

## MULTI-MODEL ANALYSIS OF TREE COMPETITION ALONG ENVIRONMENTAL GRADIENTS IN SOUTHERN NEW ENGLAND FORESTS

MICHAEL J. PAPAİK<sup>1,2</sup> AND CHARLES D. CANHAM<sup>1</sup>

<sup>1</sup>*Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA*

**Abstract.** Robust predictions of competitive interactions among canopy trees and variation in tree growth along environmental gradients represent key challenges for the management of mixed-species, uneven-aged forests. We analyzed the effects of competition on tree growth along environmental gradients for eight of the most common tree species in southern New England and southeastern New York using forest inventory and analysis (FIA) data, information theoretic decision criteria, and multi-model inference to evaluate models. The suite of models estimated growth of individual trees as a species-specific function of average potential diameter growth, tree diameter at breast height, local environmental conditions, and crowding by neighboring trees. We used ordination based on the relative basal area of species to generate a measure of site conditions in each plot. Two ordination axes were consistent with variation in species abundance along moisture and fertility gradients. Estimated potential growth varied along at least one of these axes for six of the eight species; peak relative abundance of less shade-tolerant species was in all cases displaced away from sites where they showed maximum potential growth. Our crowding functions estimate the strength of competitive effects of neighbors; only one species showed support for the hypothesis that all species of competitors have equivalent effects on growth. The relative weight of evidence (Akaike weights) for the best models varied from a low of 0.207 for *Fraxinus americana* to 0.747 for *Quercus rubra*. In such cases, model averaging provides a more robust platform for prediction than that based solely on the best model. We show that predictions based on the selected best models dramatically overestimated differences between species relative to predictions based on the averaged set of models.

**Key words:** competition; environmental gradients; forest management; information theory; multi-model inference; neighborhood analysis; neighborhood competition index; neutral theory; niche, sustainable forest management.

### INTRODUCTION

Growth and yield models and the enormous body of empirical research on which they were based provided a predictive foundation for even-aged forest management. The recent shift to partial harvesting and all-aged management on both public and private land in the northeastern United States (USDA Forest Service 2001) reflects a recognition that sustainable forestry requires managing forests to optimize a wide range of ecosystem characteristics (Kohm and Franklin 1997, Burton et al. 2003) and social values (Kimmins 1995), not simply timber yield. The shift away from even-aged management, however, presents a host of new scientific challenges. The spatial patterns of partial harvests have important implications for understory light levels for regeneration (e.g., Canham et al. 1994, Beaudet et al. 2002), including the potential for invasion by exotic species (Knapp and Canham 2000). The spatial distribution

of seed trees has strong effects on the distribution and abundance of regeneration, particularly given the limited dispersal distances of most northeastern tree species (Ribbens et al. 1994, Clark et al. 1999, Greene et al. 2004). And, perhaps most important from an economic standpoint, the spatial pattern of harvests determines the degree of release from competition with potentially dramatic effects on growth and survival of residual trees (e.g., Wimberly and Bare 1996, Coates et al. 2003, Canham et al. 2004, 2006). Predicting stand development and yield following partial harvesting requires consideration of an almost infinite variety of spatial configurations of the level of removal of different species and tree sizes within a stand.

These new challenges of managing and maintaining structurally complex stands require a shift in emphasis away from more site-specific, empirical models that emphasize prediction, to more mechanistic, spatially explicit models that incorporate the consequences of varying environments and dynamic spatial structure within stands. A number of recent analyses of models used in forest management have highlighted the need for hybrid approaches that balance the predictive power of empirical models with the generality of process models. (e.g., Pinkard and Battaglia 2001, Peng et al. 2002,

Manuscript received 10 October 2005; revised 13 March 2006; accepted 21 March 2006. Corresponding Editor: J. A. Antos.

<sup>2</sup> Present Address: University of Quebec at Montreal, CP 8888 Succ. Centre-Ville, Montreal, Quebec H3C 3P8 Canada. E-mail: papaikm@ecostudies.org

Milner et al. 2003, Robinson and Ek 2003, Seidl et al. 2005, Canham et al. 2006).

We follow an approach recently developed by Canham et al. (2006) that uses simple distance-dependent neighborhood competition models, parameterized using field data, that describe the responses of individual trees to variation in both local neighborhood competition and site environmental conditions. More generally, the models address several important theoretical questions concerning the role of competition among adult trees in structuring forest communities. These include insights into whether and which species of trees are functionally equivalent competitors; evidence for the displacement of realized niches as a result of competition; and, quantitative estimates of the strength of interspecific competition between pairs of species.

Traditional modeling approaches (including Canham et al. 2006) estimate parameters for a set of candidate models specified independently of the data analysis. Inference is then normally based only on the parameter estimates and structure of the best model (i.e., best-model inference or BMI). This is appropriate when comparisons between alternate models are used as a form of hypothesis testing (Johnson and Omland 2004). When prediction is an explicit goal of a model (as in many forest management applications), however, BMI may be misleading if there are alternate models with reasonable support in the data (Burnham and Anderson 2002). Information theory provides a basis for evaluating the weight of evidence in support of alternate models relative to the "best" model (Burnham and Anderson 2002) that hypothesis testing methods do not. This multi-model inference (MMI) provides an alternative framework, in which inference is based on the relative merits of the subset of all the models tested which have sufficient support in the data as measured by their weight of evidence (Burnham and Anderson 2002). MMI is particularly important if the predictions vary markedly among the set of alternate models (Burnham and Anderson 2002). Failure to incorporate information from alternate models may represent an unappreciated form of prediction error in ecological models. In this paper, we expand on the approach of Canham et al. (2006) and explore the use of multi-model inference for predicting the effects of neighborhood competition on tree growth along environmental gradients in southern New England forests.

#### METHODS

Our method analyzes tree growth in mapped stands (Canham et al. 2004, 2006, Uriarte et al. 2004a, b) to simultaneously estimate (1) average potential growth on an optimal site in the absence of competition as a function of target tree size, (2) variation in potential growth along environmental gradients, and (3) the magnitude of the competitive effects of neighboring trees on target tree growth as a function of the species, size, and distance to neighboring trees. Full details of the

approach we use can be found in Canham et al. (2006). We review the most salient aspects here. All model functions have been designed to be incorporated into the forest dynamics model SORTIE-ND, which is a platform for spatially explicit, individual tree modeling of forest dynamics, based on the earlier SORTIE model (Pacala et al. 1996; SORTIE-ND, *available online*).<sup>3</sup>

#### Study area and data

Our study area covers western and central Connecticut, western and central Massachusetts, and southeastern New York, roughly centered on Great Mountain Forest (GMF) in northwestern Connecticut, where SORTIE was first parameterized (Pacala et al. 1996). There are a variety of forest types in this region ranging from oak-dominated forests on drier and more southern and eastern sites, to northern hardwood forests on more mesic and northern sites. We analyze growth of adult trees of eight of the most common species across the region: American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula allegheniensis* Britton), red maple (*A. rubrum* L.), northern red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.), and white pine (*Pinus strobus* L.) (Table 1, listed in rank order of shade tolerance; Kobe et al. 1995).

Our analyses make use of data on tree growth collected by the USDA Forest Service forest inventory and analysis (FIA) program. The FIA data sets comprise a random sample, stratified by land cover, with approximately one plot per 6000 acres (2428 ha) of forestland. Of the 597 FIA plots in our study region, we used the 420 plots which had not been logged during the census interval. Plots used in our analysis had growth data from censuses taken between 1978 and 1984 and between 1992 and 1998, at intervals of 12–14 years. Specific field methods vary slightly among the three states, but are easily reconciled for our analysis. The earlier sampling protocols in all three states used 16.1 or 14.7 m radius circular plots in which all trees >12.5 cm diameter at breast height (dbh) were mapped and measured. The most recent New York census kept the original plot and also sampled all trees >12.5 cm dbh. The more recent censuses in Massachusetts and Connecticut, however, used a slightly modified plot structure, where each plot consists of four distinct subplots that are ~7.3 m radius. One subplot is embedded in the center of the older plot (USDA 1998). The change in sampling protocol allows calculation of growth for trees only within the central 7.3 m radius subplot. The original plot gives the configuration of the competitive neighborhoods as they existed at the time of the earlier census, (i.e., the spatial locations, species, and dbh of all trees) within at least a 7.3 m radius around each tree in the remeasured subplot. Based on studies in other

<sup>3</sup> ([www.sortie-nd.org](http://www.sortie-nd.org))

TABLE 1. Summary statistics of forest inventory and analysis (FIA) plots in the study area.

Species	Code	No. target trees	No. plots	dbh		Neighbors/target tree			Conspecific (%)	Mean distance (m)		
				Median	Max.	Min.	Max.	Mean		All	Conspecific	Interspecific
<i>Fagus grandifolia</i>	FAGR	100	43	20.6	62.7	0	18	8.82	39.6	4.78	4.57	4.90
<i>Tsuga canadensis</i>	TSCA	312	78	23.2	56.4	0	23	11.08	57.5	4.86	4.83	4.90
<i>Acer saccharum</i>	ACSA	169	79	24.7	98.6	0	16	7.85	32.5	4.86	4.68	4.98
<i>Betula alleghaniensis</i>	BEAL	69	41	20.8	38.1	1	20	8.70	15.6	4.77	4.77	4.76
<i>Acer rubrum</i>	ACRU	590	197	21.7	104.9	0	24	8.54	48.6	4.67	4.37	4.96
<i>Quercus rubra</i>	QURU	260	103	24.4	55.6	1	18	7.85	49.0	4.78	4.48	5.00
<i>Fraxinus americana</i>	FRAM	100	58	21.9	52.6	2	17	7.46	37.8	4.94	4.82	4.98
<i>Pinus strobus</i>	PIST	239	82	26.7	76.2	0	19	8.98	57.4	4.72	4.65	4.82
Weighted averages				23.2				8.82		4.75		

systems (Canham et al. 2004, Uriarte et al. 2004a, b), the 7.3 m radius is sufficient to capture the bulk of the effects of neighboring trees. There was ample variation among plots in the numbers of neighboring trees and their spatial configurations and species mixtures to allow us to estimate growth across a wide range of competitive conditions (Table 1).

#### Characterizing environmental variation among plots

FIA field protocols called for direct site assessment at the time of the surveys, but the data were too subjective and inconsistent to be of use in this analysis. Thus, we used ordination of plots based on the relative basal area among species within plots to generate an indirect measure of site conditions in each plot. Using relative basal area minimizes the influence of overly large trees or many small ones. Detrended correspondence analysis (DCA; Hill and Gauch 1980) and nonmetric multidimensional scaling (NMS; Kruskal 1964, Mather 1976) are both commonly used to ordinate forest community data (McCune and Grace 2002, McGarigal et al. 2000, Gotelli and Ellison 2004). We tried both methods using the implementations in PC-Ord version 4.28 (McCune and Mefford 1999) with the most recent census data for the full set of 597 plots to further minimize the potential for outliers to influence the results. The full data set had sufficient numbers of 15 species that were common enough to be used in the ordination (>350 trees and present in >7.5% of the 597 plots).

Our basic criterion for determining the usefulness of the ordination was whether the axis scores of the species centroids were interpretable as environmental gradients given knowledge of the autecologies of the major tree species in the region (McGarigal et al. 2000). For the NMS ordination, we used the Sorensen distance measure and followed the procedure outlined by McCune and Grace (2002:131–136). The recommended data reduction was to three dimensions and the stress was 21.1, indicating unreliable results (Kruskal 1964, Gotelli and Ellison 2004, McCune and Grace 2002). Moreover, the NMS ordination did not reveal interpretable patterns of species distribution along the axes.

The two axes of the DCA ordination with the highest coefficients of determination, in contrast, appeared to represent gradients in soil moisture (axis 1) and soil fertility (axis 3), so these two axes were used for our analyses.

#### A spatially explicit analysis of tree growth

The analyses provide empirical estimates of parameters that quantify the relative effects of tree size, site conditions and the sum of all competitive effects of neighboring trees on the growth of a target tree species. Growth of each of the eight species of trees was analyzed separately. The basic model has four components (Canham et al. 2006): (1) peak average potential diameter growth in the absence of competition (PotG, in mm/yr), and three sets of scalar modifiers ranging from 0 to 1 that quantify the effects on average potential growth of (2) initial target tree size (dbh, in cm), (3) local environmental (site) conditions, as measured by ordination axis scores, and (4) crowding by neighboring trees,

$$\text{growth} = \text{PotG} \times \text{size effect} \times \text{site effect} \times \text{crowding effect} \quad (1)$$

where growth is measured in mm/yr.

*Tree size effect.*—We estimate the effect of the size of the target tree on potential growth using a lognormal function:

$$\text{size effect} = e^{-1/2 \left[ \frac{\ln(\text{dbh}/\delta)}{\sigma} \right]^2} \quad (2)$$

where  $\delta$  is the dbh (of the target tree) at which PotG occurs, and  $\sigma$  determines the breadth of the function. The function can be monotonically increasing (i.e., when  $\delta$  is very large), decreasing (i.e., when  $\delta$  is very small), or have a single “hump” and a skew to the left when  $\delta$  is within the normal range of dbh (Canham et al. 2004).

*Site effect.*—Ordination results identified two major axes of variation in relative abundance of species that could be readily interpreted as variation in site conditions among plots. We used two alternative

functions to estimate the relationship between growth of trees in a plot and variation in environmental conditions as reflected in the ordination scores (Eqs. 3 and 4). The following equation produces a Gaussian distribution along an environmental axis, but can also produce sigmoidal, monotonic curves:

$$\text{site effect} = e^{-1/2 \left( \frac{\text{axis}1_i - X1_0}{X1_b} \right)^2} \times e^{-1/2 \left( \frac{\text{axis}2_i - X2_0}{X2_b} \right)^2} \quad (3)$$

where axis<sub>1</sub><sub>*i*</sub> and axis<sub>2</sub><sub>*i*</sub> are the observed ordination axis scores for plot *i*, X<sub>10</sub> and X<sub>20</sub> are the estimated axis 1 and 2 scores, respectively, at which maximum potential growth occurs, and X<sub>1b</sub> and X<sub>2b</sub> are estimated parameters that control the breadth of the function (i.e., the variance of the Gaussian distribution). Note that axes 1 and 2 are abstractions and can refer to any two axes of environmental information, whether they are from ordinations of data or any other approach to indexing or scoring environmental variables. As an alternate model, we test the bivariate logistic equation, which produces a non-sigmoidal monotonic curve:

$$\text{site effect} = \left( 1 + \frac{\text{axis}1_i}{X1_0} \right)^{-X1_b} \times \left( 1 + \frac{\text{axis}2_i}{X2_0} \right)^{-X2_b} \quad (4)$$

where all of the terms are as defined for Eq. 3, except that the original axis scores have been rescaled to be greater than zero by adding the minimum axis score plus 0.1 to each value. For both Eqs. 3 and 4, we also tested univariate functions in which terms for one of the two axes were dropped from the analysis if initial results indicated that there was no response of a target species to that axis.

**Competition.**—We assume that growth declines monotonically as a function of a neighborhood competition index (NCI):

$$\text{competition} = e^{-C \cdot \text{NCI}^D} \quad (5)$$

If *D* = 1, this is a traditional negative exponential function. If *D* > 1, the function is sigmoidal, with an initially slow rate of decline that steepens as NCI increases. NCI specifies the net competitive effect of all neighbors on the target tree as a function of species ( $\lambda_i$ ), size ( $\alpha$ ), and distance ( $\beta$ ) to neighbor trees (Canham et al. 2004, 2006):

$$\text{NCI} = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(\text{dbh}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \quad (6)$$

The species-specific competition index ( $\lambda_i$ ) ranges from 0 to 1 and allows for differences among species in their competitive effect on the target tree. To facilitate comparisons of  $\lambda_i$  across different species of target trees, the values for each species or group of competitors are rescaled as a fraction of the highest  $\lambda_i$ . As in Canham et al. (2006), we evaluated three alternate sets of competition models with different groupings of neighbors. The

“full” model used separate  $\lambda_i$  for each species of competitor for which there were greater than 20 neighbors (summed across all target trees) in the 420 plots. All other neighboring species were pooled into an “other species” category. We also specified an “intra-specific vs. interspecific” model that estimated separate  $\lambda_i$  for intraspecific competitors and interspecific competitors, and an “equivalent competitors” model in which all species of competitors had equivalent effects (i.e.,  $\lambda_i = 1$  for all neighbors).

We also tested whether a given level of crowding had a greater or lesser effect as a function of the size of the target tree by allowing the exponential decay coefficient (*C*) in Eq. 5 to vary as a function of target tree size (*dbh<sub>t</sub>*) (Canham et al. 2004, 2006):

$$C = C' \times \text{dbh}_t^\gamma \quad (7)$$

If  $\gamma < 0$ , then sensitivity to crowding declines as target tree *dbh* increases (i.e., smaller trees suffer a greater reduction in growth from a given level of crowding than do larger trees). This effect is independent of the underlying effect of target tree size on potential growth in the absence of competition (Eq. 2). The crowding function distinguishes between the competitive “effects” of neighbors ( $\lambda_i$ ,  $\alpha$ , and  $\beta$  in Eq. 6) and the competitive “response” of the target plant (*C* and *D* in Eq. 5, and  $\gamma$  in Eq. 7) (Goldberg 1990, Goldberg and Landa 1991).

#### Analytical approach

**Parameter estimation and model evaluation.**—We use simulated annealing (a global optimization procedure, Goffe et al. 1994) to estimate the maximum likelihood parameters and support intervals for all terms in the models. The analyses were done using software written specifically for this study using Delphi for Windows (Version 6, Borland Software Corporation, Cupertino, California, USA). As in many of the earlier studies (e.g., Canham et al. 2004, 2006, Uriarte et al. 2004a) an assumption of normally distributed residuals with the variance proportional to the mean was appropriate for the data. This was incorporated into the analysis by estimating an additional parameter to determine the scaling of the variance to the mean (e.g., Pacala et al. 1994). We compared models using the Akaike information criterion corrected for small sample size (AIC<sub>c</sub>; Burnham and Anderson 2002). Goodness of fit of the models was evaluated using *R*<sup>2</sup> (defined as 1 – sse/sst) and the slope of the regression of observed vs. predicted (as a measure of bias).

**Multi-model inference.**—Together, Eqs. 2–7 comprise the complete model described by Eq. 1. Alternate models are formed in two ways: (1) by using Eqs. 3 and 4, which represent two different (i.e., non-nested) possible theoretical models of growth along an environmental gradient, and (2) by forming nested models by dropping selected components or parameters for which there is at most a weak response of the target tree as suggested by predicted values using the complete model.

TABLE 2. Parameter values with support intervals (in parentheses) for the AIC<sub>c</sub> selected best model for each species.

Species	Best model			ε <sub>1</sub>	MaxRG	NCI scaling parameters		Neighbor size, α	Neighbor distance, β
	Slope	R <sup>2</sup>	Comp.			C	D		
FAGR	0.975	0.342	inter.	0.59 (0.57, 0.60)	5.15 (4.93, 5.19)	35.43 (34.93, 35.93)	1.48 (1.44, 1.50)	0.91 (0.9, 1.02)	0.005 (0, 0.17)
TSCA	1.000	0.397	inter.	0.55 (0.54, 0.57)	5.62 (5.56, 5.73)	14.89 (14.38, 15.38)		1.18 (1.17, 1.27)	0.25 (0.24, 0.28)
ACSA	0.979	0.190	full	0.85 (0.84, 0.86)	3.89 (3.86, 3.93)	453.45 (448.9, 457.9)	1.77 (1.75, 1.79)	1.35 (1.34, 1.37)	0.72 (0.72, 0.73)
BEAL	1.019	0.364	equi.	0.52 (0.50, 0.53)	5.82 (5.76, 6.0)	2.33 (1.83, 2.83)		0.94 (0.93, 1.0)	1.00 (0.99, 1.09)
ACRU	0.991	0.191	full	1.06 (1.05, 1.07)	5.06 (5.01, 5.11)	47.54 (47.03, 48.03)		1.49 (1.48, 1.52)	0.33 (0.325, 0.331)
QURU	0.996	0.498	full	0.42 (0.41, 0.43)	7.27 (7.20, 7.34)	332.44 (329.1, 335.8)		1.40 (1.39, 1.41)	0.00 (0.00, 0.002)
FRAM	0.983	0.353	full	0.83 (0.81, 0.84)	8.54 (8.37, 8.63)	90.32 (89.42, 91.22)		2.49 (2.44, 2.52)	0.00 (0.00, 0.002)
PIST	0.991	0.382	full	1.09 (1.09, 1.15)	11.04 (10.93, 11.15)	636.96 (624.2, 643.3)		1.94 (1.93, 1.96)	0.47 (0.44, 0.47)

Notes: Species are listed in approximate decreasing order of shade tolerance. Species codes are as in Table 1. A support interval is defined as the range of the parameter value that results in less than a two-unit difference in AIC<sub>c</sub>. It is roughly equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel 1997). The parameter ε<sub>1</sub> is the error variance proportionality, MaxRG is the estimated maximum radial growth (PotG in Eq. 1), C and D control the shape of the function describing the response of a target tree to variation in NCI (Eq. 5), α and β estimate the effect of neighbor tree size and distance (Eq. 6), γ estimates the effect of target tree size (Eq. 7), and δ and σ are from Eq. 2: δ describes the dbh at which MaxRG occurs; σ determines the breadth of the function. Finally, X<sub>0</sub> and X<sub>b</sub> are from Eq. 3 or 4 depending on whether the best model included the Gaussian or the logistic equation: X<sub>0</sub> describes the size at which maximum potential growth is estimated to occur, and X<sub>b</sub> controls the breadth of the function (i.e., the variance of the normal distribution).

The model with the lowest AIC<sub>c</sub> is the most parsimonious model and is considered the best. The absolute magnitude of the differences in AIC<sub>c</sub> between alternate models (ΔAIC<sub>c</sub>) provides an objective index of the strength of empirical support for the competing models (Burnham and Anderson 2002). Most studies using BMI typically stop here (e.g., Canham et al. 2006) and base both scientific inferences and subsequent simulation on the selected best model. However, AIC<sub>c</sub> can also be used to assess the relative strength of evidence for competing models, using Akaike weights (ω<sub>i</sub>) derived from the differences between AIC<sub>c</sub> values:

$$\omega_i = \frac{e^{-0.5\Delta_i}}{\sum_{r=1}^R e^{-0.5\Delta_r}} \tag{8}$$

where Δ<sub>i</sub> is ΔAIC<sub>c</sub> between the best model and the *i*th model and R is the number of models used in the analysis (Burnham and Anderson 2002). The Akaike weight of model *i* can be interpreted as the expected probability of that model being selected best if one were to take repeated independent samples from the same population. If ω<sub>best</sub> ≥ 0.9, there is little basis for including alternate models and the best model is typically used (BMI). If ω<sub>best</sub> < 0.9, however, then no single model is clearly superior, and there may be benefits to model averaging using Akaike weights. In particular, model averaged estimates often have reduced bias compared to the best model (Burnham and Anderson 2002). For nonlinear models, as in our case, model averaged growth is calculated as follows:

$$E(\hat{y}) = \sum_{i=1}^R \omega_i E(y_i) \tag{9}$$

where E(ŷ) is the model averaged estimate of the predicted expected response variable E(ŷ<sub>i</sub>) (i.e., growth) across models for a given value of the predictor variable (Burnham and Anderson 2002).

*Prediction using multi-model inference: a simplified application.*—To illustrate the utility of MMI in forest simulations designed to help improve predictions for forest managers, we present an example predicting growth of *Q. rubra* and *F. americana* as a function of target tree size and conditions at three sites along one resource gradient.

## RESULTS

### Model evaluation

All of the models produced unbiased estimates of growth (i.e., slopes of predicted vs. observed growth were all ~1.0, Table 2). Model R<sup>2</sup> for the best models for each species ranged from 0.19 to 0.50 (Table 2). The variance in predicted growth increased as a linear function of predicted growth for all of the best models, with slopes ranging from 0.42 to 1.1 (Table 2) and intercepts of 0 for all species except *B. allegheniensis* (data not shown). Factors such as pests, pathogens, physical damage, and the residual effects of suppression and release (Wright et al. 2000, Jones and Thomas 2004) all increasingly contribute to variation in growth as growth increases, making such heteroscedasticity common in studies of tree growth (Pacala et al. 1994,

TABLE 2. Extended.

Target tree size, $\gamma$	Size effect		Axis 1		Axis 3	
	$\delta$	$\sigma$	$X_0$	$X_b$	$X_0$	$X_b$
-0.94	12.8	1.43				
(-0.95, -0.93)	(12.8, 12.93)	(1.24, 1.44)				
-0.64	80.37	10.83				
(-0.649, -0.630)	(27.33, 81.17)	(10.72, 20)				
-1.60	24.24	1.02	0.38	0.99		
(-1.62, -1.59)	(23.27, 24.49)	(1.01, 1.03)	(0.37, 0.39)	(0.95, 1.0)		
	12.7	1.14				
	(12.7, 13.21)	(1.12, 1.24)				
-1.14	98.44	2.95			1.7	2.92
(-1.15, -1.13)	(97.46, 99.43)	(2.92, 2.98)			(1.68, 1.7)	(2.86, 2.95)
-1.79	81.01	4.91	0.95	1.27	0.10	1.76
(-1.81, -1.77)	(80.20, 95.60)	(4.52, 4.96)	(0.94, 0.96)	(1.26, 1.3)	(0.07, 0.10)	(1.71, 1.78)
-1.09	26.17	12.03	0.93	0.65	0.84	2.66
(-1.10, -1.77)	(25.91, 82)	(1.92, 12.15)	(0.92, 0.94)	(0.58, 0.66)	(0.83, 0.84)	(2.47, 2.68)
-1.67	12.83	1.62			0.45	0.75
(-1.69, -1.65)	(12.7, 12.96)	(1.55, 1.63)			(0.44, 0.45)	(0.74, 0.76)

Canham et al. 2004, 2006). One factor that limits the predictive power of our current study is plot size. There was evidence that the plot size is too small to estimate the full effects of neighboring trees for three of the eight species (based on predicted values of  $\beta \approx 0$ ; Table 2). Canham et al. (2006) used the same sized plots and found similar limitations for some of their species. Other studies that have used the same approach (e.g., Canham et al. 2004, Uriarte et al. 2004a, b) have used larger plots and found the effective neighborhood radius varied among species from 3.2 to 19.8 m.

*Effects of target tree size on potential growth*

Predicted maximum growth (maxRG, Table 3) was positively correlated with shade tolerance ranking (Spearman's  $r_S = 0.74$ ,  $P = 0.025$ ,  $n = 8$ ). There was a

striking difference between the magnitudes of predicted growth of the three most shade intolerant species and the more shade-tolerant species as a function of target tree dbh in the best models (Fig. 1). This pattern was also remarkably consistent across all models in the prediction set (predicted growth varied  $<2\%$  for seven of the eight species). The greatest disparity was among the models for *F. americana*, for which predictions varied by up to 6.7% for 15 cm dbh trees, but decreased to  $<1\%$  by 40 cm dbh trees (results not shown).

*Variation in potential growth of tree species along environmental gradients*

The two axes of the DCA ordination with the highest coefficients of determination were readily interpretable as gradients in soil moisture (axis 1) and soil fertility

TABLE 3. List of models included in the prediction set as determined by  $\Sigma\omega_i > 0.9$ .

Species	$\omega_{best}$	$\Sigma\omega_i$	$N(n)$	Competition model				$\gamma$	Axis 1		Axis 3	
				Full	Inter.	Equiv.	None		L	G	L	G
FAGR	0.404	0.924	6 (2)	0.022	<b>0.902</b>	NA	NA	<b>0.544</b>	0.031	0.063	0.024	NA
TSCA	0.331	0.917	6 (4)	0.117	<b>0.800</b>	NA	NA	<b>0.917</b>	0.031	0.307	NA	0.162
ACSA	0.560	0.901	4 (2)	<b>0.833</b>	0.068	NA	NA	<b>0.901</b>	0.068	<b>0.781</b>	NA	0.281
BEAL	0.261	0.902	13 (2)	0.135	0.231	<b>0.576</b>	NA	0.370	NA	NA	0.231	0.078
ACRU	0.449	0.921	5 (2)	<b>0.921</b>	NA	NA	NA	<b>0.921</b>	0.162	0.051	<b>0.540</b>	0.381
QURU	0.437	0.923	3 (3)	<b>0.923</b>	NA	NA	NA	<b>0.923</b>	0.237	<b>0.686</b>	0.249	<b>0.674</b>
FRAM	0.207	0.916	7 (5)	<b>0.721</b>	0.195	NA	NA	<b>0.571</b>	NA	<b>0.815</b>	<b>0.400</b>	0.516
PIST	0.747	0.944	4 (1)	<b>0.866</b>	0.078	NA	NA	<b>0.944</b>	0.060	0.059	NA	<b>0.944</b>

*Notes:* This set forms the basis for multi-model inference. This table can also be used to determine the relative importance of several key variables conditioned on the full set of models tested. For example, we can see that *A. rubrum* is well-behaved in the sense that species-specific competition, tree size, and axis 3 (fertility) are important in all models that make up the prediction set. However, there is only weak support that axis 1 (moisture) is important. *B. allegheniensis*, on the other hand, shows mixed support for the importance of the different competition models ( $\Sigma\omega_{eq} = 0.536$ ,  $\Sigma\omega_{int} = 0.231$ ,  $\Sigma\omega_{full} = 0.135$ ), and tree size and axis 3 have no effect ( $\Sigma\omega = 0.542$  and  $\Sigma\omega = 0.593$ , respectively). Despite the weak support for the best model ( $\omega_{best} = 0.261$ ), MMI reveals very strong support that axis 1 has no effect on the growth of *B. allegheniensis* ( $\omega_{(A1)} = 0/0.902$ ). In this way, MMI improves our understanding of which components of a system we can be more certain about and which we are less certain about and warrant more study. Parameters with values in boldface text indicate their presence in the best model;  $N$ , number of models in the prediction set;  $(n)$ , number of models with  $\omega > 0.1$ ;  $\gamma$ , response of target tree to competition as a function of its size; L, logistic model; G, Gaussian model of variation of tree growth along axis; NA, the effect did not show up in any of the models in the prediction set.

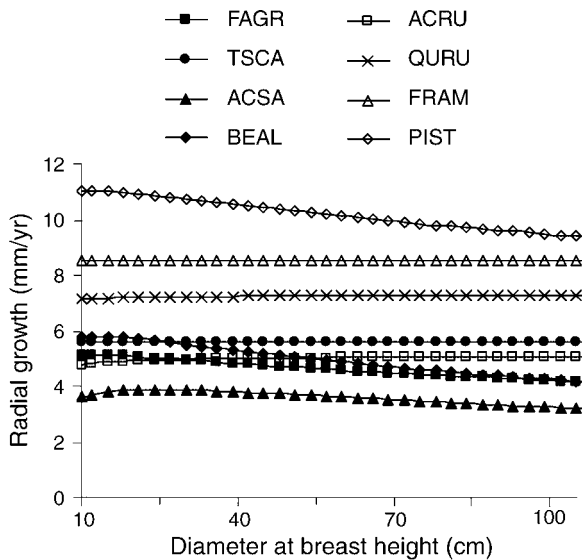


FIG. 1. Effect of target tree size on potential growth for the AIC<sub>c</sub> best models of each species. Potential growth of the less shade-tolerant species (open symbols) was generally greater than potential growth of more shade-tolerant species (solid symbols) for all sizes of trees. Species codes are in Table 1.

(axis 3; Fig. 2). The species at the low end of axis 1 (e.g., *A. saccharum*, *T. canadensis*, and *Prunus serotina*) are known to reach greatest abundance on mesic sites, while species at the high end of axis 1 (e.g., *Quercus* spp. and *P. strobus*) are typically found on more xeric sites (Burns and Honkala 1990). The species at the low end of axis 3 (e.g., *F. americana* and *A. saccharum*) are well known for their occurrence on richer soils (Fowells 1965), whereas *T. canadensis* and *F. grandifolia* are typically found on more acidic soils with lower base saturation (Kobe et al. 1995, Kobe 1996, Van Breeman et al. 1997).

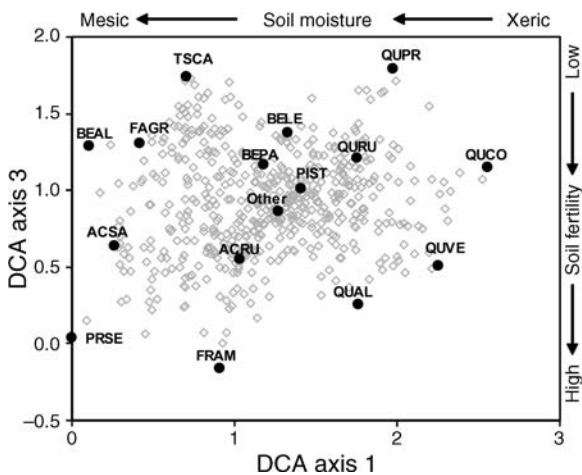


FIG. 2. DCA ordination plot scores with species centroids for axes 1 and 3. Autecologies of key species (codes identified in Table 1) indicate that these two axes may represent ecosystem gradients in soil moisture (axis 1) and soil fertility (axis 3).

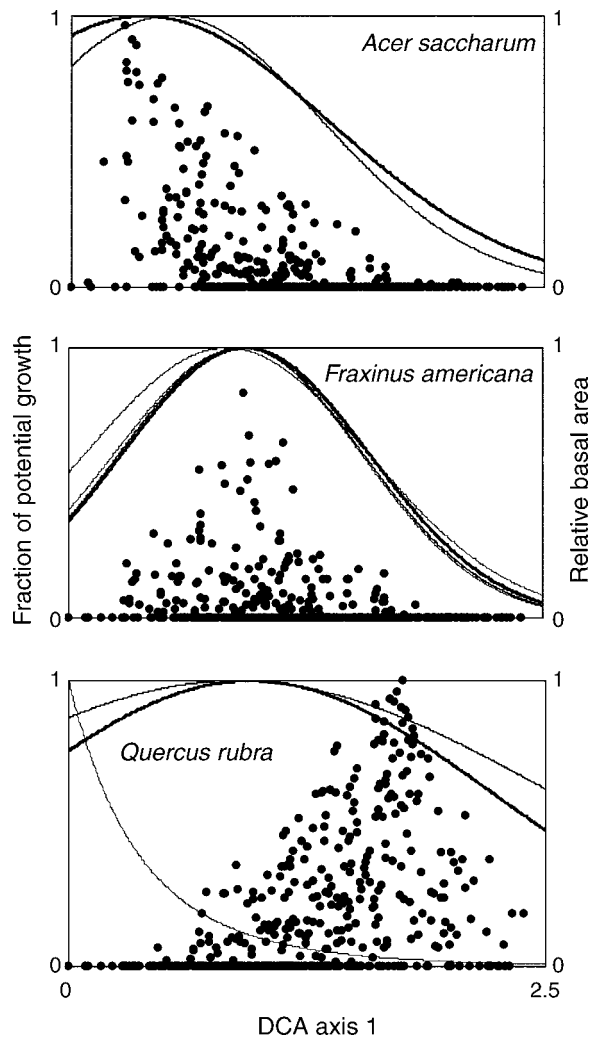


FIG. 3. Comparison of the fraction of potential growth (solid lines) with relative basal area in each plot (solid circles) as a function of DCA axis 1 scores. The heavy line shows the AIC<sub>c</sub> best model; lighter lines show alternate models for which  $\omega_i > 0.1$ .

Potential growth of five of the eight species showed a response to at least one of the ordination axes, *F. americana*, *Q. rubra* on both axes, *A. saccharum* on axis 1, and *Acer rubrum* and *P. strobus* on axis 3 (Figs. 3 and 4). On axis 1 (the putative moisture gradient), *A. saccharum* and *F. americana* were most abundant at sites where they reached their predicted optimal growth, while abundance of *Q. rubra* was displaced toward the poorer end of the gradient (i.e., higher axis scores) from where it was predicted to achieve greatest growth (Fig. 3). On axis 3 (the putative fertility gradient), *F. americana* and *A. rubrum* reached their greatest abundance toward the richer end of the gradient (i.e., lower axis scores); peak abundances of *P. strobus* and *Q. rubra* were displaced toward the poorer end of the gradient

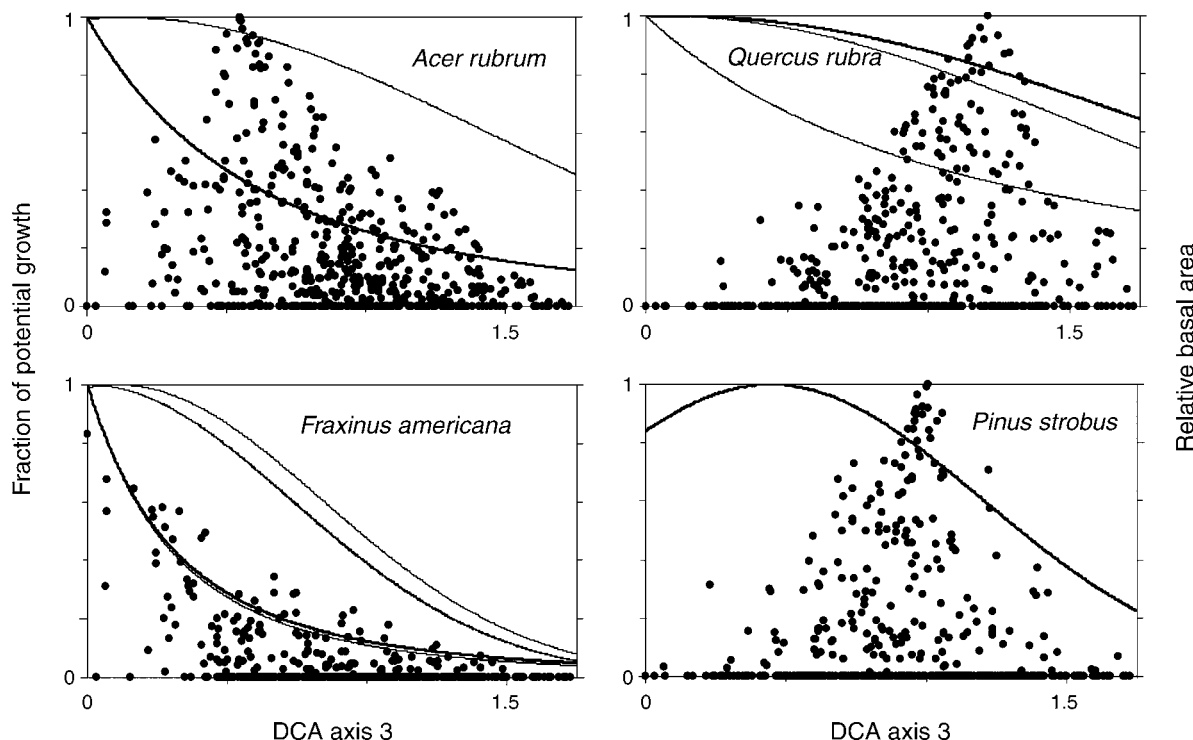


FIG. 4. Comparison of the fraction of maximum potential growth (solid lines) with relative basal area in each plot (solid circles) as a function of DCA axis 3 scores. The heavy weighted line shows the AICc best model; lighter weighted lines show alternate models for which the  $\omega_i > 0.1$ .

away from the sites where they were predicted to reach their optimal growth (Fig. 4).

#### Variation in competitive effects of neighboring species

The parameters  $\lambda_i$ ,  $\alpha$ , and  $\beta$  (Eq. 6) estimate the competitive effects of neighboring species. The parameter  $\lambda_i$  estimates the species-specific relative competitive strength of neighboring trees independently of their size or distance from the target tree. Evidence for the effect of competition from neighbors on growth of target trees was overwhelming ( $\omega_{\max} < 0.0005$ , for the “no competition” model); however, the strength of evidence for differences among neighboring species in their competitive effect on a target species varied among the target species. The “full” species-specific competition model was the best model for five of the eight target species (Table 3). The simpler model that discriminated between conspecific and interspecific competitors was most parsimonious for the two most shade-tolerant species, *F. grandifolia* and *T. canadensis* (Table 3). The equivalent species competition model was the best competition model only for *B. allegheniensis* (Table 3). The parameter  $\alpha$  provides a measure of how a target tree responds to neighbor size averaged across all species of neighbors (Eq. 5). Estimates for  $\alpha$  in the best models varied from just less than 1 to 2.5 (Table 2). The sensitivity of target trees to the size of neighboring trees was positively correlated with shade tolerance rank

(Spearman's  $r_S = 0.88$ ,  $P = 0.005$ ,  $n = 8$ ). The parameter  $\beta$  provides a measure of how the effect of neighboring trees decreases as a function of distance from a target tree. The maximum likelihood estimates of  $\beta$  were zero for three of the species, indicating that the effects of neighbors did not decline within the 7.3 m radius of the plot. The three species do not fall into any grouping with respect to shade tolerance. This suggests that the effective competitive neighborhoods for these three species are larger than the plot size. For the remaining five species, estimates of  $\beta$  ranged from 0.25 to 1.0 (Table 2) and there was no correlation between the magnitude of  $\beta$  and the shade tolerance rank of those species (Spearman's  $r_S = 0.35$ ,  $P = 1.000$ ).

#### Variation in competitive responses of target trees

The parameters  $C$ ,  $D$  (Eq. 5), and  $\gamma$  (Eq. 7) estimate the competitive responses of target trees to crowding. The effects of target tree size on the response of a tree to crowding by neighbors is controlled by the parameter  $\gamma$  (Eq. 7); when  $\gamma < 0$ , sensitivity to crowding declines as target tree dbh increases (i.e., smaller trees suffer a greater reduction in growth from a given level of crowding than do larger trees). The best models for seven of the eight species included  $\gamma$ , with  $\gamma < 0$  in all seven species (Table 2). There was a positive correlation between the magnitude of  $\gamma$  and shade tolerance rank (Spearman's  $r_S = 0.64$ ,  $P = 0.1$ ,  $n = 7$ ), with more shade-



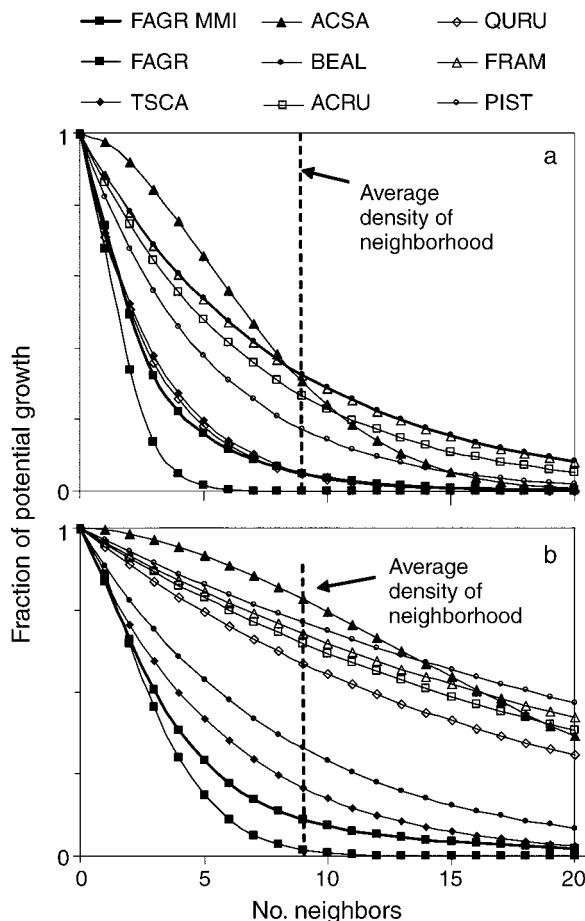


FIG. 5. Fraction of potential growth as a function of the number of trees of a given dbh and distance from (a) a 15 cm dbh target tree and (b) a 40 cm dbh target tree of each species. The neighborhood consists of a set of trees all of which are 23.2 cm dbh and 4.75 m away. Species are sorted in approximate inverse shade-tolerance order. With the exception of *Acer saccharum*, there is a clear shade-tolerance relationship that is stronger with the size of the target tree. Also, due to the effect of  $\gamma$ , the more shade tolerant a species is, the less its growth decreases as a function of target tree size. Species codes are in Table 1.

tolerant species generally having values of  $\gamma$  closer to zero (Table 3). Support for the importance of  $\gamma$  is buttressed using MMI, as the one species for which  $\gamma$  was unimportant in the best model (*B. allegheniensis*) had some support in the prediction set ( $\Sigma\omega_\gamma = 0.370$ , Table 2), and there was reasonable model selection uncertainty between this and the best model ( $\omega_{\text{best}} = 0.261$  vs.  $\omega_{\text{alt}} = 0.110$ ,  $\Delta\text{AIC}_c = 1.70$ ). Moreover, the value of  $\gamma$  in this alternate model ( $\gamma = -0.820$ ) did not change the significance of the correlation of shade tolerance rank (Spearman's  $r_S = 0.58$ ,  $P = 0.1$ ,  $n = 8$ ).

Growth declined as a simple exponential function of NCI for six of the eight species (Table 2, parameter  $D \approx 1$ ). The parameter  $C$  describes the slope of decrease in growth as NCI increases. The magnitude of  $C$  was

negatively correlated with shade tolerance ranking (Spearman's  $r_S = 0.6$ ,  $P = 0.1$ ,  $n = 8$ ). The best models for *F. grandifolia* and *A. saccharum* both predicted  $D > 1$ , however, support for  $D > 1$  was decidedly mixed for *F. grandifolia* ( $\omega_{D>1} = 0.49$  vs.  $\omega_{D=1} = 0.43$ ). To illustrate the effect of NCI on predicted growth, we compared the effect of equivalent neighborhoods on each species (Fig. 5). Fig. 5 shows the response of a 15 cm and 40 cm dbh target tree to a simplified representation of an "average" neighborhood in which all neighborhood trees are the median dbh for the data set and the median distance away from the target tree (Table 1). Because predictions of  $D$  were consistent for all species except *F. grandifolia*, we highlight the MMI inferred growth only for that species. Sensitivity to crowding varied dramatically among these species under these "average" conditions; growth of the more tolerant species declined more steeply as the neighborhood became denser (Fig. 5). In this example, the effects of  $\alpha$ ,  $\beta$ , and  $\gamma$  are held constant. Thus, variation in response among species is due entirely to the effect of the parameter  $C$ . *Fagus grandifolia* had the greatest decline of maximum potential growth, whether one considers the best model alone or model averaged predictions (Fig. 5), suggesting that MMI is unlikely to substantially alter predictions in the relative effect of NCI on growth among these species.

#### Analysis of the relative importance of processes using multi-model inference

The weight of evidence for the best models ranged from 0.207 (*F. americana*) to 0.747 (*P. strobus*) (Table 3) indicating considerable uncertainty in model selection. Depending on species, it took three to 13 models before  $\Sigma\omega_i > 0.9$  (Table 3, data tables in Appendix). We call this subset of models for each species the "prediction set." One simple use of MMI is in improving estimates of our confidence in inferences based on BMI, by estimating the relative importance of parameters (or groups of parameters) among the models in the prediction set. For example, we can estimate the importance of the effect of target tree size on sensitivity to competition ( $\gamma$ ) by calculating  $\Sigma\omega_\gamma$  of those models in which  $\gamma$  appears, over the subset of all models included in the prediction set. Based on this criterion, target tree size was very important in determining the sensitivity to competition for five of eight species, was less so for *F. grandifolia* and *F. americana*, and ambivalent for *B. allegheniensis* (Table 3). Support for the effect of variation in site conditions (as inferred from plot scores along the two ordination axes) also varied among species. Axis 1 was important to *Q. rubra* and only slightly less so to both *A. saccharum*, and *F. americana* (Table 3), whereas axis 3 was important to *A. rubrum*, *F. americana*, *P. strobus*, and *Q. rubra*. The most shade-tolerant species, *F. grandifolia*, did not respond to either axis ( $\Sigma\omega_{A1} = 0.094$ ,  $\Sigma\omega_{A3} = 0.024$ ; Table 3), and the next most shade tolerant, *T. canadensis*, also probably did not ( $\Sigma\omega_{A1} = 0.338$ ,  $\Sigma\omega_{A3} = 0.162$ ; Table 3). Support is

overwhelming that all species were subject to the competitive effect of neighbors (Table 3); however, the manner in which species responded to the identities of trees in their neighborhood varied. Five species showed strong support for the model in which neighboring species had different competitive effects (Table 3). Two species were sensitive to different competitive effects of conspecific neighbors vs. interspecific neighbors (Table 3). Only one species, *B. allegheniensis*, responded to all neighbors equivalently regardless of species identity, and support for this was decidedly ambivalent ( $\omega_{eq} = 0.536$ , Table 3).

*Prediction using multi-model inference:  
a simplified application*

Using MMI to predict growth requires incorporating the effects of all the models with sufficient support based on Eq. 8, for each species in the prediction set, using Eq. 9. We consider three hypothetical sites each with the same axis 1 scores, but different axis 3 scores, and illustrate the differences in predictions of growth using BMI vs. MMI. Sites were selected to represent environments where *F. americana* is most abundant (site A), where *Q. rubra* is most abundant (site B), and where both species are fairly common (site C). All plots have a hypothetical mean neighborhood (Table 1) and consist of eight 23.2 cm dbh trees, each of which are 4.75 m away. For simplicity, we set  $\beta = 0$  and  $\lambda_i = 1$  for all species.

Because no single model was overwhelmingly best for any of the eight species (max  $\omega = 0.747$ ; Table 3), predictive efficacy of the best models is likely weak. Our MMI analysis showed that the magnitudes of several important parameters are remarkably consistent among models (e.g., tree size effect,  $D$ ,  $\alpha$ ), thus increasing our confidence in their effects. Other parameters, however, varied considerably for at least some species (e.g., axis 1, axis 3,  $\gamma$ ) and revealed important areas of uncertainty. In particular, there was considerable uncertainty in the effects of axis 3 on potential growth of *F. americana* and *Q. rubra* (Table 3, Fig. 4). The data were ambivalent in choosing between a logistic and a Gaussian shaped effect of axis 3 on growth for both species (Table 3). It is important to note that scientific inference with respect to axis 3 is consistent whether one uses BMI or MMI: *F. americana* is most common where it grows best, and competition displaces *Q. rubra* from where it grows best. Nevertheless, MMI suggests that the different possible quantitative effects of this axis on growth could be important, because the magnitude of predicted growth across the gradient differed considerably among models in the prediction set (Fig. 4).

The effect of  $\gamma$  (i.e., target tree size) on sensitivity to crowding, in terms of weight of evidence, was considerably more important to *Q. rubra* ( $\Sigma\omega = 0.92$ ) than *F. americana* ( $\Sigma\omega = 0.57$ ). The predicted values of  $\gamma$  for *Q. rubra* were consistent among alternate models (i.e., between  $-1.698$  to  $-1.876$ ; Appendix, Table A8) showing a strong decreasing effect of competition on

trees as they got larger. As might be expected for a parameter without strong support in the data, the predicted values of  $\gamma$  for *F. americana* varied considerably among alternate models ( $-0.5$  to  $-2.0$ ; Appendix, Table A6). The consistency in the estimates of  $\gamma$  for *Q. rubra* suggest that predictions of this effect based on only the best model would not differ much from prediction based on the entire prediction set. The effect of  $\gamma$  is strongly nonlinear, however, and simulations using model-averaged predictions of both *Q. rubra* and *F. americana* could vary considerably from those based only on the best models.

## DISCUSSION

*Variation in potential growth of tree species  
along environmental gradients*

Our analyses allowed us to explore the relationship between the fundamental niche of each species as represented by potential growth (Figs. 3 and 4, heavy solid lines) and their realized niche as represented by relative abundance (Figs. 3 and 4, dots) across the inferred environmental gradients. Both axes showed clear, but distinct, relationships of shade tolerance ranking with growth and abundance. Along axis 1 (moisture), the fundamental and realized niches of the two more shade-tolerant species coincided, but the realized niche of the less shade-tolerant *Q. rubra* was displaced toward the poorer end of the gradient (Fig. 3). In contrast, only less shade-tolerant species responded to axis 3 (Fig. 4), and maximum potential growth was at or near the rich end of the gradient for all four species. All four species showed varying degrees of displacement of their realized niches towards the poorer end of the gradient. The prediction set of models shows similar qualitative interpretations of these patterns, and our inference of a relationship between shade tolerance and patterns of fundamental vs. realized niche displacement is consistent across all models in the prediction set. Multi-model inference, however, reveals important variation among the models in the magnitudes of the predicted effect of each axis on some species. In particular, *Q. rubra* showed considerable variation in predicted growth along both axes, as did predicted growth of *F. americana* and *A. rubrum* along Axis 3. We conclude that since several of these key species reach their peak growth at different points along both gradients, and because this is consistent across models in the prediction set, fundamental niche differentiation sensu Whittaker (1975) plays an important role in structuring these forests. Nevertheless, there is a substantial amount of competitive displacement, especially for less shade-tolerant species.

*Variation in competitive effects of neighbors  
and competitive responses of target trees*

Hubbell's (2001) neutral model assumes that all individuals are functionally equivalent competitors, and works well despite measurable differences among

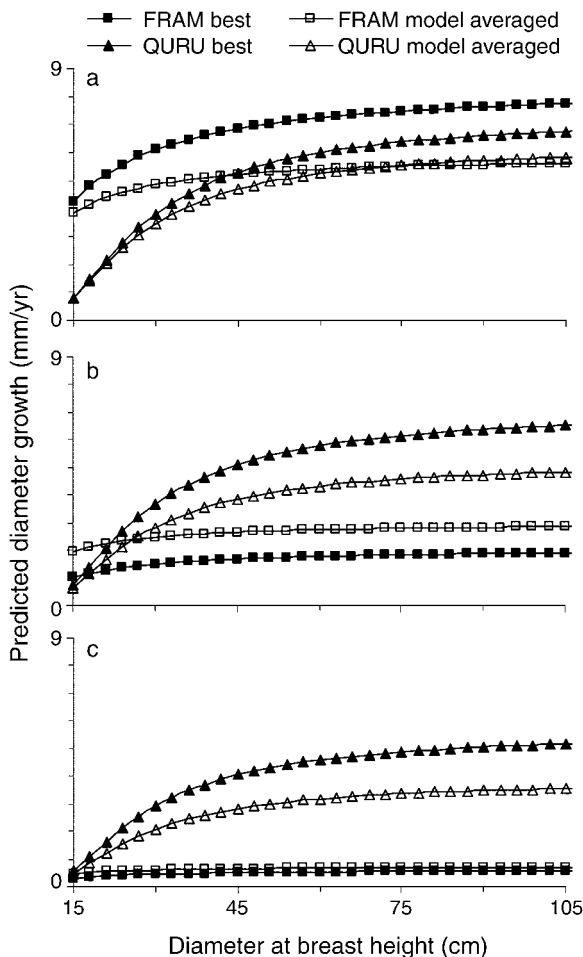


FIG. 6. Example of the importance of model averaging on predicted growth as a function of tree dbh at three points along axis 3 with two neighborhoods: (a) a rich site (axis 3 = 0.0), near where *Fraxinus americana* (FRAM) is most abundant (see Fig. 4); (b) an intermediate site (axis 3 = 0.78), where both species are roughly equally abundant; and (c) at a poorer site (axis 3 = 1.2), where *Quercus rubra* (QURU) is most abundant. Each target tree has eight neighbors at 23.2 cm dbh. Axis 1 = 1 for all graphs;  $\beta = 0$  for all models; therefore, there is no change in competitive effect with distance;  $\lambda = 1$  for all neighbors.

species and individuals. It is reasonable to expect, however, that the model performs better in some communities than others. Taken together, recent papers using our approach (Canham et al. 2004, 2006, Uriarte et al. 2004a, b, and results presented here) suggest that the assumption of competitive equivalence breaks down in less diverse forests. Over half of the species examined in tropical forests of Central America responded to conspecific vs. interspecific identities of neighboring tree species equivalently (Uriarte et al. 2004b). In the less diverse tropical forests of Puerto Rico, and temperate forests of North America, greater than 95% of the species examined responded differently to conspecific vs. interspecific neighbors (Canham et al. 2004, 2006, Uriarte et al. 2004a). These studies suggest that the

breakdown of the assumption of competitive equivalence occurs at a fairly high level of diversity, since the tropical rainforest species in Puerto Rico forests showed similar degrees of sensitivity to the identity of neighbors as was observed at the temperate forest sites.

#### Comparisons to forests of northern New England

Canham et al. (2006) used similar methods to explore competitive interactions among tree species of northern New England (Vermont and New Hampshire), basing inference solely on the best model (BMI). Both that study and the results of our analyses from southern New England were consistent in concluding that maximum relative abundance of shade intolerant species tended to be displaced from sites where predicted growth was greatest, whereas shade-tolerant species showed little if any displacement. More specifically, the four species in our analysis that responded to axis 3 (Fig. 4, the putative fertility gradient) respond to the fertility axis in the same way in Vermont and New Hampshire forests (Fig. 3 in Canham et al. 2006).

Consistency between the two studies in results for both the competitive response of target trees to neighbors ( $C$ ,  $\gamma$ ) and the competitive effects of neighbors ( $\alpha$ ,  $\beta$ ) were mixed. The magnitudes of two of the four parameters ( $\alpha$ ,  $\gamma$ ) in the two studies were significantly correlated for the eight species in common ( $\alpha$ , Spearman's  $r_S = 0.81$ ,  $P < 0.025$ ,  $n = 8$ ;  $\gamma$ , Spearman's  $r_S = 0.726$ ,  $P < 0.03$ ,  $n = 8$ ), but were not correlated for  $\beta$  and  $C$ . The lack of correspondence of  $\beta$  is not surprising considering the limitations of plot size. Nor are the inconsistencies in the estimates of  $C$  between the two studies particularly surprising, since the absolute value of  $C$  reflects scaling of the effects of neighbors by other parameters. However, the consistency in the predicted magnitudes of  $\alpha$  and  $\gamma$  on target tree growth reveals a remarkable consistency across a broad north-south gradient in the scaling of the effect of neighboring tree size on their competitive effect, and in variation in the sensitivity of target trees to crowding as a function of their size.

#### Prediction using multi-model inference

There were clear differences in the predictions of the best model vs. the averaged model for both target species at all three sites. The differences were sufficient to have profound impacts on the results of a simulation model (Fig. 6). At site A, both BMI and MMI predicted that the growth of smaller trees decreased dramatically, as we would expect given the results for  $\gamma$ . BMI predicts much greater growth of *F. americana* than *Q. rubra* at all sizes at this site, whereas MMI suggests that they converge (that is, given these neighborhood conditions). At the intermediate (site B) and poor (site C) sites, the differences between the best model predictions and model averaged predictions were more dramatic (Fig. 6b, c). At the intermediate site (B), the best model for *F. americana* underpredicted growth relative to model

averaged predictions. These results demonstrate that both the magnitudes and directions of the differences between the predictions of the best models and averaged models can change dramatically along a resource gradient, even in a relatively simple neighborhood. In all cases, model averaging resulted in smaller differences in predicted growth between these two species than predictions using only the best model. The best model predicted distinctly higher growth at the rich site for *F. americana* and for *Q. rubra* at the poor site, and thus seems to perform best at those sites where one species was clearly more abundant. Our results suggest that using MMI may be most important at sites where species are more equal in abundance (Fig. 6b).

BMI selects the model that best explains the observed data. No other model, or group of models, from the set of models used in the analysis does a better job of explaining that data. Therefore, we cannot expect model averaged predictions to do a better job in predicting the observed data. In fact, the reverse is actually true. MMI is a way of hedging bets when model selection uncertainty is high (i.e., when the differences between AICs of competing models are less than between 2 to 7 in most cases). Repeated samples drawn from a population would be expected to select different models as the best model roughly in proportion to their weights. Thus, our best estimates for the population from which the observed data were drawn may be given by MMI, and predictions of the behavior of the population may be more accurate using model averaging.

Modern mixed-species uneven-aged silviculture presents a host of new scientific challenges that require us to improve our understanding of how tree growth and survival vary among species across a wide range of stand structure, community composition, and environmental conditions. While BMI and MMI showed qualitatively consistent results for all species in our study, MMI revealed considerable uncertainties in the predicted magnitude of growth, especially away from sites where the species were expected to grow best. We have shown using a very simple example that predictions based on model averaging vs. the best models can vary dramatically as site and neighborhood conditions change. Thus, MMI augments the information in BMI and may lead to improved predictions of variation in the growth of trees as a function of site characteristics and local neighborhoods. In the face of imperfect data (and models), our results suggest that recommendations for forest management could benefit from judicious use of MMI.

#### ACKNOWLEDGMENTS

We thank Will McWilliams and the USDA Forest Service Forest Inventory and Analysis program for providing access to their remarkable datasets. We also thank two anonymous reviewers for their thoughtful criticisms of earlier drafts of this paper. This research was supported by the U.S. Environmental Protection Agency through the STAR Graduate Fellowship Program, Award #U91578401-0, and by the Andrew W. Mellon Foundation. The views expressed herein are those of the authors and do not represent positions taken by the EPA. This

study is a contribution to the program of the Institute of Ecosystem Studies, Millbrook, New York.

#### LITERATURE CITED

- Beaudet, M., C. Messier, and C. D. Canham. 2002. Predictions of understorey light conditions in northern hardwood forests following parameterization, sensitivity analysis, and tests of the SORTIE light model. *Forest Ecology and Management* **165**:235–248.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second ed. Springer-Verlag, New York, New York, USA.
- Burns, R. M., and B. H. Honkala, technical coordinators. 1990. *Silvics of North America: 1. conifers; 2. hardwoods*. Agriculture handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Burton, P. J., C. Messier, G. F. Weetman, E. E. Prepas, W. L. Adamowicz, and R. Tittler. 2003. The current state of boreal forestry and the drive for change. Pages 1–40 in P. J. Burton, C. Messier, D. W. Smith, and W. L. Adamowicz, editors. *Towards sustainable management of the boreal forest*. NRC Research Press., Ottawa, Ontario, Canada.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* **24**:337–349.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* **34**:778–787.
- Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J. Twery. 2006. Neighborhood analysis of canopy tree competition along environmental gradients in New England forests. *Ecological Applications* **16**:xx–xx.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**:1475–1494.
- Coates, K. D., C. Messier, M. Beaudet, D. L. Sachs, and C. D. Canham. 2003. Use of a spatially explicit individual-tree model SORTIE-BC to explore the implications of patchiness in structurally complex forests. *Forest Ecology and Management* **186**:297–310.
- Fowells, H. A. 1965. *Silvics of forest trees of the United States*. Agricultural Handbook #271. U.S. Forest Service, Washington, D.C., USA.
- Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* **60**:65–99.
- Goldberg, D. E. 1990. Components of resource competition in plant communities. Pages 27–49 in J. B. Grace and D. Tilman, editors. *Perspectives in plant competition*. Academic Press, San Diego, California, USA.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits. Pages 281–290 in J. Silvertown, M. Franco, and J. L. Harper, editors. *Plant life histories: ecology, phylogeny and evolution*. Cambridge University Press, Cambridge, UK.
- Gotelli, N. J., and A. M. Ellison. 2004. *A primer of ecological statistics*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Greene, D. F., C. D. Canham, K. D. Coates, and P. T. LePage. 2004. An evaluation of alternative dispersal functions for trees. *Journal of Ecology* **92**:758–766.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**:47–58.

- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in population biology 32. Princeton University Press, Princeton, New Jersey, USA.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19**: 101–108.
- Jones, T. A., and S. C. Thomas. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. *Canadian Journal of Forest Research* **34**:1525–1533.
- Kimmins, J. P. 1995. Sustainable development in Canadian forestry in the face of changing paradigms. *Forest Chronicle* **71**:33–40.
- Knapp, L. B., and C. D. Canham. 2000. Invasion of old-growth forests by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *Journal of the Torrey Botanical Society* **127**: 307–315.
- Kobe, R. K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs* **66**:181–201.
- Kobe, R. K., S. W. Pacala, J. A. Silander, Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5**:517–532.
- Kohm, K. A., and J. F. Franklin. 1997. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Covelo, California, USA.
- Kruskall, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**:1–27.
- Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons, London, UK.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data. PC-Ord version 4.28. Gleneden Beach, Oregon, USA.
- McGarigal, K., S. A. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York, New York, USA.
- Milner, K., D. Coble, A. McMahan, and E. Smith. 2003. FVSBGC: a hybrid of the physiological model STAND-BGC and the forest vegetation simulator. *Canadian Journal of Forest Research* **33**:466–479.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–43.
- Pacala, S. W., C. D. Canham, J. A. Silander, Jr., and R. K. Kobe. 1994. Sapling growth as a function of resources in a northern temperate forest. *Canadian Journal of Forest Research* **24**:2172–2182.
- Peng, C. H., J. X. Liu, Q. L. Dang, M. J. Apps, and H. Jiang. 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. *Ecological Modelling* **153**:109–130.
- Pinkard, E. A., and M. Battaglia. 2001. Using hybrid models to develop silvicultural prescriptions for *Eucalyptus nitens*. *Forest Ecology and Management* **154**:337–345.
- Ribbens, E., J. A. Silander, Jr., and S. W. Pacala. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**:1794–1806.
- Robinson, A. P., and A. R. Ek. 2003. Description and validation of a hybrid model of forest growth and stand dynamics for the Great Lakes region. *Ecological Modelling* **170**:73–104.
- Seidl, R., M. J. Lexer, D. Jager, and K. Honninger. 2005. Evaluating the accuracy and generality of a hybrid patch model. *Tree Physiology* **25**:939–951.
- Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004a. A maximum-likelihood, spatially explicit analysis of tree growth and survival in a tropical forest. *Ecological Monographs* **74**:591–614.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004b. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbors matter? *Journal of Ecology* **92**:348–360.
- USDA. 1998. Field instructions for the fourth inventories of southern New England: Massachusetts, Rhode Island, Connecticut. Version 1.0, March 1998. Forest Inventory and Analysis Unite, Northeastern Forest Experimental Station, Radnor, Pennsylvania, USA.
- USDA Forest Service. 2001. 2000 RPA assessment of forest and range lands. FS687. USDA Forest Service, Washington, D.C., USA.
- Van Breeman, N., A. C. Finzi, and C. D. Canham. 1997. Canopy tree–soil interactions within temperate forests: effects of fine-scale variation in soil texture and elemental composition on species distributions. *Canadian Journal of Forest Research* **27**:1110–1116.
- Whittaker, R. H. 1975. Communities and ecosystems. Second edition. MacMillan, New York, New York, USA.
- Wimberly, M. C., and B. B. Bare. 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. *Forest Ecology and Management* **89**:1–11.
- Wright, E. F., C. D. Canham, and K. D. Coates. 2000. Effects of suppression and release on sapling growth for eleven tree species of northern British Columbia. *Canadian Journal of Forest Research* **30**:1571–1580.

#### APPENDIX

Tables reporting results of ordinations and the parameter estimates and two-unit support intervals for the models for which weight of evidence > 0.1 for each of the eight target species (*Ecological Archives* A016-063-A1).