Height Response Functions for White Ash Provenances Grown at Different Latitudes*)[1]

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(Received 8th February 1989)

Summary

Variation among fifth-year height total height response functions was analyzed for provenances of white ash (*Fraxinus americana* L.). Mean height for each provenance was determined at four to seven locations of differing latitude. The Gaussian function was fitted to these growth data with plantation latitude as the dependent variable. Patterns of variation observed among provenances with respect to the response function parameters indicated the presence of northern and southern ecotypes in this species. Within the southern ecotype, two of the response function parameters decreased linearly with increasing latitude of provenance whereas the third parameter increased. In the northern ecotype, parameters increased with provenance latitude or remained constant. Applying the value function described by Roberds and Namkoong (1989) to the patterns of response function variation observed, the determination of optimal seed sources and planting zones was illustrated for reforestation programs involving two and three sources of seed.

Key words: Ecotypes, clinal variation, value function, seed transfer zonation, breeding zones, Gaussian function, homeostasis of response.

Introduction

In tree breeding research, the importance of growth responses to changes in environmental variables has been recognized for some time. Such responses, which are nonlinear for many environmental variables, affect rules for choosing sources of seed and for seed transfer in forest regeneration. As breeding efforts have intensified, it has become clear that nonlinear growth models also provide information useful for forming breeding populations and for specifying environmental and geographic boundaries for planting the improved stock. A number of nonlinear response functions have been used to determine seed transfer and breeding zones, and an optimization theory for such purposes has been proposed by Namkoong (1976) and Roberds and Namkoong (1986, 1989). This theory utilizes Gaussian response functions in conjunction with normal density functions which represent distributions of available planting sites. Planting zones have also been determined by modeling growth responses with the Cauchy function (Raymond and Lindgren, 1986; 1990). In addition, methods based on multiple regression techniques been suggested for determining zone boundaries (Rehfeldt, 1979; Clausen, 1984).

Little is known about variations of nonlinear response functions among populations within a species. Furthermore, it is unclear how such variation affects choices of seed source populations and boundaries for their use. In this report we describe variation patterns in response function parameters among provenances of white ash (*Fraxinus americana* L.). Using response functions, optimum choices for arrays of two and three provenances are determined and zones for their use described.

Materials and Methods

Description of Data

The data for this investigation are a subset of data from a range-wide provenance and progeny test of white ash initiated in 1975 by the North Central Forest Experiment Station at Carbondale, Illinois (Bey et al., 1977). Total heights of trees were measured after 5 growing seasons in the field (age 6 from seed). Seed sources and field planting sites are described in Clausen (1984). Each provenance at a test location was represented by 1 to 5 open pollinated families. In most plantings, 5-tree row plots were established in 5 replications in a randomized complete block design.

Of the 20 planting locations in the range-wide study, we excluded three from consideration: the New Brunswick plantation due to its eastern isolation from the other planting locations, the West Virginia plantation because of high elevation, and the Missouri plantation because of repeated deer browsing (Clausen, 1984).

In a sample of 17 provenances, mean total height for each provenance was plotted against latitude of plantation location (*Figure 1*). These line graphs indicate that planting locations can be partitioned into two distinct groups, one with good height growth for all provenances in the sample and one with poor growth. Locations with good growth were indicated by peaks (arrows in *Figure 1*), whereas locations with poor growth were represented by valleys. On this basis, at least five locations appeared to have good growth. Above 45° N latitude, however, designation of locations into growth categories was difficult. At both of the high latitude plantations (above 45° N latitude), some provenances showed increased growth over their performance at the adjacent lower latitude location, so we included these in the good growth group. Seven locations were thus designated as good growth locations. A similar designation of locations into good and poor growth categories based on the pattern obtained from plantation means after 5 years (Clausen, 1984), agreed with our assignment except for two plantations. Both plantations at locations above 45° N latitude (Ontario and Wisconsin) included in the good growth group on the basis of the sample would have been placed in the poor

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*) This paper is dedicated to the memory of Dr. S. K. Hyun whose life and work continue to be an inspiration to many scientists.

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growth category if plantation means had been used as the basis for assignment.

Differences in growth for the two groups of locations probably are attributable partly to differences in site conditions and partly to plantation management. In some plantations, weeds and brush were controlled and in others they were not (K. Clausen, personal communication).

In this investigation, only provenances that were tested in at least four of the good growth locations were studied. Mean heights of these provenances by planting location are given in *table 1*. Locations for the planting sites and provenances investigated are shown in *figure 2*.

Estimation of Response Function Parameters

The Gaussian function has been used to model responses of traits varying in environmental gradients in a theory developed for determining optimum breeding and seed transfer zones (Roberds and Namkoong, 1986; 1989). A similar use for the Gaussian function occurs in ecology where it is employed to represent the utilization function in niche theory (Christiansen and Fenchel, 1977). Its parameters can be interpreted in a biologically meaningful way and its properties are well known. We therefore chose to use it to model height response of the white ash provenances to changes in latitude of the planting locations. For this purpose, the response function can be represented as:

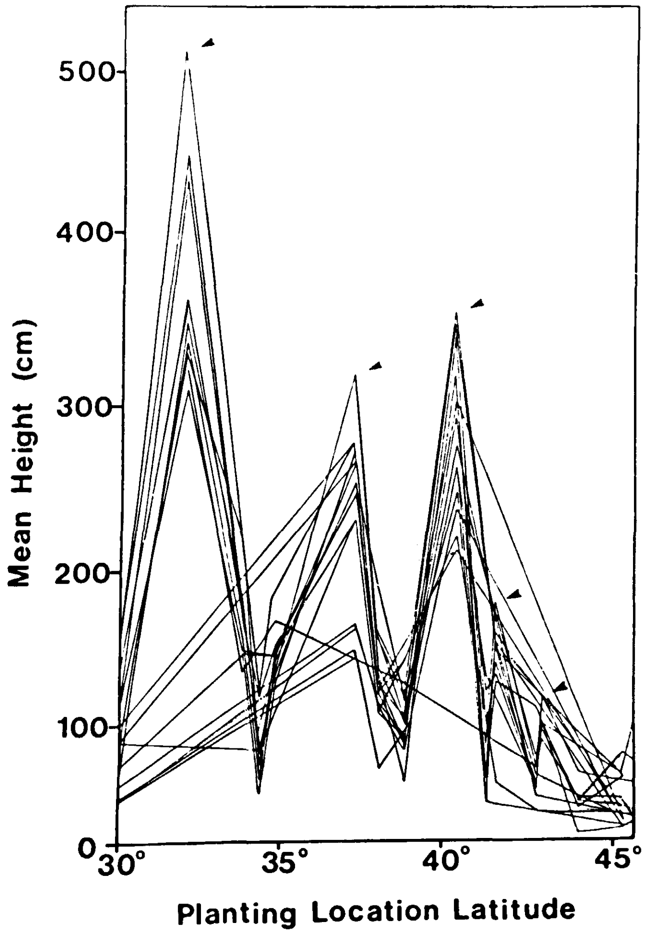


Figure 1. — Mean heights of sample provenances at planting location latitudes. Arrows indicate growth peaks.

$$f_i(x) = [k_i/\sqrt{2\pi\eta_i}]e^{-(x-\mu_i)^2/2\eta_i} \tag{1}$$

where $f_i(x)$ is mean height for the i^{th} provenance grown at latitude x; k_i is the scale parameter; η_i is the homeostatic parameter; and μ_i is the mode latitude for the i^{th} provenance. The scale parameter (k_i) scales function values from the interval (0,1) to the appropriate range of values for total height. A measure of the uniformity of response over the range of latitudes for planting white ash is given by homeostatic parameter (η_i) and the latitude at which maximum height is achieved is given by the mode parameter (μ_i).

Parameters of the response function for each provenance were estimated by fitting growth values to the Gaussian function using the least squares procedure suggested by Wright (1968). Logarithms of mean growth for each provenance were fitted to latitudes of the test plantings. In logarithmic form, the model for growth response for the i^{th} provenance is linear and can be represented as:

$$\ln f_{ij}(x) = b_{i0} + b_{i1}x_j + b_{i2}x_j^2 + e_{ij} \tag{2}$$

where $f_{ij}(x)$ is the mean height for the i^{th} provenance grown at the j^{th} location, and x_j is the latitude of the j^{th} location. The b_{ik} are regression coefficients and e_{ij} is the error term. Estimators for the Gaussian function parameters in terms of estimates for the regression coefficients are:

$$\hat{\eta}_i = -1/2\hat{b}_{i2},\ \hat{\mu}_i = -\hat{b}_{i1}/2\hat{b}_{i2} \quad \text{and}$$
$$k_i = (-\pi/\hat{b}_{i2})^{1/2}\ e^{[\hat{b}_{i0}-(\hat{b}_{i1})^2/4\hat{b}_{i2}]} \tag{3}$$

Values of R^2 were computed to indicate the fit of the logarithm data to the linear model.

Results

Response Function Variability

Parameter estimates for the Gaussian response functions and R^2 values for the logarithmic model are given by provenances in *Table 2*. Data for the southern provenances fitted the linearized form of the response function well. All provenances studied from latitudes south of 39° N had R^2 values larger than 0.93. Data for sources between 39° N and 42° N fitted the model moderately well with R^2 values that ranged from 0.85 to 0.92. Fit of the model was somewhat poorer for the four northernmost provenances which had R^2 values that varied from 0.58 to slightly above 0.77.

For the extreme southern and northern sources, latitudes at which maximum height was achieved (mode latitudes) were somewhat different from the latitudes of origin. These two characteristics of provenances, however, did not differ substantially for provenances near the central latitudes of the species range. Mode latitudes of the southernmost provenances were higher than latitudes of origin by more than 1.5°, whereas for the northernmost seed sources, mode latitudes were more than 5° below latitudes of origin (*Table 2*). Only provenances from the central latitudes attained best growth at latiudes near their origins. Nevertheless, there was a positive association between mode latitude and provenance latitude ($r > 0.82$; *Table 3*). Since provenances north of 39° N had maximum growth at a latitude of approximately 39° N, this relationship was nonlinear. A quadratic model fitted the data

Table 1. — Mean height (cm) of white ash provenances after 5 growing seasons (age 6) for plantations with good growth.

Provenance State	Number	Latitude of Origin	AL[a] (32.4)	IL (37.5)	OH (40.0)	NY (41.8)	ONT (43.2)	WI (45.6)	ONT (46.0)
TX	6768	30.3	458.7	279.3	207.3	-	-	37.2	-
MS	6737	30.8	443.7	252.2	244.3	-	-	34.0	-
MS	6740	33.4	367.3	321.6	273.1	-	-	40.5	-
AL	6733	34.5	336.9	228.6	233.2	-	-	37.0	-
TN	6728	35.2	351.6	243.8	319.6	148.7	-	39.7	-
TN	6871	35.5	311.2	262.8	302.3	-	-	38.4	-
KY	6734	36.7	-	265.4	318.7	148.9	-	34.5	-
KY	6792	37.2	341.2	250.5	350.6	147.4	97.8	32.5	36.7
IL	6721	37.7	-	278.3	320.6	164.5	-	43.8	-
IN	6795	38.6	-	271.5	342.3	175.2	93.8	46.3	43.3
WV	6778	39.0	-	141.1	278.99	144.7	-	65.4	-
IL	6771	39.1	-	228.0	360.8	146.2	88.7	51.6	37.7
CT	6794	41.3	-	172.9	267.9	123.8	108.3	64.4	53.4
VT	6782	44.0		139.5	320.1	-	94.4	83.0	92.3
ME	6785	45.9		149.5	235.9	-	83.6	70.0	70.7
WI	6723	45.7	-	162.4	299.0	136.1	98.7	79.7	72.1
MI	6736	46.6	-	146.2	258.6	-	88.1	66.9	100.3
	MEAN		372.94	223.15	290.19	148.39	94.18	50.88	63.31

a) Plantation locations. Figures in parentheses indicate degrees North latitude.

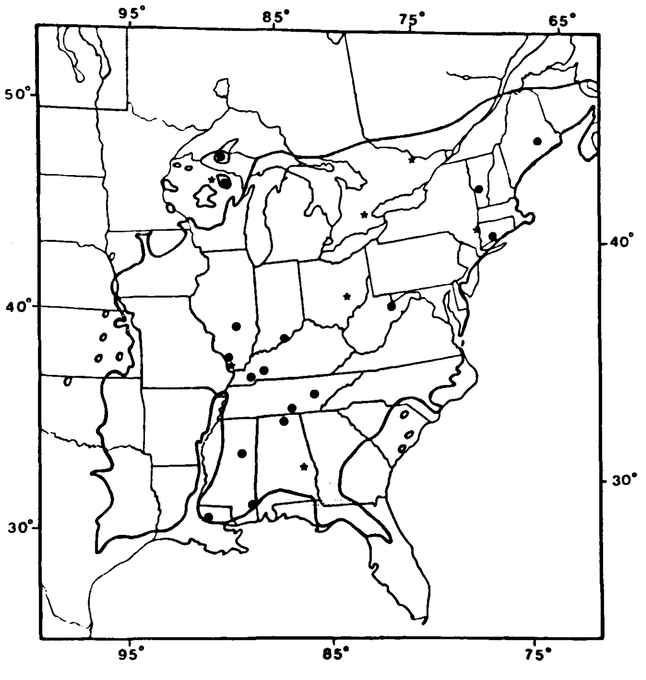


Figure 2. — Natural range of white ash (dark line), locations of provenances (dots), and locations of test plantations (stars).

well ($R^2 = 0.8213$) and can be used to predict mode latitude from latitude of origin (*Figure 3a*). Based on the equation given in the *figure*, latitude of provenance origin equaled latitude of best growth at 37.06° N, which is near the center of the white ash range.

Unlike the modes, the homeostatic parameters displayed a strong negative association with provenance latitude for the 12 sources below 40° N latitude (*Table 3* and *Figure 3b*). The largest estimate for a homeostatic parameter (37.04) was obtained for the southernmost seed source, while the smallest value (12.17) was observed for the provenance at latitude 39° N. These parameters, however, increased in value as the provenance latitude increased beyond 40° N. As a result, the correlation between this measure of homeostasis and provenance latitude was not large ($r = -0.1716$) when considered over all provenances. A second-degree polynomial with source latitude as the dependent variable, however, did fit the data well ($R = 0.8543$) and is illustrated in *figure 3b*.

The scale parameters displayed a pattern of variation similar to that found for the homeostatic parameters. The largest value observed for a scale parameter (6899.4) was found for the southernmost provenance and the smallest value (1814.07) was observed for provenance 6778 at 39° N (*Table 2*). As provenance latitude increased, the scale

Table 2. — Parameter estimates for the Gaussian response function.

Provenance	Latitude of Origin	Mode Latitude (μ)	Homeostatic Parameter (η)	Scale Parameter (k)	R^2	Response at Mode Latitude
	Degrees	Degrees				
6768	30.3	32.03	37.04	6899.40	.9965	452.26
6737	30.8	33.03	31.64	6030.65	.9759	427.72
6740	33.4	34.96	24.54	5094.93	.9921	410.31
6733	34.5	34.11	30.29	4679.84	.9716	339.23
6728	35.2	35.00	25.51	4776.23	.9339	377.26
6871	35.5	35.33	22.88	4398.39	.9596	366.84
6734	36.7	38.34	12.18	2538.13	.9743	290.14
6792	37.2	35.29	23.12	4649.25	.9486	385.74
6721	37.7	38.29	13.72	2780.04	.9772	299.42
6795	38.6	37.47	17.68	3610.36	.9550	342.55
6778	39.0	40.20	12.17	1814.07	.8456	207.45
6771	39.1	37.92	16.66	2727.12	.9159	266.55
6794	41.3	38.57	20.85	2271.10	.8923	198.42
6782	44.0	39.88	19.76	2187.65	.5785	196.33
6785	44.9	38.40	28.38	2375.25	.7723	177.87
6723	45.7	38.56	25.97	2497.12	.7505	195.49
6736	46.6	38.51	32.51	2515.63	.5824	176.01

Table 3. — Correlation coefficients for estimates of response function parameters and latitude of origin. Values above the diagonal represent correlations for the 12 provenances occurring below 40° N latitude. Values below the diagonal are correlations for all 17 provenances investigated.

	Latitude of Origin	Mode Latitude (μ)	Homeostatic Parameter (η)	Scale Parameter (k)
Latitude of Origin	-	.8966**	-.8814**	-.9027**
Mode Latitude (μ)	.8221**	_	-.9776**	-.9826**
Homeostatic Parameter (η)	-.1716	-.6612**	-	.9616**
Scale Parameter (k)	-.8366**	-.9828**	.6259*	-

**) Significant at the 1% level
*) Significant at the 5% level

parameter decreased for the southern and central sources but increased slightly for provenances north of 40° N. The second-degree polynomial fitted these data reasonably well, R = 0.9254 (*Figure 3c*). As might be expected for this pattern of variation, the linear correlation between source latitude and the scale parameter was large and negative both for the data set of all sources and the set excluding the 5 northern sources (above 40° N latitude) (*Table 3*).

The fitted growth functions (*Figure 4*) indicated that the largest differences among provenances in height occurred within a zone extending from 30° N latitude to approximately 35° N. North of this zone, variation in height among provenances gradually declined to about latitude 41° N. Above 41° N, variation in growth was small and remained at approximately the same level.

To clarify the pattern in which response functions varied as latitude of provenance increases, data from

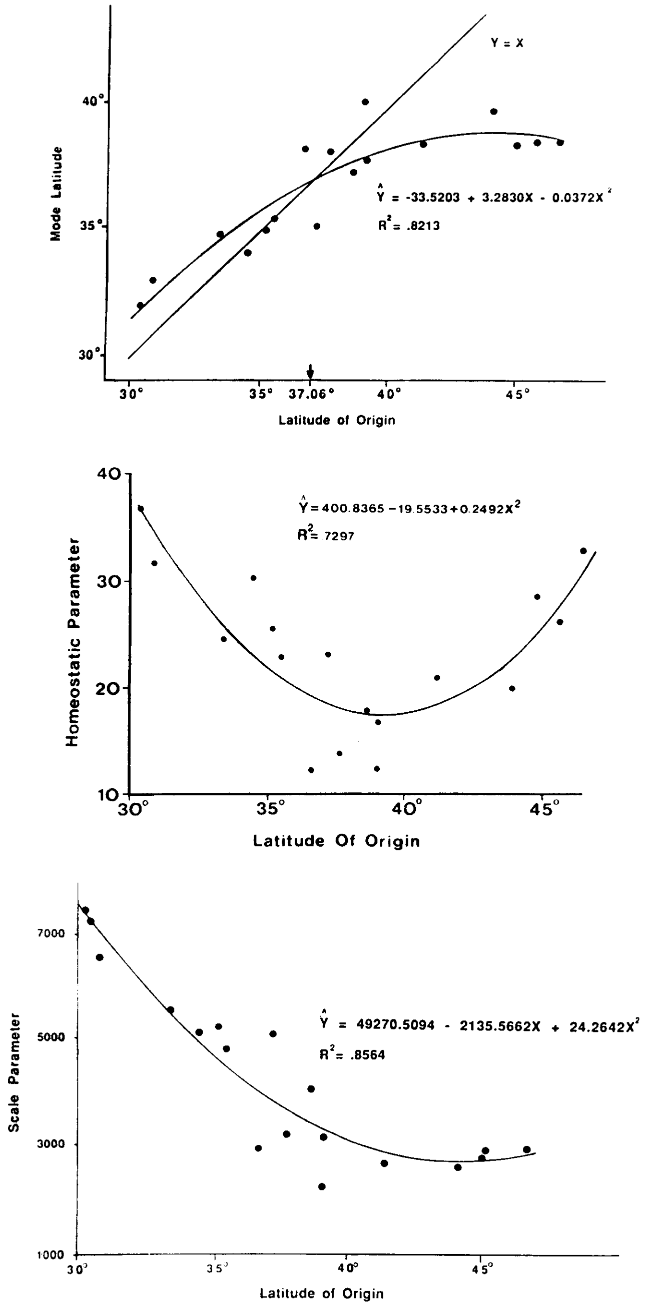


Figure 3. — Relationships between the three response function parameters and latitude of origin: a) mode latitude, b) measure of homeostasis, and c) scale parameter.

provenances of similar latitude were combined to obtain estimates of response function parameters. Comparison of these average response functions (*Figure 5*) indicated that height at mode latitude decreased linearly with increasing latitude of origin within the interval from 30° N to 40° N. The correlation between these variables was large, negative, and significantly different from zero (r = −0.8964). Similarly, correlations computed for the 12 provenances located south of 40° N indicated a strong negative relationship between mode latitude and both the homeostatic and scale parameters, (r = −0.9776 and r = −0.9826 respectively (*Table 3*)). Such strong associations suggest that these two parameters can be predicted with little error from mode latitude. In addition, there was a positive association between provenance and mode latitudes, r = 0.8966, for these same provenances. Regression equations describing these linear associations are illustrated in *Figure 6*.

Optimum Choice of Seed Sources

A value function initially introduced by NAMKOONG (1976) has been proposed as a suitable basis for determining proper seed sources, breeding populations, and zones for their use (ROBERDS and NAMKOONG, 1986; 1989). This value function is applicable to traits that have a continuous response to an environmental variable that varies in a gradient. The value function for the ith population, $v_i(x)$ is defined as

$$v_i(x) = \int_a^b f_i(x)g(x)dx \qquad (4)$$

where x represents value of the environmental variable, $f_i(x)$ is the response function for the ith population defined in (1), g(x) is the probability density function for available planting sites, and b and a represent upper and lower extrema for the environmental variable.

Generally, forest tree improvement programs involve development and use of a number of different populations because the existence of a single best population for all environments is rare. It is customary to use propagules from a particular population only in environments for which that population performs as well or better than other populations. The planting zones or intervals of use for each population along the environmental gradient are bounded by end points that truncate their response functions. The value function for a set of populations is the sum of the contributions of individual populations to the total value and can be expressed as

$$v(x) = \sum_{i=1}^{n} \sum_{j=1}^{m_i} \int_{a_{ij}}^{b_{ij}} f_i(x)g(x)dx \qquad (5)$$

where n is the number of populations in the set, m_i is the number of different contributions to value for the ith population, and b_{ij} and a_{ij} are the upper and lower truncation points for the jth interval of use for the ith population. Interior truncation points are a subset of the points of intersection for response functions. Points of intersection for two populations (t_{jk}) are given by

$$\begin{aligned} t_{ik} = {} & (\eta_i\mu_k - \eta_k\mu_i)/(\eta_i - \eta_k) \\ & \pm (\eta_i\eta_k)^{1/2}\,[(\mu_i - \mu_k)^2 - 2(\eta_i - \eta_k) \\ & \cdot \ln(k_i\eta_k^{k}/k_k\eta_i^{k})]^{1/2}/(\eta_i - \eta_k) \end{aligned} \qquad (6)$$

where i and k are such that $\eta_i > \eta_k$. The two external truncation points are the values for the environmental variable at opposing ends of the gradient.

White ash seed sources and planting zones that maximize the value function in (5) were determined for the cases of two and three sources of seed. The value function was numerically evaluated and truncation points determined for combinations of mode parameter values occurring at 0.1° intervals in the range extending from 30° N through 40° N. Mode values fell within this interval for virtually all provenances regardless of origin (*Table 2* and *Figure 3*). Within this range, values for the scale and homeostatic parameters of response functions were closely correlated with values for the mode parameter

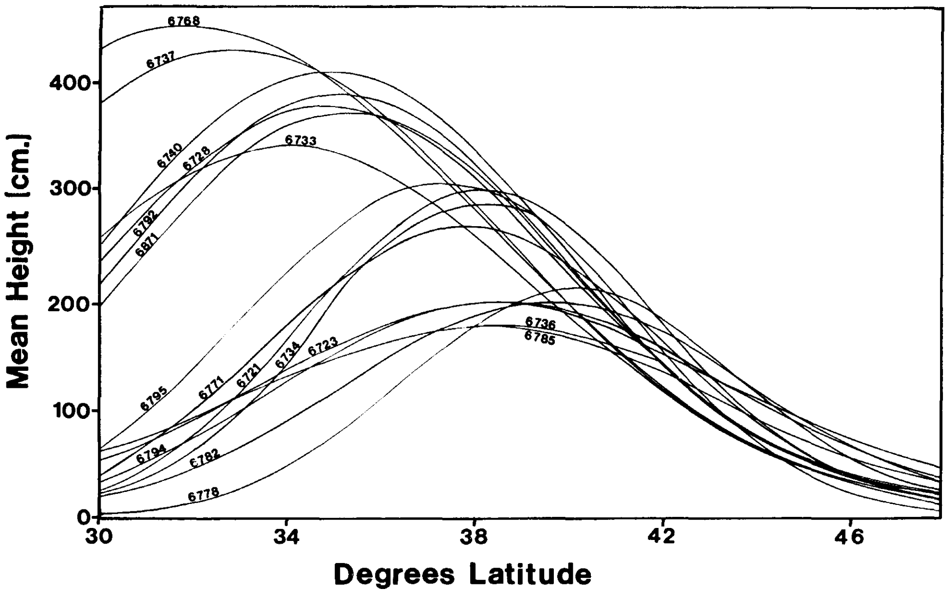


Figure 4. — Fitted response function curves for provenances.

(*Table 3* and *Figure 6a* and *6b*) and can be accurately predicted from mode values by the following linear equations.

$$\hat{Y}_1 = 139.0331 - 3.2417X$$

and

$$\hat{Y}_2 = 26281.5489 - 614.8336X \tag{7}$$

where $\hat{Y}_1$ is the predicted η_i, and $\hat{Y}_2$ the predicted k_i, and X indicates the μ_i. The probability density for white ash planting environments, g(x), is also required to evaluate (5). A normal distribution was assumed for this density function. Since we could find little information about the frequency of white ash sites, we assumed a value of 37° N for the mean latitude. This value is near the center of the north-south span of the white ash range. We considered two cases for the variance parameter of g(x), $\sigma^2_e = 6.25$, which places 95.5% of the white ash plantings within a zone extending from 32° N to 42° N latitude, and $\sigma^2_e = 2.25$, which places 99.75% of the planting sites within a zone extending from 32.5° N to 41.5° N latitude.

For the cases of both two and three seed source populations, the combination of mode parameter values to the nearest 0.1° of latitude which produced the largest value for v(x) was identified for each environmental distribution. It is clear from *Table 2* and *Figures 4* and *5* that provenances from 40° N and greater latitudes can not be part of a seed source combination that has potential to yield maximum value. These provenances each have a mode latitude identical to that of a provenance south of 40° N, but the more southerly provenances have greater responses over most of the white ash range. For this reason, attention can be restricted to provenances below 40° N for provenance combinations that produce maximum value.

Since attention need only be focused on provenances below 40° N latitude, proper seed sources can be identified using the linear relationship between mode latitude and latitude of origin that exists for provenances found below 40° N latitude. These two variables were highly correlated (*Table 3*) and the linear equation $\hat{Y} = 3.9904 + 1.1012X$ illustrated in *Figure 6c* can be used to determine latitudes of origin from the appropriate combination of mode parameters. Latitudes of optimal provenances, their mode parameters, and their planting zones are given in *Table 4* for both two and three seed sources. Response functions for three optimal provenances are illustrated in *Figure 7* for an environmental variance of 6.25.

Several patterns are evident for these optimal selections. For both variance cases and for two as well as three populations, optimal sources are from latitudes south of the assumed mean latitude for white ash planting sites. Furthermore, truncation points are not always located between the mode latitudes of the optimal sources. Planting zones for some provenances, therefore, do not include the environments that produce maximum growth for these provenances. These two patterns are mostly a reflection of the larger scale and homeostatic parameters characteristic of the southern sources. Increasing the number of provenances used as seed sources from two to three increases value, but the advantage is small less than 1.5% for both environmental distributions investigated.

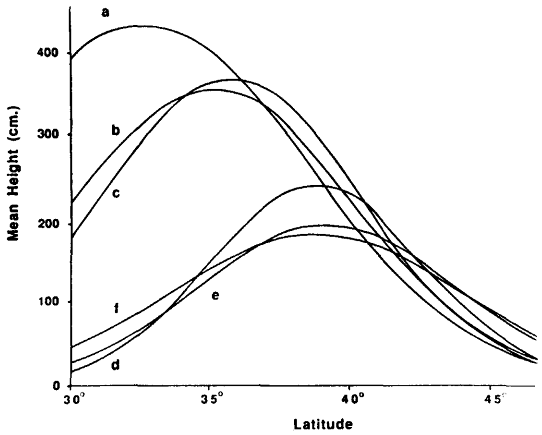
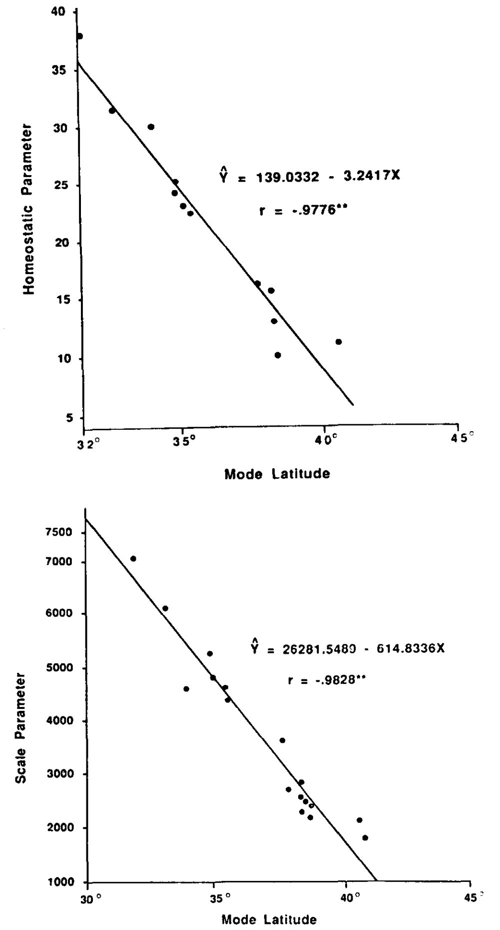


Figure 5. — Response function curves for provenances grouped according to latitude of origin. a) Curve for provenances centered at latitude 30.6° N. b) Curve for provenances centered at latitude 35.1° N. c) Curve for provenances centered at latitide 37.2° N. d) Curve for provenances centered at latitude 38.9° N. e) Curve for provenances centered at latitude 42.7° N. f) Curve for provenances centered at latitude 45.7° N.



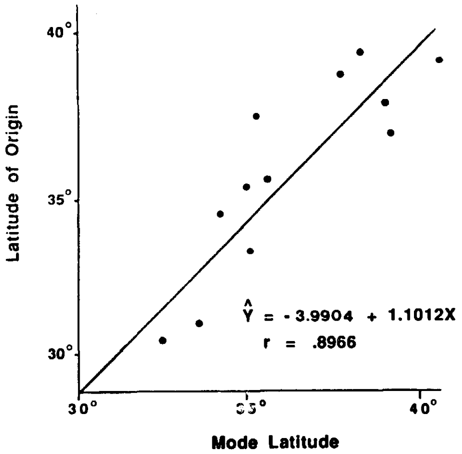


Figure 6. — Linear relationships between the mode parameter and (a) the homeostatic parameter, (b) the scale parameter and (c) the latitude of origin for seed sources below 40° N latitude.

Discussion

The pattern of variation among response functions for white ash provenances indicates the presence of a northern and a southern ecotype for this species. The boundary between these two ecotypes appears to occur in the vicinity of 40° N latitude. Provenances below 40° N latitude have response function parameters that are linearly related to latitude of seed source. Within this southern ecotype, the mode parameter increases linearly with latitude of provenance origin, whereas the homeostatic and scale parameters decrease linearly with provenance latitude, indicating clinal variation for response functions within this ecotype. On the other hand, in the northern ecotype the mode and scale parameters are constant, or nearly so, with increasing latitude of provenance but the homeostatic parameter increases with increasing latitude. Because of the contrasting variation among provenances within the two ecotypes, the relationship of all three response function parameters to latitude of provenance is nonlinear when examined across the entire latitudinal breadth of the species' range (*Figure 3*).

Our classification of ecotypes, agrees remarkably well with the demarcation of Wright (1944). His description was based on variation in such diverse characters as cold

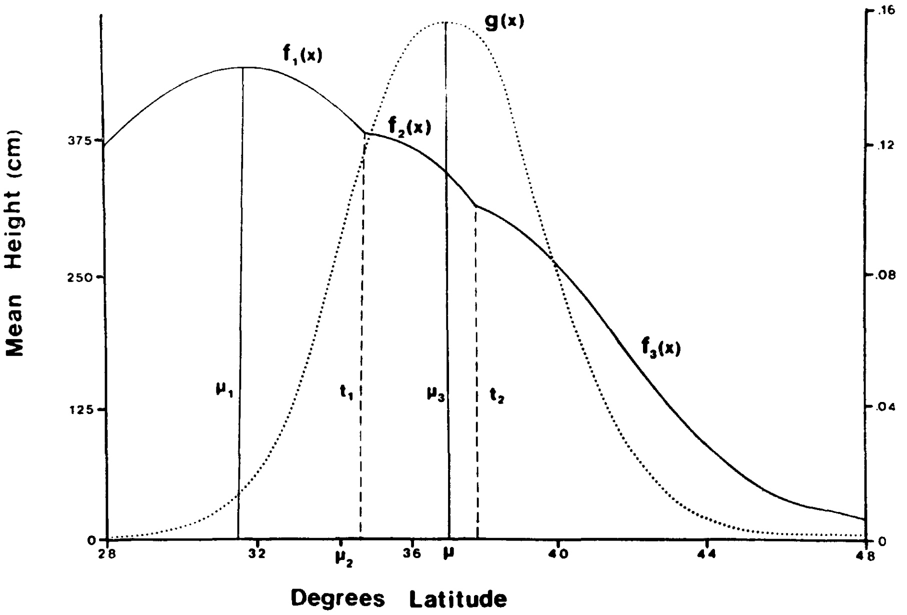


Figure 7. — Response function curves representing optimal choices for three provenances. Solid curves indicate provenance response functions ($f_i(x)$) and the dotted curve represents the probability density function ($g(x)$) for planting environments with mean 37.0° N latitude and variance 6.25.

Table 4. — Optimum choices of white ash provenances based on fifth year heights. Choices are given for two environmental distributions. Distribution A has an environmental mean of 37.0° N latitude and a variance of 6.25. Distribution B has the same environmental mean but a variance of 2.25.

Environmental Distribution							
A				B			
Provenance latitude	Mode latitude	Planting zone	Value	Provenance latitude	Mode latitude	Planting zone	Value
Two Provenances							
31.9	32.6	28.0-36.4		33.1	33.7	28.0-36.8	
35.8	36.1	36.4-48.0		35.5	35.9	36.8-48.0	
			332.37				341.19
Three Provenances							
30.9	31.7	28.0-35.0		32.6	33.2	28.0-36.0	
34.0	34.5	35.0-37.8		34.4	34.9	36.0-37.7	
36.8	37.0	37.8-48.0		36.2	36.5	37.7-48.0	
			336.36				342.91

hardiness, root system type, leaf color and pubescence, and numbers of chromosomes for progenies grown in nursery tests. The major difference in our two classifications is that Wright recognized a third intermediate ecotype for the zone in which our northern and southern ecotypes meet. Since our response function results followed closely the patterns recognized by Wright (1944), differences in response function behavior could well be a result of the same selective influences that shaped the morphological, chemical, and cytological variations observed by Wright.

The nonlinear relationship between the homeostasis parameter and provenance latitude (*Figure 3*) indicates that provenances near the southern and northern limits of the species' range are more broadly adapted than provenances near the center of the range. Provenances at the boundary of the northern and southern ecotypes. approximately 39° N latitude, are the most narrowly adapted. Because of this broad adaptability, large values for the scale parameter, and production of maximum growth at locations north of their origin, southern provenances grew well in latitudes considerably to the north of their origin. Thus, our results support the conclusion of Clausen (1984) that seed from southern provenances may be transfered considerably to the north of the collection location. Broad adaptability of provenances near the northern limit of the species' range, however, does not imply that seed from northern sources should be transferred to more southerly locations. Because latitudes for maximum growth for these provenances are in the zone 38° N to 39° N and scale parameter values are among the lowest for all provenances, seed from more southern locations will produce greater height growth. Therefore, provenances in the northern ecotype can be excluded from consideration in regeneration programs. Central provenances have maximum growth at locations only slightly lower in latitude than provenances of the northern ecotype, and southern and central provenances have greater growth at their optimum locations. Southern and central sources, therefore, also have greater growth than provenances of the northern ecotype throughout the white ash range except at the extreme northern latitudes (*Figure 5*).

Properties of solutions for response functions that maximize yield for situations in which homeostatic and scale parameters are equal have been reported by Roberds and Namkoong (1986; 1989). Some characteristics of these solutions are: (1) mode parameters and truncation points are symmetrical about environmental means, (2) distances between modes and environmental means increase with the size of the homeostatic index (hs) - - the ratio of the homeostasis parameter (η) to the environmental variance, (3) truncation points between populations are located exactly midway between the modes of their response functions. Characteristics of the response functions for the combination of white ash provenances that maximize growth are quite different. The two or more provenances that make up an optimal combination of sources have different response function parameters. Hence, the response functions are not symmetrically arrayed about the environmental mean. Mode parameters for all selected provenances will, in some situations, all lie below the environmental mean (*Table 4*). Truncation points for two response functions do not always fall between the modes of the corresponding response functions. These properties result primarily from the large magnitude of the scale parameters, the high homeostasis of the southernmost provenances, and the linear decline in these response function parameters with increasing latitude of the seed source which is characteristic of provenances in the southern ecotype. As with populations with constant homeostasis and scale parameters, intervals between provenance response function modes and the environmental mean increase with rising environmental variance.

Finally, we should point out that the patterns of variation we have observed are based on fifth year heights of white ash provenances on good sites and that we have only accounted for variation among provenances with respect to latitude. CLAUSEN (1984) reported that there is also a smaller longitudinal component to the variation among white ash provenances both for fifth year height and survival. While we have accounted for most of the geographical variation among the provenances, our analysis is incomplete and additional analyses involving parameters of multidimensional nonlinear response functions are needed. The optimal provenance prescriptions and their planting zones were described primarily to illustrate use of the value function and distribution of planting environments for determination of appropriate seed sources and zones for their use. These solutions are applicable for fifth-year height on good, and well-managed white ash sites provided the assumptions pertaining to parameters of the environmental distribution are reasonable, and the number of provenances used in the illustrations are an acceptable base for a regeneration program. Whether these allocations are appropriate for growth at later stages or for different site conditions depends on whether growth response functions and their variation patterns are substantially changed from those that we observed.

Acknowledgement

The authors wish to express grateful appreciation to Dr. HYUN KANG for helpful suggestions pertaining to data analysis and computer programming.

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Population Genetic Structure of Baldcypress (Taxodium distichum) in a Thermally Affected Swamp Forest

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(Received 30th January 1989)

Summary

Genetic structure of a mature baldcypress (*Taxodium distichum*) population in a swamp forest affected by thermal effluents from nuclear production reactors was measured by differences in allele frequencies at three loci. Tree mortality that resulted from discharge of hot water into the swamp was not selective on the basis of genotype. Allele frequencies were heterogeneous over space. Spatial autocorrelation indicated that the radii of genetically interacting groups of baldcypress do not extend across the entire swamp. The levels of gene flow detected among baldcypress samples were sufficiently high to prevent the differentiation of subpopulations due to drift in a population at equilibrium. However, a few trees breeding during unpredictable periods of low water and leaving large numbers of progeny may be responsible for the spatial hetrogeneity in allele frequencies. Population processes can amplify small differences due to drift even in the presence of gene flow.

Key words: baldcypress, gene flow, genetic differentiation, heterozygosity, population, population structure, spatial autocorrelation, *Taxodium distichum*.

Zusammenfassung

Genetische Struktur einer maturen *Taxodium distichum* Population wurde an den unterschiedlichen Allelfrequenzen dreier Loci gemessen. Die Population war Teil eines Sumpfwaldes, der von den Kühlwassern einiger Nuklearreaktoren beeinflußt war. Baummortalität, bedingt durch das Ablassen heißer Kühlwasser, war nicht korreliert mit dem Genotyp. Die gefundenen Allelfrequenzen waren heterogen im Raum verteilt. Räumliche Autokorrelation deutete an, daß die Radien genetisch interagierender Gruppen von *Taxodium distichum* sich nicht über das gesamte Sumpfgebiet erstreckten. Genfluß zwischen den untersuchten *Taxodium distichum* Proben war groß genug, um innerhalb einer sich im Gleichgewicht befindenden Popu-

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