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Geographic extension of an uneven-aged, multi-species matrix growth model for northern hardwood forests

Audra E. Kolbe [a], Joseph Buongiorno [a,*], Michael Vasievich [b]

[a] *Department of Forest Ecology and Management, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA*
[b] *USDA Forest Service, North Central Forest Experiment Station, 1407 S. Hamison Road, Suite 220, East Lansing, MI 48823, USA*

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Abstract

The objective of this study was to update and extend the geographic range of a forest growth model for northern hardwoods, developed previously with data from the fourth Wisconsin inventory (Lin et al., 1996. Ecol. Model., 91: 193–211.). To this end, Lin's model was recalibrated with data from the recent fifth inventory of Wisconsin and Michigan, and with the addition of a site variable to reflect variations in land productivity. After the introduction of site effects, there were still statistically significant differences between the equations of ingrowth, upgrowth, and mortality for Wisconsin and Michigan. Thus, two models were maintained, one for each state. Each model predicted well the growth of trees on post-sample plots, and simulated adequately the tree distribution in old stands in its own state. Applied to stands of the same initial distribution of tree species and size, the equations predicted faster early growth and higher basal area in the steady state in Michigan than in Wisconsin, with more marked differences on good than poor sites.

Keywords: Growth; Matrix model; Forest ecosystems; Ecological diversity; Statistics

1. Introduction

Forests are important in the Great Lakes region of the United States. They contribute valuable economic and ecological services, and provide for recreational interests. The majority of Wisconsin's timberland is of the Maple–Beech–Birch forest type, which is dominated by shade-tolerant trees. Wisconsin's neighboring state of Michigan is also known for its northern hardwood forests. Northern hardwoods occupy about one-third of Wisconsin's timberland area (Schmidt, 1998) and almost two-fifths of Michigan's timberland (Leatherberry et al., 1996). About three-fourths of this land is privately owned, mainly by private citizens. Due to natural succession, many stands consisting of early suc-

* Corresponding author. Fax: +1-608-262-9922.
E-mail address: buongior@facstaff.wisc.edu (J. Buongiorno)

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cessional species, such as quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), are being replaced by later successional species, such as sugar maple (*Acer saccharum*) and American basswood (*Tilia americana*).

Some private land owners manage their forests with the intent of maximizing their profits. However, recent interest in conserving biological diversity and developing sustainable forests has been growing in private, as well as public, forests (Niese and Strong, 1992; Önal, 1997). It is often assumed that diversity must come at the expense of financial returns, but this need not be the case. Buongiorno et al. (1994)found that they could keep tree size diversity in maple-birch stands at levels up to 90% of its maximum without sacrificing monetary value. Thus, it is necessary to understand how growth and management effect diversity, in order for land owners to make the best decision on how to manage their lands.

In uneven-aged northern hardwoods, both diameter distribution and species composition are important. The reverse-*J* diameter distribution of an uneven-aged stand is necessary for natural regeneration and sustainable production (Leak and Filip, 1975). This diameter distribution also induces a high level of vertical stratification, which helps maintain biological diversity (Buongiorno et al., 1994; Hunter, 1990). Northern hardwoods are also rich in tree species (Eyre, 1980). They tend to be dominated by late-successional, shade-tolerant species, but also contain less tolerant species, which grow and respond to management differently.

Our understanding of these differences could be enhanced greatly by long-term field studies, but such studies are necessarily slow and expensive to conduct. Mathematical growth models are a viable alternative. In particular, matrix models have been used widely to describe stands of diverse tree size. Matrix models have a long history of applications in forestry, dating back at least to Usher (1966), Bruner et al. (1973), and Rorres (1978). Most of the applications have been to selection silviculture, but there have also been applications to even-aged stands (Pukkala and Kolstrom, 1988). In a matrix model, the diameter distribution of the stand is represented by a vector, and the transition from one stand state to the next is described by matrices. Buongiorno and Michie (1980) built a density-independent model based on regeneration, growth and mortality. Solomon et al. (1986), Mengel and Roise (1990), and Buongiorno et al. (1995) made incremental diameter growth and mortality depend on density. Several models have also investigated how growth differs between species or groups of species (Solomon et al., 1986; Bowling et al., 1989; Vanclay, 1989; Buongiorno et al., 1995). The models have been applied to a wide variety of temperate forest ecosystems in North America (Michie and McCandless, 1986; Miller, 1991; Lin et al., 1998), Europe (Buongiorno et al., 1995; Volin and Buongiorno, 1996), and Asia (Masuki et al., 1998), and to tropical forests in Africa and South-East Asia (Mendoza and Setyarso, 1986; Osho, 1991; Houde and Ledoux, 1995; Boscolo et al., 1997).

The objective of this study was to improve and generalize a growth model to predict the growth of northern hardwood stands in the Lake States region. The starting point was the model of Lin et al. (1996), based on the methods developed by Buongiorno et al. (1995). Lin et al. (1996) calibrated their model with data from the North Central Forest Inventory and Analysis' (NC-FIA) fourth inventory of Wisconsin. Data from Wisconsin's fifth inventory have recently become available. Thus, Lin's model was modified to include possible site effects on growth, and the model was recalibrated with Wisconsin's fifth inventory data. Next, the new model structure was estimated with data from Michigan's fifth inventory. The parameters of the two models proved to be statistically different, and simulation results suggested faster stand growth in Michigan, other things being equal.

2. Model form

Lin's model is the density-dependent, multi-species matrix growth model described in Lin et al. (1996). Stand growth from time t to $t+1$ is represented by three equations: Upgrowth, the probability that a tree grows from size j to $j+1$,

$$b_{ijt} = \beta_{i0} + \beta_{i1}\left[\sum_{i=1}^{m}\sum_{j=1}^{n} B_j(y_{ijt} - h_{ijt})\right] + \beta_{i2}D_j + \beta_{i3}D_j^2 + \beta_{i4}SD; \quad (i = 1,\ldots,m; j = 1,\ldots,n) \tag{1}$$

Mortality, the probability that a tree dies,

$$d_{ijt} = \delta_{i0} + \delta_{i1}\left[\sum_{i=1}^{m}\sum_{j=1}^{n} B_j(y_{ijt} - h_{ijt})\right] + \delta_{i2}D_j + \delta_{i3}D_j^2 + \delta_{i4}SD; \quad (i = 1,\ldots,m; j = 1,\ldots,n) \tag{2}$$

Ingrowth, the rate at which trees appear in the smallest size class, per unit area,

$$I_{it} = \alpha_{i0} + \alpha_{i1}\left[\sum_{i=1}^{m}\sum_{j=1}^{n} B_j(y_{ijt} - h_{ijt})\right] + \alpha_{i2}\sum_{j=1}^{n}(y_{ijt} - h_{ijt}) + \alpha_{i3}S \quad (i = 1,\ldots,m) \tag{3}$$

where i is tree species, j is the size, y is the number of live trees per unit area, h is the number of cut trees per unit area, B is the basal area, D is diameter, S is the site index, and α, β, δ are parameters.

Thus, upgrowth and mortality are functions of residual stand basal area, tree size, and site, while ingrowth is a function of residual stand basal area, number of trees of the same species, and site. Site index, S, did not figure in Lin's model and is added here as a first step in extending it to a larger geographic area.

Once estimated, equations (1) to (3) provide the parameters in the matrix growth model:

$$\boldsymbol{y}_{t+1} = \boldsymbol{G}_t(\boldsymbol{y}_t - \boldsymbol{h}_t) + \boldsymbol{c} \tag{4}$$

where the matrix $\boldsymbol{G}_t$ depends on stand basal area, after harvest.

3. Data

The data used to calibrate and test the growth model came from the NC-FIA database. Lin's original model had been calibrated from the fourth inventory of Wisconsin's forests. In 1996 the NC-FIA released a new set of data, corresponding to Wisconsin's fifth forest inventory. Data were from the periods 1981 through 1984 and 1993 through 1996, respectively. Even though both the fourth and fifth inventories were in the Eastwide Data Base (EWDB) format, there were differences in the classification, and in the measurement, of ingrowth trees (Kolbe, 1998; Miles, 1998). To facilitate comparisons, only plots classified as timberland were used, and ingrowth was measured only from points one through three, as in the study of Lin et al. (1996).

As a result, the fifth inventory data base gave 623 plots containing 18 359 observed trees with diameters of at least 2.5 cm. The number of years between measurements ranged from 10 to 15, with an average of 12 years. Most of the 623 plots came from the northeast (226 plots) and northwest (249 plots) units of Wisconsin. The remaining plots came from the central unit (77 plots), the southeast unit (50 plots), and the southwest unit (21 plots).

As in Lin et al. (1996), the trees were divided into three species groups: shade-tolerant species, mid-tolerant species, and shade-intolerant species, based on Preston (1989). The most common shade-tolerant species were sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and American basswood (*Tilia americana*). Mid-tolerant species included yellow birch (*Betula alleghaniensis*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*), while the major shade-intolerant species were quaking aspen (*Populus tremuloides*), northern red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). The trees were then divided into twelve 5 cm diameter size classes ranging from 5 to 61 + cm. Each class is denoted by its midpoint diameter. The 5 cm class includes trees with diameter at breast height (DBH) from 2.5 cm up to, but not including, 7.5 cm, and the 61 + cm diameter class includes trees 58.8 cm and larger in DBH.

Michigan's fifth forest inventory was completed in 1993, with remeasured plots averaging 13 years between measurements. The data are also in the Eastwide Data Base format and are similar to those of Wisconsin's fifth inventory. 1259 maple-beech-birch plots were found, which had been remeasured and were classified as timberland at both measurements. Further details on the NC-

Table 1
Number of plots by site index, fifth inventory

	Site index [a]							
	9–11	12–14	15–17	18–20	21–23	24–26	27–30	Total
Wisconsin	2	18	77	221	181	86	38	623
Michigan	11	70	221	383	336	176	62	1259
Total	13	88	298	604	517	262	100	1882
% of Total	1	5	16	32	27	14	5	100

[a] Site index measured in meters at 50 years (Hansen et al., 1992).

FIA database and plot selection criteria can be found in Kolbe (1998).

To extend Lin's model to Michigan, and to account for the effects of variations in land productivity within each state, site index was added to the growth equations. The EWDB designates a site index for each plot, measuring the average total height of the dominant and codominant trees at 50 years (Hansen et al., 1992). Table 1 shows that the majority of the plots fall between site indexes of 15 and 26 m, with an average of 21 m. Trees on the best sites in Wisconsin had more than four times the amount of annual net cubic meter growth than those on the poorest (Table 2). Although these are rough comparisons, without control for other effects on growth, they still suggest that site index should be added to Lin's model structure.

Table 2
Average net growth (m^3/year) per tree of different sites in Wisconsin, fifth inventory

	Good site [a]	Poor site [b]
Average	0.022	0.005
St. Dev. [c]	0.028	0.008
S.E. [d]	0.002	0.001
t [e]		6.30
p-value [f]		0.00

[a] Site index = 30 m at 50 years.
[b] Site index = 16 m at 50 years.
[c] St. Dev. = standard deviation.
[d] S.E. = standard error.
[e] t = t-statistic.
[f] p-value = level at which the hypothesis of equal average growth would be just rejected.

4. Model estimation and stability tests

The upgrowth, mortality and ingrowth equations were estimated by multiple regression across all plots. The observed rates, which ranged over 9–18 years were converted to yearly rates by linear interpolation. Each plot gave, for each species, one observation for ingrowth, I_{it}, while each size class with at least one tree contributed one observation of upgrowth, b_{ijt}, or mortality, d_{ijt}. For example, for Wisconsin there were up to 623 observations on ingrowth, and up to three species groups*12 size classes*623 plots = 22428 observations on upgrowth or mortality, for each species.

The equations were first estimated separately for Wisconsin and Michigan, with 80% of the plots, selected at random. The other 124 in Wisconsin and 248 in Michigan were left for validation. After the validation tests, presented below, the models were each reestimated with the complete data sets, to increase efficiency, and to test the stability of parameters between samples. The parameters in Tables 3 to 5 were statistically significant at least at the 1% level[1], with both 80% of the data and with all the data. The data from Wisconsin and Michigan were also pooled to determine if a single model could be applied to both states.

In the upgrowth equations (Table 3), all the coefficients of basal area, diameter, and diameter squared had the expected signs and were highly

[1] The 1% significance level was preferred because the standard error of the mean is inversely proportional to the square root of the number of degrees of freedom, which is generally large.

Table 3
Coefficients of upgrowth equations

		Basal area (m^2/ha)	Diameter (m)	Diameter^2 (m^2)	Site x Diameter (m^2)	Constant	R^2	df
Shade-tolerant species								
Wisconsin		−0.00056	0.22	−0.32		0.016	0.08	3490
	S.E. [a]	0.00007	0.01	0.02		0.002		
Michigan		−0.00085	0.23	−0.40	0.000024	0.013	0.17	6176
	S.E.	0.00005	0.01	0.02	0.000004	0.001		
Wisconsin & Michigan		−0.00073	0.21	−0.37	0.000021	0.014	0.14	9670
	S.E.	0.00004	0.01	0.01	0.000003	0.001		
Mid-tolerant species								
Wisconsin		−0.0008	0.20	−0.38	0.000032	0.013	0.10	1148
	S.E.	0.0001	0.04	0.05	0.000010	0.005		
Michigan		−0.0011	0.25	−0.43	0.000017	0.016	0.15	2182
	S.E.	0.0001	0.02	0.03	0.000006	0.003		
Wisconsin & Michigan		−0.0010	0.24	−0.41	0.000022	0.015	0.13	3335
	S.E.	0.0001	0.02	0.02	0.000005	0.002		
Shade-intolerant species								
Wisconsin		−0.0004	0.23	−0.29		0.007	0.08	1693
	S.E.	0.0001	0.03	0.04		0.004		
Michigan		−0.0004	0.21	−0.40	0.000034	0.009	0.12	2251
	S.E.	0.0001	0.02	0.03	0.000006	0.002		
Wisconsin & Michigan		−0.0005	0.20	−0.35	0.000026	0.009	0.10	3950
	S.E.	0.0001	0.02	0.03	0.000005	0.002		

[a] S.E. = standard error.

significant, confirming the findings of Lin et al. (1996) with the fourth inventory Wisconsin data. Other things equal, trees of any species grew slower in more dense stands, and the growth rate tended to increase with tree size, up to a maximum, and then decline. The site effect was highly significant in all equations except those for shade-tolerant and shade intolerant-species in Wisconsin. The parameters were similar for Wisconsin and Michigan, suggesting that a single model of upgrowth based on pooled data from the two states might be suitable. However, a formal test rejected the hypothesis of equality of the coefficients at the 1% significance level for the shade-tolerant and shade-intolerant species, and the addition of a dummy variable to distinguish between Wisconsin and Michigan was not enough to eliminate the differences (Table 6).

The results for the mortality equations (Table 4) confirmed the findings of Lin et al. (1996) regarding the quadratic relationship between mortality and size, mortality being highest in the smallest and largest trees. This result extended well to the Michigan data. However, the effects of other variables were less stable. High stand basal area increased mortality in Michigan only and for shade-tolerant and mid-tolerant species only. Mortality was lower on better sites in both states, but for shade-tolerant species only. A test of the stability of the mortality parameters across states rejected the hypothesis that the coefficients were the same, at the 1% significance level, even after allowing for a different intercept (Table 6).

The ingrowth equations (Table 5) confirmed the negative effect of stand basal area on ingrowth found by Lin et al. (1996). The effect was highly

Table 4
Coefficients of mortality equations

	Basal area (m^2/ha)	Diameter (m)	Diameter^2 (m^2)	Site x Diameter (m^2)	Constant	R^2	df
Shade-tolerant species							
Wisconsin		−0.07	0.20	−0.000022	0.034	0.03	3490
S.E. [a]		0.02	0.02	0.000005	0.002		
Michigan	0.00019	−0.14	0.22	−0.000012	0.034	0.09	6176
S.E.	0.00004	0.01	0.01	0.000003	0.001		
Wisconsin & Michigan	0.00018	−0.12	0.21	−0.000011	0.032	0.05	9670
S.E.	0.00004	0.01	0.01	0.000003	0.001		
Mid-tolerant species							
Wisconsin		−0.13	0.17		0.042	0.02	1150
S.E.		0.03	0.04		0.004		
Michigan	0.00052	−0.20	0.27		0.036	0.10	2183
S.E.	0.00008	0.01	0.02		0.002		
Wisconsin & Michigan	0.00048	−0.17	0.23		0.035	0.06	3336
S.E.	0.00007	0.01	0.02		0.002		
Shade-intolerant species							
Wisconsin		−0.04			0.042	0.01	1697
S.E.		0.01			0.002		
Michigan		−0.19	0.22		0.052	0.10	2253
S.E.		0.02	0.03		0.002		
Wisconsin & Michigan		−0.13	0.15		0.049	0.05	3952
S.E.		0.01	0.02		0.002		

[a] S.E. = standard error.

significant, and systematic across species groups, in Michigan and Wisconsin. There was, however, little evidence of a relationship between the ingrowth of a given species and the number of trees of the same species already living in the stand. The stability tests (Table 6) suggested that data for Michigan and Wisconsin could be pooled into one single equation of ingrowth for shade-tolerant and intolerant trees, but not for mid-tolerant tress. As for mortality, the coefficients of determination, R^2, were very low, so little might be lost by modeling mortality and ingrowth as constant. Nevertheless, the low standard errors of the constant terms in the equations show that the mean expected value of ingrowth and mortality are well defined. Furthermore, the statistical significance, and the biological plausibility of the variables (e.g. negative effect of stand density on ingrowth, effect of tree size on upgrowth) argue for keeping them, at the cost of non-linear complications (Lin and Buongiorno, 1997). The adequacy of the models is best judged from post-sample validations.

5. Model validations

Two types of validations were done. First, short-term forecasts on 20% of the plots not used for model calibration. Second, comparisons of the long-term steady states predicted by the models, with some of the oldest and least disturbed stands in the FIA data base. The first test is technically more rigorous, but limited by its

Table 5
Coefficients of ingrowth equations

		Basal area (m^2/ha)	Trees of same species (tree/ha)	Constant	R^2	df
Shade-tolerant species						
Wisconsin		−1.0		45	0.02	617
	S.E. [a]	0.3		5		
Michigan		−0.5		34	0.01	1247
	S.E.	0.2		3		
Wisconsin & Michigan		−0.7		37	0.01	1866
	S.E.	0.1		2		
Mid-tolerant species						
Wisconsin		−0.4		11	0.02	617
	S.E.	0.1		2		
Michigan		−0.5	0.004	12	0.04	1246
	S.E.	0.1	0.001	1		
Wisconsin & Michigan		−0.5		13	0.03	1866
	S.E.	0.1		1		
Shade-intolerant species						
Wisconsin		−0.6		19	0.03	617
	S.E.	0.2		3		
Michigan		−0.9		22	0.04	1247
	S.E.	0.1		2		
Wisconsin & Michigan		−0.8		21	0.04	1866
	S.E.	0.1		1		

[a] S.E. = standard error.

short time horizon. The second is 'softer', but important to check that the models behave as they should over long time periods.

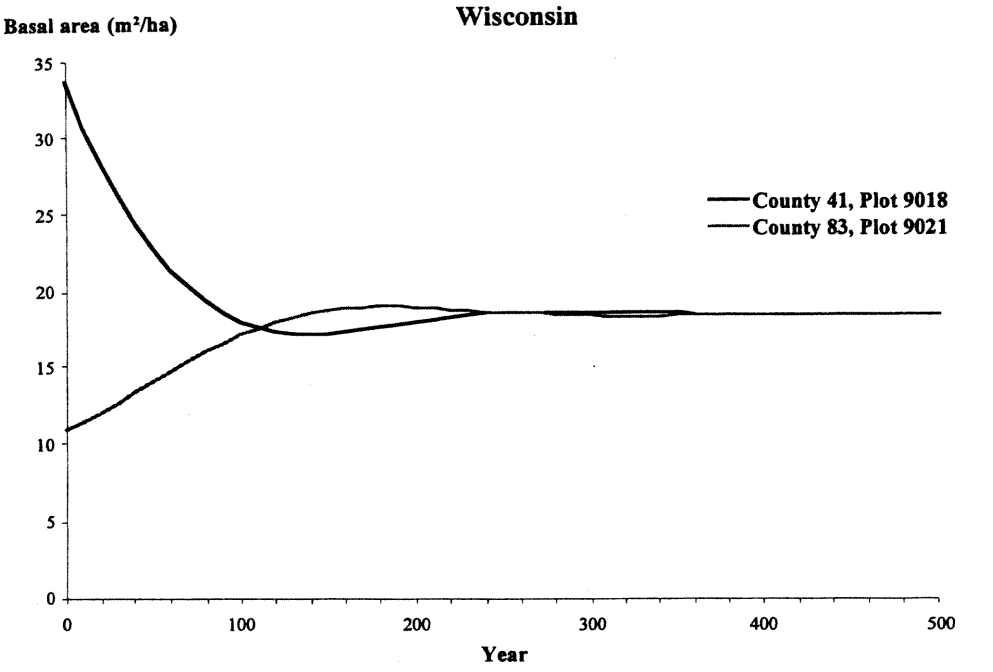
5.1. Validation on post-sample plots

Random selections of 20% of the Wisconsin plots and of 20% of those from Michigan were used to validate the models estimated from the remaining plots. Model (4) was applied to predict the state of each plot at the second measurement, i.e. after 10 to 18 years depending on the plot, given its initial state and any harvest that took place between the two measurements.

The results are summarized in Table 7, which shows the means, across all validation plots, of the actual and predicted number of trees per unit area, by size and species, at the time of the second measurement. Table 7 also shows the results of paired t-tests comparing the difference between observed and predicted number of trees. The most accurate projections were obtained with the Wisconsin model. For those 124 validation plots, only two tree categories were statistically different at the 5% significance level. The worst forecasts were those produced by the model based on pooled Wisconsin and Michigan plots, in which 1/3 of the tree categories had predictions that were statistically different from observations. This result is consistent with the findings of the within sample tests showing statistically significant differences between the Wisconsin and Michigan models. The Michigan model itself seems less accurate than the Wisconsin model, although in all the cases where the errors are statistically significant, they are generally not large in absolute value. The implication of such differences in predicting the long-term evolution of a forest is hard to tell, and calls for more long-term validation.

5.2. Long-term validation of steady states

This second test of model validity compares the long-term condition of forests predicted by the



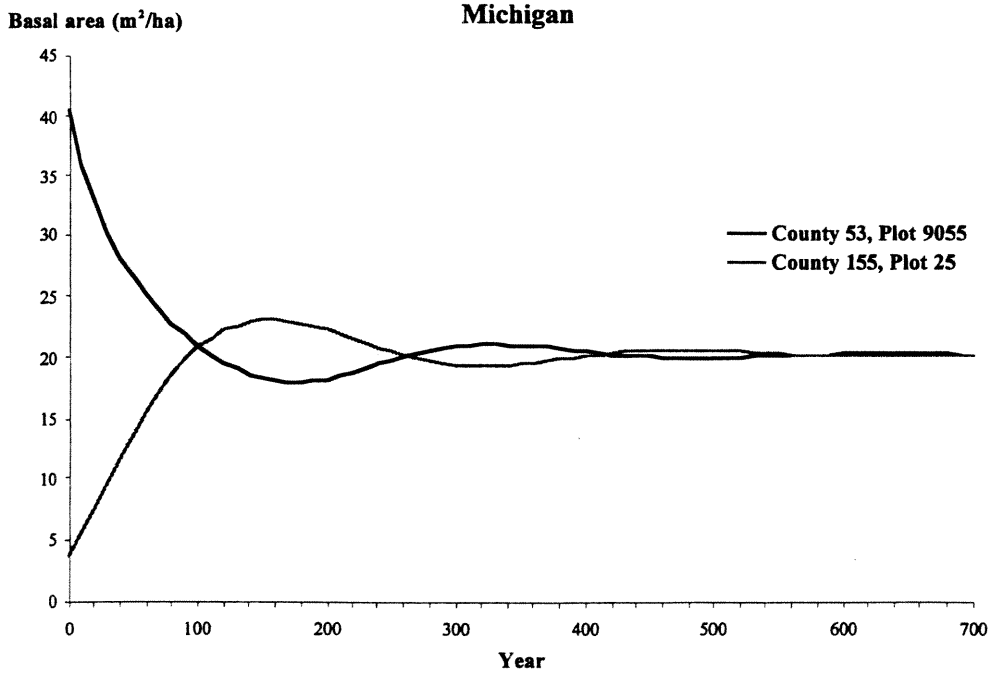


Fig. 1. Long-term development of widely different initial stands in Wisconsin and Michigan, on same site (site index = 21 m at 50 years).

Table 6
Tests of equality of parameters in Wisconsin and Michigan

Equation	Species	Model					
		Pooled			Pooled with dummy [d]		
		F	p-value [b]	df [c]	F	p-value [b]	df [c]
Upgrowth							
	Shade-tolerant	5.36	0.00	9670	[a]	[a]	[a]
	Mid-tolerant	2.36	0.04	3335	[a]	[a]	[a]
	Shade-intolerant	5.87	0.00	3950	8.17	0.00	3949
Mortality							
	Shade-tolerant	68.25	0.00	9670	42.32	0.00	9669
	Mid-tolerant	18.71	0.00	3336	4.22	0.01	3335
	Shade-intolerant	58.26	0.00	3952	16.38	0.00	3951
Ingrowth							
	Shade-tolerant	2.12	0.12	1866	[a]	[a]	[a]
	Mid-tolerant	5.17	0.00	1866	[a]	[a]	[a]
	Shade-intolerant	1.02	0.36	1866	[a]	[a]	[a]

[a] dummy variable for different states not significant at.01 level.
[b] p-value = level at which the hypothesis of equality of coefficients would be just rejected.
[c] df = degrees of freedom.
[d] dummy = variable to allow for different intercepts for Wisconsin and Michigan.

model to the states of old stands observed in nature. That stands in widely different initial conditions converge towards the same equilibrium state, after a very long time and in the absence of violent natural or human disturbance, is itself a useful test of model validity. Given the non-linear form of the model, this convergence property, consistent with the notion of climax or steady-state forest, cannot be assessed from the model parameters alone. An alternative is to simulate the growth pattern implied by the system of non-linear difference Eq. (4).

The results of such simulations are illustrated in Fig. 1, which shows the evolution of stand basal area for two stands in extremely different initial conditions, but similar sites, in Wisconsin and Michigan. In both cases, the pattern is the same: the basal areas of the poorly stocked stands increase, while those of the well stocked stands decrease, and both converge after damped oscillations towards a constant equilibrium basal area, which is the same regardless of the initial stand condition. However, the equilibrium basal area reached in Michigan is higher than in Wisconsin, despite the same site index.

To check the plausibility of the steady state predicted by the models in terms of species composition and tree size, we compared it with data from old forests. In Wisconsin, the data came from plots from the Menominee Indian Reservation. The Menominee's forests contain some of the oldest stands in Wisconsin, and they are managed very conservatively on a sustained yield basis (Pecore, 1992). Among the FIA plots on the Menominee forest, we selected seventeen for comparison with the model predictions. They had been classified as maple–beech–birch at both measurements, and the stand history record from the NC-FIA data base indicated no severe disturbance on these plots during the 20 years before the inventories. For Michigan, the predicted steady state was compared with twenty plots from the Ottawa National Forest. They all had a stand age of more than 100 years and had not been harvested during the fifth inventory period.

Figs. 2 and 3 show how the predicted steady state compares with the state of the old undis-

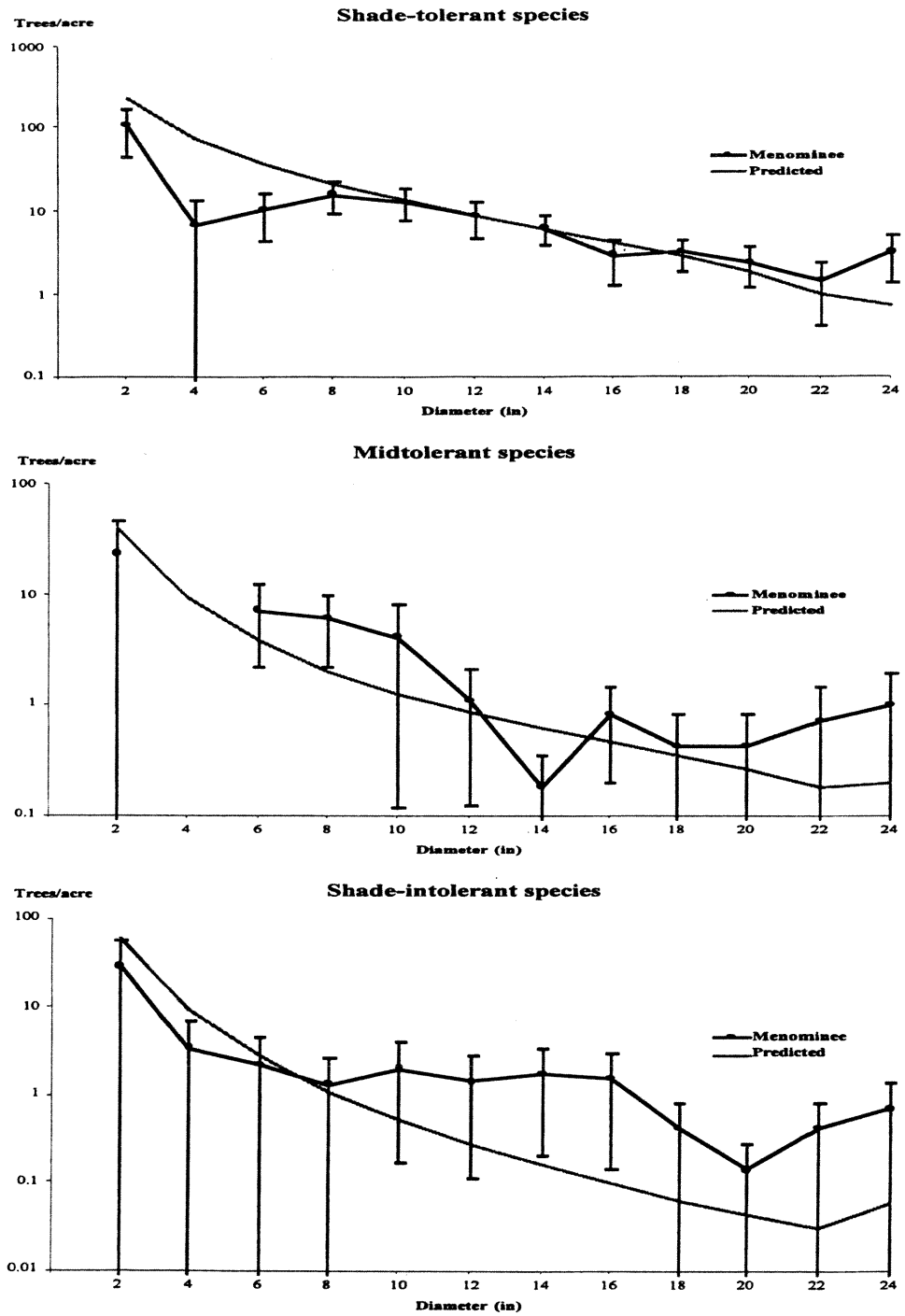


Fig. 2. Steady state predicted with Wisconsin model and sample of 17 stands in Menominee Tribal Forests, with 95% confidence intervals.

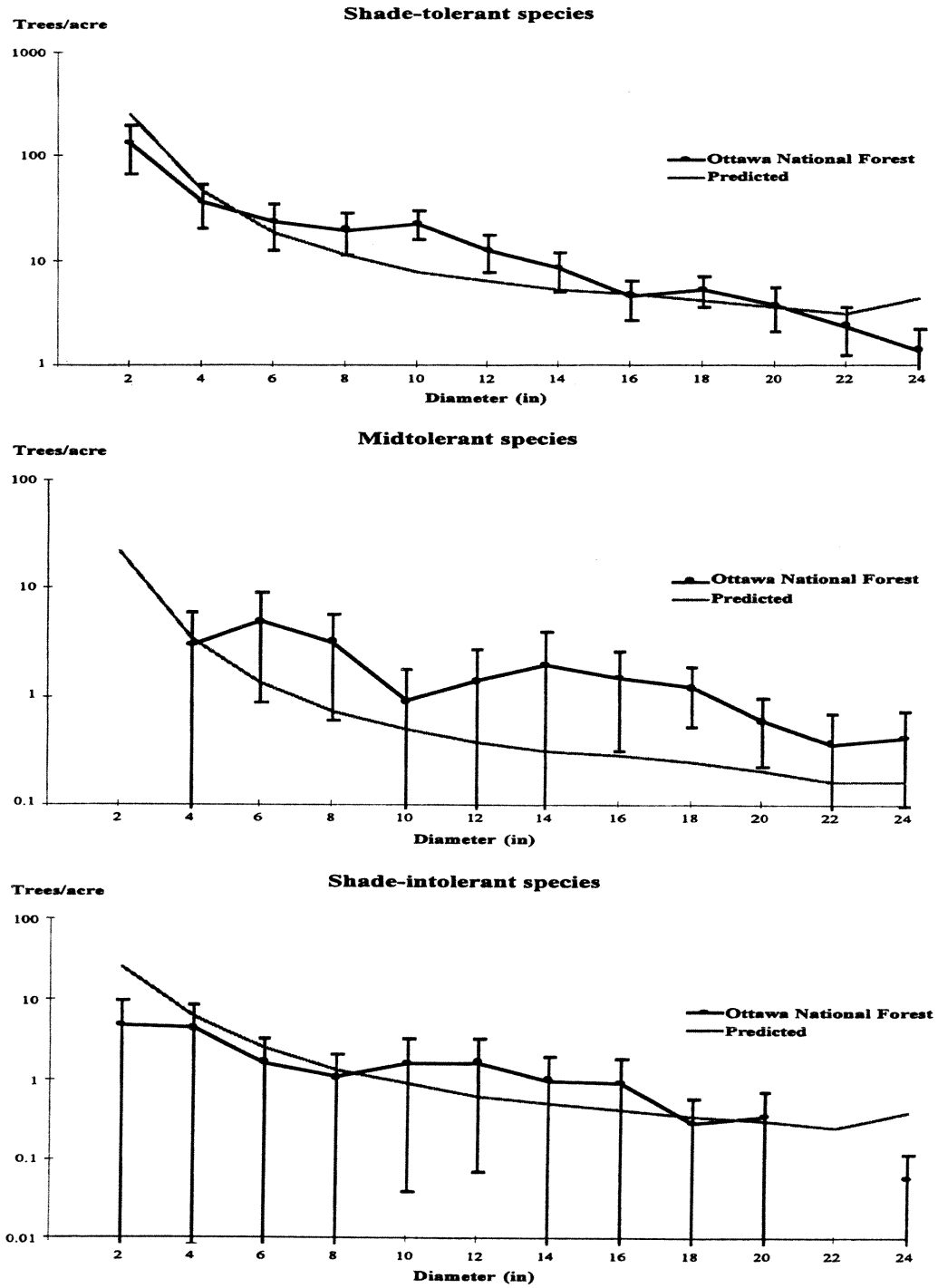


Fig. 3. Steady state predicted with Michigan model and sample of 20 stands in Ottawa National Forest, with 95% confidence intervals.

Table 7
Predicted and observed average number of trees per hectare [b]

Diameter class	Wisconsin		Michigan		Wisconsin and Michigan	
	Predicted	Observed	Predicted	Observed	Predicted	Observed
Shade-tolerant species						
5	362.9	385.6	458.2	436.9	424.4	419.9
10	86.0	79.0	93.4	80.0	93.1 [a]	79.8
15	69.4 [a]	55.1	60.8 [a]	49.2	64.0 [a]	51.1
20	52.6	50.9	41.5	44.0	45.2	46.4
25	35.6	37.3	27.4	28.4	30.4	31.4
30	21.2	22.2	17.3	17.3	18.8	19.0
36	11.9	12.1	10.1 [a]	8.4	10.6 [a]	9.6
41	6.4	5.9	5.7 [a]	4.9	5.9[a]	5.2
46	3.2	4.0	3.2	2.7	3.2	3.2
51	1.5	1.2	1.7 [a]	1.2	1.7 [a]	1.2
56	0.7	1.0	0.7	0.7	0.7	0.7
61+	0.5	1.0	1.2	1.0	1.0	1.0
Mid-tolerant species						
5	58.8	16.8	99.8	102.8	84.2	82.3
10	6.9	3.3	22.2	18.8	17.0	15.3
15	8.4	3.1	10.9	8.2	9.9	8.2
20	9.1	3.1	6.7	5.4	7.7 [a]	6.2
25	6.9[a]	1.8	4.9	5.4	5.7	4.9
30	4.0	1.5	3.5	3.0	3.7	3.2
36	2.5	0.8	2.2	2.5	2.2	2.2
41	1.2	0.6	1.5	1.2	1.5	1.5
46	0.7	0.4	1.0	1.0	1.0	1.0
51	0.5	0.3	0.5	0.5	0.5	0.5
56	0.3	0.1	0.3	0.5	0.3	0.3
61+	0.3	0.2	0.3	0.5	0.3[a]	0.5
Shade-intolerant species						
5	96.1	94.4	153.1	173.6	132.4	482.6
10	14.3	25.9	32.6	22.7	25.7	85.5
15	19.0	11.6	12.8 [a]	7.2	14.6 [a]	26.2
20	17.3	14.1	7.4 [a]	4.0	10.9 [a]	18.5
25	12.4	9.9	5.2	4.2	7.7 [a]	16.1
30	8.7	6.4	3.5	2.5	5.4 [a]	9.4
36	4.7	5.2	2.2	2.2	3.2	7.2
41	2.2	2.2	1.2	1.2	1.5	4.5
46	1.0	1.0	0.5	0.5	0.7	2.2
51	0.5	0.5	0.3	0.3	0.3	1.2
56	0.3	0.3	0.0	0.3	0.3	1.0
61+	0.3	0.3	0.0	0.0	0.3 [a]	1.0

[a] Significantly different means at 5% level.
[b] Notes: Averages of 124 post-sample plots in Wisconsin and 248 in Michigan.

turbed plots on the Menominee and Ottawa forests, by species and size class[2]. The error bars indicate 95% confidence intervals about the observed average distribution. The predicted distri-

[2] The steady states in Fig. 2 were those predicted by the model after 500 years. However, Fig. 1 shows that the predicted state would be close to this steady state after 100–200 years, making it possible to compare with the Menominee and Ottawa plots.

Table 8
Summary statistics for predicted steady state and observed old stands

	Basal area (m^2/ha)		Size diversity [d]		Species diversity [e]	
	Predicted	Observed	Predicted	Observed	Predicted	Observed
Wisconsin [a]	18.4	20.5	2.4	2.3	0.5	0.8
Michigan [b]	20.5	24.6	2.4	2.4	0.5	0.6
Wisconsin and Michigan [c]	20.0		2.5		0.5	

[a] Observed on 17 plots in Menominee Indian Tribal.
[b] Observed on 20 plots in Ottawa National Forest.
[c] Predicted with data pooled from the two states.
[d] Shannon's index, according to basal area in three species groups.
[e] Shannon's index, according to basal area in 12 size classes.

butions had the same general shape as the observed, both for Wisconsin and Michigan. And, the predicted number of trees fell generally within the 95% confidence interval of the observed mean. However, there were differences in detail, some of which may be important. For example, the model for Wisconsin seemed to underpredict the number of largest shade tolerant trees (Fig. 2), although this was not the case for the Michigan model (Fig. 3). The total average basal area per hectare predicted by the steady-state solution of the models tended to underpredict the observed, in both Wisconsin and Michigan (Table 8). However, the predicted diversity indices of species and size were remarkably close to the observed, especially for Michigan. Diversity was measured with Shannon's index, based on basal area in each species and size class (Pielou, 1977). Maximum species diversity of 1.10 would be achieved with equal basal area in each of the three species groups, and maximum size diversity of 2.48 with equal basal area in each of the 12 size classes.

More data on the differences between the Wisconsin and Michigan models are documented in Figs. 4 and 5. They show the results of simulations with the two models, starting with the same initial stand condition[3], on lands of highest and lowest productivity (site index 30 and 16, respectively). In terms of basal area, the growth on both sites is much more rapid in Michigan than in Wisconsin during the first century (Figure 4). The difference diminishes after many years, but still shows a tendency, already noted above, for stands in Michigan to carry more basal area in the steady state than those in Wisconsin. Despite the long-term convergence, the strong differences in the initial rates of growth between Michigan and Wisconsin suggest that the statistical differences between the two models are also operationally important and that it would be better to use separate models for each state to predict developments during the next decades.

Fig. 5 illustrates the differences in diversity of tree species and size, predicted with the Wisconsin and Michigan models, for stands of the same initial condition. On the poor site, the diversity indices predicted by the two are almost identical, both for species and size. On a good site, the diversity of size tends to be lower in Michigan after a long time period because the Michigan model predicts a high number of large diameter trees in the steady state, and the diversity of species tends also to be lower in Michigan, corresponding to the dominance of shade-tolerant trees. However, even on a good site the differences are not large, and it is questionable whether they are biologically significant, especially because the results are for extreme sites, while most lands in Wisconsin and Michigan have site indices between 60 and 80 (Table 1).

[3] The initial stand condition is the average stand state, across Wisconsin and Michigan.

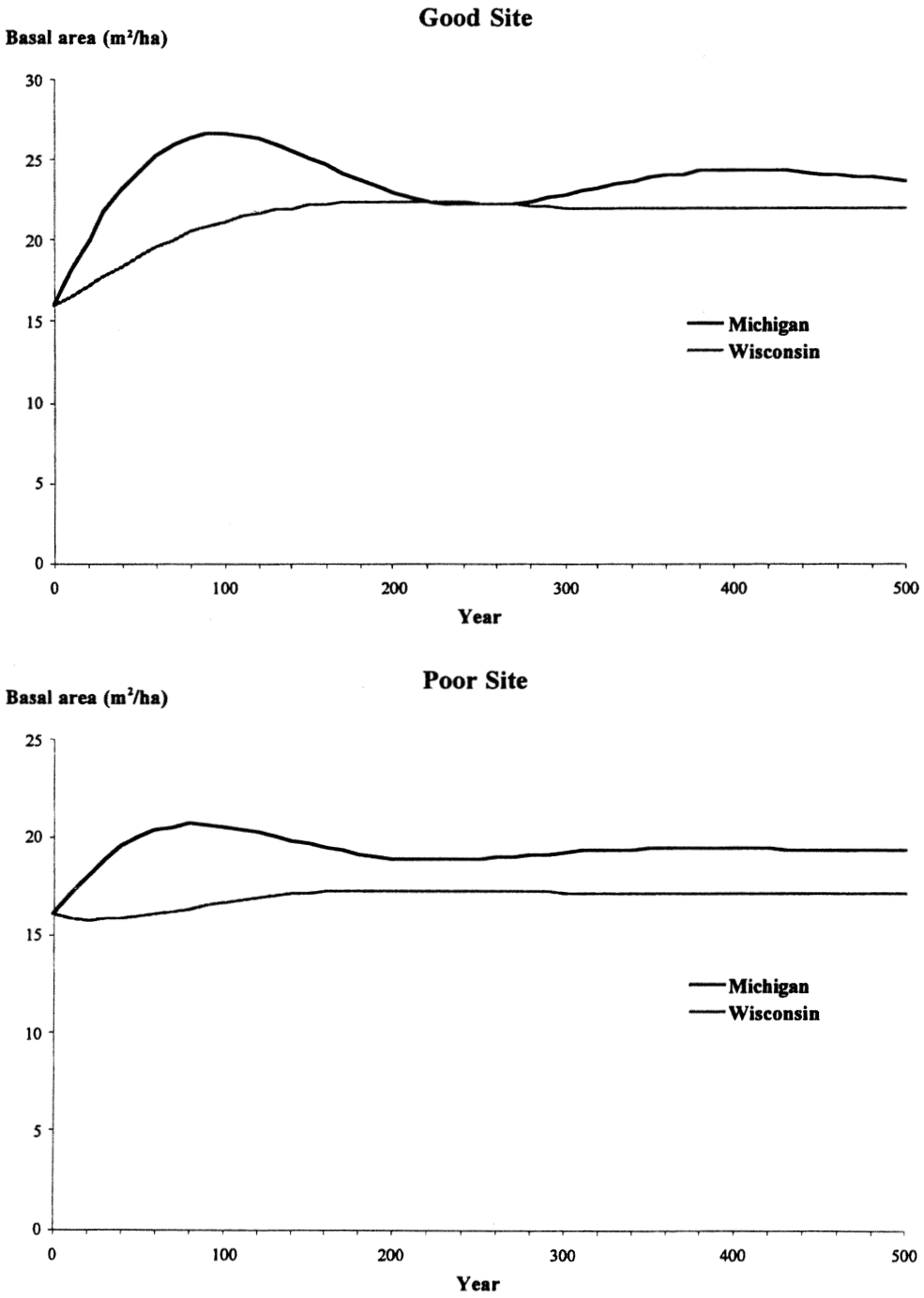


Fig. 4. Predicted basal for stands in same initial condition, growing in Wisconsin or Michigan, on good or poor site (site index = 30 or 16 m at age 50).

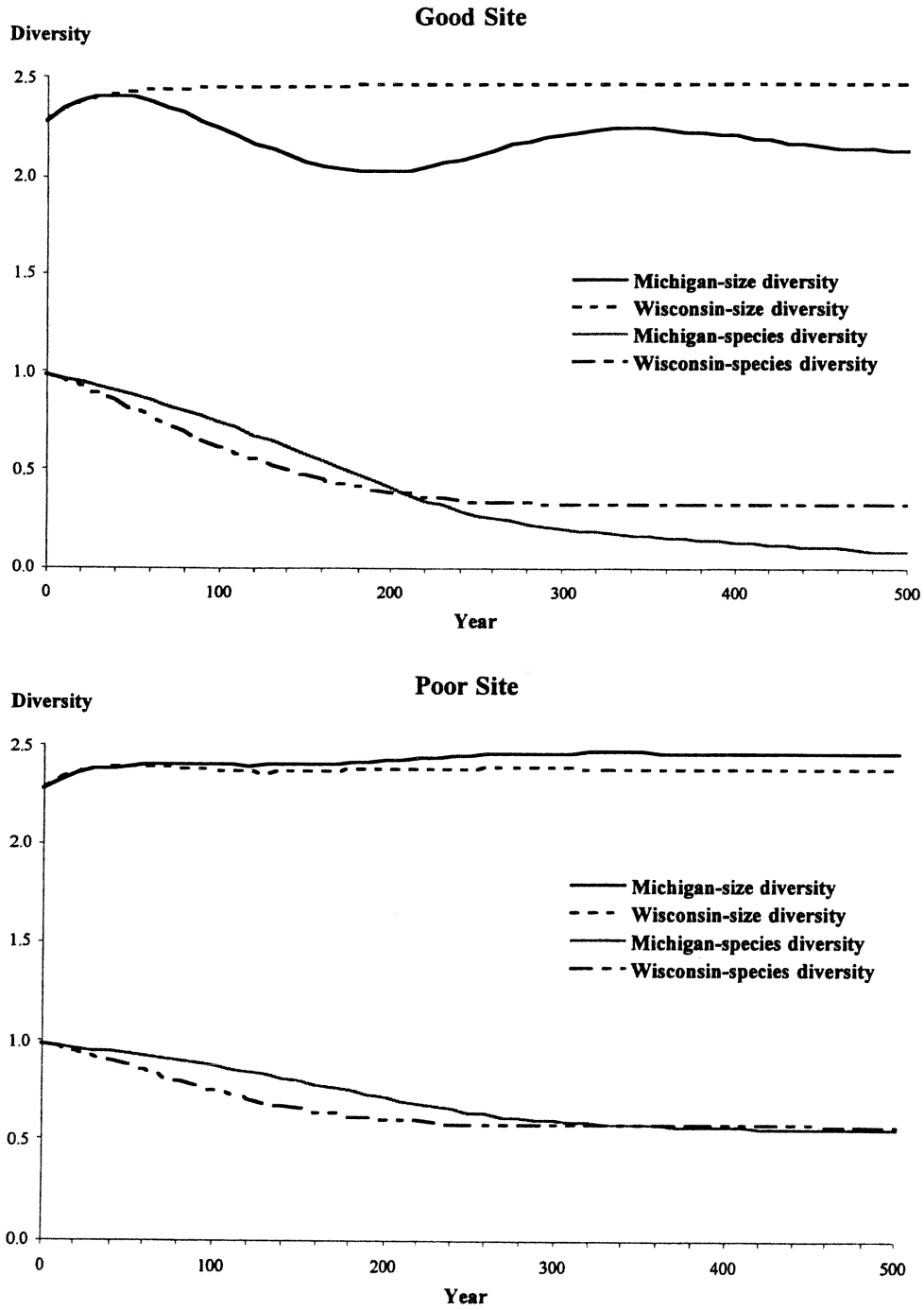


Fig. 5. Predicted tree diversity of stands in same initial condition growing in Wisconsin or Michigan, on a good or poor site (site index = 30 or 16 m at age 50).

6. Summary and conclusion

The objective of this study was to extend the geographic range of the forest growth model for northern hardwoods, developed previously by Lin et al. (1996) for Wisconsin, to cover the much larger area of same forest type, in the contiguous state of Michigan.

In searching for a single, general model, Lin's model was re-estimated with more recent data from the fifth Wisconsin inventory, and with Michigan data from the same inventory, after introducing a new variable to account for variations in site quality. Site index did have a statistically significant effect in determining upgrowth and mortality, but variations in site quality were not enough to explain the differences between the two geographic areas. Although all the parameters of the Wisconsin and Michigan models had the same signs and same order of magnitude, there were still statistically significant differences in the equations even after including the site index variable.

Post-sample tests confirmed that two separate models would predict better stand growth in each state than a single model based on the pooled data. Long-term simulations showed that each separate model predicted steady-state distributions that were independent of initial conditions, and compatible in terms of diameter and species distribution with those observed in undisturbed old stands in Wisconsin and Michigan. Applied to stands of the same initial conditions, the Michigan model predicted faster initial growth in Michigan than in Wisconsin and higher basal area in the steady state. The differences were more marked on good than poor sites.

There are several possible reasons for the differences in stand growth between Wisconsin and Michigan. One of them is the difference in tree species between states, of which there tend to be more in Michigan than Wisconsin (Table 9). These differences are masked in the aggregation of trees in the three categories of shade-tolerant, mid-tolerant, and intolerant species. An obvious improvement would be to increase the number of species categories, but this quickly leads to difficulties due to the scarcity of observations by individual species, of which there are 70. Another possible reason for the differences is the age of trees: Michigan forests were cut over at the turn of the century before those of Wisconsin, and they tend to be older. Tree age is not a variable in the model, because the inventory data do not carry this information. It is well known that tree size is not synonymous of tree age, although there is a very strong correlation between the two, especially if one controls for stand density, as in the present model. Climatic and pedologic differences may also cause differences in growth, some of which are not reflected by the site index variable used here. Since the inventories in the two states were not taken at the same time, it is possible that climatic differences may have contributed to the differences in growth rates. This should be explored in further research by including temperature, rainfall, and climatic disturbance as explanatory variables in the growth and mortality models.

Regardless of the causes for the geographic differences observed here, the results suggest that besides being statistically significant, the differences have sufficiently large implications for stand growth to warrant the use of separate parameters for Wisconsin and Michigan in current applications. Nevertheless, by pursuing 'Occam's razor' ideal of parsimony, further research may succeed in producing a single general model, by altering the model structure, and/or including new variables, though the possible changes in that direction are limited severely by data availability.

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Table 9
Species and shade-tolerance of trees of the maple–beech–birch forest type in Wisconsin and Michigan

FIA code	Common name	Scientific name	Frequency of observed trees (%)	
			Wisconsin	Michigan
Shade-tolerant species				
318	Sugar maple	*Acer saccharum*	23.24	27.76
316	Red maple	*Acer rubrum*	13.2	15.14
951	American basswood	*Tilia americana*	8.66	4.33
972	American elm	*Ulmus americana*	4.77	4.00
12	Balsam fir	*Abies balsamea*	3.88	4.17
261	Eastern hemlock	*Tsuga canadensis*	3.39	4.15
701	Ironwood	*Ostrya virginiana*	2.41	1.60
241	Northern white-cedar	*Thuja occidentalis*	1.08	0.42
391	American hornbeam	*Carpinus caroliniana*	0.81	0.42
94	White spruce	*Picea glauca*	0.43	0.87
531	American beech	*Fagus grandifolia*	0.42	2.78
975	Slippery elm	*Ulmus rubra*	0.40	0.11
319	Mountain maple	*Acer spicatum*	0.11	0.19
95	Black spruce	*Picea mariana*	0.09	0.27
313	Boxelder	*Acer negundo*	0.04	0.04
317	Silver maple	*Acer saccharinum*	0.02	0.16
315	Striped maple	*Acer pensylvanicum*	[a]	0.08
491	Flowering dogwood	*Cornus florida*	[a]	0.05
91	Norway spruce	*Picea abies*	[a]	0.02
682	Red mulberry	*Morus rubra*	[a]	0.02
693	Black gum	*Nyssa sylvatica*	[a]	0.01
314	Black maple	*Acer nigrum*	[a]	0.00
Mid-tolerant species				
371	Yellow birch	*Betula alleghaniensis*	4.14	4.59
541	White ash	*Fraxinus americana*	2.28	2.38
129	White pine	*Pinus strobus*	1.95	1.69
802	White oak	*Quercus alba*	1.32	0.66
762	Black cherry	*Prunus serotina*	1.27	3.63
977	Rock elm	*Ulmus thomasii*	0.38	0.09
823	Bur oak	*Quercus macrocarpa*	0.35	0.07
125	Red pine	*Pinus resinosa*	0.26	0.42
763	Chokecherry	*Prunus virginiana*	0.14	0.19
804	Swamp white oak	*Quercus bicolor*	0.04	0.10
462	Hackberry	*Celtis occidentalis*	0.03	[a]
373	River birch	*Betula nigra*	0.02	[a]
130	Scotch pine	*Pinus sylvestris*	[a]	0.13
403	Pignut hickory	*Carya glabra*	[a]	0.05
409	Mockernut hickory	*Carya tomentosa*	[a]	0.02
68	Eastern redcedar	*Juniperus virginiana*	[a]	0.02
405	Shellbark hickory	*Carya laciniosa*	[a]	0.01
826	Chinkapin oak	*Quercus muehlenbergii*	[a]	0.01
Shade-intolerant species				
746	Quaking aspen	*Populus tremuloides*	7.98	6.26
375	Paper birch	*Betula papyrifera*	4.53	2.44
833	Northern red oak	*Quercus rubra*	4.46	2.64
743	Bigtooth aspen	*Populus grandidentata*	1.99	2.71
543	Black ash	*Fraxinus nigra*	1.94	1.09
544	Green ash	*Fraxinus pennsylvanica*	0.88	0.58

Table 9 (continued)

FIA code	Common name	Scientific name	Frequency of observed trees (%)	
			Wisconsin	Michigan
402	Bitternut hickory	*Carya cordiformis*	0.66	0.19
837	Black oak	*Quercus velutina*	0.58	0.23
809	Northern pin oak	*Quercus ellipsoidalis*	0.48	0.07
601	Butternut	*Juglans cinerea*	0.29	0.05
105	Jack pine	*Pinus banksiana*	0.27	0.65
71	Tamarack	*Larix laricina*	0.15	0.01
741	Balsam poplar	*Populus balsamifera*	0.15	0.37
407	Shagbark hickory	*Carya ovata*	0.11	0.13
500	Hawthorn	*Crataegus* sp.	0.11	0.46
602	Black walnut	*Juglans nigra*	0.08	0.09
742	Eastern cottonwood	*Populus deltoides*	0.05	0.18
761	Pin cherry	*Prunus pensylvanica*	0.04	0.26
766	Wild plum	*Prunus americana*	0.02	660
660	Apple sp.	*Malus* sp.	0.01	0.14
552	Honeylocust	*Gleditsia triacanthus*	0.01	0.00
901	Black locust	*Robinia pseudoacacia*	0.01	0.08
931	Sassafras	*Sassafras albidum*	[a]	0.39
621	Yellow-poplar	*Liriodendron tulipifera*	[a]	0.13
935	American mountain-ash	*Sorbus americana*	[a]	0.06
923	Diamond willow	*Salix eriocephala*	[a]	0.04
731	Sycamore	*Platanus occidentalis*	[a]	0.03
922	Black willow	*Salix nigra*	[a]	0.03
921	Peachleaf willow	*Salix amygdaloides*	[a]	0.01
830	Pin oak	*Quercus palustris*	[a]	0.00
Total			100.0	100.00

[a] Absent

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