COMPARISON OF INDIVIDUAL-TREE COMPETITION METRICS IN AN UNEVEN-AGED, BALDCYPRESS AND BLACK WILLOW FLOODPLAIN FOREST

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Abstract—Forest competition is typically assessed at the stand scale, but metrics that account for individual-tree competition may be more useful for understanding controls over growth in disturbed stands with heterogeneous structure. We evaluated whether local competition measures and crown dimension measures in an uneven-aged floodplain forest were capable of accounting for the effect of competition on baldcypress (*Taxodium distichum*) and black willow (*Salix nigra*). Contrary to our hypothesized inverse relationships, various metrics of local competition and individual crown dimension variables were poorly correlated with each other for dominant and codominant trees of the two species. The variability between species and overall poor relationships were likely attributable to physiological and morphological differences, complex stand structure, and the relatively low levels of competition experienced by dominant and codominant trees.

INTRODUCTION

Stand structure and composition affect the trajectory of forest development through inter-tree competition (Franklin and others 2002). Numerous measures have been used to quantify the effects of competition at both the stand and individual-tree levels, but none have proven useful in all situations. Nonetheless, individual-tree competition measures remain important when interpreting patterns in growth. This can be especially true when stands are highly heterogeneous, such as forested wetlands where flooding may alter tree establishment patterns and thereby limit the occupancy of available aboveground growing space (Allen and others 2015).

There is a need to determine which measure best represents competition for such applications. Distance-dependent measures have been most commonly used to evaluate local competition effect on trees (Tome and Burkhart 1989). These measures (such as local basal area, local trees per hectare, and local stand density index) have been used to predict growth, but none have been consistently useful for quantifying competition effects on tree structure (Daniels and others 1986). Another type of competition measure involves quantifying the number of neighboring trees that influence the crown of a subject tree through shading. The effects of neighboring trees are dependent on distance (crowding) and shade influence (Canham and others 2004).

Competition is also manifested in tree size and shape (Curtis 1970, Krajicek and others 1961). Local competition reduces resource availability (especially light availability), and thus can influence both crown shape and size (Pacala and others 1996, Thorpe and others 2010). Some competition measures take advantage of this influence of density on crown size, using the restriction of crown dimensions of subject trees to infer and quantify local competition. For example, Meadows and others (2001) introduced a classification system for characterizing crown shape and quality in uneven-aged bottomland hardwoods of the Southeastern United States, which Dimov and others (2008) have shown to be a useful predictor of tree growth in competitive environments. Regardless of crown class (for example, dominant or codominant), increased stand density decreases crown dimensions, hence the association can provide insight on competitive effects (Holdaway 1986). Tree height, crown length, and live crown ratio can also be used to evaluate competition effects and dominance of a tree.

We evaluated various metrics of both local stand density and individual-tree crown characteristics (1) to assess the validity and interchangeability of each metric and (2) to further our understanding of whether and how competition and crown structure covary for two important species in a floodplain forest, baldcypress (*Taxodium distichum*) and black willow (*Salix nigra*). We hypothesized, for both species, that there would be

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strong inverse relationships between local competition and crown dimension metrics.

MATERIALS AND METHODS

Study stands were adjacent to Bayou Sorrel, a distributary of the Atchafalaya River in south-central Louisiana. Species dominating the sites were baldcypress, black willow, green ash (*Fraxinus pennsylvanica*), Drummond's red maple (*Acer rubrum* var. *drummondii*), and water tupelo (*Nyssa aquatica*), with water-elm (*Planera aquatica*) and swamp-privet (*Forestiera acuminata*) common in the understory. Trees were selected from three stands varying in their degree of hydrological connectivity to flowing water (McAlhaney 2018), but we lumped all trees from all stands for this analysis because there was no indication that site affected relationships. All stands were uneven-aged, with a history of frequent disturbance from flooding and sediment deposition on a rapidly accreting floodplain (Hupp and others 2008).

A total of 37 baldcypress and 39 black willow trees from dominant and codominant crown classes were sampled. These trees were chosen for minimum visible signs of damage and were competitively independent of other sampled trees. Ages of trees, determined by coring, were 54–145 years old (324 years old for two sampled trees) for baldcypress and 38–58 years old for black willow. The condition of trees was variable. Baldcypress crowns were conical but becoming flat topped (a common characteristic of maturity). Black willow crowns were irregular, many with signs of damage and epicormic sprouting, and trees were approaching age of senescence. Average diameters were 49 cm (range 35–64 cm) for baldcypress and 60 cm (19–92 cm) for black willow. The average height for both species was 24 m (range 20–27 m for baldcypress and 17–28 m for black willow).

Several measurements were made of the dimensions of each sample tree and local competition. Total height and height to crown base were measured using a TruPulse 200x laser rangefinder to the nearest 1 m. Crown length and live crown ratio were calculated from these measurements. A numerical crown classification rating system for floodplain forests developed by Meadows and others (2001) quantified the crown of each sample tree, using visual estimates of the amount of sunlight the crown received from above (MTop; scale: 1-10), the amount of sunlight the crown received from the sides (MSide; scale: 1-10), crown balance (MBal; scale: 1-4), and crown size (MSize; scale: 1-4).

We also devised and evaluated a new competition metric derived from Biging and Dobbertin (1992) that counted the number of trees occupying an inverted cone extending from the crown base of the sample tree. For each subject tree, we tallied the number of other tree crowns occupying that cone as a measurement of competition. These cone-of-influence (COI) metrics were calculated using 30°, 35°, 40°, and 45° angles from the crown base of each subject tree. To ascertain whether each neighbor was in each cone, its distance from the sample tree and its height were measured (to the nearest meter), allowing calculation of whether it intersected each inverted cone.

Local stand density was evaluated using variable-radius, point samples using basal area factors (BAF) of 20 and 10 basal-area-factor (BAF; ft^2 ac^{-1} $tree^{-1}$, converted to equivalent metric units of 4.59 and 2.29 m^2 ha^{-1} $tree^{-1}$) using angle prisms with sample trees at point center. All trees were tallied, which allowed calculation of local basal area (local BA20 and BA10), trees per hectare (local TPH20 and TPH10), and Reineke's (1933) stand density index (local SDI20 and SDI10). Simple relationships between competition measures were then determined by correlation analyses, using Spearman rank correlation coefficients to improve robustness of fit in the context of highly variable local stands including outliers containing large numbers of small trees.

RESULTS

Local stand density was relatively low, with most trees inhabiting areas with local density near or below 660 SDI20 (S.I. units), the density at which self-thinning begins. Although the ranges of local stand density data for baldcypress and black willow suggest that baldcypress inhabited locations of lower local densities, the majority of the data (excluding outliers) suggest that trees from both species occupied locations of similar stand density (table 1).

Table 1—Mean (range) of local competition indices for baldcypress and black willow

	Competition measure					
Species	BA20	TPH20	SDI20	BA10	TPH10	SDI10
Baldcypress	25(5-60)	1198(8-17017)	541(58-1296)	23(9-41)	1121(54-4585)	507(146-943)
Black willow	28(5-83)	3094(26-52902)	699(100-3325)	27(5-66)	2977(104-43811)	689(97-2689)

BA = basal area (m^2 ha^{-1}), TPH = trees per hectare, SDI = stand density index (S.I. units).

Competition measures calculated based on prism basal area factors of 20 and 10 (U.S. units).

Relationships between current levels of local tree competition and size and shape of the dominant or codominant crowns varied by species (table 2). Crown size (length) response to competition for baldcypress was stronger than for black willow, but crown shape (from Meadows crown scores) was most related to competition for black willow. The most consistent relationship was that black willow crowns were less symmetrical in the presence of competition, mostly regardless of metric used (table 2).

The relationships between COI and sample tree dimensions were generally weak except that the number of trees occupying narrow cones (i.e., low COI) was correlated with smaller crowns, especially in black willow (table 3). As the cone angle increased, implying a larger area and thus larger number of trees potentially competing with the sample tree, there were weaker relationships. The mean number of tallied trees by angle was low: 1 – COI30, 1.5 – COI35, 3.5 – COI40, and 5 – COI45, limiting the precision of this metric. Even at the widest angle of 45°, there were no trees within the COI45 of four sample trees, although there were 27 trees in COI45 of one sample tree. There were 20 trees in COI40 of two sample trees. There were fewer than 13 trees in the 30–45° cones of 73 of the 78 sample trees.

Most crown dimensions only weakly correlated with each other, with the exception of weakly positive correlations between the amount of overhead sunlight received (MTop) and crown sizes or tree total height (table 4). However, the range for MTop was 9 or 10 for every tree because the study was designed to focus on more dominant trees, with only three trees having MTop score of 9; therefore, the marginally statistically significant relationships involving this variable were not especially meaningful. In black willow, more balanced crowns also tended to be longer.

Only black willow had many significant relationships between local competition measures and number of trees in the COI (table 5). The number of trees occupying the large COIs were positively correlated with other stand-density metrics for black willow, but in baldcypress there was only a single, unexpectedly negative, relationship with TPH10. Both total heights and

Table 2—Correlations (Spearman's *ρ*) between local competition measures and individual tree dimension metrics of baldcypress and black willow

Species	Competition measure					
Crown dimension measure	BA20	TPH20	SDI20	BA10	TPH10	SDI10
Baldcypress						
MTop	-0.15	0.01	-0.07	-0.10	0.13	-0.01
MSide	0.08	0.03	0.09	-0.06	0.30*	0.14
MBal	0.13	0.07	0.08	-0.04	-0.07	-0.07
MSize	-0.09	-0.02	-0.05	-0.07	0.00	-0.04
MTotal	0.07	0.06	0.09	-0.09	0.27	0.11
Height (m)	-0.09	0.07	0.00	-0.01	0.05	-0.03
Crown length (m)	-0.32*	-0.20	-0.27	-0.38**	-0.24	-0.39**
Live crown ratio	-0.15	-0.07	-0.11	-0.32*	-0.19	-0.30*
Black willow						
MTop	0.06	0.09	0.11	0.25	0.25	0.28*
MSide	-0.24	0.00	-0.17	-0.26	-0.01	-0.14
MBal	-0.35**	-0.29*	-0.34**	-0.37**	-0.30*	-0.39**
MSize	-0.29*	-0.13	-0.26	-0.27	-0.06	-0.21
MTotal	-0.40**	-0.15	-0.33**	-0.43**	-0.14	-0.33**
Height (m)	0.11	-0.18	0.01	0.13	-0.14	0.00
Crown length (m)	0.02	0.04	0.06	0.14	0.03	0.10
Live crown ratio	-0.13	0.10	0.01	-0.01	0.13	0.09

BA = basal area (m^2 ha^{-1}), TPH = trees per hectare, SDI = stand density index (S.I. units).

Competition measures calculated based on basal area factors of 20 and 10 (U.S. units).

Meadows and others (2001) crown scores: MTop, top light; MSide, side light; MBal, balance; MSize, size; MTotal, total score.

Asterisks indicate $p < 0.10$, double asterisks indicate $p < 0.05$.

Table 3—Correlations (Spearman's ρ) between local competition measures (trees in the cone of influence) and individual tree dimension metrics of baldcypress and black willow

Species / Crown dimension measure	Competition measure			
	COI30	COI35	COI40	COI45
Baldcypress				
MTop	-0.17	-0.07	0.00	0.03
MSide	0.07	0.03	-0.04	-0.28*
MBal	-0.04	0.14	0.23	0.17
MSize	-0.17	-0.06	-0.02	0.01
MTotal	0.01	0.07	0.02	-0.20
Height (m)	-0.05	-0.05	-0.15	-0.04
Crown length (m)	-0.26	-0.10	-0.03	0.20
Live crown ratio	-0.39**	-0.22	-0.06	0.18
Black willow				
MTop	-0.34**	-0.20	-0.09	0.00
MSide	-0.14	-0.20	-0.11	-0.21
MBal	-0.01	0.07	-0.12	-0.12
MSize	0.18	0.20	0.13	-0.04
MTotal	-0.05	-0.04	-0.10	-0.23
Height (m)	-0.05	-0.08	-0.09	-0.05
Crown length (m)	-0.45**	-0.45**	-0.36**	-0.19
Live crown ratio	-0.37**	-0.37**	-0.30*	-0.18

COI = cone-of-influence metrics.

Meadows and others (2001) crown scores: MTop, top light; MSide, side light; MBal, balance; MSize, size; MTotal, total score.

Asterisks indicate $p < 0.10$, double asterisks indicate $p < 0.05$.

Table 4—Correlations (Spearman's ρ) between Meadows crown scores and crown dimension measures of baldcypress and black willow

Species / Crown dimension measure	Crown dimension measure				
	MTop	MSide	MBal	MSize	MTotal
Baldcypress					
Height (m)	-0.05	-0.14	-0.16	-0.11	-0.15
Crown length (m)	0.25	-0.08	0.04	0.14	-0.01
Live crown ratio	0.31*	-0.12	0.02	-0.02	-0.11
Black willow					
Height (m)	0.30*	-0.20	0.23	0.27	0.06
Crown length (m)	0.27*	-0.05	0.34**	0.09	0.13
Live crown ratio	0.01	0.03	0.17	-0.04	0.08

Meadows and others (2001) crown scores: MTop, top light; MSide, side light; MBal, balance; MSize, size; MTotal, total score.

Asterisks indicate $p < 0.10$, double asterisks indicate $p < 0.05$.

Table 5—Correlations (Spearman's ρ) between local competition measures and cone-of-influence competition metrics of baldcypress and black willow

Species	Competition measure					
COI angle	BA20	TPH20	SDI20	BA10	TPH10	SDI10
Baldcypress						
COI30	0.09	---0.05	0.00	0.18	0.07	0.17
COI35	0.00	-0.11	-0.10	0.00	-0.12	-0.05
COI40	0.07	-0.08	-0.04	0.09	-0.18	0.00
COI45	-0.06	-0.17	-0.16	0.01	-0.38**	-0.18
Black willow						
COI30	0.14	0.06	0.11	0.04	-0.04	-0.08
COI35	0.07	0.01	0.04	-0.04	-0.08	-0.16
COI40	0.22	0.21	0.25	0.19	0.16	0.14
COI45	0.36**	0.38**	0.42**	0.36**	0.28*	0.30*

COI = cone-of-influence metrics.
BA = basal area (m^2 ha^{-1}), TPH = trees per hectare, SDI = stand density index (S.I. units).
Competition measures calculated based on basal area factors of 20 and 10 (U.S. units).
Asterisks indicate $p < 0.10$, double asterisks indicate $p < 0.05$.

crown lengths were similar for baldcypress (24 m and 13 m, respectively) and black willow (23 m and 14 m, respectively), so there was no reason to expect different relationships among the variables by species.

DISCUSSION

Contrary to expectation, the local competition metrics correlated poorly with the individual crown dimension variables, which may originate in physiological and morphological differences. The lack of correlation between local stand density and common crown dimensions (height, crown length, live crown ratio) for black willow was unexpected, because black willow is shade intolerant, and because there was correlation for the more shade-tolerant baldcypress. However, there were generally less-symmetrical crowns in black willow facing greater competition. Although not evaluated in this study, differences in growth physiology and the resulting crown shape response may be the cause for variability in relationship strengths of competitive effect on sample trees. For example, hardwoods such as black willow have the ability to develop highly asymmetric crowns to reduce competition influence (Lorimer 1983) by phototropic growth, and indeed the crowns of our sample black willow trees were generally irregular in shape.

The competition indices may have been poorly correlated with crown characteristics because the local stand densities in this study did not create enough competition effect. The stand density for sampled trees was mostly at or below the threshold of competition at which self-thinning begins for baldcypress (SDI ≈ 660, Keim and others 2010). Although similar stand density measures for black willow have never been studied, this study suggests black willow crown size is relatively insensitive to these levels of competition.

The weak relationships between both local competition and crown dimensions and both Meadows crown scores and COI measures suggest these measures were insufficient for both species. However, these weak relationships potentially originated because the samples consisted of only dominant and codominant trees. Similarly, the low data range of trees within the cone of influence in this study may contribute to the lack of predictive utility in competition effect. Also, much of the stand density near the sampled trees originated from smaller species such as Drummond's red maple and swamp-privet. Stand structure was irregular and multi-layered, which also potentially contributed to inconsistencies between species and among competition metrics.

CONCLUSIONS

We tested relationships between many metrics of stand density, competition, and crown morphology in an uneven-aged, forested wetland, and found few of these metrics demonstrated consistent suitability for explaining or predicting dimensions of dominant and codominant trees. Contrary to expectation, the competition metrics were weakly significant predictors of crown dimensions for both species. The nature of this stand—frequently disturbed and generally of low density—may have contributed to the relative lack of sensitivity of trees to neighbors. Also, because the sample was only of dominant and codominant trees, the results may be insufficient for inferences across the entire range of competition intensity.

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