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White Oak Growth after 23 Years in a Three-Site Provenance/Progeny Trial on a Latitudinal Gradient in Indiana

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To increase the availability of improved, adapted white oak (*Quercus alba* L.) for midwestern United States landowners, we analyzed data from three 23-year-old provenance/progeny tests of 70 open-pollinated progenies from 17 provenances. Our goal was to estimate the heritability of height growth and range of adaptation and ultimately to determine the value of converting the sites to seed orchards. Tree growth was marked by positive spatial autocorrelation (SA) for height in all three test sites despite differences in management and mortality. Microsites with the highest SA changed little from age 10 to age 23. Nearest neighbor and iterative spatial or kriging analyses were used to remove effects of SA from the data, resulting in little change in heritability estimates but important changes in family means and rank. Within sites, provenances were a relatively unimportant source of variation (mostly $<2\%$), and there was no evidence local sources grew best. Genetic correlation was 0.81 for height between ages 10 and 23. Considering heritability estimates, significant differences among families, and large predicted breeding zones, once the sites are thinned, seedlings produced from the progeny tests should grow well above average on suitable sites in Indiana and would probably be acceptable in nearby states as well.

Keywords: *Quercus alba*, forest genetics, mixed model, spatial autocorrelation, tree improvement

White oak (*Quercus alba* L.) grows in every state of the eastern United States and is one of the most ecologically and economically important species in the central hardwood forest (Piva and Gallion 2005). Oak regeneration has been an important issue for the past 50 years or so (Dey 2014). O'Connor and Coggeshall (2011) reported that an average of 292,000 white oak seedlings were sold per year from the Indiana State Tree Nursery from 2006 to 2010, but how well white oak grows in plantations is poorly documented. A white oak provenance/progeny trial focused on Indiana is one of the few mid-rotation genetic resources for this species (Rink and Coggeshall 1995). An analysis of this multilocation trial found that variation for height growth after 16 years was significant for families but not provenances (=stands) (O'Connor and Coggeshall 2011). The importance of provenance effects and the ranking of nearby versus distant provenances can shed light on the size of seed and breeding zones for white oak. Results from the 2011 study were not used as a basis to convert the locations to seed orchards, an important operational goal. We remeasured the same locations at age 23 with the awareness that the trees had become large enough that competition effects and trends within the sites would probably complicate estimation of the relative performance of individuals, families, and provenances (Hamann et al. 2002).

Nongenetic variability in large progeny tests on heterogeneous sites can be controlled using single-tree plots, incomplete blocks, and other designs (Costa e Silva et al. 2001), but legacy experimental designs such as randomized complete block (RCB) designs often fail to adequately compartmentalize environmental variance. Whatever experimental design is used, it is assumed that the environment

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; kilometers (km): 1 km = 0.6 mi.

Table 1. Characteristics of the three test sites analyzed in this study, planting designs at each site, and tree growth, including spatial autocorrelation statistics.

Characteristic	HC	JP	SH
Latitude	38°15′ N	41°09′ N	38°49′ N
Longitude	86°15′ W	86°54′ W	86°05′ W
Plant hardiness zone[a]	6a	5a	5b
Soil type and traits	Haymond silt loam, deep, well drained, high capacity, moderate permeability	Maumee sandy loam, deep, poorly drained rapidly permeable	Bloomfield sandy loam, deep, well drained, moderate to rapidly permeable
Provenances	16	17	17
Initial trees planted	2,012	1,339	1,744
Trees at age 10	1,605	643	407
Trees at age 23	1,492	638	141
Families at age 10	63	57	68
Families at age 23	63	57	58
Initial spacing	2.4 m	2.4 m	1.2 m, 2.4 m between plots
Spacing at age 23[b]	3.2 m	5.0 m	14.8 m
Family plot size/type	4 tree row	4 tree row	4 tree square
Height age 10 ± SD (dm)	29.2 ± 10.3	32.9 ± 8.2	70.0 ± 15.3
Height age 23 ± SD (dm)	106 ± 16.1	94.2 ± 14.7	165 ± 16.9
Diameter age 23 (cm)	12.8 ± 3.6	15.1 ± 3.9	28.6 ± 4.3
Gingrich stocking	Fully-stocked (65%)	Understocked (35%)	Understocked (<10%)
A_0 age 10, 23 height	7.14, 6.44	19.27, 7.46	17.62, 15.46
A_0 age 23 dbh	13.07	0.033	0.0
c_0/c_n age 10, 23 height	0.37, 0.68	0.39, 0.91	2.98, 1.2
c_0/c_n age 23 dbh	0.02	0.01	0.0

[a] For more information, see planthardiness.ars.usda.gov/phzmweb/.
[b] Average spacing estimated based on tree number at age 23 and site area.

within a block is homogeneous (Zobel and Talbert 2003). When neighboring trees share a distinct environment, e.g., soil condition or microclimate, their phenotypes can become more alike than expected (positive spatial autocorrelation [SA]). Negative autocorrelation arises when growth is adversely affected by neighbors; thus, autocorrelation affects traits differently over space and time but in general it reduces the precision of estimates of treatment effects (Costa e Silva 2001). It has been argued that some sort of spatial adjustment of the data from forest tree progeny trials is essential (Magnussen 1994) because gradients inevitably develop, increasing error variance within blocks, especially as trees mature and compete. In such cases, ex post facto removal of heterogeneity can improve selection accuracy (Dutkowski et al. 2002, Piepho et al. 2008).

One of the oldest and simplest approaches for removing SA is nearest-neighbor analysis (NNA), also called moving average adjustment (Correll and Anderson 1983, Papadakis 1984). In a typical NNA, the value of a tree is adjusted in proportion to the departure of neighbor trees from clone or family means (Anekonda and Libby 1996). Other solutions for removing intrabock and block × family effects include iterative kriging (Zas 2006) or the addition of spatially dependent error vectors to analytical models (Grondona et al. 1996, Gilmour et al. 1997).

The objectives of our study were to (1) measure tree growth and determine whether growth was spatially autocorrelated, (2) apply analytical methods that remove SA to produce best linear unbiased predictions (BLUP) of family breeding values (their departure from the population mean growth), (3) estimate heritabilities for height and diameter growth and age-age genetic correlations for white oak in a multilocation progeny trial, (4) determine whether local provenances outgrew nonlocal sources, and (5) estimate the value of forward selection to establish seed orchards.

Materials and Methods

Study Sites and Data Collection

Seed sources (provenances), planting sites, and site management were described in detail in Rink and Coggeshall (1995) (Table 1). In general, trees were planted in a randomized complete block design at two sites in southern Indiana (Harrison-Crawford State Forest [HC] and Starve Hollow [SH]), and a third site (Jasper-Pulaski [JP]) was in northern Indiana. All sites were planted with 1 + 0 bareroot nursery stock in spring 1984 and managed using standard methods (Rink and Coggeshall 1995). The sites spanned 320 km and three plant hardiness zones (Table 1). The open-pollinated seeds were collected in 1982 from 70 trees in 17 stands (considered provenances). Trees were visually favorable, but no criteria regarding spatial separation between sources were observed. Five families were from Missouri (1 provenance), 6 families from Illinois (1 provenance), and 59 families from Indiana (15 provenances). The trial was slightly unbalanced because of insufficient seed (Table 1). At HC and JP, trees were planted in four-tree plots along rows. Herbivory by deer led to low survival at JP. The SH site, near the Vallonia State Tree Nursery, received more maintenance than the other sites. Trees at SH were rogued at ages 6 and 9 years, leaving a single ("best") tree per plot (O'Connor and Coggeshall 2011) and equalizing growing space. Some families but no provenances were removed during thinning (Table 1).

General Considerations for Analysis

We obtained data for 10-year height (at about the time of crown closure for the nonrogued sites), 23-year height, and 23-year dbh (Table 1). We removed suppressed trees from all analyses (Bouvet et al. 2005): 103 trees at HC (all in suppressed canopy class) and 12 at JP (>3 SD below plantation mean height). Suppressed trees at SH were previously rogued.

Because site and management differences had a large effect on tree height of the families (Table 1) and because each site will be converted to a seedling seed orchard, we analyzed the sites separately. We compared results from NNA with a standard mixed model (no adjustment for local autocorrelation) and iterative kriging by comparing Akaike information criterion (AIC) values. To find the BLUP of family and provenance effects (Piepho et al. 2008), we used REML in PROC MIXED of SAS (SAS Institute, Inc.,

Cary, NC). Because of the large number of provenances in the study, family nested in provenance and provenance were considered random effects. The relative proportion of genetic variance allocated among families versus provenances (Θ) and the correlated response to selection were calculated as described by Sierra-Lucero et al. (2002). Age-age genetic correlation between height at age 10 and age 23 across all environments was determined using SAS code provided by Fikret Isik.[1] Model effects were deemed significant at $P \leq 0.05$, and we used AIC values to compare how well models fit the data. Differences in mortality among families were tested using a χ^2 test followed by a Z test to compare each family's survival versus the site average.

Standard Mixed Model

The standard mixed model we used was

$$Y_{ijklm} = \mu + P_i + F(P)_{j(i)} + B_k + BF(P)_{kj(i)} + R_l + \varepsilon_{ijklm} \quad (1)$$

where Y_{ijklm} represents the original measurements of each trait from tree m of provenance i and family j in row l of block k, μ is the overall mean, and B_k and R_l are the fixed effects of block k and row l. Rows were considered fixed effects because rows were significant in a univariate analysis, because adding rows decreased the model AIC, and because plots of height and dbh against row number showed strong linear trends, especially for trees in codominant and intermediate crown classes (data not shown). P_i,$F(P)_{j(i)}$ and $BF(P)_{kj(i)}$ are the random effects of provenance i, family j (nested in provenance), and the block $\times$ family (nested in provenance) interaction effects, and ε_{ijklm} is the independent error term.

Iterative Spatial Analysis (ISA)

Using the method of Zas (2006) to remove SA from the data, we fit an exponential theoretical semivariogram to the observed semivariogram to model the spatial structure of residuals from the model $Y = \mu + P + F(P) + \varepsilon$, where P denotes provenance effects and $F(P)$ denotes family effects (nested in provenance). With the estimated range, patch variance, and nugget effects of the exponential semivariogram, we fit the model $\varepsilon = k + \delta$ using PROC KRIG2D of SAS to obtain the kriging estimates for each location. The kriging estimates (k) represent the spatially autocorrelated component, and δ is the random error within residuals. The kriging estimates were subtracted from the original observations to get adjusted values ($Y - k$) to remove the SA within residuals, and then the adjusted values were used for reanalysis to fit the model

$$Y - k = \mu + P + F(P) + BF(P) + B + R + \varepsilon' \quad (2)$$

and obtain new family effects (nested in provenance) ($F(P)$) and new residuals (ε'). Notations were defined as in Equation 1.

Nearest Neighbor Model

To determine the effect of removal of patchy SA, we used NNA developed by Papadakis (1937). We first fit the model $Y_{ij} = \mu + F_i + \varepsilon_{ij}$ and obtained residuals from PROC MIXED. We then applied an analysis of covariance (PROC MIXED) in which covariates for each observation were weighted averages over the neighbors' residuals (Magnussen 1993)

$$Y = \mu + P + F(P) + X + \varepsilon \quad (3)$$

where X is the covariate for each observation. After initial data exploration, we settled on a neighborhood size of eight (most proximal) trees as there was little evidence of SA at greater distances (Table 1). Trees on the edge of the planting site had smaller neighborhoods, as did those next to missing or suppressed trees.

Test of SA

After each model was fitted, we constructed semivariogram plots using PROC VARIOGRAM of SAS to check the independence of residuals. To check for SA, we fit an exponential theoretical semivariogram [$\gamma(h) = c_n + c_0(1 - e^{-h/a_0}$] to the observed semivariogram using PROC NLIN of SAS where a_0, c_0, and c_n are the range, the patch variance, and nugget effects respectively. Larger values of the c_0/c_n ratio indicated greater intensity of SA. The distance where the model first flattens out is the range a_0; observations within the range (a_0) are spatially dependent. Moran's I (Moran 1950) and Geary's C (Geary 1954) were calculated using PROC VARIOGRAM to determine whether SA was positive or negative.

Heritability Estimates

Estimates of variance components were obtained from PROC MIXED with the option REML (all model effects random). Individual (h_i^2), family (h_f^2), and within family (h_w^2) heritabilities from the standard model and ISA were calculated separately for each site using the methods of Sierra-Lucero et al. (2002) as follows

$$h_i^2 = \frac{\sigma_A^2}{\sigma_{f(p)}^2 + \sigma_{bf(p)}^2 + \sigma_e^2}$$

$$h_f^2 = \frac{0.25\sigma_A^2}{(k_1\sigma_{f(p)}^2 + k_2\sigma_{bf(p)}^2 + \sigma_e^2)/k_1}$$

$$h_w^2 = \frac{0.75\sigma_A^2}{\sigma_{bf(p)}^2 + \sigma_e^2}$$

where σ_A^2 is additive genetic variance and σ_f^2, $\sigma_{bf(p)}^2$, and σ_e^2 are the family (nested in provenance), block $\times$ family (nested in provenance), and error variances, respectively. Additive genetic variance was calculated as $\sigma_A^2 = \sigma_f^2$. Estimates of k_1 and k_2 were obtained from PROC MIXED using TYPE1 sums of squares. In all cases, we used the Kenward-Rogers denominator degrees of freedom. We replaced $\sigma_{bf(p)}^2$with the variance component of covariates (σ_c^2) to calculate heritabilities for NNA. The significance of random effects was tested using a likelihood ratio test; standard errors for family heritability were calculated as described in Becker (1984). For individual and within-family heritability, standard errors were estimated using the approximation method of Dickerson (1969).

Results

Descriptive Statistics

We observed that, in general, white oak grew well at JP and HC and extremely well at SH (Table 1) as typical diameter growth is about 0.3 cm/year (Rogers 1990). Based on univariate analysis of variance, site effects alone explained 64% of total variation in 10-year height and 51% of total variation for 23-year height and 23-year dbh. A display of the distribution of the residuals (Figure 1) and tests of SA showed that SA was considerable for most of the trait $\times$ site combinations (although SA was greater for height than for dbh).

Provenances were not significant sources of variation at HC or SH but were significant for 23-year height and 23-year dbh at JP. Overall, provenance means for 23-year height ranged from 99.9

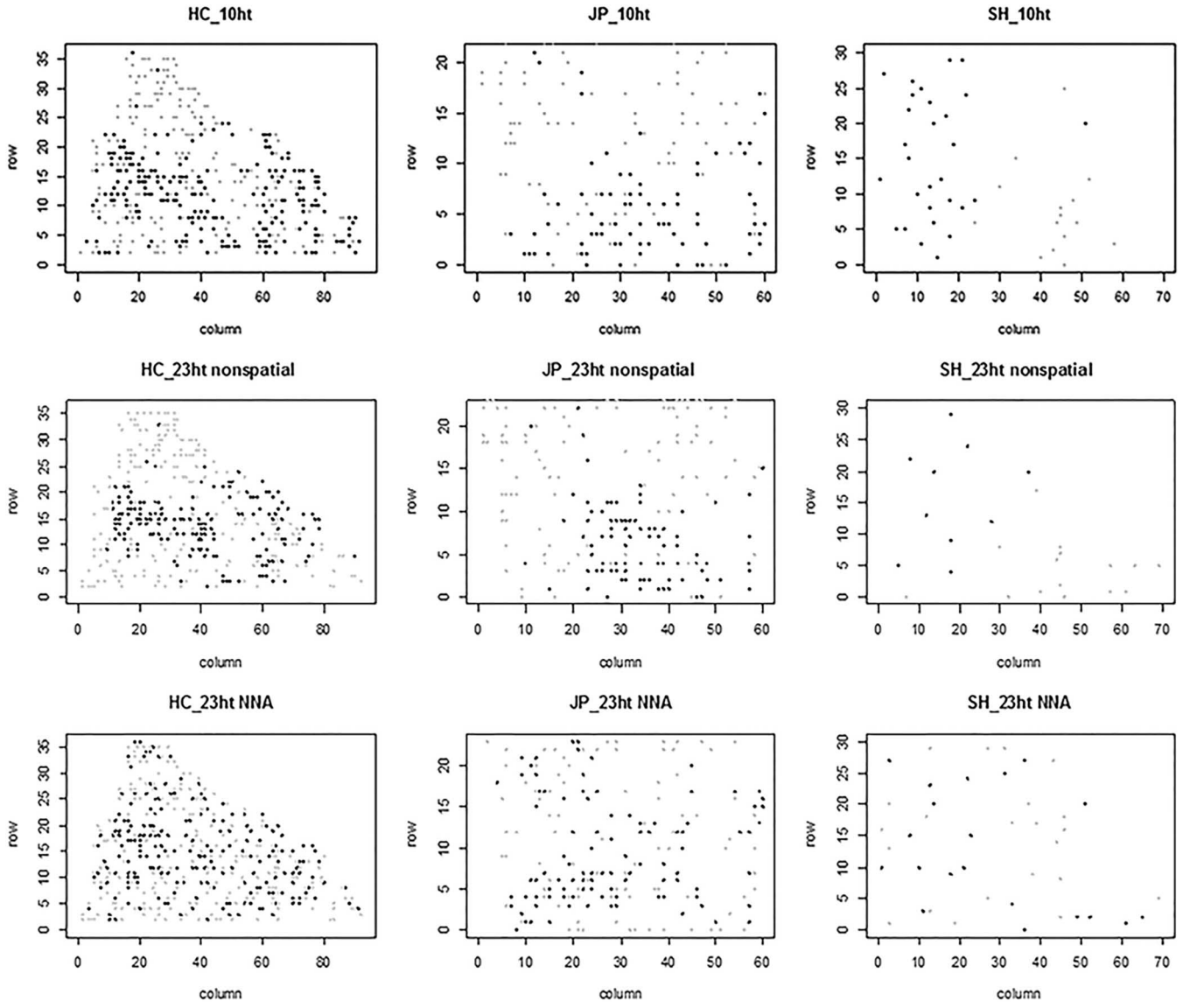

Figure 1. Plots of residuals from the standard nonspatial model for 10-year (top row) and 23-year height (ht) without adjustment for spatial autocorrelation (middle row) and with NNA adjustment (bottom row) at three sites. Extreme residual values are shown as black dots (<−1 SD) or gray dots (>+1 SD), where SD denotes the standard deviations of the original 10-year or 23-year height at each of the three test sites.

to 110.3 dm at HC, from 88.1 to 108.7 dm at JP, and from 152.7 to 173.3 dm at SH (Table 2). Provenances shifted rank among sites to a considerable extent, and there was no clear association between test site latitude and the latitude of provenances that grew or survived best or worst (Table 2). The proportion of genetic variance among provenances and families within provenances that was due to differences among provenances alone (Θ) (Sierra-Lucero et al. 2002) was 19%.

Family was a highly significant source of variation for all three traits at HC irrespective of analytical model, but at JP family was significant only for 23-year dbh. Family was significant for all traits at SH only when ISA and NNA analytical approaches were used. The shortest family at SH (IN-06−03; 131 dm; a family originating near the JP site) was considerably taller than the tallest family at JP (IN-08−01; 105 dm; a family from the northern edge of the latitudes sampled). If the best individual from every family (based on deviation from site mean height) was selected, the mean height of the selected trees would be about 135 dm or 27% greater than the overall mean. Using an index to optimally weight family means and within-family deviations for selection (Lush 1947), the best 15 trees at age 23 from HC (about 1% selection intensity, i) were about 40 dm taller than the site mean (135%). At JP, the best 25 trees (i = 4%) were 138% of site mean, and at SH the best 14 trees (i = ~10%) were 124% of site mean. The best 15 trees at each site at age 23 based on Lush's index included 28 families, although at HC and JP several families were represented three to five times among the top 15 trees (data not shown).

SA

Residuals were spatially autocorrelated for 23-year height and 10-year height at all three sites, but there was little evidence of SA for 23-year dbh (Table 1). Based on patch-nugget ratios (c_0/c_n) (Zas 2006), SA generally increased as trees aged. The increasing trend over time and the strength of SA was reflected in the size of the

Table 2. Mean height (dm) at age 23 of each provenance at each site (rank within site) with percent survival (top row) and mean height (dm) at age 23 and (rank within site) after adjustment using nearest neighbors (bottom row).

Provenance	Latitude	HC	SH[a]	JP
IL-01	37°44′	103.8 (14); 70%[a]	167.3 (7); 6%	88.7 (16); 58%[b]
		104.6 (12)	170.5 (4)	88.3 (16)
IN-14	37°58′	104.1 (13); 69%[a]	173.3 (2); 5%	91.8 (13); 46%[b]
		103.6 (13)	169.5 (5)	91.2 (13)
MO-03	37°58′	101.8 (15); 77%	154.6 (15); 5%	88.1 (17); 53%
		101.2 (16)	156.5 (14)	87.5 (17)
IN-15	38°07′	105.2 (10); 82%	167.6 (6); 6%	103.9 (2); 31%
		106.4 (9)	166.3 (8)	101.7 (2)
IN-13	38°15′	107.4 (7); 77%	160.5 (12); 12%	94.6 (7); 32%
		106.9 (7)[c]	163.1 (11)	94.9 (9)
IN-05	38°42′	107.9 (6); 78%[a]	172.3 (4); 12%	94.5 (8); 38%
		108.4 (3)	173.0 (2)	95.0 (8)
IN-01	38°49′	109.0 (3); 85%	170.7 (5); 12%	94.2 (9); 50%
		108.5 (2)	168.8 (6)[c]	95.9 (6)
IN-04	39°00′	107.1 (8); 69%	172.7 (3); 12%	96.9 (5); 25%
		107.2 (6)	171.6 (3)	97.2 (5)
IN-02	39°08′	108.3 (5); 88%	165.5 (10); 8%	90.8 (14); 38%
		108.1 (4)	163.0 (12)	89.1 (15)
IN-03	39°10′	110.0 (2); 75%	194.3 (1); 15%	90.0 (15); 46%
		108.0 (5)	186.8 (1)[d]	89.5 (14)
IN-12	39°39′		158.5 (14); 8%	108.7 (1); 21%[b]
			160.1 (13)	103.0 (1)[d]
IN-10	40°25′	110.3 (1); 88%	167.0 (8); 8%	95.2 (6); 46%
		109.2 (1)[d]	166.8 (7)	95.4 (7)
IN-11	40°33′	108.5 (4); 78%	160.2 (13); 8%	94.1 (10); 59%
		106.8 (8)	165.2 (9)	94.1 (11)
IN-09	41°04′	105.7 (9); 85%	152.7 (16); 7%	94.0 (11); 53%
		105.6 (10)	154.1 (16)	94.2 (10)
IN-06	41°05′	99.9 (16); 84%	142.5 (17); 3%	92.5 (12); 55%
		101.5 (15)	147.5 (17)	93.1 (12)[c]
IN-07	41°37′	104.7 (11); 79%	163.1 (11); 5%	99.5 (3); 43%
		103.2 (14)	156.3 (15)	99.2 (3)
IN-08	41°40′	104.7 (12); 81%	166.8 (9); 5%	98.6 (4); 53%
		105.3 (11)	164.6 (10)	97.9 (4)

[a] Survival at SH was affected by rogueing at 6 and 9 yr, see Table 1 for details concerning tree density.
[b] Provenance contained a family with significantly lower survival than average at HC (IL-01-05, IN-05-05, and IN-14-03) or JP (IL-01-05, IN-12-01, and IN-14-05).
[c] Provenance closest to each test site.
[d] Tallest provenances.

Table 3. Percentage of the total variance attributed to provenance, families, block × family (nested in provenance) interactions, and error for each analytical method at each site studied.

Site	Trait	Model	Variance component (%)[a] σ_p^2	$\sigma_{f(p)}^2$	$\sigma_{bf(p)}^2$[b]	σ_e^2
HC	10-yr h	Standard	1.0	9.1***	16.4	74.5
		ISA	0.0	8.3***	0.0	91.6
		NNA[b]	0.0	8.6***	0.7	90.3
	23-yr ht	Standard	0.8	6.4***	27.9	64.9
		ISA	0.6	8.4***	0	91
		NNA	0.6	8.3***	0.4	90.4
	23-yr dbh	Standard	0	4.7***	0	95.3
		ISA	1.5	4.6***	0.8	93.1
		NNA	1.4	4.6***	0.0	94.0
JP	10-yr ht	Standard	0.9	1.0	19.9	78.2
		ISA	0.5	3.6	3.6	92.2
		NNA	0.5	1.2	0.5	97.7
	23-yr ht	Standard	4.4	2.9	20.6	72.3
		ISA	0.1	5.2	0	94.7
		NNA	4.9	2.5	0.4	92.5
	23-yr dbh	Standard	4.7	6.1**	0	89.2
		ISA	1.2	5.6**	0	93.2
		NNA	4.4	5.6**	0	90.0
SH	10-yr ht	Standard	4.2	6.4	75.8	13.5
		ISA	1.8	9.6*	22.0	66.6
		NNA	13.5	48.5***	1.9	36.1
	23-yr ht	Standard	16.6	23.9*	49.7	9.8
		ISA	7.2	8.5*	47.9	36.4
		NNA	17.8	42.5***	1.1	38.6
	23-yr dbh	Standard	0	18.2	0	81.8
		ISA	0	20.0	0	80.0
		NNA	0	42.9***	14.1	42.9

[a] For definitions of variance components, see Materials and Methods. Significance: *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.
[b] For the NNA analysis, σ_c^2, the covariate, was used instead of $\sigma_{bf(p)}^2$ as described in Materials and Methods.

block × family interaction term of the standard model. At HC, block × family variance was almost 28% of the total (Table 3). The intensity of SA was higher in SH than in HC and JP, but at HC and JP the (c_0/c_n) ratios were as high as or higher than those reported by Zas (2006) as benefiting from ISA. The range of spatial dependence decreased as trees aged, especially at JP (Table 1), and was smaller than the block size in general. Moran's I and Geary's C both indicated positive autocorrelation for 10- and 23-year height at all three sites (i.e., nearby trees were more alike than expected).

ISA

We applied the iterative kriging method of Zas (2006) to data from all three sites. After two or three iterations, the semivariograms of residuals all became flat, indicating a random spatial pattern. After adjustment for SA, family × block interactions were reduced to zero in most cases (Table 3). As a result, we observed higher family heritability estimates from ISA than the standard mixed model except for 23-year height in SH (Table 4).

NNA

NNA (Equation 2) uses information from neighbors to locally adjust for site variability. When we fit the model $Y_{ij} = \mu + F_i + \varepsilon_{ij}$ to obtain the residuals, family was a significant effect ($P < 0.01$) for all three traits at HC but was only significant for 23-year dbh at JP and 23-year height at SH. After we added the covariate (neighborhood mean residual, X) into the model [$Y = \mu + P + F(P) + X + \varepsilon$], family was significant for all traits at all sites except for 10- and 23-year height at JP. NNA had little effect on variance allocation for any trait based on the proportion of variance explained by the covariate term (Table 3), but this did not mean that NNA adjustment did not affect the results. At HC, NNA resulted in an average change in height of 6.6 ± 6.1 dm or about 6% at age 23. In one case, NNA changed height estimates at HC by 45 dm. NNA shifted family ranks. For example, in HC four families in the top 10 based on the standard analysis dropped out of the top 10 based on NNA, and the 25th ranked family based on the standard analysis was ranked 8th best based on NNA (Table 5). The effect of NNA on 23-year height at the other locations was similar. The effect of neighbor tree height on dbh was nonsignificant. Iterating the NNA model provided little added benefit.

Model Comparisons

The AICs for the standard mixed model were the largest (i.e., worst fit) for all traits at all sites. NNA produced lowest the AICs for 10-year height and 23-year dbh at HC and SH, but ISA generally produced the best fit for 23-year height.

The proportion of variance explained by families nested in provenances was considerably greater than the among-provenance variance (Table 3). Because SA was low for 23-year dbh, all three analytical models produced similar results for this trait. The interaction

Table 4. Heritability estimates for individuals, families, and within families.

Site	h^2 type	Trait	Heritability estimate ± SE[a,b]		
			Standard	ISA	NNA
HC	h_i^2	10-yr ht	0.36 ± 0.12	0.34 ± 0.12	0.34 ± 0.12
	h_i^2	23-yr ht	0.26 ± 0.06	0.32 ± 0.08	0.33 ± 0.08
	h_i^2	23-yr dbh	0.19 ± 0.24	0.21 ± 0.24	0.19 ± 0.24
	h_f^2	10-yr ht	0.64 ± 0.11	0.66 ± 0.12	0.64 ± 0.11
	h_f^2	23-yr ht	0.49 ± 0.10	0.54 ± 0.10	0.60 ± 0.11
	h_f^2	23-yr dbh	0.54 ± 0.10	0.55 ± 0.10	0.52 ± 0.10
	h_w^2	10-yr ht	0.30 ± 0.04	0.26 ± 0.05	0.28 ± 0.05
	h_w^2	23-yr ht	0.21 ± 0.02	0.25 ± 0.03	0.27 ± 0.03
	h_w^2	23-yr dbh	0.15 ± 0.09	0.16 ± 0.09	0.14 ± 0.08
JP	h_i^2	10-yr ht	0.04 ± 0.05	0.15 ± 0.10	0.05 ± 0.06
	h_i^2	23-yr ht	0.12 ± 0.05	0.20 ± 0.08	0.20 ± 0.05
	h_i^2	23-yr dbh	0.26 ± 0.26	0.22 ± 0.24	0.25 ± 0.25
	h_f^2	10-yr ht	0.08 ± 0.03	0.27 ± 0.06	0.11 ± 0.04
	h_f^2	23-yr ht	0.20 ± 0.05	0.34 ± 0.07	0.18 ± 0.05
	h_f^2	23-yr dbh	0.44 ± 0.09	0.46 ± 0.09	0.43 ± 0.09
	h_w^2	10-yr ht	0.03 ± 0.02	0.08 ± 0.04	0.04 ± 0.02
	h_w^2	23-yr ht	0.09 ± 0.02	0.14 ± 0.03	0.08 ± 0.02
	h_w^2	23-yr dbh	0.21 ± 0.10	0.16 ± 0.08	0.20 ± 0.09
SH	h_i^2	10-yr ht	0.27 ± 0.08	0.36 ± 0.11	2.24 ± 0.15
	h_i^2	23-yr ht	1.14 ± 0.13	0.54 ± 0.08	2.06 ± 0.15
	h_i^2	23-yr dbh	0.73 ± 0.39	0.62 ± 0.40	1.71 ± 0.15
	h_f^2	10-yr ht	0.29 ± 0.07	0.37 ± 0.08	0.84 ± 0.14
	h_f^2	23-yr ht	0.46 ± 0.09	0.18 ± 0.05	0.58 ± 0.11
	h_f^2	23-yr dbh	0.32 ± 0.07	0.34 ± 0.07	0.57 ± 0.11
	h_w^2	10-yr ht	0.22 ± 0.03	0.28 ± 0.04	3.82 ± 0.33
	h_w^2	23-yr ht	1.20 ± 0.07	0.44 ± 0.03	3.21 ± 0.18
	h_w^2	23-yr dbh	0.67 ± 0.16	0.63 ± 0.17	2.25 ± 0.48

[a] For details on models, see Equations 1, 2, and 3; for method of heritability estimates, see Materials and Methods.
[b] For calculation of SE using the method of Becker (1984), heritability estimates of >1 were considered = 1.

Table 5. Rank changes of tallest families at ages 10 and 16 and at age 23 with and without nearest neighbor adjustment for spatial autocorrelation.

Family	Rank height at age			
	10 yr	16 yr	23 yr	
			No NNA	With NNA
IN-01-03	13	1	2	3
IN-10-02	3	2	20	18
IN-02-05	4	3	1	1
IN-13-03	7	4	15	7
IN-10-05	15	5	12	10
IN-11-02	5	6	11	14
IN-07-04	1	7	6	9
IN-10-04	24	8	5	4
IN-06-03	6	9	8	5
IN-14-01	19	10	36	34
IN-10-01	9	11	3	2
IN-05-01	25	ND	13	6
IN-15-02	47	ND	25	8

Age 16 data reported by O'Connor and Coggeshall (2011). ND, not determined.

term $\sigma^2_{bf(p)}$ was substantial for 10- and 23-year height under the standard mixed model, and the variance for this factor was completely reallocated using ISA at HC and JP but not SH. In SH, where ISA failed to remove $\sigma^2_{bf(p)}$, heritability estimates for 10- and 23-year height based on ISA were much lower than estimates based on NNA and, in one case, even lower than the estimate based on the standard model.

In general, ISA and NNA models did not improve estimates of family heritability over the standard mixed model at HC and JP (Table 4). At SH, heritability estimates for all three traits were considerably higher under the NNA model versus the other two models, but NNA produced unusual estimates of individual (h_i^2) and within-family heritability (h_w^2) at SH for all traits, well above the theoretical maximum (1.0). This occurred although the AIC for NNA was the lowest (best) of all three models for all three traits at SH. Heritability estimates based on NNA were in line with those for the other two methods at the other two sites. Surprisingly, even standard analysis produced unusual estimates of individual (h_i^2) and within-family heritability (h_w^2) for 23-year height at SH (Table 3).

Correlations and Correlated Response to Selection

Although there were substantial rank shifts among families over the 23 years of the study (Table 5), the genetic correlation between 10-year height and 23-year height across all sites, families, and provenances was fairly high (0.81 ± 0.08). The correlated response (gain from indirect selection) of 23-year height due to selection of parents at age 10 was 0.27 m at HC, assuming a selection intensity of 0.2 and selection among 50 families; the expected direct response to selection at age 23 in HC was only slightly better (about 0.3 m). Selection within families would probably produce additional gains.

Discussion

Effect of Site on Growth and SA

Although white oak is adapted to a wide range of soils, climates, and conditions (Rogers 1990), site and microsite had a large and significant effect on white oak height and dbh in this trial (Table 1) (Rink and Coggeshall 1995). Rink and Clausen (1989) saw similar "site-sensitivity" (their term) in a multilocation RCB trial of *Juglans nigra* L. They described how the analysis of their RCB design was compromised by SA, which was high in the white oak sites at age 10 and continued to be present at subblock spatial scales. Blocking in the original planting design was ineffective for removing SA, but high block × family interaction variance (in the standard model) did not strongly or adversely affect heritability estimates. Nevertheless, adjustment of analysis to account for SA produced models with better fit (lower AIC) that resulted in greater differences among families (at SH) and that more accurately estimated individual and family means. There is no single best analytical method to account for SA (Dutkowski et al. 2002), but in this study the use of complementary analyses increased our confidence in the heritability estimates and BLUP of family and provenance means. Surprisingly, SA was positive (i.e., neighbor trees were more similar in height than expected), although trees were clearly competing at all three sites by age 23.

White Oak Breeding Zones

What constitutes a "local" source is not clear for many hardwood species. Nearby provenances did not outgrow distant ones at any of the three sites in our study (at HC and SH provenances were nonsignificant factors), nor was there a pattern where the best sources were consistently from higher or lower latitudes than the test site or where northern or southern provenances grew faster in general. After analysis of a large-scale northern red oak (*Quercus rubra* L.) provenance trial, Kriebel et al. (1976) recommended "phenotypic selection without regard to geographic origin." For black walnut (*Juglans nigra* L.), Bresnan et al. (1994) recommend sources from 100 to 200 km south of the planting site, but many of the best

provenances at their seven test sites were considerably more distant than that. In contrast, in a large test of white ash (*Fraxinus americana* L.), provenance accounted for about three times more variance for growth than family, but the best provenance for a planting site was not usually nearby, and it could not be predicted based on latitude (Clausen 1984).

Several lines of evidence indicate that a clonal seed orchard propagated from selections from this trial would be suitable for producing nursery stock for large areas of the central hardwood region: predicted seed zones for native species in the central hardwoods are wide (Bower et al. 2014), a relatively small proportion of the total genetic variance for white oak was among provenances ($\Theta = 0.19$), local sources showed no growth advantage (Table 2), and the genetic correlation between height at age 10 and age 23 was high (0.81), so family rank would be expected to remain fairly consistent across environments, although the genetic correlation was biased (possibly reduced) by rogueing at SH (Wei and Borralho 1998). Site conditions overwhelmingly determined growth, and expected gain from family selection at age 10 was about 0.3 m. A joint analysis of all three sites might shed some light on the importance of genotype × environment (G × E) and the value of a single seed orchard, but meaningful inferences regarding G × E require at least five planting sites (Magnussen 1993).

Possible Sources of Bias in Results and Their Consequences

High levels of among-family variance, together with the effective removal of environmental variance, contributed to moderately high family mean heritability estimates (Table 4). Some heritability estimates were beyond expected ranges (>1), a result that occurred using both standard analysis and NNA at one site only. The cause of the unexpectedly high values may have been related to the small sample size of some families after rogueing, the reduction of within but not among family variance by rogueing, or the underestimation of total phenotypic variance caused by selective thinning. All of these factors may inflate heritability (Matheson and Raymond 1984) or not (Wei and Borralho 1998), probably depending on the particular thinning or rogueing regime and the traits. It was surprising that heritability estimates at SH based on ISA did not show the inflation seen using other methods. Provenance and family effects were not independent in this study as provenances were unbalanced, families were not randomly chosen, and seed sources may have shared genetic covariance.

Lessons for Future White Oak Research and Regeneration

Progeny tests of selections from these trials should not take 23 years. High genetic juvenile-mature correlations (0.81) indicated that genetic gains in white oak can be made more efficient through early selection. Early forward selection might also be possible because although white oak juvenility can exceed 20 years (Rogers 1990), M.V. Coggeshall and P.A. O'Conner (unpubl. data, October 2006) indicated that seedlings in some families in this study began bearing seeds by age 9. The effect of SA on G × E and juvenile-mature correlations probably depends on the (spatial) range of autocorrelation relative to plot size, how competition changes over time, and how G × E changes. Factors causing SA in juveniles, e.g., herbivory and shallow soil, may not do so in adult trees and vice versa but we observed that the regions of the plantations where tree height was strongly autocorrelated did not change much over time. The best microsites within the plantations were obvious by age 10 (Figure 1). The precision of forward selection can be improved by removal of SA (Dutkowski et al. 2002) as exemplified in this study where NNA changed overall mean 23-year height estimates at each site by about 6%, although the means of some individuals were adjusted by NNA more than 25%, strongly affecting forward selection and family rank within site. A seed orchard representing selections from this study could have high diversity because the top individuals from all families still provided excellent estimated gain. Alternatively, use of Lush's optimal index to select individuals would capture more among and within family variance and result in greater gain (Lush 1947).

Endnote

1. For more information, see www4.ncsu.edu/~fisik/Multivariate.htm.

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