for each analysis (if required) and also to be resubmitted for any number of different analyses.

Step 7. Analyses of Data: In step 7 the analyses of the data are carried out. In the version of DAG presented in Figure 1 the four analyses outlined in this article are carried out. Each analysis is based on a reduction of the overall model and produces a residual which is used in subsequent calculations to obtain information about the desired model terms.

Step 8. Coefficients for Expected Mean Squares: Relevant k coefficients can be estimated in two ways by DAG-either by using the harmonic mean (used here to estimate the number of individuals per plot) or using the synthesis procedure of HARTLEY (1967) (used here to estimate the number of individuals per cross).

Step 9. Genetic Parameters: In this final step the total sums of squares and products for these effects. Mean sums of squares and products and residuals formed following the analyses in step 7 are differenced to obtain the squares are calculated and equated with their expectations to form the variance and covariance components. Standard errors of these components are also computed.

Genetics of Growth Rate in Quercus rubra: Provenance and Family Effects by the Early Third Decade in the North Central U.S.A.[1])

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Abstract

Northern red oak trees from seed origins at latitudes 43° to 46° N from the Mississippi River to western Maine were consistently high in growth rate in relation to trees of other origins in 3 provenance tests in the North Central region of the U.S.A. Seed sources from farther north, south or west were less promising, although the trees from some of these sources were above average in relation to test means. About 16 percent of measured variance in height growth was attributable to provenance and 7 percent to family. Age-age correlations in the Ohio test showed that selection for growth rate was not possible at age 8, probably partly because of early mortality and rabbit injury. We could have selected the best provenances from the standpoint of growth rate at age 14, but not the best individual trees. Early selection might be more feasible now, considering improvements in technology for red oak plantation establishment.

Key words: Quercus rubra, northern red oak, growth rate, provenance, family, juvenile selection.

Zusammenfassung

Aus Samen gezogene Bäume von *Quercus rubra* (amerik. Roteiche) aus dem Ursprungsgebiet von 43° bis 46° nördl. Breite vom Mississipi bis zum westl. Maine, zeigten übereinstimmend hohe Wachstumsraten im Vergleich zu anderen Herkünften bei drei Provenienzversuchen im mittleren Norden der USA. Herkünfte, die aus entfernteren Regionen in nördlicher, südlicher oder westlicher Richtung stammten, waren weniger versprechend, obgleich einige davon überdurchschnittlich erschienen. Die Varianz im Höhenwachstum wurde zu ca. 16 Prozent von Herkünften und zu 7 Prozent von Familien verursacht. Die Alters-Alters-Korrelationen im Ohio-Versuch waren für die 8jährigen Bäume nicht möglich, teilweise wegen Mortalität und Verbiß durch Kaninchen. Wir hätten die besten Herkünfte im Höhenwachstum im Alter von 14 Jahren selektieren können, jedoch nicht die besten Bäume. Frühselektion wäre jetzt besser durchführbar, wenn die technischen Verbesserungen bei der Begründung von Roteichenplantagen berücksichtigt werden.

Introduction

The economic importance of northern red oak (*Quercus rubra* L.) in the eastern United States gave the species a high priority for genetic research when a committee for cooperative regional research was organized by the state experiment stations of the North Central region in 1959. Seven provenance tests were established in six states in the early 1960s. The objective was to evaluate range-wide genetic variation to provide a basis for selecting seed sources for high vigor and other desirable traits. Three other previously-established smaller-scale provenance tests of *Quercus rubra* evaluated at an early age demonstrated significant provenance-related variation in vigor. The number of samples was small in each case and the nature of the variation patterns could not be defined (SCHREINER and SANTAMOUR, 1961; KRAHL-URBAN, 1966; GALL and TAFT, 1973). A nursery evaluation of our own material at age 1 showed that there were both parental and provenance effects on early vigor (KRIEBEL, 1965). Analysis of all seven of our experiments at ages 12 to 14 indicated that there was significant seed source variation in growth rate, even within limited geographic areas. There was also some indication of a regional pattern of moderately high vigor among samples from southern Illinois, southern Indiana, and western Ohio (KRIEBEL *et al.*, 1976). DENEKE (1975), SCHLARBAUM and BAGLEY (1981) and SCHLARBAUM *et al.*, (1982) also found source-related differences in height growth, survival and other traits in their early reports on our experiments in Kansas and Nebraska.

In this paper, we report early third decade results of analysis of height growth differences attributable to provenance and family, from observations made in the Ohio, Indiana and Michigan plantations. We describe an emerging pattern of geographic variation, appraise the effect of seed tree relative to that of provenance, and estimate the pos-

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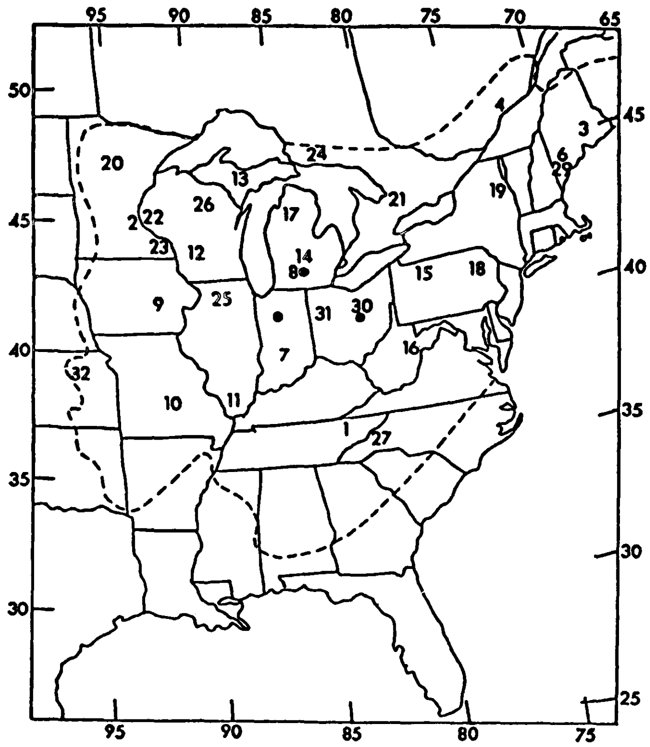

Figure 1. — Test locations (dots), provenances (numbers) and distribution of *Quercus rubra* L. (broken line) from LITTLE 1949.

sibility of early selection of individual trees for vigor by correlations of height growth at three different ages.

Methods

Populations were sampled in 30 locations scattered throughout most of the species distribution (*Figure 1* and *Table 1*). In sampling, an effort was made to obtain genotype diversity within a provenance. Seed trees were usually scattered over several stands within an area of from one to several square kilometers. In a few cases, a provenance consisted of a single stand 10 hectares or more in size. Areas where dysgenic treatments ("high-grading") might have been applied were avoided. Collections were made over a 3-year period because of the intermittent nature of seed crops in red oak. Seeds were sown each autumn soon after collection because long-term storage techniques had not been developed for the species. Thus trees of some sources were 1 or 2 years younger than others and tree age had to be considered in evaluation of growth. Seeds were sown at a single nursery at Green Springs, Ohio. A part of each seedlot was sown in 4 replicates for analysis of responses after one year in the nursery (KRIEBEL, 1965).

Two of the 3 experiments on which we are reporting (Ohio and Indiana) were laid out in randomized blocks containing 16-tree square plots. The smaller Michigan test (*Table 2*) contained 4-tree linear plots and did not include trees from the third year's seed collections. In Ohio, at least one tree of each seed parent of the provenance was includ-

Table 1. — Origin and planting years of the red oak collections in the Ohio (OH), Indiana (IN) and Michigan (MI) provenance tests.

Provenance no.	Seedlot numbers	State and county of origin		North latitude ° '		West longitude ° '		Elevation (m)
		1962 planting stock (OH, IN, MI)[a]						
1	701-2,704-10	Tennessee	Anderson	36	10	84	10	350
2	711-720	Minnesota	Hennepin	44	50	93	35	275
3	721-730	Maine	Penobscot	44	50	68	30	50
6	751-760	Maine	Cumberland	43	45	70	35	90
7	761-770	Indiana	Orange	38	30	86	30	250
11	801-4,807-10	Illinois	Jackson	37	35	89	30	165
13	821-827	Michigan	Marquette	46	30	87	20	355
17	861-870	Michigan	Missaukee	44	15	85	20	420
19	881-890	New York	Essex	44	10	73	20	110
20	891-900	Minnesota	Cass	47	20	94	30	400
21	902-5,908-10	Ontario	Simcoe	44	30	80	00	180
24	931-8,940	Ontario	Algoma	46	10	83	20	200
26	951-960	Wisconsin	Oneida	45	35	89	20	490
29	981-990	Maine	York	43	30	70	45	90
31	1002,1005-10	Ohio	Allen	40	45	84	10	270
		1963 planting stock (OH, IN, MI)[a]						
9	781-790	Iowa	Iowa	41	40	91	20	315
10	791-800	Missouri	Dent	37	40	91	30	385
12	1141-1150	Wisconsin	Vernon	43	35	90	50	400
22	911-920	Wisconsin	Pierce	45	45	92	40	420
23	1151-1160	Minnesota	Winona	44	05	92	05	300
25[b]	941-950	Illinois	Ogle	42	00	89	15	230
		1964 planting stock (OH, IN)[a]						
4[b]	1171-1180	Quebec	Jacques Cartier	46	50	73	50	40
8	1161-1170	Michigan	Kalamazoo	42	20	85	20	260
14	831-840	Michigan	Ingham	42	45	84	20	265
15	841-850	Pennsylvania	Warren	41	50	79	15	375
16[b]	851-860	West Virginia	Tucker	39	10	79	40	700
18	871-880	Pennsylvania	Lucerne	41	15	76	05	425
27	961-970	North Carolina	Buncombe	35	35	82	30	880
30	1181-1190	Ohio	Wayne	40	45	81	55	295
32	1011-1020	Kansas	Riley	39	10	96	30	335

a) Trees were one year old when planted.

b) Provenance samples marked b were only planted in Ohio.

Table 2. — Description of the experimental plantations.

Plantation location[a]	Number of provenances	Number of blocks	Number of trees/plot	Number of trees	Last growth year before measurement	No. of trees at measurement time
Apple Creek, OH	30	7	16	3360	1982	1836
W. Lafayette, IN	27	3	16	1296	1983	726
Augusta, MI	20[a]	5[b]	4	492	1983	234

a) 1964 planting stock was not planted in Michigan.

b) Some blocks contained duplicate plots.

ed in each plot, and identities of these trees were retained. This made it possible to compare the effects of provenance and seed parent on growth in this experiment. In the other plantations, the seedlots were bulked within provenances before planting.

Measurements were made in Ohio after the 1982 growing season at ages 20 to 22, age depending on provenance. Data were taken in Indiana and Michigan after the 1983 growing season, at ages 21 to 23 in Indiana and 22 to 23 in Michigan. We examined the effect of provenance on tree survival by one way analysis of variance in each plantation. We ranked all provenances within an experiment regardless of age of planting stock, to visually assess the age effect on height growth by examining the dispersion of provenance samples of different ages in the overall ranking. The statistical validity of combining data over all 3 planting sites was determined in 2 ways: (1) interaction of provenance rank with planting site was evaluated by the SAS General Linear Models Procedure in separate analyses of the 20 provenances common to all three experiments and of the 7 provenances of the youngest age class common to the Ohio and Indiana experiments; (2) rank correlations were computed to compare the provenance rankings of the 3 plantations.

Records of seedlot identities on maps of the Ohio plantation made possible a nested analysis of genetic components of variance to estimate the relative effects of family (seedlot) and provenance on growth rate. To evaluate the effectiveness of early within-plot selection for rapid growth, correlation coefficients were computed from the plot means of the 5 replications measured at 3 ages in the Ohio plantation. All 30 provenances were included in correlations of cumulative growth to: (1) 1968 *vs.* 1983; (2) 1974 *vs.* 1983.

Table 3. — Spearman coefficients of correlation between provenance rankings by mean total height growth in the 3 test sites [ab].

Planting stock	Variable pair	Number of provenances	r	p
1962	Ohio with Indiana	15	.55	.017
	Ohio with Michigan	15	.61	.008
	Indiana with Michigan	15	.77	.001
1963	Ohio with Indiana	5	.75	.042
	Ohio with Michigan	5	-.07	.445
	Indiana with Michigan	5	.23	.329
1964	Ohio with Indiana	7	.14	.385

a) The Michigan test did not include 1964 planting stock.

b) Symbols: r = correlation coefficient; p = significance of r.

Results and Discussion

Seed source had no effect on survival rate in any of the three experiments. Age appeared to affect total height because older population samples tended to outrank younger ones. Since the effects of seed source and age could not be statistically separated, comparisons were made within age class (*Table 4*). However, our provenance ranking for the Indiana test seemed to have no relation to age when we combined the 1962 and 1963 planting stock. In fact, the two top-ranking provenance samples in that experiment were from the 1963 origins. Therefore we pooled the two years and ranked them by mean annual increment (MAI) for more meaningful comparisons of seed source effects (*Table 5*). Any effect of the one year age difference was small in relation to growth over the total age of the trees, on which MAI was based.

The three experiments have similarities in the relation of seed source to growth rate, but from a statistical standpoint they differ. The interaction between srovenance and planting site is significant. In addition, rank correlations do not justify combining results from different planting sites (*Table 3*), although a case could be made for a pooled ranking of 1962 Indiana and Michigan seed sources.

A relationship between growth rate and latitude appears in *Tables 4* and *5*. In the two age classes of planting stock inclusive of a wide latitudinal range of seed sources (1962 and 1963), all but one of the provenance samples exceeding the MAI of its group in any experiment by more than one standard deviation was of Wisconsin, Michigan, Ontario, New York or Maine origin. The relation of every 1962 and 1963 provenance MAI to its *own group mean within an experiment* is shown in *Figure 2* as the number of standard deviations by which it is above or below its group mean, with the horizontal distribution based on latitude. Eight of the 9 sampling points producing trees categorized as superior by being more than one standard deviation above their group mean were within north latitudes 43° and 46° (*Figure 2*). The exception, provenance 31 growing in Michigan, is in western Ohio. In Ohio and Indiana, where it was represented by much larger numbers of trees than in Michigan, provenance 31 was only average in rank. Analysis of *Figure 2* shows that:

(1) 8 of 18 MAIs (42%) of provenances south of 43° N latitude were above their group average, and one (5%) was more than one standard deviation above the group average;

(2) 22 of 33 MAIs (67%) of provenances between 43° and 46° N latitude were above their group average, and 8 (24%) were more than one standard deviation above the group average;

(3) None of the 9 MAIs (0%) of provenances north of 46° latitude was above its group average, i.e. neither was

Table 4. — Mean total height growth and mean annual increment (MAI) by provenance, ranked within age class of planting stock [ab]

Ohio provenance test			Indiana provenance test			Michigan provenance test		
Provenance	Height growth (m)		Provenance	Height growth (m)		Provenance	Height growth (m)	
	Total	MAI		Total	MAI		Total	MAI
			1962 Planting stock					
	(at age 22)			(at age 23)			(at age 23)	
29	11.8	.54*	21	11.8	.51*	17	14.4	.63*
21	11.8	.54*	17	11.3	.49	21	14.0	.61*
17	11.4	.52*	29	11.2	.49	31	13.9	.60*
26	11.3	.51	11	11.2	.49	19	13.8	.60*
7	10.9	.49	26	11.1	.48	7	13.5	.59
11	10.8	.49	19	11.1	.48	26	13.3	.58
19	10.8	.49	2	10.9	.48	6	13.2	.57
31	10.7	.49	31	10.9	.48	11	13.1	.57
13	10.5	.48	6	10.9	.47	3	12.9	.56
6	10.3	.47	7	10.8	.47	29	12.8	.55
1	10.2	.47	20	10.3	.45	20	12.7	.55
3	10.0	.45	24	10.1	.44	2	12.7	.55
20	9.6	.44	3	10.0	.44	24	12.4	.54
24	9.4	.43	1	9.9	.43	1	12.1	.53
2	8.9	.41	13	9.7	.42	13	11.7	.51
			1963 Planting stock					
	(at age 21)			(at age 22)			(at age 22)	
22	10.1	.48*	22	12.3	.56*	22	12.7	.58*
12	9.9	.47	12	11.9	.54	10	12.4	.56
25	9.9	.47	10	10.8	.49	23	12.4	.56
9	9.7	.46	23	10.8	.49	9	12.2	.55
23	9.7	.46	9	9.9	.45	12	12.0	.54
10	9.6	.46						
			1964 Planting stock					
	(at age 20)			(at age 21)				
15	10.0	.50*	15	9.4	.45*			
14	9.2	.46	8	9.3	.44*			
16	9.2	.46	18	9.1	.43			
8	9.1	.46	14	8.6	.41			
4	9.1	.45	30	8.6	.41			
18	8.8	.44	27	8.6	.41			
27	8.8	.44	32	8.3	.40			
30	8.5	.43						
32	7.9	.40						

a) Ranked by decreasing mean total height and MAI before rounding off.

b) Asterisk indicates that the provenance MAI is more than one standard deviation above the average MAI of the group.

any MAI more than one standard deviation above its group average.

About 23 percent of the variance in height growth was related to provenance or family, with about 16 percent attributable to provenance and 7 percent to family (*Table 6*).

Age comparisons in Ohio showed that relative height of 6- to 8-year-old trees was not closely correlated with height 14 years later (*Figure 3A*). There were big shifts in plot mean heights *relative to each other* during that period, as indicated by the wide vertical dispersion of points. It is possible that this is attributable to incomplete recovery from rabbit damage by 1968. There was a much closer correlation between 1974 and 1983 height (*Figure 3B*).

We examined the efficiency of selecting the best trees within the 5 measured plots of the best provenances, because this is the procedure we would have used for early genetic selection, using the plot mean as baseline to minimize environmental effects and seeking to capture gains from both provenance and family selection. At the earliest age, we did not have much information about the best provenances, because provenance differences were not significant. If we had fortuitously selected provenance 21 at age 8, we would have picked the source ranking number 1 at age 14 (Kriebel *et al.*, 1976) and tied for first place at age 22 (*Table 4*). Analysis of the positions of the 5 provenance 21 plots in *Figures 3A* and *3B* (identities not shown) reveals that the number of plots exceeding the test mean by one or more standard deviations was:

Year	Age	Plantation mean, m.	Standard deviation	No. of plots > 1 std. dev. above mean
1968	8	0.78	0.40	3 of 5
1974	14	4.69	1.01	4 of 5
1983	22	10.01	1.45	5 of 5

Table 5. — Mean total height growth and mean annual increment (MAI) in Indiana, with 1962 and 1963 planting stock combined [abc].

Provenance	Total height (m)	MAI (m)
22	12.3	.56*
12	11.9	.54*
21	11.8	.51
10	10.8	.49
17	11.3	.49
23	10.8	.49
29	11.2	.49
11	11.2	.49
26	11.1	.48
19	11.1	.48
2	10.9	.48
31	10.9	.48
6	10.9	.47
7	10.8	.47
9	9.9	.45
20	10.3	.45
24	10.1	.44
3	10.0	.44
1	9.9	.43
13	9.7	.42

a) Age-related differences in total height of 1962 and 1963 planting stock are not significant at $p < .05$ (Duncan's New Multiple Range Test).

b) Ranked by decreasing MAI before rounding off.

c) Asterisk indicates that the provenance MAI is more than one standard deviation above he average MAI of the group.

Analysis of the raw data shows that if we had used one or more standard deviations above each provenance 21 plot mean as our selection criterion for individual trees, we would have obtained the following results:

Table 6. — The relative contributions of provenance and family to height growth of red oak in Ohio [a]).

Variance source	Degrees of freedom	Mean square	Variance components	Percent of total
Provenance	29	3902	92	15.9
Family (provenance)	261	603	42	7.2
Trees (family (provenance))	822	446	446	76.9
Total	1113	576	580	100.0

a) Based on 1983 total height in Ohio at age 20 to 22, depending on planting stock age.

(1) By genetic selection at age 8, we would have picked 4 of the 9 trees of provenance 21 (44%) that exceeded their plot means by one or more standard deviations at age 22;

(2) Using the same criterion at age 14, we would have selected 5 of the 9 provenance 21 trees (56%) that were superior at age 22.

Under conditions of better early plantation protection and better weed control, as is now possible, mortality and juvenile damage would be lower and the potential for early selection might be greater.

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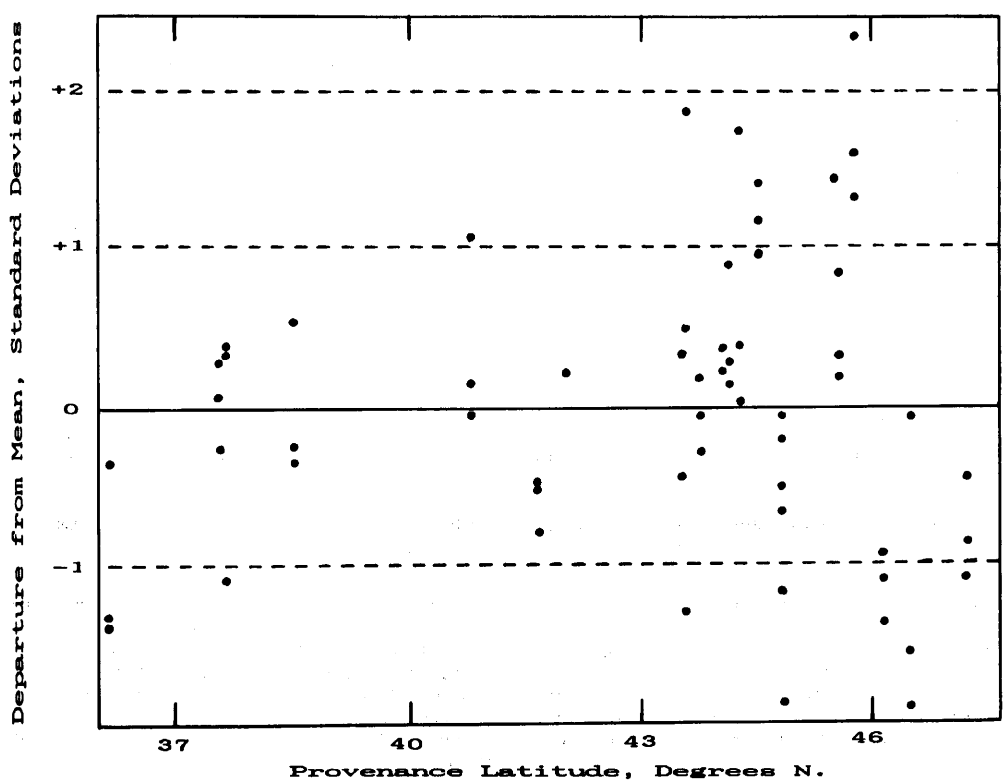

Figure 2. — Relationship of each of the 1962—1963 provenance MAIs of *Table 4* (OH, MI) and *Table 5* (IN) to the mean and standard deviation of its own age group within its plantation and to provenance latitude. MAI is mean annual increment over the life of the trees.

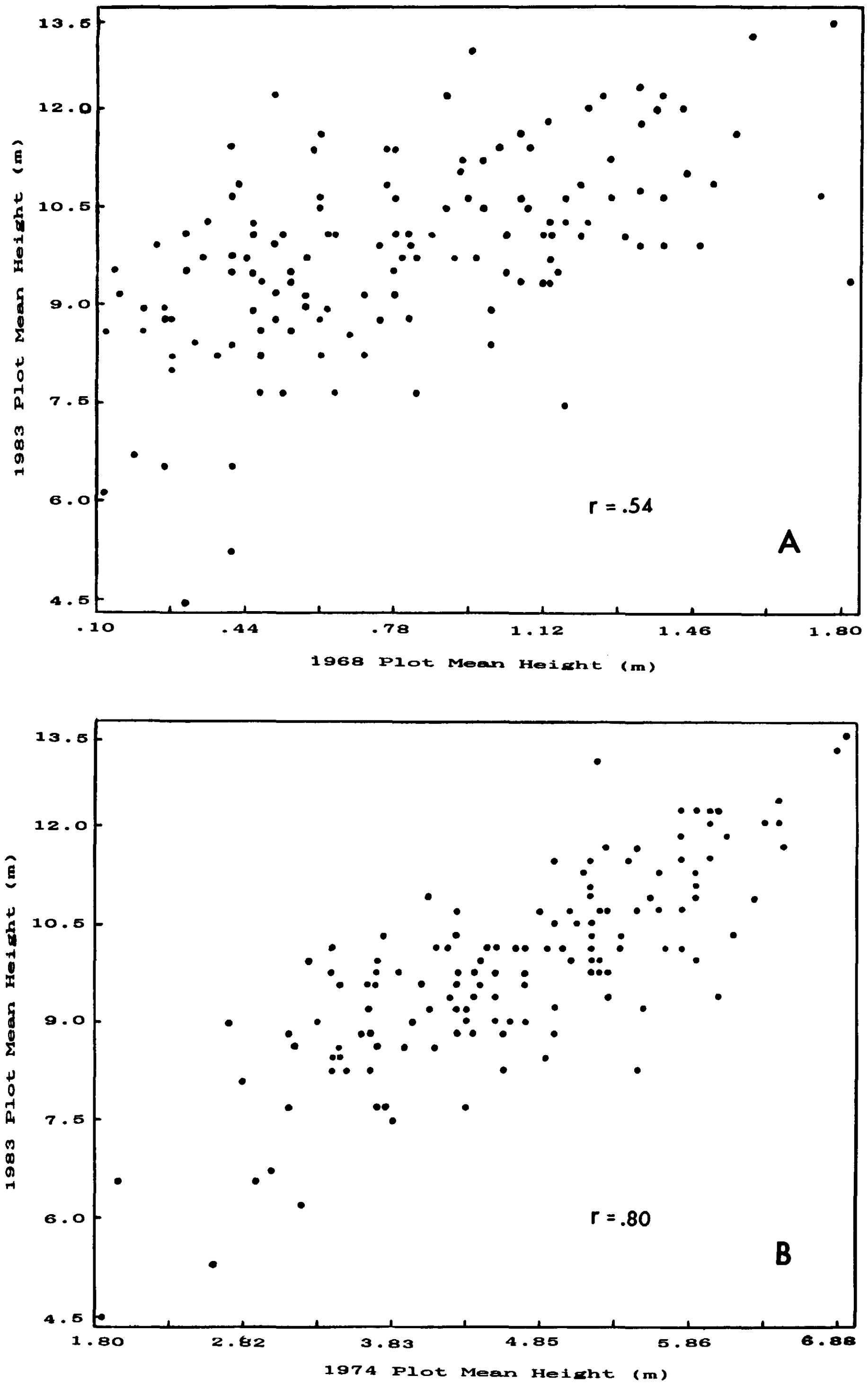

Figure 3. — Relationship of the mean height of each provenance plot by 1983 to that by 1968 and 1974; r = correlation coefficient.

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