Intertree competition in uneven-aged ponderosa pine stands

C.W. Woodall, C.E. Fiedler, and K.S. Milner

Abstract: Intertree competition indices and effects were examined in 14 uneven-aged ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) stands in eastern Montana. Location, height, diameter at breast height (DBH), basal area increment, crown ratio, and sapwood area were determined for each tree (DBH >3.8 cm) on one stem-mapped plot (0.2–0.4 ha) in each sample stand. Based on tree locations, various competition indices were derived for each sample tree and correlated with its growth efficiency by diameter class. In addition, trends in individual tree attributes by diameter class and level of surrounding competition were determined. For trees with a DBH <10 cm, growth efficiency was most strongly correlated with the sum of surrounding tree heights within 10.6 m. The index most highly correlated for larger trees was the sum of surrounding basal area within 6.1 m. Regardless of tree size, individual tree growth efficiency, basal area increment, and crown ratio all decreased under increasing levels of competition, with the effect more pronounced in smaller trees. These results suggest that individual trees in uneven-aged stands experience competition from differing sources at varying scales based on their size, with response to competition diminishing as tree size increases.

Résumé : Les indices et les effets de la compétition entre les arbres ont été examinés dans 14 peuplements inéquiennes de pin ponderosa (*Pinus ponderosa* var. *scopulorum* Engelm.) dans l'Est du Montana. Pour chaque peuplement, la localisation, la hauteur, le diamètre à hauteur de poitrine (DHP), l'accroissement en surface terrière, la proportion de houppier et la surface de l'aubier ont été mesurés sur chaque arbre (DHP >3,8 cm) dans une placette (0,2–0,4 ha) dont les tiges ont été cartographiées. Sur la base de la localisation des arbres, différents indices de compétition ont été dérivés pour chaque arbre et corrélés avec leur efficacité de croissance par classe de diamètre. De plus, les tendances dans les attributs des arbres ont été déterminées par classe de diamètre et par niveau de compétition avoisinante. Pour les arbres avec un DHP <10 cm, l'efficacité de croissance est plus fortement corrélée avec la somme de la hauteur des arbres avoisinants situés à moins de 10,6 m. Pour les arbres plus gros, l'indice le plus fortement corrélé correspond à la somme de la surface terrière des arbres voisins situés à moins de 6,1 m. Indépendamment de la taille des arbres, l'efficacité de croissance des arbres, l'accroissement en surface terrière et la proportion de houppier diminuaient avec l'augmentation des niveaux de compétition, avec un effet plus prononcé pour les petits arbres. Ces résultats montrent que les arbres des peuplements inéquiennes subissent une compétition provenant de sources différentes à des échelles variables, en fonction de leur taille et avec une réponse à la compétition qui diminue à mesure que la taille de l'arbre augmente.

[Traduit par la Rédaction]

Introduction

Competition is a term often used to describe the interaction among plants in a community, whereby at least two plants are competing for the same resource (i.e., light, nutrients, water). Foresters have sought to quantify competition and its effects for decades (see for instance Opie 1968; Bella 1971). In even-aged stands, efforts to quantify competition have been reasonably successful because all trees are approximately the same size and have random spatial distributions (Newton and Jolliffe 1998; Hökkä and Groot 1999). Irregular diameter and spatial distributions have constrained the quantification of competition and subsequent growth prediction in uneven-aged stands (Hökkä and Groot 1999). Further examination of the dynamics of competition at the individual tree level in uneven-aged stands is needed to refine future modeling and management efforts.

The objective of this study is to investigate intertree competition dynamics in uneven-aged ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) stands by (*i*) quantifying site occupancy (competition) surrounding subject trees through use of various sizes of fixed-radius plots, sizes of subject trees, and alternative measures of competition; and (*ii*) determining the effects of competition on individual tree attributes (growth efficiency, basal area increment, sapwood area, crown ratio, and tree height).

Past work

Quantifying competition

Intertree competition is most often quantified using competition indices. A competition index is a mathematical formulation derived to represent or describe competition from

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adjacent trees that could be affecting the growth of any considered tree (Daniels 1976; Schreuder and Williams 1995). Opie (1968) proposed a "zone of influence" as a crucial component of any competition index based on the assumption that every tree has a certain area in which it exerts demand for limited resources. Distance-dependent indices attempt to quantify an individual tree's zone of influence, while distance-independent competition models use subject tree attributes or stand-level estimates of density for growth prediction and thus may not actually gauge competition surrounding individual trees (Biging and Dobbertin 1995). Distance-dependent indices, at best, only marginally improve estimates of individual tree growth over distance-independent indices (Biging and Dobbertin 1992, 1995; Tome and Burkhart 1989; Martin and Ek 1984; Daniels et al. 1986). Additional research is needed to gain a broad understanding of the relationships that underlie competition in uneven-aged stands. Examination of competition across a range of tree sizes and spatial scales in stands with heterogeneous structures can contribute to this understanding.

Numerous tree and stand attributes have been proposed as estimators of competition. Stand size/density measures serve as vital components of most competition indices (Stoll et al. 1994). For example, summations of basal area surrounding individual trees at various scales have been used as robust gauges of competition (Bella 1971; Wykoff et al. 1982). A refinement of basal area such as sapwood area may also be used to gauge competition. Lorimer (1983) and Biging and Dobbertin (1992) found that inclusion of crown class ratings for competitors refined competition estimation, a role that sapwood area could potentially fulfill based on the pipe-stem model (Waring et al. 1982). To date, scant research has been conducted to determine the best tree and (or) stand attribute(s) for gauging competition around trees of different sizes in uneven-aged stands.

Effects of competition

Growth efficiency (GREFF), defined as a sensitive, physiologically based measure of individual tree vigor (Coyea and Margolis 1994), may vary by tree size and surrounding level of competition in any given stand (Long and Dean 1986; O'Hara 1996). GREFF is usually calculated as tree growth divided by leaf area (Waring 1983); however, basal area increment divided by sapwood area may serve as a GREFF surrogate. Generally, individual tree GREFF has been shown to decrease with increasing tree size and age (Ryan 1989; Yoder et al. 1994; Maguire et al. 1998; Kaufman and Ryan 1986). The behavior of individual tree GREFF in uneven-aged stands may also depend on the influence of stand structure, which may create variable levels of competition (Maguire et al. 1998). Trends of individual tree GREFF under varying levels of competition and across a range of tree sizes have never been quantified for uneven-aged stands.

Individual tree growth usually decreases under increasing competition (Bella 1971; Biging and Dobbertin 1992), a response that may be asymmetric across the range of tree sizes (Weiner 1990). Hökkä and Groot (1999) found that growth of codominant and intermediate trees in even-aged stands was only slightly reduced by competition, while the growth of suppressed trees rapidly decreased as competition increased. Results from Bella (1971) also support the hypothesis that the growth of suppressed and intermediate trees is much more affected by competition than that of larger, more dominant trees. However, information is sparse concerning trends in individual tree sapwood area and crown ratio under increasing levels of competition for uneven-aged stands. Based on research into the response of tree social classes to increasing competition in even-aged stands, it might be expected that trees will have thinner crowns and shorter crown lengths under increasing levels of competition (Smith and Long 1989; Hökkä and Groot 1999). Increasing levels of competition should have less effect on individual tree height than on diameter growth (Assman 1970), although a study by Biging and Dobbertin (1992) found that height growth was slightly affected by competition. Overall, individual tree attribute response to increasing competition has been scarcely studied in uneven-aged stands.

Materials and methods

Study area

Ponderosa pine occupies approximately 0.9 × 10^6 ha in eastern Montana, often in monocultures (O'Brien and Conner 1991*a*, 1991*b*). Ponderosa pine forests occur on lowlands and hilly terrain (850 to 1350 m in elevation) in the northern Great Plains of eastern Montana (Arno 1979), where soils are typically shallow and poorly developed, and precipitation averages 260–420 mm/year (Pfister et al. 1977). Because of the historic low-intensity fire regimes, sporadic regeneration events, and harsh environmental conditions of eastern Montana, many of these stands are uneven aged.

Field

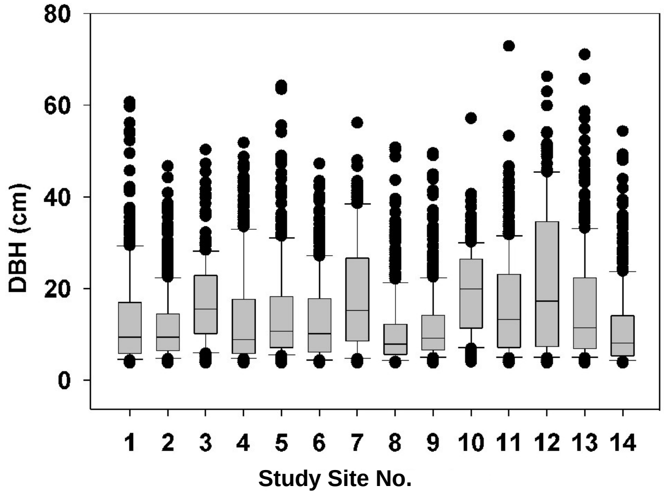
Fourteen sample sites were located in pure ponderosa pine stands exhibiting negligible evidence of recent human or natural disturbances (Table 1, Fig. 1). Although sample sites were located in stands across the range of site qualities found in eastern Montana ponderosa pine ecosystems, in a larger context these stands occupy the lower end of the range of site qualities inhabited by ponderosa pine. For a more detailed quantification of site qualities for these sample sites see Woodall (2000).

A 0.2- to 0.4-ha fixed-radius plot was subjectively established at each site to minimize variation in physiographic attributes. The location of every plot tree ≥3.8 cm diameter at breast height (DBH, 1.37 m) was mapped by distance and azimuth from plot center using a laser range-finding device and digital compass. Plot trees between 3.8 and 12.7 cm DBH were cored once to the pith, and plot trees ≥12.7 cm in 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 future analysis in the laboratory. In addition to core work, all trees were measured for DBH (nearest 0.25 cm), tree height (nearest 0.03 m), and crown base height (nearest 0.03 m). Approximately 5000 trees were sampled across the 14 sites (210–605 trees per site) (Table 1, Fig. 1). Since an uneven-aged stand may be defined as a stand containing groups of

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

Site No.	Sample plot size (ha)	No. 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

Fig. 1. Box plots of diameter (DBH) distributions for 14 uneven-aged ponderosa pine stands in eastern Montana. The median is shown by a horizontal line within a lower and upper quartile box. Whiskers extending from each box show the 1.5 inter-quartile range. Solid dots represent outliers.



trees of varying ages with rather complicated development patterns (Smith et al. 1997), age and size distributions indicated that all study stands could be defined as uneven aged (Table 1, Fig. 1).

Laboratory data tabulation

Every core taken in the field was dried, mounted on a grooved board, and sanded for subsequent analysis. Age at breast height was estimated by reading annual rings for one core from each tree using a dissecting scope. Sapwood width and inside-bark bole radius were measured to the nearest millimetre. Ten-year radial growth increment was measured to the nearest 0.0254 mm using an Acu-Gage Coordinate Measuring Machine (Acu-Gage Systems, Manchester, N.H.) with attached zoom video system. Inside-bark basal area (BA), sapwood area (SA), and 10-year basal area increment (BAI) were calculated for each tree, averaging dual estimates for trees that were cored twice. In this study, GREFF was defined as an individual tree's BAI divided by its SA. Individual tree crown ratio was determined by subtracting crown base height from total tree height then dividing the remainder by total tree height.

Table 2. Levels of competition by DBH class.

Level	DBH 3.8–10 cm	DBH ≥10.1 cm
1	0–125	0–0.075
2	126–250	0.076–0.150
3	251–375	0.151–0.225
4	376–500	0.226–0.300
5	501–625	0.301–0.375
6	≥626	≥0.376

Note: For the 3.8–10 cm DBH class, the estimated competition levels are sums of tree heights (metres) within 10.0 m. For the ≥10.1 cm DBH class, the estimated competition levels are sums of basal areas (square metres) within 6.1 m.

Estimates of surrounding competition were calculated for each individual tree. Since the location and attributes of all individual trees were known, database queries were developed to establish sample plots of various fixed radii (1.6, 3.1, 4.6, 6.1, 7.6, 9.1, 10.6, and 12.1 m) around each tree. For each sample plot radius, trees closer to the plot border than the plot radius were discarded as subject trees. For each sample plot, SA, BA, BAI, GREFF, and height of all "in" trees were summed by attribute to serve as estimates of competition (excluding attributes of the respective subject tree).

Data analysis

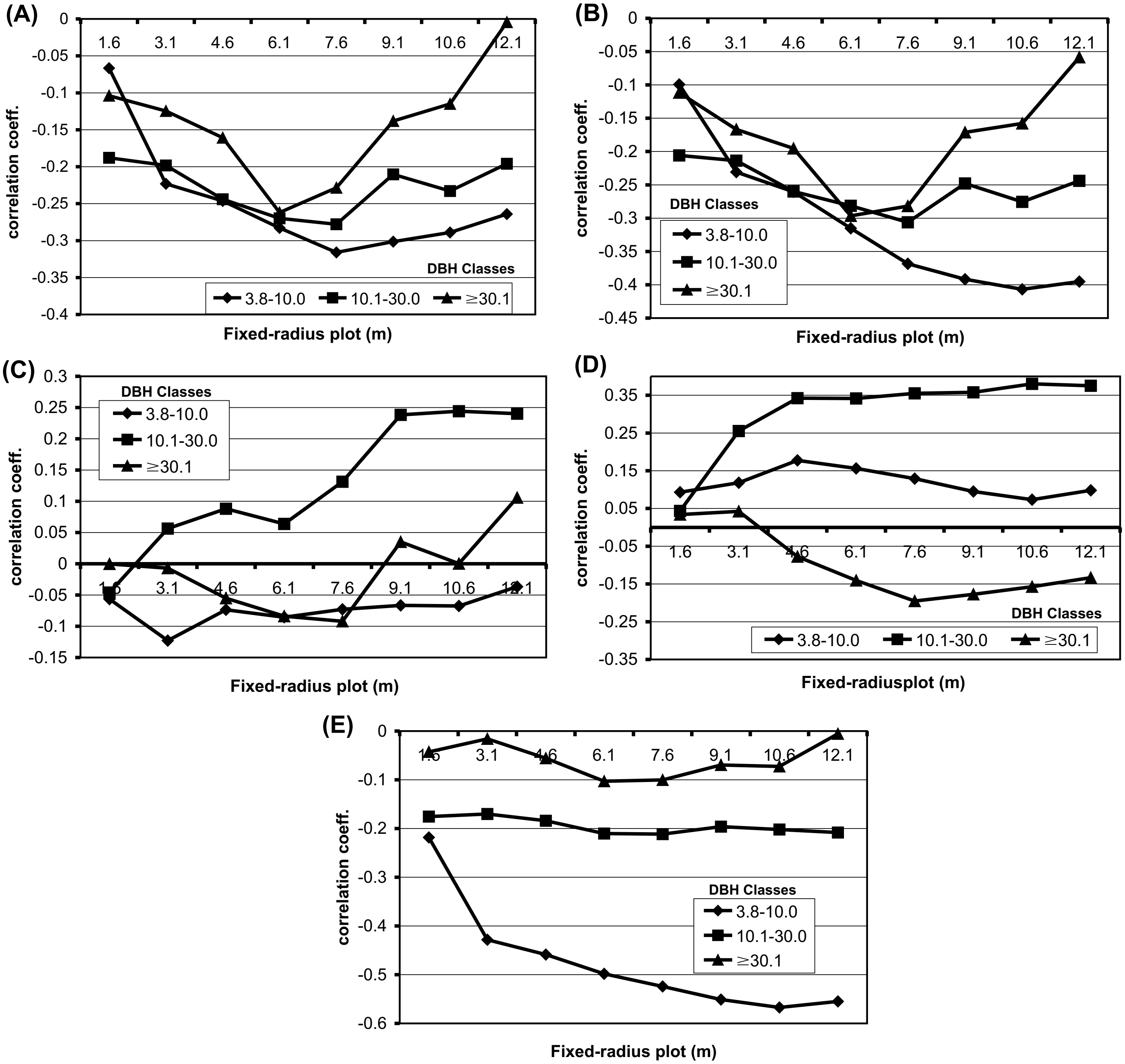
To evaluate measures of competition, Pearson's correlation coefficients were calculated between individual tree GREFF (stratified by three diameter classes) and estimates of surrounding competition (various plot sizes and summed tree attributes) with preliminary graphs indicating linear relationships. Only subject trees around which all sizes of fixed-radius plots could be established were used in this part of the study. The effects of competition were determined through computation of means and associated standard errors for various tree attributes under varying levels of competition. Levels of competition were estimated using results from completion of the competition quantification analysis, with the most highly correlated tree attribute and fixed-radius plot size used for each of the three diameter classes, respectively (Table 2). For small trees with a DBH from 3.7 to 10.0 cm, 10.1-m fixed-radius plots of summed tree heights were used as an estimate of competition. For medium trees with a DBH from 10.1 to 30.0 cm and large trees with a DBH ≥30.1 cm, 6.1-m fixed-radius plots of summed basal area were used as an estimate of competition. Although individual tree GREFF for medium trees had a slightly higher correlation with 7.6-m than 6.1-m fixed-radius plots, the slight increase in correlation (0.024) was not worth the decrease in sample size (103 observations) that resulted when using the larger (7.6 m) fixed radius.

Results

Gauging competition in uneven-aged stands

Individual tree GREFF was negatively correlated with in-

Fig. 2. Pearson's correlation coefficients between individual tree growth efficiency and the sums of (A) sapwood areas, (B) basal areas, (C) basal area increments, (D) growth efficiencies, and (E) total tree heights on various fixed-radius plots (associated probabilities are shown in Table 3).



creasing levels of surrounding BA and SA (Figs. 2A and 2B). Estimates of surrounding BA displayed stronger correlation with individual tree GREFF than did estimates of SA (Figs. 2A and 2B). The GREFF of medium trees (DBH 10.1–30.0 cm) was positively correlated with estimates of surrounding BAI, while the GREFF of large and small trees (DBH ≥30.1 cm and DBH ≤10.0 cm, respectively) showed weak correlation with estimates of surrounding BAI (Fig. 2C). The GREFF of the smallest and midsized diameter classes was positively correlated with the sum of surrounding tree GREFFs, but the GREFF of the largest trees was negatively correlated with the sum of surrounding tree GREFFs (Fig. 2D). Individual tree GREFF was negatively correlated with total surrounding tree heights, with the strength of the correlation diminishing as subject tree DBH increased (Fig. 2E). Diameter-class correlations between GREFF and estimates of surrounding competition varied not only by tree attribute, but also by plot size. If we use the correlation between individual tree GREFF and estimates of surrounding BA as an example, small trees had the strongest

Table 3. Associated probabilities for Pearson's correlation coefficients between individual tree growth efficiency and the sums of sapwood areas, basal areas, basal area increments, and growth efficiencies on various fixed-radius plots.

			Plot radius (m)							
Competition surrogate	DBH class (cm)	*n*	1.6	3.1	4.6	6.1	7.6	9.1	10.6	12.1
Sapwood	3.8–10.0	464	0.0265	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	10.1–30.0	407	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	≥30.1	82	0.2995	0.3108	0.1698	0.0386	0.0453	0.4661	0.5575	0.7876
Basal area	3.8–10.0	464	0.0326	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	10.1–30.0	407	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	≥30.1	82	0.2897	0.1584	0.0867	0.0159	0.0124	0.2876	0.3069	0.7961
Basal area increment	3.8–10.0	464	0.2240	0.0081	0.1127	0.0660	0.1174	0.1524	0.1463	0.4298
	10.1–30.0	407	0.3647	0.2586	0.0745	0.1980	0.0075	<0.001	<0.001	<0.001
	≥30.1	82	0.9008	0.8588	0.7997	0.6459	0.4355	0.5758	0.7266	0.2232
Growth efficiency	3.8–10.0	464	0.0450	0.0109	<0.001	0.0007	0.0054	0.0409	0.1154	0.0347
	10.1–30.0	407	0.3615	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	≥30.1	82	0.9554	0.7515	0.4272	0.1732	0.0574	0.0682	0.1263	0.1767
Height	3.8–10.0	464	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	10.1–30.0	407	0.0004	0.0005	0.0002	<0.001	<0.001	<0.001	<0.001	<0.001
	≥30.1	82	0.6994	0.8166	0.7575	0.4628	0.4112	0.5918	0.6632	0.9375

correlation with 10.6 m radius plots, medium trees with 7.6 m radius plots, and large trees with 6.1 m radius plots (Figs. 2A and 2B). By diameter classes, the strongest correlation between individual tree GREFF and estimates of surrounding competition was found with estimates of total tree heights using 10.6 m radius plots for small trees, with estimates of surrounding BA using 7.6 m radius plots for medium trees, and with estimates of surrounding BA using 6.1 m radius plots for large trees (Figs. 2A–2E). Correlation coefficient probabilities were significant ($P < 0.05$) for the majority of individual tree GREFF – competition surrogate combinations (Table 3). For small and medium trees with a DBH ≤30.0 cm, most nonsignificant correlations were found between individual tree GREFF and smaller fixed-radius plots of surrounding BAI (Table 3). For large trees with a DBH ≥30.1 cm, correlation coefficients between individual tree GREFF and surrounding competition indices were usually only significant when using 4.6-, 6.1-, and 7.6-m fixed-radius plots (Table 3).

Effects of competition

Mean individual tree GREFF decreased as competition increased, regardless of tree size (Fig. 3A). However, the decrease was more pronounced in smaller trees than in larger ones (Fig. 3A). Trends in mean individual tree BAI were similar to trends in GREFF. As competition increased, mean BAI decreased for all diameter classes (Fig. 3B). The change in mean BAI under increasing competition was greatest for small and medium trees (Fig. 3B). Mean individual tree SA values appeared to be less affected by increasing levels of surrounding competition than did BAI values (Fig. 3C). Mean individual tree heights by diameter class were greater under higher levels of competition — a relationship observed across all diameter classes (Fig. 3D). Mean crown ratio values decreased under increasing competition, regardless of subject tree size (Fig. 3E). In addition to standard error (Figs. 3A–3E) and sample size (Table 4) interpretations, a two-way ANOVA indicated significant differences among the means of all examined tree attributes by diameter class and level of competition ($P < 0.001$).

Discussion

The correlation between individual tree GREFF and alternative competition indices depended on both the specific competition index and the subject tree size. The GREFF of small diameter trees may be most affected by overtopping competition, an effect best represented by total (summed) tree heights on large fixed-radius plots. The GREFF of medium- and large-diameter trees was most affected by more proximate competition, which may be estimated using relatively small fixed-radius plots for estimating surrounding BA. For medium and large trees, higher surrounding densities may result in water and nutrient competition, while for the smallest trees, light may be the most limiting resource. Results from this study suggest that the appropriate sampling procedure for gauging competition depends on the size of the subject tree, which supports previous research suggesting that the radius of sample plots should depend on the size of the subject tree to appropriately gauge individual tree competition (Lorimer 1983; Martin 1982). In addition, the individual tree attributes used to estimate surrounding competition, whether BA or tree height, may depend on the size of the subject tree. The results of our study lend support to the assertion by Biging and Dobbertin (1992) that it is difficult to define a universal gauge of intertree competition.

Correlations between individual tree GREFF and surrounding plots of total BAI and total GREFF may provide information on uneven-aged stand dynamics. Medium tree GREFF was positively correlated with increasing total GREFF and BAI, while the GREFF of the largest trees was negatively correlated with surrounding sums of individual tree GREFF and BAI. Because regeneration in these stands is often spatially clustered, medium trees may experience most of their competition from growth-efficient medium and small trees. For larger trees, their associated regeneration

Fig. 3. Mean values and associated standard errors for individual tree characteristics by DBH class and level of surrounding competition: (A) growth efficiency, (B) basal area increment, (C) sapwood area, (D) total tree height, and (E) crown ratio. Descriptions of competition levels are provided in Table 2.

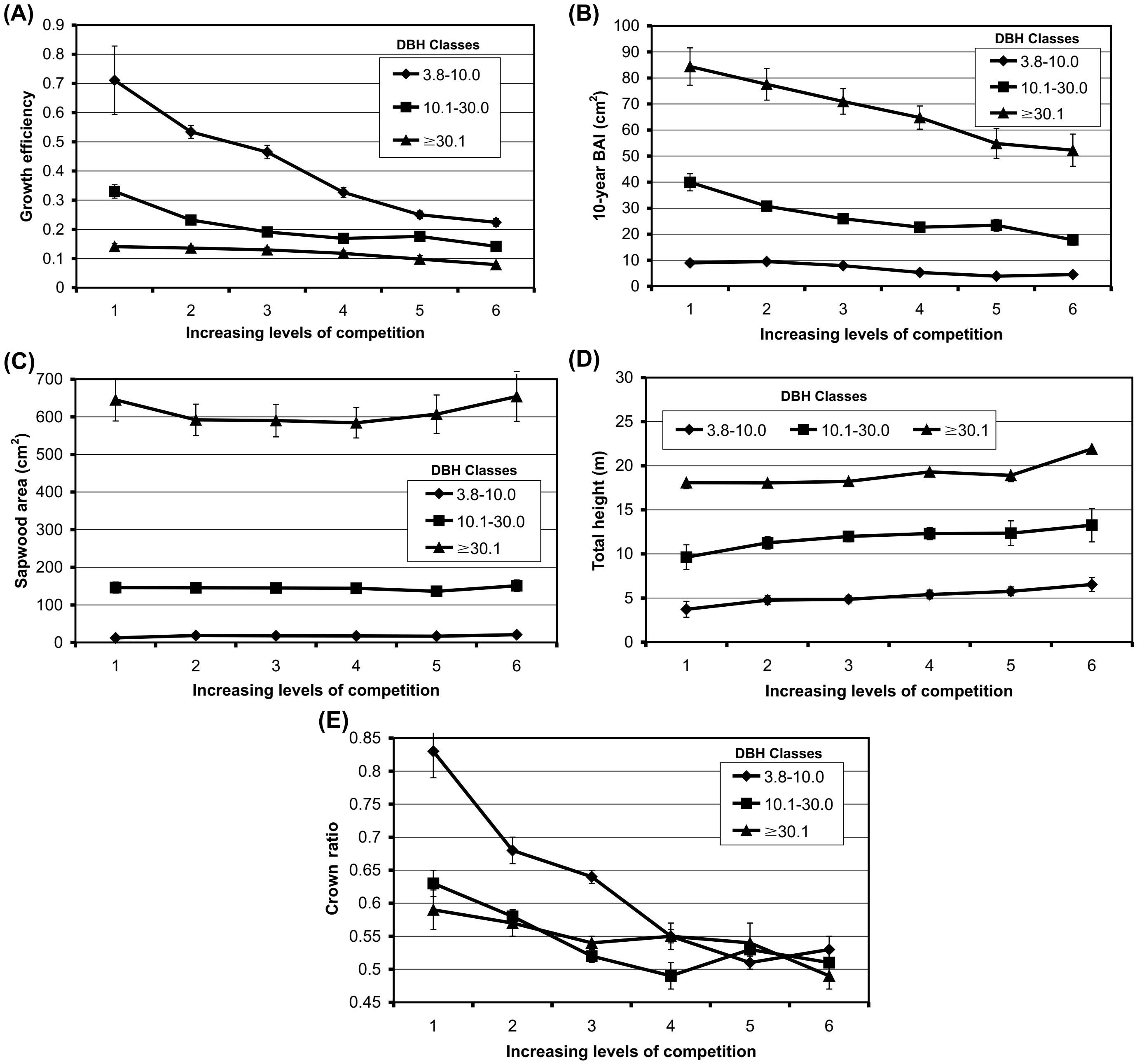


Table 4. Sample sizes for examination of individual tree attributes by DBH class and level of surrounding competition.

DBH class (cm)	Levels of competition*					
	1	2	3	4	5	6
3.8–10.0	5	76	95	101	92	55
10.1–30.0	54	195	291	231	79	50
≥30.1	20	44	36	34	16	35

*Descriptions of competition levels are provided in Table 2.

clusters may have thinned out a century ago, allowing establishment of growth-efficient young trees that provide new and intense competition from below. Other studies have found that compared with large trees, small trees have a greater than size-proportional effect on subject trees when included in competition indices (Stoll et al. 1994; Biondi 1996). There may be two types of trees shaping the distribution of individual tree GREFF for a given diameter class. There are the trees that are vigorous members of a recent regeneration event, and there are the suppressed members of a regeneration event that were left behind during differentiation. This may explain why some midsized trees are very growth efficient, although surrounded by numerous growth-efficient trees, and why some medium trees are growth inefficient, although surrounded by fewer growth-inefficient trees. This broader view of intertree competition, in which general sources of competition for tree size classes are identified, may provide a foundation for conceptualization of uneven-aged stand dynamics.

Tree response to competition depended on the size of the subject tree and on the particular response being examined. Some past work has indicated that individual tree GREFF increases with uneven-aged cohort age (O'Hara 1996), while other research has shown a decrease in GREFF with increasing tree age (Ryan 1989; Yoder et al. 1994; Maguire et al. 1998). However, no conclusions were drawn in these studies about the effects of competition (Ryan 1989; Yoder et al. 1994; O'Hara 1996; Maguire et al. 1998). In our study, not only did the mean values of individual tree GREFF show distinct declines with increasing tree size, GREFF also declined under increasing BA and height competition, an effect more pronounced in small trees. Results of previous work involving other species in other regions provide no consistent pattern. For example, Gilmore and Seymour (1996) found that suppressed trees had low levels of GREFF, while Kaufman and Ryan (1986) and Smith and Long (1989) reported that suppressed trees had high levels of GREFF due to the self-shading of crowns. A study by Penner and DeBlonde (1996) also found that small trees had marginally higher aboveground GREFF in stands where competition is great.

Variations in individual tree BAI and SA, the two components of GREFF, may explain observed trends in individual tree GREFF. The BAI of small trees is more negatively affected by increasing competition than that of large trees. However, for a given diameter class, we found no evidence of individual tree SA substantially changing across the range of competition. Therefore, an individual tree maintaining a rather stable amount of SA under increasing competition, but adding less BAI, may explain the behavior of GREFF. The carbon allocation strategy of trees would support this result. As trees fix less carbon, they allocate less to basal area growth and attempt to maintain their leaf area (Waring and Schlesinger 1985). It may be difficult to find highly growth efficient trees under very high levels of competition. Hökkä and Groot (1999) and Bella (1971) found that growth of codominant and intermediate trees in even-aged stands was only slightly reduced by competition, while the growth of suppressed trees rapidly decreased as competition increased. As concluded by this and recent research, the GREFF of individual trees in uneven-aged stands varies not only by tree size (Maguire et al. 1998), but also by levels of surrounding competition.

Tree height and crown ratio response to competition supported conventional hypotheses. Within a given diameter class, mean tree height was greater at higher levels of competition. Higher stand densities have been shown to reduce height growth less than diameter growth (increasing height/diameter ratios; Assman 1970), an effect that may be more pronounced with larger, older trees that have had a longer period of time to allow height growth differences to accrue. Mean crown ratio decreased with increasing competition. As intertree competition increases, shading of lower branches will result in higher crown bases and lower crown ratios. In addition to shading, competition for water at higher surrounding densities may require trees to maintain only the most growth-efficient parts of the crown. However, the apparent contradiction between tree maintenance of SA over a range of competition levels and a reduction in crown ratio over the same range needs to be resolved. As a tree grows under increasing competition, it may reallocate its resources to a more compact, growth-efficient crown. Therefore, under increasing competition, a tree may grow less BAI, have a lower crown ratio, but possibly maintain its SA.

Conclusions

The dynamics of plant competition define the character of all plant ecosystems. The intertree competition dynamics that drive the development pattern(s) of uneven-aged stands have been poorly understood. Results from this study may refine understanding of intertree competition in uneven-aged stands. Individual trees experience competition from different sources at varying scales based on their size. The GREFF of small diameter trees was found to be most strongly correlated with estimated sums of surrounding tree heights using 10.6-m fixed-radius plots, while the GREFF of medium and large trees was found to be most strongly correlated with estimates of surrounding BA using 6.1- and 7.6-m fixed-radius plots, respectively. The effects of this competition can be seen as a reduction in individual tree GREFF, an effect more pronounced in small trees. Reductions in GREFF may be attributed to trees attempting to maintain stable levels of SA, but growing less BAI under increasing competition. Other effects of increasing competition, regardless of tree size, include reductions in crown ratio and increases in tree height for a given diameter. Better understanding of the general relationships of intertree competition may benefit numerous aspects of uneven-aged stand management such as prioritizing stands for treatment, providing guidance for reserve density targets, aiding in marking efforts, and facilitating more accurate growth modeling.

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References

Arno, S.F. 1979. Forest regions of Montana. USDA For. Serv. Res. Pap. INT-218.

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

Bella, I.E. 1971. A new competition model for individual trees. For. Sci. **17**: 364–372.

Biging, G.S., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**: 695–720.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **41**: 360–377.

Biondi, F. 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? Can. J. For. Res. **26**: 1397–1406.

Coyea, M.R., and Margolis, H.A. 1994. Historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Can. J. For. Res. **24**: 2208–2221.

Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. **22**: 454–456.

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.

Gilmore, D.W., and Seymour, R.S. 1996. Alternative measures of stem growth-efficiency in central Maine, USA. For. Ecol. Manage. **84**: 209–218.

Hökkä, H., and Groot, A. 1999. An individual tree basal area growth model for black spruce in second-growth peatland stands. Can. J. For. Res. **29**: 621–629.

Kaufman, M.R., and Ryan, M.G. 1986. Physiographic, stand, and environmental effects on individual tree growth efficiency in subalpine forests. Tree Physiol. **2**: 47–59.

Long, J.N., and Dean, T.J. 1986. Sapwood area of *Pinus contorta* stands as a function of mean size and density. Oecologia, **68**: 410–412.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360.

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. 1982. Estimation of individual tree competition from horizontal point sample data. For. Sci. **28**: 45–48.

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.

Newton, P.F., and Jolliffe, P.A. 1998. Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. Can. J. For. Res. **28**: 259–275.

O'Brien, R.A., and Collins, D.C. 1991*a*. Forest statistics for land outside national forests in west-central Montana. USDA For. Serv. Res. Bull. INT-72.

O'Brien, R.A., and Conner, R.C. 1991*b*. Forest statistics for land outside national forests in eastern Montana. USDA For. Serv. Res. Bull. INT-71.

O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. For. Sci. Monogr. 33.

Opie, J.E. 1968. Predictability of individual tree growth using various definitions of competing basal area. For. Sci. **14**: 314–323.

Penner, M., and DeBlonde, G. 1996. The relationship between leaf area and basal area growth in jack pine and red pine trees. For. Chron. **72**: 170–175.

Pfister, R.D., Kovalchik, B.L., Arno, S.F., and Presby, R.C. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34.

Ryan, M.G. 1989. Sapwood volume for three subalpine conifers: predictive equations and ecological implications. Can. J. For. Res. **19**: 1397–1401.

Schreuder, H.T., and Williams, M.S. 1995. Assessing measures of tree competition using fixed-area, variable-radius, and horizontal plot sampling. Can. J. For. Res. **25**: 1578–1582.

Smith, F.W., and Long, J.N. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. J. Appl. Ecol. **26**: 681–691.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1997. The practice of silviculture. 9th ed. Wiley, New York.

Stoll, P., Weiner, J., and Schmid, B. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology, **75**: 660–670.

Tome, M., and Burkhart, H.E. 1989. Distance dependent competition measures for predicting growth of individual trees. For. Sci. **35**: 816–831.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Adv. Ecol. Res. **13**: 327–354.

Waring, R.H., and Schlesinger, W.H. 1985. Forest ecosystems: concepts and management. Academic Press, New York.

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.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. **5**: 360–364.

Woodall, C.W. 2000. The growth and structural dynamics of uneven-aged ponderosa pine stands in eastern Montana. Ph.D. dissertation, University of Montana, Missoula, Mont.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User's guide to the Stand Prognosis Model. USDA For. Serv. Gen. Tech. Rep. INT-133.

Yoder, B.J., Ryan, M.G., Waring, R.H., Shoettle, A.W., and Kaufman, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. **40**: 513–527.