The influence of compositional and structural diversity on forest productivity

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Summary

Data from ~1500 ponderosa pine (*Pinus ponderosa* C. Lawson) stands in the western United States were used to examine the potential influence of compositional and structural diversity on forest productivity. Relative density, height and site quality were combined in a conceptually sound expression of the relationship between growth and growing stock for ponderosa pine-dominated stands of relatively simple structure. Predictions from this model were compared with productivity of more compositionally and structurally diverse stands. Our results are consistent with the common observation in forest production ecology that stand growth is not strongly influenced by either compositional or structural diversity.

Introduction

The relationship between production and diversity has long been an important focus of research in forest production ecology (Assmann, 1970; Scherer-Lorenzen *et al.*, 2005). In the broader plant ecological literature, the nature of the production–diversity relationship has also received a great deal of attention and indeed is a subject of considerable debate and even contention (e.g. Schmid, 2002). A subset of production–diversity research deals with species richness as a function of potential or actual productivity, e.g. how does species richness respond to a gradient in site quality or potential productivity? (Gillman and Wright, 2006; Bai *et al.*, 2007; Nightingale *et al.*, 2008). The more typical approach, certainly in forest production ecology, is represented by the general question, is production influenced by diversity? (Chen *et al.*, 2003; Fridley, 2003; Pretzsch, 2005). Despite an extensive literature, there are no definitive answers to either of these questions.

Diversity, of course, can be characterized in a number of ways. For example, in contrast to the relatively simple composition and structure of even-aged single-species populations, Dhote (2005) highlights diversity represented by (1) species mixtures in a single canopy layer; (2) vertical stratification with different canopy layers dominated by different species; (3) size and/or age unevenness within canopy layers and (4) horizontal diversity (e.g. the mosaic of age-classes associated with gap-phase reproduction). These categories represent various combinations of compositional and structural diversity, the influences of which can almost certainly be confounded (Pretzsch, 2005).

In forest ecology, greater attention has been focused on the influence of structural rather than species diversity compared with plant population ecology in general. In the classic forestry literature, the potential influence of structural diversity on production has typically been framed as a comparison of even-aged *vs* uneven-aged silvicultural systems (Assmann, 1970). Similarly, the potential influence of species diversity on production has most often been framed as a comparison of monocultures *vs* mixed-species stands, with the later most commonly represented by two-species mixtures (e.g. Pretzsch, 2005; Kelty, 2006). There is a common intuitive expectation that production ought to be positively associated with both compositional and structural diversity. Nevertheless, the predominance of studies in forest production ecology do not support this optimism. Indeed, most results are either ambiguous or negative (Assmann, 1970; Pretzsch, 2005; Kelty, 2006).

What has been unambiguously established is that growth of forest stands is strongly inflenced by relative density, age and site quality (e.g. Assmann, 1970; Long and Smith, 1988; Oliver and Larson, 1996; Innes *et al.*, 2005). We share with Pretzsch (2005) the suspicion that confounding influences of these stand and site characteristics may be responsible for at least some of the ambiguity associated with the relationship between production and diversity.

Our objective is to establish a general relationship between growth, growing stock and site quality for ponderosa pine (*Pinus ponderosa* C. Lawson) stands in the western US and to use this relationship to explore possible influences of compositional and structural diversity on stand growth.

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Methods

The data used in this study were drawn from USDA Forest Service Forest Inventory and Analysis (FIA) surveys completed between 1981 and 2007 in the states of Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, South Dakota, Wyoming and Utah (Figure 1). These states include most of the range of ponderosa pine in which it occurs in both pure stands and mixtures with a variety of other species. Ponderosa pine occurred on 5597 FIA plots in this area.

FIA plots are generally composed of a set of subplots, the spatial arrangement of which was variable prior to 1995. These early plot designs were placed such that they sampled a single homogeneous condition (i.e. a stand). Since 1995, FIA surveys have used a standardized mapped plot design (Conkling and Byers, 1993), meaning that two or more conditions (e.g. stand types or ages or forest and non-forest cover) could be present on a plot. We eliminated multi-condition plots to ensure that the entire plot footprint sampled a relatively homogeneous condition. In order for a plot to qualify for further analysis, it had to meet the following criteria: (1) annual volume increment could be calculated for all live trees on the plot at the time of last measurement; (2) site index (SI) of ponderosa pine was measured on the plot, using base age of 50 years and (3) average stand height could be calculated. Only the most recent data were used from plots that had been visited more than once.

Few plots had been remeasured using the same protocol on successive visits, so diameter growth was based primarily on the measurement of increment cores. Periodic height growth was based on height growth curves and the measured site index. Annual volume growth for each tree was calculated using species-specific volume equations with breast-height diameter and height as independent variables; volume of the tree estimated from 1 year prior to the time of measurement was subtracted from the volume at the time of measurement to give annual volume growth. Periodic annual increment (PAI), expressed as $m^3\ ha^{-1}\ yr^{-1}$, was calculated by summing the periodic growth for all trees on the plot. Stand height (HT) was calculated as an average height of trees on a plot.

Our conceptualization of the growth–growing stock relationship is based on the premise that growth is a function of site quality and site occupancy. We characterize growth as net PAI, site quality as SI and site occupancy as a combination of relative density and stand height. Site index is the average height of dominant and codominant trees of the target species at a reference or index age (50 years for our data). It is commonly used as an indicator of potential productivity (Tesch, 1981; Smith *et al.*, 1997).

Stand density index (SDI; Reineke, 1933) is a metric of relative density commonly assumed to be independent of both site quality and age (Jack and Long, 1996; Innes *et al.*, 2005). For each stand in our dataset, we calculate SDI in two ways—using Dq (equation 1) and by the summation method (Long and Daniel, 1990; Shaw, 2000) (equation 2):

$$SDI_{Dq} = TPH \times (Dq/25)^{1.6}, \quad (1)$$

where Dq is quadratic mean diameter at breast height (1.37 m) in centimetres and TPH is trees per hectare.

$$SDI_{sum} = \sum(TPH_i \times (D_i/25)^{1.6}), \quad (2)$$

where D_i is the diameter at breast height of the ith tree in the sample and TPH_i is the number of trees per $hectare^{-1}$ represented by the i^{th} tree.

The two versions of SDI are essentially equivalent for even-aged stands but diverge for stands with skewed diameter frequency distributions (Long and Daniel, 1990; Shaw, 2000; Ducey and Larson, 2003). The ratio of SDI_{sum}:SDI_{Dq} has been used to separate even-aged stands from those with more complex structures (Long and Shaw, 2005; Shaw and Long, 2007; Ducey, 2009). In the current study, we use the ratio of SDIs as an index of structural diversity. We also express ponderosa pine dominance as the proportion of SDI_{sum} for the ponderosa pine in relation to the SDI_{sum} of all species [per cent ponderosa pine (PP)].

Site occupancy is represented by the combination of SDI_{sum} and HT and, with the inclusion of site quality (i.e. SI), our model of the growth–growing stock relation becomes:

$$PAI = f(SDI, HT, SI). \quad (3)$$

This conceptualization reflects that a stand with high site occupancy (i.e. a large amount of growing stock) occurring on a site with poor growth potential (i.e. low site quality) will have relatively low growth. Similarly, a stand occurring on a high-quality site, but with limited growing stock, will also have relatively low growth.

The model was fitted using non-linear regression (SAS version 9.1, SAS Institute, Inc., Cary, NC, USA). Goodness of fit was assessed by computing adjusted R^2 and root mean square error and parameters assessed for significance. Residuals were examined for bias with respect to independent variables and relevant stand characteristics (e.g. stand age and basal area).

Analysis of possible influences of structural and compositional diversity on production was done in the context of the basic growth-growing stock model (equation 3). Structural diversity was assumed to be negatively related to the ratio of SDI_{sum}:SDI_{Dq} (SDIrat). For example, high values (e.g. 1.0) of the ratio are associated with regular, unimodal, diameter frequency distributions and low structural diversity. Conversely, bimodal or skewed diameter frequency distributions are associated with ratio values < 1.0. Ducey and Larson (2003) and Ducey (2009) suggest that limiting values may approach 0.8 for extremely irregular diameter distributions. Compositional diversity was characterized by the percentage of a stand's total SDI_{sum} contributed by ponderosa pine. For example, per cent PP of pure ponderosa pine stands would equal 100 per cent.

Results

The data were filtered to include stands with a preponderance of ponderosa pine, defined as at least 75 per cent

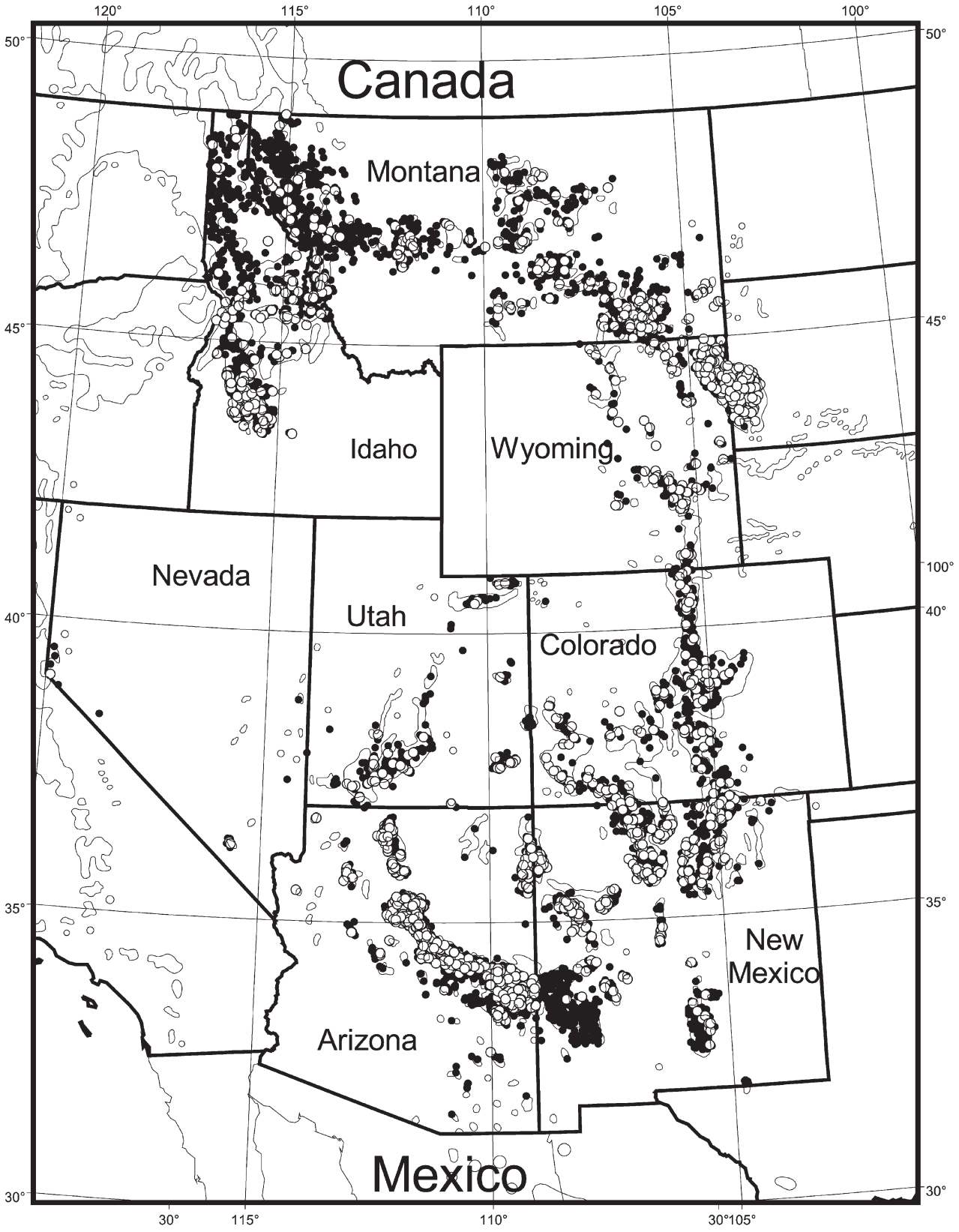

Figure 1. Locations of FIA plots used in this study. Closed circles represent all FIA plots with ponderosa pine present and open circles represent plots selected for analysis. Polygons show the range of ponderosa pine in the US (Little, 1971).

of total SDI contributed by ponderosa pine (per cent PP > 0.75) and SDIrat > 0.95 (n = 997). The resulting dataset therefore represents stands with limited compositional and structural diversity (see Figure 2a for illustration). Fitting these data to the basic growth–growing stock relation (equation 3) results in:

$$\mathrm{PAI} = 0.0302 \times \mathrm{SDIsum}^{0.7050} \times \mathrm{HT}^{0.4783} \times \mathrm{SI}^{1.5191}. \quad (4)$$

PAI is periodic annual increment (m^3 ha^{-1} yr^{-1}) and the independent variables are as previously defined. Estimated R^2 ~0.86. Examination of residuals suggests that estimates of PAI are unbiased with respect to the independent variables and relevant stand characteristics, including stand age and stand basal area. This growth–growing stock relation serves as a reference against which to compare growth of more diverse stands. A non-linear least-squares fit of the frequency distribution of residuals was normalized to facilitate comparison with results from data subsets with different numbers of observations (Figure 3a).

To explore the potential influence of compositional diversity on the growth–growing stock relation, the original data were filtered to include stands with limited structural diversity, defined as SDIrat > 0.95 and a range of compositional diversity represented by per cent PP from 0.75 to 0.5 (n = 202) (e.g. Figure 2b). For each of these stands, we calculated the difference between observed PAI and the prediction based on the growth–growing stock relation developed for stands of limited structural and compositional diversity (equation 4). We reject (P = 0.05) the hypothesis that the difference between observed and predicted PAI is zero; mixed-species stands are, on average, actually growing slightly slower than stands dominated by a single species (Figure 3b).

To explore the potential influence of structural diversity on the growth–growing stock relation, the original data were filtered to include stands with a preponderance of ponderosa pine (SDIpp/SDIsum > 0.75) and SDIrat < 0.95 (i.e. 0.8–0.94). The resulting dataset (n = 169) therefore represents stands with limited compositional diversity but relatively high structural diversity (e.g. Figure 2c). For each of these stands, we calculated the difference between observed PAI and the prediction based on the growth–growing stock relation developed for stands of limited structural and compositional diversity (equation 4). We failed to reject (P = 0.05) the hypothesis that the difference between observed and predicted PAI is zero (Figure 3c). In other words, our analysis suggests that structurally complex ponderosa pine-dominated stands are growing neither faster nor slower than stands with more limited structural diversity.

As a final comparison, the original data were filtered to include stands with both structural diversity (SDIrat < 0.95) and compositional diversity (per cent PP 0.75–0.5) (n = 106) (e.g. Figure 2d). For each of these stands, we calculated the difference between observed PAI and the prediction based on the growth–growing stock relation developed for stands of limited structural and compositional diversity (equation 4). We reject (P = 0.05) the hypothesis that the difference between observed and predicted PAI is zero; stands with high structural

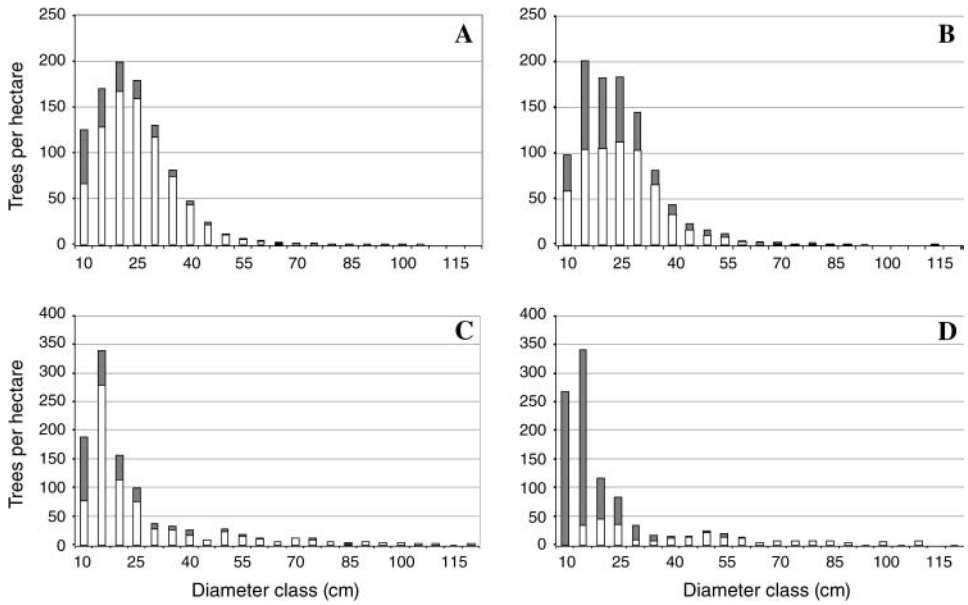

Figure 2. Diameter distributions representative of the four classes of stands used in this study: (A) nearly pure stand with simple structure, (B) mixed-species stand with simple structure, (C) nearly pure stand with complex structure and (D) mixed-species stand with complex structure. White portions of bars represent ponderosa pine component and black portions represent other species. Histograms are composites of data from several stands that share similar ranges of composition and structure.

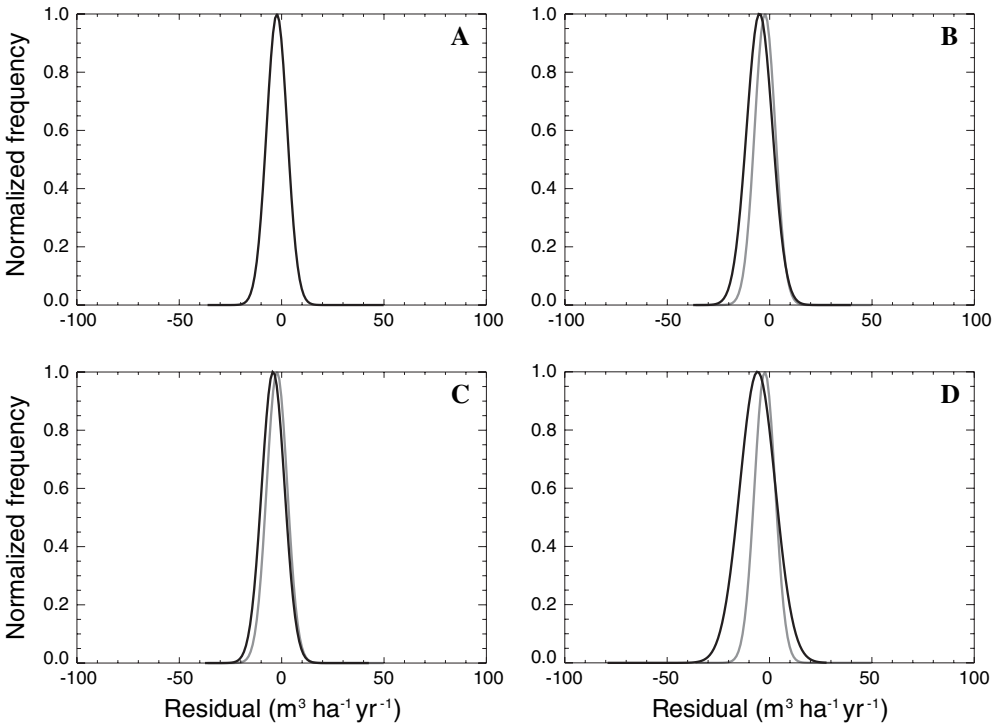

Figure 3. Non-linear least squares fit of the frequency distribution of residuals (equation 4) normalized to facilitate comparison with results from data subsets with different numbers of observations: (A) stands of low compositional and structural diversity, (B) stands of high compositional and low structural diversity, (C) stands of low compositional and high structural diversity and (D) stands of high compositional and structural diversity.

and compositional diversity are, on average, actually growing slightly slower than stands with simple structure and dominated by a single species (Figure 3d).

Discussion

Size–density indices, like SDI, are surrogates for relative site occupation (Innes *et al.*, 2005). This argument is supported by observations that stand leaf area is proportional to site occupancy, sapwood area is proportional to leaf area and SDI is proportional to sapwood area (Long and Dean, 1986; O'Hara and Valappil, 1995; Woodall *et al.*, 2003). Combining relative density with stand height completes the expression of site occupancy and this, combined with site index (i.e. potential productivity), characterizes the growth–growing stock relation (Innes *et al.*, 2005).

Equation 4 represents a robust expression, both conceptually and quantitatively (i.e. goodness of fit and residual analysis), of the relationship between growth and growing stock for ponderosa pine-dominated stands of relatively simple structure. In his assessment of diversity and productivity of forests, Pretzsch (2005) uses long-term experimental plots and avoids less reliable inventory data; however, he also warns against generalizing results obtained from a limited spectrum of site conditions. Our dataset includes a very broad spectrum of site conditions for stands from throughout much of the range of ponderosa pine in the western US, representing a wide range of stand ages, elevations and site quality (Table 1). The model is realistic in that it reflects a positive relationship between growth and both relative density and site quality. The negative exponent for HT is also biologically realistic. Height and age are, of course, related, and for a given relative density and potential productivity, growth culminates at a fairly early stand age and height (Smith and Long, 2001). For many of the stands in our data, set growth has culminated; therefore, across the range of data, growth is negatively related to height.

There are, of course, alternative ways to quantify structural and compositional diversity (Staudhammer and LeMay, 2001). Brassard *et al.* (2008) quantify stand structure diversity with tree-size variability, measured using Shannon's diversity index and coefficient of variation. Our characterization, using the ratio SDI_{sum}:SDI_{Dq}, is intended to capture a conventional view of structural diversity, reflected, for example in the contrast between even-aged *vs* uneven-aged stands (Long and Shaw, 2005; Shaw and Long, 2007; Ducey, 2009). There are, however, important differences within these broad structural categories. For example, Smith and Long (1989) demonstrate that the way total LA is apportioned among trees within essentially even-aged stands, e.g. many small trees *vs* fewer big trees, makes a difference in production. Because

Table 1: Mensurational characteristics of the database (n = 1474)

Parameter	Mean	SD	Range
Elevation (m)	1871	562	549–3035
Density (trees ha^{-1})	247	195	3–1324
Volume (m^3 ha^{-1})	101	88	0.5–699
Dq (cm)	29.5	10.8	7.6–96.5
HT (m)	14.0	5.3	4.0–46.9
Age (year)	95	41	5–379
Site index (m)	12.4	4.2	3–31.7
Basal area (m^2 ha^{-1})	16	18	1–61
% Ponderosa pine	89	15	50–100
SDIrat	0.96	0.03	0.8–1.0

equation 4 includes height as well as relative density, we suspect that the model may account for variability in growth associated with differences in mean crown size.

It is also important to note that our characterization of compositional diversity is a reflection of the relative amount of ponderosa pine and there are certainly other ways to characterize this component of diversity. For example, per cent PP = 50 per cent could reflect a 50:50 mix of ponderosa pine and either one or many other species. It may also make a difference if the other species is/are more or less tolerant than ponderosa pine. Pretzsch (2005) observes that examples of overyielding are most commonly observed with mixtures of a shade-tolerant and a shade-intolerant species, rather than, for example, two shade-tolerant species.

Our results are consistent with the fairly common observation in forest production ecology that stand growth is positively related to neither compositional nor structural diversity (e.g. Assmann, 1970; Smith and Long, 1992; Pretzsch, 2005; Kelty, 2006; O'Hara and Nagel, 2006). Absolute superiority (*sensu* Pretzsch, 2005) of growth by mixtures requires that, for a given site, a mixture will produce more than a pure stand of any of the component species. In spite of the effects of competitive reduction or facilitation associated with species mixture, absolute superiority appears to be uncommon (Kelty, 1992). Special examples of absolute superiority of growth in mixtures appear to be associated with specific edaphic amelioration effects. The interplanting of pine or larch with Sitka spruce on infertile peat bogs in Scotland prevents check of the spruce and results in growth greatly in excess of a pure plantation (Miller, 1990). Planted mixtures of Douglas-fir and nitrogen-fixing red alder (*Alnus rubra*) on extremely nitrogen-deficient sites in Washington, USA, is another example of absolute superiority (Miller and Murray, 1978).

There are certainly many situations where compositional and structural diversity are desirable (Ashton, 1992). For example, a positive relationship between overstorey and understorey species diversity might be associated with ecological benefits independent of production (Berger and Puettmann, 2000). Reduced probability of ponderosa pine infestation by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) appears to be associated with some aspects of tree species and structure diversity (Negron and Popp, 2004). Among possible reasons for the culture of species mixtures, Pretzsch (2005) suggests that risk distribution or insurance might be among them but concludes that increased production will not. With respect to risk of wind damage, Dhote (2005) concludes neither species mixtures nor irregular canopy structure provides much if any inherent benefit compared with even-aged monocultures, i.e., this aspect of resistance is not a good argument for diversity.

Conclusions

Data used in this analysis represent a broad array of stand and site characteristics (Table 1). A metric of compositional diversity, the relative proportion of ponderosa pine, and a metric of structural diversity, the ratio of alternative calculations of SDI, were used to parse the data into four subsets reflecting various combinations of compositional and structural diversity. The subset representing ponderosa pine-dominated stands of relatively simple structure was used to construct an expression of the relationship between growth and growing stock. Growth was defined as PAI and growing stock as a combination of relative density, height and site index. This growth–growing stock relation was used as a reference against which growth of more diverse stands was compared.

Our results are consistent with the common observation in forest production ecology that stand growth is positively related to neither compositional nor structural diversity. There are undoubtedly situations when compositional and structural diversity will be desired but with the exception of some special edaphic situations, increases in production should not be expected.

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Conflict of Interest Statement

None declared.

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