NURSERY EVALUATION OF A PITCH PINE PROVENANCE TRIAL

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ABSTRACT

First- and second-year heights of pitch pine provenances, representing the entire range, were closely correlated with climate at the origin when grown in the Connecticut State Nursery. The correlation between second year height and April-May mean maximum temperature was 0.91. The variation in height among a sample of pitch pine provenances from the coastal plain was largely explained by regression on latitude. Initation and cessation of growth were also related to provenance origin.

Selection of the best provenance would result in gains of 43 percent relative to the local, Connecticut provenance. There was apparently little or no variation among stands within geographic areas and no additive genetic variation among families within stands.

INTRODUCTION

The range of pitch pine (*Pinus rigida* Mill.) extends from Georgia north to Quebec and over this range it encounters a diversity of climates and, presumably, selection pressures. Phenotypic variation has been reported in growth form, wood properties, and cone characteristics (Saucier and Clark 1969, Smouse 1972, Smouse and Saylor 1973, Ledig and Fryer 1972, 1974, Ledig 1974, Ledig et al. 1975). However, there have been

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no reports of provenance or progeny variation in uniform environments. Information on genetic variation among provenances and among families within provenances is necessary for improvement of pitch pine by either selection or hybridization, We report patterns of variation in height of pitch pine during its first two years in the nursery,

MATERIALS AND METHODS

Materials.--Seed was collected throughout the range of pitch pine in 1969 and 1970 according to a nested sampling scheme that employed geographic areas, stands in areas, and trees in stands, There were 29 areas with 2 stands each, one area represented by a single stand, and one with 3 stands, Nominally, there were 6 trees per stand but accidental loss reduced the number to 5 in a few cases, Stands within areas were usually 1 to 20 miles apart and trees in stands were separated by 200 ft. to reduce the probability of relationship. Stand locations are pictured in Figure 1 and detailed information was presented in Ledig et al. (1975).

In 1971 the coastal plain from southern New Jersey to Cape Cod was subjected to more intensive sampling. Seed was collected from 15 stands at approximately 20 mile intervals (Figure 1, Table 1). The number of trees per stand varied from 8 to 10, usually the latter.

Nursery Methods.--Seed from both the rangewide and the coastal plain collections was dried to ca. 4.5 percent moisture content (dry weight basis) and refrigerated until sown in the Pachaug State Nursery of the Connecticut Department of Environmental Protection at Voluntown in spring 1972. Seed lots were randomized according to mother tree (half-sib families). Sixty lots were replicated twice, and the remainder were represented by single plots. Plots were 1 or 1.5 ft. wide and 4 ft. across the bed, Distance between plots was 1 ft. and they were separated by wood laths. Though sowing rates were adjusted to account for differences in germinative capacity and plots were thinned before the second growing season, final density varied from only a few seedlings per plot to 15 per square foot. Most of the variation in density resulted from washing of one bed accidentally left uncovered after sowing. All seedlots received standard nursery practices with respect to irrigation, fertilization, and weed control.

Statistical Methods.--Heights of 5 randomly chosen, interior seedlings per plot were measured at the end of the first and second year and twice during the second growing season. Components of variance for areas, stands, and families were estimated from analysis of variance of plot means. Plot to plot variance was estimated from the 60 replicated seed lots, and within plot variance was calculated from the entire experiment.

Dates of height growth initiation and cessation were estimated with a procedure suggested by Teich and Holst (1970). Cumulative height growth during the second growing season (two dates of observation) was expressed as a percent of final height and transformed to probits, The two points defined a straight line which was extrapolated to horizontal intercepts at 2 percent and 98 percent of total growth (there are no probit values for 0 or 100 percent). The intercepts were estimates of the dates of initiation and cessation of growth (Figure 2). Because only two points were available to define probit lines, results were occasionally erratic.

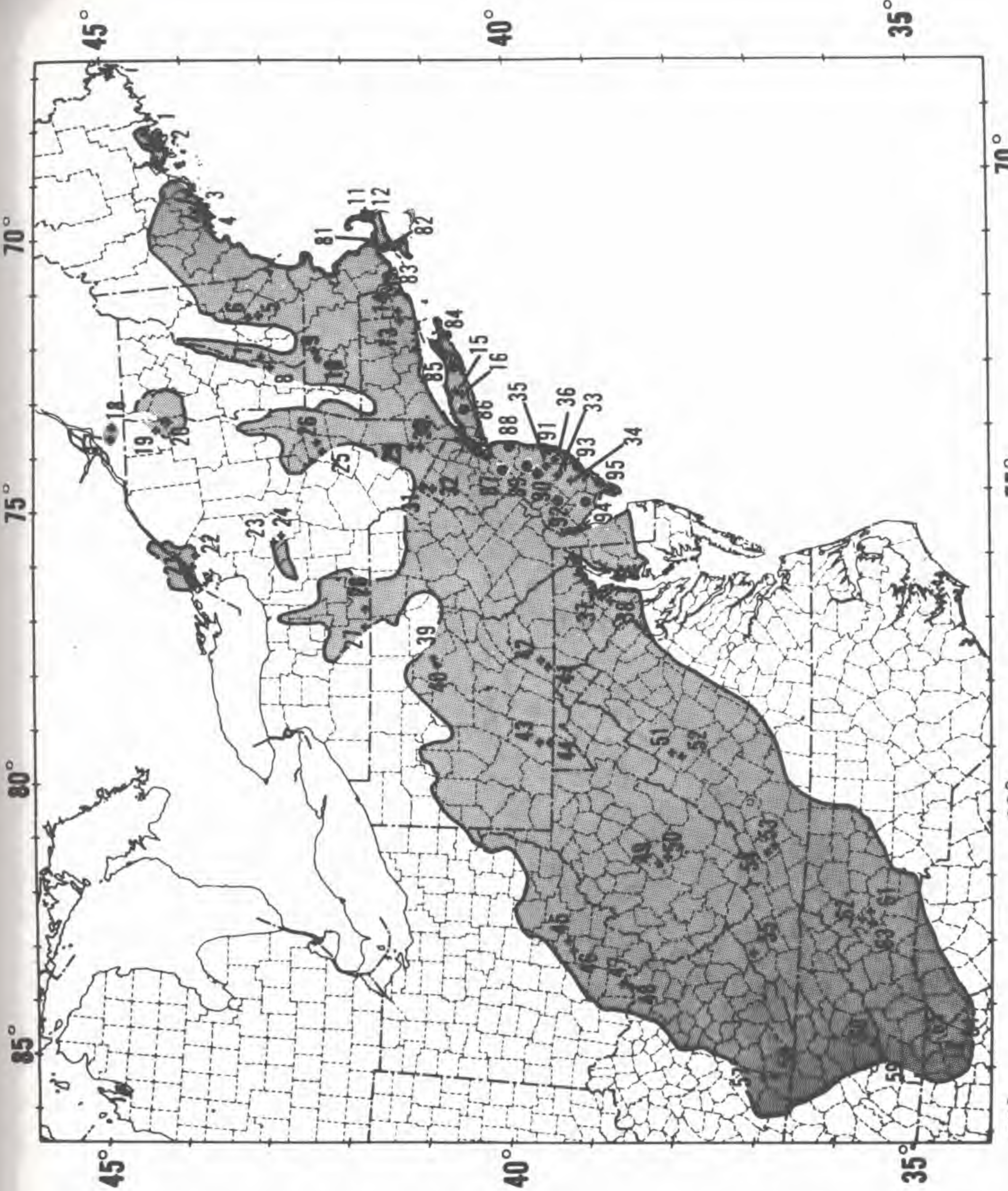

Fig. 1.--Range of pitch pine (modified from Critchfield and Little 1966), showing location of stands in rangewide (+) and coastal plain (•) collections.

Table 1.--Provenance location data for coastal plain pitch pine provenance collection.

Provenance	County	State	Code No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Trees in seed collection
Sagamore	Barnstable	Massachusetts	81	41°46'	70°32'	200	10
Bourne	Barnstable	Massachusetts	82	41°43'	70°35'	100	10
Fall River	Bristol	Massachusetts	83	41°39'	71°01'	90	8
Beach Hampton	Suffolk	New York	84	40°59'	72°06'	10	10
Hampton Bays	Suffolk	New York	85	40°53'	72°33'	20	10
Commack	Suffolk	New York	86	40°48'	73°16'	150	10
Helmetta	Middlesex	New Jersey	87	40°23'	74°26'	50	10
Green Cove	Monmouth	New Jersey	88	40°15'	74°05'	100	10
Lakehurst	Ocean	New Jersey	89	40°01'	74°18'	60	10
Lebanon Lakes	Burlington	New Jersey	90	39°53'	74°34'	110	10
Waretown	Ocean	New Jersey	91	39°48'	74°12'	20	10
Fries Mills	Gloucester	New Jersey	92	39°40'	75°76'	130	9
Oceanville	Atlantic	New Jersey	93	39°28'	74°28'	40	10
Cumberland	Cumberland	New Jersey	94	39°23'	74°57'	40	10
Clermont	Cape May	New Jersey	95	39°10'	75°46'	10	10

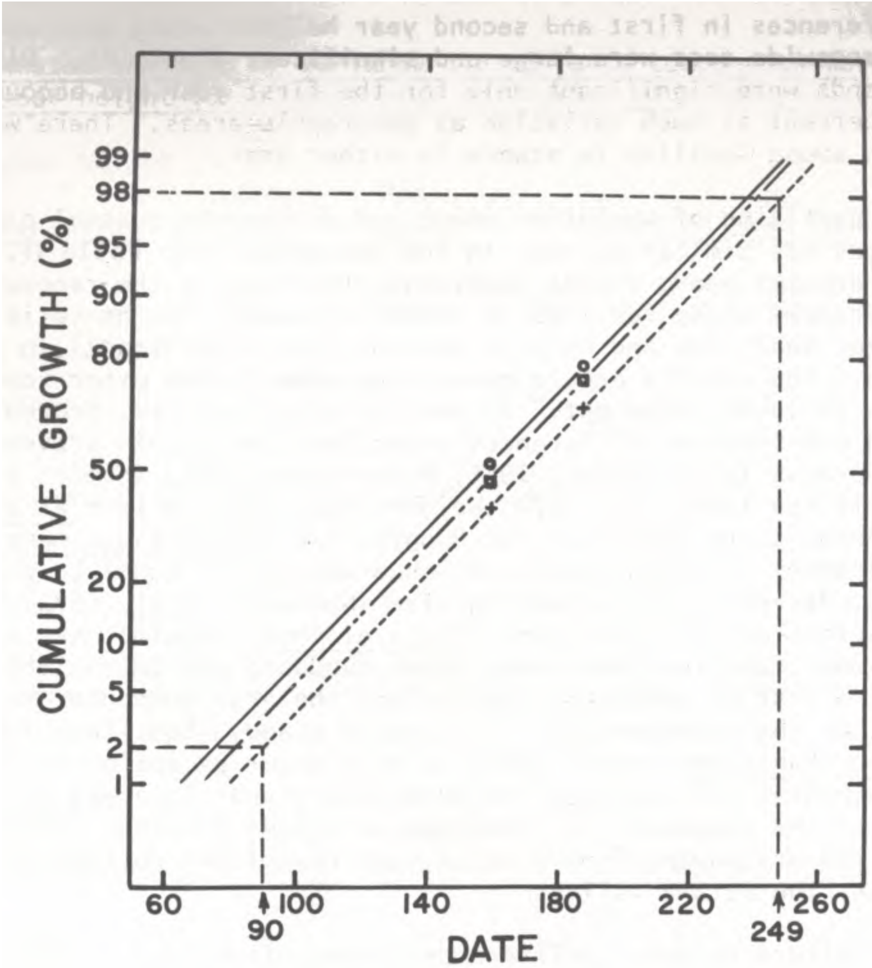

Figure 2.--Probit plots of cumulative height growth as percent of second-year growth for three provenances of pitch pine: St. Chrysostome, Quebec; — – Michaux State Forest, Pennsylvania; - - - Chattahoochee National Forest, Georgia. Under the assumption that growth fits a probit relationship, the lines were extrapolated to intercepts at 2 percent and 98 percent of yearly growth. The values at the intercepts were taken as the dates of initiation and cessation of growth. In the example, date of growth initiation for the provenance from Georgia is estimated at 90 days and date of cessation at 249 days (n = 60).

Therefore, estimates for initiation of growth earlier than March 1 or of cessation later than October 31 were excluded from further analysis.

The relationships of height, initiation of growth, and cessation of growth to provenance origin were analyzed by regression analysis on latitude and 69 climatic variables. Climatic data was obtained from monthly records for local weather stations, and spanned ca. 30 years.

RESULTS AND DISCUSSION

Differences in first and second year heights among geographic areas in the rangewide test were large and significant (Table 2), Differences among stands were significant only for the first year and accounted for only 15 percent as much variation as geographic areas. There was no variation among families in stands in either year,

The partition of variation among and within the coastal plain provenances was similar to that in the rangewide test (Table 3). There were differences among stands (analogous to areas in the rangewide test) but differences among families in stands accounted for no variation in second year seedlings and only 16 percent (non-significant) in first year seedlings, The results are in general agreement with other reports on variation in juvenile height. In several other species, provenance variation overshadowed differences among families within provenances, often by wide margins (e.g. Kriebel 1965, Morgenstern 1969, Schmitt and Webb 1971, Squillace 1966, Thor 1974, Wright 1962, 1963, Wright et al. 1958, 1970), Results are equivocal for Douglas-fir (Pseudotsuga menziessi (Mirb.) Franco) in which family variance was nil or equal to provenance variation, depending upon planting site (Namkoong et al. 1972). For seed orchard selections of slash pine (Pinus elliotii Engelm). variance was greater among families than among areas (Goddard and Smith 1969), but for a rangewide test of geographic variation, the area component was 17 times greater than the component for families in stands (Squillace 1966). Jack pine (Pinus banksiana Lamb.) seems to be a major exception to the general rule. Components of variance for areas and stands in areas were insignificant compared to the component for families in stands (Yeatman 1974). However, all families originated from a relatively restricted portion of the jack pine range, the Ottawa Valley.

The failure to detect differences among pitch pine families in stands was in contrast to the results of a phenotypic study of the parents of these seedlings, Among parents in situ, trees within stands accounted for 36 percent of the total variation in height adjusted for age, and differences among stands within areas accounted for an additional 36 percent (Ledig 1974). Perhaps, high error resulting from variation in seedbed density in the present study obscured family differences, but it is unlikely. If the results are real, they may indicate that most of the genetic variation among trees within geographic areas is of the dominance or epistatic type, reflected in the high within family variance component. Large differences among populations coupled with no variation among families within populations may also suggest inbreeding. Whatever the cause, the results indicate that mass selection among trees within stands would be largely unrewarding while provenance selection should yield large gains. The best provenance was 71 percent taller than the worst and 43 percent taller than the local, Connecticut provenance collected within a few miles of the nursery.

Because height and age of parent trees were measured, it was possible to calculate heritability from the offspring-parent relationship. Family height was compared with parental mean annual increment (height/age) over the entire range and within stands, Heritability was estimated by the correlation coefficient rather than the regression coefficient because of the difference in scale between offspring and parent (Falconer 1960, Steinhoff and Hoff 1971). For the entire rangewide collection, heritability was 0.36, However, such a heritability is difficult to interpret. To be valid, heritabilities should be estimated within random-mating populations

Table 2.--Nested analysis of variance and variance components for first and second year height for a range-wide collection of pitch pine provenances.

A. First year height

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square	Variance Component
Areas	30	21.645	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2 + 6.056\sigma_s^2 + 12.082\sigma_a^2$	1.466
Stands in areas	31	3.929	$\frac{1}{4.968}\sigma_w^2 + \sigma_P^2 + 6.036\sigma_s^2$	0.222
Families in stands	303	2.573	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2$	0[a]
Plot to plot	60	2.687	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2$	1.778[b]
Within plot	1488	4.044	^2_w	4.044

B. Second year height

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square	Variance Component
Areas	30	512.517	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2 + 12.082\sigma_a^2$	39.658
Stands in areas	31	30.971	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2$	0[a]
Families in stands	303	33.481	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2$	0[a]
Plot to plot	60	34.059	$\frac{1}{4.968}\sigma_w^2 + \sigma_p^2$	18.844[c]
Within plot	1488	72.172	σ_w^2	72.172

[a] Negative components estimated as zero

[b] Pooled families in stands plus plot to plot component

[c] Pooled stands in areas, families in stands, plus plot to plot component

Table 3.--Nested analysis of variance and variance components for first and second year height for coastal plain provenances of pitch pine.

A. First year height

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square	Variance Component
Stands	16	16.575	$\frac{1}{5}\sigma_w^2 + \sigma_p^2 + 1.392\sigma_{t/s}^2 + 12.717\sigma_s^2$	1.070
Families in stands	141	2.963	$\frac{1}{5}\sigma_w^2 + \sigma_p^2 + 1.377\sigma_{t/s}^2$	0.201
Plot to plot	60	2.687	$\frac{1}{5}\sigma_w^2 + \sigma_p^2$	1.891
Within plot	876	3.979	σ_w^2	3.979

B. Second year height

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square	Variance Component
Stands	16	293.037	$\frac{1}{5}\sigma_w^2 + \sigma_p^2 + 12.717\sigma_s^2$	20.898
Families in stands	141	24.387	$\frac{1}{5}\sigma_w^2 + \sigma_p^2$	0[a]
Plot to plot	60	34.059	$\frac{1}{5}\sigma_w^2 + \sigma_p^2$	20.879[b]
Within plot	876	65.899	σ_w^2	65.899

[a] Negative components estimated as zero

[b] Pooled families in stands plus plot to plot component

with equal gene frequencies among sub-populations, which is obviously not the case for pitch pine. Heritability from pooled within stand regressions was 0.06. Though the standard error was many times larger than the estimate, so that it is not significantly different from zero, 0.06 is close to the heritability expected for vigor traits in wild populations of southern pines (Namkoong 1970). The family analysis indicated that heritability within populations was zero.

Two major stands of dwarf vegetation, the East and West New Jersey Pine Plains, were included in the tests, and it was interesting to compare their growth with that of trees from the surrounding Pine Barrens. In the first year, mean height of seedlings from the Pine Plains was slightly greater than that of Pine Barrens' seedlings, but the difference was not significant. By the end of the second year, the Pine Plains' provenance were shorter than any of the other 11 provenances from the New Jersey coastal plain. Although statistically significant, the difference was slight. Mean height for the Plains was 48.5 cm compared to 52.4 cm for the Barrens. We expect the "dwarf" nature of the Plains' seedlings to be fully expressed only after the trees reach the cone bearing stage, because the precocious Plains' trees tend to channel most of their productivity into reproduction, to the exclusion of vegetative growth. By analogy, precocious provenances of white spruce (*Picea glauca* (Moench) Voss) suffered a 14 percent reduction in height growth after the start of cone production, relative to provenances that were not producing cones (Teich 1975).

Provenance height and estimated dates of initiation and cessation of growth in the rangewide test were related to several variables describing climate at the provenance origin, but the annual or April-May mean maximum temperature accounted for the most variation (Table 4). Multiple correlations with two or more variables explained little more variation in the dependent traits than simple correlation. The correlation between area means for second year height and April-May mean maximum temperature was 0.91 (Figure 3).

Mean seed weight varied with latitude and could conceivably account for the differences in height among areas. However, the correlations of first and second year height with seed weight were only 0.62 and 0.67, respectively. Stepwise regression was used to further explore the relative influence of seed weight and April-May mean maximum temperature on height. The standardized partial correlation coefficient for height on temperature was over seven times larger than the standardized partial correlation coefficient for seed weight (0.83 vs. 0.11), suggesting that geographic variation in height was not the result of differences in seed weight. Apparently, genetic differences in juvenile growth reflect close adaptation to climate at the provenance origin.

Climatic data were not available for the rather closely spaced stands in the coastal plain collection. However, the correlation of second year height on latitude was highly significant (r = 0.91; Figure 4), despite the relatively restricted range of latitude (only 2° 36'). Twelve of the 15 stands seemed to describe an almost perfect line. If the three most divergent stands were excluded, the correlation between the remaining 12 and latitude was 0.99. The regression also fits the coastal plain provenances from the rangewide test.

Table 4.--The best five of 70 simple correlation coefficients between nursery growth of a rangewide collection of pitch pine provenances (area means) and the parental environment (latitude and climatic variables at the seed origin).

Environment at Origin	Nursery Growth			
	First-year height	Second-year height	Date of growth initiation	Date of growth cessation
April-May mean maximum temperature	0.82	0.91		0.66
Date of spring mean temperature of 6°C	0.79	0.89		0.65
September-October mean maximum temperature	0.78	0.87		
Daylength on spring date of mean temperature of 6°C	0.78	0.88		0.65
Annual mean maximum temperature	0.77	0.88		0.68
February precipitation			0.52	
Annual precipitation			0.37	
Precipitation in driest year			0.29	
Date of Fall mean temperature of 6°C			0.29	
Days between spring and fall occurrence of 0°C			0.26	
Latitude				0.68

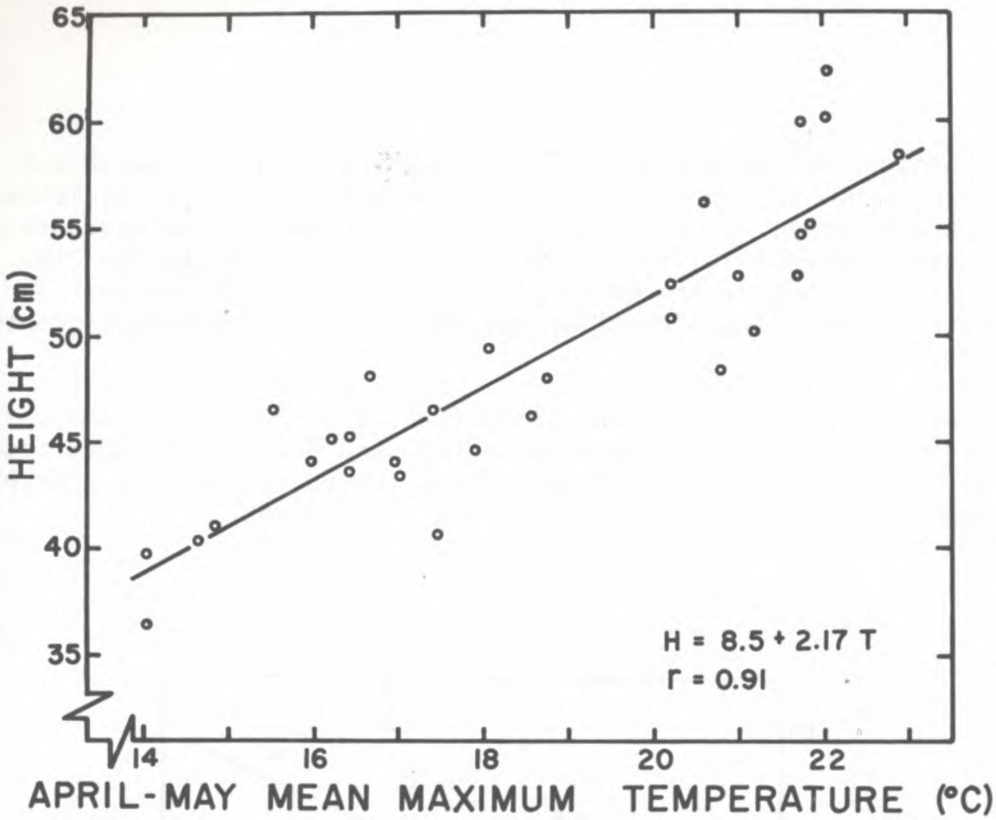

Figure 3.--Second year height for a rangewide sample of pitch pine provenances as related to April-May mean maximum temperature at the origin (n ≃ 60).

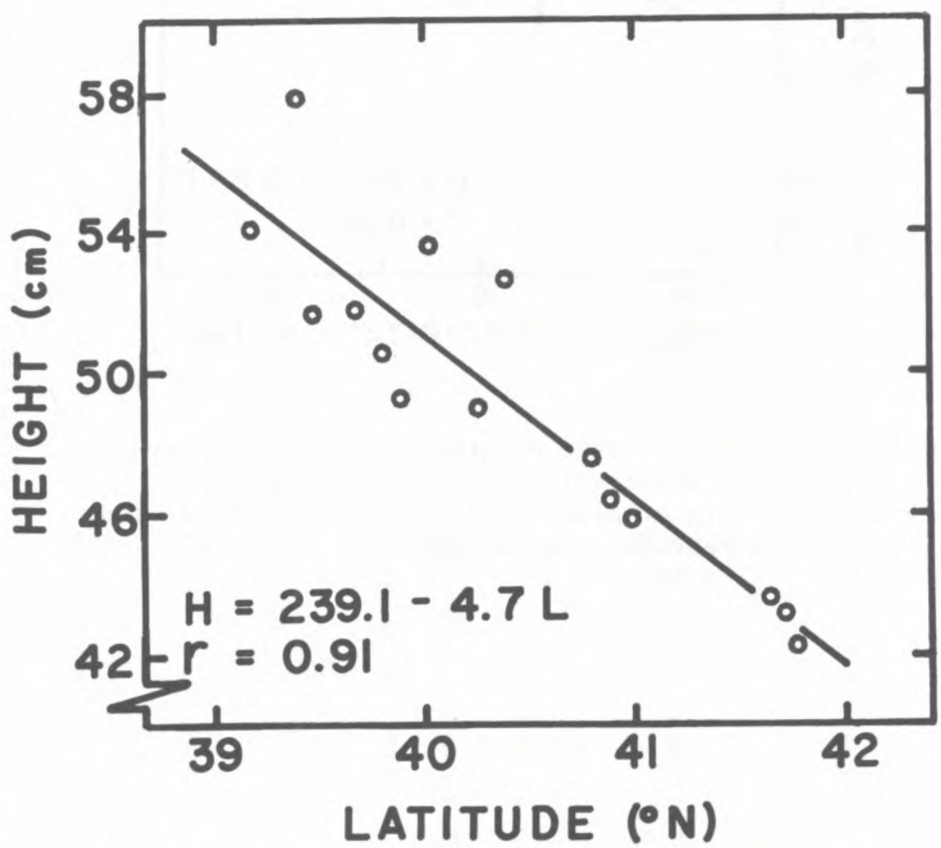

Figure 4.--Second year height of an intensive sample of coastal plain pitch pine provenances as related to latitude of origin. Note that 12 of the 15 points would fit a straight line almost perfectly (n ≃ 50).

Regressions for estimated dates of height growth initiation and cessation were not as strong as those for height (Figures 5, 6; Table 4), but were significant, Correlations might be improved if more accurate measurements of growth initiation and cessation were available. The present method of estimation based on two measurements is crude. In addition, the probit transformation may not be valid for height growth in pitch pine.

All significant correlations among first year height, second year height, growth initiation, growth cessation, and seed weight were positive (Table 5). Provenances that flushed early tended to continue growth later in the season, but the correlation was not significant.

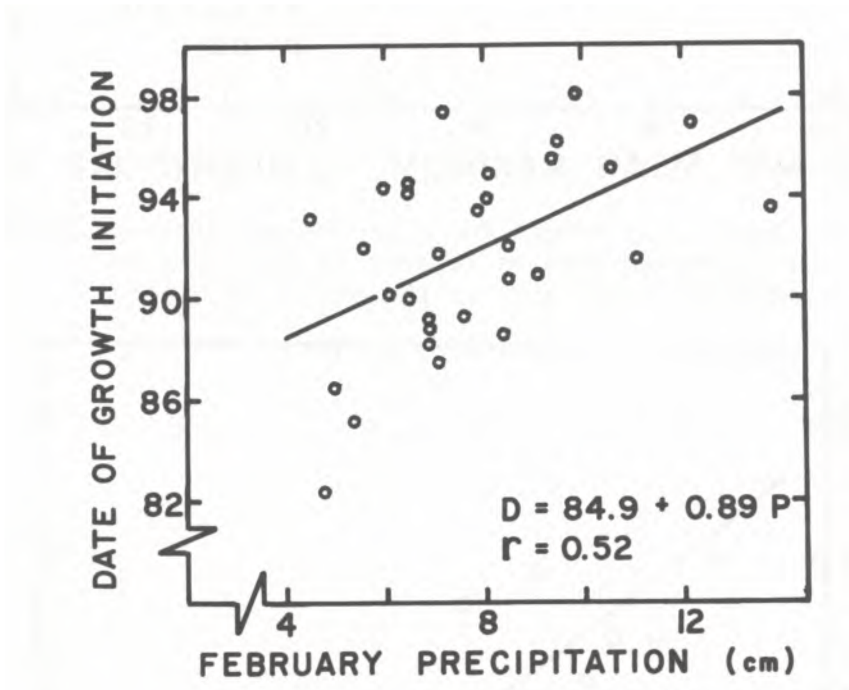

Figure 5,--Estimated date of growth initiation (days from January 1, 1973) for a rangewide sample of pitch pine provenances as related to February precipitation at the origin (n = 60).

Table 5.--Correlation matrix[1] among area means for growth traits, April-May mean maximum temperature, and seed weight in nursery trial of pitch pine provenances from a rangewide collection.

	First-year height	Second-year height	Date of growth initiation	Date of growth cessation	Seed weight	April-May mean maximum temperature
First-year height	1.00	0.89	0.30	0.50	0.62	0.82
Second-year height		1.00	0.24	0.74	0.67	0.91
Date of growth initiation			1.00	-0.27	-0.01	0.15
Date of growth cessation				1.00	0.50	0.66
Seed weight					1.00	0.67
April-May mean maximum temperature						1.00

[1] Correlation required for significance at 5 percent level is ± 0.36 and at 1 percent level ± 0.46.

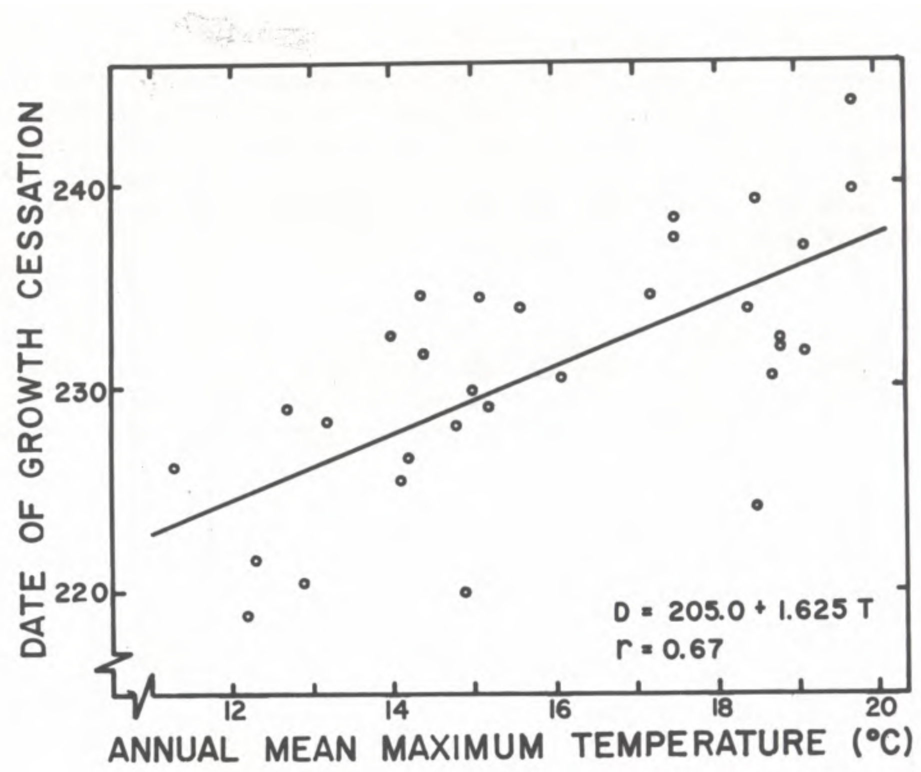

Figure 6.--Estimated date of growth cessation (days from January 1, 1973) for a rangewide sample of pitch pine provenances as related to annual mean maximum temperature (n = 60).

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