Research paper

Distance-Dependent Competition Measures for Individual Tree Growth on a Taiwania Plantation in the Liuguei Area

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【Summary】

Competition among trees within a stand occurs when resource availability is insufficient to meet the total requirements of a tree population for optimal growth. Six distance-dependent competition measures that incorporate tree sizes and distances from neighbors, evaluated over varying competition zones, were used to assess the competition stress among trees. A reduction in the mean square error relative to the no-competition index involved was used to judge the performance of each competition index for 3 growth components (i.e., diameter at breast height (DBH), basal area, and volume). The results showed that except for Martin-Ek, the other competition indices investigated were significantly correlated with periodic growth in the 3 growth components ($p < 0.0001$). The performance of the competition indices in predicting 5-yr growth indicated that the inclusion of competition indices in the growth-prediction model reduced the mean square error from 14% for volume growth to 17% for DBH growth. Moreover, expanding the search zones in the Hegyi competition index was found to have slightly improved the ability to estimate competition effects.

Key words: competition index, individual tree growth, distance-dependent tree model.

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研究報告

距離相依競爭指數應用在六龜地區台灣杉單木生長之研究

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摘　要

人工林林分生長樹冠鬱閉後，為爭取林木生長所需之各項資源時，林木彼此間開始競爭有限之環境資源。林木間之競爭作用視主林木大小，競爭木數量、大小和主林木與競爭木間之距離會承受不同之競爭壓力。本研究使用距離相依之競爭指數來衡量各株單木承受之競爭壓力。使用Bella, Staebler, Hegyi, Martin-Ek, Alemdag和樹冠體積比六種競爭指數公式，並配合競爭木三種不同半徑之搜尋方式，計算台灣杉林分內各林木之競爭指數，以表示各林木在生長過程中遭遇競爭壓力之程度。此外，使用台灣杉林木5年胸徑、斷面積和材積之生長資料配置林木單株生長式，評估在單株生長式中納入競爭指數之效果，以瞭解競爭指標對林木生長之貢獻。研究結果顯示5年單木生長量和各競爭指數除了Martin-Ek外，皆呈現極顯著之相關($p < 0.0001$)。初步資料分析結果顯示在台灣杉單木生長配置中納入競爭指數會減少模式配置之MSE，而增加模式之配置效果。單株生長式中納入競爭指數之效果在不同之林木屬性間有所差異。個案研究顯示納入競爭指數株後之單株生長式會比原有之生長式對林木定期生長之預測能力提昇14~17%。

關鍵詞：競爭指數、林木單木生長、距離相依生長模式。

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INTRODUCTION

Competition among trees within a population occurs when adjacent trees are forced to share limited resources in a restricted area (Tilman 1982, Shainsky and Radosevich 1992). Due to the competition that occurs, trees in populations usually exhibit large variations in growth (Harper 1977). Understanding this variation in growth is central to forest ecology because of its significance to the forest structure, mortality, and biomass (Peet and Christensen 1987, Nishimura et al. 2002, Coomes and Allen 2007a, b).

In studying forest growth and yields, tree competition can be investigated on a stand basis or individual tree basis (Bella 1971). Variations in tree growth inherent from competition based on the stand level are evaluated from a range of stand densities, expressed as the number of trees or basal area per area unit, and calculated as tree averages (Clutter et al. 1983). While useful and practical, such averages tend to obscure cause-effect relationships between trees and growth. In order to gain better insights into basic tree-growth relationships, attention has shifted to competition on an individual-tree basis (Bella 1971, Perot et al. 2010).

The main problem in analyzing individual tree growth arises from the difficulty in measuring and evaluating competition from neighboring trees. In the past, different approaches were used to evaluate the effects of competition on individual tree growth. A competition measurement or index for an individual tree is defined as "any index that estimates the total competition from adjacent trees thought to be affecting the growth of the subject tree" (Biging and Dobbertin 1992).

Based on the relationship between competition and spatial distance, competition measurements (indices) are categorized as distance-independent and -dependent ones (Munro 1974). For the former, the competitive status is expressed as ratios of various trees' individual sizes (e.g., diameter, basal area, or height) to the average in the stand (Glover and Hool 1979, Daniels et al. 1986). While no tree spatial information is explicitly involved in the formulation, this type of index does quantify the relative size position of an individual tree in a stand that may be highly related to its competitive position and was found to be useful in mortality prediction studies (Daniels et al. 1986).

In distance-dependent competition measurements, in addition to individual tree size, a tree's spatial information is involved to estimate the competitive status of an individual tree. Several concepts are used to calculate competition indices, including point density (Spurr 1962), the area of influence overlap (Bella 1971, Adlard 1974), a weighted size-ratio distance (Hegyi 1974, Martin and Ek 1984), the area potentially available or polygons (Brown 1965, Pelz 1978), and the growing space (Holmes and Reed 1991, Biging and Dobbertin 1992). Size-ratio indices calculate sums of ratios of subject tree dimensions (e.g., diameter at breast height (DBH), total height, and basal area) to competitor tree dimensions, and are often weighted by distances of the subject tree to its competitors.

For influence-zone overlap indices, an area of an influence zone related to the tree size around each tree is calculated; then a sum of the ratio of the area of overlap between the influence zone of subject tree *i* and the influence zone of competitor *j* to the influence zone of the subject tree is used, weighted by the DBH ratio, as a competition index. In growing-space indices, the growing space of each tree is described as a polygon to represent the area potentially available to each tree within the stand. The area is determined either by positioning perpendicular bisectors at points half the distance to neighboring trees (Brown 1965) or at a point proportional to the relative dimensions of the subject tree and competitors (Pelz 1978), and a polygon is formed by connecting the intersections of the perpendicular bisectors.

Identifying competitors of a subject tree is a prerequisite for calculating the competition indices. Generally 3 methods widely used to identify the search radius for competitors are (a) a fixed radius, (b) crown overlap and, (c) DBH angle gauge or point tree samples (Biging and Dobbertin 1992). In the case of a fixed radius, based on the center of the subject tree, competitors are found by the circle with a radius of 10 feet (3.04 m) (Hegyi 1974). In the case of crown overlap, trees the crowns of which overlap with the subject tree crown are chosen as competitors (Bella 1971). Angle-gauge methods use angles based on either the DBH or tree height of neighboring trees and the subject tree. In the former, trees with a DBH greater than the specified angle are chosen as competitors (Alemdag 1978). In the latter, trees the heights of which surpass a certain critical height determined by the angle and distance to a subject tree are selected as competitors (Biging and Dobbertin 1992).

The objective of this study was to compare the predictive capability of selected distance-dependent competition indices used in conjunction with an individual growth model of DBH, basal area, and volume of Taiwania plantations. It is expected that through this study, the most relevant competition index will be used to subsequently build up an individual tree growth simulation model for Taiwania plantations.

MATERIALS AND METHODS

Data for this study were collected in permanent plots of Taiwania (*Taiwania cryptomerioides*) plantations in the Liuguei Experimental Forest (southwestern Taiwan) of the Taiwan Forestry Research Institute. In order to encompass a variety of site conditions, plots of different ages, sites, and management regimes were used to investigate the competition effect in Taiwania plantations. On each plot, trees were tagged, the stems were mapped, and the DBH, total height, and crown length were recorded following different survey periods. The 5-yr diameter and basal area growth data were obtained from measurements in different survey periods. Twenty-five plots, aged 20~38 yr, located in compartments 3, 10, 12, 14, 18, and 20 including thinned and no-thinning practices were used to establish the individual-tree competition model for Taiwania plantations.

At each plot, individual trees were treated as observations in calculating the competition index for each tree. In this study, distance-dependent competition indices utilizing the size-ratio, influence-overlap, and growing-space approaches in the formulation were calculated. The distance-dependent competition indices and their formulas used in this study are listed in Table 1. Complete descriptions of these formulas can be found in Wang et al. (2004). Four types of search radii were used to determine competitors for subject trees (Table 2).

All competition indices investigated in this study were evaluated in conjunction with growth models of DBH, basal area, and volume for Taiwania plantations in the Liuguei Experimental Forest. The goodness of fit of the regression models was determined using the mean squared error (MSE), percentage of MSE, and R^2 to assess the validity of the competition indices.

Table 1. Distance-dependent competition indices (formulas) investigated

Variable name	Variable abbreviation	Equation	Index type and weighting
Staebler	S	$\Sigma\,(OLij \times CRi)/2$	influence zone overlap
Bella	B	$\Sigma\,(OAij/Zi) \times (Dj/Di)$	influence zone overlap
Hegyi	H	$\Sigma\,Dj/Di \times [1/(Lij+1)]$	size-ratio
Martin-Ek	ME	$\Sigma\,Dj/Di \times EXP\,(16 \times Lij/(Di+Dj))$	size-ratio
Alemdag	A	$\Sigma\,\{\pi[Lij \times Di/(Di+Dj)]\}^2 \times [(Dj/Lij)/\Sigma\,(Dj/Lij)]$	growing space
Crown volume	CV	$\Sigma\,(CVj/CVi) \times [1/(Lij+1)]$	size-ratio

Di, diameter at breast height (DBH) of subject tree *i* (cm); Dj, DBH of competitor trees ($j \neq i$) (cm); Lij: distance of subject tree *i* to competitor *j* (m); CVi: crown volume of subject tree *i* (m^3); CVj: crown volume of competitor tree *j* (m^3); OAij: crown overlap (or influence zone overlap) between subject tree *i* and competitor tree *j* (m^2); Zi: crown projection area (or influence zone) of subject tree *i* (m^2); OLij: distance of crown projection overlap between subject tree *i* and competitor tree *j* (m); CRi: crown radius of subject tree *i* (m).

Table 2. Competition index search radii used

Variable name	Tree is included as a competitor if:
D1	$Lij < (Di + Dj)/8$
D2	$Lij < (Di + Dj)/6$
D3	$Lij < (Di + Dj)/4$
H1	$Lij < (Hj/\sqrt{3})$

Di, diameter at breast height (DBH) of subject tree *i* (cm); Dj: DBH of competitor trees ($j \neq i$) (cm); Lij: distance of subject tree *i* to competitor tree *j* (m); Hj: height of competitor trees ($j \neq i$) (m).

RESULTS AND DISCUSSION

Growth of forest trees depends on their ability to compete for potentially limited resources such as moisture, nutrients, and light. Partitioning of a resource for which neighboring individuals compete depends on the type of resource and whether the competition is mediated by depletion or preemption of the resource (Nord-Larsen et al. 2006). Usually, 3 types of competitions exist. Completely symmetrical competition occurs when contested resources are divided equally among competitors irrespective of their size, whereas size-symmetrical competition occurs when uptake of contested resources is proportional to size. Finally, completely asymmetrical competition involves 1-sided interactions in which the few largest individuals receive all contested resources leaving nothing for their smaller competitors (Brand and Magnussen 1988, Schwinning and Weiner 1998). In forest stands, competition among individual trees involves competition for several resources; therefore, the resulting interactions are somewhere on a continuum in which completely symmetrical and completely asymmetrical competition form the extremes. The competition indices examined in the studies mentioned above belong to size-symmetrical or completely symmetrical competition.

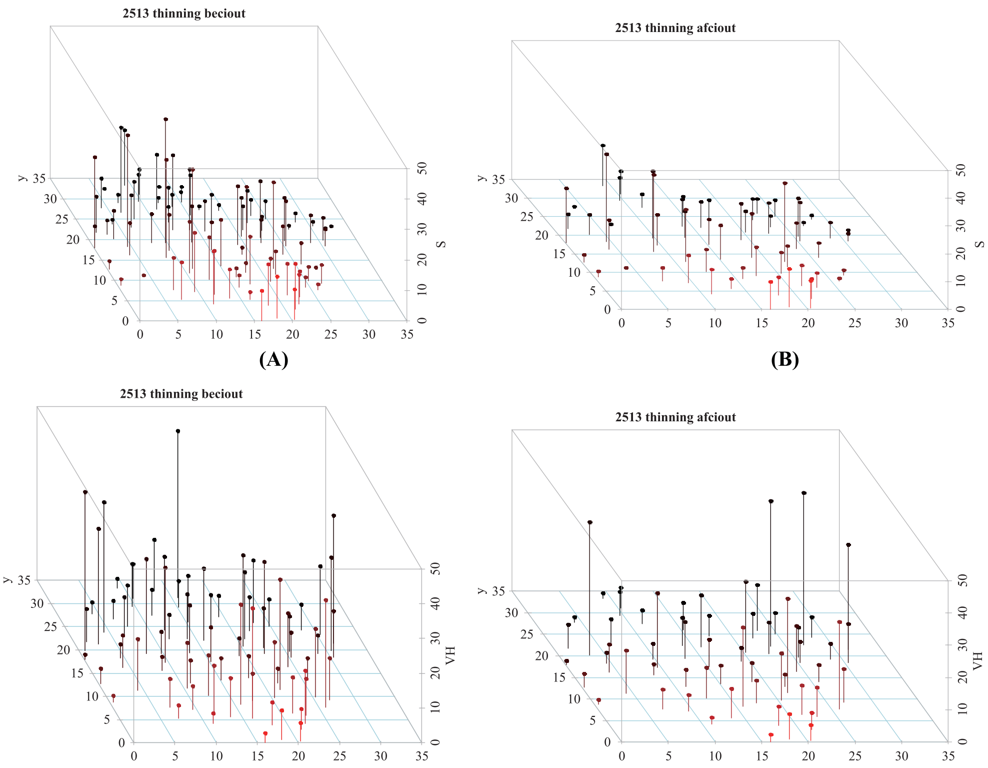
Variables of size dimensions of subject trees and assumed competitors and distances between them are often used to calculate the competition indices using the formulas. Values of competition indices for each individual tree depend on the mathematical formulation of relationships between the variables chosen and on the method used to define neighboring trees as competitors. These 2 factors are mentioned by a 2-part nomenclature where the former is referred as the CI-formula and the latter is the CI-search radius (Biging and Dobbertin 1992). In this study, based on the CI-formula and CI-search radius, 12 competition indices were computed.

In the search for competitors with the size-ratio approach, any tree surrounded by a subject tree is considered to be a competitor if the distance is less than the sum of their DBHs (expressed in centimeters x 100) divided by 8, 6, and 4. No competition radius is used for the influence-overlap indices because only those trees exhibiting crown overlap with a subject tree crown are considered to be competitors. In the height-angle method, an angle from the base of the subject tree using 60° from the horizontal is used to determine competitors. In practice, this means that for a given tree to be regarded as a competitor, its distance from the subject tree has to be $< 1/\sqrt{3}$ of its own height (Biging and Dobbertin 1995). The competition search radii used in this study are listed in Table 2.

Size-ratio indices calculate the sum of the ratios of subject tree dimensions to competitor tree dimensions. Size-ratio competition indices are often weighted by distances of a subject tree to its competitors so that for a given size, more competition is exerted as distances decrease from the subject to competitor trees. In this study, several size-ratio competition indices were investigated. They included Hegyi's (1974) DBH-ratio index (H), Martin and Ek's (1984) exponential weighting scheme for relative diameters (ME), and Alemdag's potentially available growing-space index (A).

For computation of distance-dependent competition indices, plot-edge bias control is necessary when those indices are calculated from plot sample data and potential competitors lie outside of the sample plot. Without the plot-edge bias control, biased estimates of the true competition measures are possible (Martin et al. 1977). In this study, under the assumption that the underlying spatial pattern of forest trees outside the plot was the same as that of trees within the plot, a method proposed by Yang and Wang (1987) was used to control plot-edge bias to obtain an unbiased estimator of the true competition of each subject tree for the plot data.

A comparison of the thinning effect on the competition indices showed that the overall competition stress suffered for all trees was affected by the stand density. Before thinning, a higher overall value was found for each competition index; however, the overall competition stress became less after thinning (Fig. 1). Moreover, a *t*-test of changes in competition indices caused by thinning showed that a very significant change occurred in the competition stress for individual trees by thinning. For those competition indices measuring the growth space for a subject tree, the subject



(A) (B) (C) (D)

Fig. 1. Spatial distribution for the competition index of Staebler before thinning (A), after thinning (B), crown volume before thinning (C), and crown volume after thinning (D) in a given stand.

tree became more vigorous after thinning, and those measuring the growth space of competitors indicated that the subject suffered less competition stress after thinning (Table 3).

The 5-yr growth increments in DBH, basal area, and volume used in this study are shown in Fig. 2. To evaluate the contributions of competition indices to individual tree growth, the consistency of the empirical competition indices with their theoretical relationships had to be checked (Daniels et al. 1986). All indices showed a significant consistency in correlations with 5-yr increments in DBH, basal area, and volume (Table 4). The sign of the correlation coefficient depends on the competition index used. As the Staebler, Bella, and Alemdag indices focused on measuring the subject tree's influence zone or growing space, a positive correlation with tree growth was shown. However, for the Hegyi and Martin-Ek indices, negative correlations existed with crown volumes because competitors' growing space was measured instead. Among these indices, the Staebler index was not significantly correlated with the DBH increment ($\alpha = 5\%$), but was significantly correlated with both the basal area and volume increments ($p < 0.0001$). The Bella index was not correlated with any of the 3 attribute increments (Table 4). Moreover, the wider radius used in determining competitors resulted in the higher correlation because more competitors were involved (Table 4). This finding is consistent with previous studies which empirically showed that a larger search area provided better correlations with tree growth (Daniels et al. 1986). In order to ensure the correlation with increments, different competition indices were used to fit the growth equations (Table 5).

To assess the performances of the competition indices in predicting individual tree growth, a growth prediction without a competition index was established. In this prediction model, variables such as the initial tree size, tree height, and crown ratio were considered explanatory variables and selected by stepwise regression techniques. The associated MSE was assigned 100%. In the DBH-growth prediction model, the significant variables were the initial DBH and tree crown ratio (Table 6); for basal-area growth, the significant variables were the initial basal area and tree crown ratio (Table 7), and for

Table 3. Results of *t*-tests of changes in the competition indices by thinning

Competition index-search radius	*n*	*t*-value	*p* value
S	62	7.3569	< 0.0001
B	62	7.5649	< 0.0001
H-D1	62	-13.3188	< 0.0001
H-D2	62	-16.1139	< 0.0001
H-D3	62	-20.3283	< 0.0001
ME-D1	62	-13.4763	< 0.0001
ME-D2	62	-15.535	< 0.0001
ME-D3	62	-17.4516	< 0.0001
A-D1	62	2.2267	0.0297
A-D2	62	0.2431	0.8087
A-D3	62	0.9436	0.3477
CV-H1	62	-8.7977	< 0.0001

Competition indices are defined in Tables 1 and 2.

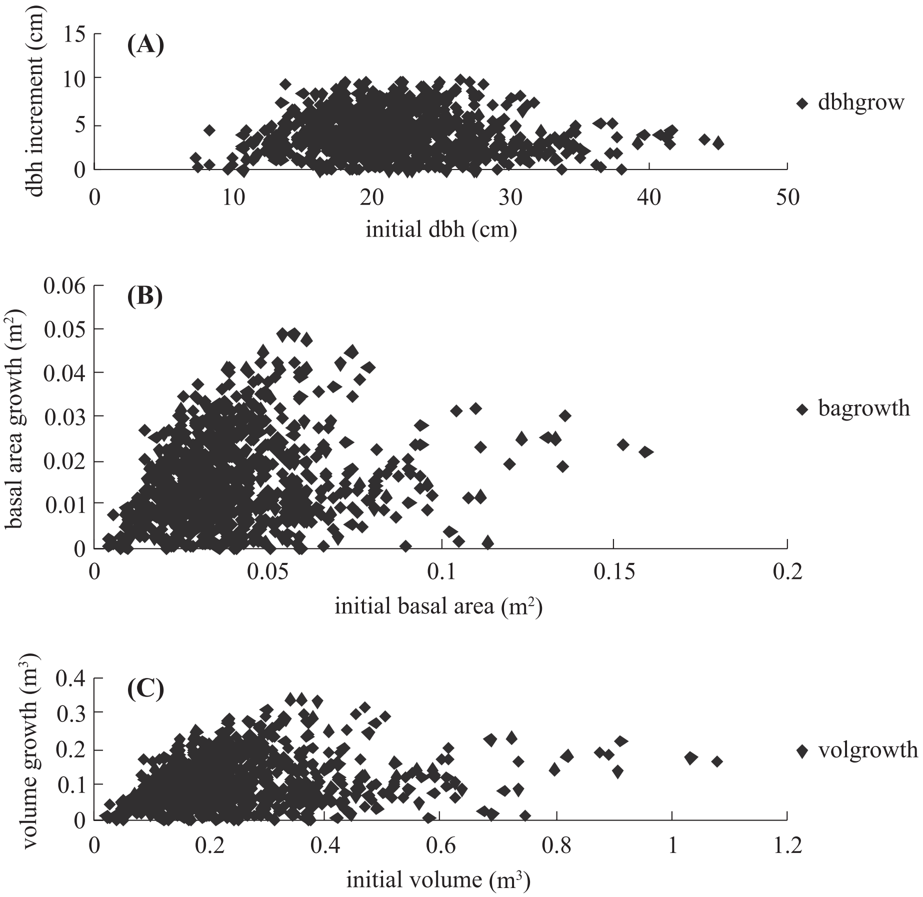


Fig. 2. Five-year increment in diameter at breast height (DBH) (A), basal area (B) and volume (C).

volume growth, the significant variables were the initial volume and tree crown ratio (Table 8). Moreover, due to the insignificance of the intercept, the regression constants were omitted from all growth component models.

The inclusion of competition indices in the tree growth model produced decreases in MSEs for all competition indices relative to the no-competition index involved in all 3 growth components. Comparing the different competition formulas used (Tables 6-8), the Staebler index performed the worst for basal area and volume growth because of little or no improvement in the prediction. There was no substantial improvement using the Alemdag index for all 3 growth models. However, good performances were found for the Hegyi and crown-volume indices.

In all growth-prediction models, the reduction in the MSE caused by the crown volume (CV-H) index was the largest (MSE% = 83.38% in Table 6, 85.27% in Table 7, and 86.45% in Table 8), meaning that the performance of crown volume in increasing the precision of the predictive model was the best among the competition indices studied (Tables 6-8). In addition, the Hegyi index also performed quite well. With the simple formulation used to calculate the Hegyi index, it is in practice quite useful to use the Hegyi index

Table 4. Correlation coefficients with *p* values in parenthesis of various competition indices (CIs) with 5-yr growth of individual Taiwania trees

Attribute (CI)	DBH increment	Basal area increment	Volume increment
DBH1/BA1/Vol1[1)]	0.30580 (< 0.0001)	0.55810 (< 0.0001)	0.59223 (< 0.0001)
S	0.10162 (0.0956)	0.31324 (< 0.0001)	0.34381 (< 0.0001)
B	0.07447 (0.2226)	0.03405 (0.5774)	0.04990 (0.4141)
H-D1	-0.23710 (< 0.0001)	-0.23077 (0.0001)	-0.22772 (0.0002)
H-D2	-0.26102 (< 0.0001)	-0.25696 (< 0.0001)	-0.25384 (< 0.0001)
H-D3	-0.28202 (< 0.0001)	-0.29078 (< 0.0001)	-0.28934 (< 0.0001)
ME-D1	-0.19654 (0.012)	-0.13640 (0.0650)	-0.12660 (0.0576)
ME-D2	-0.20672 (0.062)	-0.14199 (0.0196)	-0.13138 (0.0609)
ME-D3	-0.21540 (0.045)	-0.15185 (0.0125)	-0.14137 (0.0701)
A-D1	0.30560 (< 0.0001)	0.53165 (< 0.0001)	0.56111 (< 0.0001)
A-D2	0.30494 (< 0.0001)	0.54392 (< 0.0001)	0.57553 (< 0.0001)
A-D3	0.28977 (< 0.0001)	0.52932 (< 0.0001)	0.56085 (< 0.0001)
CV-H1	-0.27492 (< 0.0001)	-0.31335 (< 0.0001)	-0.31467 (< 0.0001)

[1)] DBH1, BA1, Vol1 represents the initial value for the diameter at breast height, basal area, and volume, respectively.

Competition indices are defined in Tables 1 and 2.

Table 5. Competition indices used in fitting growth equations for the diameter at breast height (DBH), basal area, and volume growth

Competition index-search radius	DBH increment	Basal area increment	Volume increment
S		X	X
B			
H-D1	X	X	X
H-D2	X	X	X
H-D3	X	X	X
ME-D1			
ME-D2			
ME-D3			
A-D1	X	X	X
A-D2	X	X	X
A-D3	X	X	X
CV-H1	X	X	X

X indicates that the competition index was used in the growth equation.

Competition indices are defined in Tables 1 and 2.

in conjunction with other variables to predict tree growth.

This study showed that gains in expansion of search zones when determining competitors varied among the competition indices. For the Alemdag index, there was little or no difference in the MSEs for the 3 search zones. However, for the Hegyi index, a slight improvement in the ability to estimate a competition effect was found.

Table 6. Coefficient and mean square error (MSE) for competition indices (CIs) as a percentage of the no-competition index for diameter at breast height (DBH) growth of Taiwania trees

Competition index-search radius	Initial DBH	Crown ratio	CI inverse	Adjusted R^2 (%)	MSE	MSE (%)
No CI	0.04679**	2.00977**		81.03	1.2512	100
H-D1	0.04521**	1.83162**	0.80508*	83.15	1.1581	92.56
H-D2	0.04536**	1.87531**	0.88286*	83.46	1.1433	91.38
H-D3	0.0444**	1.82713**	1.85294*	84.00	1.1068	88.46
A-D1	0.05067**	2.23336**	-2.86640**	82.78	1.1826	94.52
A-D2	0.05004**	2.20460**	-3.96844**	83.37	1.1654	93.15
A-D3	0.04956**	2.17913**	-6.65836**	83.90	1.1619	92.87
CV-H1	0.04771**	2.20285**	-0.93782*	85.54	1.0432	83.38

* $\alpha < 0.05$; ** $\alpha < 0.01$.

Competition indices are defined in Tables 1 and 2.

Table 7. Coefficient and mean square error (MSE) for competition indices (CIs) as a percentage of the no-competition index for basal area growth of Taiwania trees

Competition index-search radius	Initial basal area	Crown ratio	CI inverse (10^{-3})	Adjusted R^2 (%)	MSE (10^{-4})	MSE (%)
No CI	0.12130**	0.00677**		80.98	0.2762	100
S	0.12010**	0.00711**	-0.31712*	81.02	0.2638	95.51
H-D1	0.12016**	0.00617**	2.300**	82.57	0.2471	89.45
H-D2	0.12085**	0.00658**	1.040**	82.86	0.2447	88.61
H-D3	0.12012**	0.00635**	3.48**	83.05	0.2403	87.02
A-D1	0.11893**	0.00976**	-19.71*	81.78	0.2555	92.52
A-D2	0.11887**	0.00962**	-30.06*	82.06	0.2538	91.89
A-D3	0.11884**	0.00942**	-54.21*	82.59	0.2511	90.92
CV-H1	0.13538**	0.00787**	-1.2356*	83.94	0.2355	85.27

* $\alpha < 0.05$; ** $\alpha < 0.01$.

Competition indices are defined in Tables 1 and 2.

The type of zone of influence model describes a circle determined by the size of the tree, and from which the tree can potentially draw resources and within which it competes with other trees. Trees compete when their zones of influence overlap. As the radius of the influence zone for a subject tree was proportional to its size (crown size DBH, or height), using a specific radius (e.g., 10 feet (3.04 m) in Hegyi 1974) to determine competitors was not used by many studies. On the contrary, a variable radius reflecting the variety of influence zones among trees is widely used (Daniels et al. 1986, Biging and Dobbertin 1992).

Reductions in the MSE caused by competition indices varied among growth components. This study showed that the benefit obtained with basal area was highest followed by the DBH and volume growth. For DBH and basal area, a consistent result was found with previous studies (Bella 1971, Biging and

Table 8. Coefficient and mean square error (MSE) for competition indices (CIs) as a percentage of the no-competition index for volume growth of Taiwania trees

Competition index-search radius	Initial volume	Crown ratio	CI inverse	Adjusted R^2 (%)	MSE	MSE (%)
No CI	0.07801**	0.06135**		74.59	0.00129	100.00
S	0.08448**	0.0510**	0.00952*	74.67	0.00124	96.51
H-D1	0.07614**	0.05416**	0.02664**	75.14	0.00117	91.05
H-D2	0.07497**	0.05127**	0.05246**	75.55	0.00115	89.12
H-D3	0.07429**	0.05086**	0.08157**	75.93	0.00114	88.62
A-D1	0.07569**	0.07142**	-0.06412*	74.61	0.00121	93.93
A-D2	0.07595**	0.06938**	-0.08073*	74.82	0.00122	94.83
A-D3	0.07601**	0.06886**	-0.14576*	74.85	0.00122	94.29
CV-H1	0.08017**	0.06328**	-0.012559*	76.10	0.00112	86.45

* $\alpha < 0.05$; ** $\alpha < 0.01$.

Competition indices are defined in Tables 1 and 2.

Dobbertin 1992, Wang et al. 2004). As to volume growth, the finding that a slight reduction in the MSE using volume growth rather than basal-area growth can probably be explained by the fact that the uncontrolled variation which occurred in tree height growth may increase the MSE in the growth model, therefore lessening the contribution incurred by competition indices.

Considerable debate has occurred in the literature as to whether information on tree spacing improves predictions of individual tree growth. Intuitively, it seems likely that knowledge of tree locations and their sizes should improve our ability to characterize competition among trees. However, answers from the literature are inconsistent. Some studies proved the superiority of distance-dependent competition indices in predicting individual tree growth (Alemdag 1978, Daniels et al 1986, Biging and Dobbertin 1992). Other studies reported that distance-dependent measures were not superior to distance-independent measures for predicting growth (Hatch et al. 1975, Lorimer 1983, Martin and EK 1984). In Taiwania plantations where the spacing is relatively controlled and knowledge of tree location is of lesser value, this study showed that 14~17% better predictions than no-competition indices involved were obtained by recognizing spatial information.

Performances of competition indices on individual tree growth vary by species and growth component (Biging and Dobbertin 1992, Wang et al. 2004). Compared to other studies, the gain in MSE reduction by including competition indices in individual growth predictions obtained in this study was lower than that obtained in a previous study (Wang et al. 2004). This is probably because in the previous study, even though examining the same species, only 1 age stand was used to determine the initial value of the growth component; however, in this study, different ages of stands were pooled together. In other words, competition indices used in differently structured plantations such as by age or tree size may play various roles in predicting individual tree growth.

CONCLUSIONS

Competition for resources among individual trees has considerable impacts on

DBH, basal area, and volume growths. This study showed considerable improvement in predicting individual tree periodic growth when including distance-dependent competition indices. In these indices studied, the crown-volume index performed the best among all growth components because crown information of competitors was incorporated into the index. Furthermore, this result can subsequently be used to develop individual tree growth simulations.

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LITERATURE CITED

Adlard PG. 1974. Development of an empirical competition model for individual trees within a stand. Proceeding in growth models for tree and stand simulation. Fries J editor. Stockholm, Sweden: Royal College of Forestry. p 22-37.

Alemdag IS. 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. Forest Management Institute Information Report FMR-X-108. Ottawa, Canada: Canadian Forestry Service, Department of the Environment. 39 p.

Bella IE. 1971. A new competition model for individual trees. For Sci 17:364-72.

Biging GS, Dobbertin M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For Sci 38(3):695-720.

Biging GS, Dobbertin M. 1995. Evaluation of competition indices in individual tree growth models. For Sci 41(2):360-77.

Brand DG, Magnussen. 1988. Asymmetric, two-sided competition in even-aged monocultures of red pine. Can J For Sci 18:901-10.

Brown GS. 1965. Point density in stems per acre. New Zealand Forest Research Notes no. 38. Rotorua, NZ: Forest Research Institute, New Zealand Forest Service. 11 p.

Coomes DA, Allen RB. 2007a. Effects of size, competition and altitude on tree growth. J Ecol 95:1084-97.

Coomes DA, Allen RB. 2007b. Mortality and tree-size distributions in natural mixed-age forests. J Ecol 95:27-40.

Clutter JL, Fortson JC, Piennar LV, Brister GH, Bailey RL. 1983. Timber management: a quantitative approach. Hoboken, NJ: J Wiley. 333 p.

Daniels RF, Burkhart HE, Clason TR. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can J For Res 16:1230-7.

Glover GR, Hool JN. 1979. A basal area ratio predictor of loblolly pine plantation mortality. For Sci 25:275-82.

Harper JL. 1977. Population biology of plants. Maryland Heights, MO: Academic Press.

Hatch CR, Gerrard DJ, Tappeiner II JC. 1975. Exposed crown surface area: a mathematical index of individual tree growth potential. Can J For Res 5:224-8.

Hegyi F. 1974. A simulation model for managing jack-pine stands. Proceeding in growth models for tree and stand simulation. Fries J, editor. Stockholm, Sweden: Royal College of Forestry. p 74-90.

Lorimer CG. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For Ecol Manage 6:343-60.

Martin GL, Ek AR. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. For Sci 30(3):731-43.

Martin GL, Ek AR, Monserud RA. 1977. Control of plot edge bias in forest stand growth simulation models. Can J For Res 7(1):100-5.

Munro DD. 1974. Forest growth models-a prognosis. Proceeding in growth models for tree and stand simulation. Fries J, editor. Stockholm, Sweden: Royal College of Forestry. p 7-21.

Nishimura N, Hara T, Miura M, Manabe T, Yamamoto S. 2002. Tree competition and species coexistence in a warm-temperate old-growth evergreen broad-leaved forest in Japan. Plant Ecol 164:235-48.

Nord-Larsen T, Damgaard C, Weiner J. 2006. Quantifying size-asymmetric growth among individual beech trees. Can J For Res 36:418-25.

Peet RK, Christensen NL. 1987. Competition and tree death. Bioscience 7:586-95.

Pelz DR. 1978. Estimating individual tree growth with tree polygons. Growth models for long term forecasting of timber yields. Fries J, Burkhart HE, Max TA, editors. FWS-1-78. Blacksburg, VA: School of Forestry and Wildlife Resources, Virginia Ploytechnic Institute and State Univ. p 172-8.

Perot T, Goreaud F, Ginisty C, Dhote JF. 2010. A model bridging distance-dependent and distance-independent tree models to simulate the growth of mixed forests. Ann For Sci 67(5):501-11.

Schwinning S, Weiner J. 1998. Mechanisms determining the degree of size-asymmetry in competition among plants. Oecologia 113(4):447-55.

Shainsky LJ, Radosevich SR. 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology 73:30-45.

Spurr SH. 1962. A measure of point density. For Sci 8:85-96.

Tilman D. 1982. Resource competition and community structure. Monographs in Population Biology Number 17. Princeton, NJ: Princeton Univ. Press. 296 p.

Wang DH, Wang CH, Kao YB, Wu YJ. 2004. Growth competition in mixed plantation of Taiwania and red alder in Doa-Na area. Taiwan J For Sci 19(4):337-51. [in Chinese with English summary].

Yang YC, Wang CH. 1987. Expectation and variance of basal area estimates using remeasured horizontal line sampling. For Sci 174-84.