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Effects of tree size and spatial distribution on growth of ponderosa pine forests under alternative management scenarios

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Abstract Forest ecosystems may be actively managed toward heterogeneous stand structures to provide both economic (e.g., wood production and carbon credits) and environmental benefits (e.g., invasive pest resistance). In order to facilitate wider adoption of possibly more sustainable forest stand structures, defining growth expectations among alternative management scenarios is crucial. To estimate the effect of tree size and spatial distributions on growth for forest structures commonly considered in uneven-aged forest stand management, large (0.2 ha+) plots were established in 14 uneven-aged ponderosa pine stands in eastern Montana. All study trees were stem-mapped and measured for diameter and 10-year sapwood and basal area increment. A generalized growth model was developed to predict both total and merchantable 10-year basal area increment for nine hypothetical stand structures [three diameter distributions (reverse-J, irregular, flat) × three spatial distributions (clumpy, partial clumpy, uniform)]. Results indicate that the size and spatial distributions of individual trees have a considerable effect on overall stand growth. The greatest total stand growth was in stands with reverse "J" shaped tree size distributions, while the greatest merchantable stand growth was in stands with "flat" diameter distributions and uniform spatial distributions. Through better comprehension of generalized uneven-aged stand growth dynamics, forest managers may better assess the effects of alternative stand structures on stand growth while providing forest stand structures that may be more resilient in a changing climate.

Keywords Uneven-aged · Ponderosa pine · Restoration · Stand growth · Growth efficiency

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1 Introduction

Forest ecosystems across the U.S. have been providing a myriad of resources (e.g., clean air, water, recreation, wildlife habitat, wood, fuel, aesthetics) to the populace for centuries (Smith et al. 2004). Substantial portions of U.S. forestland have been directly managed for resource extraction or indirectly altered through fire suppression and fragmentation. More recently, the effects of climate change, increased fire occurrence, and invasive pests/plants have further impacted the Nation's forests (Malmsheimer et al. 2008). Taken collectively, the sustainability of U.S. forests is now being more closely monitored than at any previous point in U.S. history (e.g., USDA 2004).

Given the threats facing U.S. forests, numerous ecologists/foresters have been proposing that forest management paradigms shift from one where forest vegetation is manipulated to maximize wood production toward one where vegetation is manipulated to resemble a pre-European-American settlement condition. The theory is postulated that historic forest stand structures evolved over millennia toward conditions sustainable with natural disturbance processes/patterns. Some foresters seek to create ranges of forest stand density, structure, and species composition that approximate historically sustainable conditions (Fiedler 2000). Others seek to remove nearly all trees established after Euro-American settlement and approximate pre-settlement tree locations with as much fidelity as possible given existing tree sizes and locations (Fule et al. 1997, 2001). These pre-settlement forest stand structures may be more resilient in the face of the mounting threats facing contemporary forest ecosystems (e.g., climate change).

Forest managers that seek to "restore" forest stand structures to pre-settlement conditions often adopt uneven-aged stand management practices compared to traditional even-aged management. Even-aged forest stands typically consist of one age cohort of trees often of the same species. Uneven-aged stands may be defined as forest stands that consist of more than two age-cohorts often with a mixed-species composition (O'Hara 1996). Growth in even-aged stands has been studied for decades (Assman 1970) resulting in numerous well-established management indices (for example, see Long 1985). In contrast, a similar knowledge is not available for structurally complex uneven-aged stands with trees of different sizes, diameter distributions, and spatial arrangements. To date, growth models such as the Forest Vegetation Simulator (Wykoff et al. 1982) or the General Growth and Yield Model (Edminster et al. 1991) have been the only tools available for foresters to predict growth responses to management activities in uneven stands in some forests of the U.S. However, these models do not account for tree spatial distributions, a stand variable that may significantly affect growth and yield (Miina 1994; Shao and Shugart 1997). Defining growth dynamics in relation to tree diameter distribution *and* spatial arrangement, and proposing generalized principles of growth in uneven-aged structures, could aid managers facing restoration implementation decisions. If the forest management strategy of adopting possibly more resilient uneven-aged stand structures across landscapes is to be more widely adopted by the forestry profession, tools for projecting stand growth are necessary. Because most forestland in the U.S. is owned by private citizens (Smith et al. 2004), the efficacy of alternative forest management paradigms may need to be evaluated both ecologically (e.g., invasive pest resistance) and economically (e.g., wood production and carbon credits).

The widespread ponderosa pine (*Pinus ponderosa*) forests of the intermountain west of the U.S. provide a unique opportunity to examine the effect of various alternative forest stand structures on forest stand growth. It has been estimated that there are over 12.7 million ha of ponderosa pine forests in the western U.S. (Smith et al. 2004). The benefits of uneven-aged management of ponderosa pine have been demonstrated for decades and provide a context for exploring the effects of alternative forest management practices on stand growth (for examples see Covington and Moore 1994; Covington et al. 2001; Arno and Fiedler 2005; Fule et al. 1997). If differences in stand growth can be broadly conceptualized among varying forest stand structures for one forest ecosystem, this information may inform uneven-aged management practices in forest ecosystems in other temperate regions around the world. The goal of our study was to generalize growth dynamics for a range of hypothetical uneven-aged stand structures in ponderosa pine. Specific objectives of this study were: (1) develop models to estimate individual tree sapwood area by DBH (diameter breast height −1.37 m) and individual tree GREFF (growth efficiency) per unit sapwood area by level of surrounding competition (spatial distributions) and DBH size-class; (2) develop a generalized uneven-aged growth model based on individual tree sapwood area and GREFF models; and (3) evaluate growth predictions from the generalized growth model for nine alternative stand structures (three diameter distributions × three spatial distributions).

2 Methods

2.1 Study sites

Study sites were located in ponderosa pine forests to the east of the Continental Divide in the northern Rocky Mountains (Montana, United States) predominantly within the Bull Mountains, Snowy Mountains, and Powder River uplands (for study site map and detailed descriptions refer to Woodall 2000, 2008). Sites were located in 14 pure ponderosa pine stands that exhibited negligible evidence of recent human or natural disturbances (Table 1, see Woodall 2000). The relatively xeric study sites of eastern Montana represent the poorer site qualities that ponderosa pine inhabits along its range stretching from British Columbia and Canada to the southwestern U.S. Although the majority of land in eastern Montana is dominated by agriculture or grazing, ponderosa pine monocultures still occupy nearly 0.9 million ha (O'Brien and Conner 1991; O'Brien and Collins 1991) on lowlands and hilly terrain (850–1350 m in elevation) (Arno 1979), where soils are typically shallow and poorly developed with precipitation averaging 260–420 mm a year (Pfister et al. 1977). Due to the historic low-intensity fire regimes, sporadic regeneration events, and harsh environmental conditions of eastern Montana, these forests are often mosaics of tree sizes and stand densities making up irregular multistoried stands (Alexander 1986). Given that many of these forests have never been actively managed, these study sites present the unique opportunity to evaluate stand growth dynamics of "target" forest restoration conditions for a widespread ponderosa pine resource.

Table 1 Summary information for 14 study sites in uneven-aged ponderosa pine stands in eastern Montana

Site number	Sample plot size (ha)	Number of sample trees	Quadratic mean diameter (cm)	DBH range (cm)	Age range (years)
1	0.32	347	13.9	3.8–60.7	12–362
2	0.28	545	10.7	3.8–46.7	20–138
3	0.32	255	15.5	3.8–50.3	25–330
4	0.23	349	14.5	3.8–51.8	17–187
5	0.20	257	15.7	3.8–64.3	33–206
6	0.30	373	12.5	3.8–47.2	21–140
7	0.32	202	17.5	3.8–56.1	8–199
8	0.27	604	10.2	3.8–50.8	14–178
9	0.29	566	11.2	3.8–49.5	23–244
10	0.41	208	17.5	4.0–57.2	22–236
11	0.32	348	15.7	3.8–72.9	14–116
12	0.35	250	21.6	3.8–66.3	10–155
13	0.29	383	15.7	3.8–71.1	13–240
14	0.26	345	12.2	3.8–54.4	12–213

2.2 Field and lab methods

A 0.2- to 0.4-ha fixed-radius circular plot was established at each study site. The location of every plot tree, ≥3.8 cm DBH, was mapped by distance and azimuth from plot center using a laser range-finding device and digital compass. An increment borer was used to extract a single core from each plot tree between 3.8 and 12.7 cm DBH; trees ≥ 12.7 cm DBH were cored twice to the pith [once from an upslope position (occasionally downslope if excessive branching or an adjacent tree physically precluded boring upslope), then on contour (perpendicular to slope)]. Once a core was extracted, its sapwood/heartwood boundary was marked with a pen and the core was inserted into a labeled plastic straw for later analysis in the laboratory. In addition to core work, all trees were measured for DBH (nearest 0.25 cm). Approximately 5,000 trees were sampled across the 14 sites (210–605 trees per site). Because uneven-aged stands may be defined as stands containing groups of trees of varying ages with rather complicated development patterns (Smith et al. 1997), tree age and size distributions indicated that all study stands could be defined as uneven-aged. Individual trees were sampled across a range of naturally occurring stand conditions, providing the basis to assess growth by tree size, diameter distribution, and spatial arrangement.

Every increment core taken in the field was dried, mounted on a grooved board, and sanded for subsequent analysis. Sapwood width and inside-bark bole radius were measured to the nearest mm. Ten-year radial growth increment was measured to the nearest 0.0254 mm using an ACU-GAGE Coordinate Measuring Machine and Javelin Smart Cam video system. Sapwood area and 10-year basal area increment were calculated for each tree, averaging dual estimates for trees that were bored twice. In this study, GREFF was defined as an individual tree's 10-year basal area increment divided by its sapwood area (for similar sapwood area measurement techniques refer to O'Hara and Valappil 1995; O'Hara 1996). The sum of basal areas (BACOMP) of all trees (≥3.8 cm DBH) located within 6.1 m of each individual tree (excluding the basal area of the subject tree) was used to estimate surrounding competition. Basal area growth of individual ponderosa pine trees in uneven-aged stands was found to be highly correlated to this measure of competition (Woodall et al. 2003). Trees in clumpy spatial distributions were assumed to have high levels of BACOMP around individual trees, while trees in uniform distributions had lower levels of BACOMP.

2.3 Analysis

The vertical and horizontal heterogeneity in uneven-aged stands complicates efforts to estimate growth differences among the various ponderosa pine stand structures considered by forest managers. To help resolve this complexity, this study adopts the approach of combining aspects of both process-based and empirical based growth models. One assumption of our analysis is that an uneven-aged stand may be viewed as a given amount of leaf area occupying a site (O'Hara 1996). This leaf area, partitioned into individual trees, has an associated rate of growth per unit leaf area that can be expressed as growth efficiency (GREFF) (Waring 1983; Coyea and Margolis 1994). GREFF of ponderosa pine trees in uneven-aged stands has been shown to vary with tree size and level of surrounding competition (tree spatial arrangement) (Woodall et al.

2003). Thus, the growth of an entire uneven-aged stand can be generalized by assessing a stand's leaf areas and associated GREFF. Because of the high correlation between sapwood area and leaf area (pipe model theory—Shinozaki et al. 1964; Waring et al. 1982), and because the measurement of sapwood area is much more practical, it is often used as a surrogate for leaf area in models calibrated using field data (Long and Dean 1986; O'Hara 1996). Ultimately, the effect of varying site quality among sample sites is controlled through the adoption of tree-level sapwood area competition models, whereas it does not matter if one site supports more leaf area than another since sapwood area competition is directly included in growth models.

Analytical methods consisted of three parts: developing individual tree growth models, linking individual models into a general growth model, and finally predicting growth for a variety of uneven-aged stand structures considered in ponderosa pine restoration efforts. Nonlinear models were developed for individual tree sapwood area versus DBH (Eq. 1) and individual tree GREFF versus DBH class and level of competition (Eq. 2),

$$E(\text{sapwood area}) = b_1 + b_2\text{DBH} + b_3\text{DBH}^2, \quad (1)$$

where $E(\cdot)$ denotes statistical expectation, b's are parameters to be estimated, and DBH is diameter at breast height.

$$E(\text{GREFF}) = b_1 e^{\left[b_2(\text{DBH}-3.8)^{b_3} + b_4\text{BACOMP}^{b_5}\right]}, \quad (2)$$

where $E(\cdot)$ denotes statistical expectation, b's are parameters to be estimated, e is base for natural logarithms, BACOMP is the summed basal area of all trees within 6.1 m of the subject tree (surrogate for tree spatial distributions), the constant 3.8 accounts for the minimum diameter of the study data set, and DBH has been previously defined.

The nonlinear equations (1, 2) were fitted using the SAS NLIN procedure with the Gauss-Newton option. A general growth model was developed based on the parameterized individual tree models (Eqs. 1 and 2). Equations 1 and 2 were linked such that for each diameter class, the individual tree sapwood area and GREFF could be predicted, with subsequent growth (10-year basal area increment/ha) being estimated for each diameter class (3) and merchantable growth being considered basal area increment in trees with DBH >30.0 cm.

$$\widehat{\text{DBH}}_{\text{CG}} = \text{TPH}_\text{d} * \text{GREFF}_\text{p} * \text{SAP}_\text{p}, \quad (3)$$

where $\widehat{\text{DBH}}_{\text{CG}}$ is the 10-year basal area stand growth for one diameter class, TPH_d is the trees per hectare for a given diameter class, GREFF_p is the predicted growth efficiency for the midpoint diameter of the DBH class (Eq. 2), and SAP_p is the predicted sapwood area for the diameter class midpoint (Eq. 1). In the generalized growth model, the various diameter distributions are reflected by TPH_d. The spatial distributions are reflected by the GREFF_p, which varies by the amount of competition within 6.1 m of individual trees (BACOMP) (Eq. 3).

The final step of the analysis involved evaluating the growth predictions for nine hypothetical uneven-aged stand structures based on output from the generalized growth model. The nine structures were based on combinations of three diameter distributions (reverse-J, flat, and irregular) (Fig. 1 and Table 2) and three spatial arrangements (clumpy, partial clumpy, and uniform) (Fig. 2) of trees in uneven-aged stands (Fig. 1a–c) with a stand basal area density of 11.3 m^2/ha. The spatial arrangements were not modeled. Instead, levels of competition surrounding individual trees were used as a surrogate for spatial distribution (Table 3). For example, in a tightly clumped tree arrangement there would be intense competition within 6.1 m of any individual tree, whereas in a uniform distribution tree competition would be less (Fig. 2 and Table 3). Therefore, spatial distributions are represented by the variable BACOMP in Eq. 2. For overall stand density, we used 11.3 m^2/ha in our analysis because it is a recommended reserve density for maintaining tree vigor and inducing regeneration of shade-intolerant ponderosa pine (Arno and Fiedler 2005). Evaluation at moderately lower or higher densities had little effect on the relationships reported here.

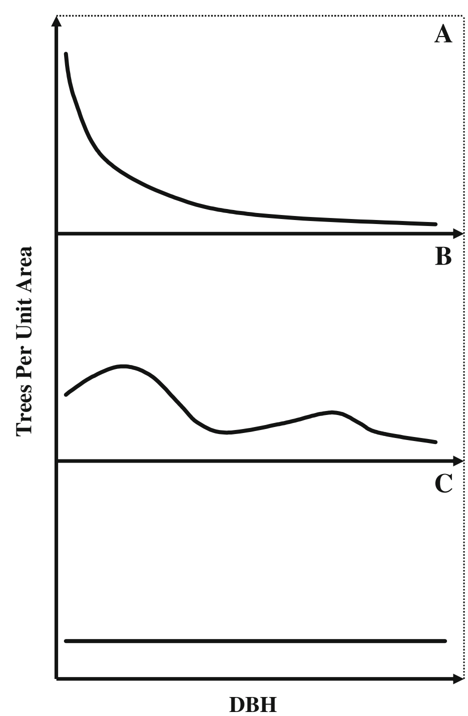

Fig. 1 Hypothetical diameter distribution of trees used in model process (a = reverse-J, b = irregular, c = flat)

Table 2 Number of tree per hectare by diameter classes and diameter distributions for hypothetical stands

Diameter distributions	DBH classes (cm)				
	0.0–15.0	15.1–30.0	30.1–45.0	45.1–60.0	60.0–75.0
Reverse-J	2006	109	18	6	3
Flat	14	14	14	14	14
Irregular	55	65	10	22	6

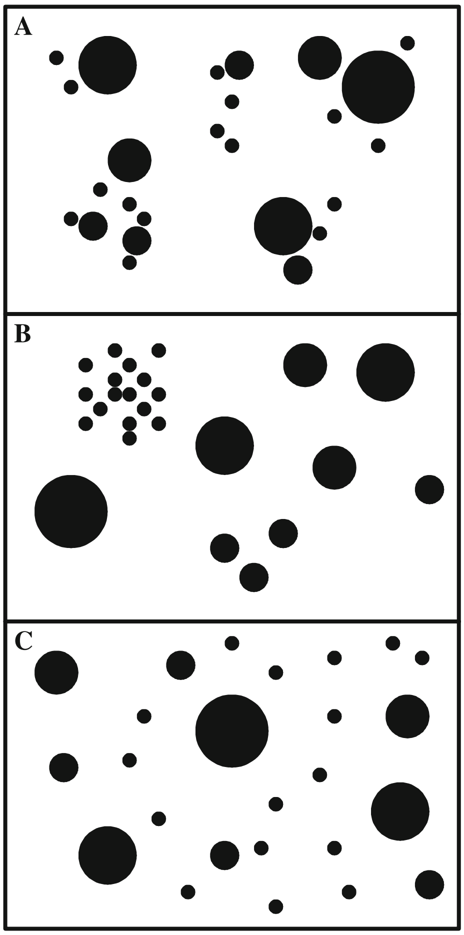

Fig. 2 Hypothetical spatial arrangement of trees used in model process (**a** = clumpy, **b** = partial clumpy, **c** = uniform)

Table 3 Growth model competition levels for three hypothetical spatial distributions using the amount of competing basal area (m^2) within 6.1 m of individual trees as a surrogate for spatial distributions

DBH class (cm)	Hypothetical spatial distributions (m^2)		
	Clumpy	Partial clumpy	Uniform
0.0–15.0	0.7	0.7	0.1
15.1–30.0	0.7	0.7	0.1
30.1–45.0	0.7	0.5	0.1
45.1–60.0	0.7	0.3	0.1
60.0–75.0	0.7	0.1	0.1

3 Results

3.1 Individual tree models

The cross-sectional sapwood area of individual ponderosa pine trees in uneven-aged stands appears to increase exponentially with increasing tree DBH, a trend that is more pronounced after a minimum DBH of about 30 cm is reached (Fig. 3) (Eq. 1) (SE($\hat{b}_1$) = 0.000482, SE($\hat{b}_2$) = 0.000049, SE($\hat{b}_3$) = 0.000001; approximate $R^2 = 0.87$; F-value = 7643.86, total degrees of freedom = 2253; p-value <0.0001). Reflecting this trend, the nonlinear model form (Eq. 1) accommodates the exponential increase in sapwood area found in increasingly larger trees (parameter estimates, Table 4). Individual tree GREFF is dependent both on individual tree size and the amount of surrounding basal area competition (clumpy or uniform spatial distributions) (Fig. 4). Smaller trees under the lowest levels of competition attain the highest levels of GREFF, while larger trees have lower levels of GREFF, but are less affected by increasing levels of surrounding competition (Fig. 4). A nonlinear multivariate model (Eq. 2) was required given the differences in trends of GREFF among diameter classes and levels of surrounding competition (Table 4) (SE($\hat{b}_1$) = 0.4415, SE($\hat{b}_2$) = 0.0292, SE($\hat{b}_3$) = 0.0423, SE($\hat{b}_4$) = 0.1880, SE($\hat{b}_5$) = 0.0163; approximate $R^2 = 0.76$; F-value = 1958.03, total degrees of freedom = 2253; p-value <0.0001). The dynamics between the individual sapwood area and GREFF models provide the

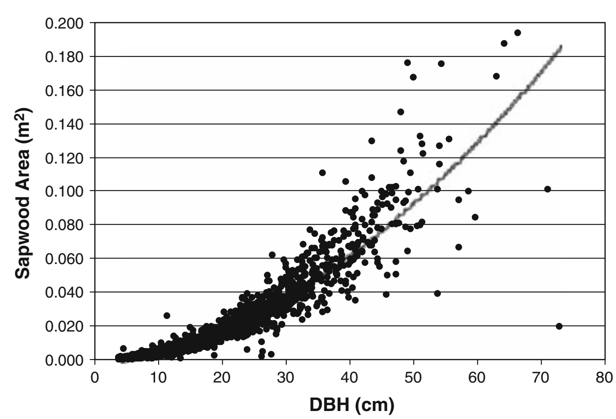

Fig. 3 Individual tree sapwood area versus DBH for ponderosa pine trees measured on study plots in uneven-aged stands, eastern Montana

Table 4 Parameter estimates for sapwood and growth efficiency individual tree models

Model	Equation	b_1	b_2	b_3	b_4	b_5
Sapwood area	1	−0.000300	−0.000020	0.000042	–	–
Growth efficiency	2	5.717800	−0.129900	0.632100	−3.407700	0.116800

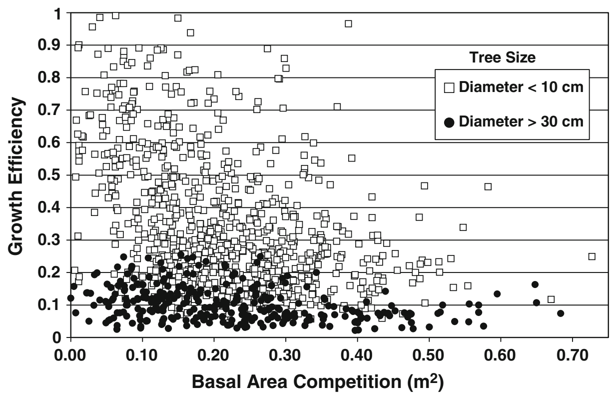

Fig. 4 Individual tree growth efficiency versus surrounding basal area competition (within 6.1 m of subject tree) for small and large ponderosa pine trees measured on study plots in uneven-aged stands, eastern Montana

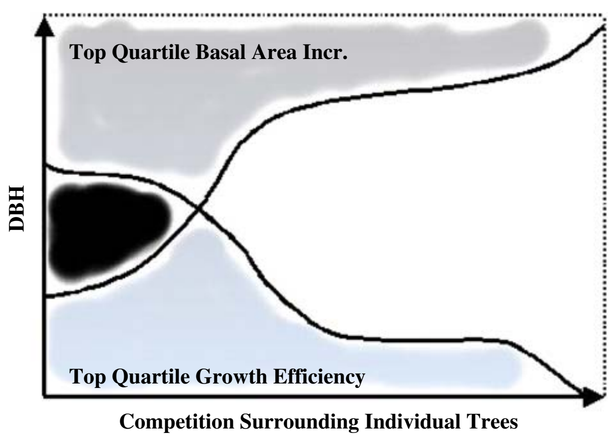

Fig. 5 Conceptual relationships between individual tree growth, growth efficiency, tree size, and surrounding competition for individual trees in uneven-aged stands, eastern Montana

theoretical basis for understanding how stand growth varies among stands with the same stand basal area but with varying tree size and spatial distributions (Fig. 5).

3.2 Generalized growth model

Growth model output for the nine hypothetical stand structures indicates substantial differences in total 10-year basal area growth related to the diameter distribution and spatial arrangement of constituent trees (Fig. 6a and Table 5). For all three diameter distributions, stand-level

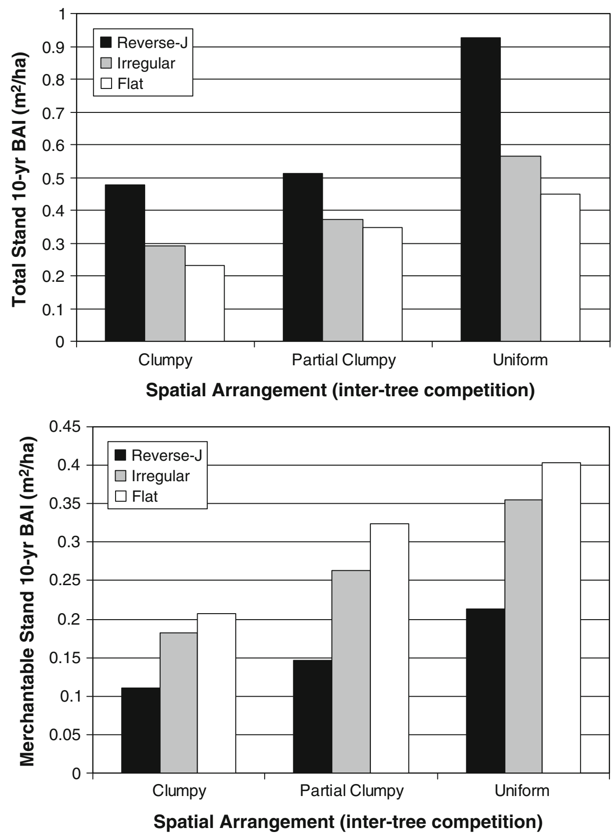

Fig. 6 Effect of varying competition levels (spatial arrangements) of individual trees and diameter distributions on stand total (**a**) and merchantable (**b**) 10-year basal area increment

growth was greatest under the spatial arrangement that minimized intertree competition (uniform) (Fig. 6a and Table 5). In contrast, total stand growth was reduced by nearly 50% under a clumpy arrangement (Fig. 6a and Table 5). The reverse-J distribution produced the greatest disparity between total and merchantable growth of the three diameter distributions (Fig. 6a, b and Table 5). Total stand growth of reverse-J stands appears driven by the large proportion of small-diameter trees. Because small trees are more affected by competition than larger trees, the clumping (heavy competition) of small trees greatly reduced total stand growth. If competition is to be allowed in some component of reverse-J stand structures, leaving high levels of competition around larger trees may reduce total stand growth by only about 15% (Fig. 6a and Table 5).

Total stand growth for the flat-diameter distribution was least affected by the spatial arrangement of individual trees

Table 5 Total and merchantable stand 10-yr basal area growth expressed as percentage of maximum 10-year basal area growth for nine hypothetical stands (both total and merchantable) for stands with 11.2 m^2 basal area

Spatial distribution	Diameter distribution					
	Reverse-J		Irregular		Flat	
	Total	Merch.	Total	Merch.	Total	Merch.
Uniform	100	53	60	88	48	100
Partial clumpy	55	36	40	65	37	80
Clumpy	51	27	31	45	24	51

(Fig. 6b and Table 5). The irregular and flat-diameter distributions showed relatively little difference between total and merchantable stand growth (Fig. 6a, b and Table 5). Because high numbers of growth-efficient smaller trees drive total stand growth, the modest number of small trees in these distributions results in lower total stand growth. Although minimizing competition among individual trees may be an unrealistic (or undesirable) goal for most stand treatments, stand growth for the flat-diameter distribution with partially clumpy spatial distributions was nearly the same as when trees were uniformly spatially distributed (Fig. 6b). Because much of the stand site is occupied by larger trees, minimizing competition on these trees, while allowing smaller trees to “crowd,” may still produce appreciable stand growth.

The irregular diameter distribution represents a rather common structure in western ponderosa pine stands—scattered large-diameter trees left from late 1800 to early 1900 logging activities, numerous medium trees that regenerated following these early harvests, and thickets of small trees in the understory that regenerated following patchy mortality of trees in the middle or upper canopy. Overall growth of the hypothetical stand with an irregular diameter distribution was less affected by changes in tree spatial arrangements than the stands with the two other diameter distributions (Fig. 6a, b and Table 5). Growth differences between tree spatial arrangements providing the most competition (clumpy) versus those with less individual tree competition (uniform) indicate that the large numbers of medium trees were major growth contributors in stands with irregular diameter distributions (Fig. 6a, b and Table 5). Stands with relatively large numbers of medium trees may give managers the flexibility to vary spatial distributions with the least impact on merchantable stand growth.

4 Discussion

The growth of structurally complex uneven-aged stands was quantified by first observing patterns in site occupancy and GREFF for individual trees by tree size and spatial distribution. Although some assumptions and caveats (i.e., competition reflected by tree spatial distributions) were stated to generalize the growth of uneven-stands, our study’s results may augment the base of forest restoration information. Different size components of uneven-aged stand structures (small, medium, and large trees) contribute substantially different proportions of growth to overall stand growth, depending on tree diameter distribution and spatial arrangement (Fig. 5). Maximum individual tree growth is found in the largest trees growing under the least competition, while maximum individual tree GREFF occurs in the smallest trees. Evaluating growth across the full range of diameters and spatial distributions indicates that only medium trees growing under the uniform spatial arrangements (least competition) achieve both high levels of growth and GREFF (Fig. 5). With site occupancy limitations setting sapwood area occupancy bounds for any given forest site (Grier and Running 1977), a forest manager may influence the complicated process of stand growth by recognizing trends in individual tree GREFF and growth for stands containing infinite combinations of individual tree diameters and spatial distributions. Whereas in even-aged stands the mean size and number of trees predominate predictions of stand growth (Long 1985), in uneven-aged stands growth may be viewed in a different light as being affected by tree size and spatial distributions.

Our use of a semi-empirical uneven-aged model here is hardly unique (O’Hara 1996). The purpose of this study’s growth model was to highlight obvious trends in growth dynamics across diverse restoration treatments, rather than to serve as an operational tool for forest managers. Growth model results indicated that growth among stands with even the same diameter distribution and stand basal area may vary as much as 49%. The spatial arrangement of different-size trees within an uneven-aged stand strongly influenced total and merchantable increment—sometimes as much as the diameter distribution itself. Reverse-J diameter distributions produce the greatest total growth, but are most affected by tree spatial arrangement. Flat-diameter distributions produce the lowest total stand growth of the three distributions, but are least affected by tree spatial arrangement. Additionally, the total stand growth of all three diameter distribution scenarios appears to be greatly affected by the spatial arrangement of the smaller-diameter trees, as opposed to the spatial arrangement of larger-diameter trees that are least affected by surrounding competition. Uniform spacing that minimized the clumping of small trees resulted in the highest stand growth, whereas clumpy spatial distributions (most competition) reduced growth the most. It is typically difficult for forest managers to predict the growth response of stands with irregular diameter distributions. In our study’s irregular distribution scenario, stands had high levels of total growth, while not sacrificing merchantable growth. This was due to a large number of intermediate-size trees accruing substantial increment relative to their sapwood area, while growth of the largest trees remained relatively unaffected by their surrounding competition (Fig. 5). The management of intermediate-size trees may be the most important component controlling the growth of uneven-aged stands. Hall (1993) came to a similar conclusion: the younger half of an uneven-aged stand may be the most important component to consider in terms of management and manipulation.

Generalizing growth relationships in uneven-aged ponderosa pine stands may provide broad guidance for forest managers considering adoption of alternative management scenarios in temperate, uneven-aged single-species forests. There are measurable tradeoffs between individual tree GREFF and actual growth increment. These tradeoffs can be broadly summarized in tree size/competition diagrams, and can be used to develop restoration prescriptions for uneven-aged ponderosa pine stands. Forest managers have much influence over growth in uneven-aged stands, because growth variations appear driven by basic stand parameters such as the number, diameter distribution, and spatial arrangement of constituent trees. If forest managers can manipulate these stand attributes, they can influence stand growth and highlight the yield potentials of complex alternative management scenarios.

5 Conclusions

Our study quantified trends in the individual tree attributes of sapwood area and GREFF among various stand structures with respect to tree size and spatial distributions. Models to predict these individual tree attributes were joined in a generalized growth model to estimate total and merchantable 10-year basal area stand growth, whereby sapwood area and GREFF served as surrogates of site occupancy and growth, respectively. Total stand growth may be maximized in stands with reverse-J shaped diameter distributions where trees are arranged uniformly. Merchantable stand growth may be maximized in stands with flat-diameter distributions with uniform tree spatial distributions. Given the strong effect that tree size and spatial distributions have on stand growth, forest managers can greatly control the yield of any treated stand while maintaining uneven-aged stand structures. Although not always the first priority when adopting alternative forest management scenarios, the quantification of growth implications of treatments may allow their more widespread acceptance and management flexibility in the face of possible climate change.

References

Alexander RR (1986) Silvicultural systems and cutting methods for ponderosa pine forests in the Front Range of the Central Rocky Mountains. General technical report RM-128. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station

Arno SA (1979) Forest regions of Montana. Research paper INT-218. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station

Arno SA, Fiedler CE (2005) Mimicking nature's fire: restoring fire-prone forests in the West. Island Press, Covelo, CA

Assman E (1970) Growth and yield study. Pergamon Press, New York, NY

Covington WW, Moore MM (1994) Southwestern ponderosa pine structure: changes since Euro-American settlement. J Forest 92:39–47

Covington WW, Fule PZ, Hart SC, Weaver RP (2001) Modeling ecological restoration effects on ponderosa pine structure. Restor Ecol 9:421–431. doi:10.1046/j.1526-100X.2001.94011.x

Coyea MR, Margolis HA (1994) Historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Can J Forest Res 24:2208–2221. doi:10.1139/x94-284

Edminster B, Mowrer HT, Mathiasen RL, Schuler TM, Olson WK, Hawksworth FG (1991) GENGYM: a variable density stand table projection system calibrated for mixed conifer and ponderosa pine stands in the Southwest. Research paper RM-297. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO

Fiedler CE (2000) Restoration treatments promote growth and reduce mortality of old-growth ponderosa pine (Montana). Ecol Res 18:117–119

Fule PZ, Moore MM, Covington WW (1997) Determining reference conditions for ecosystem management in southwestern ponderosa pine forests. Ecol Appl 7:895–908. doi:10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2

Fule PZ, McHugh C, Heilein TA, Covington WW (2001) Potential fire behavior is reduced following forest restoration treatments. In: Vance RK, Edminster CB, Covington WW, Blake JA (compilers) Ponderosa pine ecosystems restoration and conservation: steps toward stewardship. Proceedings RMRS-22. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp 28–35

Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893–899. doi:10.2307/1936225

Hall FC (1993) Stocking considerations in uneven-aged management. In: Growth basal area handbook. USDA PNW-R6-Ecol-181b-1984

Long JN (1985) A practical approach to density management. Forest Chron 61:23–27

Long JN, Dean TJ (1986) Sapwood area of *Pinus contorta* stands as a function of mean size and density. Oecologia 68:410–412. doi:10.1007/BF01036747

Malmsheimer RW, Heffernan P, Brink S, Crandall D, Deneke F, Galik C et al (2008) Forest management solutions for mitigating climate change in the United States. J Forest 106:115–171

Miina J (1994) Spatial growth model for Scots pine on drained peatland. Silva Fenn 28:15–27

O'Brien RA, Collins DC (1991) Forest statistics for land outside national forests in west-central Montana. Resource bulletin INT-72. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT

O'Brien RA, Conner RC (1991) Forest statistics for land outside national forests in eastern Montana. Resource bulletin INT-71. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT

O'Hara KL (1996) Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. Forest Science Monograph 33

O'Hara KL, Valappil NI (1995) Sapwood: leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Can J Forest Res 25:1553–1557

Pfister RD, Kovalchik BL, Arno SF, Presby RC (1977) Forest habitat types of Montana. General technical report-34. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT

Shao G, Shugart HH (1997) A compatible growth-density stand model derived from a distance-dependent individual tree model. Forest Sci 43:443–446

Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form—the pipe model theory. Jpn J Ecol 14:97–104

Smith DM, Larson BC, Kelty MJ, Ashton PMS (1997) The practice of silviculture, 9th edn. Wiley, New York, NY

Smith WB, Miles PD, Vissage JS, Pugh SA (2004) Forest resources of the United States, 2002. Gen. Tech. Rep. NC-241. U.S. Department of Agriculture, Forest Service. North Central Research Station, St. Paul, MN

U.S. Department of Agriculture (2004) Natl Rep Sustain Forests 2003: FS-766. U.S. Department of Agriculture, Forest Service. Washington, DC

Waring RH (1983) Estimating forest growth and efficiency in relation to canopy leaf area. Adv Ecol Res 13:327–354. doi:10.1016/S0065-2504(08)60111-7

Waring RH, Schroeder PE, Oren R (1982) Application of the pipe model theory to predict canopy leaf area. Can J Forest Res 12:556–560. doi:10.1139/x82-086

Woodall CW (2000) The growth and structural dynamics of uneven-aged ponderosa pine stands in eastern Montana. PhD dissertation, University of Montana, Missoula, MT

Woodall CW (2008) When is one core per tree sufficient to characterize stand attributes? Results of a *Pinus ponderosa* case study. Tree Ring Res 64:55–60

Woodall CW, Fiedler CE, Milner K (2003) Competition in uneven-aged stands. Can J Forest Res 33:1719–1726. doi:10.1139/x03-096

Wykoff WR, Crookston NL, Stage AR (1982) User's guide to the stand prognosis model. General technical report-133. U.S. Department of Agriculture, Forest Service. Intermountain Forest and Range Experiment Station, Ogden, UT