

# The effect of local stand structure on growth and growth efficiency in heterogeneous stands of ponderosa pine and lodgepole pine in central Oregon

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**Abstract:** Basal area and height growth were analyzed for individual trees in uneven-aged ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands in central Oregon. Basal area growth was modeled as a function of other stand and tree variables to address three general objectives: (1) to compare the predictive ability of distance-dependent versus distance-independent stand density variables; (2) to determine the degree to which small trees negatively affect the growth of overstory trees; and (3) to test for differences in growth efficiency between species and between indices of spatial occupancy used to define efficiency (area potentially available, crown projection area, and a surrogate for total tree leaf area). Distance-dependent variables were found to improve growth predictions when added to models with only distance-independent variables, and small trees were found to have a quantifiably negative effect on the growth of larger trees. While volume growth efficiency declined with increasing levels of spatial occupancy for lodgepole pine, ponderosa pine volume growth efficiency was greatest at the highest levels of crown base sapwood area and crown projection area. The behavior in ponderosa pine resulted from the previously recognized correlation between tree height and total leaf area or crown size. The final statistical models distinguished between the positive effect of relative height and the negative effect of increasing tree size.

**Résumé :** La croissance en surface terrière et en hauteur d'arbres individuels a été analysée dans des peuplements inéquiennes de pin ponderosa (*Pinus ponderosa* Dougl. ex Laws.) et de pin lodgepole (*Pinus contorta* Dougl. ex Loud.) situés dans le centre de l'Oregon. La croissance en surface terrière a été modélisée en fonction d'autres variables du peuplement et des arbres en tenant compte de trois objectifs généraux : (1) comparer le pouvoir de prédiction des variables de densité du peuplement dépendantes et indépendantes de la distance; (2) déterminer dans quelle mesure les arbres de petite dimension affecte négativement la croissance des arbres dominants; et (3) vérifier s'il y a des différences dans l'efficacité de croissance entre les espèces et entre les indices d'occupation spatiale utilisés pour définir l'efficacité (la surface potentiellement disponible, le couvert vertical au sol et un substitut pour la surface foliaire totale d'un arbre). Les variables dépendantes de la distance améliorent les prédictions de la croissance lorsqu'elles sont ajoutées aux modèles composés seulement de variables indépendantes de la distance et les arbres de petite dimension ont un effet négatif quantifiable sur la croissance des arbres plus gros. Tandis que l'efficacité de croissance en volume diminue avec l'augmentation du niveau d'occupation spatiale dans le cas du pin lodgepole, l'efficacité de croissance en volume du pin ponderosa est maximale lorsque la surface de bois d'aubier à la base de la cime et le couvert vertical au sol sont à leur niveau le plus élevé. Le comportement du pin ponderosa est le résultat d'une corrélation déjà observée entre la hauteur d'un arbre et la surface foliaire totale ou la dimension de la cime. Les derniers modèles statistiques permettent de distinguer entre l'effet positif de la hauteur relative et l'effet négatif de l'augmentation de la dimension des arbres.

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## Introduction

Many interior conifer forests in western North America contain dense, multicohort stands that reflect past and current disturbance patterns (Covington et al. 1994; Starr et al. 2001; Hemstrom 2001). Fire, insects, disease, and logging can all create growing space within a stand, allowing establishment of new tree cohorts. Conversely, frequent ground

fires can eliminate or thin successive waves of conifer regeneration without disturbing the overstory. Deviation from historic disturbance regimes that maintained fire resilience and insect and disease resistance has led to stand structures that are currently at risk and suboptimal for current management objectives (Hessburg et al. 1994; Oliver et al. 1994). Broad implementation of restoration treatments has been proposed to mitigate currently undesirable conditions, with stand

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density reduction identified as a high priority for reducing fire hazard and for enhancing residual tree vigor and insect resistance (Campbell and Liegel 1996).

Although growth of residual trees does accelerate after thinning in single-cohort stands (Cochran and Dahms 1998, 2000; and Cochran and Barrett 1995, 1998), the specific effect of density reduction on residual growth remains uncertain in multicohort stands, particularly if accomplished by understory removal in very heterogeneous stands. Three primary questions arise when designing silvicultural treatments to enhance residual stand vigor under these conditions. First, what characterization of local stand density is most appropriate for representing its influence on tree growth and vigor? Second, is competition two-sided, that is, do understory trees have a significant influence on overstory tree growth and vigor? Finally, do conclusions about stand structural effects on tree growth efficiency (and inferred insect and disease resistance) vary among alternative measures of site occupancy?

The high degree of spatial heterogeneity in many central Oregon pine stands suggests the need to determine the relative importance of average stand density versus local stand density as a descriptor of the competitive environment and predictor of tree growth. Previous studies in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) have shown that correlations between local basal area and tree growth were highest if sampling was conducted with a small basal area factor, that is, over a greater area around the subject tree (Lemmon and Schumacher 1962). Conversely, other studies have demonstrated that a high degree of intertree competition associated with high local stand density was an important risk factor for bark beetle attack (Olsen et al. 1996).

Spatially explicit measures of local competition have been used to improve both predictions of tree growth and understanding of the stand structural components influencing growth. The most common spatially explicit competition indices include distance-weighted size ratio indices; crown or influence zone overlap indices; and area occupancy indices. The performance of these indices in models depends on the index selected and species targeted, but many have been found to add statistically significant predictability to growth models in a variety of forest types, including mixed conifer (Biging and Dobbertin 1992), northern hardwoods (Holmes and Reed 1991), red pine (*Pinus resinosa* Ait.) (Martin and Ek 1984), and Tasmanian blue gum (*Eucalyptus globulus* Labill.) (Tome and Burkhart 1989). Because collecting data necessary to compute such variables is expensive, the marginal value of this extra predictability has been questioned in the context of growth and yield models (Daniels et al. 1986).

Of particular interest in central Oregon pine forests is the high stand density resulting from copious natural regeneration that has accumulated during the era of fire exclusion (Weaver 1959). Competition in such forests is often thought to be one-sided; that is, the overstory trees inhibit the growth of the understory, while the overstory itself experiences little or no competition from the understory. In the dry pine forests of central Oregon, regeneration density beyond that necessary for future replacements may be deleterious to the growth of older cohorts as a result of their belowground resource utilization (Van Sickle and Hickman 1959; Barrett and Youngberg 1965; Riegel et al. 1992). The effect of removing or thinning dense understory cohorts in these complex stands

is largely unknown. Decisions about the desirability of removing small trees must at least partly consider the effects on tree growth, in addition to risk of catastrophic loss. Growth efficiency, as one measure of vigor and potential risk of insect damage, provides diagnostic value beyond the obvious economic implications of enhanced volume growth (Mitchell et al. 1983).

Because site occupancy or growing space has been measured in numerous ways, growth efficiency patterns may vary from study to study depending on the type of growth and the measure of site occupancy (Waring 1983; Roberts et al. 1993; O'Hara 1988). Three appealing surrogates for growing space are leaf area, crown projection area, and ground area potentially available. The quantity of leaf area on a fully occupied site can be considered representative of maximum potential growing space, and the proportion of total leaf area contributed by an individual tree can be considered representative of its relative occupancy (O'Hara 1988, 1996). Leaf area is a biologically appealing measure of site occupancy for calculating growing efficiency, and estimation of leaf area has been made practical by the correlation between leaf area and sapwood cross-sectional area (Grier and Waring 1974).

In stands at full crown closure, the relative amount of growing space occupied by an individual tree is closely approximated by its vertical crown projection area (Assmann 1970). This measure of occupancy has been successfully applied to closed-canopy stands where crown overlap is negligible (O'Hara 1988). When leaf area index of individual trees (ratio of leaf area to crown projection area) does not vary over space or time, crown projection area will yield results similar to leaf area. However, where crown shape and density vary, or where tree leaf area index changes in response to silvicultural treatment, leaf area may be preferable.

The third option, area potentially available, also has merit as a measure of site occupancy, because optimal spacing of residual trees is directly related to this variable and because it may be operationally more practical than allocating growing space by leaf area. For sites where a fully stocked stand does not necessarily exhibit a closed canopy, the extent of the root system should be an effective indicator of ground space occupancy. In such sites, root spread has been found to greatly exceed crown projection (Hall 1989). Also, in stands that have been repeatedly entered, ground space being used may not be proportional to the tree's leaf area, especially immediately after harvest. Growing space occupancy under these conditions would best be represented by crown projection area plus some portion of the open area between trees. For open-canopy stands, area potentially available (APA) (Assmann 1970) is a useful surrogate for ground space occupancy, since it includes estimation of a tree's share of the "open" ground between trees (Assmann 1970).

In repeatedly disturbed stands, growth efficiency based on these three alternative measures of site occupancy may lead to slightly different conclusions. However, differences in respective growth efficiency may also provide a more comprehensive view of stand structural effects on growth and growth efficiency and, hence, on our ability to design stand structures and silvicultural systems that maintain desirable tree vigor. The goal of this study was to gain a better understanding of the growth dynamics in mixed ponderosa pine / lodgepole

**Table 1.** Attributes of the nine 0.4-ha study plots sampled in the pumice region of Oregon.

Plot	Ponderosa pine					Lodgepole pine				
	Mean DBH (cm)	Mean tree basal area growth (cm <sup>2</sup> /year)	Max height (m)	Tree density (no./ha)	Basal area (m <sup>2</sup> /ha)	Mean DBH (cm)	Mean tree basal area growth (cm <sup>2</sup> /year)	Max height (m)	Tree density (no./ha)	Basal area (m <sup>2</sup> /ha)
BL2	29.4	14.7	23.3	227	13.4	19.7	10.5	18.1	257	5.7
BL3	24.6	16.7	28.5	126	5.9	18.1	11.8	20.0	338	4.3
BM	25.4	9.4	26.6	207	7.5	19.5	9.2	21.3	914	16.5
BH1	25.4	11.4	26.6	170	7.6	18.5	8.2	19.0	1529	11.7
BH2	24.6	10.7	22.7	306	11.0	14.4	5.0	20.5	2376	13.3
TL1	18.0	11.3	21.5	252	6.1	18.3	16.3	14.3	54	1.3
TM	17.0	7.9	28.7	1010	8.1	16.0	6.6	11.3	7	0.1
TH1	18.0	4.9	30.8	1539	13.4	17.7	8.6	22.9	321	4.0
TH2	18.5	6.8	21.2	1067	15.9	18.1	8.2	14.2	114	0.9

Note: DBH, diameter at breast height.

pine (*Pinus contorta* Dougl. ex. Loud.) stands in central Oregon, particularly after different types and intensities of silvicultural treatments. Specific objectives were to test the following hypotheses: (1) spatially explicit measures of local stand structure provide significant gains in predictive power over stand- or plot-averaged variables; (2) understory trees have a deleterious effect on overstory tree growth; and (3) relative growth efficiency of individual trees depends on how site occupancy is measured (leaf area vs. crown projection area vs. area potentially available).

## Materials and methods

The questions of interest in this study required careful selection of study sites and a very structured approach to subsequent regression analysis. In regard to the study site, stand structural heterogeneity had to be the result of previous harvest entries rather than inherent site differences within the stand. This restriction ensured that effects of stand structure were minimally confounded with effects of local variation in site quality and that effects of silvicultural treatments on tree and stand growth could be assessed in a manner similar to a manipulative experiment.

Basal area growth of individual trees was selected as one of the primary responses, because it was more accurately measured than volume growth. Basal area growth depends on various tree and stand attributes, including tree size, tree vigor, tree position, stand density, and site productivity (Wykoff 1990; Hann and Larsen 1991). Multiple linear regression techniques allowed testing of stand density effects while correcting for other unavoidable tree, stand, and site covariates. In constructing the regression models, features from previous models of stem diameter growth were considered (Hann 1980; Ritchie and Hann 1985; Dolph 1988, 1992; Wykoff 1990; Hann and Larsen 1991). Volume growth was also explored because (1) it has more obvious economic implications than basal area; (2) it is a superior surrogate for total aboveground primary productivity; and (3) it is a more biologically meaningful basis for estimating growth efficiency.

## Study sites

The study area was part of Crown Pacific's central Oregon tree farm, centered approximately at Gilchrist, Oregon (43°28'N, 121°42'W). The target population consisted of multicohort ponderosa pine / lodgepole pine stands. Nine, square, 0.4-ha plots were subjectively selected to meet the following requirements: (1) high variability in local stand density, vertical stratification, diameter range, and presence of small trees and regeneration, all imposed by past harvesting; (2) no large treeless areas or large areas of high stem densities prohibitive to stem mapping; (3) no management activity for the past 10 years; and (4) common aspect and no obvious differences in soil type, plant association, or landform.

The nine plots were split between two sites, but both were characterized as a *Pinus ponderosa* / *Purshia tridentata* plant association (Franklin and Dyrness 1973). The first site, hereafter referred to as Timbers, consisted primarily of multiaged ponderosa pine (87% of basal area in *Pinus ponderosa*). The second site, hereafter referred to as Blackrock, contained a significant component of lodgepole pine (45% of basal area in *Pinus contorta*) in addition to ponderosa

pine. Much of the lodgepole pine occurred in single-cohort patches, and the understory of both sites was dominated by bitterbrush (*Purshia tridentata* (Pursh) de Canolle). Individual plots were selected to cover a wide range in stand density within both the Timber and Blackrock sites. Basal area ranged from 7.3 to 24.3 m<sup>2</sup>/ha, and tree density ranged from 306 to 2682 trees/ha (Table 1). Other stand structural features were also quite variable.

Central Oregon, like much of the Interior West, is characterized by cold winters, warm and dry summers, and limited precipitation falling mostly as snow during the winter months. The dry summers are further characterized by periodic drought. Over the last 30 years, the mean January minimum was -8 °C, and the mean July maximum was 27 °C. Total annual precipitation during this time averaged 54 cm, with approximately 70% of this falling as snow (<http://www.ocs.orst.edu/allzone/allzone5.html>)

Soils in this part of central Oregon are strongly influenced by pumice and ash deposition from past volcanic eruptions. The Mazama pumice deposited at the study sites generally extended greater than 3 feet (1 foot = 0.3048 m) in depth, were coarse textured and well-drained, and had low fertility, low bulk density, and low thermal conductivity.

### Sampling design and field measurements

Following establishment of plot corners in the summer of 1998, all trees >1.37 m in height were tagged and stem mapped. All tagged trees were measured for diameter at breast height (DBH, 1.3 m) to the nearest 0.1 cm. For each plot tree greater than 10 cm DBH, the following additional attributes were measured: Ht, height from the ground to the topmost whorl, representing height at the end of the 1998 growing season (nearest 0.1 m); Ht<sub>5</sub>, height from the ground to the fifth whorl from the tip of the tree, representing total height at the end of the 1993 growing season (nearest 0.1 m); HCB, height to the live crown base (nearest 0.1 m), defined as the lowest whorl in which 75% of the branches were still alive; CW, geometric mean of N-S and E-W crown widths; ΔR, radial increment for the past 5 years (nearest 0.5 mm) measured on two cores separated by 180°; and SR, geometric mean of sapwood widths (nearest 1 mm) measured on each increment core. On 60 trees of each species, diameter inside bark at breast height (DIB<sub>1.3</sub>) was recorded as the sum of the pith-to-cambium distances from the two increment cores.

### Analysis data set

Numerous variables were calculated from the basic field measurements. These variables included the following: APA, area potentially available, computed as the constrained, tree-weighted polygon for each tree (Nance et al. 1988); CPA, crown projection area, computed as  $(\pi/4)CW^2$ ;  $H(\theta)$ , point relative height, computed as the ratio of the subject tree height to the tallest neighboring tree, with neighboring trees defined as those with height penetrating the inverted cone of fixed angle  $\theta$  from the tip of the subject tree ( $\theta = 30^\circ$  or  $45^\circ$ ); ST<sub>k</sub>, total basal area of trees with DBH < 10 cm and located within zones of influence surrounding each subject tree, with zone radii equal to  $k$  crown radii of the subject tree ( $k = 1.5, 2, 2.5, 3$ , and  $3.5$ ); DIB, DIB<sub>1.3</sub> estimated from the regression equation

$$DIB = b_1 DBH^{b_2}$$

where  $b_1$  and  $b_2$  are parameters estimated from the 60 trees of each species on which DIB<sub>1.3</sub> was measured directly; SAP, sapwood cross-sectional area, estimated as  $\pi[(DIB/2)^2 - (DIB/2 - SR)^2]$ ; CSAP, crown base sapwood cross-sectional area, estimated from SAP by applying a ponderosa pine sapwood taper equation to both species (S.M. Garber, unpublished data; based on data set in Garber and Maguire (2003)); and V<sub>98</sub>, individual tree volume in 1998, estimated from measured height and diameter (Cochran 1985).

Crown base sapwood area was selected as the most appropriate surrogate for leaf area, given the wide variability in stand densities among plots and corresponding differences in heights to crown base (Waring et al. 1982). Empirical studies have confirmed this expectation in several species (Dean and Long 1986; Maguire and Bennett 1996).

Backdating of some variables was necessary to relate past 5-year growth to initial conditions. During fieldwork, 1993 height was measured directly at the fifth whorl below the tree tip, and 1993 diameters (DBH<sub>93</sub>) were determined using the 5-year diameter increments and the DIB estimation equation. Because lodgepole pine exhibits a degree of multinodality, backdating heights by whorl counting is less accurate for this species than for ponderosa pine (Franklin and Callahan 1970). Nevertheless, measured growth rates conform to the expected height growths calculated from the study area's site index (Dahms 1975). Individual tree volume in 1993, V<sub>93</sub>, was estimated from the 1993 DBH and height measurements by application of existing volume equations (Cochran 1985). Five-year basal area growth for the small trees (DBH < 10 cm) was estimated for each plot with the appropriate forest vegetation simulator variant (SORNEC). These growth estimates were then expressed as a percentage of the initial basal area, and these percentages were used to estimate past 5-year growth of the small tree stand component. With the exception of crown attributes, all individual tree and stand variables were calculated using these backdated values. Because no reliable methods exist to estimate past change in crown attributes, sapwood cross-sectional area, crown width, and crown ratio were assumed to be constant since 1993.

### Statistical analysis

Three forms of growth efficiency (VGE) were computed for each tree with DBH > 10 cm, specifically by dividing its volume growth by each of three site occupancy variables: CSAP (leaf area surrogate), APA, and CPA. Consistency in tree rankings by the three alternative VGEs was tested with Spearman's rank correlation coefficient. The null hypothesis was that the growth efficiency ranking of trees did not depend on the form of VGE applied.

Growth efficiencies were initially assessed for both species by plotting VGE on the measure of site occupancy represented in that VGE. VGE<sub>CSAP</sub> and VGE<sub>CPA</sub> were also plotted against the ratio APA/CPA, an index of degree of disengagement between a subject tree and its neighbors (Assmann 1970). Likewise, a surrogate for tree-level leaf area index (CSAP/CPA) was plotted against APA/CPA to examine the relationship between total leaf area (CSAP),



**Table 2.** Parameter estimates for distance-independent model [1] fit to ponderosa pine and lodgepole pine data.

Parameter	Ponderosa pine		Lodgepole pine	
	Parameter estimate	Standard error	Parameter estimate	Standard error
$\alpha_0$	-1.24664	0.21429	-0.44792	0.25245
$\alpha_1$	0.86651	0.05848	0.71012	0.07133
$\alpha_2$	2.33587	0.14258	1.89263	0.10784
$\alpha_3$	-0.01209	0.00540	-0.02602	0.00608
$\alpha_4$	-0.05448	0.00701	-0.02692	0.00908
$\alpha_5$	-0.33599	0.03296	-0.20966	0.05082

crown projection area (CPA), and the amount of aerial growing space available to the tree (APA/CPA).

The relationships between individual tree growth and stand structure were evaluated with two basic statistical models: spatially explicit (or distance-dependent) models incorporating information on tree locations to compute various competition measures and spatially implicit (or distance-independent) models disregarding tree locations. All models were constructed separately for lodgepole pine and ponderosa pine, because their behavior under similar conditions was expected to differ. During initial screening for appropriate predictor variables, individual-tree basal area was logarithmically transformed as the response variable, and alternative models were evaluated on the basis of variance inflation factors (VIF), Mallow's  $C_p$  statistics, correlation coefficients, current growth theory, biological rationality of predicted growth trends, interpretability, and consistency in model form between species.

The spatially implicit model relied on variables obtained or easily calculated from standard timber cruise or stand exam information, with competition measures based on plot-level averages. The spatially explicit model was then developed as an expansion of the spatially implicit form, with competition surrogates constructed from stem locations and individual tree attributes. Variables related to competition in the spatially explicit model included local site occupancy (APA), relative height ( $H(\theta)$ ), and basal area of small trees ( $DBH < 10$  cm) within a zone of potential interaction with the subject tree ( $ST_3$ ). The relative contribution of spatially explicit variables to the spatially implicit model was evaluated by a series of extra-sums-of-squares tests. The null hypothesis was that the expanded or full models (spatially implicit model) with various sets of spatially explicit variables represented no significant improvement over the reduced model (with no spatially explicit variables).

The models developed for periodic annual basal area growth over the past 5 years were then refit with periodic annual volume growth (VG) as the response variable. Smoothed or mean trends in growth efficiencies were assessed by analysis of the spatially explicit explanatory models, refit with successive replacement of the site occupancy variable (CSAP, APA, CPA). Implied growth efficiencies and their relationships to the explanatory variables were derived by dividing both sides of the growth equations by the corresponding surrogate for site occupancy, yielding VGE on the left-hand side of the equation. Implied VGEs were then assessed graphically in two ways. First, the trend in VGE was plotted

**Table 3.** Parameter estimates for distance-dependent basal area growth model [2] fit to ponderosa pine and lodgepole pine data.

Parameter	Ponderosa pine		Lodgepole pine	
	Parameter estimate	Standard error	Parameter estimate	Standard error
$\beta_0$	-0.5202	0.1956	0.1249	0.2422
$\beta_1$	0.4863	0.0521	0.2754	0.0761
$\beta_2$	1.7741	0.1373	1.6618	0.1078
$\beta_3$	0.1720	0.0148	0.1824	0.0215
$\beta_4$	-0.0540	0.0046	-0.0380	0.0063
$\beta_5$	0.2074	0.0533	0.1556	0.0757
$\beta_6$	-0.3765	0.2115	-1.3068	0.2670
$\beta_7$	-0.2887	0.0305	-0.1170	0.0500

over the occupancy variable, with other explanatory variables set at their mean values. One drawback to this approach is that explanatory variables in this type of study are characterized by multicollinearity to some degree, causing the average level of other explanatory variables to change as the level of site occupancy increases. In the second approach, therefore, observations were grouped into approximately 10 intervals along the site-occupancy axis. Volume growth and implied VGE were then computed, with the other explanatory variables fixed at their mean values within each interval, and the trend in VGE was depicted by plotting VGE over site occupancy (CSAP, CPA, or APA).

## Results

### Growth trends

Nonlinear models have been preferred for describing basal area growth in other studies primarily because of non-normality of the residuals on the logarithmic scale (Ritchie and Hann 1985). Normality plots for residuals from the ponderosa and lodgepole pine models, however, failed to reject normality on the transformed scale, and Furnival's (1961) index likewise suggested that the logarithmically transformed model was better. The final model form was

$$[1] \quad \ln(\text{BAG}) = \alpha_0 + \alpha_1 \ln(\text{DBH}_{93}) + \alpha_2 (\text{CR}) + \alpha_3 (\text{BA}) + \alpha_4 (\text{BAL}) + \alpha_5 (T) + \epsilon_1$$

where BAG is tree basal area growth (square centimetres per year),  $\text{DBH}_{93}$  is initial DBH (1993), CR is live crown ratio, BA is initial plot basal area (square metres per hectare), BAL is initial basal area in trees larger than the subject tree (square metres per hectare),  $T$  is site indicator (1 if Timbers site, 0 if Blackrock site), and  $\epsilon_1 \approx N(0, \sigma_1^2)$ . The model explained 79% and 66% of the variation in the logarithm of ponderosa pine and lodgepole pine basal area growth, respectively, with corresponding RMSEs of 0.360 and 0.342. Residual plots suggested close conformity to constant variance and normality of residuals. Parameter estimates indicated positive effects of increasing initial diameter and crown ratio, but negative effects of increasing basal area and BAL (Table 2).

The best spatially explicit model form for both ponderosa and lodgepole pine was

**Table 4.** Results of extra-sums-of-squares tests on adding spatially explicit variables to the distance-independent basal area growth model [1].

Full model	Reduced model	<i>p</i> values	
		Ponderosa pine	Lodgepole pine
[1] Distance independent			
[1] + ln(APA)	[1]	<0.0001	<0.0001
[1] + $H(\theta)$	[1]	0.0027	0.0001
[1] + ST <sub>3</sub>	[1]	0.0007	0.0637
[1] + ln(APA) + $H(\theta)$	[1]	<0.0001	<0.0001
	[1] + ln(APA)	0.0121	<0.0001
	[1] + $H(\theta)$	<0.0001	<0.0001
[1] + ln(APA) + ST <sub>3</sub>	[1]	<0.0001	<0.0001
	[1] + ln(APA)	0.0003	0.0355
	[1] + ST <sub>3</sub>	<0.0001	<0.0001
[1] + ln(APA) + $H(\theta)$ + ST <sub>3</sub>	[1]	<0.0001	<0.0001
	[1] + ln(APA)	0.0002	<0.0001
	[1] + $H(\theta)$	<0.0001	0.0003
	[1] + ST <sub>3</sub>	<0.0001	<0.0001
	[1] + ln(APA) + $H(\theta)$	0.0008	0.0969
	[1] + ln(APA) + ST <sub>3</sub>	0.0306	0.0001

**Table 5.** Parameter estimates (with standard errors in parentheses) for distance-dependent volume growth model fit to ponderosa pine and lodgepole pine data with APA as the measure of site occupancy (model [2] with ln(VG) as the response variable).

	Ponderosa pine			Lodgepole pine		
	APA	CPA	CSAP	APA	CPA	CSAP
$\beta_0$	-3.2445 (0.1700)	-3.2495 (0.1795)	-2.8935 (0.1593)	-1.7081 (0.1900)	-1.5895 (0.2164)	-1.6952 (0.1482)
$\beta_1$	1.6106 (0.0452)	1.6117 (0.0521)	0.7550 (0.0833)	1.1033 (0.0597)	1.0921 (0.0702)	0.3085 (0.0635)
$\beta_2$	0.7635 (0.1191)	0.8486 (0.1225)	-1.3919 (0.2121)	0.9459 (0.0846)	0.9489 (0.0964)	-1.5818 (0.1493)
$\beta_3$	0.0703 (0.0128)	0.0889 (0.0292)	0.7145 (0.0555)	0.0883 (0.0169)	0.0953 (0.0304)	0.8244 (0.0414)
$\beta_4$	-0.0240 (0.0040)	-0.0268 (0.0040)	-0.0049 (0.0041)	-0.0209 (0.0049)	-0.0243 (0.0049)	-0.0034 (0.0040)
$\beta_5$	0.3550 (0.0462)	0.3610 (0.0469)	0.3694 (0.0427)	0.3563 (0.0594)	0.3870 (0.0601)	0.3325 (0.0473)
$\beta_6$	-0.0724 (0.2187)	-0.2886 (0.1895)	-0.1914 (0.1690)	-0.4790 (0.2094)	-0.6399 (0.2145)	-0.3816 (0.1669)
$\beta_7$	-0.1064 (0.0265)	-0.1207 (0.0267)	-0.0629 (0.0247)	-0.1071 (0.0392)	-0.1359 (0.0403)	-0.0972 (0.0312)

Note: APA, area potentially available; CPA, crown projection area; CSAP, crown base sapwood cross-sectional area; VG, volume growth.

$$\begin{aligned}
 [2] \quad \ln(\text{BAG}) = & \beta_0 + \beta_1 \ln(\text{DBH}_{93}) \\
 & + \beta_2(\text{CR}) + \beta_3 \ln(\text{APA}) + \beta_4(\text{BAL}) \\
 & + \beta_5[H(\theta)] + \beta_6(\text{ST}_3) + \beta_7(T) + \epsilon_2
 \end{aligned}$$

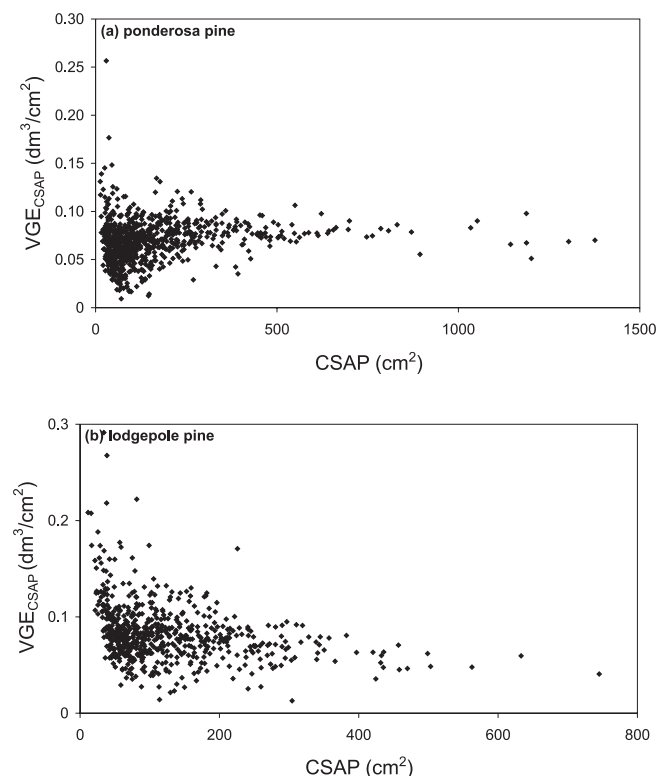
where  $\theta = 45^\circ$  for ponderosa pine and  $30^\circ$  for lodgepole pine, ST<sub>3</sub> is basal area in trees with DBH < 10 cm and within three crown radii of the subject tree, and  $\epsilon_2 \sim N(0, \sigma_2^2)$ . This model explained 83% and 71% of the variation in the logarithm of ponderosa pine and lodgepole pine basal area growth, respectively, with corresponding RMSEs of 0.329 and 0.320. Residual plots indicated close conformity to constant variance and normality of residuals. Total plot basal area (BA) dropped out of the model ( $p > 0.5$ ) when APA, BAL, and  $H(\theta)$  were introduced. Parameter estimates indicated positive effects of increasing initial diameter, crown ratio, APA and  $H(\theta)$  (point relative height), but negative effects of increasing BAL and ST<sub>3</sub> (basal area of small stems) (Table 3). Although  $H(45)$  was a more powerful predictor than  $H(30)$  for ponderosa pine, the reverse was true for lodgepole pine.

Understory trees exhibited a consistently negative effect on volume growth of lodgepole and ponderosa pines. This negative effect ranged from 0.1 to 5 dm<sup>3</sup>·tree<sup>-1</sup>·year<sup>-1</sup> at the highest levels of understory basal area, depending on individual tree attributes.

Extra-sums-of-squares tests indicated that almost any combination or subset of the spatially explicit variables from the spatially explicit model (eq. 2) — APA,  $H(\theta)$ , and ST<sub>3</sub> — yielded a full model that accounted for significantly more variation in volume growth than the reduced model (eq. 1) (Table 4). The only cases in which addition of one of these variables proved to be nonsignificant (at  $\alpha = 0.05$ ) were for small tree basal area added to the distance-independent ponderosa pine model ([1]) and for this same variable added to the ponderosa pine model with APA and  $H(\theta)$  already present. In both cases, ST<sub>3</sub> was marginally significant ( $p = 0.06$  and 0.09, respectively), but the majority of gain in predictive power was achieved through APA as opposed to  $H(\theta)$  and ST<sub>3</sub>.

When the basal area growth models mentioned before were refit with periodic annual volume growth as the response variable, all explanatory variables remained signifi-

**Fig. 1.** Observed volume growth efficiency ( $VGE_{CSAP}$ ) plotted on CSAP (crown base sapwood area as a surrogate for leaf area) for (a) ponderosa pine and (b) lodgepole pine.



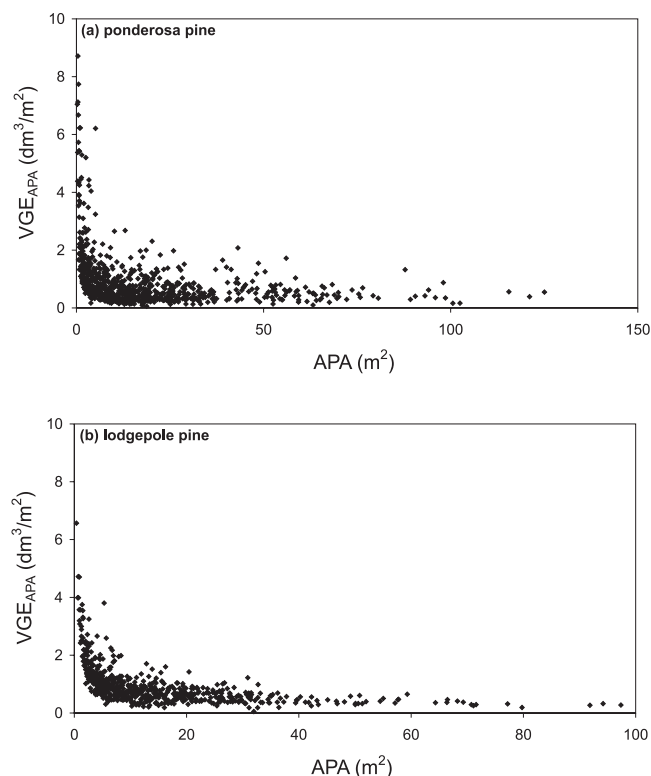
cant except for small tree basal area ( $ST_3$ ) for ponderosa pine and basal area in larger trees (BAL) for both ponderosa and lodgepole pine when CSAP was the spatial occupancy index (Table 5). However, these variables were retained to keep the models consistent.

### Observed growth efficiency

The rank of trees by VGE changed significantly when alternative expressions of site occupancy were applied, suggesting that each VGE reflects a slightly different aspect of site utilization. For example, a given tree may appear very efficient with regard to growth per unit crown projection area (CPA), yet if its degree of disengagement (sensu Assmann 1970) is great, APA is much larger than CPA, and the efficiency by which the same tree uses APA growing space is low.

Several generalizations can be drawn from observed growth efficiencies and their relationship to the three site occupancy measures. First, VGE based on both CSAP and CPA is greater for lodgepole pine than for ponderosa pine, but VGE based on APA is similar between the two species (Figs. 1–3). In addition, VGE generally declines in a negative exponential fashion with increasing level of site occupancy, with the possible exception of  $VGE_{CSAP}$  over CSAP for ponderosa pine. VGE of both species maintained moderate values with increasing CSAP; for example, trees with  $CSAP > 300 \text{ cm}^2$  grows faster per unit sapwood than many of the smaller trees (Fig. 3). For ponderosa pine in particular,  $VGE_{CSAP}$  maintains moderate VGE with increasing CSAP. Because the leaf area / sapwood area ratio for ponderosa pine is greater than for lodgepole pine (Waring et al. 1982), VGE based on actual leaf area would probably be

**Fig. 2.** Observed volume growth efficiency ( $VGE_{APA}$ ) plotted on APA (area potentially available) for (a) ponderosa pine and (b) lodgepole pine.



similar for the two species. It is also important to keep in mind that these scatterplots (Figs. 1–35) are not corrected for levels of other covariates that would increase or decrease with measure of site occupancy.

In both ponderosa and lodgepole pine,  $VGE_{CPA}$  increases with increasing degree of disengagement (APA/CPA), as does  $VGE_{CSAP}$ , although the trend is not nearly as strong in the latter (Figs. 4 and 5). The total amount of leaf area packed above a given crown projection area (measured by CSAP/CPA) also increases with increasing degree of disengagement (Fig. 6).

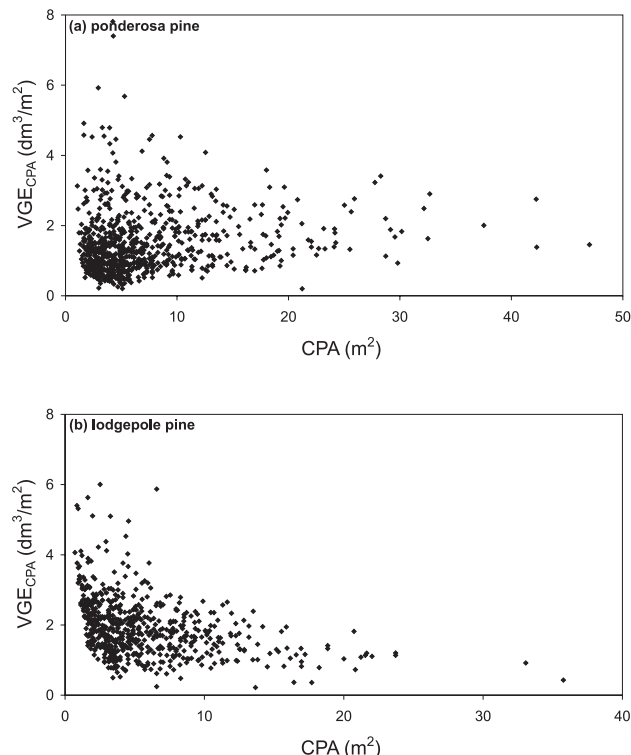
### Growth efficiency

When other covariates were set at their mean values for the entire data set, VGE declined with increasing measure of site occupancy (Figs. 7a, 8a, 9a). Lodgepole pine had higher volume growth per unit CSAP than ponderosa pine, but displayed similar efficiencies when site occupancy was measured with APA and CPA. When VGE in a given interval of site occupancy was estimated from the mean value of other covariates within the same interval, the trend in VGE was considerably more variable (Figs. 7b, 8b, 9b). Although VGE still generally declined with increasing site occupancy, two notable exceptions were apparent. In ponderosa pine, VGE generally increased with increasing CSAP (Fig. 5b) and with increasing CPA (Fig. 7b).

### Discussion

The relative importance of accounting for local stand structure in these heterogeneous stands of ponderosa and lodgepole

**Fig. 3.** Observed volume growth efficiency ( $VGE_{CPA}$ ) plotted on CPA (crown projection area) for (a) ponderosa pine and (b) lodgepole pine.



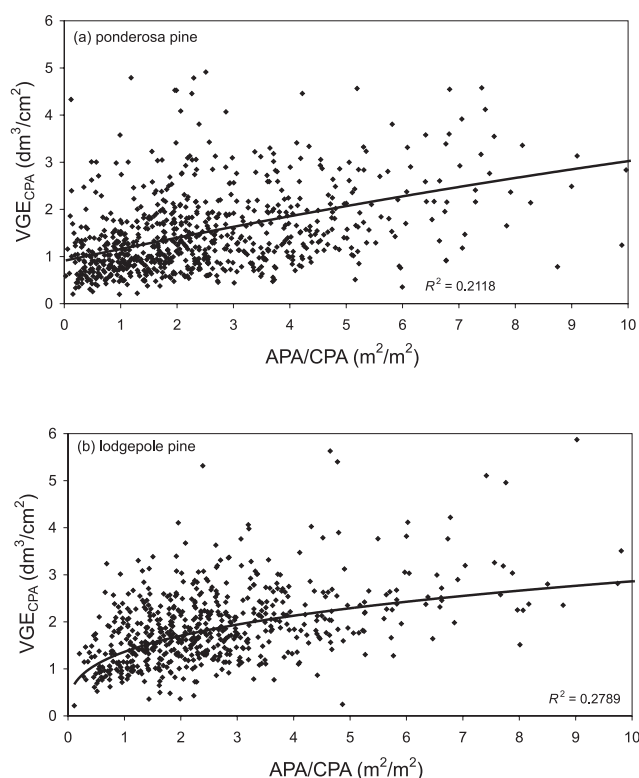
pine was indicated by the marginal contribution of spatially explicit competition measures. The spatially explicit models explained approximately 4% more of the variability in basal area growth than the spatially implicit model. Ground space occupancy, measured as the area potentially available (APA), was the preferred index of site occupancy in the final model, but other spatially explicit variables made significant contributions as well ( $H(\theta)$  and  $ST_3$ ). The extra-sums-of-squares tests underscored the fact that these variables all explained a slightly different aspect of local stand structure that was important to tree growth. All else being equal, greater available ground area beyond a tree's crown projection leads to greater basal area growth. APA thus may act partly as a surrogate for the belowground resource reservoir from which the subject tree's roots can draw water and nutrients.

The greater basal area growth with increasing height of the subject tree relative to its neighbors ( $H(\theta)$ ) is consistent with the concept of dominance and is supported by previous studies (Maguire et al. 1998; O'Hara 1996; Roberts et al. 1993) and by equations included in any individual-tree growth model (Hann and Ritchie 1988). The more favorable light environment experienced by trees with a height advantage generally enhances their growth.

#### Growth effect of small understory trees

Growth analysis with the variable representing density of trees with  $DBH < 10$  cm ( $ST_3$ ) allows separation of the competitive effect of these trees from the two-sided effects of larger trees represented in BAL and BA or in APA and  $H(\theta)$ .

**Fig. 4.** Increase in volume growth per unit crown projection area ( $VGE_{CPA}$ ) with increasing degree of disengagement for (a) ponderosa pine and (b) lodgepole pine.



The spatially explicit model confirmed growth inhibition by smaller trees within three crown radii of the subject tree.

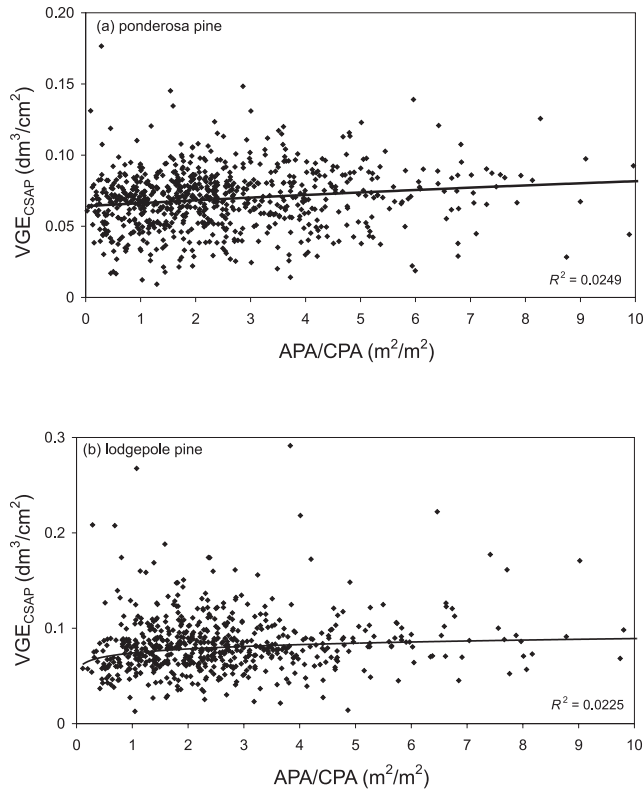
Because the zone of influence around a particular tree has significant overlap with the zones of other trees, removal of these trees would positively affect other nearby trees as well. In plot TH1, for example, 10 randomly selected trees with  $DBH < 10$  cm were found to be within the zone of influence of 10.3 trees on average. If all trees smaller than 10 cm  $DBH$  were removed from plots TH1 and BH2, 552 and 813 trees would be cut, respectively, and volume growth in larger trees would be predicted to increase by approximately  $0.16 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$  ( $160 \text{ dm}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ ). Although this operation would not be profitable for the purpose of improving future timber value, some of the costs of this treatment could be offset by using the cut trees, but value also accrues from avoidance of catastrophic losses by improving tree vigor, insect and disease resistance, or fire risk. Furthermore, reduction of stand density to levels recommended by Cochran et al. (1994) may necessitate removal of additional stems that would be larger and have greater potential use. In short, the benefits to be gained from removal of small trees would depend on management objectives for a particular stand.

#### Growth efficiency

Assessment of tree vigor by growth efficiency ( $VGE$ ) depends heavily on the definition of growth efficiency applied. The difference in tree rank by growth efficiency suggests that the three growth efficiencies examined in the ponderosa and lodgepole pine stands reflect slightly different aspects of site use. For example, a given tree may appear very efficient with regard to growth per unit leaf area, yet if its degree of



**Fig. 5.** Increase in volume growth per unit sapwood area at crown base ( $VGE_{CSAP}$ ) with increasing degree of disengagement for (a) ponderosa pine and (b) lodgepole pine.

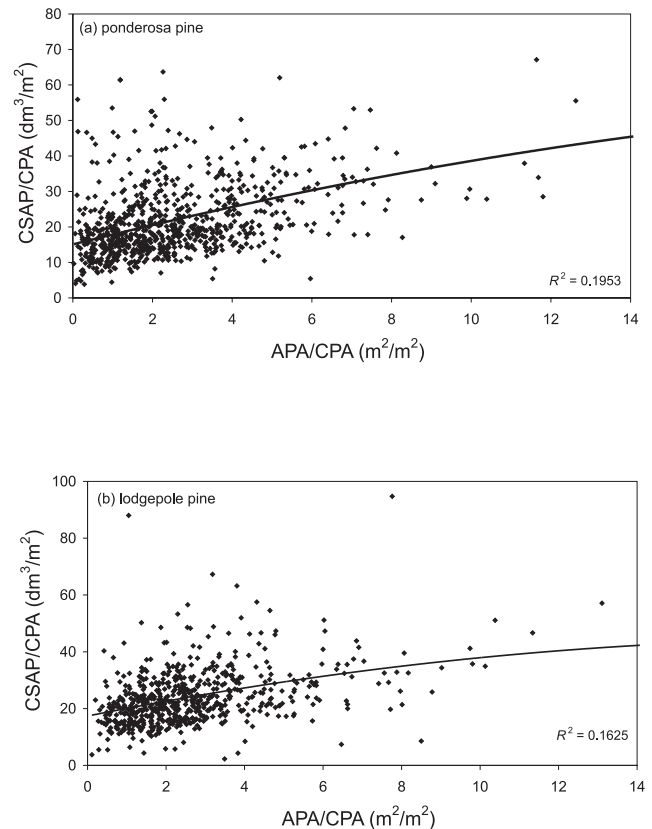


disengagement (Assmann 1970) is great, APA is much larger than CPA and efficiency by which the same tree uses available growing space is low.

The influence of specific covariates on growth efficiency was directly related to their effect on volume growth. All else being equal, diameter and crown ratio positively affected growth and growth efficiency. Conversely, stand basal area, BAL, and small tree basal area negatively affected growth and growth efficiency. Increases in each of the occupancy indices, while positively affecting growth, had a negative effect on VGE, all else being equal.

However, because tree height and the light environment improved with increasing CSAP in ponderosa pine, this simultaneous change in social position resulted in a slight increase in VGE initially. This result was similar to that found by Roberts et al. (1993) in subalpine fir (*Abies lasiocarpa* (Hook.) Nutt., by O'Hara (1996) in uneven-aged ponderosa pine, and by Seymour and Kenefic (2002) in eastern hemlock (*Tsuga canadensis* (L.) Carr.) / red spruce (*Picea rubens* Sarg.) stands; that is, the tallest trees exhibited the greatest volume growth per unit leaf area. The ponderosa pine in the central Oregon study plots generally exhibited complex vertical canopy stratification, similar to O'Hara's (1996) uneven-aged stands. The beneficial effect of greater height for capturing light is underscored by the positive effects of relative height on volume growth. In a previous analysis, the effects of relative height on red spruce growth efficiency were explicitly separated from the effects of tree size (Maguire et al. 1998). In this case, the marginal effect of increasing relative height was positive, and the marginal effect of increasing tree size

**Fig. 6.** Increase in CSAP/CPA ratio (surrogate for tree-level leaf area index) with increasing degree of disengagement for (a) ponderosa pine and (b) lodgepole pine. CSAP, crown base sapwood area as a surrogate for leaf area; CPA, crown projection area.

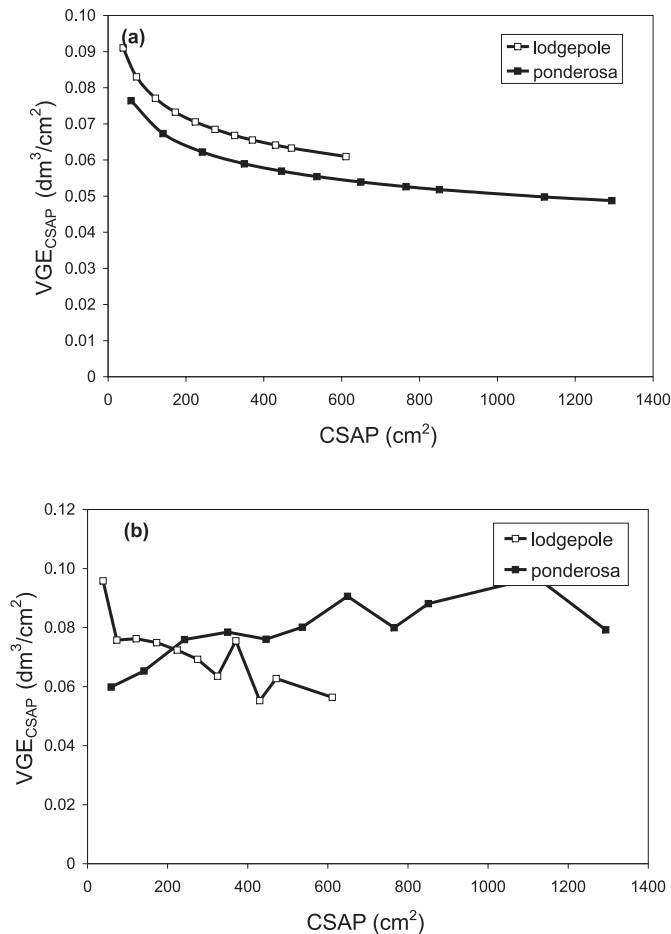


was negative. Even without correcting for relative height,  $VGE_{CSAP}$  in the ponderosa pine from the current study appeared to decline at the highest leaf areas, because these larger trees were quite old and had larger crowns without much corresponding improvement in light environment. Diminished growth rates of large or old trees have been attributed to hydraulic limitations, greater respiratory demand, and (or) tissue maturation (Yoder et al. 1994; Day et al. 2001).

In contrast with ponderosa pine,  $VGE_{CSAP}$  in lodgepole pine declined with increasing CSAP. Many if not most of the trees within these study plots were in single-cohort patches. Studies analyzing  $VGE_{CSAP}$  in lodgepole pine and subalpine fir have suggested that VGE in lodgepole pine decreases with increasing leaf area because the lodgepole pine analyzed were growing in single-cohort stands with little vertical stratification; hence, an increased leaf area corresponds to a very small improvement in light environment and does not offset the other factors that lead to a decline in VGE of larger trees (Roberts et al. 1993). This result is likely to be different in unevenaged lodgepole stands, where both leaf area index and leaf area-defined growing efficiency have been found to be greatest in the oldest cohorts (Kollenberg and O'Hara 1999).

An increase in APA does not result in increased  $VGE_{APA}$ , regardless of whether corresponding changes in other covariates are accounted for. Ponderosa and lodgepole pine with greater amounts of available space around a tree grew

**Fig. 7.** Predicted trend in volume growth efficiency ( $VGE_{CSAP}$ ) across increasing CSAP (crown base sapwood area, as a surrogate for leaf area) (a) setting all other explanatory variables at mean values for the entire dataset and (b) setting explanatory variables to their mean values within specific intervals along the CSAP axis.

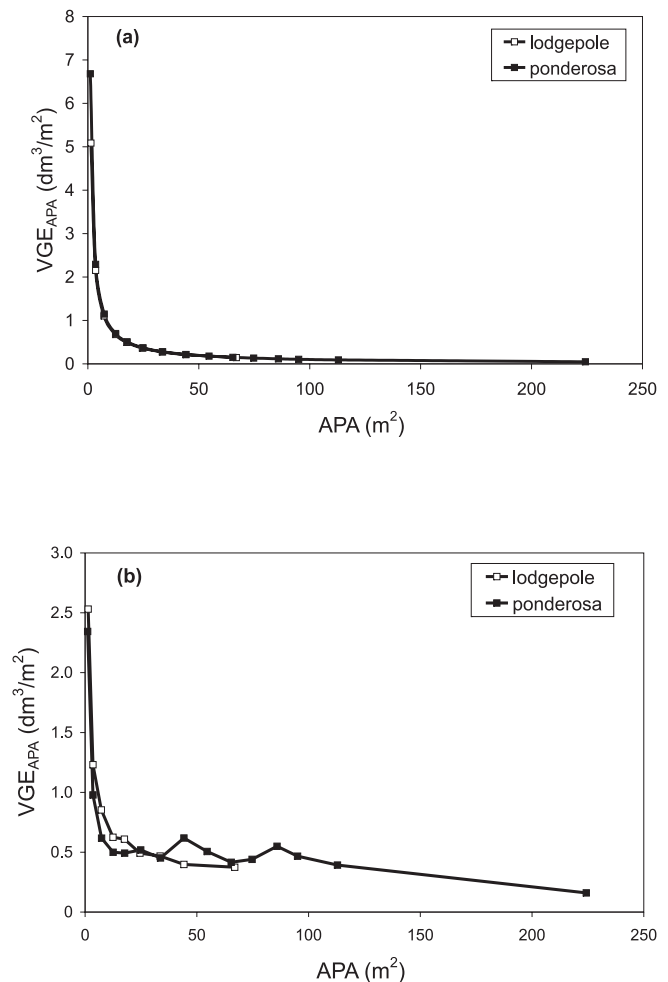


more rapidly, but at a marginally decreasing rate as APA increased. The decrease in efficiency quickly slows for both species at values of APA above 20  $m^2$ . The sustained  $VGE_{APA}$  of ponderosa pine for APA values between 20 and 90  $m^2$ , even when other covariates are accounted for, was due to the fact that the area available was occupied by trees with large crowns (high CPA/APA).

The similarity in behavior of  $VGE_{CPA}$  and  $VGE_{CSAP}$  was likely a result of the strong correlation between crown projection area and tree leaf area (represented by CSAP). For a given CPA, high  $VGE_{CPA}$  may be expected in trees that have particularly long and full crowns (higher leaf area per unit CPA) (Kuuluvainen 1988). Additionally, Pukkala and Kuuluvainen (1987) suggested that this type of crown promotes greater light availability in the lower canopy, while Roberts et al. (1993) also noted the lower investment in branches relative to a tree with the same leaf area but wider crown.

The greater amount of above- and below-ground resources per unit crown associated with a large degree of disengagement (APA/CPA) is expected to yield a greater growth efficiency (Assmann 1970). The positive correlation between

**Fig. 8.** Predicted trend in volume growth efficiency ( $VGE_{APA}$ ) across increasing APA (area potentially available) (a) setting all other explanatory variables at mean values for the entire data set and (b) setting explanatory variables to their mean values within specific intervals along the APA axis.

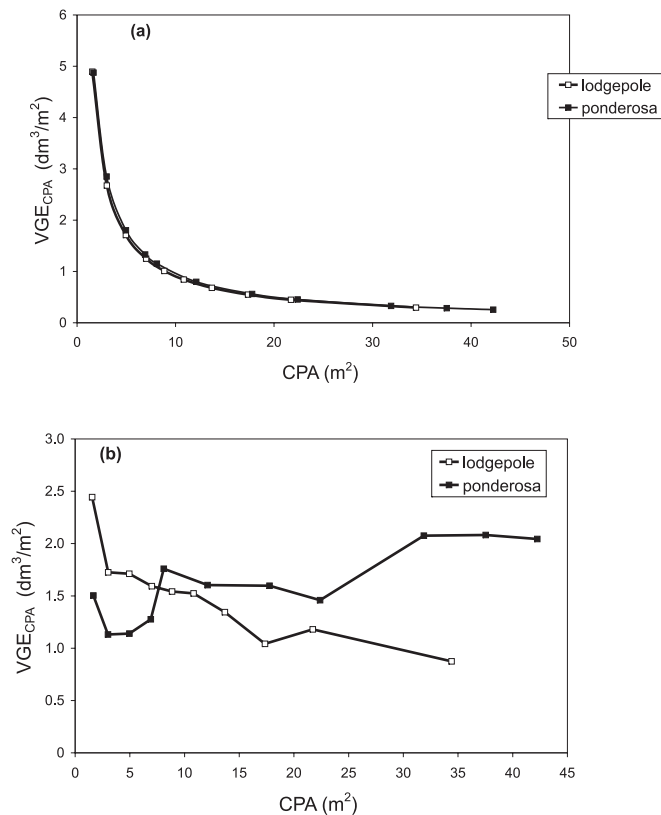


$VGE_{CPA}$  and APA/CPA (degree of disengagement) for these ponderosa and lodgepole pine trees was consistent with this expectation, although the relationship was very weak for  $VGE$  defined by growth per unit CSAP. The general increase in CSAP/CPA (a surrogate for leaf index of an individual tree) with increasing degree of disengagement (APA/CPA) suggested that the mechanism for these responses is a densification of the crown (sensu Oliver and Larsen 1996) with increasing thinning intensity and enhanced disengagement.

## Conclusions

The high  $VGE$  of a tree whose spatial occupancy is minimal suggests that stand growth would theoretically be maximized by decreasing the leaf area or ground area per tree, that is, increasing the stem density. Although total wood production is of ultimate interest where timber production is emphasized, only under a pulpwood regime and in the absence of potential insect or disease would individual tree growth be rationally subordinated to stand growth. In gen-

**Fig. 9.** Predicted trend in volume growth efficiency ( $VGE_{CPA}$ ) across increasing CPA (crown projection area) (a) setting all other explanatory variables at mean values for the entire data set and (b) setting explanatory variables to their mean values within specific intervals along the CPA axis.



eral, this strategy is inappropriate under a variety of ecosystem management constraints and objectives. However, natural stand dynamics would cause trees to differentiate in most cases, leading to differentiation in growth efficiency as well. As addressed by Roberts et al. (1993), individuals in even-aged subalpine fir stands differentiate strongly, to a large extent because its shade tolerance allows suppressed individuals to persist below the main canopy. Hence, an increase in leaf area is associated with a significant improvement in their light environment for the smallest trees in the stand. Vertically stratified, uneven-aged ponderosa pine stands are more analogous to even-aged and differentiating subalpine fir stands than are even-aged, but weakly differentiating lodgepole pine stands. The effect of improved light environment may be further enhanced by the even greater vertical stratification found in the multicohort ponderosa pine. Regardless, at any given level of differentiation, wider spacing would lead to an increase in degree of disengagement (APA/CPA) and an increase in  $VGE_{CSAP}$ . This form of growth efficiency has served as the basis for defining thresholds above which resistance to insects and disease is conferred (Mitchell et al. 1983; Larsson et al. 1983).

Area potentially available, a surrogate for the degree of root spread, the available belowground resource pool, and (or) the degree of crown crowding, is an appealing measure of spatial occupancy because of its direct relevance to tree spacing as a common specification in silvicultural treat-

ments. However, APA is only a very rough estimator of relative or proportional growing space available to an individual tree and has limited value without an additional index of tree size relative to APA. In other words, optimal spacing and density depends on tree size, particularly crown dimensions (Briegleb 1952). Those trees most efficiently using the larger APAs will be those whose crowns occupy an appropriate portion of their APA.

Light environment has been put forward as one of the most important determinants of growth and growth efficiency in an uneven-aged stand (O'Hara 1996; Maguire et al. 1998). In this study, the demonstrated ability of small trees to continue showing acceptable growth rates was no doubt due to the relatively low leaf area index for ponderosa and lodgepole pine on these sites. A previous study in the pumice region of central Oregon found that diameter and height growth responded quickly among 40–70-year-old ponderosa saplings (averaging 5 cm in diameter) following overstory removal and spacing (Barrett 1965). Where overstories were retained, similar saplings responded to thinning, but did so more slowly (Barrett 1969). The high VGE of small trees underscores the feasibility of maintaining some of these stems for replacing overstory trees as they are harvested. Overstory density needs to be controlled so that young ingrowth maintains a straight stem form with enough crown to ensure postharvest release and, conversely, the negative effect of subordinate trees, both on trees within the same cohort and on their larger neighbors, emphasizes the need to maintain low densities of these trees. Thinning or removing understorey trees can increase overstorey growth and growth efficiency. However, the decision to remove any or all of this material will depend on other management objectives, the size and density of the understorey, and the corresponding cost of this type of restoration treatment.

## References

- Assmann, E. 1970. The principles of forest yield study. Pergamon Press Ltd., Oxford.
- Barrett, J.W. 1965. Spacing and understorey vegetation affect growth of ponderosa pine saplings. USDA For. Serv. Res. Note PNW-RN-27.
- Barrett, J.W. 1969. Crop-tree thinning of ponderosa pine in the Pacific Northwest USDA For. Serv. Res. Note PNW-RN-100.
- Barrett, J.W., and Youngberg, C.T. 1965. Effect of tree spacing on water use in a pumice soil. Soil. Sci. Soc. Am. J. **29**: 472–475.
- Biging, G.S., and Dobberty, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**: 695–720.
- Bravo, F., Hann, D.W., and Maguire, D.A. 2001. Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir in southwestern Oregon. Can. J. For. Res. **31**: 2237–2247.
- Briegleb, P.A. 1952. An approach to density management in Douglas-fir. J. For. **50**: 529–536.
- Campbell, S., and Liegel, L. (Technical coordinators). 1996. Disturbance and forest health in Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-381.
- Cochran, P.H. 1985. Site index, height growth, normal yields, and stocking levels for larch in Oregon and Washington. USDA For. Serv. Res. Note PNW-RN-424.

- Cochran, P.H., and Barrett, J.W. 1995. Growth and mortality of ponderosa pine poles thinned to various densities in the Blue Mountains of Oregon. USDA For. Serv. Res. Pap. PNW-RP-483.
- Cochran, P.H., and Barrett, J.W. 1998. Thirty-five year growth of thinned and unthinned ponderosa pine in the Methow Valley of northern Washington. USDA For. Serv. Res. Pap. PNW-RP-502.
- Cochran, P.H., and Dahms, W.G. 1998. Lodgepole pine development after early spacing in the Blue Mountains of Oregon. USDA For. Serv. Res. Pap. PNW-RP-503.
- Cochran, P.H., and Dahms, W.G. 2000. Growth of lodgepole pine thinned to various densities on two sites with differing productivities in central Oregon. USDA For. Serv. Res. Pap. PNW-RP-520.
- Cochran, P.H., Geist, J.M., Clemens, D.L., Clausnitzer, R.R., and Powell, D.C. 1994. Suggested stocking levels for forest stands in northeastern Oregon and southeastern Washington. USDA For. Serv. Res. Note PNW-RN-513.
- Covington, W.W., Everett, R.L., Steele, R., Irwin, L.L., Daer, T.A., and Auclair, A.W.D. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. *J. Sustain. For.* **2**: 13–63.
- Dahms, W.G. 1975. Gross yield of central Oregon lodgepole pine. *In* Proceedings, Symposium on Management of Lodgepole Pine Ecosystems, Pullman, Washington, 9–11 October, 1973. *Edited by* D.M. Baumgartner. Cooperative Extension Service, Washington State University, Pullman, Wash. pp. 208–232.
- Daniels, R.F., Burkhart, H.E., and Clason, T.R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. *Can. J. For. Res.* **16**: 1230–1237.
- Day, M.E., Greenwood, M.S., and White, A.S. 2001. Age related changes in foliar morphology and physiology in red spruce and their influence in declining photosynthetic rates and productivity with tree age. *Tree Physiol.* **21**: 1195–1204.
- Dean, T.J., and Long, J.N. 1986. Variation in sapwood area-leaf area relations within two stands of lodgepole pine. *For. Sci.* **32**: 749–758.
- Dolph, K.L. 1988. Prediction of periodic basal area increment for young-growth mixed conifers in the Sierra Nevada. USDA For. Serv. Res. Pap. PSW-RP-190.
- Dolph, K.L. 1992. A diameter increment model for red fir in California and southern Oregon. USDA For. Serv. Res. Pap. RP-PSW-210.
- Franklin, E.C., and Callaham, R.Z. 1970. Multinodality, branching, and forking in lodgepole pine. *Silvae Genet.* **19**: 180–184.
- Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-8.
- Furnival, G.M. 1961. An index for comparing equations used in constructing volume tables. *For. Sci.* **7**: 337–341.
- Garber, S.M., and Maguire, D.A. 2003. Modeling stem taper of three central Oregon species using nonlinear mixed effects models and autoregressive error structures. *For. Ecol. Manage.* **179**: 207–522.
- Grier, C.C., and Waring, R.H. 1974. Conifer foliage mass related to sapwood area. *For. Sci.* **20**: 205–206.
- Hall, F.C. 1989. The concept and application of growth basal area: a forestland stockability index. USDA For. Serv. Ecol. Tech. Pap. PNW-007-89.
- Hann, D.W. 1980. Development and evaluation of an even and uneven aged ponderosa pine/Arizona fescue stand simulator. USDA For. Serv. Res. Pap. RP-INT-267.
- Hann, D.W., and Larsen, D.R. 1991. Diameter growth equations for fourteen tree species in southwest Oregon. *Ore. State Univ. For. Res. Lab. Res. Bull.* **69**.
- Hann, D.W., and Ritchie, M.W. 1988. Height growth rate of Douglas-fir: a comparison of model forms. *For. Sci.* **34**: 165–175.
- Hemstrom, M.A. 2001. Vegetative patterns, disturbances and forest health in eastern Oregon and Washington. *Northwest Sci.* **75**: 91–109.
- Hessburg, P.F., Mitchell, R.G., and Filip, G.M. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-327.
- Holmes, M.J., and Reed, D.D. 1991. Competition indices for mixed species northern hardwoods. *For. Sci.* **37**: 1338–1349.
- Kollenberg, C.L., and O'Hara, K.L. 1999. Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. *Can. J. For. Res.* **29**: 687–695.
- Kuuluvainen, T. 1988. Crown architecture and stemwood production in Norway spruce. *Tree Physiol.* **4**: 337–346.
- Larsson, S., Oren, R., Waring, R.H., and Barrett, J.W. 1983. Attacks of mountain pine beetle as related to tree vigor in Ponderosa Pine. *For. Sci.* **29**: 395–402.
- Lemmon, P.E., and Schumacher, F.X. 1962. Stocking density around pine trees. *J. For.* **8**: 397–403.
- Maguire, D.A., and Bennett, W.S. 1996. Patterns in vertical distribution of foliage in young coastal Douglas-fir. *Can. J. For. Res.* **26**: 1991–2005.
- Maguire, D.A., Brissette, J.C., and Gu, L. 1998. Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine. *Can. J. For. Res.* **28**: 1233–1240.
- Martin, G.L., and Ek, A.R. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For. Sci.* **30**: 731–743.
- Mitchell, R.G., Waring, R.H., and Pitman, G.B. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* **29**: 204–211.
- Nance, W.L., Grissom, J.E., and Smith, W.R. 1988. A new competition index based on weighted and constrained area potentially available. *In* Forest growth modeling and prediction. *Edited by* A.R. Ek, S.R. Shifley, and T.E. Burk. USDA For. Serv. Gen. Tech. Rep. GTR-NC-120. pp. 134–142.
- O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even aged Douglas-fir stand. *Can. J. For. Res.* **18**: 859–866.
- O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. *For. Sci.* **42**.
- Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley and Sons, Inc., New York.
- Oliver, C.D., Irwin, L.L., and Knapp, W.H. 1994. Eastside forest management practices: historical overview, extent of their applications, and their effect on the sustainability of ecosystems. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-324.
- Olsen, W.K., Schmid, J.M., and Mata, S.A. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *For. Sci.* **42**: 310–327.
- Pukkala, T., and Kuuluvainen, T. 1987. Effect of canopy structure on the diurnal interception of direct solar radiation and photosynthesis in a tree stand. *Silva Fenn.* **21**: 237–250.
- Riegel, G.M., Miller, R.F., and Krueger, W.C. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. *Ecol. Appl.* **2**: 71–85.
- Ritchie, M.W., and Hann, D.W. 1985. Equations for predicting basal area increment in Douglas-fir and grand fir. *Ore. State Univ. For. Res. Lab. Res. Bull.* **51**.
- Roberts, S.D., Long, J.N., and Smith, F.W. 1993. Canopy stratification and leaf area efficiency: a conceptualization. *For. Ecol. Manage.* **60**: 143–156.



- Seymour, R.S., and Kenefic., L.S. 2002. Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed species, multiaged northern conifer stands. *Can. J. For. Res.* **32**: 2032–2042.
- Starr, L., Hayes, J.L., Quigley, T.M., Daterman, G.E., and Brown, S. 2001. A framework for addressing forest health and productivity in eastern Oregon and Washington. *Northwest Sci.* **75**: 1–10.
- Tome., M., and Burkhart, H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.* **35**: 816–831.
- Van Sickle, F.S., and Hickman, R.D. 1959. The effect of understory competition on the growth of ponderosa pine in north central Oregon. *J. For.* **57**: 852–853.
- Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* **13**: 327–354.
- Waring, R.H., Schroeder, P.E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* **12**: 556–560.
- Weaver, H. 1959. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. *J. For.* **57**: 15–20.
- Wykoff, W.R. 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. *For. Sci.* **36**: 1077–1104.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufmann, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* **40**: 513–527.