio of not more than 80 (measured at 15cm above ground) are suggested thresholds to guide this evaluation. Trees taller than 10m, especially from vigor class 1, are unlikely to be worth releasing. The ability of taller trees to attain post-release growth rates comparable to trees that were not suppressed is likely to be lower, and lag time before response may be so long that it may be faster and involve less risk of stem failure to start with new regeneration.

The assessments and height thresholds regarding overstory recruitment and release potential for the four vigor classes are conservative estimates based on incomplete information. Complete information is rarely available in forest management, and management decisions have to be made with a combination of the best information available, knowledge of what is not known, and human judgement. Further research should be undertaken to empirically test these estimates to avoid unforeseen consequences.

Factors influencing vigor: individual tree level

The increasing difference in RVG between trees with high and low crown overlap as overstory stocking decreases supports the finding that light is the primary factor influencing understory growth at low lights levels but declines in importance as light increases (Carter and Klinka 1992, Wang et al. 1994, Drever and Lertzman 2001, Duchesneau et al. 2001). At low light levels the effect of small changes in sunfleck activity can have a large impact on growth (Chadzon 1988, Lieffers et al. 1999) that may overshadow the effects of crown crowding and not be detectable with visual methods or hemispherical photographs (Comeau 2000). This does not mean that crown crowding from intra-cohort competition and tall shrubs is not an important influence on growth or crown morphology in low light environments. Givnish (1988) theorizes that high intra-cohort competition levels force understory trees in low light environments to invest scarce carbon resources in growing upward to access available light, instead of remaining shorter and extending their crowns laterally. Greater height growth in low light results in higher HD ratios and lower vigor as the amount of carbon demanding, non-photosynthetic tissue is proportionally higher with increasing tree size. While results from this study show a trend of high crown overlap affecting HD ratios and live crown ratios at low light levels (Figure 10), the light measurements methods used in this study were not sufficiently precise to fully test this theory.

The relatively high R^2 values of low crown overlap light models are similar to those found by other investigators using percent of full sun light measures and relative or log transformed measures of growth with trees with little or no intra-cohort competition (Carter and Klinka 1992, Wright 1998, Drever and Lertzman 2001). The much lower R^2 values of high crown overlap models reflects the difficulty in explaining differences in growth when the relative increases in growth rates per increase in light levels are much lower, and other factors such as pests, pathogens, genetics, site differences, and measurement error play a proportionally larger role (Duchesneau et al. 2001, Canham et al. 2004).

The fact that using a 30% 3-dimensional or 50% 2-dimensional threshold of crown overlap as an indicator variable performed better than using it as a continuous variable suggests that either understory trees can withstand a certain level of crown crowding before growth reductions occur, or that effects of small changes in competition levels are not detectable within the range of other factors influencing growth or with the measurement techniques used. However, the fact that distant dependent neighborhood competition (NCI) models of crown overlap did not perform better than the 3-dimensional percent overlap method confirms the findings of Wagner and Radosevich (1991, 1998) that percent cover estimates are as good at predicting changes in growth as neighborhood models and suggests that more detailed measures of competition will not improve predictive power. Caution is advised in using the 2-dimensional crown overlap method, however. Occasionally a tree had lot of competition at the base of the live crown from short neighbors, but very little in the upper 2/3^{rds} of the live crown. These trees, although relatively uncommon in this data set, had a high percent crown overlap but little crown crowding in the majority of the crown. A way to account for this and make the 2-dimensional method more precise would be to estimate percent overlap at the base of the live crown and also halfway up the live crown and then average the two estimates together. Also, one of the main sources of measurement error in any of these approaches is including dead neighbors that have no current effect, but clearly influenced crown development of the sample tree in the past. Dead neighbors were not common in this study and were mostly found on the ground; and were not included in any analysis.

Similar to other studies (Table 1), 45% full sunlight was found to be the average level where understory trees with little intra-cohort competition could achieve vigor levels where recruitment into the overstory without further release is likely (vigor class four) (Figure 5, 6, 8 & 9). For vigor class three trees, this average is 35% full sunlight. For vigor classes one and two, the average was found to be 10-15% full sunlight. Below 10 % full sunlight, regeneration was scarce and of poor vigor. The linear relationship of measures of light and RVG, and the wide scatter in the models, is consistent with other studies on Douglas-fir saplings for the range of light levels sampled (Williams et al. 1999, Deisenhofer 2000, Drever and Lertzman 2001). Although Drever (2001) used a non-linear regression model, the relationship of height growth and log radial growth to percent full sun is almost linear for the site index that is closest to the stands sampled in this study. He attributes the wide scatter around the best fit line and high variability in growth at a given light level to genetics, mycorrhizal associations, previous periods of suppression, disturbance history, competition for resources, morphological differences, and micro-site factors. The variance introduced by using the regression model to predict RVG, as well as measurement error, are undoubtedly other factors in this study.

The linear relationship of light to RVG should not be extrapolated to trees smaller than the 1.4m cutoff used in this study. Other authors investigating Douglas-fir seedlings have found that growth increases linearly to a certain light threshold and then declines in slope thereafter (Carter and Klinka 1992, Mailly and Kimmins 1997, St.Clair and Sniezko 1999). This pattern is common for more shade tolerant conifer species of all size classes (Wright 1998), and suggests that Douglas-fir may grow equally well under partial overstories as in full sunlight at the seedling stage, at least on harsh sites. Once seedlings are established and able survive the summer drought, the asymptotic relationship then disappears. In mixed conifer forests of eastern Oregon and Washington, Seidel (1983) noted that Douglas-fir regeneration in clearcuts often failed and that the shelterwood system resulted in satisfactory regeneration. Plantations have been successfully established on prairie soils at Ft. Lewis (Foster, pers comm.). Natural regeneration, however, may have greater or equal survival and growth during the first few years after germination under partial canopies.

The strong relationship of visual open sky, weighted for southern exposure, to percent full sunlight from hemispherical photographs and the similar power in predicting response of RVG shows that visual estimates of crown cover or open sky can be a practical and efficient method when a high degree of accuracy is not needed, as long as consistency can be assured. Brandeis et al. (2001a) and Deisenhofer (2000) found similar results. Another advantage of visual methods is that tall shrubs or intra-cohort competition can be “looked through” when estimating percent openness of the overstory is the goal. The relative nature of VOS, however, makes it difficult to compare absolute light levels with other studies.

The inferiority of stand level density measures over light measures at predicting growth responses of individual trees is consistent with findings that density measures are weaker predictors of growth (Wampler 1994, Deisenhofer 2000, Brandeis et al. 2001b, Page et al. 2001) and not well correlated with light (Chan et al. 1997, Brandeis et al. 2001a, Aukema and Carey 2003). Similar to this study, Wampler (1994) found a quadratic relationship between overstory basal area and percent of maximum height growth with a similar wide but clear band in the data and sharp increase at a 100 ft^2/acre. This corresponds to roughly 125 SDI, which is slightly lower than the sharp increase in growth found at 150 SDI in this study (Figure 6b). These results indicate that 125-150 SDI (25-30% of full site occupancy, (Long 1985); 20-24 Relative Density (Curtis 1982)) represents a threshold where overstory density is low enough to begin to let enough light through for RVG to exceed 30% and create conditions for trees with a vigor category of 3 or 4. An upper threshold for class one and two trees appears to be around 275-300 SDI (54-59% full site occupancy; 44-48 Relative Density (Curtis 1982)) as less than 25% of class one and two trees were found above 275 SDI (Figure 8b). These SDI thresholds are line with conclusions from other studies (Table 1).

Factors influencing vigor: stand level

Overstory SDI has a strong influence on understory vigor at the stand level (Figure 11a). However, the moderate R^2 value shows that other factors are involved. The much higher R^2 values of the non-linear models in predicting stand average RVG for all trees and crop trees indicate that the variables included capture other important factors influencing understory vigor (Figure 11c). The fact that overstory SDI and shrub cover were weak or non-significant predictors of RVG at the individual tree level but important factors at the stand level, suggests that the stand level is a more appropriate scale to use SDI as the primary metric to analyze the growth consequences of the distribution of growing space. The power form of the model shows that the variables have multiplicative, and not additive, interactions.

Most of the signs and the proportional effect on RVG of the significant coefficients make biological sense. Overstory SDI is the dominant driver in the model confirming the basic idea that it is the main occupier of growing space (Oliver and Larson 1996). Understory SDI is also a significant factor. Stands with low overstory SDI but high understory stocking have lower than expected RVG. An extreme example of this is Recondo Johnson (Rj, Table 3), a stand with an evenly distributed overstory and intense understory regeneration and competition. It has an overstory SDI of 140, but an average crop tree RVG of only 26% due in large part to the understory SDI of 59. West wier (Ww, Table 3), in contrast, has an overstory SDI of 223 and a crop tree RVG of 23%, but only has an understory SDI of 7.

Understory SDI is a product of both trees per acre and average tree size. Larger understory tree size increases understory SDI and drives down average RVG in the model, which supports the hypothesis that larger trees need more growing space (Givnish 1988, Messier et al. 1999). For example, Rodomsky (Rd) has an overstory SDI of 226, a crop tree tpa of 19, and a crop tree RVG of 16% (Table 3). Somemore (Sm) has a higher overstory SDI of 252, a similar crop tree tpa of 15, but a crop tree RVG of 23%. While low percent shrub cover and a higher SDI plot ratio (ratio overstory SDI of plots with understory trees to SDI of all plots) account for part of this difference, the greater understory tree size in Rodomsky, and thus understory SDI, accounts for 3.5% of the difference. The average tree height is 7.4m, which is high for a stand with such a high level of overstory stocking.

Percent cover of tall shrubs substantially reduces understory RVG in the models, indicating the competitive effect that may other authors have shown (Chan and Walstad 1987, Cole and Newton 1987, Wagner and Radosevich 1991, Emmingham et al. 2000, Brandeis et al. 2001b). Low shrubs, on the other hand, increase RVG suggesting that they do not have a net negative competitive effect on trees and are perhaps a sign of greater moisture and/or light reaching the understory. Although examining wetter Douglas-fir forest types, Van Pelt and Franklin (1999) found a strong correlation between light reaching the understory and shrub cover. Shrubs communities are commonly used as indicators of soil moisture (Henderson et al. 1989, Harrington et al. 2003). If multi-collinearity is not the cause of the positive sign of low shrubs, and greater low shrub cover is indeed an indication of higher soil moisture, the results of this model may provide insight into the contradictory findings that Douglas-fir is more shade tolerant on drier sites (Carter and Klinka 1992, Bailey 1996, Chen et al. 1996, Williams et al. 1999) and more tolerant on wetter sites (Aztet and Waring 1970, Marshall 1986). At the same light level, greater soil moisture may increase growth potential of understory trees but also support more abundant and taller shrub communities. The net effect of greater soil moisture would thus depend on the height and moisture demand of the shrub communities present and their ability to compete for light and moisture with the understory cohort being sampled.

Despite the fact that the coefficients for crown overlap and the SDI plot ratio were not significant, their role in the model suggests that the horizontal distribution of both understory and overstory has an effect on the relationship of understory vigor and overstory stocking. Advanced regeneration often tends to establish in clumps that can lead to high levels of intra-cohort competition at relatively low per acre stocking levels. Clumps are often in canopy gaps, however. The positive sign of crown overlap in the model may be explained by the fact that the positive effect of the increased light overrides the negative effect of intra-cohort competition. Also, the effects of intra-cohort competition may be partially accounted for in the model by understory SDI.

Other authors have found that for the same amount of overstory stocking, a more clumped overstory distribution with gaps provides more microsites with light levels sufficient for Douglas-fir than a uniform distribution (Bailey and Tappeiner 1998, Lieffers et al. 1999, Coates et al. 2003, Drever and Lertzman 2003). Comparing several stands with similar overstory SDI confirms this (Table 3). Kalipso (KP) has an overstory SDI of 242, an average VOS of 36, and a crop tree RVG of 30% while Cherry Hill (CH) has an SDI of 163, VOS of 35, and a crop tree RVG of 29%. According to the model, the ability of Kalipso to have such a high RVG for its relatively high amount of overstory stocking is due to low understory stocking (5), low percent cover of tall shrubs (4%) and low SPR (70%). If understory stocking and tall shrubs are increased to levels more similar of other stands with the same level of overstory SDI, crop tree RVG is still 3-8% higher than these other stands. This patchy stand had the majority of its regeneration in gaps while parts of the stand with high overstory densities had no regeneration. The fact that it has such a high average VOS compared to other stands with similar levels of overstory SDI (Table 3) suggest that this clumpy distribution of overstory trees results in a higher average understory light level for similar levels of SDI.

Through sensitivity analysis, the model showed that to achieve an average crop RVG of 35% or a vigor category 3, the highest overstory SDI possible is 210 and the average SDI is 150. For a crop tree RVG of 50%, vigor category 4, the highest SDI is 170, whereas the average is 120. The higher levels of SDI needed to achieve 35 and 50% RVG predicted by the stand model compared to the individual tree model (Figure 6) is due to the fact the stand model is taking into account the overstory in the whole stand and not just overstory trees that are affecting understory trees. All stands had plots with no understory trees that increased average overstory SDI without influencing RVG. Although experimentation with the model did not involve values for predictor variables outside of the ranges found in the stands sampled, actual stands with a crop tree RVG above 36% were not found. The model is not a predictive model, and the results should be used only as general guidelines.

The results and overall structure of the model confirm the underpinnings of the stand level, multi-cohort growth model developed by O’Hara (1996) and O'Hara and Valappil (1999). Average vigor of an understory cohort is determined by the growing space available to the cohort divided by the number of trees in the cohort. Using leaf area index to measure growing space, the total available leaf area is apportioned between the overstory and understory cohorts to determine the leaf area available to a particular understory cohort. The model in this study uses SDI to measure growing space occupancy and includes shrubs and the spatial arrangement of the cohorts. The following diagram (Figure 12) explains this concept using the non-linear model form derived in this study.

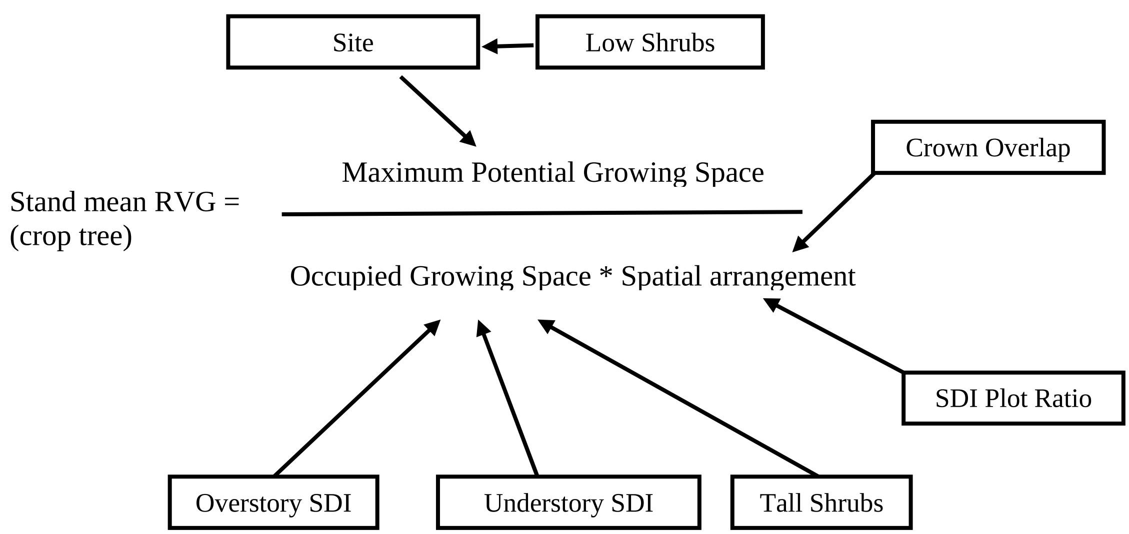


Figure 12 : Diagram of conceptual model of factors influencing vigor of understory regeneration.

This stand level model was developed from only 13 stands at a single point in time and cannot be used to predict the effects of treatments. The high R^2 value of the model is likely to be a product of having only 13 data points and five or six variables. With more stands, the R^2 value would likely decrease. However, the fact that between 85-90% of the variation in RVG was predicted with only overstory SDI, understory SDI, and tall or low shrubs, suggests that strong, stand level relationships between understory vigor, overstory and understory SDI, and shrub cover do exist. Until more stands are included, this model should be used as a conceptual model and a rough guide of the quantitative relationships between understory vigor and the predictor variables.

Separate from the stand level model, overstory SDI is well correlated with understory stocking, whether measured by tpa or SDI (10b). The exponential relationship suggests that as stands are opened up during future thinnings, natural regeneration will provide sufficient understory stocking levels to maintain adequate growing stock under current thinning regimes. Miller and Emmingham (2001) also found that natural regeneration provided sufficient growing stock in selection thinning systems in similar Douglas-fir forests. However, many gaps in the stands surveyed in this study had low understory stocking and understory crop tree stocking levels are currently on the low side for most of the stands (Table 3). Crop tree stocking should be monitored and a more detailed analysis of growing stock under different thinning regimes should be undertaken to ensure that growing stock is adequate.

Conclusions and Management Recommendations

To assess vigor of understory Douglas-fir, height growth, LC ratio, HD ratio, and crown density rating (a visual estimate or measured variable of crown density, such as number of internodal branches or branch length) can be combined together into a powerful indicator of vigor: relative volume growth (RVG). RVG allows for comparisons across a wide range of size classes, relates easy to measure growth metrics to volume growth, and provides managers with a concrete measure of how understory trees are growing compared to the maximum potential for that site. The qualitative crown density rating can be dropped if necessary with only a small loss in predictive power (Appendix B). Constructing a maximum volume growth curve and predictive regression models for a site, however, requires intensive sampling and an initial investment of time to reconstruct volume growth in the laboratory.

Understory tree vigor can also be assessed via a classification system that uses thresholds of height growth, HD ratio, and LC ratio to place trees into four vigor classes. This simpler system is sufficient for most management applications and can be easily integrated into most stand exam, marking, or cruising protocols. With some training, field technicians can quickly classify trees in the field using only visual estimates of these growth metrics, or by taking height and diameter measurements and visually estimating height growth and live crown ratio.

It is very likely that most of the Douglas-fir regeneration (vigor classes 1-3) found in this study will need release from overstory removal in order to recruit into the overstory. Although Douglas-fir appears to be able to maintain slow growth rates, reasonable LC ratios and HD ratios, and release potential in low light environments for several decades, it is unlikely that Douglas-fir can persist at slow growth rates in the understory for the many decades and centuries it would take for the overstory to be thinned by natural mortality. Understory trees from vigor class one are currently at some risk of mortality from suppression and growth rates of trees from higher vigor classes will decline as the overstory closes over time.

If released, however, evidence from this study and all other studies reviewed suggest that Douglas-fir will respond. In all but the most severely suppressed trees, released trees appear able to regain growth rates comparable with trees that were never suppressed, recover from high HD ratios, and become viable replacement trees. The lag time before response to release, degree of response, and decline in HD ratio after release will depend on the level of overstory removal, the degree of crown crowding from understory competition after release, and pre-release live crown ratio and growth rates. Trees in vigor classes one and two will likely take a period of time to respond, while class three and four will likely respond very quickly. Furthermore, risk of stem failure from high HD ratios and lag time before response to release appear to increase with increasing tree height. Trees taller than 5m in both vigor class one and two should be carefully evaluated to determine if they are worth releasing. A LC ratio of at least of 50% and an HD ratio of not more than 80 (measured at 15cm above ground) are suggested thresholds to guide this evaluation. Trees taller than 10m, especially from vigor class 1, are unlikely to be worth releasing.

At the individual tree level, dominant and co-dominant Douglas-fir with low levels of crown crowding (less than 50% 2-dimensional crown overlap) need an average of 45% full sunlight to achieve vigor levels where recruitment into the overstory without further release is likely (vigor class four). For vigor class three trees, this average is 35% full sunlight. For vigor classes one and two, the average was found to be 10-15% full sunlight. Below 10% full sunlight, regeneration is likely to be scarce and in vigor class one. SDI levels are 150 (30% full site occupancy; 24 Curtis Relative Density) or less to achieve vigor classes three and four, 150-275 for classes one and two, and 275+ (55% full site occupancy; 44 Curtis Relative Density) for scarce stocking and class one trees. These percent of full sunlight and SDI levels are means, however, and growth rates of individual trees will vary considerably for a given level of light or overstory density.

Trees with high levels of crown crowding (greater than 50% 2-dimensional crown overlap) require more light to achieve the same vigor classes, and this effect increases in higher light environments. Only in very high light environments do they reach 35% RVG (Figure 5 & 6). Even in low light environments, negative effects on HD ratios and live crown ratios are apparent (Figure 10). Without release from crown crowding, trees with greater than 50% crown overlap will suffer serious losses in potential volume growth. Pre-commercial thinning is recommended for crop trees that have crown overlap over 50% or are likely to before the next stand entry. Pre-commercial thinning should be done after overstory thinning treatments as harvesting will damage a proportion of crop trees.

While maintaining the overstory below 150 SDI is necessary for recruitment of Douglas-fir advanced regeneration into the overstory, entire stands do not need to be thinned to these low levels. Most volume growth and stand structure exists in the overstory and thus early, heavy thinning across an entire stand will result in a major loss of potential volume growth (O'Hara 1996). It can also result in intense natural regeneration or shrub colonization of open areas. Between approximately 150-275 SDI, understory Douglas-fir grows slowly but appears able to maintain its release potential as long as understory cohorts do not get too tall. To balance the tradeoff between total stand volume growth and vigor of regeneration, patchy or spatially heterogeneous stands can be created and maintained in a shifting mosaic.

A three stage progression of overstory treatment types is recommended for patches within a stand. First, some patches can be managed to maximize volume growth in the overstory for one or more stand entries with light thinning from below treatments that keep stocking levels over 275 SDI. Although some regeneration may establish after these light thinning entries, it should not be a primary treatment objective as regeneration establishment will be a focus of the second stage. In this second stage, the overstory should be opened up enough (150-275 SDI) for regeneration to establish and maintain at an average vigor of class two. Depending on stand conditions and the objectives of the landowner, overstory trees can be removed across all diameter classes or from below, and small gaps can be created. These two cohort patches can be maintained for several stand entries by progressively reducing overstory density towards 150 SDI which will allow the regeneration to keeping growing, albeit slowly, and maintain its release potential. Depending on how vigorous the regeneration cohort is, the patch should be moved to the third stage once the regeneration is between 5-10m in height. In this stage, overstory SDI should be reduced below 150 to provide enough light for regeneration to grow vigorously and recruit into the overstory. To maximize growth of the regeneration cohort, all the overstory trees should be removed in one entry. If a multi-layered canopy is a management goal, however, the overstory can be removed over several stand entries and some overstory trees can be indefinitely retained for long term structure. Clumped retention, rather than dispersed retention, should be used as it provides more micro-sites with high light levels for the same amount of overstory SDI (Lieffers et al. 1999, Drever and Lertzman 2003) and thus uses growing space more efficiently. A third cohort may establish after scarification from successive stand entries in areas of the patch that are not stocked with regeneration. Once the main regeneration cohort reaches commercial size, the patch can be moved back to the first stage and begin the cycle again. If some members of the original overstory cohort are retained, a three cohort structure is likely to be achieved in the next cycle, if it is not already present.

By ensuring that different patches within a stand are at different stages in the progression, a horizontally and vertically complex stand with multiple cohorts will be created. Although each patch may only have 1-3 cohorts, the patches put together will have more. Minimum patch size should be 0.25 ha (0.6 ac), as this appears to be the minimum gap size necessary for Douglas-fir to achieve high vigor levels in gaps (Ketchum 1994, Mailly and Kimmins 1997). Larger patch sizes, however, will be easier to manage. By varying patch size and the spatial arrangement of patch stages, a high degree of structural complexity can be created.

Active management of the regeneration cohort should be also considered during the second and third stages of overstory treatments. As described above, pre-commercial thinning and shrub control around crop trees has the potential to significantly increase vigor levels. While natural regeneration appears to be providing sufficient stocking under thinned understories, gaps captured by shrubs and grasses may need shrub control and or planting to ensure timely stocking and full utilization of growing space. Gaps occupied with native shrubs provide important wildlife habitat, but many gaps are filled with non-native Scotch Broom (*Cytisus scopariu)* in the stands inventoried in this study.

Prescriptions for individual stands will need to take into account the current vigor, height, crown crowding, spatial arrangement, and stocking levels of both overstory and understory cohorts, as well as shrub cover. Relatively uniform, even-age stands with high overstory SDI and little regeneration should be thinned to different densities throughout the stand to create a mix of stage one and two patches. Stage three patches can be added if large gaps are desired for wildlife habitat. Stands that already have a high level of patchiness can be treated by moving different patches to different stages depending on the stocking, vigor and height of the regeneration in each patch. Stands with overstory stocking below 150 SDI and high levels of understory competition will likely require a greater emphasis on pre-commercial thinning over further overstory removal to move the regeneration into vigor classes three and four. To provide an approximate assessment of stands at the patch level, inventory data can be broken down by plot to show the distribution of overstory SDI and understory trees per acre, average height, relative volume growth, and crown overlap. Displaying this information on stand map using GIS can provide an idea of the spatial distribution of different cohorts (Appendix F).

To help managers determine the stand level tradeoffs between structural goals, wood production needs, habitat value, understory vigor, and risk tolerance, stand level models that are based on existing inventory information and accessible to managers are needed (Lieffers et al. 1999, Hasenauer and Kindermann 2002). While light based models are clearly superior at predicting growth of advanced regeneration at the individual tree level, density based models appear to work well at the stand level (O'Hara 1996). Although spatially explicit models are powerful tools to understand forest ecosystems and the effects of experimental treatments, they will require substantial investment of time and resources for development. At the same time, traditional inventory metrics and growth models designed for even-age management are often not sufficient for uneven-age management. Incorporating light measurements and simple metrics for intra-cohort competition, spatial distribution of cohorts, and shrub cover into distant independent stand models shows promise to make them versatile and powerful enough for most management needs.

The results of this study support the conclusions of other investigators that uneven-age management is possible with Douglas-fir on dry sites using two-aged shelterwood systems (Seidel 1983b, Tesch and Korpela 1993), group selection (Coates and Burton 1997), or single tree selection systems that include heavy thinning at some point (Deisenhofer 2000, Miller and Emmingham 2001). By combining elements of all three systems, structurally complex, multi-cohort stands can be created that also produce significant wood volume. These stands will be structurally different from west-side, late-successional forests that contain shade tolerant conifers, however, and require ongoing, periodic thinning to maintain.

List of References

Anderson, W. W., A. O. Ness, and A. C. Anderson. 1955. Soil survey of Pierce County, Washington. USDA Soil Conservation Service, Washington, D.C.

Aukema, J. E., and A. B. Carey. 2003. Management History and thinning affect growth and survival of tree seedlings planted underneath experimentally thinned Douglas-fir. A report to Ft. Lewis. USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington.

Aztet, T., and R. H. Waring. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Can. J. Bot. **48**:2163-2167.

Bailey, J. D. 1996. Effects of Stand Density Reductions on Structural Development in Western Oregon Douglas-fir forests - A reconstruction study. PhD dissertation. Oregon State University, Corvallis, OR.

Bailey, J. D., and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40-100 years Douglas-fir stands in western Oregon. For. Ecol. Manage **108**:99-113.

Becker, R. 1995. Operational considerations of implementing uneven-aged management. *in* K. L. O'Hara, editor. Uneven-aged Management: Opportunities, Constraints, and Methodologies. Montana Forest and Conservation Experiement Station, Missoula, Montana.

Biging, G. S., and M. Dobbertin. 1995. Evaluation of competition indices in individual tree growth models. Forest Science **41**:360-377.

Bitterlich, W. 1947. Measurement of basal area per hectare by means of angle measurement. Allg. Forest. Holzwirtsch, Ztg. **58**:94-96.

Brandeis, T. J., M. Newton, and E. C. Cole. 2001a. A comparison of overstory density measures for describing understory conifer growth. For. Ecol. Manage **152**:149-157.

Brandeis, T. J., M. Newton, and E. C. Cole. 2001b. Underplanted conifer seedling survival and growth in Douglas-fir stands. Can. J. For. Res. **31**:302-312.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**:620-631.

Canham, C. D., P. T. LePage, and D. K. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading vs. crowding. Can. J. For. Res. **34**:778-787.

Carey, A. B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forests inducing spatial heterogeneity with variable density thinning. Forestry **76**:127-136.

Carlson, C. E., and W. C. Schmidt. 1989. Influence of overstory removal and western spruce budworm defoliation on growth of advance conifer regeneration in Montana. **Res. Paper INT-409**.

Carter, R. E., and K. Klinka. 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western redcedar in coastal British Columbia." For. Ecol. Management **55**:87-105.

Chadzon, R. L. 1988. Sunflecks and their importance to understory plants. Advanced Ecological Research **18**:1-63.

Chan, S., and J. D. Walstad. 1987. Correlations between overtopping vegetation and development of Douglas-fir saplings in the Oregon Coast Range. Western Journal of Applied Forestry **2**:117-119.

Chan, S. S., M. Bailey, D. Karnes, R. Metzger, and W. Kastner. 1997. Riparian Silviculture in the Oregon Coast Range; A partnership between management and research, pp 190-198. USDA Forest Service, Northeastern Forest and Range Experiment Station, General Tech Report **GTR 238**.

Chen, H. Y. H., and K. Klinka. 1997. Light availability and photosynthesis of Pseudotsuga menziesii seedlings grown in the open and in the forest understory. Tree Physiol. **17**:23-29.

Chen, J. M., K. Klinka, and G. J. Kayahara. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established Pinus contorta and Pseudotsuga menziesii var. glauca saplings. Can. J. For. Res. **26**:1149-1157.

Coates, D. K., and P. J. Burton. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage **99**:337-354.

Coates, D. K., C. D. Canham, M. Beaudet, D. L. Sachs, and C. Messier. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage **186**:297-310.

Cole, E. C., and M. Newton. 1987. Fifth-year responses of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. **17**:181-186.

Comeau, P. 2000. Measuring light in forests. British Columbia Ministry of Forests Extension Notes.

Curtis, R. O. 1982. A simple index of stand density for Douglas-fir. Forest Science **28**:92-94.

Curtis, R. O. 1998. Selective Cutting in Douglas-fir. Journal of Forestry **96**:40-46.

Curtis, R. O., D. S. DeBell, C. A. Harrington, D. P. Lavender, J. B. St.Clair, J. C. Tappeiner, and J. D. Walstad. 1998. Silviculture for multiple objectives in the Douglas-fir Region. USDA Forest Service, Gen. Tech. Rep. **PNW-GTR-435**.

Deisenhofer, F. U. 2000. Influence of light on the growth of advance regeneration in the understory of Douglas-fir dominated forests in western Oregon. Masters. Oregon State University, Corvallis.

Drever, C. R., and K. P. Lertzman. 2001. Light growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Can. J. For. Res. **31**:2124-2133.

Drever, C. R., and K. P. Lertzman. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Can. J. For. Res. **33**:137-146.

Duchesneau, R., I. Lesage, C. Messier, and H. Morin. 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. For. Ecol. Manage **140**:215-225.

Emmingham, B., S. Chan, D. Mikowski, P. Owston, and B. Bishaw. 2000. Silviculture practices for riparian forests in the Oregon Coast Range. Oregon State University, College of Forestry, Forest Research Laboratory, Corvallis, OR.

Emmingham, W. H. 2002. Status of uneven-aged management in the Pacific Northwest, USA. Forestry: An International Journal of Forest Research **75**:433-436.

Foster, J. R., and S. E. Shaff. 2003. Forest colonization of puget lowland grasslands at Fort Lewis, Washington. Northwest Science **77**:283-296.

Franklin, J. F., D. R. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting. Pages 111-140 *in* J. F. Franklin, editor. Creating a forest for the 21st century: the science of ecosystem management. Island Press, Washington, D.C.

Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyser (GLA), Version 2.0: Imaging software to extract canopy structure and gap light light transmission indices from true-colour fisheye photographs Copyright 1999. Inf. Rep. BC-X-373, Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Frazer, G. W., J. A. Trofymow, and K. P. Lertzman. 1997. A method for estimating canopy openess, effective leaf area index, and photosynthetically active photon flux density using hemipherical photography and computerized image analysis techniques. Inf. Rep. BC-X-373, Canadian Forest Service, Pacific Forest Center.

Gersonde, R. F. 2003. Developing a hybrid growth model for multiaged Sierra Nevada mixed-conifer forests. PhD Dissertation. University of California, Berkeley, Berkeley.

Givnish, T. J. 1988. Adaptation to Sun and Shade: A whole-plant perspective. Aust. J. Plant Physiology **15**:63-92.

Gordon, J. C. 1994. From vision to policy: a role for foresters. J. Forestry **92 .**16 - 19.

Harrington, C. A., K. R. Buermeyer, L. C. Brodie, and B. W. Wender. 2003. Factors influencing growth and flowering of understory plants in conifer stands in western Washington. *in* Proceeedings from the wood compatibility initiative workshop, N 17.

Hasenauer, H., and G. Kindermann. 2002. Methods for assessing regeneration establishment and height growth in uneven-aged mixed species stands. Forestry **75**:385-394.

Helms, J. A., and Standiford. 1985. Predicting release of advanced reproduction of mixed conifer species in California following overstory removal. Forest Science **31**:3-15.

Henderson, J. A., D. H. Peter, R. D. Lesher, and D. C. Shaw. 1989. Forest plant associations of the Olympic National Forest. USDA Forest Service, Pacific Northwest Region **R6 ECOL Technical Paper 001-99**.

Herman, R. K., and D. P. Lavender. 1990. *Psuedostsuga Menziesii* (Mirb.) Franco. Pages 527-540 *in* Silvics of North America. USDA Forest Service Agric. Handbook 654, Washington, D.C.

Howard, G., and M. Newton. 1984. Overtopping by successional Coast Range vegetation slows Douglas-fir seedlings. Journal of Forestry **82**:178-180.

Hunter, M. G. 2001. Communiqué No. 3: Management in young forests. Cascade Center for Ecosystem Management, Corvallis, Oregon.

Issac, L. A. 1956. Place of partial cutting in old-growth stands of the Douglas-fir region. USDA Forest Service, Res. Pap. **PNW-16**:48p.

Issac, L. A., and E. J. Dimock 1958. Silvicultural Characterisitcs of Doulgas-fir. USDA Pacific Northwest Forest and Range Experiment Station **Silvical Series N0. 9**.

Ketchum, S. J. 1994. Douglas-fir, grand fir and plant community regeneration in three silvicultural systems in Western Oregon. Masters thesis. Oregon State University, Corvallis, OR.

King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. No. 8, Weyerhaeuser Forestry Paper, Weyerhaeuser Forestry Research Center, Centralia, WA.

Kneeshaw, D. D., H. Williams, E. Nikinmaa, and C. Messier. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. Can. J. For. Res. **32**:255-265.

Kobe, R. K., and D. K. Coates. 1997. Models of saping mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**:227-236.

Kohm, K. A., and J. F. Franklin. 1997. Creating a forest for the 21st century: the science of ecosystem management. Island Press, Washington D.C.

Kollenberg, C. L., and K. L. O'Hara. 1999. Leaf area and tree increment dynamics of even-aged and multiaged lodge pole pine stands in Montana. Can. J. For. Res. **29**:687-695.

Lieffers, V. J., C. Messier, K. J. Stadt, F. Gendron, and P. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. **29**:796-811.

Long, J. N. 1985. A practical approach to density management. Forestry Chronicle **61**:23-27.

Long, J. N. 1995. Using stand density index to regulate stocking in uneven-aged stands. *in* K. L. O'Hara, editor. Uneven-aged Management: Opportunities, Constraints, and Methodologies. Montana Forest and Conservation Experiement Station, Missoula, Montana.

Long, J. N., and T. W. Daniel. 1990. Assessment of growing stock in uneven-aged stands. Western Journal of Applied Forestry **5**:93-96.

Mailly, D., and K. P. Kimmins. 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* along a light gradient:resource allocation and morpholigcal acclimation. Canadian Journal of Botany **75**:1424-1435.

Malcolm, D. C., W. L. Mason, and G. C. Clarke. 2001. The transformation of conifer forests in Britain: regeneration, gap size and silvicultural systems,. Forest Ecology and Management **151**:7-23.

Maquire, D. A., and A. Kanaskie. 2002. The ratio of live crown length to sapwood area as a measure of crown sparseness. Forest Science **48**:93-100.

Marshall, J. D. 1986. Drought and shade tolerance interact to cause fine root mortality in Douglas-fir seedlings. Plant Soil **91**:51-60.

McCaughey, W. W., and D. E. Ferguson. 1988. Response of advanced regeneration to release in the inland mountain west: a summary. USDA Forest Service, Gen. Tech. Rep. **INT-GTR 243**:255-266.

Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly, and M. J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. **29**:812-823.

Miller, M., and B. Emmingham. 2001. Can selection thinning convert even-age douglas-fir stands to uneven-age structures? Western Journal of Applied Forestry **16**:35-43.

Monserud, R. A., and A. P. Robinson. 2003. How adaptable are forest growth models for simulating alternative silvicultures in the Northwest. *in* Proceeedings from the wood compatibility initiative workshop, N 17. USDA, Forest Service, Pacific Northwest Research Station.

Munger, T. T. 1950. A look at selective cutting in Douglas-fir. Journal of Forestry **48**:97-99.

Mustard, J., and G. Harper. 1998. A summary of the available information on the height to diameter ratio. Forest Dynamics Research, Research Branch, B.C. Ministry of Forests, Victoria, B.C.

Newton, M., and P. Comeau. 1990. Control of competing vegetation. Pages 256-265 *in* D. Winston, editor. Regenerating British Columbia's Forests. U.B.C. Press, Vancouver, B.C.

O'Hara, K. L. 1996. Dynamics and stocking-level relationships of multi-aged Pondersoa Pine Stands. Forest Science, Monograph 33 **42**:1-34.

O'Hara, K. L., and N. I. Valappil. 1999. Masam - a flexible stand density management model for meeting diverse structural objectives in multi-aged stands. For. Ecol. Manage **118**:57-71.

Oliver, C. D. 1995. Uneven-age Stand Dynamics. *in* K. L. O'Hara, editor. Uneven-aged Management: Opportunities, Constraints, and Methodologies. Montana Forest and Conservation Experiement Station, Missoula, Montana.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. John Wiley & Sons, Inc., New York.

Oliver, W. W. 1985. Growth of California red fir advance regeneration after overstory removal and thinning. USDA Forest Service, Research Paper **PSW-RP-180**:1-6.

Page, L. M., A. D. Cameron, and G. C. Clarke. 2001. Influence of overstorey basal area on density and growth of advanced regeneration in Sitka spruce in variably thinned stands. For. Ecol. Manage **151**:25-35.

Perdue, V. 1997. Land use and the Fort Lewis prairies. Pages 17-28. *in* K. Ewing, editor. Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, WA.

Ralston, R., J. Buongiorno, S. Benedict, and F. J. 2003. Westpro: A computer program for simulating uneven-aged Douglas-fir stand growth and yield in the Pacific Northwest. USDA Forest Service, General Tech Report **PNW-GTR-574**.

Reineke, L. H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. **46**:627-639.

Ruel, J.-C., C. Messier, R. Doucet, Y. Claveau, and P. Comeau. 2000. Morphological indicators of growth response of coniferous advance regeneration to overstory removal in the boreal forest. The Forestry Chronicle **76**:633-642.

Seidel, K. W. 1983a. Growth of suppressed grand fir and shasta red fir in central Oregon after release and thinning 10-year results. USDA Forest Service, Research Note **PNW-RN-404**.

Seidel, K. W. 1983b. Regeneration in mixed conifer and Douglas-fir shelterwood cuttings in the cascades range of Washington. USDA Forest Service, Research Paper **PNW-RP-314**.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The Practice of Silviculture, 9th edition. John Wiley & Sons.

SPSS, I. 2003. SPSS for Windows, version 12.0 ed. SPSS, Inc. Chicago, Ill.

St.Clair, J. B., and R. A. Sniezko. 1999. Genetic variation in response to shade in Coastal Douglas-fir. Can. J. For. Res. **29**:1751-1763.

Tappeiner, J. C., W. H. Emmingham, and H. D. E. 2002. Silviculture in the Oregon Coast Range forests. Pages 172-190 *in* G. E. Wells, editor. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Tappeiner, J. C., D. P. Lavender, J. D. Walstad, R. O. Curtis, and D. S. DeBell. 1997. Silvicultural systems and regeneration methods:current practices and new alternatives. *in* J. F. Franklin, editor. Creating a forest for the 21st century: the science of ecosystem management. Island Press, Washington, D.C.

Tesch, S. D., and E. J. Korpela. 1993. Douglas-fir and white fir advance regeneration for renewal of mixed-conifer forests. Can. J. For. Res. **23**:1427-1437.

Van Pelt, R., and J. F. Franklin. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. Ecological Applications **9**:504-512.

Wagner, R. G., and S. R. Radosevich. 1991. Neighborhood predictors of interspecfic competition in young Douglas-fir plantations. Can. J. For. Res. **21**:821-828.

Wagner, R. G., and S. R. Radosevich. 1998. Neighborhood approach for quantifying interspecific compeition in coastal Oregon forests. Ecological Applications **8(3)**:779-794.

Wampler, M. 1994. Growth of Douglas-fir under partial overstory retention. M.S. thesis. University of Washington, Seattle, WA.

Wang, G. G., H. Qian, and K. Klinka. 1994. Growth of *Thuja plicataI* seedlings along a light gradient. Canadian Journal of Botany **72**:1749-1757.

Waring, R. H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advanced Ecological Research **13**:325-354.

Williams, H., C. Messier, and D. D. Kneeshaw. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Can. J. For. Res. **29**:222-231.

Wilson, J. S., and C. D. Oliver. 2000. Stability and density management in Douglas-fir plantations. Can. J. For. Res. **30**:910-920.

Wonn, H. T., and K. L. O'Hara. 2001. Height:diameter ratios and stability relationships for four northern Rocky Mountain tree species. Western Journal of Applied Forestry **16**:87-94.

Wright, E. F., D. D. Canham, and K. D. Coates. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. **30**:1571-1580.

Wright, E. F., Coates,K.D., Canham,D.D.,Bartemucci,P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. **28**:871-886.

Zar, J. H. 1999. Biostatiscal Analysis, 4th ed. edition. Simon & Schuster, Upper Saddle River, NJ.

Appendices

Appendix A

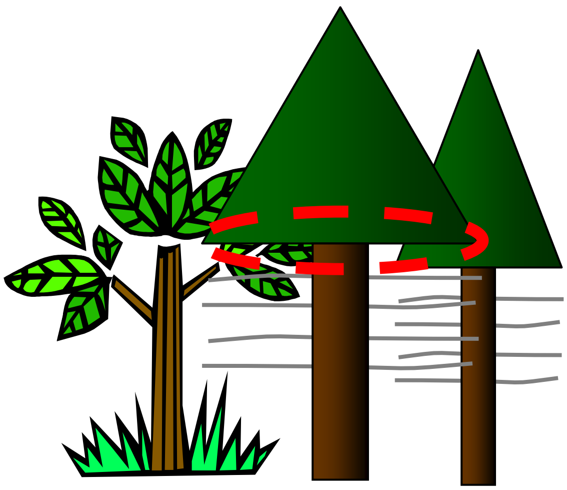
Crown metrics and criteria used to estimate crown density rating. The last 3 years of growth was examined and averaged together. Trees were rated based on which category they met the most number of criteria for.

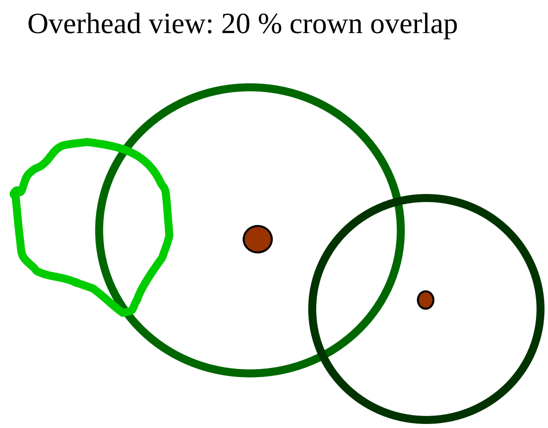
Rating	Branch length (cm)	Branch thickness (mm)	# of Internodal buds and branches	# of Whorls
1	<=10	<=1.5	<=4	3-4
2	11-15	1.6-2.5	5-10	3-4
3	15-24	2.6-3.5	5-10	5
4	25-34	3.6-4.5	11-15	5-6
5	35+	4.6+	16+	5-6

\

Appendix B

Diagram of crown overlap method of measuring crown crowding from intra-cohort competition and tall shrubs.



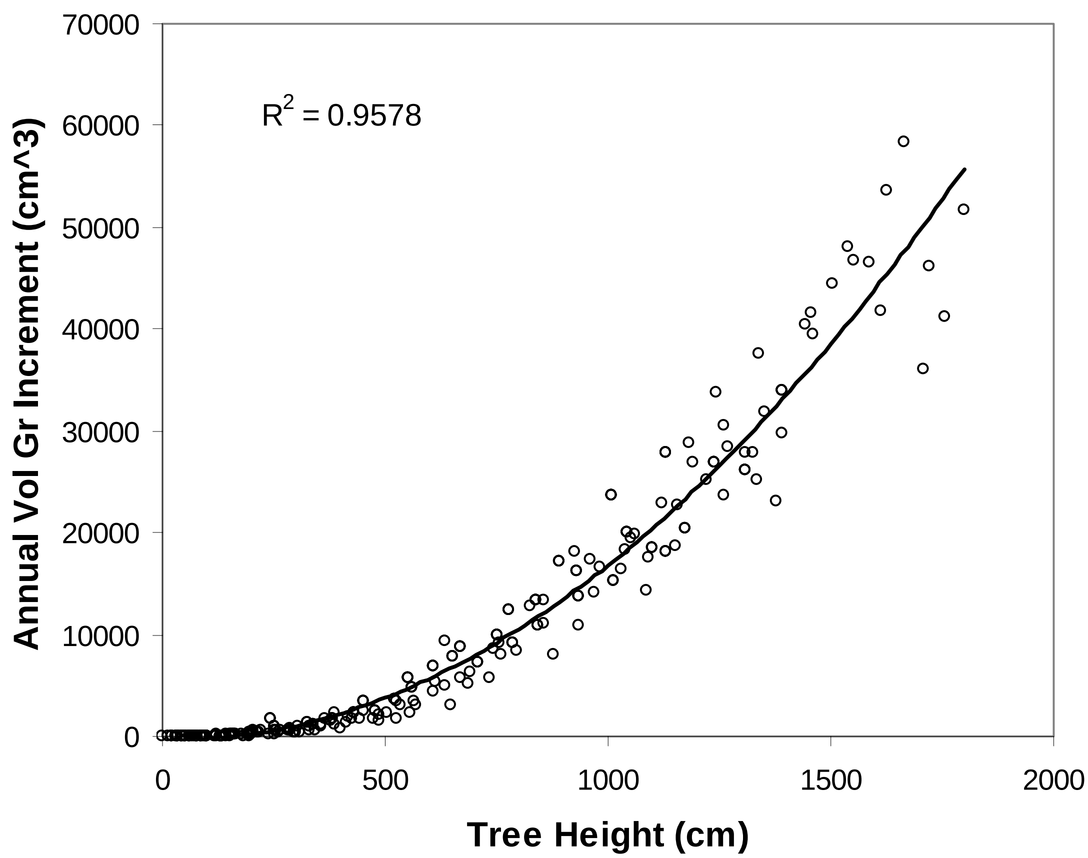


Appendix C

Scatterplot and fitted regression line for maximum site potential height (Ht) to volume growth curve. Data is from 19 naturally regenerated, open grown “best” trees growing near the study sites on the same soil type. Each data point represents the annual volume growth increment for a single height of a tree. Multiple data points for each of the 19 trees are included.

Annual volume growth increment (cm^3/yr) = *0 .018(Ht)*^{2} *- 0.27(Ht) - 466.74*

(R^2= 0.96, p<0.0001)



Appendix D

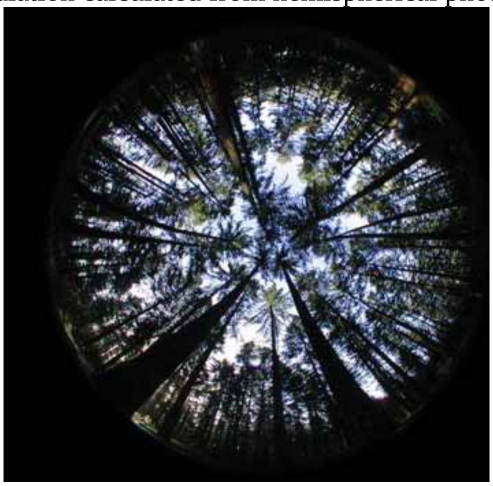
Relative volume growth regression without crown density rating. Live crown ratio drops out of the model.

$$\textit{Predicted RVG} = 1.721 - 0.367\ \textit{ln(HD Ratio)} + 0.005\ \textit{HG(cm)} - 0.0001\ \textit{Ht(m)}$$

(R^2= 0.86, SE=0.064, p<0.0001, all coefficients are significant p<0.001)

Appendix E

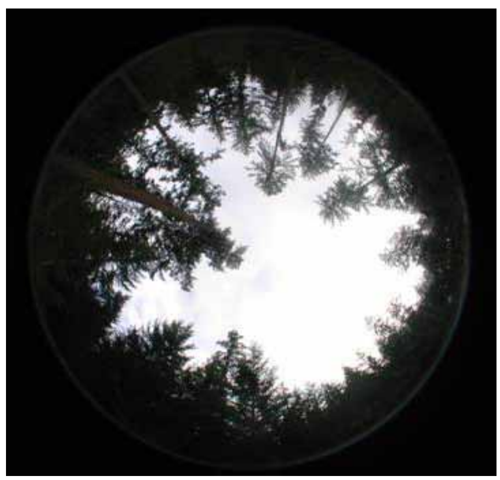
Examples of hemispherical photos of 4 vigor classes. Percent full sun is percent of total solar radiation calculated from hemispherical photographs.



Vigor Class 1: 12% Full Sun

Vigor Class 2: 25% Full Sun

Vigor Class 3: 43% Full Sun



Vigor Class 4: 67% Full Sun

Appendix F

Sample diagram of plot layouts for Kalipso stand. Number above and to left of point shows Tpa of understory crop trees and percent below and to left of points is average relative volume growth of the understory crop trees.