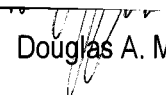AN ABSTRACT OF THE THESIS OF

Alexa K. Michel for the degree of Master of Science in Forest Science presented on January 27, 2005

Title: Morphological Characteristics of Ponderosa Pine and Lodgepole Pine Regeneration Nine Years after Stand Density Reduction at Three Sites in Central Oregon

Abstract approved

Douglas A. Maguire

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Without the natural occurrence of fire in ponderosa pine forests of the western US, lodgepole pine has started to dominate regeneration in many forest stands and may be gradually replacing ponderosa pine over time. This development, however, conflicts with recent efforts in this region to restore old-aged, open ponderosa pine forests, and active management may be needed to ensure the establishment and survival of ponderosa pine. The objectives of this study were to test the effects of various stand densities on ponderosa pine and lodgepole pine regeneration between 0.1 and 1.3 m in height, compare their seedling density, morphological characteristics, and height growth rates and determine the best morphological predictors of height growth at three sites in central Oregon.

Ponderosa pine seems more persistent in forest understory conditions than lodgepole pine and a high percentage of ponderosa pine seedlings originated from advance regeneration with ages of more than 30 years commonly measured in these seedlings. Lodgepole pine seedlings, on the other hand, seemed to have established primarily after stand density reduction, as indicated by their younger minimum ages and low survival of tall seedlings, especially at high overstory densities. After stand density reduction, high rates of seedling establishment, rapid height growth and rapid crown development seem to enable this species to more quickly occupy growing space than ponderosa pine.

The morphological variables best predicting absolute height growth in both species and at all three sites were absolute height growth in the previous year, the number of needle fascicles on the main stem, stem diameter at the root collar, and initial seedling height. In addition to initial seedling height and in addition to initial seedling height and overstory density, the best predictors were the number of needle fascicles on the main stem and needle density on the main stem and terminal leader. In general, there were significant effects of species, initial seedling height, and overstory density on morphological characteristics and height growth.

Silvicultural treatments should consider the effects that different stand densities have on the competitive ability of ponderosa pine and lodgepole pine. Light and frequent reductions in stand density that leave significant residual canopy in these stands (>20 m²/ha), may be more favorable to ponderosa pine than to lodgepole pine regeneration. Conversely, after a higher stand density reduction more growing space is available to seedlings in the absence of serious competition with understory vegetation and may be a competitive advantage of lodgepole pine over ponderosa pine. This advantage may last into maturity and conflict with restoration efforts by inevitably changing the structure and dynamics of these ponderosa pine forests.

Morphological Characteristics of Ponderosa Pine and Lodgepole Pine Regeneration

Nine Years after Stand Density Reduction at Three Sites in Central Oregon

by

Alexa K. Michel

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TABLE OF CONTENTS

Chapter Three: Height Growth Responses of Ponderosa Pine and Lodgepole Pine Regeneration Nine Years after Stand Density Reduction at Three Sites in Central Oregon

LIST OF FIGURES

LIST OF TABLES

Morphological Responses of Ponderosa Pine and Lodgepole Pine Regeneration Nine Years After Stand Density Reduction at Three Sites in Central Oregon

Chapter One: Introduction

Background

Ecosystem Dynamics in Ponderosa Pine and Lodgepole Pine Forests in Central Oregon

Fire exclusion since the 1900s has resulted in major changes in forest ecosystems in the Pacific Northwest, threatening their structural and functional attributes, e.g. species diversity, habitat, productivity, and stability. The alteration of successional patterns has led to an increased risk of high-intensity fire, insect and disease damage, and severe competition between trees and between trees and other vegetation. These changes are especially dramatic in forests long dominated by shade-intolerant species that depend on large-scale catastrophic disturbances such as ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *ponderosa*) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.) (Walker 1999, Steele 1994).

Ponderosa pine is the most widely distributed pine species in the United States, and it is the primary species used for timber in central Oregon. Although it is considered a shade-intolerant species and a pioneer that depends on large-scale disturbances for regeneration, it often appears to occur in uneven-aged stands (Walker 1999). These stands, however, commonly consist of a mosaic of even-aged cohorts (Oliver and Ryker 1990). Ponderosa pine produces seeds after 16-20 years (Minore and Laacke 1992) and bears significant seed crops at only irregular intervals of about 4-5 years (Barrett 1979).

Lodgepole pine is the most widely distributed conifer in western North America with extreme ecological and genetic variability. The subspecies *latifolia* is a fast growing shade-intolerant pine species, even more shade-intolerant than ponderosa pine (Spurr and Barnes 1980, p. 385). Lodgepole pine produces serotinous cones (i.e. high temperatures lead to the opening of cones and distribution of seeds), and it seeds prolifically after fire when the mineral

soil is exposed. Often, regeneration occurs in gaps leading to small groups of even-aged seedlings in an uneven-aged matrix of mixed species (Volland 1985), but in general, it is found in dense pure stands. Lodgepole pine produces a high abundance of seeds beginning at an early age of 5-10 years (Lotan and Critchfield 1990).

In the absence of large-scale disturbances, lodgepole pine often fails to regenerate in forest understory conditions. As a result of fire or logging in ponderosa pine forests, however, dense stands of lodgepole pine can establish and prevent establishment of any other conifer in the absence of further catastrophic disturbance (Volland 1985). Its behaviour after fire has been called aggressive (Wheeler and Critchfield 1985), and it is regarded as highly invasive (Rejmánek and Richardson 1996). Lodgepole pine is a rather short-lived species, and heavy disturbances at frequencies less than 15-20 years are critical for its persistence relative to other species that are considered long-lived, shade-tolerant, and sensitive to perturbations but slow growing (Volland 1985). If lodgepole pine is present in a cone-bearing age on the site, site preparation techniques such as underburning, slash piling, or strip scarification can provide conditions conducive to establishment (Lotan and Critchfield 1990, Crossley 1976). However, in young stands that are composed of fire-tolerant species such as Douglas-fir, western larch, or ponderosa pine, underburning can be a measure to select against the more fire sensitive lodgepole pine. On very wet, cold, or dry sites, lodgepole often grows in a mixture with other species and its active removal from the site to promote more valuable species will not be cost-effective (Volland 1985). At a later stand age, precommercial thinning lodgepole pine or simply accepting lodgepole as dominant are management options to be considered. However, fire and insect susceptibility of dense lodgepole pine stands, the species' lower commercial value, and recent restoration efforts in ponderosa pine forests make lodgepole a less favorable option if ponderosa pine is the alternative.

Without naturally occurring fires, large numbers of lodgepole pine seedlings have established in many ponderosa pine stands. Lodgepole pine may start to dominate the stand if active management does not ensure the establishment and survival of ponderosa pine regeneration. To better judge silvicultural options regarding future desirable stand structures and yield, the amount, dynamics, and spatial pattern of natural regeneration of both species need to be quantified.

Silvicultural Options for Regenerating Ponderosa Pine Forests

The shift to forest ecosystem management in recent years has led to increased scientific attention on responses of tree regeneration to partial forest overstory reductions under various silvicultural systems. Because of the relative shade-intolerance of ponderosa and lodgepole pine, traditional management calls for removing all overstory trees to maximize seedling growth. However, after canopy reduction, competition from shrubs like manzanita (*Arctostaphylos patula* Greene) and ceanothus (*Ceanothus velutinus* Dougl. ex. Hook.) can be as harmful to newly germinated seedlings as a dense overstory. Seeds of these understory species can survive many years in the ground, germinate quickly and grow vigorously after canopy opening, resulting in severe competition to tree regeneration (Miller 1988, White 1987, Barrett 1970, Zavitkovski and Woodard 1970). In central Oregon, regeneration of pine is also difficult because of climatic extremes, low precipitation and young, poorly developed soils that are covered with pumice from historic volcanic activity and that have low water holding capacity (Hermann and Petersen 1969). Thinning treatments and promotion of advance regeneration may therefore be a reasonable option in these forest ecosystems. On poor to moderate ponderosa pine sites, these management options can provide shelter from severe climatic conditions and inhibit competing vegetation by means of a residual overstory canopy.

Environmental Factors Affecting the Establishment and Growth of Regeneration in Ponderosa Pine and Lodgepole Pine Forests and the Role of Advance Regeneration

Microclimate beneath a closed canopy and its influence on tree regeneration differs from open habitat. In the forest understory, for example, air and soil temperature extremes decline, light and water availability are reduced, spectral composition is altered (e.g. red / far red ratio), and wind speed is diminished (Huggard 2002, Kremsater and Bunnell 1999, Cadenasso et al. 1997, Chen et al. 1995, Chen et al. 1993). Advance regeneration is a term that describes seedlings and small saplings that develop in forest understory conditions and can survive for many years until a disturbance in the overstory canopy releases them to grow into the canopy (Tesch and Korpela 1993). It plays a crucial role in the regeneration of shade-tolerant species, but it has received relatively little attention in the management of light-demanding species such as lodgepole pine and ponderosa pine. Pacific silver fir *(Abies amabilis* Dougl. ex. Loud.*)* is one

example of an extremely shade-tolerant species. Seedlings of this species beneath a forest canopy and with a height of less than 1.0 m were over 100 years old (Utzig und Herring 1974 in Oliver and Larson 1996). In contrast, southern pine seedlings survive only one or two growing seasons beneath a closed canopy (Oliver and Larson 1996).

Various studies have addressed inter- and intraspecific strategies in genetic adaptation and phenotypic acclimation of species to forest understory conditions (review by Ruel et al. 2000). Survival and growth of plants in the shade are enabled by responses not only at the leaf-level but also at the shoot-, crown-, and whole-plant levels (Messier et al. 1999a, Kobe and Coates 1997, Givnish 1988). Beaudet et al. (2000) noted that whole-plant level carbon gain seems to be a better indicator for growth and survival of a species than leaf level photosynthesis. For example, canopy attributes such as leaf inclination and clumping influence light absorption at constant values of LAI (i.e. leaf area index - foliage area per ground area), thereby determining the average amount of light intercepted by a given unit of foliage area (Niinemets and Kull 1995). However, physiological acclimations are also important: for example, LMA (leaf dry mass per unit leaf area), generally plays an important role in whole-canopy carbon acquisition, and its plasticity is an important feature of shade-tolerant species (Niinemets 1998, Niinemets and Kull 1998). In comparison to morphological characteristics, physiological processes are more dynamic, enabling species to respond quickly to changes in resource availability.

Pine species can tolerate closed canopy conditions, but overall their shade-tolerance is low. Acclimation mechanisms are generally more pronounced in shade-adapted species as they experience a range of different environmental conditions during their life-span. Their ability to change physiological and morphological characteristics after release from the overstory is, therefore, essential for survival and reproductive success (Claveau et al. 2002, Messier et al. 1999b, Williams et al. 1999, Chen et al. 1996). Messier (2003) suggested that shade-tolerant species modify mainly their biomass allocation, morphology, and growth pattern to maximize the capture of the growth-limiting resources, whereas shade-intolerant species modify primarily their physiological activity. In general, the ability of advance regeneration to endure conditions in the understory is not only dependent on their light and water use efficiency, but also on a variety of "post-photosynthetic processes" such as carbon partitioning, respiration, and allocation to sinks in different parts of the whole plant (Farrar 1999).

Although some measure of canopy openness may be better correlated with light conditions on the forest floor than basal area, particularly in structurally diverse stands (Chrimes 2004, Mitchell and Popovich 1997), stand basal area can be very effective for measuring the effects of overstory trees on seedbed conditions, light, understory composition, and other biotic and abiotic factors. As a result, basal area is strongly correlated with seedling height growth (Wampler 1993) and probably success of seedling establishment in North American boreal forest species (Greene et al. 1999). The growth of regeneration generally increases with decreasing stand density as measured by basal area, especially in light-demanding conifer species (Page et al. 2001, Bailey and Tappeiner 1998, Wampler 1993). At higher residual stand densities and if stand density is gradually reduced over time, however, advance regeneration may be able to gradually acclimate to increased light thereby avoiding the so-called 'growth shock' (Miller and Emmingham 2001). In managed stands, a lower stand basal area can also represent heavier logging disturbance, possibly damaging advance regeneration and/or reducing brush competition but also preparing seedbed for new seedling establishment.

The effect of seedling height on growth responses has been inconsistent (Ruel et al. 2000). Nevertheless, tree height has been called important to consider in combination with light availability when predicting growth rates or morphological attributes (Claveau et al. 2002). For example, the number of nodal branches of the shade-intolerant species Jack pine (*Pinus banksiana* Lamb.) and lodgepole pine, as well as height and lateral growth, changed with seedling height (Williams et al. 1999). Messier (2003) even suggested that size determines the ability of a tree to acclimate and survive in understory conditions. Overall, the effect of tree height on seedling characteristics under varying overstory conditions is still not well understood and requires further investigation (Claveau et al. 2002).

In low light environments, tree height is generally restricted because the ratio of photosynthetic to non-photosynthetic plant material declines with tree size (Messier and Nikinmaa 2000, Messier et al. 1999a). More carbon needs to be assimilated by larger plants to sustain respiration of live cells. After a certain stage, tall advance regeneration may also experience competitive effects of adjacent vegetation, instead of facilitation experienced by germinants and small seedlings (Keyes et al. 2001). Height growth and survival can be negatively correlated in shaded understory conditions, and survival can prove to be more important in forest succession

than seedling growth (Wright et al. 1998, Chen 1997). Therefore, greater height growth under shade may not be a favorable strategy for surviving and reproducing.

OBJECTIVES

The study materials are naturally established ponderosa pine and lodgepole pine seedlings (new and advanced regeneration) growing on two sets of research plots in central Oregon. These plots have been grown under varying silvicultural regimes, the first set involving different density regimes in even-aged stands of predominantly lodgepole pine, and the second set involving different regimes for managing uneven-aged ponderosa pine stands. The objectives of this study were to investigate the species' response strategies to an increase in growing space at each site by: (1) testing the effects of stand density reduction on seedling density and morphological characteristics of ponderosa and lodgepole pine regeneration; (2) testing the effects of stand density reduction on height growth of ponderosa and lodgepole pine seedlings; and (3) testing the predictive value of morphological characteristics on seedling height growth of ponderosa pine and lodgepole pine seedlings.

Chapter 2 addresses the first objective and involves testing the following specific hypotheses:

- Seedling density, height to diameter ratio, total number of primary branches per tree, number of new whorl branches, length of 5-yr-old branches, apical dominance, number of needle fascicles on the main stem and on the 2002 terminal leader, needle fascicle density per unit length on the main stem and on the 2003 terminal leader, needle length in 2002, and needle longevity, are largely controlled by initial seedling height and stand density, and this effect differs with species.

Chapter 3 addresses the second objective and involves testing the following specific hypotheses:

- Current absolute and relative height growth, height growth immediately after stand density reduction and height growth before stand density reduction are largely controlled

by initial seedling height and local basal area, and this effect will differ with species.

- Current absolute height growth is correlated with morphological attributes and previous height growth, and some of these morphological attributes can be used as determinants of height growth in a predictive model.

The final chapter of this thesis summarizes the major results of chapters two and three and discusses silvicultural implications of this research.

CHAPTER TWO:

BRANCH AND FOLIAGE CHARACTERISTICS OF PONDEROSA PINE AND LODGEPOLE PINE

REGENERATION NINE YEARS AFTER STAND DENSITY REDUCTION

AT TWO SITES IN CENTRAL OREGON

INTRODUCTION

Fire exclusion since the 1900s has resulted in major changes in forest ecosystems in the Pacific Northwest, threatening their structural and functional attributes, e.g. species diversity, habitat, productivity, and stability. These changes are especially dramatic in forests long dominated by shade-intolerant species that depend on large-scale catastrophic disturbances such as ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *ponderosa*) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.) (Walker 1999, Steele 1994).

Ponderosa pine and lodgepole pine are two of the most widely distributed tree species in the western US (Walker 1999) and often they occur together (Franklin and Dyrness 1973). Lodgepole pine can invade many ponderosa pine forests as result of fire or logging (Volland 1985). Without the continuing occurrence of fire, lodgepole pine may be gradually replacing ponderosa pine in stands where large numbers of lodgepole pine seedlings have started to dominate regeneration. This development, however, conflicts with recent efforts to restore old-aged, open ponderosa pine forests throughout the US (Kaufmann et al. 1997). Ponderosa pine also has higher commercial value than lodgepole pine. For these reasons lodgepole pine is a less favorable option in stands where ponderosa pine is the alternative and active management may be needed to ensure the establishment and survival of ponderosa pine.

The shift to forest ecosystem management in recent years has led to increased scientific attention on responses of tree regeneration to partial forest overstory reductions under various silvicultural systems. In central Oregon, temperature extremes, low precipitation and young, poorly developed soils that are covered with pumice from historic volcanic activity and that have low water holding capacity (Hermann and Petersen 1969), may make the use of only partial

cutting and promotion of advance regeneration a reasonable option. On poor to moderate ponderosa pine sites, these management options can provide shelter from severe climatic conditions and inhibit competing vegetation by means of a residual overstory canopy (McDonald 1976, Zavitkovski and Woodard 1970).

Advance regeneration plays an important role in the regeneration of shade-tolerant species, but it has received relatively little attention in the management of light-demanding species such as lodgepole pine and ponderosa pine. In shade-tolerant species, the inter- and intraspecific strategies in genetic adaptation and phenotypic acclimation to forest understory conditions have been addressed in various studies (review by Ruel et al. 2000). Survival and growth of plants in the shade are enabled by responses not only at the leaf-level but also at the shoot-, crown-, and whole-plant levels (Messier et al. 1999a, Kobe and Coates 1997). Pine species can tolerate closed canopy conditions, but overall their shade-tolerance is low (Oliver and Larson 1996). To better judge silvicultural options regarding future desirable stand structures and yield in these ecosystems, the density, dynamics, spatial pattern, and adaptation/acclimation strategies of ponderosa pine and lodgepole pine natural regeneration need to be studied in more detail.

OBJECTIVES

The study materials are naturally established ponderosa pine and lodgepole pine seedlings (new and advanced regeneration) growing at two research sites in central Oregon. These plots have been grown under varying silvicultural regimes, the first set involving different density regimes in even-aged stands of predominantly lodgepole pine, and the second set involving different regimes for managing uneven-aged ponderosa pine stands. The objectives were to investigate the species' response strategies to an increase in growing space by testing the effects of stand density reduction on seedling density and morphological characteristics of ponderosa and lodgepole pine regeneration.

The following specific hypotheses will be tested: Seedling density, total number of primary branches per tree, number of new whorl branches, length of 5-yr-old branches, apical dominance, number of needle fascicles on the main stem and on the 2002 terminal leader, needle fascicle density per unit length on the main stem and on the 2003 terminal leader, needle

length in 2002, needle longevity, and height to diameter ratio are largely controlled by initial seedling height and stand density, and this effect will differ with species.

METHODS

Study Area

The two study sites, Finley Butte, and Twin Lakes, are situated in the Deschutes National Forest, east of the Cascade Mountain Range in central Oregon. Finley Butte is approximately 10 km east of La Pine (43° 36' N, 121° 24' W), and Twin Lakes is approximately 21 km west of La Pine (43° 42' N, 121° 45' W). Both sites are approximately 50 km south of Bend, and the elevation is approximately 1300 m above sea level.

The climate is continental with dry and hot summers and cold winters with precipitation mostly occurring as snow. Periodic droughts during the summer are common. Mean temperature at Wickiup Dam near the Finley Butte and Twin Lakes sites from 1971-2000 was 7.1 °C with monthly temperature extremes of –30.0 °C in December and 38.3 °C in August. Mean annual precipitation from 1971-2000 was 2015 mm from snow and 560 mm from rainfall with 150 mm occurring between the months of April to September. The average number of days with a temperature minimum of 0 °C or less was 212.3 with possibilities of late frost in July and early frost in August. (Data from the Oregon Climate Service at Western Regional Climate Center at http://www.wrcc.dri.edu/ and http://www.ocs.oregonstate.edu/)

The soils are well drained Entisols, low in nutrients and with a shallow, immature profile developed in dacite pumice from the eruption of Mt. Mazama approximately 7600 years ago (Hermann and Petersen 1969). Both sites have soils belonging to the Lapine series (National Cooperative Soil Survey 1992). The Finley Butte vegetation is a *Pinus ponderosa/Purshia tridentata* plant association dominated by ponderosa pines with scattered lodgepole pines in the overstory (Franklin and Dyrness 1973). The vegetation of Twin Lakes is a mix of the Pinus ponderosa/*Purshia tridentata* and *Pinus ponderosa/Purshia tridentata/Stipa occidentalis* plant associations, and it is dominated by lodgepole pine with scattered ponderosa pines in the overstory. The main species in the understory at both sites are antelope bitterbrush (*Purshia*

tridentata (Pursh) DC.), snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex. Hook.) and greenleaf manzanita (*Arctostaphylos patula* Greene). In general, herbaceous plants form relatively low cover on these soils (Dyrness and Youngberg 1966).

Study Design

The Finley Butte site is part of a study to test differences in timber productivity between even-aged and uneven-aged silvicultural systems in ponderosa pine. The study was established on the Deschutes, Ochoco, Fremont, and Winema National Forests in 1991-1994, with the USDA Forest Service Pacific Northwest Research Station taking the lead. At Finley Butte, there is one replicate of each of four silvicultural treatments: overstory removal, uneven-age 'classic', uneven-age 'best tree', and a control. These treatments were implemented in 1991 and 1994 and have led to different stand densities and age structures of the residual trees (Wood et al. no year, also see appendix). Study site parameters are summarized in Tab. 1.

The Twin Lakes site is part of a lodgepole thinning study with the last thinning in 1994 (Cochran and Dahms 2000). Two stands with a high density and two stands with a low density were selected from this study to investigate the characteristics of seedlings in the understory. Within three of the four selected stands, nine 40 m² (1/100th acre) circular subplots with a radius of 3.6 m had been installed along a grid. In the fourth stand (one of the low density plots), only one subplot was randomly selected. Study site parameters are summarized in Tab. 1.

Table 1: Study site parameters at Finley Butte and Twin Lakes

	Finley Butte			Twin Lakes		
	min	mean	max	min	mean	max
Local Basal Area (m²/ha)	6	18.3	45.5	9	21.1	34
Cover of Understory Vegetation (%)	1	16	55	<5	29	60
Cover of Woody Debris (%)	-	-	-	5	22	80
Number of Ponderosa Pine Seedlings Studied	355			79		
Number of Lodgepole Pine Seedlings Studied	162			71		
Total Number of Seedlings Studied (N = 667)	517			150		

Combining both Finley Butte and Twin Lakes, eight stands with different silvicultural treatments and overstory structures were investigated. Circular subplots of 40.5 m² (1/100 acre) each were established to sample seedlings and assess the local growing environment, resulting

in a total of 50 subplots in four stands at Finley Butte and 25 subplots in four stands at Twin Lakes. The subplots lay along a grid and were 16 m (53 ft) apart at Finley Butte and approximately 8 m (26 ft) apart at Twin Lakes. Local basal area was estimated from the center of each subplot with an angle gauge of basal area factor 1 m²/ha, distinguishing between over-, mid-, and understory strata at Finley Butte. At Twin Lakes, the overstory consisted of only one stratum with only a few trees above 1.3 m in the understory.

All measurements were taken from July to October 2003. In each subplot, all ponderosa pine and lodgepole pine seedlings between 0.10 m and 1.30 m that met the following sampling criteria were measured: no damage, no disease, no stem distortions like crooks or sweeps, no broken or forked tops, not germinated from the same seed cache (an important phenomenon for establishment in ponderosa pine (Keyes 2001)), and no cone production (observed in some lodgepole pine seedlings). The total number of seedlings was 517 at Finley Butte (355 ponderosa pines and 162 lodgepole pines) and 150 at Twin Lakes (79 ponderosa pines and 71 lodgepole pines), giving a total of 667 seedlings from both sites combined. The number of seedlings in each height class, including seedlings < 0.10 m, was tallied on each subplot to provide an estimate of total seedling density at both sites.

To quantify the architectural and growth responses of the two species, numerous attributes were measured on each individual. Total seedling height and stem diameter at the root collar were measured, and the height to diameter ratio was calculated. Annual height growth was measured downward until it was too difficult to determine visually. Apical dominance was determined in two ways: (1) as the length of the terminal leader for each year divided by the length of the corresponding leader of the longest lateral branch that same year, and (2) as the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except the current. If lodgepole pine showed evidence of multinodal or polycyclic growth, i.e. the annual shoot had produced more than one whorl of branches (Lanner 1976, Van den Berg and Lanner 1971), the lengths of the internodes within the same year were summed. A polycyclic growth pattern does not occur in ponderosa pine.

The longest 5-year-old branch was measured in detail to compute the ratio of the sum of terminal and lateral growth for five years (although not including the current growth in 2003).

Years of needle retention and number of primary branches on each tree and whorl branches per year were determined. Length was measured on one needle of average length on the south side just below the top of the terminal leader shoot, and the number of needle fascicles on each shoot was counted. Needle density was calculated as the number of needle fascicles per unit stem length. Since ages could not be determined by ring count, minimum age was calculated as the age down to the point where terminal bud scars or whorls were still discernible. This procedure performed equally well in both species.

ANALYSIS

All statistical analyses were performed using the Statistical Analysis System software (SAS Institute Inc. 1999-2001) with separate analyses for each site. The effect of species, initial seedling height, and local basal area on morphological characteristics was investigated with multiple linear regression analysis in PROC MIXED or POISSON log-linear regression in PROC GENMOD if the response was a count variable. In PROC MIXED, the best model was selected by means of forward selection and by comparing AIC values obtained with different transformations of the response variable and three explanatory variables, and their interactions. The same was done in PROC GENMOD by comparing deviances, e.g. using the drop in deviance test (McCullagh and Nelder 1989). To meet the assumptions of linearity, constant variance, and normality in PROC MIXED, the response variables and explanatory variables seedling height and local basal area were often transformed (logarithmic, square root, or reciprocal transformations). For the graphs showing average characteristics throughout the years, averages of seedlings were calculated for each height class. Current growth and needle characteristics were not included in most analyses because the growing season had not ended at the time of measurement (July and October 2003; Fowells 1941).

RESULTS

Seedling Density

Although seedlings of both species originated from before the last stand density reduction in 1994, this especially applies to ponderosa pine. Of the ponderosa pine seedlings sampled, 64 % at Finley Butte and 63 % at Twin Lakes had established before the treatments (Figs. 1 and 3). In contrast, only 24% at Finley Butte and 38 % at Twin Lakes of the lodgepole pine seedlings that were sampled had established before 1994 (Fig. 2 and 4). Since no accurate age measurements were taken, minimum age was calculated as the age down the stem to the point where terminal bud scars or whorls were still discernible. In general, bud scars could be distinguished far down the tree and often even nearly to the base of the stem in both species. Although it is difficult to determine whether trees with a low minimum age originated after silvicultural treatment, it can be concluded that many trees with a high minimum age are advance regeneration that persisted after the last stand density reduction.

At Finley Butte, only few lodgepole pine seedlings were found in subplots with a local stand density above 19 m²/ha (Fig. 6). In both species, the distribution of seedlings at Finley Butte appeared irregular and no clear trends were obvious across the studied range in basal area (6-46.5 m²/ha) (Fig. 5-6). At Twin Lakes, total seedling density of lodgepole pine was higher than that of ponderosa pine (Fig. 7-8). After distinguishing seedling density by species and height classes, however, only few large lodgepole pine seedlings (< 0.10 m) were evident at Twin Lakes, whereas small seedlings < 0.10 m were plentiful (Fig. 8). Therefore, it seems that although there is a high rate of establishment of lodgepole pine, the survival rate seems lower than that of ponderosa pine at the observed overstory densities (9.0-34.0 m²/ha), especially above 20-25 m²/ha. Seedlings < 0.10 m were not distinguished by species at Finley Butte, and for this reason, they were not included in the graphics.
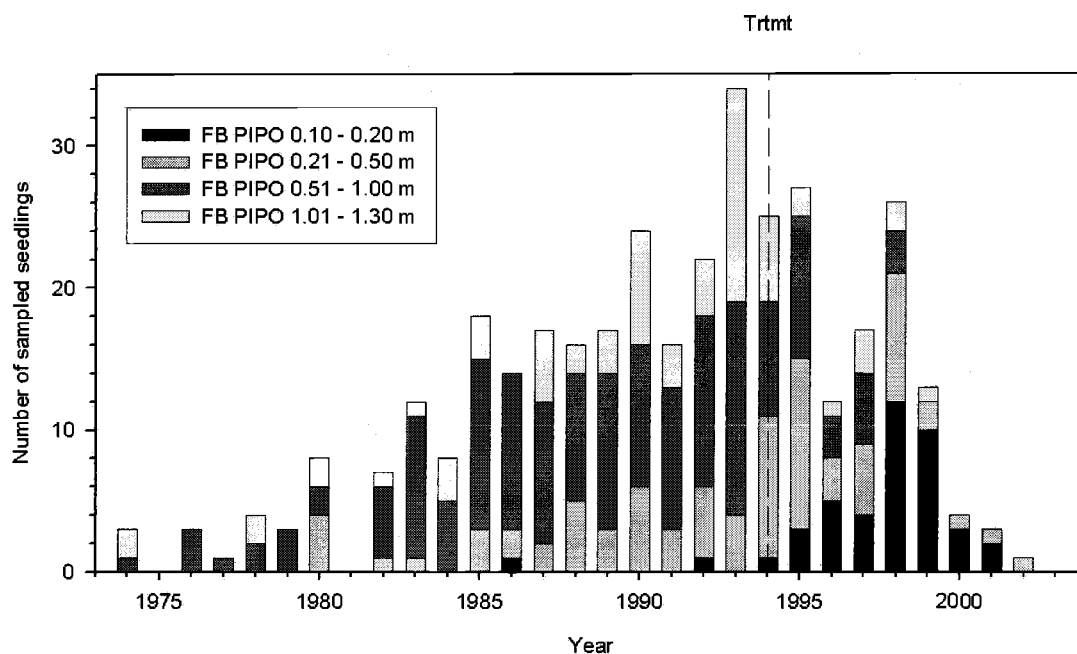
Figure 1: Seedling density of corresponding minimum age of ponderosa pine seedlings at Finley Butte (N = 355; seedlings established before 1994: 64 %)
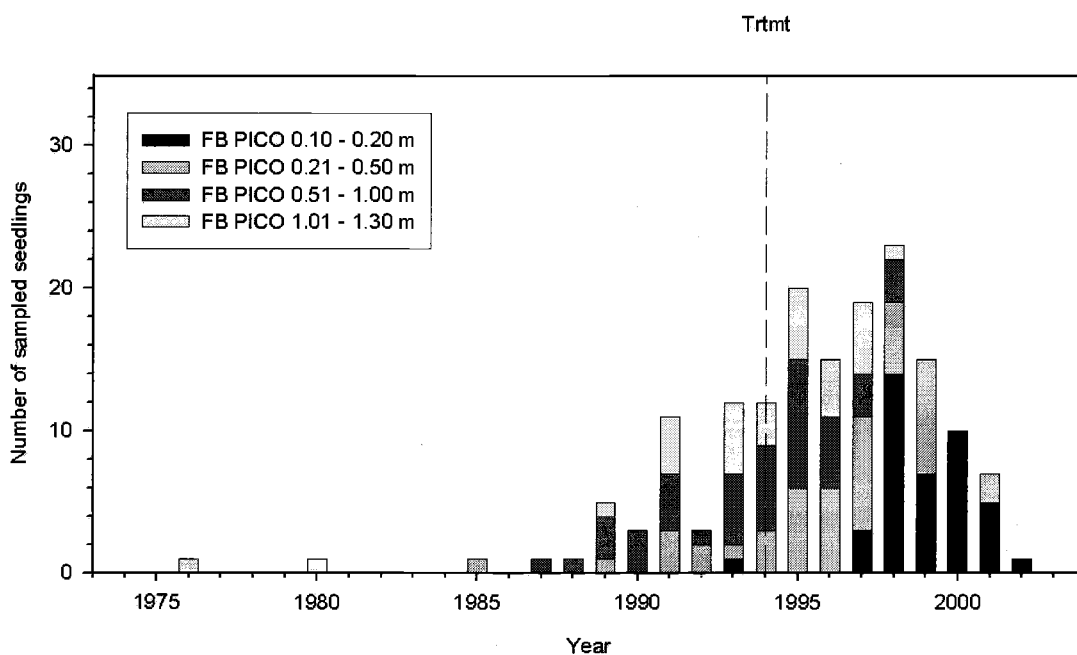
Figure 2: Seedling density of corresponding minimum age of lodgepole pine seedlings at Finley Butte (N = 161; seedlings established before 1994: 24 %)
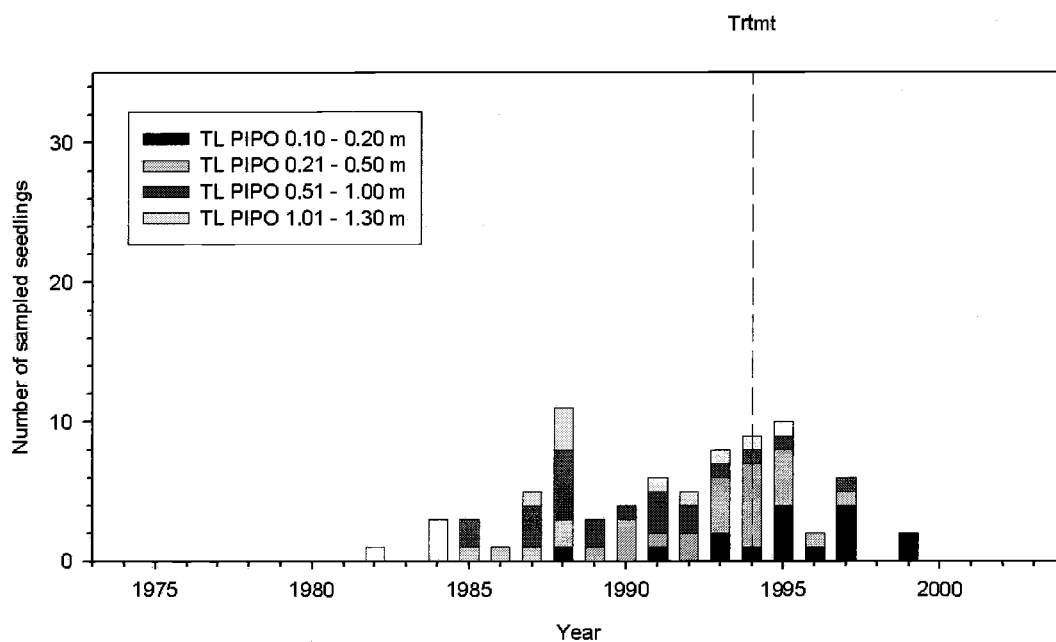
Figure 3: Seedling density of corresponding minimum age of ponderosa pine seedlings at Twin Lakes (N = 79; seedlings established before 1994: 63 %)
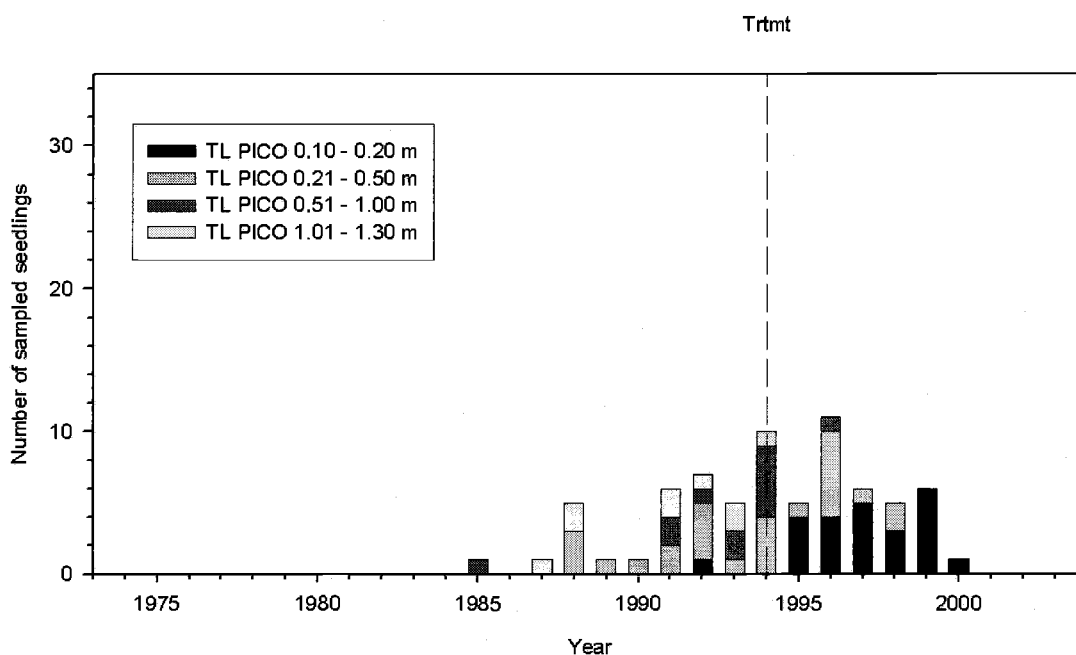
Figure 4: Seedling density of corresponding minimum age of lodgepole pine seedlings at Twin Lakes (N = 71; seedlings established before 1994: 38 %)
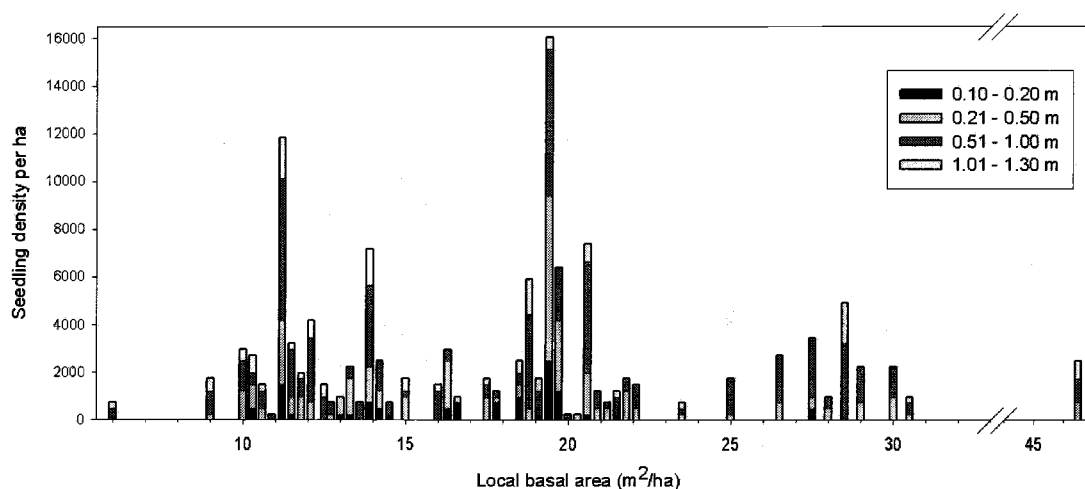
Figure 5: Ponderosa pine subplot seedling densities by height class and local stand density at Finley Butte (basal area from 1 m²/ha angle gauge at plot center)
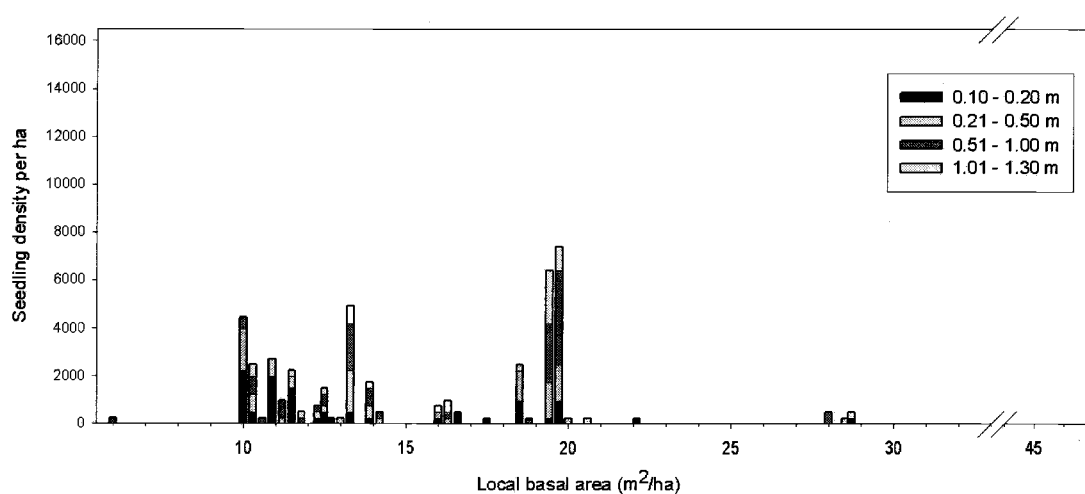
Figure 6: Lodgepole pine subplot seedling densities by height class and local stand density at Finley Butte (basal area from 1 m²/ha angle gauge at plot center)
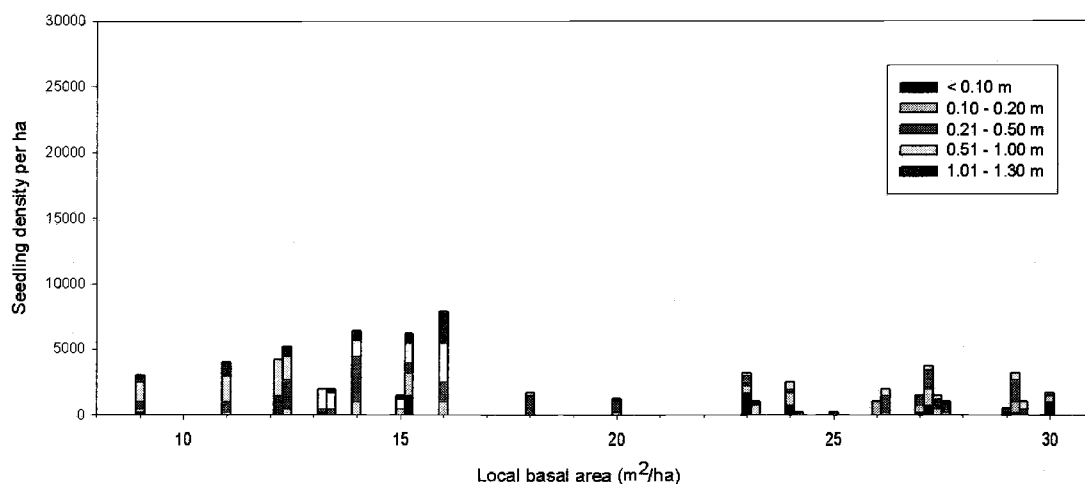
Figure 7: Ponderosa pine subplot seedling densities per ha by height class and local stand density at Twin Lakes (basal area from 1 m²/ha angle gauge at plot center)
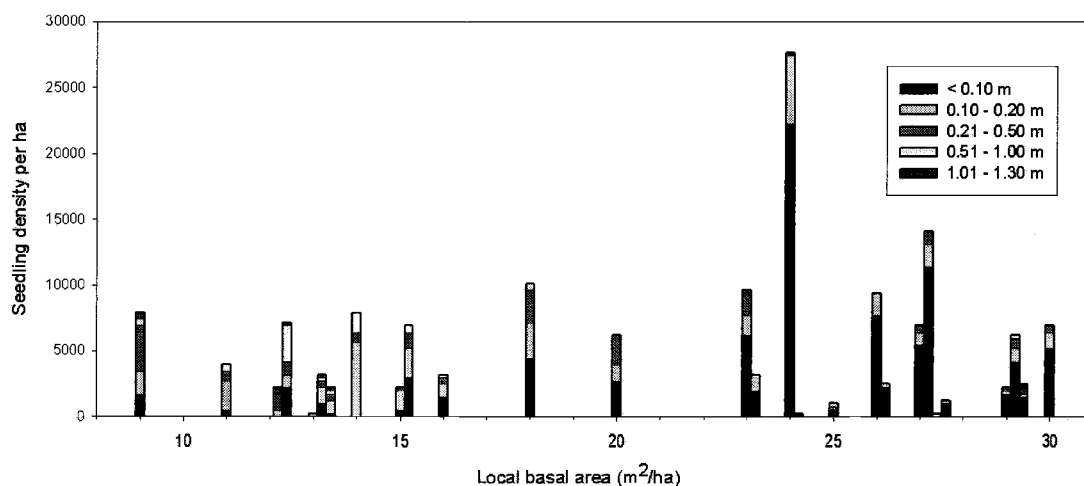
Figure 8: Lodgepole pine subplot seedling densities per ha by height class and local stand density at Twin Lakes (basal area from 1 m²/ha angle gauge at plot center)

Stem Morphology

<u>Height to Diameter Ratio (H/D)</u>

The relationship between local basal area, initial seedling height, and H/D was different at the two investigated sites. At Finley Butte, H/D increased with increasing overstory density, and this increase was a little steeper in ponderosa pine than in lodgepole pine (p-value = 0.0381 for the interaction between species and local basal area). H/D also increased with increasing seedling height, but this effect was only small, although statistically significant (p-value = 0.0168) (Fig. 9; Tab. 2).

At Twin Lakes, no significant difference between the two species was found. At low stand densities, the effect of seedling height was less pronounced than at high densities (p-value = 0.0068 for the interaction between seedling height and local basal area). At high densities, small seedlings had a much lower H/D than tall seedlings. However, seedling height was less influential for seedlings greater than 0.60 m in height (Fig. 10; Tab. 3).

Although seedlings of both species reached maximum H/D-values of approximately 120, the regression model suggests an average H/D of approximately 40 at the lowest overstory densities in both species at Finley Butte and of approximately 50 at Twin Lakes. At high overstory densities, H/D was between 60 and 70 in tall seedlings at both sites according to the model.
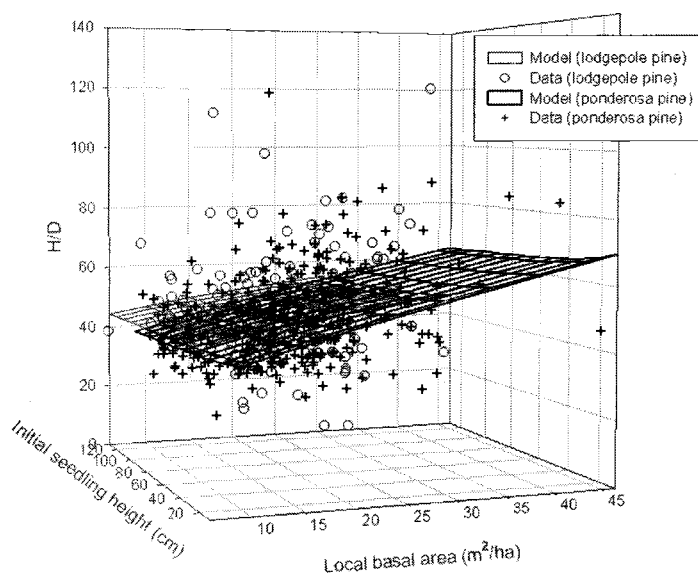
Figure 9: Height to diameter ratio at Finley Butte (R^2 = 0.16)

Table 2: Multiple linear regression model of H/D ratio at Finley Butte

ln H/D $= \beta_0 + \beta_1$ ln H $+ \beta_2$ sqrt LBA $+ \beta_3$ I $+ \beta_4$ sqrt LBA $\cdot$ I $+ \varepsilon$					
where	ln H/D	= natural logarithm of the height to diameter ratio in 2003			
	ln H	= natural logarithm of height of seedling (cm)			
	sqrt LBA	= square root of local basal area (m²/ha)			
	I	= indicator for species; 0 for lodgepole pine, 1 for ponderosa pine			
$\varepsilon \sim N(0,\sigma^2)$					
Effect	**Estimate**	**Standard error**	**df**	**F-value**	**p-value**
Intercept	3.7918	0.1176			
ln H	-0.03482	0.01452	509	5.75	0.0168
sqrt LBA	0.06933	0.02636	509	42.81	<0.0001
I	-0.3794	0.1294	509	8.60	0.0035
sqrt LBA $\cdot$ I	0.06457	0.03107	509	4.32	0.0381
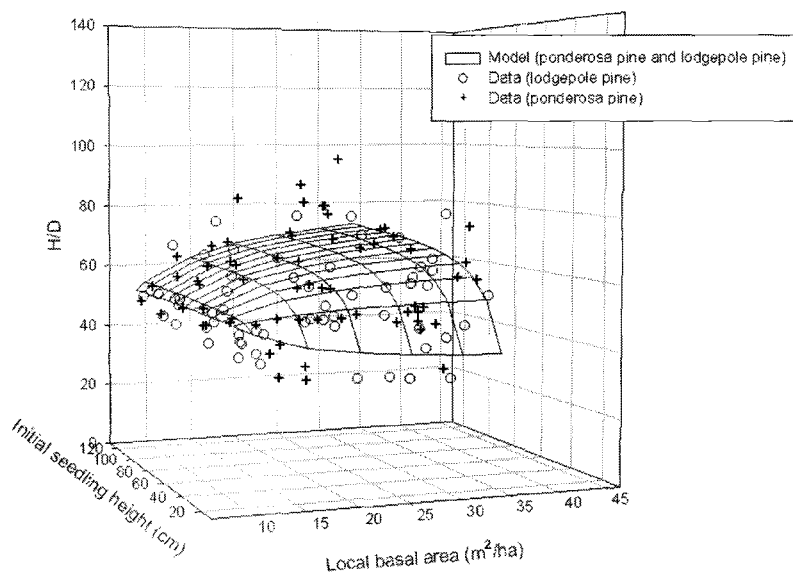
Figure 10: Height to diameter ratio at Twin Lakes (R^2 = 0.25)

Table 3: Multiple linear regression model of H/D ratio at Twin Lakes

ln H/D 2002 = β_0 + β_1 1/H + β_2 1/ LBA + β_3 1/H • 1/ LBA + ϵ	
where ln H/D 2002	= natural logarithm of height to diameter ratio in 2003
1/H	= initial height of seedling (cm)
1/LBA	= logarithm of local basal area (m²/ha)
I	= indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\epsilon \sim N(0,\sigma^2)$	

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	4.4576	0.07670			
1/H	-7.9892	1.7095	145	21.84	< 0.0001
1/LBA	-4.6976	1.0695	145	19.29	< 0.0001
1/H • 1/ LBA	69.3682	25.2677	145	7.54	0.0068

Branch and Crown Morphology

Number of Primary Branches

At both sites, lodgepole pine seedlings had up to twice as many primary branches as ponderosa pine seedlings. Both species had none to very few primary branches at seedling heights below 0.20 m but, except for tall lodgepole pine seedlings at Finley Butte, the number of primary branches gradually increased with increasing seedling height and decreasing stand basal area (Figs. 11-12; Tabs. 4-5). The highest number of primary branches on an individual seedling was approximately 60 in lodgepole pine and 30 in ponderosa pine. In both species, the number of primary branches was higher at Finley Butte than at Twin Lakes.

At Finley Butte, there was evidence that the effect of local basal area on the total number of primary branches on a seedling differed between species nine years after stand density reduction (p-value = 0.0001 from an F-test for interaction between species and local basal area), as did the effect of seedling height (p-value = 0.0039 from an F-test on the interaction between species and seedling height) (Tab. 4). There was also convincing evidence that the effect of local basal area on the number of primary branches changed with seedling height (p-value = 0.0288 from an F-test for interaction between initial seedling height and local stand basal area). According to the regression model, small seedlings increased their number of primary branches but tall lodgepole pine seedlings decreased their number of primary branches with reduction in overstory density. The data, however, do not convincingly support this result (Fig. 11).

The results at Twin Lakes differ only slightly from those at Finley Butte in that the regression model does not detect a species effect of height on the number of primary branches. But although the smallest seedlings of both species have no or only very few branches, after back-transformation of the model estimates to the original scale, the increase in the number of primary branches with increasing seedling height is much greater in lodgepole pine seedlings than it is in ponderosa pine seedlings. The regression model also suggests that the effect of overstory density is influenced by seedling height (p-value = 0.0294) (Fig. 12).
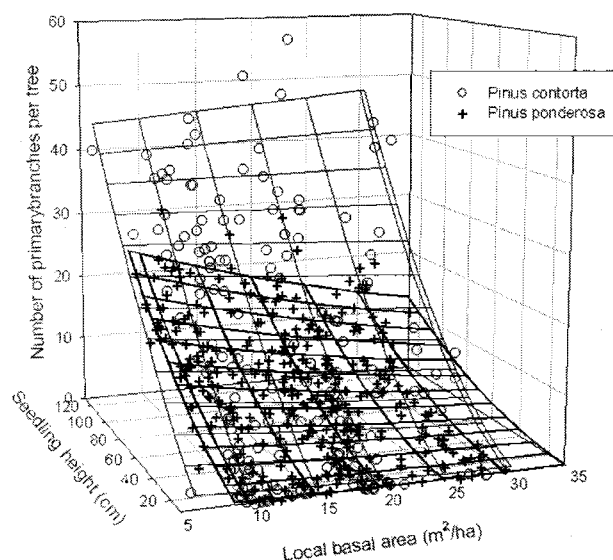
Figure 11: Number of primary branches at Finley Butte (R^2 = 0.74)

Table 4: POISSON log-linear regression analysis of number of primary branches per tree at Finley Butte

$\ln \mu = \beta_0 + \beta_1 \log H + \beta_2 LBA + \beta_3 I + \beta_4 \ln H \cdot LBA + \beta_5 \ln H \cdot I + \beta_6 \cdot LBA \cdot I$

where
μ	=	expected mean number of primary branches
LBA	=	local basal area (m²/ha)
ln H	=	natural logarithm of height of seedling (cm)
I	=	indicator for species; 0 for lodgepole pine, 1 for ponderosa pine

$Y \sim \text{Poisson} (\mu)$; $E(Y) = \mu$; $\text{Var}(Y) = \mu \cdot \Phi$;

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-1.4952	0.6758	507		
log H	1.0791	0.1517	507	66.90	< 0.0001
LBA	-0.0901	0.0398	507	6.98	0.0085
I	-1.9341	0.6758	507	14.63	0.0001
ln H • LBA	0.0193	0.0000	507	4.81	0.0288
ln H • I	0.3228	0.1126	507	8.41	0.0039
LBA • I	-0.0287	0.0073	507	15.22	0.0001
Scale	1.6245	**Deviance**	1338.0160	**Dev. / df (Φ)**	2.6391
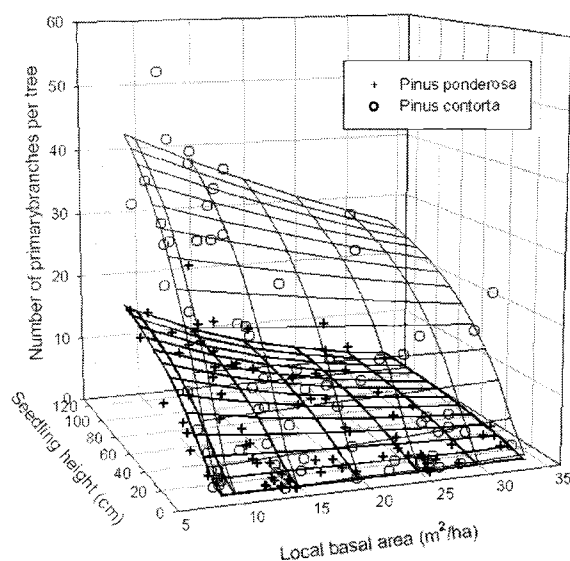
Figure 12: Number of primary branches at Twin Lakes ($R^2 = 0.72$)

Table 5: POISSON log-linear regression model of number of primary branches per tree at Twin Lakes

$\ln \mu = \beta_0 + \beta_1 \, 1/H + \beta_2 \, LBA + \beta_3 \, I + \beta_4 \, 1/H \cdot LBA + \beta_5 \cdot LBA \cdot I$

where μ =   expected mean number of primary branches
          LBA   =   local basal area (m²/ha)
          1/H   =   logarithm of height of seedling (cm)
          I   =   indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$Y \sim$ Poisson (μ); $E(Y) = \mu$; Var $(Y) = \mu \cdot \Phi$;

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	4.4985	0.1999	144		
1/H	-74.3599	9.1756	144	76.64	< 0.0001
LBA	-0.0279	0.0119	144	18.60	< 0.0001
I	-0.6632	0.2459	144	7.32	0.0076
1/H • LBA	1.0292	0.4611	144	4.84	0.0294
LBA • I	-0.0437	0.0146	144	9.33	0.0027
Scale	1.4143	**Deviance**	288.0274	**Dev. / df (Φ)**	2.0002

New Whorl Branches in 2002 and their Annual Change over Time since Stand Density Reduction

For lodgepole pine seedlings, the number of new whorl branches in 2002 included branches of all whorls produced in the annual shoot (polycyclic growth pattern in lodgepole pine; see Lanner 1976, Van den Berg and Lanner 1971). At both sites, the number of whorl branches was highest at low overstory densities, in the taller seedlings and in lodgepole pine (Figs.13-14; Tabs. 6-7). At Finley Butte, the number of new whorl branches increased more steeply with reduction in overstory density in lodgepole pine than it did in ponderosa pine. The effect of overstory density was greatest at a local basal area of approximately 15 m²/ha, in the taller seedlings, and differed by species (p-values = 0.0001 for the interaction between species and local basal area and p-value = 0.0380 for the interaction between initial seedling height and local basal area). The highest number of new whorl branches was 6 in lodgepole pine and 3 in ponderosa pine at a low overstory density.

At Twin Lakes, the increase in the number of new whorl branches with increasing seedling height was stronger in lodgepole pine than in ponderosa pine (p-value = 0.0281 from an interaction of species and initial seedling height). The effect of overstory density increased greatest at about 20 m²/ha in both species, and the highest number of new whorl branches was 8 in lodgepole pine and 3 in ponderosa pine at a low overstory density.

Over time since treatment, lodgepole pine produced more whorl branches on average than ponderosa pine in each height class, regardless of year, and the number seems to have increased after the last silvicultural treatment in 1994 at both sites (Figs. 15-16). In both species, the taller the seedlings, the higher was the number of whorl branches and the greater the increase after 1994. Fewer whorl branches were produced, on average, after a peak in 1999 at Finley Butte and, depending on height class, in 1999 and 2001 at Twin Lakes.
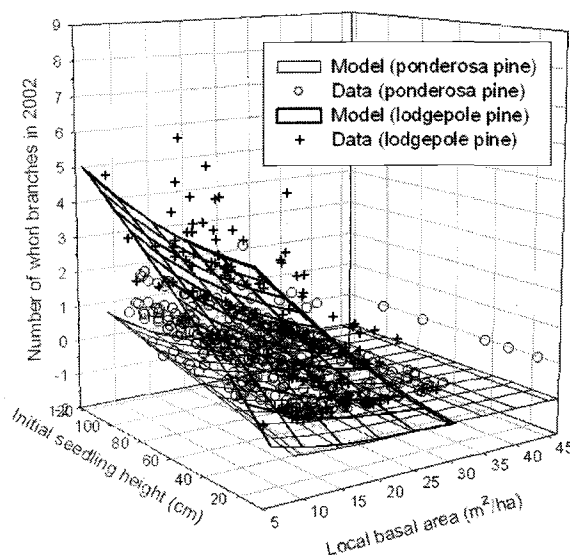
Figure 13: New whorl branches produced in 2002 at Finley Butte (R² = 0.57)

Table 6: POISSON log-linear regression model of new whorl branches produced in 2002 at Finley Butte

$$\ln \mu = \beta_0 + \beta_1 \ln H + \beta_2 LBA + \beta_3 I + \beta_4 LBA \cdot I + \beta_5 \ln H \cdot LBA$$

where μ = expected mean number of new whorl branches in 2002
$\ln H$ = natural logarithm of initial height of seedling (cm)
LBA = local basal area (m²/ha)
I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$Y \sim$ Poisson (μ); $E(Y) = \mu$; Var $(Y) = \mu \cdot \Phi$;

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-1.1987	0.8946			
ln H	0.6675	0.2105	506	10.45	0.0013
LBA	-0.1744	0.0600	506	11.95	0.0006
I	-0.6148	0.2569	506	5.72	0.0171
LBA • I	-0.0601	0.0157	506	15.12	0.0001
ln H • LBA	0.0287	0.0139	506	4.33	0.0380
Scale	0.7678	Deviance	298.3189	Dev. / df (Φ)	0.5896
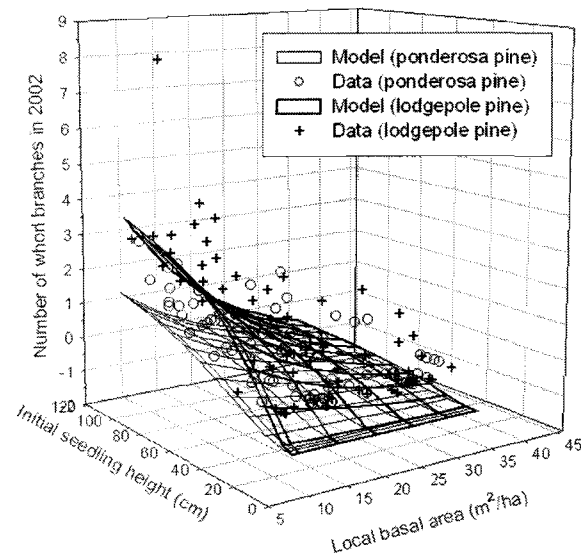
Figure 14: New whorl branches produced in 2002 at Twin Lakes ($R^2 = 0.55$)

Table 7: POISSON log-linear regression model of new whorl branches produced in 2002 at Twin Lakes

$\ln \mu = \beta_0 + \beta_1\, 1/H + \beta_2\, LBA + \beta_3\, I + \beta_4\, 1/H \cdot I$					
where μ = expected mean number of new whorl branches in 2002					
$1/H$ = reciprocal of initial height of seedling (cm)					
LBA = local basal area (m²/ha)					
I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine					
$Y \sim$ Poisson (μ); $E(Y) = \mu$; Var $(Y) = \mu \cdot \Phi$;					
Effect	**Estimate**	**Standard error**	**df**	**F-value**	**p-value**
Intercept	2.5262	0.2085	145		
1/ H	-39.1228	5.1282	145	152.38	< 0.0001
LBA	-0.0753	0.0124	145	44.51	< 0.0001
I	-0.4483	0.2696	145	2.69	0.1029
1/H • I	-28.7043	0.000	145	4.92	0.0281
Scale	0.7259	**Deviance**	76.4025	**Dev. / df (Φ)**	0.5269
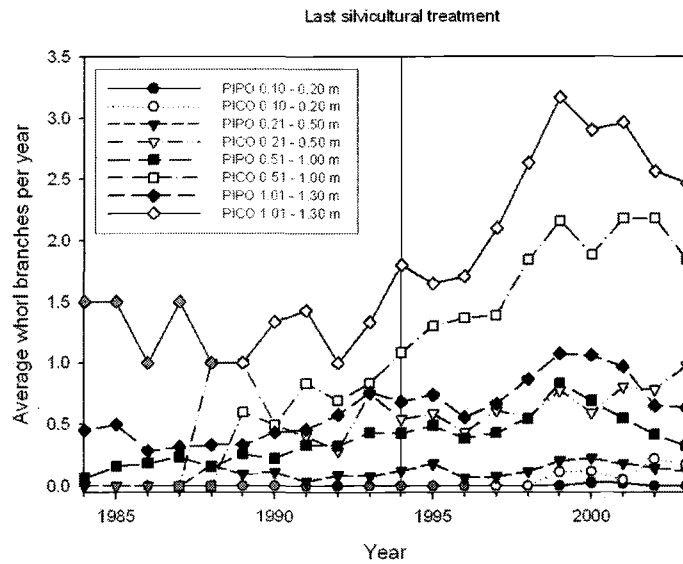
Figure 15: Average number of whorl branches per year at Finley Butte
(gray data points indicate averages computed from <3 seedlings)
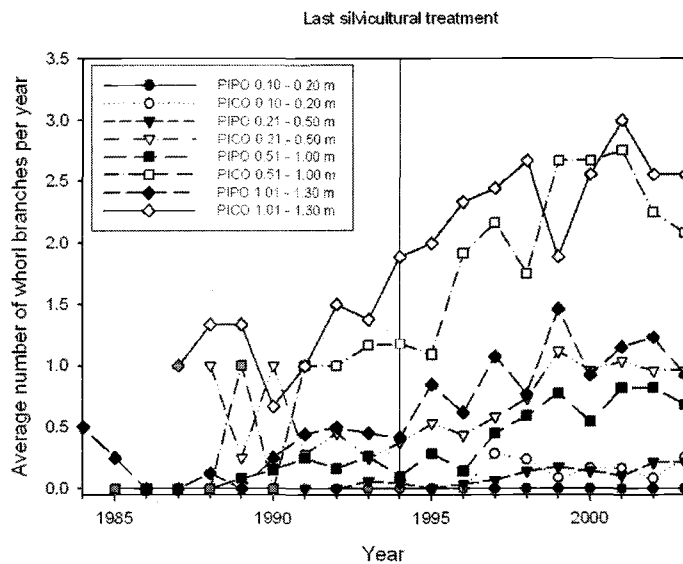
Figure 16: Average number whorl branches per year at Twin Lakes
(gray data points indicate averages computed from <3 seedlings)

Length of the Longest 5-Year-Old Branch

The width of the seedling crown was estimated by measuring the length of the longest 5-yr-old branch. The current growth in 2003 was subtracted because growth had not ceased at the time of measurement (Fowells 1941). Only seedlings that had a 5-yr-old branch were included in the analysis.
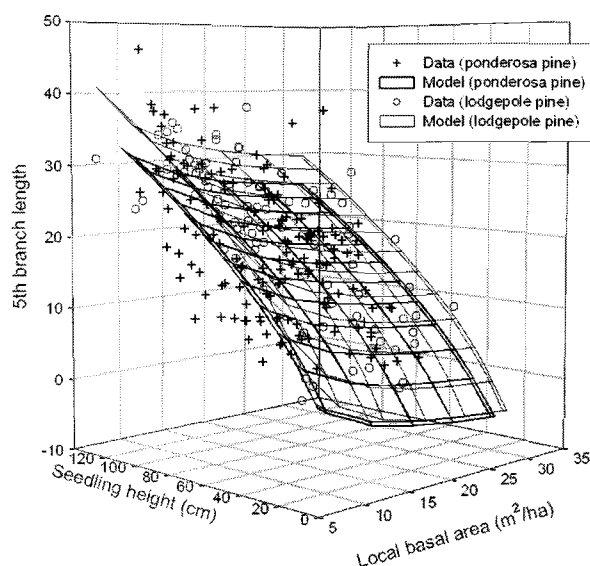
Figure 17: Length of longest 5-yr-old branch
without the current growth in 2002 at Finley Butte (R² = 0.62)

Table 8: Multiple linear regression model of length of longest 5-yr-old branch at Finley Butte

$LB = \beta_0 + \beta_1 \, sqrt \, H + \beta_2 \, 1 \, / \, LBA + \beta_3 \, I + \varepsilon$

where	LB	=	length of longest 5-yr-old branch (without growth in 2003)
	sqrt H	=	square root of height of seedling (cm)
	1 / LBA	=	reciprocal of local basal area (m²/ha)
	I	=	indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$			

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-22.5111	2.3401			
sqrt H	4.3564	0.2342	241	345.87	< 0.0001
1 / LBA	82.7626	15.9556	241	26.91	< 0.0001
I	-4.3865	0.7974	241	30.26	< 0.0001
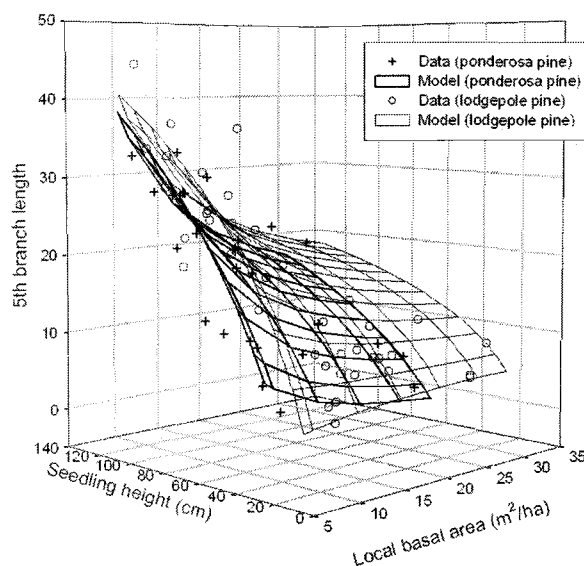
Figure 18: Length of 5-yr-old branch
without the current growth in 2002 at Twin Lakes ($R^2 = 0.78$)

Table 9: Multiple linear regression model of length of longest 5-yr-old branch at Twin Lakes

$LB = \beta_0 + \beta_1 \ln H + \beta_2 \, 1 / LBA + \beta_3 I + \beta_4 \ln H \cdot I + \beta_5 \ln H \cdot 1/ LBA + \varepsilon$

where	LB	=	length of longest 5-yr-old branch (without growth in 2003)
	ln H	=	natural logarithm of height of seedling (cm)
	1 / LBA	=	reciprocal of local basal area (m^2/ha)
	I	=	indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$			

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-5.0377	16.5050			
ln H	3.1724	4.0690	60	2.18	0.1451
1 / LBA	-593.79	235.81	60	6.34	0.0145
I	-33.9981	14.3174	60	5.64	0.0208
ln H • I	177.56	56.2996	60	9.95	0.0025
ln H • LBA	6.5068	3.2657	60	3.97	0.0509

At both sites, the extent of the longest 5-yr-old branch according to the regression models was greatest in lodgepole pine, in taller seedlings, and at low overstory densities, except for small lodgepole pine seedlings, which had smaller branches at low overstory densities than at high overstory densities (Figs. 17-18; Tabs. 8-9). At Twin Lakes, the 5-year-old branch of small lodgepole pine seedlings was shorter than that of ponderosa pine seedlings, however, it was longer in tall seedlings (p-value = 0.0025 from an interaction between species and initial seedling height). The effect of overstory density also changed with the height of the seedling so that the increase in the length of the longest 5-year-old branch was greater in tall seedlings than in small seedlings of both species (p-value = 0.0509 from an interaction between initial seedling height and local basal area). Small lodgepole pine seedlings even seemed to decrease branch growth at lower local basal areas.

Overall, differences between species were not great, and the longest 5-year-old branch was 46 cm in ponderosa pine and 38 cm in lodgepole pine at Finley Butte and 33 cm in ponderosa pine and 45 cm in lodgepole pine at Twin Lakes.

Apical Dominance: Ratio of Terminal Leader Growth to Branch Leader Growth

Apical dominance is defined as the "preferential growth of a plant shoot (or root) from the apical or terminal meristem and the corresponding suppression of lateral subtending meristems and branches" (Aarssen 1994). In this section, apical dominance is defined as the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except the current. Only seedlings that had a 5-yr-old branch were included in the analysis. Apical dominance in the following section will be defined as the ratio of the length of the terminal leader to the length of the longest new lateral of the same year.

Lateral growth of the longest 5-yr-old branch increased relative to the apical growth of the main stem, i.e. the apical dominance ratio decreased, as local basal area and seedling height increased (Figs. 19-20; Tabs. 10-11). Small seedlings at all of the investigated overstory densities had an apical dominance of >1 (i.e. the height growth of the main stem was greater than the lateral growth of the longest 5-year-old branch). Tall seedlings experiencing an overstory
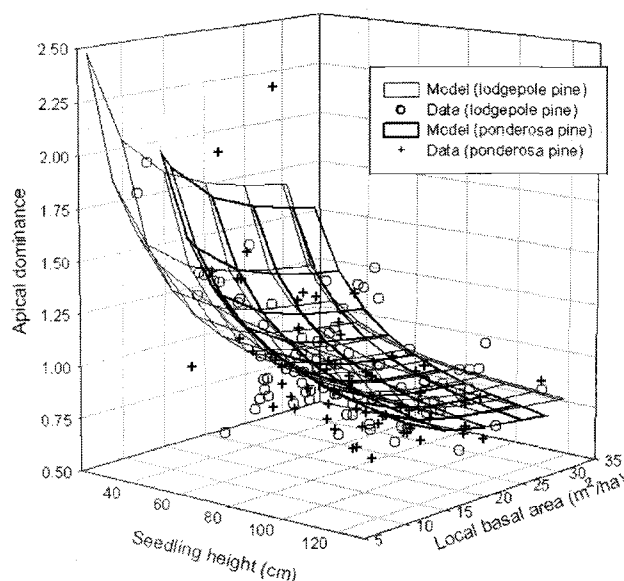
Figure 19: Apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except the current) at Finley Butte ($R^2 = 0.39$)

Table 10: Multiple linear regression model of apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except the current) at Finley Butte

$$\ln AD_{1999\text{-}2002} = \beta_0 + \beta_1\, 1/H + \beta_2\, 1/LBA + \beta_3\, I + \beta_4\, 1/H \cdot I + \varepsilon$$

where $\ln AD_{1999\text{-}2002}$ = natural logarithm of apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except for the current)

$1/H$ = reciprocal of height of seedling (cm)

$1/LBA$ = reciprocal of local basal area (m^2/ha)

I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine

$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-0.3888	0.06561			
1/ H	16.0876	2.9230	68.31		< 0.0001
1 / LBA	2.9463	0.6458	20.82		< 0.0001
I	-0.2653	0.08701	9.30		0.0027
1/ H • I	24.9455	6.9016	13.06		0.0004
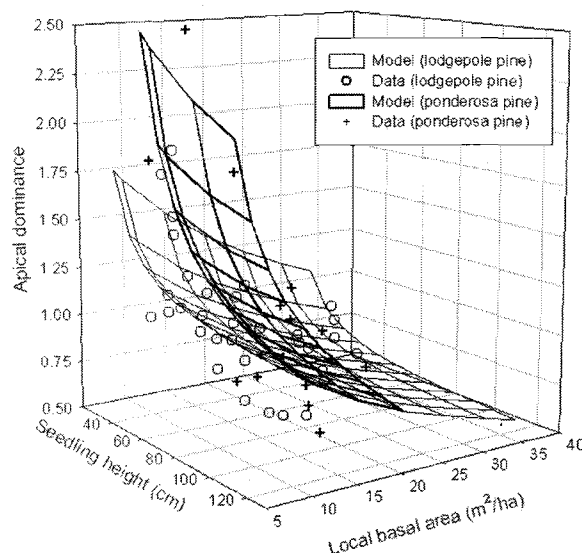
Figure 20: Apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except for the current) at Twin Lakes ($R^2 = 0.39$)

Table 11: Multiple linear regression model of apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 4-yr growth period) at Twin Lakes

$$\ln AD_{1999\text{-}2002} = \beta_0 + \beta_1\, 1/H + \beta_2\, \text{sqrt LBA} + \beta_3\, I + \beta_4\, 1/H \cdot I + \varepsilon$$

where $\ln AD_{1999\text{-}2002}$ = natural logarithm of apical dominance (the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 4-yr growth period)

$1/H$ = reciprocal of height of seedling (cm)

sqrt LBA = square root of local basal area (m²/ha)

I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine

$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.4935	0.1866			
1/ H	11.9626	4.1058	44	31.69	< 0.0001
sqrt LBA	-0.1799	0.05002	44	12.93	0.0008
I	-0.2827	0.1534	44	3.39	0.0722
1/ H • I	37.3649	10.7662	44	12.04	0.0012

> 10 m²/ha at Finley Butte and tall seedlings at all overstory densities at Twin Lakes, however, shifted their growth towards increasing crown width relative to height growth, thereby reducing apical dominance. At both sites, the effect of seedling height on apical dominance was different in both species (p-values = 0.0004 and 0.0012, respectively, for the interaction between species and seedling height). According to the regression model, small ponderosa pine seedlings at Finley Butte had higher apical dominance than small ponderosa pine seedlings but the opposite was found in tall seedlings. At Twin Lakes, apical dominance in ponderosa pine seedlings was higher than ponderosa pine at all measured seedling heights but the difference decreased with increasing seedling height.

Change in Apical Dominance

Apical dominance in the previous section was defined as the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr growth period except the current. In this section, apical dominance is defined as the ratio of the length of the terminal leader to the length of the longest new lateral of the same year. Apical dominance > 1 means that the growth of the terminal leader exceeded that of the longest new lateral of the same year. Only trees that had established before 1990 at Finley Butte and before 1992 at Twin Lakes (according to their minimum age) were analyzed (i.e. one and two years before stand density reduction). Apical dominance was defined as zero for any tree that had not produced any lateral branches in the specific year. Therefore, an increase in mean apical dominance could also have resulted from the production of whorl branches in more seedlings in that year. Height classes are determined from seedling height in 2003, i.e. at time of measurement.

At Finley Butte, mean apical dominance in ponderosa pine seedlings increased gradually after stand density reduction in 1991 and 1994 (Fig. 21). Mean apical dominance decreased after a peak in 1999 in all but the smallest height class. Mean apical dominance in lodgepole pine also increased after the first silvicultural treatment in 1990 and decreased after peaks in 1995, 1997, and 1998, respectively, depending on height class (Fig. 22). Only few seedlings were available to

calculate averages, and there is a high variation in the observed mean apical dominances in lodgepole pine.
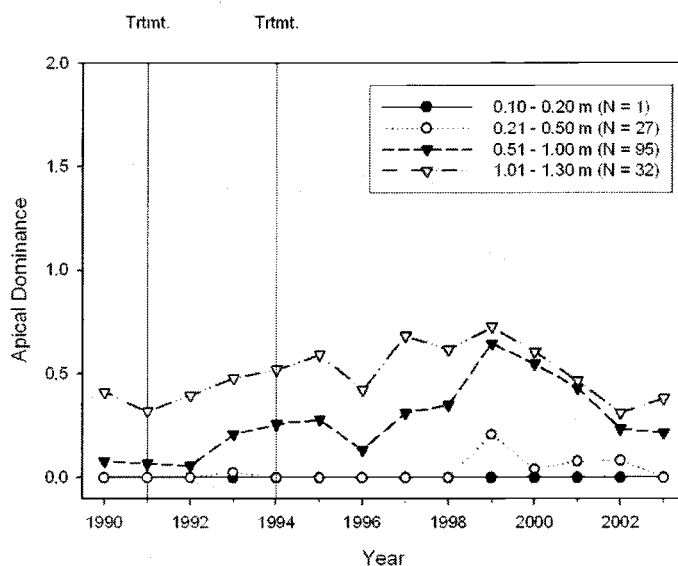
Figure 21: Apical dominance of ponderosa pine seedlings at Finley Butte
(only seedlings originating before 1990)
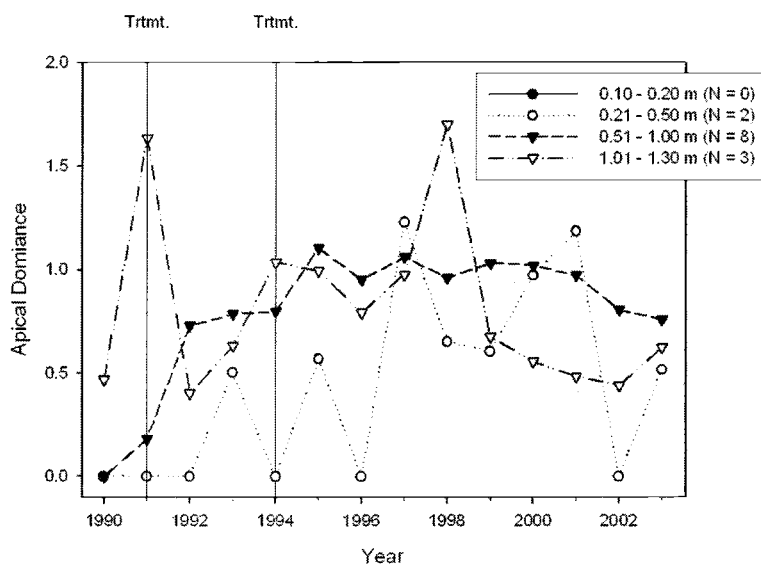
Figure 22: Apical dominance of lodgepole pine seedlings at Finley Butte
(only seedlings originating before 1990)
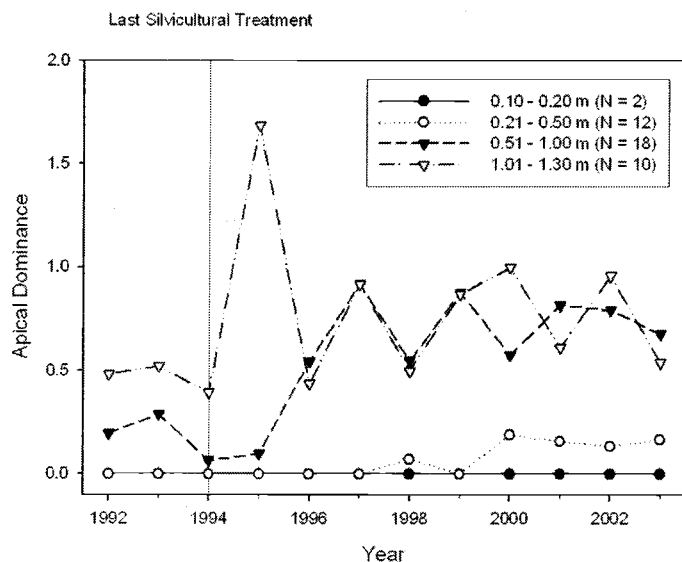
Figure 23: Apical dominance of ponderosa pine seedlings at Twin Lakes
(only seedlings originating before 1992)
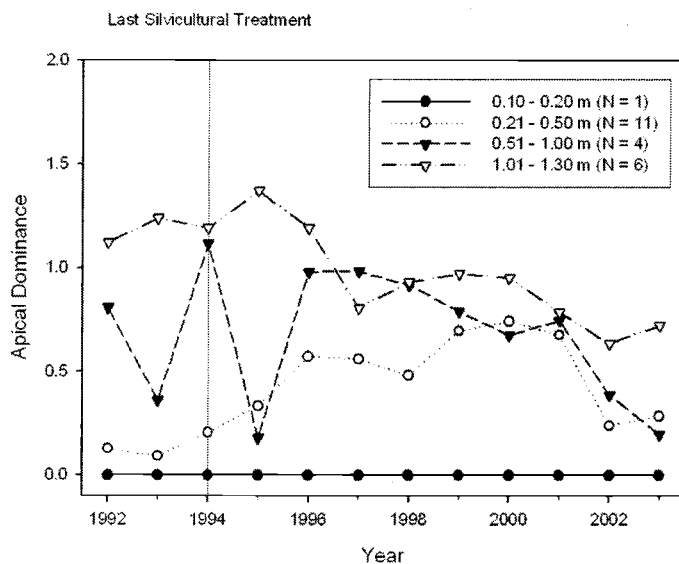
Figure 24: Apical dominance of lodgepole pine seedlings at Twin Lakes
(only seedlings originating before 1992)

At Twin Lakes, mean apical dominance in ponderosa pine seedlings increased very strongly in the now tallest seedlings one year after silvicultural treatment (Fig. 23). Ponderosa pine seedlings that are now between 0.51-1.00 m tall, increased mean apical dominance two years after the silvicultural treatment. Whether there is a decline in apical dominance in recent years is difficult to judge from the data, because there is much variation between the years. Mean apical dominance in lodgepole pine seems to have declined after silvicultural treatment, except for seedlings now 0.21 - 0.50 m tall which increased their mean apical dominance up to a peak in 2000 after which it declined again (Fig. 24). Seedlings smaller 0.20 m had not developed any lateral branches in both species and at all sites and no mean apical dominance could be calculated.

Foliage Morphology

Number of Needle Fascicles on the Main Stem

At both sites, the number of needle fascicles on the main stem was lower in ponderosa pine seedlings, in shorter trees, and decreased gradually in trees experiencing higher overstory density (Figs. 25-26; Tabs. 12-13). At Finley Butte, seedling height and local basal area influenced the number of needle fascicles on a seedling (all p-values < 0.0001), but there was no interaction between explanatory variables. Tall lodgepole pine seedlings at lower stand basal areas had the most needle fascicles on their main stem, the highest number being > 350.

At Twin Lakes, the effect of seedling height and overstory density on the number of needle fascicles on the main stem was greater in lodgepole pine than in ponderosa pine (p-value = 0.0019 from the interaction between species and initial seedling height and p-value = 0.0438 from the interaction between species and local basal area). At both sites, the number of needle fascicles on the main stem increased greatest at approximately 20 m²/ha in lodgepole pine and 15 m²/ha in ponderosa pine.
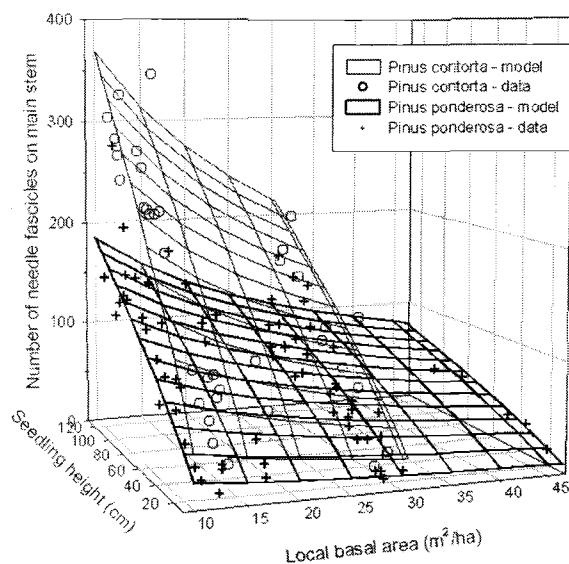
Figure 25: Number of needle fascicles on main stem at Finley Butte (R^2 = 0.88)

Table 12: Multiple linear regression model of number of needle fascicles on main stem at Finley Butte

ln NF = β_0 + β_1 ln H + β_2 sqrt LBA + β_3 I + ϵ			

where 　ln NF 　= 　natural logarithm of number of needle fascicles on the main stem
　　　　ln H 　 = 　natural logarithm of initial height of seedling (cm)
　　　　sqrt LBA = 　square root of local basal area (m²/ha)
　　　　I 　　 = 　indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\epsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	2.7639	0.1784	105		
ln H	0.7966	0.03435	105	537.60	< 0.0001
sqrt LBA	-0.2310	0.02594	105	79.26	< 0.0001
I	-0.6905	0.05791	105	142.18	< 0.0001
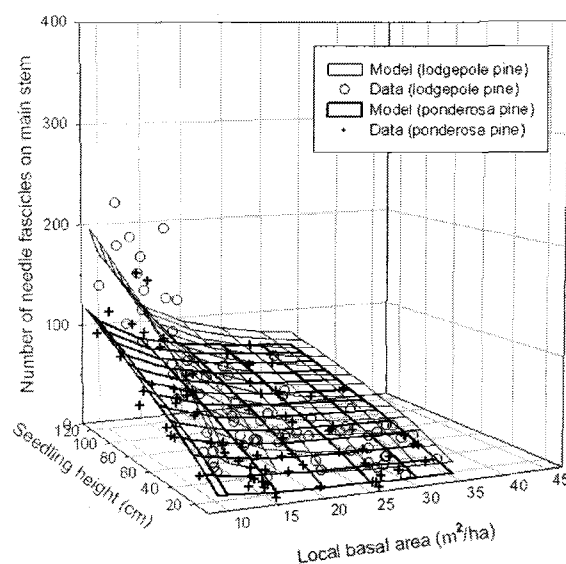
Figure 26: Number of needle fascicles on main stem at Twin Lakes (R^2 = 0.80)

Table 13: Multiple linear regression model of number of needle fascicles on main stem at Twin Lakes

ln NF = β_0 + β_1 log H + β_2 1/LBA + β_3 I + β_4 ln H • I + β_5 1/LBA • I + ε

where   ln NF   =   natural logarithm of number of needle fascicles on the main stem
           1/LBA =   reciprocal of local basal area (m²/ha)
           ln H   =   natural logarithm of initial height of seedling (cm)
           I   =   indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.2182	0.2104			
ln H	0.5686	0.05642	144	321.93	< 0.0001
1/LBA	11.5804	1.5415	144	65.48	< 0.0001
I	-1.2197	0.2953	144	17.06	< 0.0001
ln H • I	0.2428	0.07691	144	9.96	0.0019
1/LBA • I	-4.6528	2.2871	144	4.14	0.0438

Number of Needle Fascicles on the Terminal Leader from 2002

Species differ in their periods of seasonal growth (Fowells 1941). To compare species, therefore, the needles remaining from the 2002 growing season were believed to be a better indicator of number of needles produced on a per year basis than the number at the time of measurement (July to October 2003).

Lodgepole pine seedlings at Finley Butte had more needle fascicles on their terminal leader from the previous year than ponderosa pine seedlings but, except for seedlings at the lowest overstory densities and the smallest seedlings, ponderosa pine seedlings had a higher number of needle fascicles at Twin Lakes (Figs. 27-28; Tabs. 14-15). Although the number of needle fascicles was similar at both sites in ponderosa pine, in lodgepole pine the regression model suggests up to 30 more needle fascicles in tall seedlings at low overstory densities at Finley Butte than at Twin Lakes. At Finley Butte, both seedling height and stand basal area had a significant effect on the number of needle fascicles on the terminal (all p-values < 0.0001) and more needle fascicles are produced in taller seedlings and in seedlings experiencing a lower stand density. There were no significant interactions between the explanatory variables. At Twin Lakes, the effects of seedling height and stand basal area on the number of needle fascicles on the terminal leader differed by species (p-values < 0.0001 and p-value = 0.0061, respectively, for the interactions between species and initial seedling height and species and local basal area). Increases in the number of needle fascicles were gradual over the investigated overstory densities but this increase was steeper in lodgepole pine at both sites.
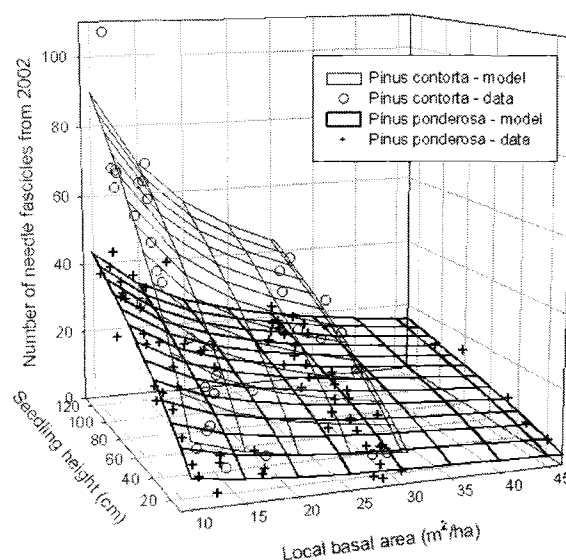
Figure 27: Number of needle fascicles on the terminal leader in 2002 at Finley Butte (R^2 = 0.76)

Table 14: POISSON log-linear regression model of number of needle fascicles on the terminal leader in 2002 at Finley Butte

$\ln \mu = \beta_0 + \beta_1 \log H + \beta_2 \log LBA + \beta_3 I$					
where	μ	= expected mean number of needle fascicles on terminal leader from 2002			
	$\ln H$	= natural logarithm of initial height of seedling (cm)			
	$\ln LBA$	= natural logarithm of local basal area (m²/ha)			
	I	= indicator for species; 0 for lodgepole pine, 1 for ponderosa pine			
$Y \sim$ Poisson (μ); $E(Y) = \mu$; Var $(Y) = \mu \cdot \Phi$;					

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	2.8528	0.2458			
log H	0.6472	0.0407	105	300.65	< 0.0001
log LBA	-0.6540	0.0606	105	123.46	< 0.0001
I	-0.7292	0.0524	105	192.81	< 0.0001
Scale	1.3213	Deviance	183.3143	Dev. / df (Φ)	1.7459
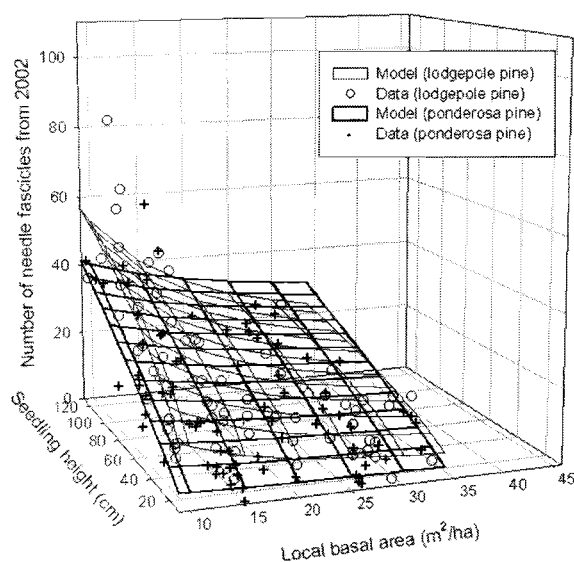
Figure 28: Number of needle fascicles on the terminal leader in 2002 at Twin Lakes ($R^2 = 0.62$)

Table 15: POISSON log-linear regression model of number of needle fascicles on the terminal leader in 2002 at Twin Lakes

$\ln \mu = \beta_0 + \beta_1 \log H + \beta_2 \log LBA + \beta_3 I + \beta_4 \log H \cdot I + \beta_5 \log LBA \cdot I + \varepsilon$

where μ =   expected mean number of needle fascicles on the terminal leader from 2002
     $\ln LBA$ =   logarithm of local basal area (m^2/ha)
     $\ln H$ =   logarithm of initial height of seedling (cm)
     I =   indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$Y \sim$ Poisson (μ); $E(Y) = \mu$; Var $(Y) = \mu \cdot \Phi$;

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	3.2476	0.3788			
ln H	0.4648	0.0540	143	233.47	< 0.0001
ln LBA	-0.6714	0.1038	143	33.72	< 0.0001
I	-3.0596	0.6155	143	25.00	< 0.0001
ln H • I	0.3685	0.0896	143	17.34	< 0.0001
ln LBA • I	0.4315	0.1575	143	7.54	0.0061
Scale	1.6106	**Deviance**	370.9536	**Dev. / df (Φ)**	2.5941

Needle Fascicle Density per 10 cm Stem Length

In contrast to the number of needle fascicles, needle fascicle density takes the length of the shoot into account. Needle fascicle density on the main stem was calculated as the number of needle fascicles per 10 cm stem length.
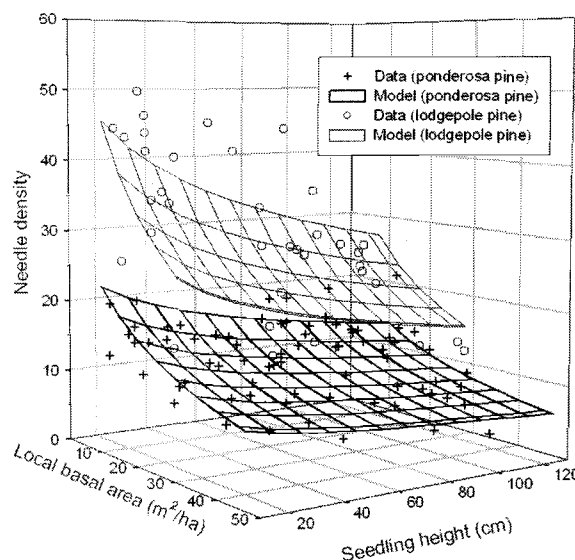
Figure 29: Needle fascicle density per 10 cm on the main stem at Finley Butte (R^2 = 0.78)

Table 16: Multiple linear regression model of needle fascicle density on main stem at Finley Butte

ln ND_10 = β_0 + β_1 sqrt H + β_2 sqrt LBA + β_3 I + ε

where ln ND_10 = natural logarithm of needle fascicle density on the main stem
(number of needle fascicles per 10 cm of the main stem)
sqrt H = square root of height of seedling (cm)
sqrt LBA = square root of local basal area (m²/ha)
I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	4.7654	0.1375			
sqrt H	-0.06404	0.009964	105	41.31	< 0.0001
sqrt LBA	-0.2334	0.02540	105	84.45	< 0.0001
I	-0.6878	0.05667	105	147.32	< 0.0001
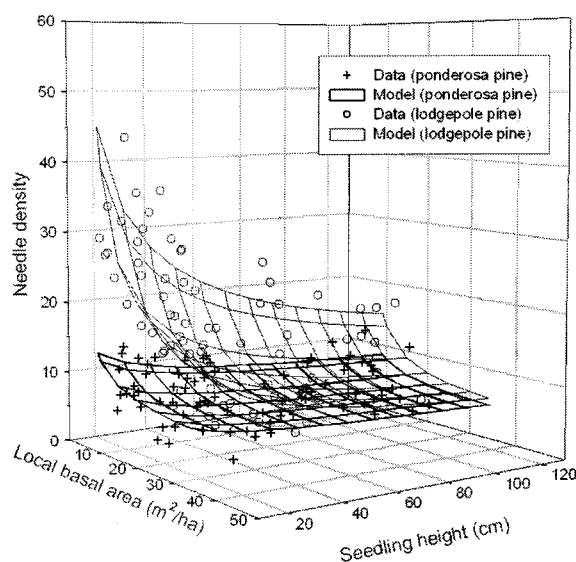
Figure 30: Needle fascicle density per 10 cm on the main stem at Twin Lakes ($R^2 = 0.67$)

Table 17: Multiple linear regression model of needle fascicle density on main stem at Twin Lakes

$\ln ND\_10 = \beta_0 + \beta_1 \log H + \beta_2\ 1/LBA + \beta_3\ I + \beta_4 \log H \cdot I + \beta_5\ 1/\ LBA \cdot I + \varepsilon$

where $\ln ND\_10 =$ natural logarithm of needle fascicle density on the main stem
(number of needle fascicles per per 10 cm of the main stem)

$\ln H \quad =$ natural logarithm of height of seedling (cm)

$1 / LBA \quad =$ reciprocal of local basal area (m^2/ha)

$I \quad\quad =$ indicator for species; 0 for lodgepole pine, 1 for ponderosa pine

$\varepsilon \sim N(0, \sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	3.5208	0.2104			
ln H	-0.4314	0.05642	144	65.02	< 0.0001
1/LBA	11.5804	1.5415	144	65.48	< 0.0001
I	-1.2197	0.2953	144	17.06	< 0.0001
ln H • I	0.2428	0.07691	144	9.96	0.0019
1/ LBA • I	-4.6528	2.2871	144	4.14	0.0438

At both sites, needle fascicle density per 10 cm stem length was significantly higher in lodgepole pine than in ponderosa pine seedlings (Figs. 29-30, Tab. 16-17). In both species, it was lower in tall seedlings and at a high overstory density (all p-values < 0.0001). At Finley Butte, needle fascicle density was about twice as high in lodgepole pine seedlings of all measured heights and at all overstory densities compared to ponderosa pine seedlings. At Twin Lakes, the decrease of needle fascicle density with seedling height was steeper in tall lodgepole pine than in tall ponderosa pine seedlings (p-value = 0.0019 for the interaction between species and seedling height) as was the decrease with overstory density (p-value = 0.0438 from the interaction between species and local basal area).

Needle Fascicle Density on the New Terminal Leader in 2003

Apical height growth and needle growth in pine do not cease until early September (Turner 1956). At the time of measurement between July and October 2003, a few seedlings may have already shed their needles from the previous year. To determine the maximum needle density these species produce under the given conditions, needle fascicle density per 1 cm shoot length was calculated and analyzed for the 2003 growing season.

At both sites, lodgepole pine produced a higher number of needle fascicles than ponderosa pine, and needle fascicle density on the new terminal leader was lowest at low overstory densities in both species. At Finley Butte, small seedlings of both species had a higher needle fascicle density than taller seedlings (p-value = 0.0231), but this effect seemed to level off in the tallest seedlings (Fig. 31; Tab. 18). Needle fascicle density also increased with increasing overstory density (p-value < 0.0001), but also seemed to level off at the highest measured local basal area values.

At Twin Lakes, the effect of overstory density was stronger in lodgepole pine than in ponderosa pine (p-value = 0.0033 for the interaction between species and local basal area) (Fig. 32; Tab. 19). Lodgepole pine seedlings reduced their needle fascicle density by a third from 34 to m^2/ha to 9 m^2/ha in local basal area whereas ponderosa pine produced around five needle fascicles per 1 cm shoot length at all investigated overstory densities. There was no effect of seedling height on the density of needle fascicles on the terminal leader at Twin Lakes.
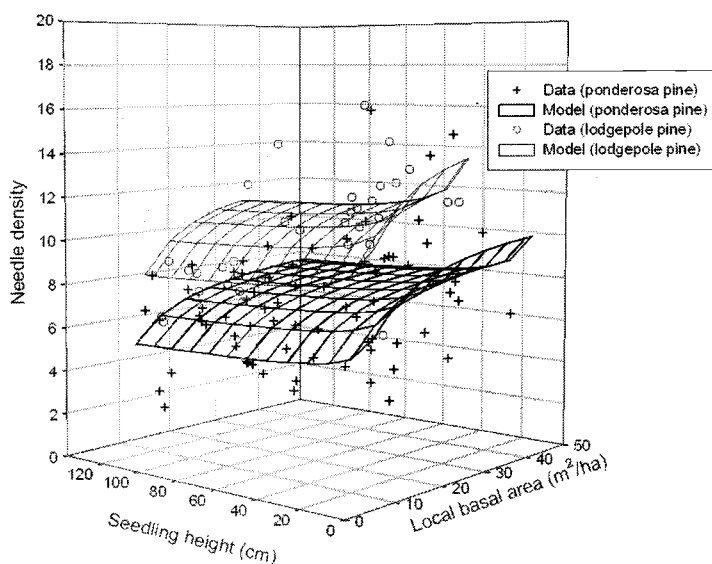
Figure 31: Needle fascicle density per cm on the terminal leader at Finley Butte ($R^2 = 0.41$))

Table 18: Multiple linear regression model of needle fascicle density per cm on the terminal leader at Finley Butte

sqrt ND 2003 = β_0 + β_1 1/H + β_2 1/LBA + β_3 I + ε

where	sqrt ND	2003 =	square root of needle fascicle density on terminal shoot in 2003 (number of needle fascicles / terminal shoot length)
	1/ H	=	reciprocal of height of seedling (cm)
	1/ LBA	=	reciprocal of local basal area (m^2/ha)
	I	=	indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$			

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	3.5754	0.1403			
1/ H	3.8935	1.6885	103	5.32	0.0231
1/ LBA	-7.3742	1.6273	103	20.53	< 0.0001
I	-0.6479	0.08783	103	54.42	< 0.0001
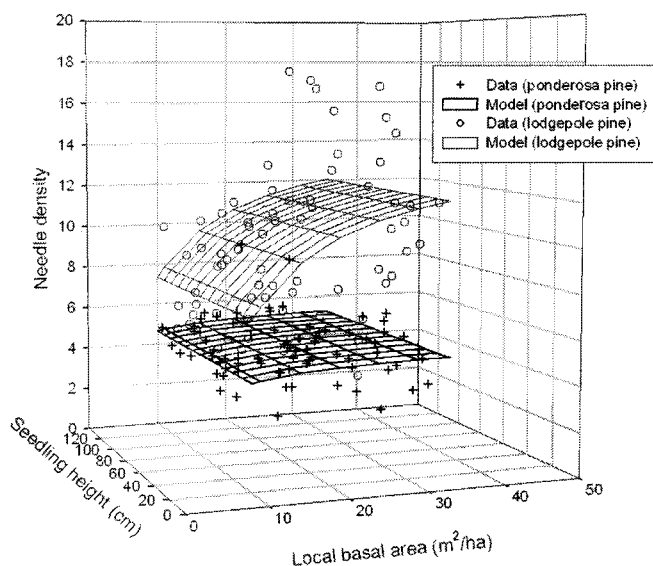
Figure 32: Needle fascicle density per cm on the terminal leader at Twin Lakes ($R^2 = 0.67$)

Table 19: Multiple linear regression model of needle fascicle density on the terminal leader at Twin Lakes

ln ND 2003 = β_0 + β_1 1 / LBA + β_2 I + β_3 1/ LBA • I + ϵ					
where ln ND 2003 = natural logarithm of needle fascicle density on terminal shoot in 2003 (number of needle fascicles / terminal shoot length)					
1/ LBA = reciprocal of local basal area (m²/ha)					
I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine					
$\epsilon \sim N(0,\sigma^2)$					

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	2.6690	0.07518			
1/ LBA	-5.8907	1.0262	144	22.63	< 0.0001
I	-0.9357	0.1054	144	78.76	< 0.0001
1/ LBA • I	4.5495	1.5203	144	8.95	0.0033

Needle Length

Needles on ponderosa pine seedlings were as much as three times as long as needles on lodgepole pine seedlings at both sites (Fig. 33-34; Tab. 20-21). The longest measured ponderosa pine needle was 12.8 cm at Finley Butte and 14.6 cm at Twin Lakes. Lodgepole pine needles reached a length of up to 5.8 cm at Finley Butte and 6.5 cm at Twin Lakes.
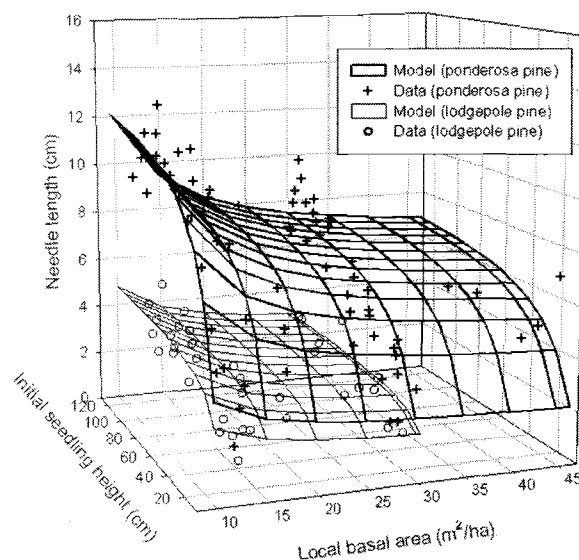
Figure 33: Needle length in 2002 at Finley Butte (R^2 = 0.81)

Table 20: Multiple linear regression model of needle length at Finley Butte

ln NL 2002 = β_0 + β_1 1/H + β_2 1/LBA + β_3 I + β_4 1/H • I + ε

where   ln NL 2002   = natural logarithm of number needle length of needles from 2002
          1/H   = reciprocal of initial height of seedling (cm)
          1/LBA   = reciprocal of local basal area (m²/ha)
          I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.8850	0.08423	105		
1/H	-4.9336	1.1490	105	118.59	< 0.0001
1/LBA	7.3086	0.9041	105	65.34	< 0.0001
I	0.9671	0.07091	105	186.02	< 0.0001
1/H • I	-6.6556	1.5190	105	19.20	< 0.0001
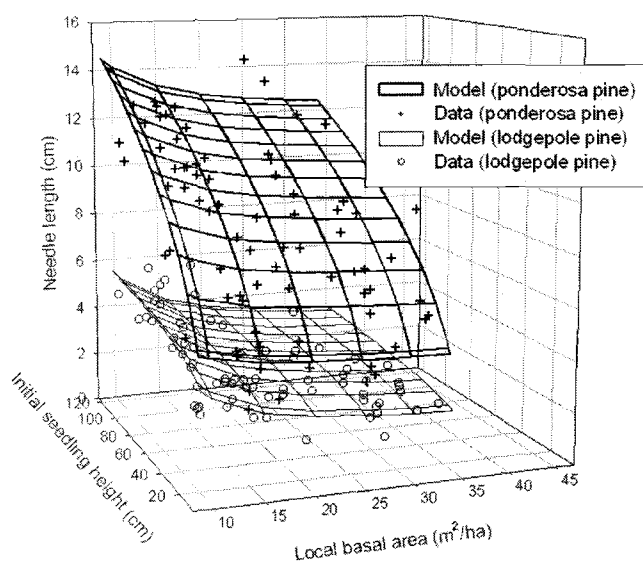
Figure 34: Needle length in 2002 at Twin Lakes (R^2 = 0.83)

Table 21: Multiple linear regression model of needle length at Twin Lakes

$$\ln NL\ 2002 = \beta_0 + \beta_1 \log H + \beta_2\ 1/LBA + \beta_3\ I + \beta_4 \log H \cdot I + \beta_5\ 1/LBA \cdot I + \varepsilon$$

where   ln NL 2002   = natural logarithm of number of needle length of needles from 2002
           ln H   = natural logarithm of initial height of seedling (cm)
           1/LBA   = reciprocal of local basal area (m^2/ha)
           I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0, \sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.5305	0.1199	143		
ln H	0.1153	0.03179	143	118.59	< 0.0001
1/LBA	6.1007	0.9393	143	32.20	< 0.0001
I	0.1325	0.1720	143	0.59	0.4423
ln H • I	0.2578	0.04485	143	33.04	< 0.0001
1/LBA • I	-4.2543	1.4004	143	9.23	0.0028

At both sites and in both species needle length was negatively affected by overstory density (p-values < 0.0001). At Twin Lakes, the influence of the overstory also differed between the two species (p-value = 0.0028 from the interaction between species and local basal area). Tall seedlings of both species and at both sites had greater needle length than small seedlings (p-values < 0.0001), and increase in needle length with height differed between species (p-values < 0.0001 from the interaction between species and seedling height).

Needle Retention and Longevity

At Finley Butte, the smallest trees and trees experiencing the lowest overstory densities had fewer years of needle retention than tall trees and trees at high overstory densities (p-values < 0.0001) (Fig. 35, Tab. 22). The reduction in needle retention with decreasing seedling height was greater in lodgepole pine than in ponderosa pine seedlings (p-value = 0.0340 for the interaction between species and initial seedling height). However, this effect of seedling height and overstory density on needle retention in both species occurred very abruptly at the lowest overstory densities and in the smallest seedlings. In general, needle retention appeared to be constant over a wide range of seedling heights and overstory densities.

At Twin Lakes, patterns in needle retention were not significantly different between the species (p-value > 0.05) (Fig. 36, Tab. 23). Needle retention increased with greater seedling height (p-value = 0.0013) and reduction in local basal area (p-value = 0.0149), and the effect was more gradual than at Finley Butte. In general, needle retention appeared shorter at Twin Lakes than at Finley Butte.
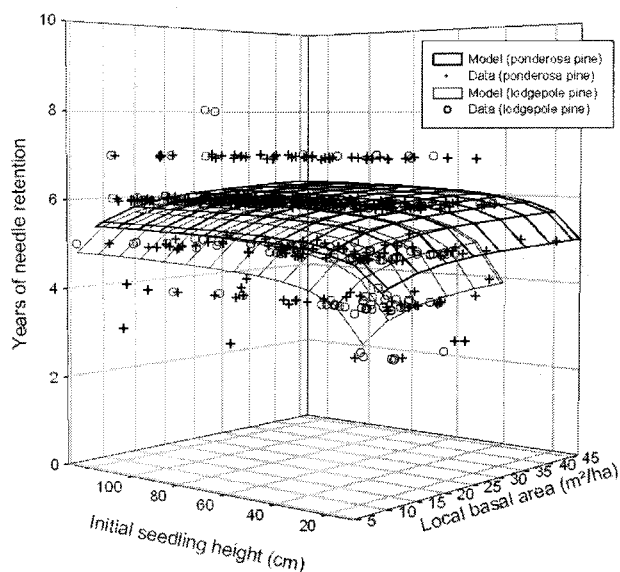
Figure 35: Needle retention at Finley Butte (R^2 = 0.22)

Table 22: Multiple linear regression model of needle retention at Finley Butte

ln NR 2002 = β_0 + β_1 1/H + β_2 1/LBA + β_3 I + β_4 1/H • I + ϵ

where   ln NR 2002   = natural logarithm of needle retention in 2003
            1/H   = reciprocal of initial height of seedling (cm)
            1/LBA   = reciprocal of local basal area (m^2/ha)
            I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\epsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.8686	0.03082			
1/H	-3.6715	0.5113	506	78.70	< 0.0001
1/LBA	-1.6359	9.3325	506	24.21	< 0.0001
I	0.009650	0.02534	506	0.15	0.7035
1/H • I	1.4202	0.6681	506	4.52	0.0340
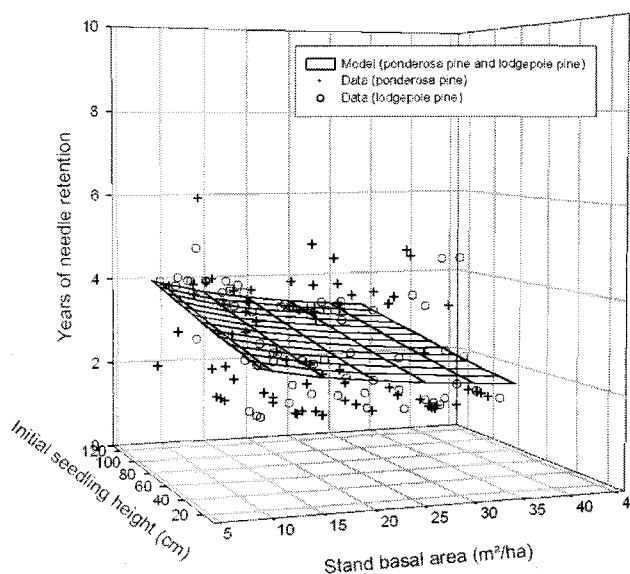
Figure 36: Needle retention at Twin Lakes ($R^2 = 0.13$)

Table 23: Multiple linear regression model of needle retention at Twin Lakes

ln NR 2002 = β_0 + β_1 H + β_2 ln LBA + ϵ

where   ln NL 2002   = natural logarithm of needle retention in 2003
          H   = initial height of seedling (cm)
          ln LBA   = natural logarithm of local basal area (m2/ha)
          I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\epsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.4061	0.1937	146		
H	0.002407	0.000732	146	10.81	0.0013
ln LBA	-0.1578	0.06402	146	6.07	0.0149

Discussion

Seedling Density

Factors determining the success of natural regeneration are the abundance of seeds produced, their viability, and the rates of predation, germination, and survival. Although many millions of seeds can be distributed from ponderosa pine trees (Foiles and Curtis 1973), in central Oregon only few survive the first years after establishment due to extremes in temperature and low water availability (Keyes 2001). Although growth rate and growth form can be key to survival (Messier et al. 1999a, Canham and Marks 1985), in the long term survival can be more important to forest succession than seedling growth (Wright et al. 1998, Chen 1997). Lodgepole produces good seed crops every 1-3 years with light crops in between, and in eastern Oregon, a serotinous cone habit is not common (Lotan and Critchfield 1990). Seedfall in Oregon, therefore, can range from about 35000 to over 1.2 million/ha per year (Dahms 1963). Low seedling density of tall lodgepole pine seedlings and their low minimum age in this study may therefore not be the result of crop failure or seed storage, but the result of low survival in the understory caused by predation or unfavorable abiotic conditions in the understory. In contrast to ponderosa pine germinants which can develop a root system that reaches depths up to 50 cm within a few months of germination (Oliver and Ryker 1990), mortality caused by drought is common in 1-year-seedlings of lodgepole pine because of a relatively shallow root system (Lotan and Critchfield 1990).

No clear relationship between seedling density and stand basal area has been found in this study (Figs. 5-8), and the literature is ambiguous as well. Although density and height of pine regeneration have been found to correlate with stand basal area (Messina and Jenkins 2000, McDonald 1976), others have not found a correlation (Morin and Laprise 1997). Greene et al. (1999) propose a threshold below which advance regeneration density and stand basal area are correlated, and above which overstory dominance results in no significant correlation. Most research seems to show that seedling growth is more responsive to canopy openings than seedling density (Greene et al. 1999). However, even small openings produce significant increases in density and height growth in ponderosa pine although a potential inhibitory effect of

overstory ponderosa pine trees has been found to extend at least 12 m and persist 4 years after tree removal (McDonald 1976).

At the stand scale, presence and germination of seed and survival of germinants strongly depend on seed production and climate, and both vary significantly from year to year (Clark et al. 1999). Overstocking is a common problem in even-aged lodgepole pine stands resulting in growth stagnation and higher susceptibility to insect outbreaks and high-intensity fires. In lodgepole pine stands between 5-20 years of age, Cole (1975) suggests stocking levels of not more than 1240 – 1980 trees/ha. These densities are exceeded in many subplots in this study, especially at low overstory densities. Stocking, therefore, seems adequate if not overabundant if establishment of a new tree regeneration had been the goal of the implemented silvicultural treatments. Further treatments to reduce densities, however, may be needed in the future to avoid overstocking and its consequences.

Stem Morphology

Species differing more strongly in their shade-tolerance have very different resource partitioning strategies, with greater investment of biomass into foliage in shade-tolerant species than in shade-intolerant species (Hara et al. 1991, King 1991, Williams et al. 1999). This difference in allocation corresponds to a reduction in stem biomass and volume growth, and a lower competitive ability in more open habitats (Niinemets 1998). In this study on the responses of two pine species that are both classified as shade-intolerant, there was no significant difference in the H/D ratio at Twin Lakes and only a minor difference at Finley Butte. So although differences in the branch morphology and investments into foliage between the two species were found, this is not represented by a change in diameter growth compared to height growth.

H/D has been consistently observed to increase with greater stand densities, and mature trees with a ratio of more than 100 are considered less resistant to mechanical forces such as wind or frozen precipitation (Smith et al. 1997). The highest measured H/D ratios in this study were approximately 120, but, according to the regression model, the estimated mean H/D was not higher than 75 for the tallest seedlings at the highest overstory densities. As was the case in

this study, Williams et al. (1999) also found that the H/D ratio of lodgepole pine seedlings increased with decreasing light availability and increasing seedling height.

Ruel et al. (2000) mention that more research is needed on H/D responses and the mechanisms involved. This ratio has been successfully applied in vegetation management studies to measure the relative vigor of seedlings and saplings under varying intensities of competing vegetation (Brandeis et al. 2001). However, its sensitivity makes it a poor predictor in this setting because both height and diameter growth can be influenced by many factors, such as climate, tree age, and genotype (Mustard and Harper 1998 in Ruel et al. 2000), and these could not be controlled.

Branch and Crown Morphology

The number of nodal and internodal primary branches have been found to be good indicators of seedling vigor for many species (Ruel et al. 2000) as they are an indication for crown development and associated leaf area. In this study, both species at Twin Lakes and ponderosa pine seedlings at Finley Butte had more primary branches and whorl branches at low overstory densities. Analogous to the findings of Clauveau et al. (2002), seedling height is an important variable that influences the effect of other explanatory variables on the response. The response of number of primary branches to overstory density, although only slight, was significantly different for seedlings of different heights, and in this study this effect of height on the response often also differed by species. Small seedlings have the tendency to allocate more carbohydrates into stem growth than into crown development, and in this study, the smallest seedlings of approximately 0.10 cm height had most often no primary branches developed. A disadvantage of a high number of primary branches may be the effect of self-shading which can result in foliage of lower branches being less productive and less capable of both supporting themselves and exporting carbohydrates.

Tall lodgepole pine seedlings had up to 3x as many primary branches than ponderosa pine and produced 3x as many whorl branches in 2002. Therefore, lodgepole pine seems to have more primary branches per tree by producing more branches per whorl in a specific year.

Vigorous trees produce more growth flushes than weak trees (Oliver and Larson 1996) and Ruel et al. (2000) suggest 3-4 nodal branches and 3 internodal branches as an indicator of good vigor in understory conditions for lodgepole seedlings over 1.00 m height. They also cite an unpublished study by Comeau et al. who suggest that less than 3 whorl branches per year indicate a stressed lodgepole pine seedling. In 2002, the tallest lodgepole pine seedlings in this study produced on average 3+ whorl branches at a local basal area of more than 12 m^2/ha at Twin Lakes and 17 m^2/ha at Finley Butte. Ponderosa pine develops only one whorl of branches per year and only one ponderosa pine tree at each site produced 3 whorl branches in 2002. On average, lodgepole pine seedlings had at least three whorl branches in tall seedlings in 1999 at Finley Butte and in 2001 at Twin Lakes, approximately 5-7 years after the last stand density reduction. Rebuilding of the overstory canopy may be responsible for a subsequent decline in the mean number of whorl branches after 1999.

Only seedlings that had a 5-year-old branch were included in the analysis of branch length (crown width) and, although statistically significant, the change with local basal area and between species was not very great in studied seedlings. This result was not expected, and it may have been that only the more vigorous trees retained a 5-year-old branch, so extending the inference to the entire seedling population at these sites may be unjustified. Of interest may be that this 5-year-old branch was often the only primary branch of many ponderosa pine seedlings, whereas it was just one of many in lodgepole pine. May 1998 (i.e. the year before this lateral was produced) was one of the wettest since weather records began in 1943 at Malheur Experiment Station in eastern Oregon, and precipitation was similarly high in central Oregon (approximately 100 mm; Malheur Experiment Station, Oregon State University http://www.cropinfo.net/weather/weathersummary98.htm, NCDC National Climatic Data Center http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/main.html). This extremely high and unusual rate of precipitation in the spring of 1998 may explain why this primary branch was produced even by ponderosa pine trees which had only very few branches altogether. But it does not explain why there was no growth difference between species and effect of overstory density after five years.

The caveat of reduced inference also applies to one of the apical dominance ratios calculated as the ratio of past periodic growth of the terminal leader to the past periodic growth of

the longest 5-yr-old branch leader. Again, only seedlings with a 5-year-old branch were included in the analysis. For both species and at both sites, the ratio decreased with increasing seedling height (i.e. taller seedlings allocated relatively more resources to lateral branch growth than into height growth than did smaller seedlings). But although apical dominance was higher in ponderosa pine than in lodgepole pine in small seedlings, the opposite was true in tall seedlings. Tall ponderosa pine seedlings, therefore, already seem to develop a wider crown at these heights compared to lodgepole pine of which a narrow crown is a typical characteristic in general (Lanner and Van den Berg 1973).

Apical dominance also decreased with increasing overstory density and trees experiencing higher local basal areas appeared to change their architecture to a more umbrella-like shape typical of low-light conditions following the theory of the maximum seedling height in understory conditions (Messier et al. 1999a). This relationship between light availability and apical dominance depends on the plasticity of a tree. Whereas shade-tolerant species have been found to alter their growth form toward an umbrella shape in forest understory conditions, this plastic response is considered absent or less strong in shade-intolerant species (Williams et al. 1999, Chen et al. 1996). In general, the ratio of terminal leader to branch leader growth can indicate stress from low resource availabilities (Little 1970), and it is regarded as a good indicator of advance regeneration vigor. It is sensitive to light availability, it indicates current and recent growing conditions, and it can easily be measured in the field by simply bending the longest lateral branch of the last whorl up and comparing its length to the length of the leader (S. Parent, unpublished report in Ruel et al. 2000).

After stand density reductions in 1991 and 1994 at Finley Butte and 1994 at Twin Lakes, there was no clear trend in mean apical dominance as defined as the ratio of the length of the terminal leader to the length of the longest lateral over time. In general, seedlings seemed to increase their leader growth compared to their lateral growth after stand density reduction but over time, this ratio decreased again. This may have been caused by a higher production of whorl branches as a response to the treatment and canopy closure over time after the treatments. Only seedlings originating from before silvicultural treatment were averaged and these were few.

Needle Morphology

No physiological or morphological measurements of leaves have been made, e.g., needle dry mass per area or number of stomata, to investigate foliage photosynthetic capacity and whole canopy carbon gain. The results of this study, therefore, only suggest photosynthetic potential by a comparison of certain characteristics and their changes with seedling height and overstory density. In a broad sense, the number of needles, their length, and density all determine the photosynthetic potential of pines (Garrett and Zahner 1973) and although, for example, the number of needle fascicles on the main stem is not an indication of the total number of needle fascicles of a tree, it may still be a valid indicator of vigor. For example, foliage on the main stem of red pine (*Pinus resinosa* Ait.) has been found to be more sensitive to sudden changes in the environment than foliage on lateral branches (Garrett and Zahner 1973). The number of needle fascicles on the main stem also reflects the combined effects of differences in fascicle density per unit length, needle longevity, and annual height growth. In lodgepole pine and ponderosa pine, all cycles of growth of the terminal leader are pre-determined as the number of stem units in the terminal bud produced during the year preceding height growth (Lanner 1976). However, in comparison to ponderosa pine, in lodgepole pine not all needle primordia are set the previous year, but may also initiate during the spring of the year they elongate. This may be an advantage if current growth conditions are exceptionally better during the current season than they have been the previous year.

Differences in height and in overstory density, in general, led to greater responses in foliage of lodgepole pine than ponderosa pine. However, more ponderosa pine seedlings seemed to have established before stand density reduction according to their minimum age (Figs. 1-4). Shade-intolerant species have been found to be less plastic in their response to changes in their environment (Chen 1996), and the strong increase in foliage as well as branches in lodgepole pine may be a result of them being young and highly vigorous in comparison to older and less responsive ponderosa pine seedlings. In addition to having more primary branches, lodgepole pine had more needle fascicles on their main stem and terminal leader except for tall seedlings at high overstory densities at Twin Lakes. Needle density on both the main stem and terminal leader was also greater in lodgepole pine than in ponderosa pine. However, needle length was up to

three times greater in ponderosa pine than in lodgepole pine. Also, ponderosa pine produces generally three needles per fascicle compared to only two in lodgepole pine, and needle retention was a little higher in small ponderosa pine seedlings than in lodgepole seedlings at one of the sites. Any analysis of foliage on the main stem of a seedling, however, does not take foliage on lateral branches into account. Since lodgepole pine had more lateral branches than ponderosa pine, it may have more leaf area per tree.

Needle density on the main stem increased but needle density on the terminal leader decreased with reduction in overstory density. Although seedlings had a higher number of needles remaining on the terminal leader at the lowest overstory densities, greater absolute height growth in tall seedlings may have resulted in lower needle density per unit length. Surprisingly, there is no difference in seedlings of different heights except for an abrupt increase in needle density on the terminal leader in seedlings smaller than 0.30 m at Finley Butte. Needle density on the terminal leader was analyzed on the current shoot between July to October 2003. Time of needle primordia development and shoot elongation is not identical, and needle density can be high if environmental conditions during shoot elongation are less favorable than they were during primordia development (Oliver and Larson 1996). Time of shoot and needle elongation may also differ with species, overstory density, and seedling height, thereby influencing needle density at time of measurement. For example, more soil water may be available to seedlings at low overstory densities after stand density reduction, and growth may continue longer during the given year (Zahner and Whitmore 1960 in Smith et al. 1997). In loblolly pine, needle length and leaf area per shoot reached their maximum much later in the year than did shoot growth (Tang et al. 1999).

Needle length is an important morphological characteristic because it is very sensitive to environmental conditions (Kozlov and Niemelä 1999, McDonald et al. 1992), and it can be an indicator of both tree vigor (McDonald et al. 1992) and site quality (Gonda 1998). Needle length has also been found to be a good predictor for shoot length of the following year (Garrett and Zahner 1973). Among the Pinaceae, genera containing less shade-tolerant species develop longer needles, e.g. *Pinus* in comparison to *Picea, Abies, Tsuga*. This trend is also often true within the genus *Pinus* itself (*P. taeda, P. palustris* compared to *P. strobus*) (Niinemets et al. 2002). However, ponderosa pine is considered less shade-intolerant than lodgepole pine (Spurr

and Barnes 1980), and its needles are as much as three times as long (Figs. 33-34). Longer needles may be disadvantageous for a tree in forest understory conditions because greater investment may be needed for an architecture that keeps the needles in a position for optimal light harvesting (Niinemets et al. 2002). As a result, transpiration rates per unit leaf area may increase with leaf size (Walter and Schurr 2000). Needle length in pine species, in general, seems to be negatively correlated with number of needle fascicles produced on the terminal leader as this was found in red pine by Garrett and Zahner (1973) and ponderosa and lodgepole pine in this study.

Leaf life-span is highly interrelated with other plant traits and has been found to increase with decreasing relative growth rates as well as leaf LAR (leaf area ratio - the ratio between total leaf area and total plant biomass in m²/kg). It also tends to be higher in shade-tolerant trees, thereby increasing their potential photosynthetic return per carbon investment (Reich et al. 1992). Both species in this study had lower needle retention at low overstory densities and in smaller seedlings. This effect, however, was only very small at Twin Lakes, and at Finley Butte, it occurred very abruptly at the lowest overstory densities and in the smallest seedlings. Needle retention at Finley Butte was, therefore, constant over a wide range of seedling heights and overstory densities. Overall, the variation in needle retention was high at both sites with regression models explaining only 22 % and 13 %, respectively.

CHAPTER THREE:

HEIGHT GROWTH RESPONSES OF PONDEROSA PINE AND LODGEPOLE PINE

REGENERATION NINE YEARS AFTER STAND DENSITY REDUCTION

AT THREE SITES IN CENTRAL OREGON

INTRODUCTION

Although the response of advance regeneration to stand density reduction has been investigated in some forest types of the western US (Ferguson 1994, Ferguson 1984, Dahms 1960), such studies have long been neglected in ponderosa pine and lodgepole pine, in part because of their shade-intolerance. In these two pine species, many questions remain regarding the quantity and quality of established seedlings after canopy opening.

Advance regeneration is a term that describes seedlings and small saplings that develop in forest understory conditions and can survive for many years until a disturbance in the overstory canopy releases them to grow into the canopy (Tesch and Korpela 1993). After release, advance regeneration may react in different ways depending on its vigor and plasticity: The seedlings and saplings may either die, stay alive and grow very little, or grow rapidly. Accurate prediction of seedling response to canopy opening is necessary for successful implementation of partial cutting strategies.

Ruel et al. (2000) reviewed the relationships between morphological indicators and the response of advance regeneration to canopy removal. They concluded that response to release depends on shade-tolerance, light conditions prior to release, and the combination of live crown ratio, bole damage during harvest, and pre-release height growth rate. Because shade-tolerant and shade-intolerant species have different responses to release and different priorities in carbon allocation, Ruel et al. (2000) suggest that variables for predicting responses should also differ. Shade-tolerant species are regarded as more plastic, with seedlings reducing their live crown ratio and expanding laterally in conditions of low light. Therefore, the apical dominance ratio and live crown ratio are effective indicators of response capacity in shade-tolerant species. Diameter

growth of shade-intolerant species on the other hand is more sensitive to changes in light availability, so the height/diameter ratio, number of buds, and number of lateral branches are useful indicators of their response potential (Ruel et al. 2000).

Tree responses to sudden release, therefore, depend on tree characteristics and site conditions, but also on the degree of the so-called "growth shock". Growth or physiological shock is a reduction in growth up to several years following a release and before growth increases in response to increased resource availability. Shock has been explained by a shift in allocation to roots and as adjustment to a higher transpiration rate under increasing light and temperature (Kneeshaw et al. 2002). It has been found after thinning in established Douglas-fir stands (Harrington and Reukema 1983), but has also been reported in ponderosa pine and lodgepole pine stands (Kneeshaw et al. 2002, Dahms 1960). In lodgepole pine seedlings, Kneeshaw et al. (2002) found an immediate increase in root growth after canopy opening, a one year delay then increase in stem diameter growth, and a 2-3 yr height growth reduction. No growth shock was observed, however, in more mesic environments of eastern Canada by the same author (Kneeshaw et al. 1998), and forest management that aims to promote the release of advanced regeneration appears to be more successful in ecosystems with abundant moisture (McCaughey and Ferguson 1988).

In this study, height growth and relationships between height growth and various morphological tree variables of ponderosa pine and lodgepole pine seedlings after stand density reduction were investigated. Height growth in this study will be examined from 1989 to 2002 to cover a time period both before and after stand density reduction in 1991 and/or 1994, depending on the site. This is a retrospective study, and only few morphological variables could be reconstructed to view a time sequence of responses.

OBJECTIVES

The study materials are naturally established ponderosa pine and lodgepole pine seedlings (new and advanced regeneration) growing on two sets of research plots in central Oregon. These plots have been grown under varying silvicultural regimes, the first set involving different density regimes in even-aged stands of predominantly lodgepole pine, and the second

set involving different regimes for managing uneven-aged ponderosa pine stands. The objectives of this study were to test the hypotheses that at the studied sites: (1) height growth of both species accelerates after treatment; (2) height growth of lodgepole pine is greater than ponderosa pine after treatment; (3) height growth increases with increasing seedling height and decreasing local stand density; (4) height growth declines again where canopies are re-closing with time since treatment, (5) some morphological characteristics are good predictors of height growth in the following year.

METHODS

Study Area

Two of the three study sites, Finley Butte and Twin Lakes, are situated in the Deschutes National Forest, east of the Cascade Mountain Range in central Oregon. Finley Butte is approximately 10 km east of La Pine (43° 36' N, 121° 24' W) and Twin Lakes is approximately 21 km west of La Pine (43° 42' N, 121° 45' W). Both sites are approximately 50 km south of Bend. Elevation above sea level is approximately 1430 m at Finley Butte and 1330 m at Twin Lakes. The third site, Stinger Creek, is situated in the Ochoco National Forest in eastern Oregon (43° 44' N, 119° 24' W), approximately 34 km northwest of Burns. At Stinger Creek, elevation above sea level is approximately 1610 m.

At all sites, the climate is continental with dry and hot summers and cold winters with precipitation mostly occurring as snow. Periodic droughts during the summer are common. Mean temperature at Wickiup Dam near the Finley Butte and Twin Lakes sites from 1971-2000 was 7.1 °C with monthly temperature extremes of –30.0 °C in December and 38.3 °C in August. Mean annual precipitation from 1971-2000 was 2015 mm from snow and 560 mm from rainfall with 150 mm occurring between the months of April to September. The average number of days with a temperature minimum of 0 °C or less was 212.3 with possibilities of late frost in July and early frost in August. Mean temperature at Burns near the Stinger Creek site from 1971-2000 was 6.8 °C with monthly temperature extremes of –33.3 °C in December and February and 38.9 °C in August. Mean annual precipitation from 1971-2000 was 1000 mm from snow and 270 mm from rainfall with 100 mm occurring during the months of April to September.

The average number of days with a temperature minimum of 0 °C or less was 205.9 with possibilities of late frost in July and early frost in August. (Data from the Oregon Climate Service at http://www.ocs.oregonstate.edu/ and Western Regional Climate Center at http://www.wrcc.dri.edu/)

The soils at Finley Butte and Twin Lakes are well drained Entisols, fairly low in nutrients and with a shallow, immature profile developed in dacite pumice from the eruption of Mt. Mazama approximately 7600 years ago (Hermann and Petersen 1969). Both sites have soils belonging to the Lapine series (National Cooperative Soil Survey 1992). The Finley Butte vegetation is a *Pinus ponderosa/Purshia tridentata* plant association dominated by ponderosa pines with scattered lodgepole pines in the overstory (Franklin and Dyrness 1973). The vegetation at Twin Lakes is a mix of *Pinus ponderosa/Purshia tridentata* and *Pinus ponderosa/Purshia tridentata/Stipa occidentalis* plant associations, and it is dominated by lodgepole pine with only scattered ponderosa pines in the overstory. The main species in the understory at both sites are antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex. Hook.), and greenleaf manzanita (*Arctostaphylos patula* Greene). In general, herbaceous plants form relatively low cover on these soils (Dyrness and Youngberg 1966).

No soil survey data has been published for the Stinger Creek site. Lodgepole pine is not present at Stinger Creek, and the main species in the understory are antelope bitterbrush, curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.), rubber rabbitbrush (*Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird), snowbrush ceanothus, wax currant (*Ribes cereum* Dougl.), and western juniper (*Juniperus occidentalis* Hook.).

Study Design

The Finley Butte and Stinger Creek sites are part of a study to test differences in timber productivity between even-aged and uneven-aged silvicultural systems in ponderosa pine. The study was established on the Deschutes, Ochoco, Fremont, and Winema National Forests in 1991 – 1994, with the USDA Forest Service Pacific Northwest Research Station taking the lead. At Finley Butte and Stinger Creek, there is one replicate of each of four silvicultural treatments: overstory removal, uneven-age 'classic', uneven-age 'best tree', and a control (Wood et al. - no

year, also see appendix). These treatments were implemented in 1991 and 1994 at Finley Butte and in 1994 at Stinger Creek and have led to different stand densities and age structures of the residual trees (see appendix for treatment information). Study parameters are summarized in Tab. 24.

The Twin Lakes site is part of a lodgepole thinning study with the last thinning in 1994 (Cochran and Dahms 2000). Two stands with a high density and two stands with a low density were selected from this study to investigate the characteristics of seedlings in the understory. Within three of the four selected stands, nine 40.5 m² (1/100 acre) circular subplots with a radius of 3.6 m had been installed along a grid. In the fourth stand (one of the low density plots), only one subplot was randomly selected. Study site parameters are summarized in Tab. 24.

Table 24: Study site parameters at Finley Butte, Twin Lakes, and Stinger Creek

	Finley Butte			Twin Lakes			Stinger Creek		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Local Basal Area (m²/ha)	6	18.3	45.5	9	21.1	34	3.5	17.1	28.5
Cover of Understory Vegetation (%)	1	16	55	<5	29	60	3	13	31
Cover of Woody Debris (%)	-	-	-	5	22	80	-	-	-
Number of Ponderosa Pine Seedlings Studied	355			79			77		
Number of Lodgepole Pine Seedlings Studied	162			71			-		
Total Number of Seedlings Studied (N = 744)	517			150			77		

Combining all three sites, Finley Butte, Twin Lakes, and Stinger Creek, ten stands with different silvicultural treatments and overstory structures were investigated. Circular subplots of 40.5 m² (1/100 acre) each were established to sample seedlings and assess the local growing environment, resulting in a total of 50 subplots in four stands at Finley Butte, 25 subplots in four stands at Twin Lakes, and 16 subplots in two stands at Stinger Creek. The subplots lay along a grid and were 16 m (53 ft) apart at Finley Butte and Twin Lakes and approximately 8 m (26 ft) apart at Twin Lakes. Local basal area was estimated from the centre of each subplot with an angle gauge of basal area factor 1 m², distinguishing between over-, mid-, and understory strata at Finley Butte and Stinger Creek. At Twin Lakes, the overstory consisted of only one stratum with only a few trees above 1.3 m in the understory.

All measurements were taken from July to October 2003. In each subplot, all ponderosa pine and lodgepole pine seedlings between 0.10 m and 1.30 m that met the following sampling criteria were measured: no damage, no disease, no stem distortions like crooks or sweeps, or broken or forked tops, not germinated from the same seed cache (an important phenomenon for establishment in ponderosa pine (Keyes 2001)), and no cone production (observed in some lodgepole pine seedlings). The total number of seedlings was 517 at Finley Butte (355 ponderosa pines and 162 lodgepole pines), 150 at Twin Lakes (79 ponderosa pines and 71 lodgepole pines), and 77 (all ponderosa pines) at Stinger Creek, giving a total of 744 seedlings from all three sites combined. The number of seedlings in each height class, including seedlings < 0.10 m, was tallied on each subplot.

To quantify the architectural and growth responses of the two species, numerous attributes were measured on each individual. Total seedling height and stem diameter at the root collar were measured, and the height to diameter ratio was calculated. Annual height growth was measured downward until it was too difficult to determine visually. Relative height growth was calculated as the absolute height growth divided by the initial seedling height. Apical dominance was determined in two ways: (1) as the length of the terminal leader for each year divided by the length of the corresponding leader of the longest lateral branch that same year, and (2) as the ratio of past periodic growth of the terminal leader to the past periodic growth of the longest 5-yr-old branch leader, for the most recent 5-yr-growth period except the current. If lodgepole pine showed evidence of multinodal or polycyclic growth, i.e. the annual shoot had produced more than one whorl of branches (Lanner 1976, Van den Berg and Lanner 1971), the lengths of the internodes within the same year were summed. A polycyclic growth pattern does not occur in ponderosa pine.

The longest 5-year old branch was measured in detail to compute the ratio of the sum of terminal and lateral growth for five years (although not including the current growth in 2003). Years of needle retention and number of primary branches on each tree and whorl branches per year were determined. Length was measured on one needle of average length on the south side just below the top of the terminal leader shoot, and the number of needle fascicles on each shoot was counted. Needle density was calculated as the number of needle fascicles per unit stem length.

ANALYSIS

All statistical analyses were performed using the Statistical Analysis System software (SAS Institute Inc. 1999-2001) with separate analyses for each site. The effect of species, initial height, and local basal area on seedling absolute and relative height growth was investigated with multiple linear regression analysis in PROC MIXED. The best model was selected by means of forward selection and comparing AIC values obtained by running models with different transformations of the response variables and the three explanatory variables, and their interactions. To meet the assumptions of linearity, constant variance, and normality, the response variable height growth was ln-transformed. Logarithmic-, square root-, or reciprocal transformations were also performed on the two explanatory variables initial seedling height and stand basal area. To investigate the change of height growth over time, average height growth was calculated by height class and graphically displayed.

A simple linear regression analysis was performed on all 508 ponderosa pine and 226 lodgepole pine seedlings, although needle variables were measured on only a subset of seedlings. Therefore, some analyses were performed on only 226 ponderosa pine and 107 lodgepole pine seedlings. PROC REG was used for analyzing the relationship between absolute height growth in 2002 and single potential predictor variables (Table 44). Multiple linear regression analysis and stepwise selection procedures in PROC REG were also performed to identify the best predictor variables in combination with initial seedling height and initial seedling height and stand density that best explain absolute height growth. The two species at the three sites were analyzed separately. Table 25 lists all variables in the regression analysis.

Table 25: Mean and range of variables introduced in simple correlation analyses

| Variable | Variable definition | Finley Butte | | | | Twin Lakes | | | | Stinger Creek | |
| | | Ponderosa Pine | | Lodgepole Pine | | Ponderosa Pine | | Lodgepole Pine | | Ponderosa Pine | |
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
AGR_{2002}	Absolute height growth (2002)	2.67	0.2 – 13.1	4.15	0.5 – 24.9	3.10	0.4 – 11.5	2.60	0.6 – 13.0	2.66	0.3 – 7.1
AGR_{2001}	Absolute height growth (2001)	2.70	0.2 – 13.0	4.26	0.5 – 22.5	3.28	0.3 – 14.5	3.50	0.5 – 13.0	2.30	0.2 – 9.4
RGR_{2002}	Relative height growth (2002)	0.0477	0.0096 – 0.2096	0.1195	0.0110 - 0.4527	0.0727	0.0204 – 0.1953	0.0904	0.0141 - 0.5098	0.0772	0.0104 – 0.3396
RGR_{2001}	Relative height growth (2001)	0.0511	0.0116 – 0.3684	0.1442	0.0186 – 1.000	0.0771	0.0172 – 0.2014	0.1230	0.0162 - 0.3235	0.0688	0.0067 – 0.3101
LBA_{2003}	Local basal area (2003) (m^2/ha)	19.4	9 – 46.5	16.5	6.0 – 30.5	18.9	9.0 – 30.5	17.7	9.0 - 34.0	14.8	3.5 – 28.5
H_{2002}	Initial seedling height (2002) (cm)	61.3	9.0 – 123.0	46.0	7.5 – 120.4	48.1	8.7 – 115.3	38.5	5.1 - 110.0	48.5	7.8 – 120.5
D_{2003}	Stem diameter at the root collar (2003) (cm)	1.49	0.12 – 4.30	1.10	0.11 – 3.33	0.94	0.20 – 3.21	0.87	0.21 - 3.56	1.28	0.16 – 3.68
H/D_{2003}	Height to diameter ratio (2003)	48.6	23.0 – 117.9	53.5	19.8 – 118.2	59.5	28.0 – 96.8	54.7	32.9 - 80.7	44.1	21.6 – 75.0
PB_{2002}	Total number of primary branches (2002)	6.2	0 - 29	12.5	0 - 50	3.2	0 - 20	11.5	0 - 42	7.4	0 - 22
WB_{2001}	Number of new whorl branches (2001)	0.5	0 - 4	1.5	0 - 6	0.5	0 - 3	1.4	0 - 7	0.4	0 - 2
AD_{2002}	Apical dominance (2002)	0.6	0 - 16	1.3	0 - 40	0.6	0 – 6.3	1.4	0 - 15.0	0.4	0 – 3.1
AD_5	Apical dominance of 5-yr-old branch (2002)	1.3	0.5 – 5.7	1.4	0.8 – 4.5	2.3	0.7 – 12.6	1.6	0.8 - 7.3	1.5	0.73 – 6.3
ND_{2003}	Needle density per 1 cm on terminal leader (2003)	7.1	1.9 – 16.0	10.9	6.0 – 29.1	5.3	3.3 – 9.2	10.0	4.1 - 17.6	6.1	1.7 – 14.3
ND_{stem}	Needle density per 10 cm main stem	12.8	4.3 – 21.3	30.8	12.4 – 50.0	8.1	1.9 – 15.4	18.3	4.6 - 43.9	12.0	2.9 – 30.8
NF_{stem}	Number of needle fascicles on main stem	83.5	12 - 277	156.1	22 - 351	41.4	5 - 157	69.4	11 - 222	47.6	14 - 176
NL_{2001}	Needle length (2001) (cm)	6.7	2.4 13.2	3.2	0.9 – 5.2	9.3	3.7 – 14.0	3.7	1.5 - 5.9	7.1	2.5 – 13.8
NR_{2002}	Needle retention (2003) (years)	5.7	3 - 7	5.2	3 - 9	3.0	1 - 6	3.2	2 - 5	4.5	2 - 7

RESULTS

Polycyclic Growth in Lodgepole Pine

Polycyclic growth (i.e. the annual shoot produces more than one whorl of branches; Lanner 1976, Van den Berg and Lanner 1971) occurred in 12.0 % of the lodgepole pine seedlings at Finley Butte and Twin Lakes (i.e. in 28 out of 233 seedlings with height growth measurements taken). Of those 28 seedlings, 75 % were in stands with a stand basal area < 15 m²/ha and 75 % were between 1.01 and 1.30 m tall. Most second whorls occurred in or after 1998. In general, the number of whorl branches was lower during the second growth flush. Lodgepole pine seedlings were not present at Stinger Creek. Ponderosa pine does not have a polycyclic growth pattern.

Absolute Height Growth in 1990, 1995, and 2002 at Finley Butte

Absolute height growth at Finley Butte increased with reduction in overstory density after the last stand density reduction in 1994 and was highest at low overstory densities in 2002. Compared to ponderosa pine seedlings, absolute height growth was greater in lodgepole pine seedlings at all overstory densities, initial seedling heights, and in all the investigated years (Figs. 37-39; Tabs. 26-28).

In 2002, absolute height growth increased more steeply with increasing seedling height and reduction in overstory density below approximately 20 m²/ha, and this increase was more pronounced in lodgepole pine than in ponderosa pine seedlings (p-value = 0.0233 from the interaction between species and local basal area; p-value = 0.0012 from the interaction between species and initial seedling height) (Fig. 37; Tab. 26). The greatest absolute growth rate at all sites in 2002 was reached by lodgepole pine seedlings at Finley Butte, the maximum being 22.5 cm from a 0.50 m lodgepole pine seedling at a low overstory density (10.5 m²/ha).

In 1995 (i.e. one year after the last stand density reduction), the effect of both, species and overstory density, was different in seedlings of different heights (p-value = 0.0018 from the interaction between initial seedling height and species and p-value = 0.0023 from the interaction between initial seedling height and overstory density) (Fig. 39; Tab. 27). Height growth of small lodgepole pine seedlings was twice that of ponderosa pine in the smallest seedling size class, but

there was not much difference between species in taller seedlings. At low overstory densities, lodgepole pine seedlings of various heights differed only very little in their absolute height growth rates, whereas absolute height growth increased clearly with increasing seedling height in ponderosa pine seedlings. As in 2002, absolute height growth in lodgepole pine increased more steeply than in ponderosa pine seedlings as overstory dropped below approximately 20 m²/ha.

In 1990, absolute height growth was significantly different between species (p-value = 0.0370), but species responded similarly to changes in overstory density and initial seedling height (no significant interaction between either species and initial seedling height or species and local basal area) (Fig. 38; Tab. 28). Although the model predicts higher growth rates in tall lodgepole pine seedlings, observed growth rates were higher in tall ponderosa pine seedlings. The effect of overstory density, however, depended on initial seedling height (p-value = 0.0423 for the interaction between initial seedling height and local basal area). Tall seedlings did not change their absolute growth rate at low overstory densities but small seedlings did.
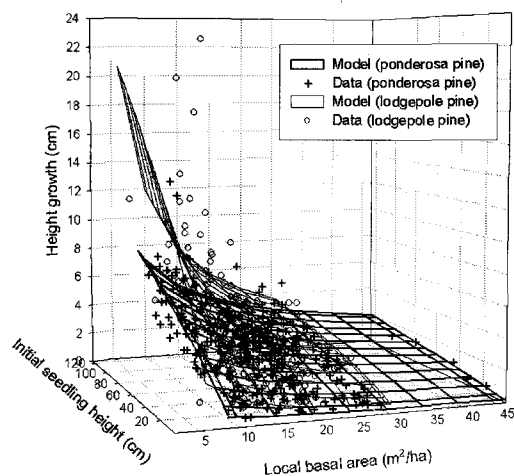
Figure 37: Absolute height growth in 2002 at
Finley Butte (R² = 0.71)
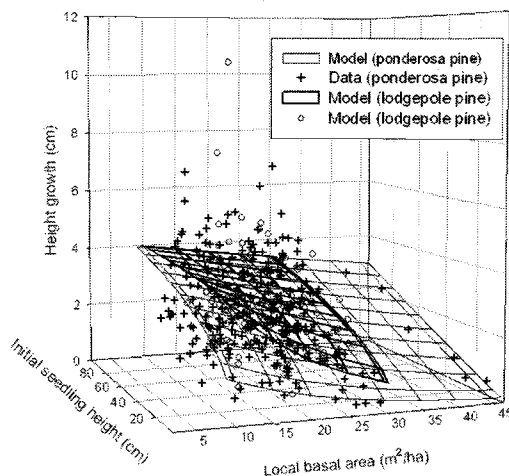
Figure 39: Absolute height growth in 1995 at
Finley Butte (R² = 0.36)

Figure 38: Absolute height growth in 1990 at
Finley Butte (R² = 0.36)

Table 26: Multiple linear regression model of absolute height growth in 2002 at Finley Butte

$\ln AH_{2002} = \beta_0 + \beta_1 \ln H + \beta_2 \ln LBA + \beta_3 I + \beta_4 \ln H \cdot I + \beta_5 \ln LBA \cdot I + \varepsilon$

where $\ln AH_{2002}$ = natural logarithm of absolute height growth in 2002
         $\ln H$ = natural logarithm of of initial height of seedling (cm)
         $\ln LBA$ = natural logarithm of local basal area (m^2/ha)
         I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0, \sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.8709	0.2779			
ln H	0.6355	0.0393	508	791.31	< 0.0001
ln LBA	-1.0666	0.0948	508	273.86	< 0.0001
I	-1.9254	0.3543	508	29.53	< 0.0001
ln H · I	0.1664	0.0511	508	10.60	0.0012
ln LBA · I	0.2578	0.1133	508	5.18	0.0233

Table 27: Multiple linear regression model of absolute height growth in 1995 at Finley Butte

$\ln AH_{1995} = \beta_0 + \beta_1 \ln H + \beta_2 LBA + \beta_3 I + \beta_4 \ln H \cdot LBA + \beta_5 \ln H \cdot I + \varepsilon$

where $\ln AH_{1995}$ = natural logarithm of absolute height growth in 1995
         $\ln H$ = natural logarithm of of initial height of seedling (cm)
         LBA = local basal area (m^2/ha)
         I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0, \sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	2.0537	0.4817			
ln H	-0.1284	0.1366	343	0.04	0.8342
LBA	-0.09479	0.02278	343	17.31	<0.0001
I	-1.4483	0.3468	343	17.44	<0.0001
ln H · LBA	0.01884	0.006142	343	9.41	0.0023
ln H · I	0.3119	0.09928	343	9.87	0.0018

Table 28: Multiple linear regression model of absolute height growth in 1990 at Finley Butte

$\ln AH_{1990} = \beta_0 + \beta_1 1/H + \beta_2 1/LBA + \beta_3 I + \beta_4 1/H \cdot 1/LBA + \varepsilon$

where $\ln AH_{1990}$ = natural logarithm of absolute height growth in 1990
         $1/H$ = reciprocal of initial height of seedling (cm)
         $1/LBA$ = reciprocal of local basal area (m^2/ha)
         I = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0, \sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.5515	0.2389			
1/ H	-29.0584	5.4192	163	28.75	< 0.0001
1/ LBA	-3.1177	4.4044	163	0.50	0.4800
I	-0.2761	0.1313	163	4.42	0.0370
1/ H · 1/ LBA	214.49	104.80	163	4.19	0.0423

Absolute Height Growth in 1990, 1995, and 2002 at Twin Lakes

In contrast to Finley Butte, at Twin Lakes the growth advantage of one species over the other differed with overstory density and year (Figs. 40-42; Tabs. 29-31).

In 2002, absolute growth rates at high overstory densities were more than 2x higher in ponderosa pine than in lodgepole pine (Fig. 40; Tab. 29). In both species, absolute height growth increased with reduction in overstory density (p-value <0.0001). The model predicts that tall lodgepole pine seedlings have higher absolute growth rates at overstory densities below 10 m²/h and small lodgepole pine seedlings below 15 m²/ha than ponderosa pine seedlings. According to the data, however, ponderosa pine reached equally high or higher absolute growth rates at low overstory densities. According to the regression model, the difference between the species was more pronounced in tall seedlings (p-value = 0.0146 from the interaction between species and initial seedling height).

In 1995, lodgepole pine had faster growth rates except for the tallest seedlings (p-value = 0.0011 from the interaction between species and initial seedling height) (Fig. 42; Tab. 30). In both species, the increase in absolute height growth was greatest below 20 m²/ha (p-value < 0.0001). Although the model suggests growth rates of 10-11 cm at the lowest overstory densities, the highest actual growth rate was 6.6 cm in 1995 in ponderosa pine and 8.5 cm in lodgepole pine.

In 1990, absolute height growth was higher at low overstory densities (p-value = 0.0319), in the taller seedlings (p-value < 0.0001), and in ponderosa pine seedlings (p-value = 0.0265) (Fig. 41; Tab. 31). This difference between species was most pronounced in the tallest seedlings (p-value = 0.0056 from the interaction between initial seedling height and species).
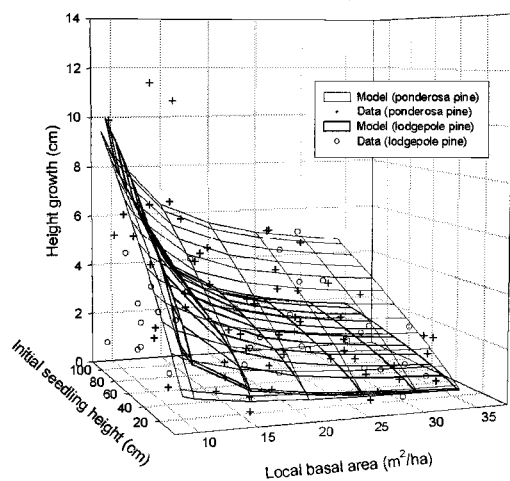
Figure 40: Absolute height growth in 2002 at Twin Lakes (R² = 0.69)

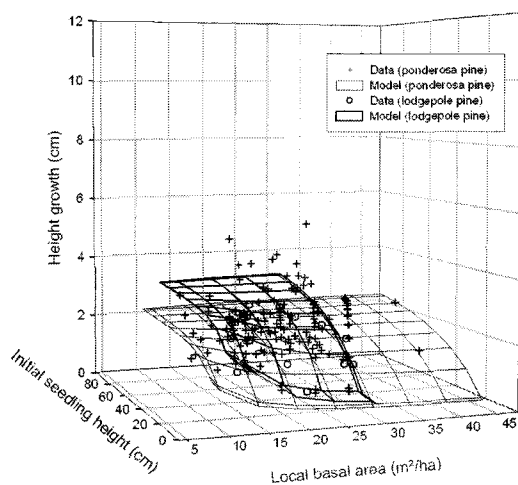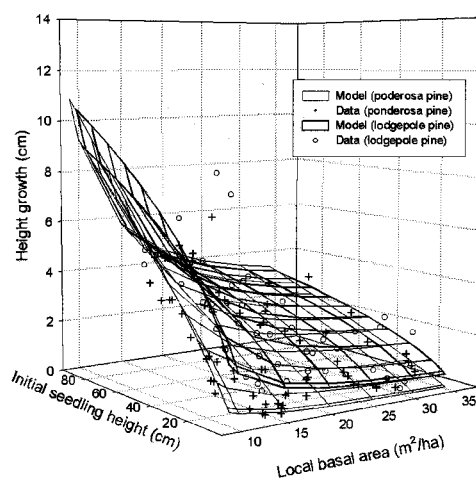Figure 42: Absolute height growth in 1995 at Twin Lakes (R² = 0.72)

Figure 41: Absolute height growth in 1990 at Twin Lakes (R² = 0.68)

Table 29: Multiple linear regression model of absolute height growth in 2002 at Twin Lakes

$\ln AH_{2002} = \beta_0 + \beta_1 \text{sqrt } H + \beta_2 1/LBA + \beta_3 I + \beta_4 \text{sqrt } H \cdot I + \varepsilon$

where $\ln AH_{2002}$ = natural logarithm of absolute height growth in 2002
            sqrt H   = square root of initial height of seedling (cm)
            1/ LBA   = reciprocal of local basal area (m²/ha)
            I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
    $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-1.0551	0.1541			
sqrt H	0.1720	0.0214	145	203.59	< 0.0001
1/ LBA	11.0113	1.3449	145	67.03	< 0.0001
I	-0.3376	0.1889	145	3.19	0.0760
ln H • I	0.0712	0.0288	145	6.10	0.0146

Table 30: Multiple linear regression model of absolute height growth in 1995 at Twin Lakes

$\ln AH_{1995} = \beta_0 + \beta_1 \ln H + \beta_2 1/LBA + \beta_3 I + \beta_4 \ln H \cdot I + \varepsilon$

where $\ln AH_{1995}$ = natural logarithm of absolute height growth in 1995
            ln H   = natural logarithm of initial height of seedling (cm)
            1/ LBA   = reciprocal of local basal area (m²/ha)
            I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
    $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-1.4515	0.2976			
ln H	0.4853	0.0909	106	140.88	<0.0001
1/ LBA	14.5347	1.7831	106	66.45	<0.0001
I	-1.7322	0.3547	106	23.85	<0.0001
ln H • I	0.3831	0.1142	106	11.25	0.0011

Table 31: Multiple linear regression model of absolute height growth in 1990 at Twin Lakes

$\ln AH_{1990} = \beta_0 + \beta_1 1/H + \beta_2 1/LBA + \beta_3 I + \beta_4 \ln H \cdot I + \varepsilon$

where $\ln AH_{1990}$ = natural logarithm of absolute height growth in 1990
            1/ H   = reciprocal of initial height of seedling (cm)
            1/ LBA   = reciprocal of local basal area (m²/ha)
            I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
    $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.4386	0.3211			
1/ H	-6.5817	3.5975	35	34.69	<0.0001
1/ LBA	9.9558	4.4536	35	5.00	0.0319
I	0.6677	0.2882	35	5.37	0.0265
1/ H • I	-13.0534	4.4261	35	8.70	0.0056

Absolute Height Growth in 1990, 1995, and 2002 at Stinger Creek

At Stinger Creek, no lodgepole pine was present. Absolute height growth in 2002, 1995, and 1990 increased with initial seedling height and, except in 1990, with overstory density, the steepest increase occurring below about 10 m²/ha (Figs. 43-45; Tabs. 32-34).
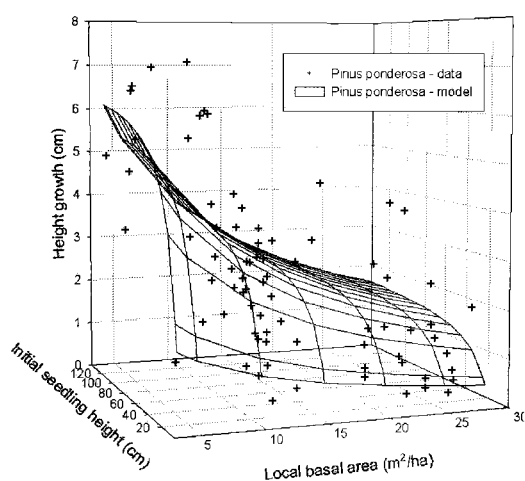
Figure 43: Absolute height growth in 2002 at Stinger Creek (R² = 0.65)

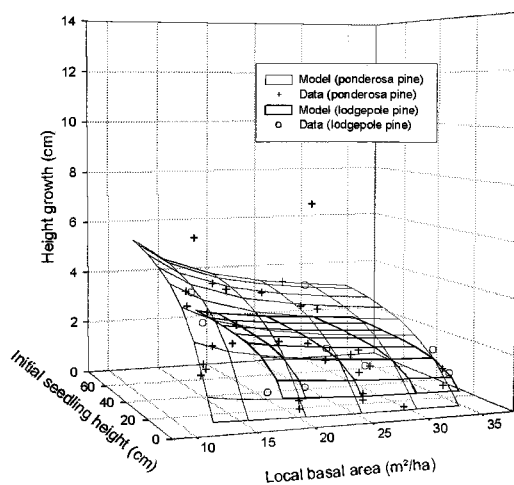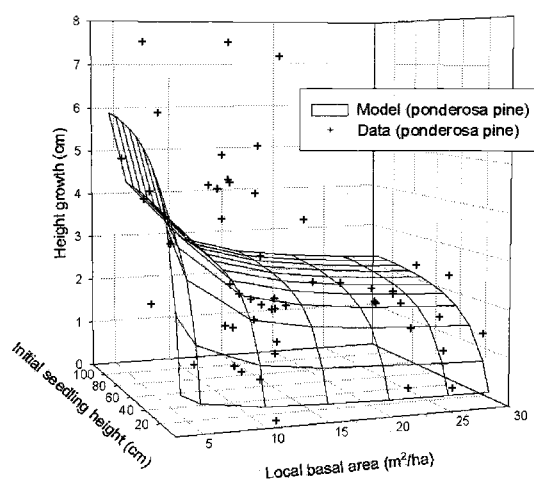Figure 45: Absolute height growth in 1995 at Stinger Creek (R² = 0.43)
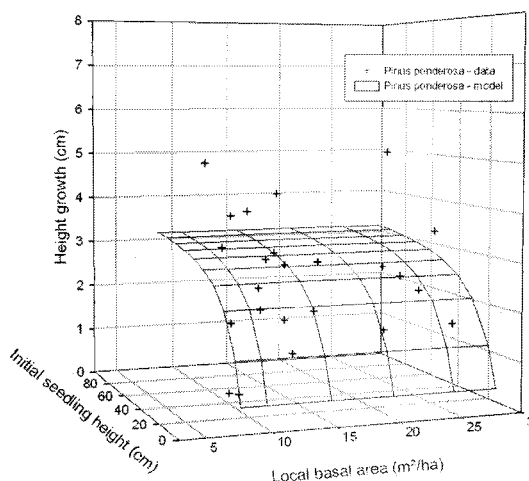
Figure 44: Absolute height growth in 1990 at Stinger Creek (R² = 0.36)

Table 32: Multiple linear regression model of absolute height growth in 2002 at Stinger Creek

$\ln AH_{2002} = \beta_0 + \beta_1 \, 1/H + \beta_2 \, \text{sqrt LBA} + \varepsilon$

where $\ln AH_{2002}$ = natural logarithm of absolute height growth in 2002

           $1/H$ = reciprocal of initial height of seedling (cm)

           sqrt LBA = square root of local basal area (m²/ha)

$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	2.5808	0.1946			
1/ H	-11.6220	1.3524	74	73.85	< 0.0001
sqrt LBA	-0.3623	0.0497	74	53.23	< 0.0001

Table 33: Multiple linear regression model of absolute height growth in 1995 at Stinger Creek

$\ln AH_{1995} = \beta_0 + \beta_1 \, 1/H + \beta_2 \, 1/LBA + \varepsilon$

where $\ln AH_{1995}$ = natural logarithm of absolute height growth in 1995

           $1/H$ = reciprocal of of initial height of seedling (cm)

           1/ LBA = reciprocal of local basal area (m²/ha)

$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.8503	0.1680			
1/ H	-10.8465	2.1551	50	25.33	<0.0001
1/ LBA	3.6380	1.0936	50	11.07	0.0017

Table 34: Multiple linear regression model of absolute height growth in 1990 at Stinger Creek

$\ln AH_{1990} = \beta_0 + \beta_1 \, 1/H + \varepsilon$

where $\ln AH_{1990}$ = natural logarithm of absolute height growth in 1990

           $1/H$ = reciprocal of initial height of seedling (cm)

$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.2869	0.1463			
1/ H	-10.5372	2.9299	23	12.93	0.0015

Relative Height Growth in 1990, 1995, and 2002 at Finley Butte

In 2002, the increase of relative height growth was greater in lodgepole pine with reduction in overstory density than it was in ponderosa pine, and this effect increased abruptly at approximately 15 m²/ha (p-value = 0.0002 from the interaction between species and local basal area) (Fig. 46; Tab. 35). Relative height growth also increased more abruptly with decreasing initial seedling height in lodgepole pine seedlings than in ponderosa pine seedlings (p-value = 0.0217 from the interaction between species and initial seedling height).

In 1995, i.e. one year after the last silvicultural treatment, relative growth rates were higher than in 2002, especially in the smaller seedlings (Fig. 48; Tab. 36). The increase in relative height growth was much stronger with decreasing initial seedling height in lodgepole pine seedlings (p-value = 0.0021 from the interaction between species and initial seedling height). The effect of overstory density on relative growth rate was much higher in small seedlings and seems only marginal in tall seedlings (p-value = 0.0019 from the interaction between local basal area and initial seedling height). The effect of overstory density on relative height growth of small seedlings increased at densities as low as approximately 25 m²/ha.

Although effects of initial seedling height and overstory density were significant in 1990 (p-values = < 0.0001 and 0.0066, respectively), they seem very slight compared to 1995 and 1990 (Fig. 47; Tab. 37). There was no difference between species at Finley Butte in 1990.
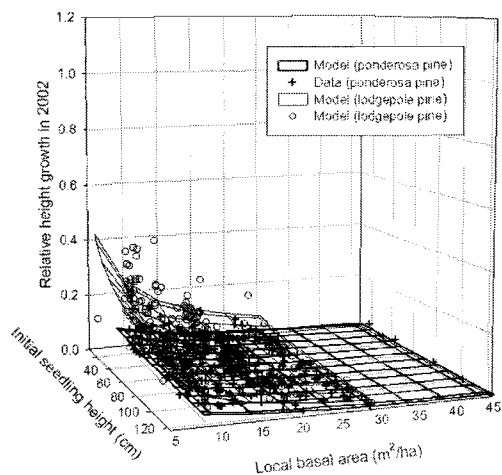
Figure 46: Relative height growth in 2002 at Finley Butte (R^2 = 0.65)
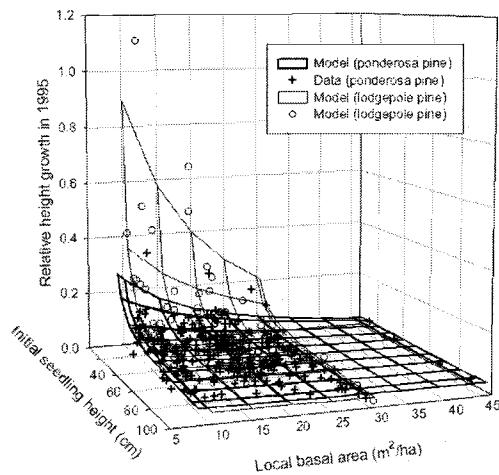
Figure 48: Relative height growth in 1995 at Finley Butte (R^2 = 0.50)

Figure 47: Relative height growth in 1990 at Finley Butte (R^2 = 0.14)

Table 35: Multiple linear regression model of relative height growth in 2002 at Finley Butte

ln RH 2002 = β_0 + β_1 sqrt H + β_2 ln LBA+ β_3 I + β_4 sqrt H • I + β_5 ln LBA • I + ε

where   ln RH 2002   = natural logarithm of relative height growth in 2002
              sqrt H   = square root of initial height of seedling (cm)
              ln LBA   = natural logarithm of local basal area (m^2/ha)
              I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	1.3800	0.2611	508		
sqrt H	-0.1254	0.01314	508	132.05	< 0.0001
ln LBA	-1.0657	0.09405	508	277.34	< 0.0001
I	-1.7355	0.3250	508	28.52	< 0.0001
sqrt H • I	0.2590	0.1124	508	5.30	0.0217
ln LBA • I	0.06109	0.01652	508	13.68	0.0002

Table 36: Multiple linear regression model of relative height growth in 1995 at Finley Butte

ln RH 1995 = β_0 + β_1 ln H + β_2 sqrt LBA + β_3 I + β_4 ln H • sqrt LBA + β_5 ln H • I + ε

where   ln RH 1995   = natural logarithm of relative height growth in 1995
              ln H   = natural logarithm of initial height of seedling (cm)
              sqrt LBA   = square root of local basal area (m^2/ha)
              I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	3.9490	0.9060	343		
ln H	-1.5232	0.2501	343	29.16	< 0.0001
sqrt LBA	-0.8584	0.2088	343	16.90	< 0.0001
I	-1.4530	0.3486	343	17.37	< 0.0001
ln H • sqrt LBA	0.1747	0.05648	343	9.56	0.0019
ln H • I	0.3127	0.09979	343	9.82	0.0021

Table 37: Multiple linear regression model of relative height growth in 1990 at Finley Butte

ln RH 1990 = β_0 + β_1 1/H + β_2 1/LBA + ε

where   ln RH 1990   = natural logarithm of relative height growth in 1990
              1/H   = reciprocal of initial height of seedling (cm)
              1/LBA   = reciprocal of local basal area (m^2/ha)
              I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-3.5668	0.1234	165		
1/ H	8.1289	2.0177	165	16.23	< 0.0001
1/ LBA	6.1893	2.2505	165	7.56	0.0066

Relative Height Growth in 1990, 1995, and 2002 at Twin Lakes

In 2002, there was no difference in relative height growth between the species according to the model, although two of the smallest lodgepole pine seedlings had relative growth rates much higher than ponderosa pine seedlings, the highest being 0.5 (Fig. 49; Tab. 40). Relative height growth increased gradually with reduction in overstory density (p-value < 0.0001) and with decreasing seedling height (p-value < 0.0001). The effect of seedling height on relative growth rate increased abruptly in seedlings smaller than 0.30 m.

In 1995, relative growth rate of lodgepole pine seedlings was approximately 2x that of ponderosa pine seedlings at all overstory densities and in trees of all measured heights (p-value < 0.0001 for species effect and no significant interaction between either species and initial seedling height or species and local basal area in the model) (Fig. 51; Tab. 39). Relative height growth increased with reduction in overstory density (p-value < 0.0001), and this increase became greater at approximately 15 m²/ha. As in 2002, the effect of initial seedling height on relative growth rate increased more abruptly in seedlings smaller than 0.30 m (p-value < 0.0001).

In 1990, there was no difference in relative height growth between species and in seedlings of different heights (Fig. 50; Tab. 40). However, relative height growth was a little higher in seedlings experiencing lower basal areas at time of measurement 2003 (p-value = 0.0167).
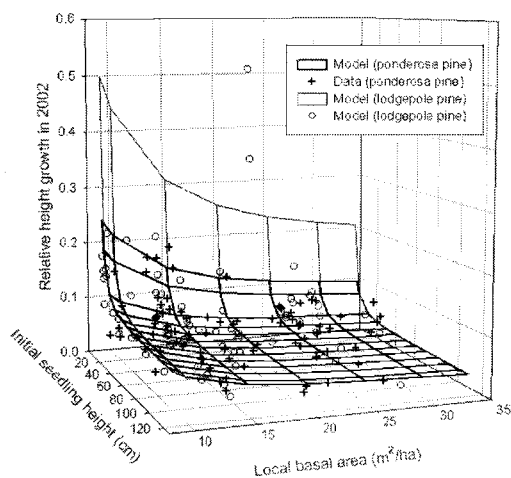
Figure 49: Relative height growth in 2002 at Twin Lakes (R² = 0.50)
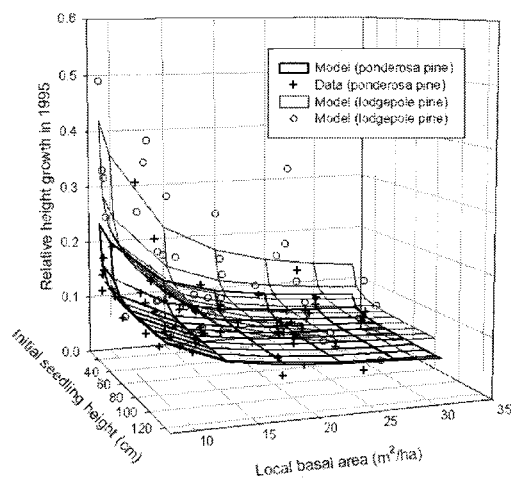
Figure 51: Relative height growth in 1995 at Twin Lakes (R² = 0.54)
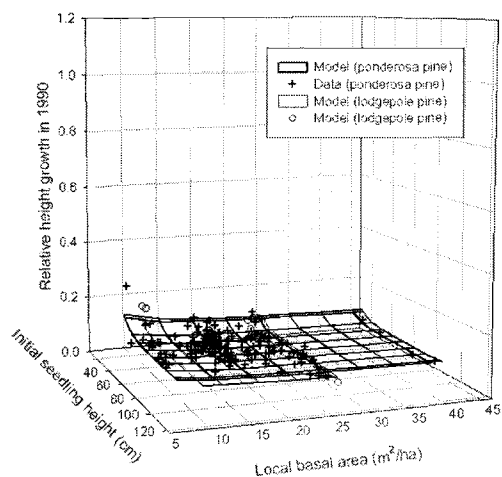

Figure 50: Relative height growth in 1990 at Twin Lakes Lakes (R² = 0.14)

Table 38: Multiple linear regression model of relative height growth in 2002 at Twin Lakes

$\ln RH\ 2002 = \beta_0 + \beta_1\ 1/H + \beta_2\ 1/LBA + \varepsilon$	

where   ln RH 2002   = natural logarithm of relative height growth in 2002
            1/H   = reciprocal of initial height of seedling (cm)
            1/LBA   = reciprocal of local basal area (m²/ha)
     $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-3.7883	0.1042	147		
1/ H	9.5497	0.9962	147	91.90	< 0.0001
1/ LBA	10.6443	1.3302	147	64.03	< 0.0001

Table 39: Multiple linear regression model of relative height growth in 1995 at Twin Lakes

$\ln RH\ 1995 = \beta_0 + \beta_1\ 1/H + \beta_2\ 1/LBA + \beta_3\ 1/LBA + \varepsilon$	

where   I RH 1995   = natural logarithm of relative height growth in 1995
            1/H   = reciprocal of initial height of seedling (cm)
            1/LBA   = reciprocal of local basal area (m²/ha)
             I   = indicator for species; 0 for lodgepole pine, 1 for ponderosa pine
     $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-3.2250	0.1516	107		
1/ H	3.7225	0.8906	107	17.47	< 0.0001
1/ LBA	14.4697	1.8954	107	58.28	< 0.0001
I	-0.5911	0.09441	107	39.20	< 0.0001

Table 40: Multiple linear regression model of relative height growth in 1990 at Twin Lakes

$\ln RH\ 1990 = \beta_0 + \beta_1\ 1/LBA + \varepsilon$	

where   log RH 1990   = natural logarithm of relative height growth in 2002
            1/LBA   = reciprocal of local basal area (m²/ha)
     $\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-3.1462	0.2440	38		
1/ LBA	11.7133	4.6786	38	6.27	0.0167

Relative Height Growth in 1990, 1995, and 2002 at Stinger Creek

In 2002 and 1995, relative height growth in ponderosa pine seedlings increased with reduction in overstory density (p-values <0.0001 and 0.0015, respectively) (Fig. 52 und 54; Tab. 41-42). This effect increased more abruptly at local basal areas below 15 m^2/ha in 2002 and 10 m^2/ha in 1995. Relative height growth also gradually increased with decreasing initial seedling height in both years (p-values <0.0001). In 1990, there was no effect of overstory density as measured in 2003 (Fig. 53; Tab. 43). Relative height growth, however, was higher in small seedlings compared to tall seedlings (p-value = 0.0015).
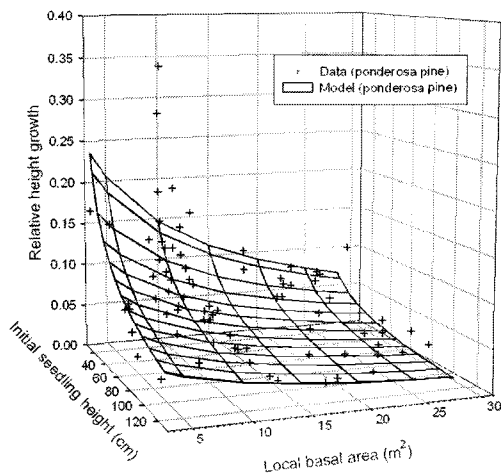
Figure 52: Relative height growth in 2002 at Stinger Creek (R² = 0.64)

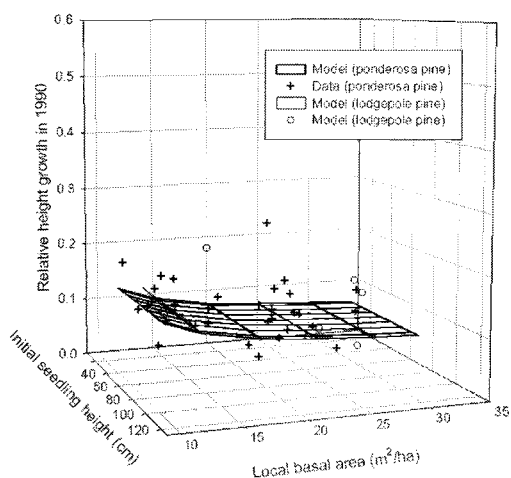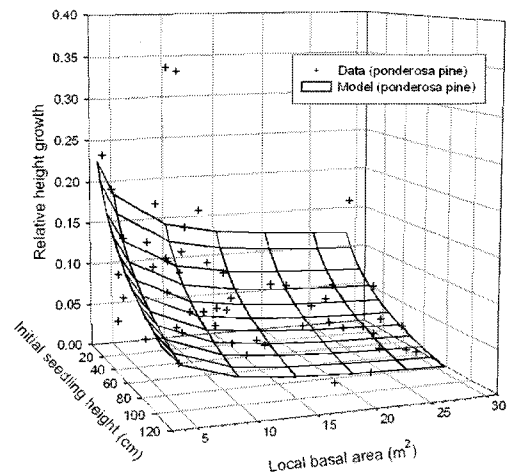Figure 54: Relative height growth in 1995 at Stinger Creek (R² = 0.43)
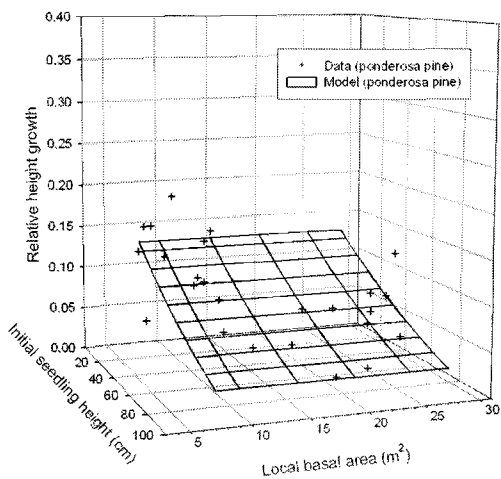
Figure 53: Relative height growth in 1990 at Stinger Creek (R² = 0.36)

Table 41: Multiple linear regression model of relative height growth in 2002 at Stinger Creek

ln RH 2002 = β_0 + β_1 sqrt H + β_2 sqrt LBA + ε

where | ln RH 2002 | = natural logarithm of relative height growth in 2002
sqrt H | = square root of initial height of seedling (cm)
sqrt LBA | = square root of local basal area (m²/ha)
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	-0.2915	0.2374	74		
sqrt H	-0.1823	0.01969	74	85.71	< 0.0001
sqrt LBA	-0.3604	0.05005	74	51.85	< 0.0001

Table 42: Multiple linear regression model of relative height growth in 1995 at Stinger Creek

sqrt RH 1995 = β_0 + β_1 sqrt H + β_2 1/LBA + ε

where | sqrt RH 1995 | = square root of relative height growth in 1995
sqrt H | = square root of initial height of seedling (cm)
1/LBA | = reciprocal of local basal area (m²/ha)
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.3908	0.04119	50		
sqrt H	-0.02722	0.005676	50	22.99	< 0.0001
1/ LBA	0.5095	0.1521	50	11.22	0.0015

Table 43: Multiple linear regression model of relative height growth in 1990 at Stinger Creek

sqrt RH 1990 = β_0 + β_1 H + ε

where | sqrt RH 1990 | = square root of relative height growth in 2002
H | = initial height of seedling (cm)
$\varepsilon \sim N(0,\sigma^2)$

Effect	Estimate	Standard error	df	F-value	p-value
Intercept	0.3707	0.02770	23		
H	-0.00225	0.000627	23	12.94	0.0015

Change of Absolute Height Growth of Seedlings in Different Height Classes Over Time

Only seedlings that had established before 1989 according to their minimum age at Finley Butte and before 1992 at Twin Lakes and Stinger Creek (i.e. 2 years before the stand density treatments) were analyzed for height growth patterns over time. Height classes were distinguished by initial seedling height either in 1989 (Finley Butte) or 1992 (Twin Lakes and Stinger Creek).

The effect of stand density reduction on absolute height growth differed between species, height classes, and sites, but the species effect was not clear (Figs. 55-59). At all sites, height growth peaked around 1998/1999 when there was a year of unusual high precipitation (see the discussion section). The smaller seedlings had the lowest absolute height growth rates. But in both species and at all sites, seedlings in the middle height class (0.21-0.50 m) often had higher growth rates after stand density reduction than seedlings in the upper height class (0.51-1.00 m).

At Finley Butte, absolute height growth of both species gradually increased until a peak was reached in 1998/1999. Thereafter, growth decreased to pre-peak levels and seemed to level off. At Twin Lakes and Stinger Creek, absolute height growth of seedlings taller than 0.20 m seemed to have decreased at least for one year after stand density reduction (but mind the precipitation data in the discussion section). Height growth after the peak at both sites returned to pre-peak levels and either further increased (ponderosa pine at Twin Lakes and Stinger Creek) or decreased (lodgepole pine at Twin Lakes).

Figure 55: Average absolute height growth of ponderosa pine seedlings in four height classes at Finley Butte

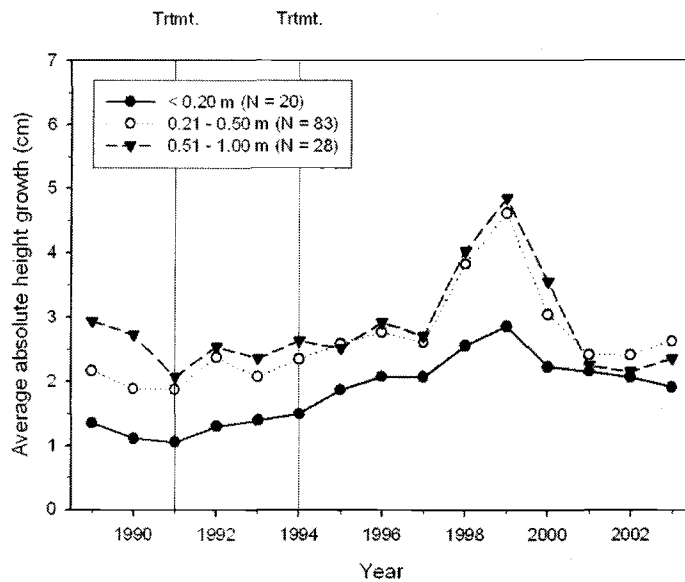Figure 56: Average absolute height growth of lodgepole pine seedlings in four height classes at Finley Butte

Figure 57: Average absolute height growth of ponderosa pine seedlings in four height classes at Twin Lakes

Figure 58: Average absolute height growth of lodgepole pine seedlings in four height classes at Twin Lakes

Figure 59: Average absolute height growth of ponderosa pine seedlings in four height classes at Stinger Creek

Change of Relative Height Growth of Seedlings in Different Height Classes Over Time

Only seedlings that had established before 1989 according to their minimum age at Finley Butte and before 1992 at Twin Lakes and Stinger Creek (i.e. 2 years before the stand density treatments) were analyzed for relative height growth patterns over time. Height classes were distinguished by initial seedling height either in 1989 (Finley Butte) or 1992 (Twin Lakes and Stinger Creek).

At Finley Butte, there was a peak in relative height growth 1999 in ponderosa pine seedlings of all height classes after which relative growth declined (Fig. 60). There is no general response to treatments apparent in these seedlings. Only very few lodgepole pine seedlings had a minimum age of 15 years or more and were averaged (Fig. 61). Relative height growth seemed to have declined after the first treatment in 1991 but increased after the second treatment. After a peak in 1999/2000, height growth decreased to levels lower than before the peak. At Finley Butte, growth rates were similar between species except for higher growth rates in the smallest lodgepole pine seedlings.

At Twin Lakes, there was no increase in relative height growth apparent in ponderosa pine and lodgepole pine seedlings after stand density reduction (Fig. 62-63) but a steady decrease with time except for a peak in 1998/1999. Except for the smallest seedlings, relative growth rates were a little higher in ponderosa pine than in lodgepole pine.

At Stinger Creek, the change of relative height growth of seedlings over time seems very different for seedlings of different height classes (Fig. 64). Relative height growth of seedlings smaller than 0.20 m increased after the last stand density reduction but relative height growth of taller seedlings decreased.
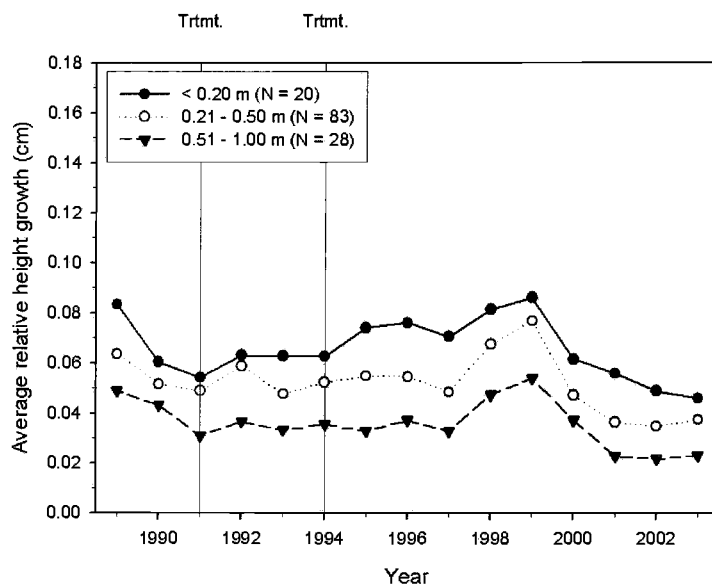
Figure 60: Average relative growth of ponderosa pine seedlings in four height classes
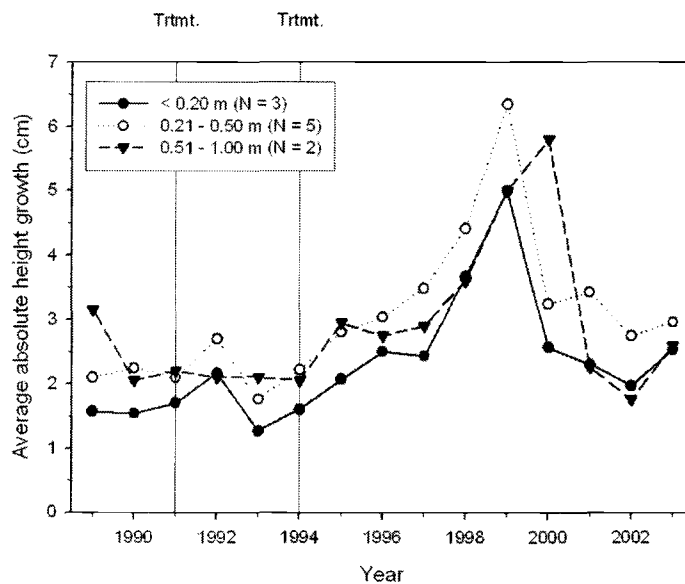at Finley Butte
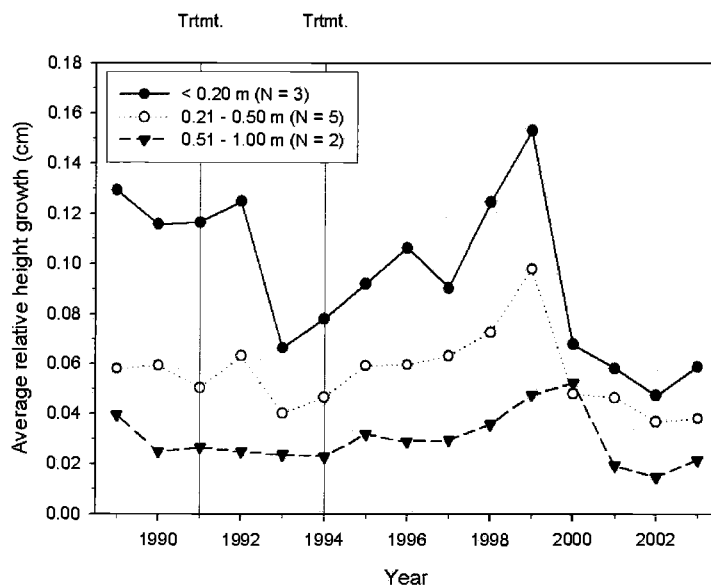
Figure 61: Average relative height growth of lodgepole pine seedlings in four height classes
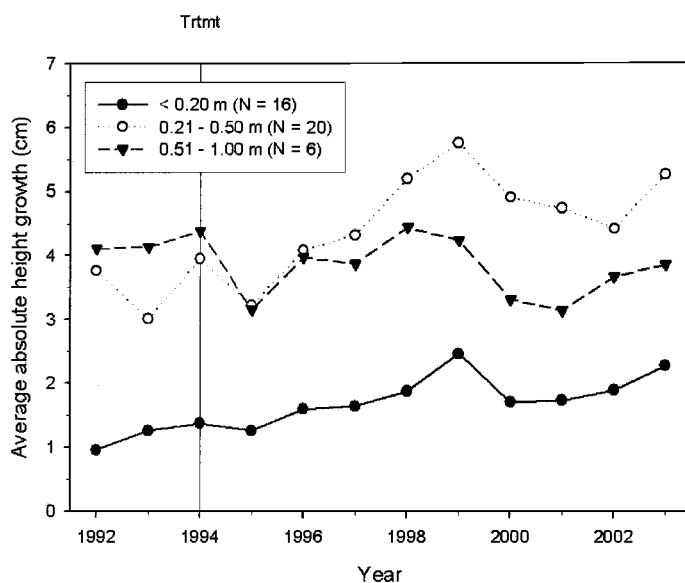at Finley Butte
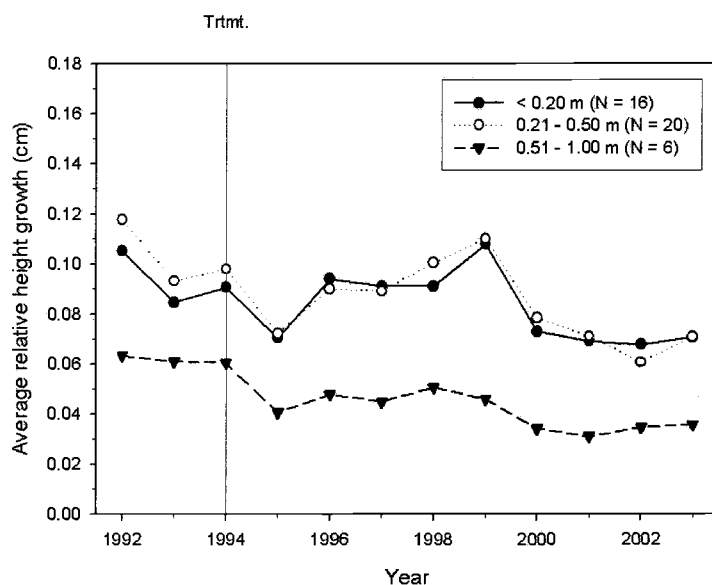
Figure 62: Average relative height growth of ponderosa pine seedlings in four height classes at Twin Lakes
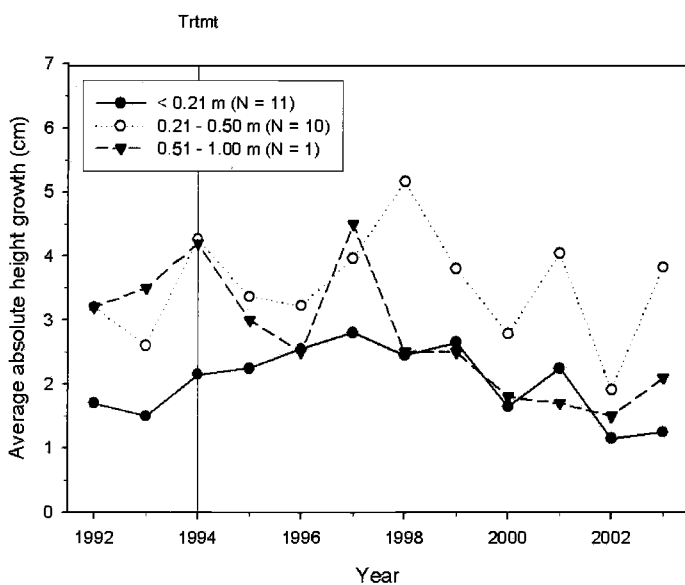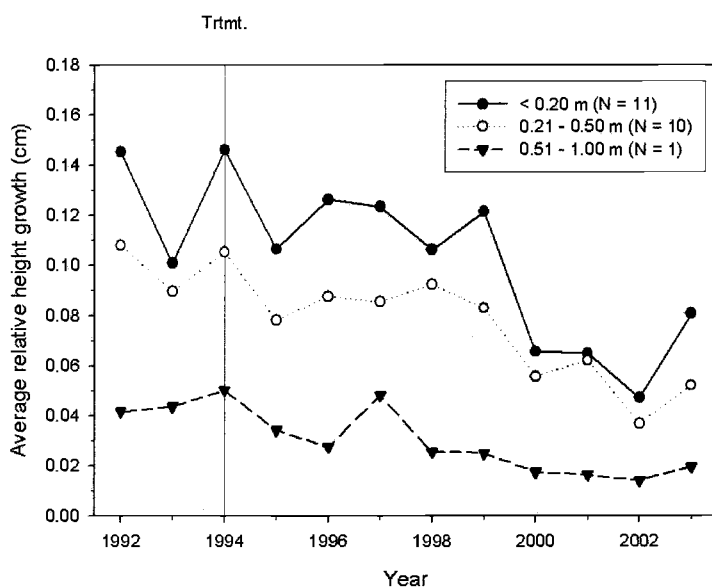

Figure 63: Average relative height growth of lodgepole pine seedlings in four height classes at Twin Lakes
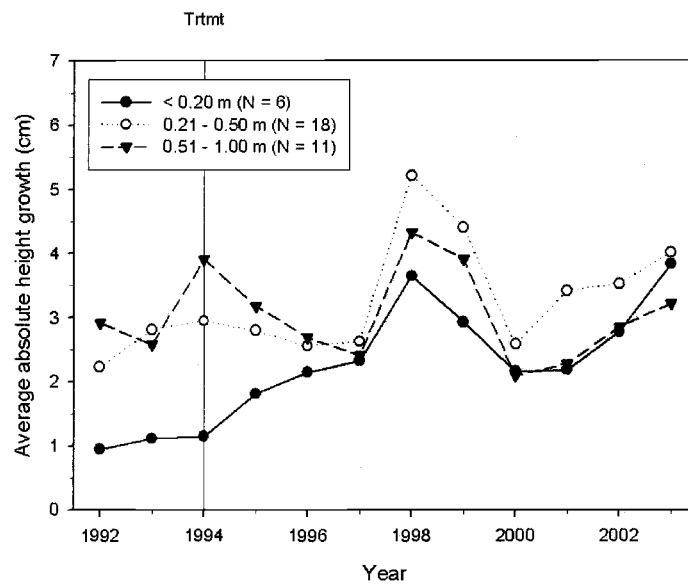
Trtmt.
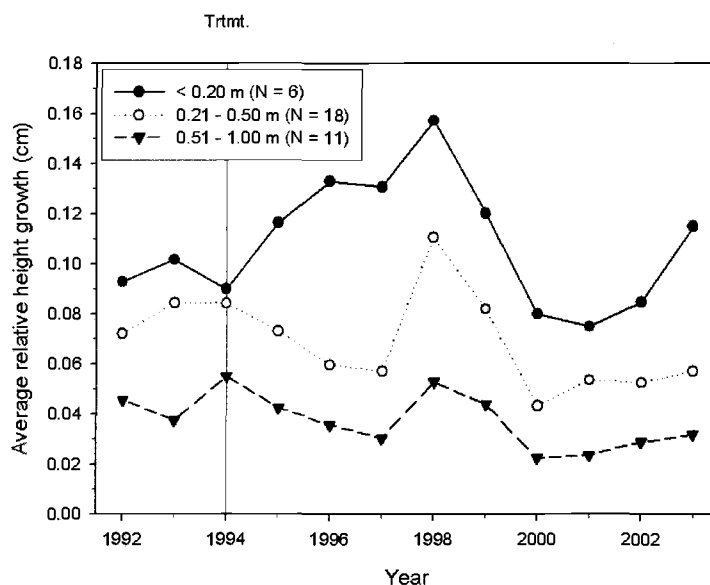
Figure 64: Average relative height growth of ponderosa pine seedlings in four height classes at Stinger Creek

Relationships of Absolute Height Growth in 2002 and Seedling Morphological Characteristics

To describe the relationship between absolute height growth in 2002 and different morphological characteristics, coefficients of determination (R^2) were computed for each species and at each site (Figs 65-79; Tab. 44). Most variables were transformed to fit the assumptions of constant variance and normality. Figures 65-79 show the original data at all sites but distinguish between species, whereas the computations in Table 44 are for each site and species separately. Foliar characteristics can be correlated with site quality (Gonda 1998), and a site specific analysis seemed more appropriate.
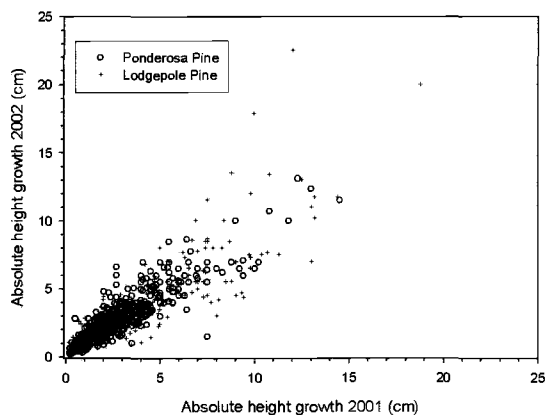
Figure 65: Relationship between absolute height growth in 2002 and absolute height growth in 2001
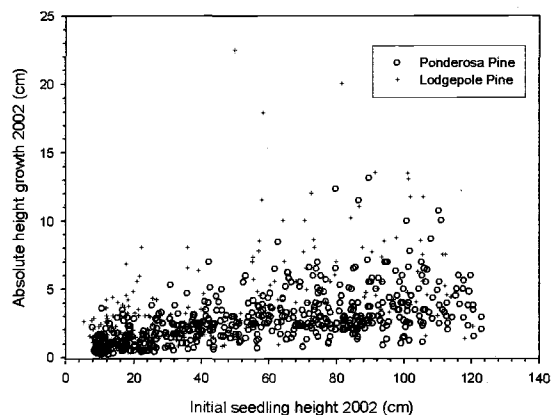
Figure 67: Relationship between absolute height growth in 2002 and initial seedling height 2002
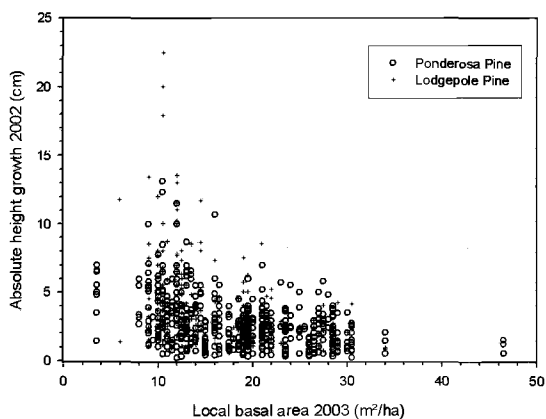
Figure 66: Relationship between absolute height growth in 2002 and local basal area in 2003
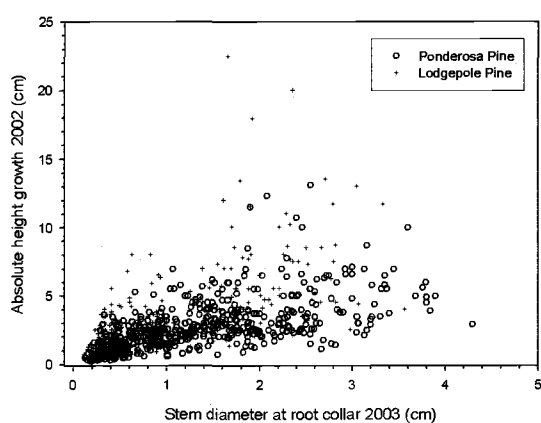
Figure 68: Relationship between absolute height growth in 2002 and stem diameter at the root collar 2003
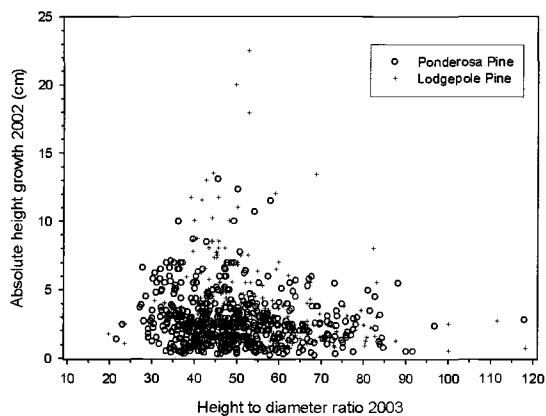
Figure 69: Relationship between absolute height growth in 2002 and the H/D ratio in 2003
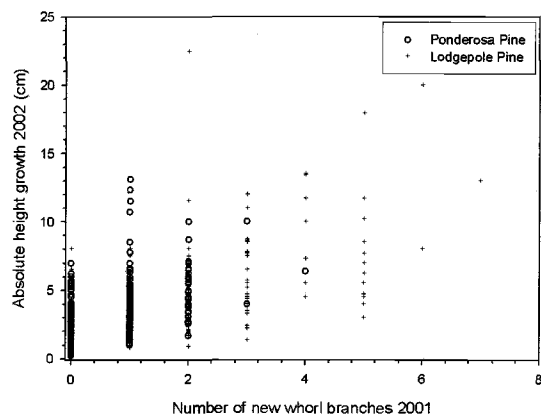
Figure 71: Absolute height growth in 2002 as a function of the number of whorl branches from 2001
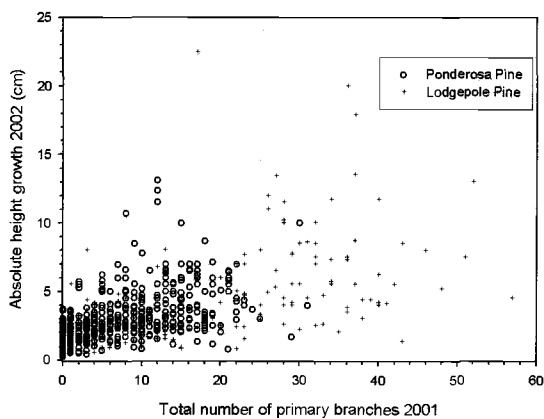
Figure 70: Absolute height growth in 2002 as a function of the total number of primary branches in 2002
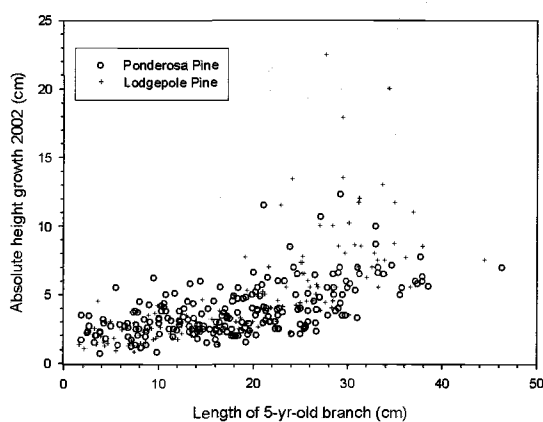
Figure 72: Absolute height growth in 2002 as a function of the length of the longest 5-yr-old branch in 2003 (after subtracting the current growth in 2003)
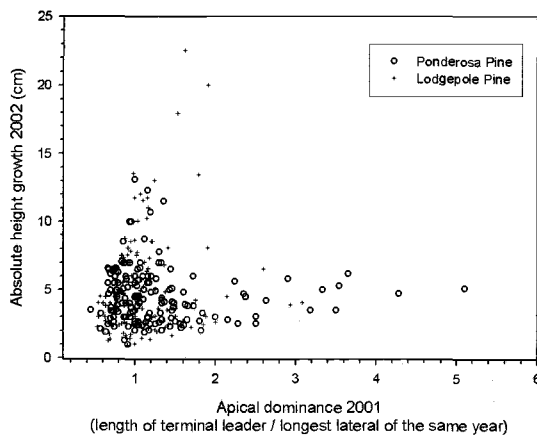
Figure 73: Relationship between absolute
height growth in 2002 and apical dominance in
2002
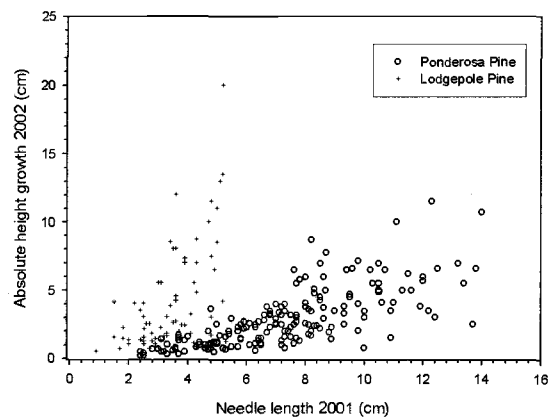
Figure 75: Relationship between absolute
height growth in 2002 and needle length in
2001
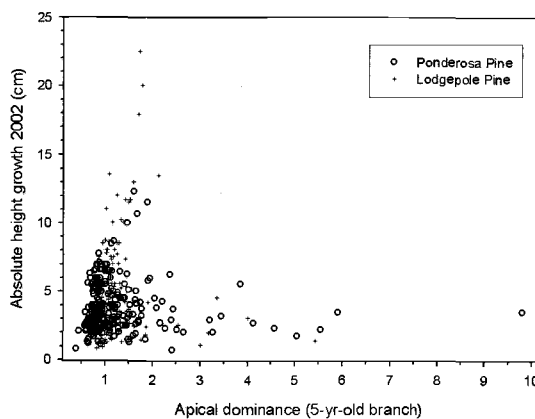
Figure 74: Relationship between absolute
height growth in 2002 and apical dominance
(the ratio of past periodic growth of the terminal
leader to the past periodic growth of the longest
5-yr-old branch leader, for the most recent 5-yr-
growth period except the current)
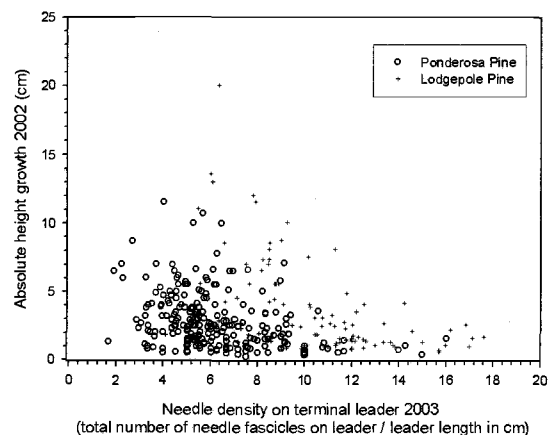
Figure 76: Relationship between absolute
height growth in 2002 and needle density on
the terminal leader 2003
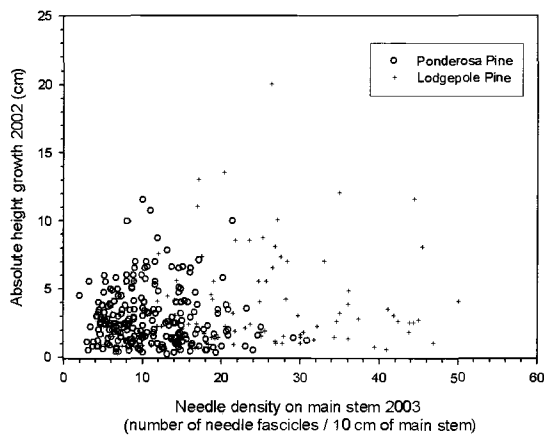
Figure 77: Relationship between absolute height growth in 2002 and needle density on the main stem 2003
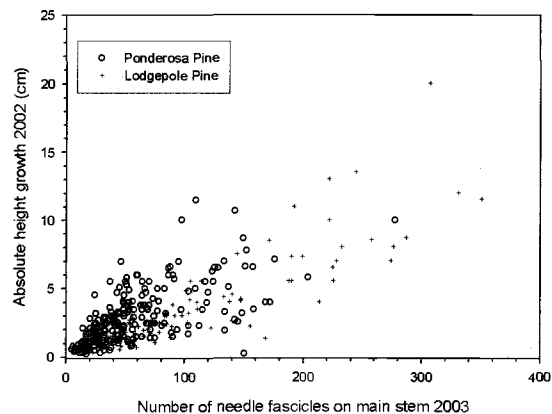
Figure 79: Relationship between absolute height growth in 2002 and the number of needle fascicles on the main stem 2003
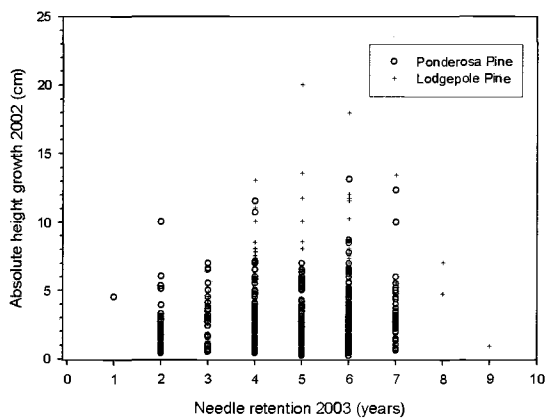
Figure 78: Relationship between absolute height growth in 2002 and needle retention 2003

The variables having the strongest relationship with relative height growth in 2002 were absolute height growth in 2001 ($r^2 = 0.39 - 0.87$), number of needle fascicles on the main stem 2001 ($r^2 = 0.57 - 0.85$), stem diameter at the root collar ($r^2 = 0.46 - 0.73$), and initial seedling height ($r^2 = 0.40 - 0.69$) (Figs. 65, 67, 68, 79; Tab. 44). Overall, the relationships between morphological characteristics and absolute height growth were similar across species and sites.

Table 44: Single predictor variables of absolute height growth in 2002

| y = LN Absolute height growth (2002)	Finley Butte		Twin Lakes		Stinger Creek
	PIPO	PICO	PIPO	PICO	PIPO
	r^2	r^2	r^2	r^2	r^2
x = Absolute height growth (2001)	0.8433 (N= 354; LN y)	0.7687 (N= 160; √ y)	0.7270 (N= 27; LN y)	0.8748 (N= 39; √ y)	0.3915 (N= 34; 1/ y)
x = Number of needle fascicles on main stem (2003)	0.6049 (N = 74; LN y)	0.7605 (N = 38; LN y)	0.8039 (N = 79; LN y)	0.8498 (N = 71; √ y)	0.5726 (N = 77; 1/ y)
x = Stem diameter at the root collar (2003)	0.6118 (N= 353; LN y)	0.5661 (N= 161; LN y)	0.7253 (N= 79; LN y)	0.5704 (N= 71; √ y)	0.4605 (N= 77; LN y)
x = Initial seedling height (2002)	0.5325 (N= 355; LN y)	0.4386 (N= 161; 1/ y)	0.6880 (N= 79; LN y)	0.3976 (N= 71; √ y)	0.4041 (N= 77; 1/ y)
x = Length of 5-yr-old branch	0.4005 (N= 158; y)	0.6157 (N= 87; y)	0.1197 (N= 27; 1/y)	0.7840 (N= 39; √ y)	0.5063 (N= 34; √ y)
x = Total number of primary branches (2001)	0.4699 (N= 355; 1/ y)	0.4267 (N= 161; LN y)	0.4786 (N= 79; LN y)	0.4544 (N= 71; y)	0.4268 (N= 77; 1/ y)
x = Number of new whorl branches (2001)	0.3102 (N= 355; LN y)	0. 5095 (N= 161; √ y)	0.4200 (N= 79; 1/ y)	0.5689 (N= 71; y)	0.2816 (N= 77; 1/ y)
x = Local basal area (2003)	0.1382 (N= 355; 1/ y)	0.1483 (N= 159; 1/ y)	0.1513 (N= 79; 1/ y)	0.3244 (N= 71; 1/y)	0.3103 (N= 77; LN y)
x = Needle density on terminal leader (2003)	0.2204 (N = 72; LN y)	0.2816 (N = 37); 1/y)	0.0538 (N = 78; 1/ y)	0.2497 (N = 71; 1/ y)	0.1633 (N = 76; √ y)
x = Needle length (2001)	0.1504 (N= 75; LN y)	0.3395 (N= 37; √ y)	0.0824 (N= 32; 1/ y)	0.0983 (N= 34; 1/y)	0.0632 (N= 74; 1/ y)
x = Needle retention (2003)	0.0194 (N= 355; 1/ y)	0.0342 (N= 157; 1/ y)	0.0987 (N= 79; √ y)	0.1579 (N= 71; 1/ y)	0.0337 (N= 77; 1/ y)
x = Needle density on main stem (2003)	0.0313 (N = 73; 1/y)	0.0097 (N = 38; 1/y)	0.0001 (N = 79; 1/y)	0.0449 (N = 71; 1/y)	0.0921 (N = 77; √ y)
x = Height to diameter ratio (2003)	0.0690 (N= 353; 1/ y)	0.0156 (N= 161; 1/ y)	0.0411 (N= 79; 1/ y)	0.0284 (N= 71; 1/ y)	0.0021 (N= 77; 1/ y)
x = Apical dominance (2001)	0.0030 (N= 128; 1/y)	0.0098 (N= 98; 1/ y)	0.0080 (N= 25; 1/y)	0.0609 (N= 40; 1/ y)	0.0139 (N= 28; 1/y)
x = Apical dominance (5-yr-old branch)	0.0155 (N= 158; 1/y	0.0195 (N = 85; 1/y)	0.0170 (N = 26; 1/ y)	0.0056 (N = 39; 1/y)	0.0257 (N = 16; √ y)

Although absolute height growth in 2001 had the strongest relationship of all variables with relative height growth in 2002, it was not included in the selection of the 'best' fitting multiple linear regression models including initial seedling height and/or local basal area (Tab. 45). Both, absolute height growth rate in 2001 and in 2002, may be influenced by the same morphological

characteristics of a seedling, and the objective was to evaluate the effects of the latter. Only seedlings with foliage measurements were included in the multiple regression analyses.

Initial seedling height already explained much of the variation in absolute height growth in both species and at all three sites (R^2 = 0.40 – 0.69) (Tab. 45,col. 3), and can be regarded as a good predictor variable. After including initial seedling height, the three 'best' two-variable regression models that explained absolute height growth in both species and at all sites included the sum of needle fascicles on the main stem, needle density on the main stem, needle density on the terminal leader, local basal area, or stem diameter at the root collar, increasing the coefficient of determination (R^2) to up to 0.85 (Tab. 45, cols. 4-5).

Table 45: Best predictor variables in addition to initial seedling height and/or overstory density in multiple linear regression models for each site and species

1	2	3 Initial seedling height R^2	4 Initial seedling height and the following variable:	5 R^2	6 Initial seedling height and overstory density R^2	7 Initial seedling height and overstory density and the following variable:	8 R^2
Ponderosa Pine	Finley Butte (N = 72)	0.54	1. NF_{stem}	0.75*	0.68	1. NF_{stem}	0.86
			2. ND_{stem}	0.66		2. ND_{leader}	0.85
			3. ND_{leader}	0.60		3. ND_{stem}	0.84
	Twin Lakes (N = 78)	0.69	1. NF_{stem}	0.83	0.76	1. NF_{stem}	0.84
			2. ND_{stem}	0.77		2. ND_{stem}	0.80
			3. LBA	0.76		3. ND_{leader}	0.77
	Stinger Creek (N = 76)	0.40	1. LBA	0.64	0.64	1. NF_{stem}	0.71
			2. NF_{stem}	0.59*		2. ND_{stem}	0.67
			3. ND_{stem}	0.51		3. ND_{leader}	0.66
Lodgepole Pine	Finley Butte (N = 36)	0.44	1. NF_{stem}	0.79*	0.65	1. NF_{stem}	0.85*
			2. ND_{stem}	0.60		2. ND_{stem}	0.75*
			3. ND_{leader}	0.49		3. ND_{leader}	0.75*
	Twin Lakes (N = 71)	0.40	1. NF_{stem}	0.85*	0.64	1. NF_{stem}	0.85*
			2. ND_{stem}	0.75		2. ND_{stem}	0.78
			3. D	0.63		3. D	0.76

* The model is significant but one of the variables included is not (p>0.05). NF_{stem} = sum of needle fascicles on the main stem 2003; ND_{stem} = needle density on the main stem; ND_{leader} = needle density on the terminal leader; D = stem diameter at the root collar; LBA = local basal area; Additional variables included in the model selection procedures: H/D, number of new whorl branches 2001, total number of primary branches 2001, needle retention. Variables NOT included in the model selection procedures: apical dominance of 5-yr-old branch, length of 5-yr-old branch. Model selection by comparing AIC values (Akaike's Information Criterion)

The two most silvicultural practical variables, overstory density and initial seedling height, explained 64 - 76 % of the variation in absolute height growth (Tab. 45; col. 6). Depending on the site and species, the sum of needle fascicles on the main stem, needle density on the main stem, needle density on the terminal leader, and stem diameter at the root collar are the variables that improve R^2 best in a three-variable model, increasing R^2 to up to 0.86 (Tab. 45; cols. 7-8).

DISCUSSION

Absolute Height Growth in 2002, 1995, and 1990 and its Annual Change over Time after Stand Density Reduction

Height growth follows species-specific patterns and determines the growth form and competitive ability of a tree in different environmental conditions. In shade-intolerant trees, fast juvenile growth ensures survival and seedlings quickly occupy growing space in highly competitive environments (Oliver and Larson 1996). In optimal conditions, the relationship between absolute height growth and age over the life of a tree follows a sigmoid pattern. In young trees, absolute height growth is comparatively low, because of a small crown and small total leaf area.

In this study, absolute height growth was positively affected by stand density reduction at all three sites and in both species. Before the treatments in 1990, absolute height growth was approximately 3 cm for the tallest seedlings at Twin Lakes and at Stinger Creek. At Finley Butte, absolute height growth was approximately 2 cm in ponderosa pine and 3 cm in lodgepole pine seedlings. The lack of relationship between 2003 overstory density and absolute height growth in 1990 confirms the assumption that stands were comparable in stand density before silvicultural treatment. All seedlings at a particular site were experiencing very similar growing conditions before stand density reduction, and as a result, height growth responses to these conditions did not differ between seedlings in different stands.

In 2002, absolute height growth rates of lodgepole pine seedlings under low overstory densities (i.e. in stands that were thinned) were > 8x higher in 2002 than they were in 1990, the maximum being 22.5 cm in lodgepole pine and 13.1 cm in ponderosa pine. Increase in absolute

height growth was sharpest as overstory density fell below approximately 20 m²/ha at Finley Butte and Twin Lakes and below approximately 10 m²/ha at Stinger Creek. The effect of reduction in overstory density was greatest in tall lodgepole pine seedlings at Twin Lakes and Finley Butte, and absolute height growth rates of small seedlings did not seem very different between species and overstory densities. Seedling differences were higher in 2002 than they were one year after the thinning (1995) at Finley Butte and Twin Lakes. There were no lodgepole pine present at Stinger Creek, and the ponderosa pine seedlings at that site grew poorly, probably due to lower precipitation.

It is not clear whether faster growth rates of lodgepole pine reflect a different potential between species on these sites or an advantage of not being advance regeneration and avoiding a period of initial suppression. Growth rates were only taken on trees that were still alive in 2003. At Finley Butte, 162 lodgepole seedlings were analyzed in 2002 but only 13 of them (8 %) in 1990. In contrast, 356 ponderosa pine seedlings were analyzed in 2002 and 155 (46 %) of them in 1990. Although only minimum age was determined, this difference in the number of trees measured and the high absolute growth rates of tall lodgepole pine seedlings suggest that many lodgepole pine seedlings established after the stand density reduction at Finley Butte. This establishment time may also explain the higher growth rates of small lodgepole pine compared to ponderosa pine seedlings one year after thinning in 1995. Higher absolute height growth rates in tall lodgepole pine seedlings in 2002 and small lodgepole pine seedlings in 1995 may be caused by their establishment just before or during the year of the silvicultural treatment, whereas ponderosa pine seedlings from advance regeneration may have had to respond to changes in overstory density by adjusting their morphology and physiology. Shade-intolerant species are regarded as having only small plasticity, especially if vigor before release was low (Ruel et al. 2000).

In 2002, the very small difference in absolute height growth between species at overstory densities below 15 m²/ha at Finley Butte may indicate a threshold for favoring or disfavoring lodgepole pine growth over that of ponderosa pine. This threshold value, however, varies with site. Although at Finley Butte absolute height growth of lodgepole pine was higher in general, at Twin Lakes absolute height growth was only greater at the lowest overstory densities. Small lodgepole pine seedlings had higher absolute growth rates than ponderosa pine of comparable

size below 15 m²/ha, and tall lodgepole pine seedlings had higher growth rates than ponderosa pine only below 10 m²/ha. These model predictions, however, did not seem to fit observed data. Many tall lodgepole pine seedlings had lower growth rates than ponderosa pine seedlings.

Average absolute height growth over time of advance regeneration indicates growth shock behaviour in the taller seedlings at Twin Lakes and Stinger Creek (i.e. height growth reduction one to a few years after overstory reduction in advance regeneration), but this decline in growth may in fact be caused by a year of unusual low precipitation in 1995. A very unusual high amount of precipitation in the spring of 1998 could explain the peak in height growth in 1989 and 1999. Water on these sites is very limited. Any change in the amount of water availability can have a great effect on the vegetation.

The fact that seedlings between 0.21-0.50 m had higher absolute growth rates than the seedlings between 0.51-1.00 m was not expected. They may have been better able to respond to the treatments than the taller seedlings. Advance regeneration of both species did not differ in its response to stand density reduction at Finley Butte, but lodgepole pine seedlings seemed to have a lower response potential than ponderosa pine at Twin Lakes as their average absolute height growth rates decreased after treatments. Ginn et al. (1991) related increased growth of 8-year-old loblolly pine seedlings after thinning to an increase in crown size, especially in the lower crown where foliage responded to increased light availability. In this study, many of the morphological characteristics indicating leaf area (see Chapter Two) were higher in seedlings on low-density plots, i.e. after stand density reduction, which may explain their higher growth rates.

Relative Height Growth in 2002, 1995, 1990 and its Annual Change over Time after Stand Density Reduction

Relative growth rate seems to be a species specific characteristic (Cornelissen et al. 1998). In woody species, it decreases with tree height because more resources are allocated to supporting structures compared to photosynthetic leaf material (Kramer and Kozlowski 1997). In this study, differences in relative height growth between species and at different overstory densities were most pronounced in the smallest seedlings.

Relative height growth in both species increased after the last silvicultural treatments in 1994, and this response was stronger in lodgepole pine than in ponderosa pine. Relative height

growth was higher in seedlings one year after the silvicultural treatment (1995) compared to eight years after treatment (2002). A decrease in recent years may have been caused by an increase in local basal area and associated building of canopy since thinning. Small seedlings had the highest relative height growth rates and the greatest positive response to overstory density reduction. Whether this response can be attributed to suppression avoidance by establishment after treatment is not clear. Lodgepole pine did not occur at Stinger Creek, but the effects of overstory density and initial seedling height were similar for ponderosa pine at that site compared to Finley Butte and Twin Lakes. Although fast height growth may confer a competitive advantage in regard to light availability, it involves trade-offs such as costs from past investments in stem and support structures and for future maintenance and respiration. Both species are considered shade-intolerant and rapid early height growth can be regarded as a strategy to avoid low light levels in lower canopy positions.

In ponderosa pine, average relative height growth over time stayed the same or even declined after silvicultural treatments in the taller seedlings but increased in the smallest seedlings at two of the three sites. This increase in the smallest seedlings over time is contrary to the results in Figs. 46-54 after which relative height growth decreased with increasing initial seedling height and it suggests a strong response potential of small ponderosa pine advance regeneration. In logepole pine, average relative height growth after stand density reduction increased in all height classes at one site but decreased in all height classes at the second site, not allowing a general statement about the response of lodgepole pine at these two sites.

All seedlings displayed a peak in growth during the years 1998 and 1999, after which the growth rates declined again. This peak can be explained by a higher than usual rate of precipitation in May 1998. This period was recorded as one of the wettest since weather records began in 1943 at Malheur Experiment Station in eastern Oregon, and precipitation was similarly high in central Oregon (approximately 100 mm; NCDC National Climatic Data Center http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/main.html and Malheur Experiment Station, Oregon State University http://www.cropinfo.net/weather/weathersummary98.htm). No physiological shock or reduced growth rate was evident after stand density reduction, except for tall ponderosa pine seedlings at Stinger Creek.

In a study by Kneeshaw et al. (2002), lodgepole pine responded to release with immediate increase in root growth and after a 1-yr delay with an increase in stem growth. Branch radial increment and leader height growth, however, experienced a 2- to 3-year growth reduction before responding positively. Ferguson (1994) also observed, on average, at least a 1-year delay in height growth response in the Inland West if buds are pre-determined, as in ponderosa pine and lodgepole pine. Height growth the first summer after release reflects conditions when the bud was developed the previous fall. Therefore, height growth the second year after release will reflect the new growing conditions and the degree of physiological shock that occurred the first year after release. In general, increases in this study were gradual. This gradual increase was consistent with a study on the effects of thinning on foliage length and mass of lodgepole pine with gradual and long-lasting responses up to four years after thinning (Yang 1998).

Predictor Variables of Absolute Height Growth in 2002

Although inferences about the predictive value of certain morphological characteristics on absolute height growth in ponderosa pine and lodgepole pine seedlings only apply to the investigated sites, the best predictors in this study are likely to be good indicators in general as they agree with findings in the literature. This, however, needs further investigation.

Many of the measured morphological characteristics were highly correlated with tree growth because they influence light harvesting and carbon gain. As in previous studies reviewed by Ruel et al. (2000) and Ferguson (1994), height growth rate of the previous year, stand basal area, and initial seedling height were good predictors for subsequent absolute height growth in 2002 at the investigated sites. The absolute height growth of the previous year was one of the best indicators for all species and at all three sites. After absolute growth rate in 2001, the second best predictor variable was number of needle fascicles on the main stem, explaining up to 85 % of the variation in absolute height growth in 2002.

McDonald et al. (1992) found that initial length of 1-year-old ponderosa pine needles was positively correlated with seedling height and diameter 2-4 years after vegetation management treatments, and they recommend needle length as predictor for future seedling growth responses. In this study, the coefficient of determination (R^2) was only between 0.06 and 0.15 in

ponderosa pine and between 0.10 and 0.34 in lodgepole pine, respectively. Stem diameter at the root collar was a reliable predictor in both ponderosa pine and lodgepole pine. Except for lodgepole pine at Twin Lakes (R^2 = 0.14), the stem height to diameter ratio (H/D) has not been found to be a good indicator for growth in this study, a result consistent with other studies (Ruel et al. 2000). Ruel et al. (2000) regard H/D to have limited value for predicting regeneration responses because variation is considerable among different sites and species. Height or diameter growth can be influenced by many other factors like climate, tree age, and genotype (Mustard and Harper 1998). One measure of apical dominance, the ratio of leader length to length of the longest lateral branch at the last whorl, was advocated as an index of suppression intensity for trees in the understory (Ruel et al. 2000). In this study, both measures of apical dominance did not perform as well as expected.

Ruel et al. (2000) suggests the use of combined predictors and critical threshold values for predictor variables. Critical threshold values for two of the most practical predictors of absolute height growth, i.e., stand basal area and initial seedling height, were difficult to determine within the range of investigated stand basal areas because increases in growth over the range of these predictors were often gradual, if not linear. However, overstory densities below 15-20 m²/ha often resulted in a sharp increase in crown development as well as height growth rates (see Chapter Two).

Initial seedling height on its own already explained up to 69% of the variation in absolute height growth. When two-variable multiple regression models with initial seedling height and one other variable were developed, the sum of needle fascicles on the main stem, needle density on the main stem, and needle density on the terminal leader were the best additional variables for explaining variation in absolute height growth (R^2 = 0.49-0.85). If both, initial seedling height and overstory density were forced into the model, both variables predict height growth well (R^2 = 0.64-0.76 for all species and at all sites). The mechanisms by which stand basal area and seedling height control seedling height growth responses of these two species is suggested by the strong relationship these two variables have to morphological characteristics (see Chapter Two).

In a three-variable model, the same variables as in the two-way model proved to be good additional predictor variables with initial seedling height and overstory density: the number of needle fascicles on the main stem, needle density on the main stem, and needle density on the

terminal leader. Growth in seedlings has been found highly correlated with LAR (leaf area ratio, i.e. ratio between total leaf area and total plant biomass) (Cornelissen et al. 1998). Although LAR was not determined in this study, an increase in the number of needle fascicles on the main stem and needle density on the main stem may be effective surrogates.

CHAPTER FOUR:

SYNTHESIS OF MORPHOLOGICAL RESPONSES OF SEEDLINGS TO SILVICULTURAL

TREATMENTS AND SILVICULTURAL IMPLICATIONS

Species differ in the amount of time they can survive in the understory, with their ranking roughly corresponding to their relative shade-tolerance (Kobe and Coates 1997). Differences in mortality between species may be more important to stand dynamics than growth responses after release (Wright et al. 1998, Chen 1997). Although ponderosa pine and lodgepole pine are both regarded as shade-intolerant species, they show different morphological responses to changes in their growing environment that may explain the relative advantage of one over the other where they grow together. And although inferences are limited to the studied sites, the results indicate species interactions that may also apply to other stands on which ponderosa pine and lodgepole pine grow together. To make broader inferences, however, further investigations are necessary.

At low overstory densities created by silvicultural treatments, lodgepole pine seedlings had a higher height to diameter ratio than ponderosa pine (at least at one site), produced more primary branches per seedling and whorl branches per year, had longer 5-year-old branches, higher annual apical dominance, more needle fascicles on the main stem and terminal leader, higher needle density on the main stem and terminal leader, a polycyclic growth pattern, and higher absolute and relative height growth rates. However, at these sites lodgepole pine does not seem to establish and survive as well as ponderosa pine, as reflected in the number of seedlings, especially under relatively dense overstories. Both species are represented in the overstory and although lodgepole pine establishment seems high (i.e. many seedlings < 0.10 m were found), its long-term survival is low (i.e. significantly fewer seedlings > 0.10 m were found), especially where overstories are retained. Ponderosa pine seedlings had stronger apical dominance in 5-year-old branches, longer needles, more needles per fascicle, and longer needle retention at one site (there was no significant species difference at the other). However, the advantage conferred by these morphological attributes is not obvious, if they are in fact a factor in the greater number of surviving seedlings in the understory. The ranking of morphological characteristics regarding their predictive value at the investigated sites was very similar in both species with absolute height

growth the previous year and the number of needle fascicles on the main stem being the best predictors of absolute height growth.

A higher percentage of ponderosa pine seedlings originated from advance regeneration with ages of more than 30 years commonly measured in these seedlings. Lodgepole pine, on the other hand, seemed to have established primarily after stand density reduction, as indicated by their younger minimum ages, greater height growth rates, and low survival of tall seedlings at high overstory densities. Valid comparisons of the species' plasticity to reduction in overstory density in advance regeneration, therefore, were not made because of insufficient seedling survival in lodgepole pine.

The results on these sites confirm the finding that lodgepole pine is the more invasive species, at least in part due to its strategy of producing large seed crops more often, its short juvenile period (early development of cones as seen in seedlings at the investigated sites), and its fast growth (Rejmánek and Richardson 1996). This strategy enables lodgepole pine to more quickly occupy growing space by high rates of seedling establishment after canopy opening and greater investment of its resources into height growth and crown development compared to ponderosa pine. Therefore, it may have an advantage in reaching canopy dominance if it can sustain higher respiration costs associated with these acclimations. Ponderosa pine, however, seems more persistent in forest understory conditions than lodgepole pine, possibly due to its ability to reduce transpiration at low soil water potentials and its extensive root system that enhances water uptake at these moisture-limited sites (Oliver and Ryker 1990).

Although the results only apply to the studied sites, they suggest that lodgepole pine may depend on larger canopy openings to successfully regenerate than ponderosa pine. Effects of overstory reduction on morphological characteristics and height growth in lodgepole pine were generally gradual but often there was a steep increase as stand densities dropped below 15-20 m²/ha. The density of lodgepole pine seedlings > 0.10 m was low at local basal areas above 19 m²/ha at Finley Butte and 24 m²/ha at Twin Lakes. Only the smallest lodgepole pine seedlings (<0.10 m) were abundant above these overstory densities, and they do not seem to survive to larger sizes. Light and frequent reductions in stand density, that still leave significant residual canopy in these stands (>20 m²/ha), therefore, may be more favorable to ponderosa pine than to lodgepole pine regeneration.

These findings may have implications for future stand development because once established, lodgepole pine may indeed remain the more dominant species until mature age. In spacing trials comparing pure and mixed plantations of ponderosa and lodgepole pine at sites very similar to those in this study, lodgepole pine did behave as the more shade-intolerant species of the mix, with respect to slightly greater initial height growth. After 30 years, lodgepole pine and ponderosa pine had similar heights (approximately 11 m) in the more open conditions (5.5 m spacing), but lodgepole pine was still approximately 2 m taller at the closest spacing (1.8 m) (Garber and Maguire 2004)

If silvicultural treatments are implemented during restoration efforts, they will have to consider the effects that different overstory densities have on the competitive ability on these two species. If treatments are heavier, and as a consequence, more growing space is available in absence of serious competition with understory vegetation as on sites in this study, lodgepole pine with its strategy to quickly occupy growing space may have a competitive advantage over ponderosa pine. This advantage may have a long-lasting effect on the structure and dynamics of these ponderosa pine forests and may conflict with restoration efforts in these ecosystems.

BIBLIOGRAPHY

Aarssen L.W. (1994): Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. Oikos 74: 149-156.

Bailey J.D. and J.C. Tappeiner (1998): Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. For. Ecol. Manage. 108: 99-113.

Barrett J.W. (1979): Silviculture of ponderosa pine in the Pacific Northwest: the state of our knowledge. USDA Forest Service, PNW Forest and Range Experiment Station, Gen. Tech. Rep. PNW-97, 106 p.

Barrett J.W. (1970): Ponderosa pine – saplings respond to control of spacing and understory vegetation. USDA Forest Service, PNW Forest and Range Experiment Station, Research Paper PNW-106, 16 p.

Beaudet M., C. Messier, D.W. Hilbert, E. Lo, Z.M. Wang, and M.J. Lecowicz (2000): Leaf- and plant level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. Can. J. For. Res. 30(3): 390-404.

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

Cadenasso M.L., M.M. Traynor, and S.T.A. Pickett (1997): Functional location of forest edges: gradients of multiple physical factors. Can. J. For. Res. 27: 774-782.

Canham C.D. and P.L. Marks (1985): The response of woody plants to disturbance: patterns of establishment and growth. In: The ecology of natural disturbance and patch dynamics. Eds.: S.T.A. Pickett and P.S. White. Academic Press, Orlando, FL. 472 pp.

Crossley D.I. (1976): The ingress of regeneration following harvest and scarification of lodgepole pine stands. For. Chron. 52: 17-21.

Chen H.Y.H. (1997): Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. 27: 1383-1393.

Chen J., J.F. Franklin, and T.A. Spies (1993): Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agr. Forest Meteorol. 63, 219-237.

Chen J., J.F. Franklin, and T.A. Spies (1995): Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecol. Appl. 5(1): 74-86.

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

Chrimes D. (2004): Stand development and regeneration dynamics of managed uneven-aged Picea abies forests in boreal Sweden. Doctoral thesis, Swedish University of Agricultural Sciences Umeå

Clark J.S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff (1999): Interpreting recruitment limitation in forests. Am. J. Bot. 86(1): 1-16.

Claveau Y., C. Messier, P.G. Comeau, and K.D. Coates (2002): Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32(3):458-468.

Cochran P.H. and W.G. Dahms (2000): Growth of lodgepole pine thinned to various densities on two sites with differing productivities in central Oregon. USDA Forest Service Pacific Northwest Research Station PNW-Research Paper 520, 59 pp.

Cole D. (1975): Culture of immature lodgepole pine stands for timber objectives. In: Management of lodgepole pine ecosystems: symposium proceedings, held at Washington University, Pullman, 9-11 Oct. 1973. Ed.: D.M. Baumgartner. Washington State University Extension Service.

Cornelissen J.H.C., P. Castro-Díez, and A.L. Carnelli (1998): Variation in relative growth rate among woody species. In: Inherent variation in plant growth. Physiological mechanisms and ecological consequences, pp. 363-392. Eds.: H. Lambers, H. Poorter and M.M.I. Van Vuuren. Backhuys Publishers, AH Leiden, The Netherlands, 592 pp.

Dahms W.G. (1960): Long-suppressed ponderosa pine seedlings respond to release. USDA Forest Service PNW Forest and Range Experiment Station No. 190.

Dahms W.G. (1963): Dispersal of lodgepole pine seed into clear-cut patches. USDA Forest Service PNW Forest Range and Experiment Station, Research Note PNW-3, Portland, OR. 7 pp.

Dyrness C.T. and C.T. Youngberg (1966): Soil-vegetation relationships within the ponderosa pine type in the central Oregon pumice region. Ecology 47 (1): 122-138.

Farrar J.F. (1999): Acquisition, partitioning and loss of carbon. In: Physiological Plant Ecology: The 39th Symposium of the British Ecological Society. Blackwell Science, Oxford; Malden, MA, USA, 480 pp.

Ferguson D.E. (1984): Needed: Guidelines for defining acceptable advance regeneration. USDA Forest Service Research Note INT-341.

Ferguson D.E. (1994): Advance regeneration in the Inland West: Considerations for individual tree and forest health. J. Sustainable Forestry 2 (3-4): 411-422.

Foiles M.W. and J.D. Curtis (1973): Regeneration of ponderosa pine in the Northern Rocky Mountain – Intermountain Region. USDA Forest Service Research Paper INT-145.

Fowells H.A. (1941): The period of seasonal growth of ponderosa pine and associated species. J. For. 39: 601-608.

Franklin J.F. and C.T. Dyrness (1973): Natural vegetation of Oregon and Washington. USDA Forest Service (Portland, OR), Gen. Tech. Rep. PNW-80.

Garber S.M. and D.A. Maguire (2004): Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. For. Sci. 50(1): 92-105.

Ginn S.E., J.R. Seiler, B.H. Cazell, and R.E. Kreh (1991): Physiological and growth responses of eight-year-old loblolly pine stands to thinning. For. Sci. 37: 1030-1040.

Givnish T.J. (1988): Adaptation to sun and shade: A whole-plant perspective. Aust. J. Plant Physiol. 15: 63-92.

Gonda H. (1998): Needle length as site quality predictor in unthinned young-growth ponderosa pine plantations in Neuquen, Patagonia, Argentina. In: Height-Diameter and volume equations, growth intercept and needle length site quality indicators, and yield equations for young ponderosa pine plantations in Neuquen, Patagonia, Argentina. Ph.D. thesis, Oregon State University, 198 pp.

Greene D.F., J.C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard (1999): A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29: 824-839.

Hara T., M. Kimura, and K. Kikuzawa (1991): Growth patterns of tree height and stem diameter in populations of *Abies veitchii. A. mariesii* and *Betula ermanii*. J. Ecol. 79: 1085-1098.

Harrington C.A. and D.L. Reukema (1983): Initial shock and long-term stand development following thinning in a Douglas-fir plantation. For. Sci. 29: 33-46.

Hermann R.K. and R.G. Petersen (1969): Root development and height increment of ponderosa pines in pumice soils of central Oregon. For. Sci. 15(3): 226-237.

Huggard D.J. (2002): Edge effects in high-elevation forests at Sicamous Creek. Extension Note 62, Ministry of Forests Forest Science Program, BC, Canada.

Kaufmann M.R., P.Z. Fulé, W.H. Romme, and K.C. Ryan (1997): Restoration of ponderosa pine forests in the interior western U.S. after logging, grazing, and fire suppression. In: Restoration of Boreal and Temperate Forests, pp. 481-500. Eds.: J.A. Stanturf and P. Madsen. CRC Press.

Keyes C. (2001): Recruitment of ponderosa pine seedlings beneath partial overstories. Ph.D. thesis, Oregon State University, Corvallis (OR).

Keyes C., S.A. Acker, and S.E. Greene (2001): Overstory and shrub influences on seedling recruitment patterns in an old-growth ponderosa pine stand. Northwest Sci. 75(3): 204-210.

King D.A. (1991): Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. Funct. Ecol. 5: 485-492.

Kneeshaw D., Y. Bergeron, and L. De Grandpré (1998): Early response of Abies balsamea seedlings to artificially created openings. J. Veg. Sci. 9(4): 543-550.

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(2): 255-265.

Kobe R.K. and K.D. Coates (1997): Models of sapling 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.

Kozlov M.V. and P. Niemelä (1999): Difference in needle length – a new and objective indicator of pollution impact on Scots pine (Pinus sylvestris). Water, Air, and Soil Pollution 116: 365-370.

Kramer P.J. and T.T. Kozlowski (1997): Physiology of woody plants, 2nd edition. Academic Press, San Diego, 411 p.

Kremsater L. and F.L. Bunnell (1999): Edge effects: theory, evidence and implications to management of western North American forests. In: Forest fragmentation: wildlife and management implications, pp. 117-153. Eds.: Rochelle J.A., Lehmann L.A., Wisniewski J.. Brill, London, UK.

Lanner R.M. (1976): Patterns of shoot development in Pinus and their relationship to growth potential, In: Tree Physiology and Yield Improvement, p. 223-243. Eds.: M.G.R. Cannell and F.T. Last. Academic Press, London, New York, San Francisco

Little C.H.A. (1970): Apical dominance in long shoots of white pine (Pinus strobus). Can. J. Bot. 48: 239-253.

Lotan J.E. and W.B. Critchfield (1990): *Pinus contorta* Dougl. ex. Loud. – Lodgepole pine. In: Silvics of North America, Vol. 1. Conifers. Agriculture Handbook 654. USDA Forest Service, Washington, DC.

McCaughey W.W. and D.E. Ferguson (1988): Response of advance regeneration to release in the Inland Mountain West: a summary. USDA Forest Service, Gen. Tech. Report INT-243, pp. 255-266.

McCullagh P. and J.A. Nelder (1989): Generalized linear models. Chapman and Hall, London, UK.

McDonald P.M. (1976): Forest regeneration and seedling growth from five major cutting methods in north-central California. USDA Forest Service Research Paper PSW-115.

McDonald P.M., C.N. Skinner, and G.O. Fiddler (1992): Ponderosa pine needle length: an early indicator of release treatment effectiveness. Can. J. For. Res. 22: 761-764.

Messier C. (2003): New ideas on growth strategies of understory trees: ecological and silvicultural implications. Presentation at the North American Forest Ecology Workshop, Corvallis, OR. http://wwwdata.forestry.oregonstate.edu/nafewabs/webppt/messierc_files/ frame.htm

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

Messier C. and E. Nikinmaa (2000): Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. Ecoscience 7(3): 345-356.

Messier C., S. Parent, M. Chengaou, and J. Beaulieu (1999b): Juvenile growth and crown morphological plasticity of eastern white pines (Pinus strobus L.) planted along a natural light gradient: results after six years. For. Chron. 75(2): 275-279.

Messina M.G. and J. Jenkins (2000): Loblolly pine stand early development under reserve-tree silvicultural systems in East Texas. South. J. Appl. For 24(1): 11-16.

Miller D.L. (1988): The influence of competing vegetation in ponderosa pine forests. In: Ponderosa pine: the species and its management : symposium proceedings, September 29-October 1, 1987 Spokane, Washington, USA / compiled and edited by D.M. Baumgartner and J.E. Lotan. Washington State University, Pullman, WA. 281 pp.

Miller M. and B. Emmingham (2001): Can selection thinning convert even-age Douglas-fir stands to uneven-age structures? West. J. Appl. For. 16(1): 35-43.

Minore D. and R.J. Laacke (1992): Natural regeneration. In: Reforestation practices in southwestern Oregon and northern California. Eds.: S.D. Hobbs, S.D. Tesch, P.W. Owston, R.E. Stewart, J.C. Tappeiner II, and G.E. Wells. Forest Research Laboratory, Oregon State University, Corvallis. pp. 258-283.

Mitchell J.E. and S.J. Popovich (1997): Effectiveness of basal area for estimating canopy cover of ponderosa pine. For. Ecol. Manage. 95: 45-51.

Morin H. and D. Laprise (1997): Seedling bank dynamics in boreal balsam fir forests. Can. J. For. Res. 27: 1442-1451.

Mustard J. and G. Harper (1998): A summary of the available information on the height to diameter ratio. Research branch. British Columbia Ministry of Forests.

National Cooperative Soil Survey (1992): Soil Survey of Upper Deschutes River Area, Oregon, including parts of Deschutes, Jefferson, and Klamath Counties. 286 p.

Niinemets Ü. (1998): Growth of young trees of Acer platanoides and Quercus robur along a gap-understory continuum: Interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. Int. J. Plant Sci. 159(2): 318-330.

Niinemets Ü., D.S. Ellsworth, A. Lukjanova, M. Tobias (2002): Dependence of needle architecture and chemical composition on canopy light availability in three North American Pinus species with contrasting needle length. Tree Physiol. 22: 747-761.

Niinemets Ü. and Kull O. (1998): Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiol. 18: 467-479.

Niinemets Ü. and O. Kull (1995): Effects of light availability and tree size on the architecture of assimilative surface in the canopy of Picea abies: variation in shoot structure. Tree Physiol. 15: 791-798.

Oliver C.D. and B.C. Larson (1996): Forest Stand Dynamics, update edition. J. Wiley & Sons, New York, 521 pp.

Oliver W.W. and R.A. Ryker (1990): *Pinus ponderosa* Dougl. ex Laws. – ponderosa pine. In: Silvics of North America, Vol. 1. Conifers. Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Page L.M., A.D. Cameron, and G.C. Clarke (2001): Influence of overstorey basal area on density and growth of advance regeneration of Sitka spruce in variably thinned stands. For. Ecol. Manage. 151 (1/3): 25-35.

Rejmánek M. and D.M. Richardson (1996): What attributes make some plant species more invasive? Ecology 77(6): 1655-1661.

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. For. Chron. 76(4): 633-642.

SAS Institute Inc., Cary, NC, USA (1999-2001): The SAS System for Windows Release 8.02.

Smith D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton (1997): The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley & Sons, Inc, New York. 537 pp.

Spurr S.H. and B.V. Barnes (1980): Forest Ecology, 3rd edition. John Wiley & Sons, Inc., New York. 687 pp.

Steele R. (1994): The role of succession in forest health. In: Assessing forest ecosystem health in the inland west, pp. 183-190. Eds.: Sampson R.N. and Adams D.L. Food Products Press, Binghampton, NY. 461 pp.

Tang Z., J.L. Chambers, S. Guddanti, S. Yu, and J.P. Barnett (1999): Seasonal shoot and needle growth of loblolly pine responds to thinning, fertilization, and crown position. For. Ecol. Manage. 120: 117-130.

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(7): 1427-1437.

Utzig G. and L. Herring (1974): Factors significant to high elevation forest management: A report emphasizing soil stability and stand regeneration, British Columbia Forestry Service Research Division, Vancouver, British Columbia, Canada.

Van den Berg D.A. and R.M. Lanner (1971): Bud development in lodgepole pine. For. Sci. 17(4): 479-487.

Volland (1985): Ecological classification of lodgepole pine in the United States. In: Lodgepole pine – the species and its management: symposium proceedings. Eds.: D.M. Baumgartner, R.G. Krebill, J.T. Arnott, and G.F. Weetman. Pullman, Wash.: Office of Conferences and Institutes, Cooperative Extension, Washington State University, 381 pp.

Walker L.C. (1999): The North American forests: geography, ecology, and silviculture. CRC Press LLC.

Walter A. and U. Schurr (2000): Spatio-temporal variation of leaf growth, development and function. In: Leaf development and canopy growth, p. 96-117. Sheffield Academic Press, Sheffield, England, 317 p.

Wheeler N.C. and W.B. Critchfield (1985): The distribution and botanical characteristics of lodgepole pine: biogeographical and management implications. In: Lodgepole pine – the species and its management: symposium proceedings. Eds.: D.M. Baumgartner, R.G. Krebill, J.T. Arnott, and G.F. Weetman. Pullman, Wash.: Office of Conferences and Institutes, Cooperative Extension, Washington State University, 381 pp.

White D.E. (1987): Competitive interactions between Douglas-fir or ponderosa pine and whiteleaf manzanita. Ph.D. thesis, Oregon State University. 138 pp.

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(2): 222-231.

Wood D., C. Linkenhoker, K. Seidel, and M. Znerold (no year): Comparison of timber growth and other site conditions between even-aged and uneven-aged management. Study plan.

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

Yang R.C. (1998): Foliage and stand growth responses of semimature lodgepole pine to thinning and fertilization. Can. J. For. Res. 28: 1794-1804.

Zahner R. and F.W. Whitmore (1960): Early growth of radically thinned loblolly pine. J. For. 58: 628-634.

Zavitkovski J. and E.S. Woodard (1970): Role of brush in ponderosa pine establishment. In: Regeneration of ponderosa pine: symposium held Sept. 11-12, 1969. Comp. and ed. by R.K. Hermann. Paper 681, School of Forestry, Oregon State University. 125 pp.

Overstory treatments at Finley Butte and Stinger Creek (Wood et al. no year)

Overstory removal: "The traditional practice of removing all mature trees, usually above 16-18" DBH, and managing the residual stocking as an even-aged stand. This would include precommercial and commercial thinning."

Uneven-age 'classical': "This is uneven-aged managment with a major effort to achieve a predetermined diameter class distribution. For this study a Q-value of 1.3 would be used and a maximum DBH of 24". A twenty year cutting cycle is planned."

Uneven-age 'best tree': "This would also have the objective of maintaining these best growing trees at a specified basal area. With an objective of producing high quality ponderosa pine with a diameter of 24" or larger. Smaller trees would be removed to maintain desired stocking and remove less desirable trees. Tree distribution by size class would not be an objective. A twenty year cutting cycle is planned."

Control: No treatment.

control   overstory removal classical   best tree

Trees were measured in at least 3 of the 9 x 1/100th acre circular subplots within all 3 x 1-acre plots. Subplots were chosen to represent extreme overstory conditions.
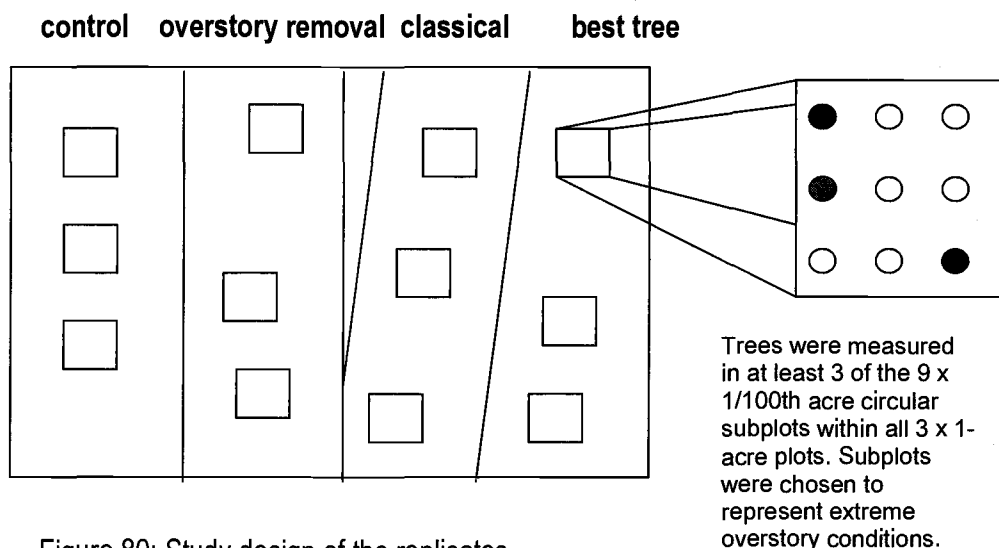
Figure 80: Study design of the replicates at Finley Butte and Stinger Creek