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Effects of competitor spacing in a new class of individual-tree indices of competition: semi-distance-independent indices computed for Bitterlich versus fixed-area plots

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Abstract: We illustrate effects of competitor spacing for a new class of individual-tree indices of competition that we call semi-distance-independent. This new class is similar to the class of distance-independent indices except that the index is computed independently at each subsampling plot surrounding a subject tree for which growth is to be modelled. We derive the effects of distance for this class as the expected value over independent samples containing a particular subject tree. In a previous paper, we illustrated distance effects implicit in eight indices of the distance-dependent class. Here, we present distance effects of four semi-distance-independent indices: density, sum of diameters, basal area, and tree-area ratio; each determined for small fixed-area plots of 0.04 ha and for Bitterlich samples of 6 $m^2 \cdot ha^{-1}$. We show that several members of this new class have distance effects very similar to the distance-dependent class and should, therefore, be equally effective in accounting for competitive effects in individual-tree increment models. The comparisons should inform selection of competition indices and sampling designs for growth modelling.

Résumé : Les effets de l'espacement entre les arbres compétiteurs sont illustrés pour une nouvelle classe d'indices de compétition d'arbres individuels appelée classe d'indices semi-dépendants de la distance. Cette nouvelle classe est similaire à la classe des indices indépendants de la distance sauf que l'indice est calculé indépendamment pour chaque sous-placette-échantillon entourant un arbre sujet dont la croissance doit être modélisée. Pour cette nouvelle classe, les effets de la distance sont considérés comme étant la valeur attendue des échantillons indépendants contenant un arbre sujet particulier. Les effets de la distance implicites dans huit indices dépendants de la distance sont illustrés dans un article précédent. Ici, les effets de la distance sont présentés pour quatre indices semi-dépendants de la distance : densité, somme des diamètres, surface terrière et quotient d'espace vital. Chaque indice est déterminé pour de petites placettes à surface fixe de 0,04 ha et pour les placettes-échantillons Bitterlich de 6 $m^2 \cdot ha^{-1}$. Pour plusieurs membres de la nouvelle classe, les effets de la distance sont très similaires à ceux des indices de la classe dépendante de la distance. Ils devraient par conséquent être aussi efficaces pour tenir compte des effets de compétition dans les modèles de croissance d'arbres individuels. Ce type de comparaisons devrait influencer la sélection des indices compétition et le mode d'échantillonnage pour la modélisation de la croissance.

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Introduction

Recent increment models of individual-tree development based on direct observations of changes in tree size have used measures of competition at two spatial scales: a mean over the entire "stand" and some more local measure of trees in the immediate neighborhood of the subject tree (e.g., Tomé and Burkhart 1989; Stage and Wykoff 1998; Lappi 2005). In this paper, we consider the local measure. The stand mean indices have been termed "distance-independent," and the local neighborhood indices are termed "distance-dependent." Both of these measures have deficiencies when applied to stands of irregular spacing using sample plots to estimate competition among trees: the latter because some competitors for trees near the edge of the plot will not be included and the former because effects of local variation in spacing are not represented. A third class, called "semi-distance-independent" has been applied to

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distance-independent indices calculated only from trees on a single, small sample plot including the subject tree (Stage and Wykoff 1998). In this case, the plot configuration is part of the definition of the measure. All of these local indices have two components: the relative attributes of the subject and competitor pairs and their spatial separation. Ledermann and Stage (2001) displayed the interactions of these two components for eight distance-dependent indices by graphing the contribution of a single tree of each of three typical crown classes of competitors to the indices of each of the same set of trees considered as subject trees, expressed as a function of the spatial separation between subject tree and competitor. In this paper, we will extend that form of display to include the effects of variation attributable to plot configuration (fixed-area plots vs. Bitterlich samples) for four semi-distance-independent indices. To assure comparability to our previous paper, we use the individual-tree data of the same three Norway spruce (*Picea abies* (L.) Karst.) trees originally selected from a permanent research plot of the Institute of Forest Growth and Yield, University of Agricultural Sciences, Vienna.

Neighbor relations in competition indices

Areas physically occupied by individual trees are often represented in distance-dependent indices of competition by contours of occupation within a finite limit (Ledermann and Stage 2001; Casper et al. 2003; Lappi 2005). The contours within the zone of influence may be defined simply as circles of radii that are multiples of tree diameter at breast height (DBH) or, in the more sophisticated indices, by the relative crown geometries of the subject and competitor pair. Empirical data of root excavations show substantial variation between the assumed area and the area actually occupied by trees. For example, roots of trees on slopes show a longer radius downslope (Curtis 1964 for ponderosa pine (*Pinus ponderosa* P.&C. Lawson), and crown measurements and root diagrams show trees tend to fill adjacent openings as the trees forage for resources (e.g., Muth and Bazzaz 2003). Thus, tree-centered competition measures include a model error component arising from the discrepancy between the size, shape, and intensity of the area actually occupied and the assumed domain of subject trees. Although more recent competition indices (CIs) have sought to include such effects, the calculated contribution to a CI can only be justified by assuming it to be true "on the average."

A major application of growth models is to project current inventories into the future for alternative management scenarios (Lessard et al. 2001; Ledermann 2003). Most large-scale inventories use plot configurations with a spatial support plane considerably smaller than the usual concept of a "stand" as commonly represented by growth models. This area discrepancy introduces a source of error into competition measures computed from the inventory data that differ in configuration from the configuration used to collect the data for model calibration. Distance-dependent CIs calculated for individual trees on small sample plots have an additional source of error arising if trees just outside the plot are not included in the index. The consequence of their omission is a negative bias in distance-dependent measures that is larger for subject trees closer to the plot boundary.[2] Schreuder and Williams (1995) examined the loss of increment prediction accuracy when using distance-dependent indices on small plots. However, they did not consider bias due to proximity to plot boundaries. Methods for accommodating discrepancy in plot sizes between calibration and application data have been derived by Stage and Wykoff (1998) and Lappi (2005) for semi-distance-independent competition measures. Alternatively, some inventory projection models have attempted to avoid the problem by limiting their calibration data to the inventory data itself (Monserud and Sterba 1996; Lessard et al. 2001). However, if the plot size in the inventory design changes with tree size, there is still a bias in long-term projections because actual plot sizes are fixed at the start of the projection, but tree sizes increase. The effect of such a bias was demonstrated by Ledermann and Eckmüllner (2004) using an individual-tree growth simulator that utilizes a semi-distance-independent competition measure. To our knowledge, effect of inventory design on the optimal definition of competition measures has not been considered.

Both classes of plot-based competition measures are functions of the attributes of subject tree and competitor and of the distance separating them plus a source of random variation. The random component in tree-centered measures lies in the discrepancy between the unobservable area (and intensity) of spatial occupancy of each member of the pair and its mathematical representation in the CI. Specific parameters of the index are usually defined by maximizing correlation with increment of the subject tree. However, note that Lappi (2005) has shown that maximizing correlation may not be the best criterion. Congruently, the random component in a semi-distance-independent measure arises from the random location of the sampling point, tree attributes, and their relation to distance between the subject tree and the competitor.

All of the distance-dependent indices discussed by Ledermann and Stage (2001) are summations over the number of competitors. The subject tree attributes in these indices are only influential through ratios to the attributes of each competitor. They are intrinsically descriptors unique to the individual subject tree. In contrast, distance-independent indices include the subject tree in the summations on the same scale as its competitors. The index is, then, a characteristic of a particular sampling point that indicates the intensity of occupancy of the site to the extent that it can be represented by the selected tree attributes and the support plane of the sampling point.

Methods

Representation of effects of separation distance in competition measures is most easily considered in the context of point sampling. Sampling in the plane can be viewed from two equivalent concepts: plot sampling or point sampling (Grosenbaugh 1958; Stage and Rennie 1994). Plot sampling (with replacement) places a geometric figure—the plot—at a random point in the area being sampled. (In later discussion, the geometric figure will be assumed to be a circle, although

[2] Provision for measuring "off-plot" trees within the search radius is certainly possible but is not part of standard practice.

it can be any shape with a constant orientation relative to the point or tree.) Then trees located at points within the plot comprise the sample at that point. In contrast, point sampling places the same geometric figure around each tree. Then, trees in the sample are just those trees for which the figures cover that particular random sampling point. Either concept yields exactly the same list of trees associated with the sampling location, and the data can be compiled with the same expressions.[3] However, in the point-sampling view, the probability of the ith tree being selected by a random sampling point is proportional to the area of its figure (a_i), which can vary by design for trees of different attributes as in Bitterlich sampling with radii proportional to DBH.

The joint probability of any pair of trees being in the same sample is proportional to the area of overlap of their respective figures: $a_{ij} = a_i \cap a_j$, which also depends on the distance (d_{ij}) between the subject tree j and the competitor i. Then, for any additive CI summed over the n competitors to the jth subject tree is

$$[1] \qquad \mathrm{CI}_j = \sum_{i=1}^{n} c_{ij}\delta_i$$

where n is a random variable depending on the number of tree circles covering the sample point that is within the tree circle of the subject tree and c_{ij} is the marginal contribution of the ith competitor to the CI for the jth subject tree. The attributes of a single competitor c_{ij} in a CI may be values of the functions graphed by Ledermann and Stage (2001) or simply its DBH, its basal area, or its contribution of unity to tree density. For distance-dependent measures, δ_i equals unity if the competing tree i is observed and measured. Thus, the effect of their distance apart is incorporated in the value of c_{ij} and not in δ_i, which may be zero if the separation exceeds the maximum search radius for competing trees.

For semi-distance-independent measures, the roles of c_{ij} and δ_i are different than for distance-dependent indices. The value of c_{ij} for the competition measures we consider is just the attribute of the ith competitor, and δ_i is unity provided that the ith competitor and jth subject tree are both included in the same sample. Otherwise, δ_i is zero. Hence, the conditional probability of δ_i being unity for semi-distance-independent indices equals the area of overlap of the subject and competitor tree circles divided by the area of the subject tree circle. For example, if the competitor and subject tree are in opposite directions from the sample point (realization of the random event), then the joint probability is likely to be less than if competitor and subject tree are both in the same direction from the sample point. However, after the sample is drawn the competitor is either in the sample or not, and for that realization, its attribute is either included in the competition measure or not. But in a sample-based data set, there are as many realizations of the random process as there are subject trees in the data set. Hence, the mean effect of a semi-distance-independent measure is represented by the expected value of $c_{ij}\delta_i$.

The expectation of $c_{ij}\delta_i$ over repeated random sampling with replacement within a_j is

$$[2] \qquad E[c_{ij}\delta_i] = c_{ij}E[\delta_i] = \frac{c_{ij}a_{ij}}{a_j}$$

Thus, this effect of distance between subject tree and competitor represented by a_{ij} in the expected value of CI is only a function of plot radii and is not the function of distance defined by a distance-dependent index per se. However, by considering the expected value in eq. 2, we can compare the effective distance functions of different plot configurations and for the several classes of CIs. Let m be the number of competing trees defined by having tree circles intersecting or within the subject-tree circle ($a_{ij} > 0$). Because the subject tree is always included in the sample, the total number of sample trees at any point in the subject-tree circle is $n \le m + 1$ depending on the spatial pattern of tree locations. However, note that, because n may vary from point to point within the subject-tree circle, the expected value of CI_j is

$$[3] \qquad E[\mathrm{CI}_j] = c_{jj} + \sum_{i=1}^{m} c_{ij}\left(\frac{a_{ij}}{a_j}\right)$$

For example, if CI_j is basal area per unit area estimated for a subject tree selected by a Bitterlich sample, c_{ij} of eq. 2 equals the basal area factor (BAF) for j and all $i = 1, 2, \ldots, m$ competitors, and $\mathrm{CI}_j = n \times \mathrm{BAF}$:

$$[4] \qquad E[\mathrm{CI}_j] = \mathrm{BAF}\left[1 + \sum_{i=1}^{m}\left(\frac{a_{ij}}{a_j}\right)\right]$$

Our methods can be extended to basal area in larger trees (BAL; Wykoff 1990) by defining c_{ij} in eq. 3 as BAF if $\mathrm{DBH}_i > \mathrm{DBH}_j$ and zero otherwise.

The area of overlap (a_{ij}) of two circles is a function of the distance (d_{ij}) between their centers and their radii, which in our case is the radius of the subject tree circle, r_j, and the competitor tree circle, r_i. The circles intersect only for distances between the difference and the sum of the radii of the two circles. For a smaller circle totally within a larger circle (distance less than the difference of their radii), the overlap is the full area of the smaller circle. One form of the equation is provided by Stoyan and Stoyan (1994, Appendix K). Although derived through rather messy algebra and trigonometry, the area is just the sum of areas of the sectors of the sampling circles minus the areas of the four right triangles bounded by the circle centers and the intersections of the two circles (Fig. 1).

Let r_i be the radius of circle i; r_j be the radius of circle j; d_{ij} be the distance between centers of circles i and j, for $(r_i - r_j) < d_{ij} < (r_i + r_j)$ and $r_i > r_j$; α be the angle (radians) between the line connecting centers and the line from center of circle i to the intersection of the two circles; and β be the angle (radians) between the line connecting centers and the

[3] Modelling of periodic diameter increment as a function of initial diameter from Bitterlich samples at a subsequent point in time requires a correction for bias arising from the fact that faster growing trees have a greater probability of being included in the sample even though their initial diameters may be equal (Lappi and Bailey 1987). Alternatively, the field procedure may be designed so that trees sampled for increments are selected with probability proportional to their initial diameter rather than their subsequent diameter.

Fig. 1. Graphical representation of the intersection area a_{ij} of two circles.

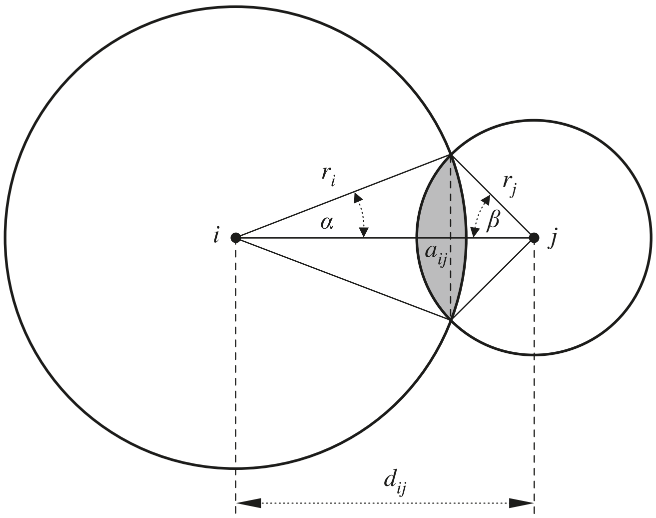
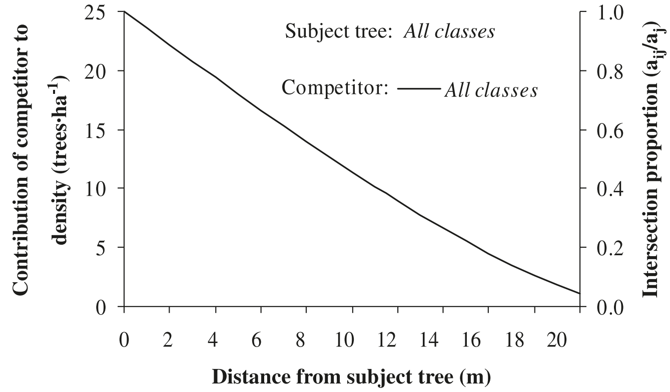


Fig. 2. Contribution of a competitor to the semi-distance-independent measure of density averaged over repeated samples from plots of 0.04 ha (left-hand axis) or as proportion of plot area (right-hand axis).



line from center of circle j to the intersection of the two circles. Then:

$$[5] \qquad \alpha = \arccos\left(\frac{d_{ij}^2 + r_i^2 - r_j^2}{2d_{ij}r_i}\right)$$

$$[6] \qquad \beta = \arccos\left(\frac{d_{ij}^2 + r_j^2 - r_i^2}{2d_{ij}r_j}\right)$$

and the areas of the two sectors are αr_i^2 and βr_j^2. The area of the two right triangles inscribed in the larger sector is $r_i^2 \sin(\alpha)\cos(\alpha)$ and of the two in the smaller sector is $r_j^2 \sin(\beta)\cos(\beta)$. Thus, the intersection area a_{ij} of the two circles is

$$[7] \qquad a_{ij} = r_i^2[\alpha - \sin(\alpha)\cos(\alpha)] + r_j^2[\beta - \sin(\beta)\cos(\beta)]$$

or:

$$[8] \qquad a_{ij} = r_i^2\left[\alpha - \frac{\sin(2\alpha)}{2}\right] + r_j^2\left[\beta - \frac{\sin(2\beta)}{2}\right]$$

The radii, r_i and r_j, are equal for all tree sizes if a fixed-area plot is used. In case of Bitterlich samples, r_i and r_j are calculated as follows:

$$[9] \qquad r_{i,j} = \frac{50\mathrm{DBH}_{i,j}}{\sqrt{\mathrm{BAF}}}$$

where r_i and r_j are the limiting distances in metres of sample trees i and j, DBH_i and DBH_j are the corresponding diameters at breast height (1.3 m) in metres, and BAF is the basal area factor in square metres per hectare. Overlap as a proportion of the subject tree area (a_j) is shown on the right-hand axis of Fig. 2 for equal radii for each member of the pair.

Semi-distance-independent competition measures

The distance functions of four semi-distance-independent CIs will be displayed: tree density (trees·ha^{-1}), sum of diameters (m·ha^{-1}), and basal area (m^2·ha^{-1}); each is measured at the spatial resolution of the single plot. Although basal area per hectare has been the most common distance-independent index, we also show an index derived from a linear combination of these three moments of the diameter distribution: tree-area ratio (TAR) of Chisman and Schumacher (1940).[4] The TAR for loblolly pine (*Pinus taeda* L.) for diameters in meters and area in hectares is

$$[10] \qquad \mathrm{TAR} = 0.0000194N + 0.001065\sum_{k=1}^{N}\mathrm{DBH}_k + 0.01677\sum_{k=1}^{N}\mathrm{DBH}_k^2$$

The individual terms are summations per hectare. Then, TAR expresses the proportion of the hectare that would be allocated to the total trees in a "normal" (fully stocked) stand of *Pinus taeda*. In calculating the expectation of the contribution of the ith tree to TAR for the jth subject tree under random sampling, we sum the expected value (eq. 2) for each of the three terms in eq. 10:

$$[11] \qquad E(\mathrm{TAR}_{ij}) = (0.0000194 + 0.001065\mathrm{DBH}_i + 0.01677\mathrm{DBH}_i^2)\frac{a_{ij}}{a_j}$$

Results

Two plot configurations are illustrated: a fixed-area plot of 0.04 ha (11.28 m radius) for all tree sizes (Figs. 2 and 3), and a Bitterlich sample with BAF of 6 m^2·ha^{-1}·tree^{-1} (Figs. 4, 5, 6, and 7). Other plot sizes and BAFs merely rescale the distance axes of the figures. Dimensions of the trees represented in the calculations of Ledermann and

[4] In the 1960s, David Bruce plotted logarithms of three popular distance-independent competition measures: tree-area ratio (TAR), crown competition factor (CCF; Krajicek et al. 1961) and stand density index (SDI; Reineke 1933) against the logarithm of tree DBH. Although the first two are linear combinations of sums of number, diameter, and diameter squared, their curves over the usual range of diameters are very nearly linear and parallel to the SDI line.

Fig. 3. Contribution of a competitor to the semi-distance-independent measures of sum of diameters (upper panel), basal area (middle panel), and tree-area ratio (lower panel) averaged over repeated samples from plots of 0.04 ha.

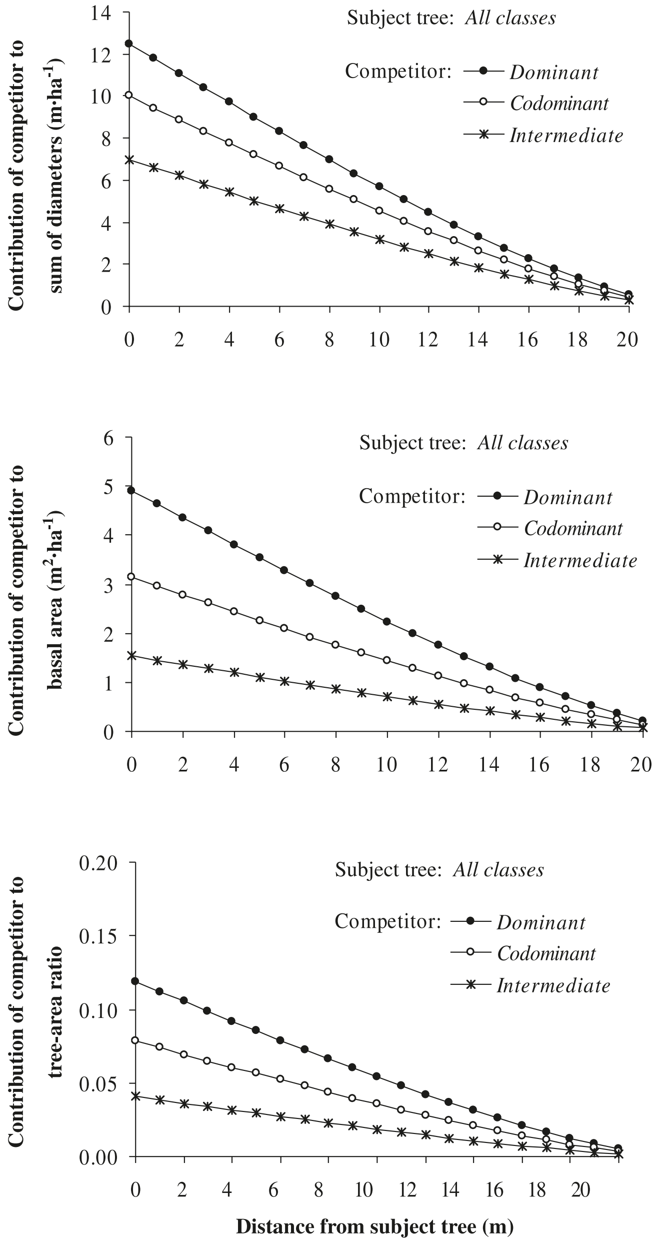
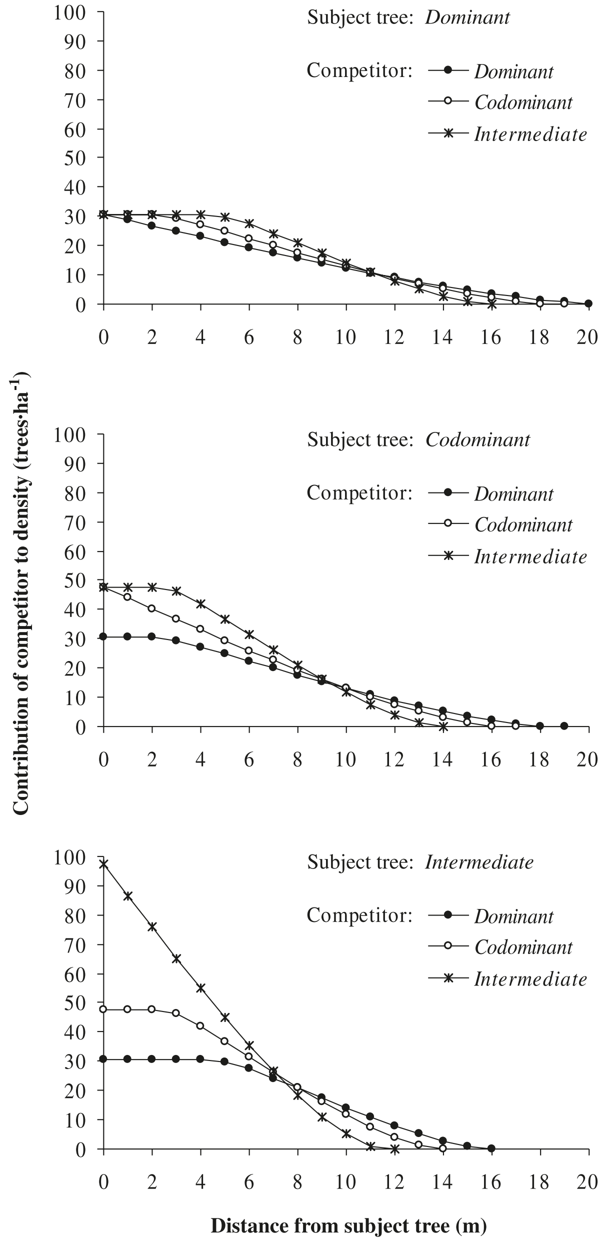


Fig. 4. Contribution of a competitor to the semi-distance-independent measure of density averaged over repeated Bitterlich samples using a BAF of 6 $m^2 \cdot ha^{-1} \cdot tree^{-1}$ for dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel).



Stage (2001) are listed in Table 1, although the competition measures illustrated in this paper only depend on DBH.

Distance effects differ markedly among combinations of the semi-distance-independent competition variables and sampling designs. Ranking of crown class effects changes, and some curves cross.

Tree density on fixed-area plots shows no discrimination among crown classes of either the subject tree or the competitor (Fig. 2). Unfortunately, the tree-density measure was chosen by Lappi (2005) to illustrate effects of sampling error of competition measures on growth-model coefficients.

An even more serious deficiency of the tree-density measure (Fig. 4) and the sum of diameters measure (Fig. 5) from Bitterlich samples is the reversal of the relative contributions of the dominance classes. Sum of diameters, basal area, and TAR calculated as semi-distance-independent competition measures from fixed-area plots show considerable discrimination among crown classes of the competitor but not among the crown classes of the subject tree (Fig. 3).

TAR calculated for trees in the Bitterlich samples is a linear combination of the curves of Figs. 4, 5, and 6. For trees in the range of diameters shown, the curves of TAR (Fig. 7) are very nearly proportional to the basal area curves (Fig. 6).

Discussion

All the distance-dependent indices displayed by Leder-

Fig. 5. Contribution of a competitor to the semi-distance-independent measure of sum of diameters averaged over repeated Bitterlich samples using a BAF of 6 $m^2 \cdot ha^{-1} \cdot tree^{-1}$ for dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel).

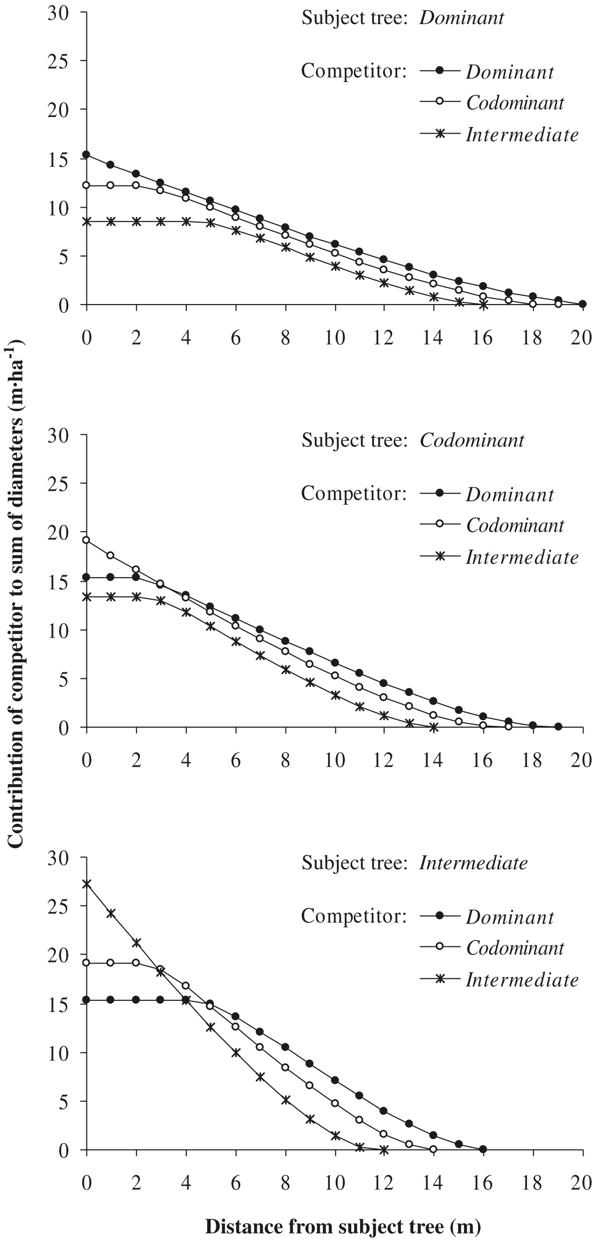
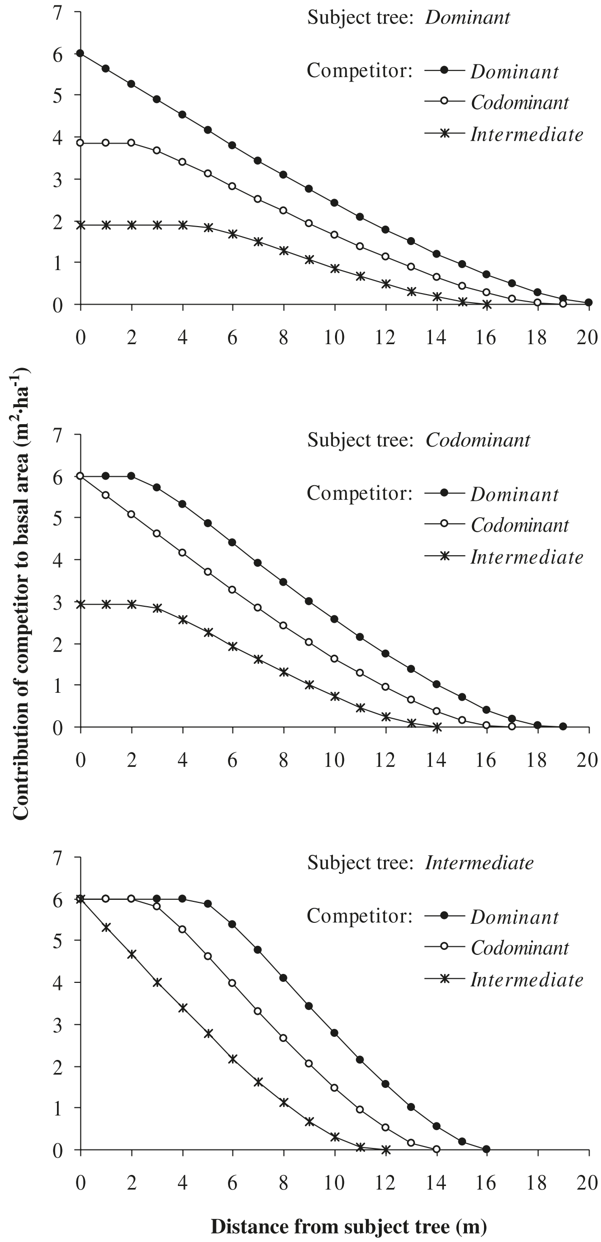


Fig. 6. Contribution of a competitor to the semi-distance-independent measure of basal area averaged over repeated Bitterlich samples using a BAF of 6 $m^2 \cdot ha^{-1} \cdot tree^{-1}$ for dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel).



mann and Stage (2001) show that competition from a tree of lower crown class contributes less to the index than competition from more dominant crown-class trees, and generally, the differences are larger for less dominant subject trees. Moreover, all the indices except the crown volume index according to Biging and Dobbertin (1992) decline with increasing distance. For comparison of our results to distance-dependent indices, we reproduce figures showing the distance effects for two indices that capture the consensus of indices shown by Ledermann and Stage (2001). Bella (1971) uses only diameters of the subject and competitor pair, whereas Pretzsch (1995) uses crown relations of the pair (Figs. 8 and 9). When the expected values of distance-dependent indices are calculated over repeated sampling with 0.04 ha plots, the curves they show would be further reduced by multiplying by the factor of the right-hand axis of Fig. 2. It is this reduction that biases the distance-dependent measures relative to their whole-stand counterparts.

Of all the combinations of variables and plot design we have evaluated, basal area from a Bitterlich sample with BAF of 6 $m^2 \cdot ha^{-1} \cdot tree^{-1}$ has a curve form that most closely corresponds to the consensus of distance-dependent measures. They are nearly proportional to the Bella (1971) and Pretzsch (1995) distance-dependent indices but spread over a somewhat longer distance (Figs. 8 and 9). More recently, Kokkila et al. (2006) have proposed a curve form in which

Fig. 7. Contribution of a competitor to the semi-distance-independent measure of tree-area ratio averaged over repeated Bitterlich samples using a BAF of 6 $m^2 \cdot ha^{-1} \cdot tree^{-1}$ for dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel).

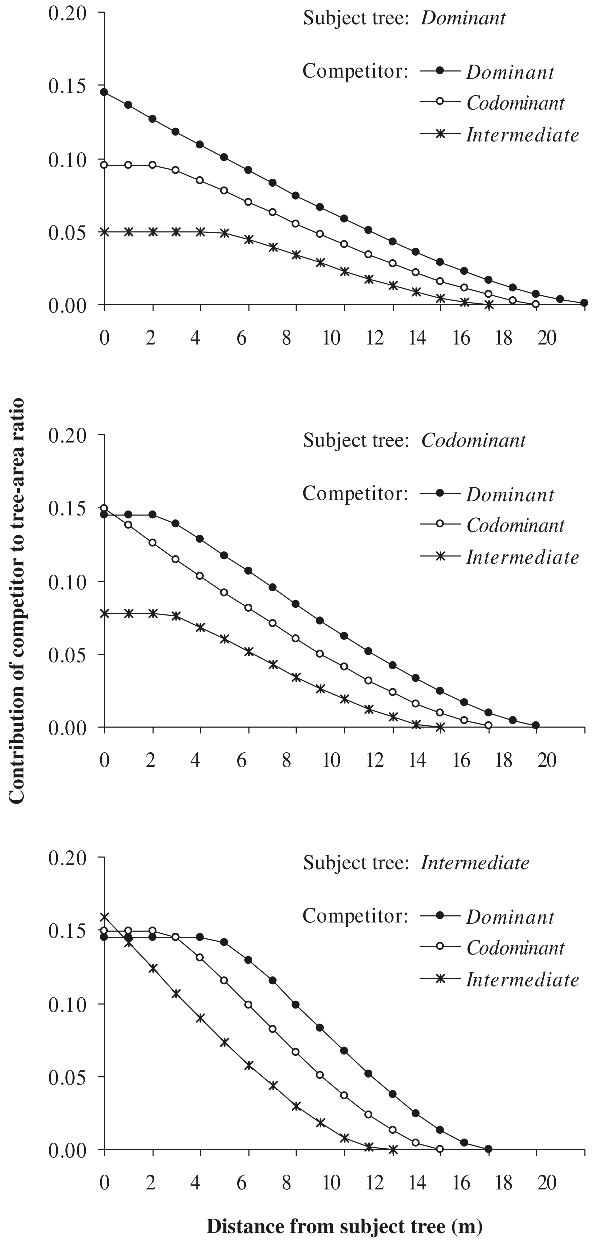
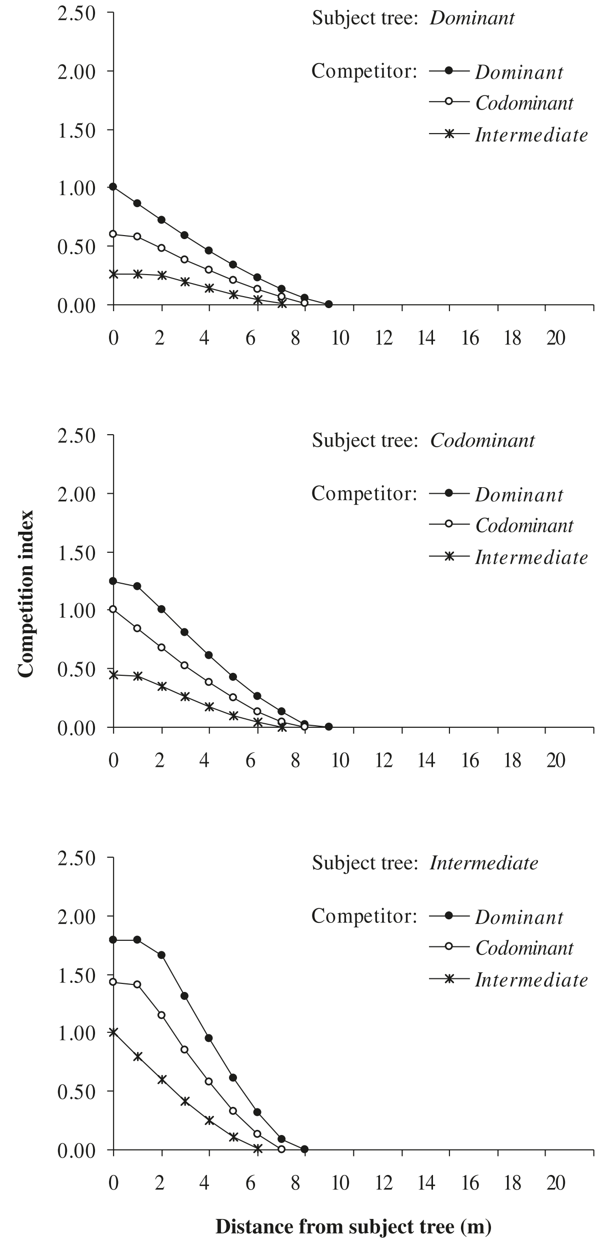


Fig. 8. Competition index according to Bella (1971) as calculated by Ledermann and Stage (2001) for combinations of dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel) and competitors of three typical crown classes.



competition is a maximum up to some distance from the subject tree then decreases to zero at a distance beyond which the competitor has no effect (0.4 m and 7.98 m, respectively, in their simulations), which is very similar to most of the curves for the Bitterlich sample design. Thus, we conclude that total basal area or some similar function of tree size, averaged over subject trees in a Bitterlich sample, should provide effective measures of competition for modelling increment of individual trees.

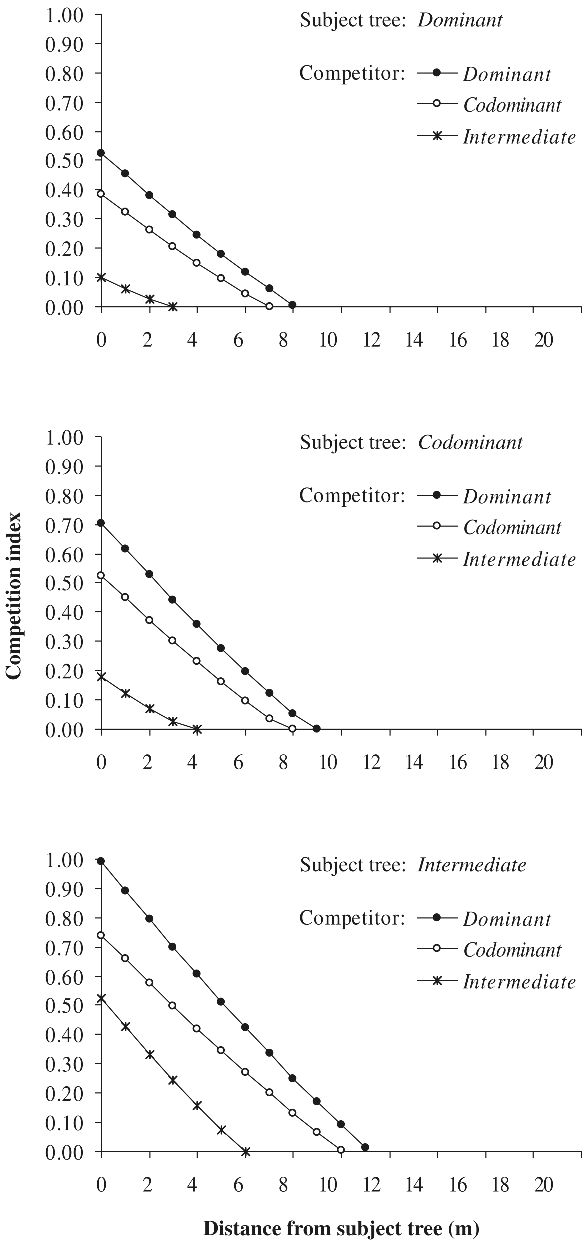
The empirical studies by Biging and Dobbertin (1995) and Windhager (1999) seem to support our conclusion. The objective of both studies was to compare the predictive capability of selected distance-independent CIs against competition measures that use tree locations. The CIs were used in conjunction with growth models of diameter squared and logarithm of diameter squared, respectively. And the results of both studies were rather unexpected. Biging and Dobbertin (1995) reported that some distance-independent relative size CIs performed as well or even better than the best distance-dependent competition measures based on their reduction in mean square error; in the analysis by Windhager (1999), the distance-independent index BAL performed best among all CIs that were evaluated. A possible explanation might be the fact that both studies were performed on rather small plots, e.g., 0.04–0.08 ha in the study by Biging and Dobbertin (1995). These plot sizes correspond rather well to the plot sizes (or plot size equivalents of Bitterlich samples) that we used in our analysis to demon-

Table 1. Tree dimensions for example trees used in calculation of competition indices.

Dimension*	Dominant	Codominant	Intermediate
DBH (cm)	50	40	28
Height (m)	35	33	26
Height to live crown (m)	20	20	17
Crown length (m)	15	13	9
Crown ratio	0.43	0.39	0.35
Crown width (m)	4.40	3.80	3.20
Crown width OGT (m)	9.11	7.90	6.28

*DBH, diameter at breast height; OGT, open-grown trees according to Hasenauer (1997).

Fig. 9. Competition index according to Pretzsch (1995) as calculated by Ledermann and Stage (2001) for combinations of dominant (upper panel), codominant (middle panel), and intermediate subject trees (lower panel) and competitors of three typical crown classes.



strate the similarities of basal area distance effects in Bitterlich samples to the distance effects implicit in distance-dependent indices.

Summary

Comparisons of effects of competitor spacing in semi-distance-independent indices of competition show that some combinations of competition variables and sample plot designs can generate CIs that are very similar to the consensus of distance-dependent indices, e.g., basal area per unit area or TAR estimated from Bitterlich samples (compare Figs. 6 and 7 with Figs. 8 and 9). However, other combinations of competition variables and plot design produce anomalous distance and (or) size effects.

The results show that modellers of growth and designers of inventory plot configuration should consider the interaction of these two parts of their system if they are intended to be used for stand growth analysis or inventory projection. Comparisons between these two classes of CIs suggest that optimum plot sizes for estimating semi-distance-independent CIs are smaller than plot sizes commonly used for estimating stand volume. In particular, the similarities of basal area distance effects, as measured by Bitterlich samples, to the effects implicit in the collection of distance-dependent indices suggest that growth models using basal area related competition variables (i.e., as semi-distance-independent indices) are able to capture the effects of tree spacing without the necessity of stem mapping. Thus, we believe that the results of this study provide the theoretical basis behind the findings of Biging and Dobbertin (1995) and Windhager (1999). However, more specific and concerted analyses remain to be done to answer the question of whether variation between actual space occupancy and that assumed to be captured by sophisticated measures of crowns and spacing in some of the distance-dependent measures explain more or less variation in actual predictions of tree increment than does the point to point variation in semi-distance-independent basal area measured from Bitterlich samples.

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References

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.

Casper, B.B., Shenk, H.J., and Jackson, R.B. 2003. Defining a plant's belowground zone of influence. Ecology, **84**: 2313–2321. doi:10.1890/02-0287.

Chisman, H.H., and Schumacher, F.X. 1940. On the tree-area ratio and certain of its applications. J. For. **38**: 311–317.

Curtis, J.D. 1964. Roots of a ponderosa pine. USDA For. Serv. Intermountain For. Range Exp. Stn. Res. Pap. INT-9.

Grosenbaugh, L.R. 1958. Point-sampling and line-sampling: probability theory, geometric implications, synthesis. USDA For. Serv. South. For. Stn. Occas. Pap. 160.

Hasenauer, H. 1997. Dimensional relationships of open-grown trees in Austria. For. Ecol. Manage. **96**: 197–206. doi:10.1016/S0378-1127(97)00057-1.

Kokkila, T., Mäkelä, A., and Franc, A. 2006. Comparison of distance-dependent and distance-independent stand growth models—is perfect aggregation possible? For. Sci. **52**: 623–635.

Krajicek, J.E., Brinkmann, K.E., and Gingrich, S.F. 1961. Crown competition—a measure of density. For. Sci. **7**: 35–42.

Lappi, J. 2005. Plot size related measurement error bias in tree growth models. Can. J. For. Res. **35**: 1031–1040. doi:10.1139/x05-019.

Lappi, J., and Bailey, R.L. 1987. Estimation of diameter increment function or other tree relations using angle-count samples. For. Sci. **33**: 725–739.

Ledermann, T. 2003. Implementierung eines Waldwachstumsmodells zur Nachhaltskontrolle. Ph.D. thesis, University of Natural Resources and Applied Life Sciences (BOKU), Vienna.

Ledermann, T., and Eckmüllner, O. 2004. A method to attain uniform resolution of the competition variable Basal-Area-in-Larger Trees (BAL) during forest growth projections of small plots. Ecol. Modell. **171**: 195–206. doi:10.1016/j.ecolmodel.2003.08.005.

Ledermann, T., and Stage, A.R. 2001. Effects of competitor spacing in individual-tree indices of competition. Can. J. For. Res. **31**: 2143–2150. doi:10.1139/cjfr-31-12-2143.

Lessard, V.C., McRoberts, R.E., and Holdaway, M.R. 2001. Diameter growth models using Minnesota forest inventory and analysis data. For. Sci. **47**: 301–310.

Monserud, R.A., and Sterba, H. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manage. **80**: 57–80. doi:10.1016/0378-1127(95)03638-5.

Muth, C.C., and Bazzaz, F.A. 2003. Tree canopy displacement and neighborhood interactions. Can. J. For. Res. **33**: 1323–1330. doi:10.1139/x03-045.

Pretzsch, H. 1995. Zum Einfluß des Baumverteilungsmusters auf den Bestandeszuwachs. Allg. Forst Jagdztg. **166**: 190–201.

Reineke, L.H. 1933. Perfecting a stand density index for even-aged forests. J. Agric. Res. **46**: 627–638.

Schreuder, H.T., and Williams, M.S. 1995. Assessing measures of tree competition using fixed-area, variable radius, and horizontal-line sampling. Can. J. For. Res. **25**: 1578–1582. doi:10.1139/x95-172.

Stage, A.R., and Rennie, J.C. 1994. Fixed-radius plots or variable-radius plots? J. For. **92**: 20–24.

Stage, A.R., and Wykoff, W.R. 1998. Adapting distance-independent forest growth models to represent spatial variability: effects of sampling design on model coefficients. For. Sci. **44**: 224–238.

Stoyan, D., and Stoyan, H. 1994. Fractals, random shapes and point fields: methods of geometrical statistics. John Wiley & Sons, New York.

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

Windhager, M. 1999. Vergleich von distanzabhängigen und unabhängigen konkurrenzbeschreibenden Faktoren und ihre Auswirkung auf den Grundflächenzuwachs. Allg. Forst Jagdztg. **170**: 133–136.

Wykoff, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For. Sci. **36**: 1077–1104.