

Early Results of a Seed Source Study of Slash Pine
In Georgia and Florida

by

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All southern foresters are aware of the extensive planting of slash pine in the South. Therefore, the need for information on racial variation in this species requires no elaboration.

In 1953 the Lake City Research Center, in cooperation with other organizations ^{1/}, began a study to get some of this needed information. The study complements the Southwide Pine Seed Source Study which incorporates six seed sources scattered throughout the range of slash pine. In contrast, the Lake City test contains more seed sources and covers only that portion of the species range occurring in Georgia and Florida.

Review of Literature

In reviewing the literature we found that apparently only two other racial variation tests have been started in slash pine. The earliest of these entails trees from eight sources planted in four localities in South Africa and was reported upon by Sherry (1947). At 9 years, average heights of trees from different sources at all plantations varied only from 35.5 to 38.1 feet. However, the locality of origin of only six of the sources was known and these were from rather similar latitudes and climates.

The second test is the "slash pine series" of the Southwide Pine Seed Source Study which has already been mentioned. Mergen (1954), reporting on one of the plantations (Baker County, Florida), showed that 2-year-old seedlings originating from Polk County, Florida, were significantly shorter than those from four other sources in more northerly portions of the species range. However, he concluded that the Polk County trees may have been hybrids between typical slash pine and its south Florida variety. Wakeley (1955) summarized over-all progress in the southwide test, and Henry and Hepting (1957) covered diseases occurring during the first 3 years.

^{1/} Cooperators in the study are: Atlantic Land and Improvement Co. , Florida National Forests, Owens-Illinois Glass Co. , East Gulf Coast Research Center, St. Joe Paper Co. , Cordele Research Center, Union Bag-Camp Paper Co. and Gair Woodlands Corp.

Methods and Materials

In the Lake City test slash pine seeds were collected from 15 localities scattered throughout south Georgia and Florida (figures 1 and 2). One of the collections was from trees of the south Florida variety of slash pine. In including this source along with typical slash pine sources, we do not mean to dispute the existence of the variety. In the test we attempt to correlate seed source differences with climatic factors and to gain some insight into the evolution of genetic variation. Such relationships, if found to exist, may be clinal and need not necessarily change abruptly at recognized varietal boundaries. Therefore, we feel that a comprehensive test should include sources from as many parts of the species range as possible, and by this means one may even be able to gain some insight into the evolution of recognized varieties.

One additional seed lot, from Escambia County, Florida, did not produce sufficient seedlings for outplanting.

Details of the seed collections were given by Mergen (1958). The seed lots and trees grown from them are designated by the counties from which they originated. One-year-old seedlings grown from the seeds were outplanted in seven localities in the winter of 1954-55, in 100-tree plots with four replications. Trees from each of the 14 typical slash pine sources were planted at 5 of the sites (Dooly and Effingham Counties, Georgia; and Liberty, Baker, and Lake Counties, Florida). Trees of six of the typical slash pine sources were also planted in Emanuel County, Georgia. Finally, trees of five of the typical slash pine sources and trees of the single South Florida slash pine source were planted in Collier County, Florida.

Our report covers growth and survival through the fall of 1957. Disease and insect damage, which was rather light at most of the planting sites, is not covered. Climatic variation within the range of slash pine and its south Florida variety was studied to aid in interpreting results on survival and growth.

Results

Growth, Survival, and Other Traits

Trees from different sources grew at different rates through their third year after outplanting and most of these differences were moderately consistent over all plantations (table 1). For example, trees from Taylor County (Fla.), Calhoun County (Fla.), and Brooks-Lowndes County (Ga.) grew relatively fast at most plantations, while those from Volusia County, (Fla.), Citrus County (Fla.), Laurens County (Ga.), and Dooly County (Ga.) grew slowly at most plantations. The former group grew an average of about 16

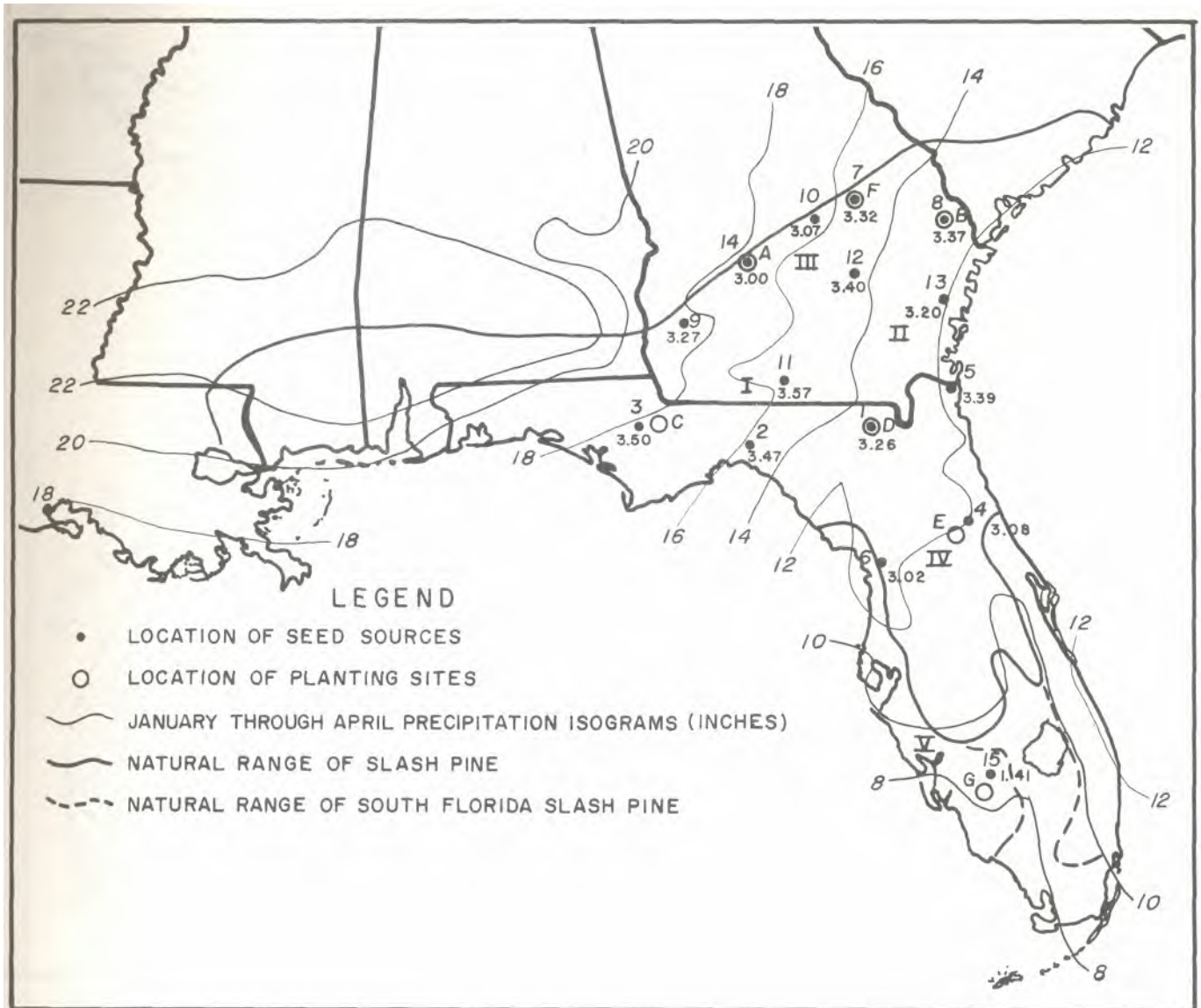


Figure 1.—A portion of Southeastern United States showing (1) the pattern of early-season rainfall, (2) approximate location of climatic zones (Roman numerals) discussed in text, (3) the location of seed sources and planting sites with their respective number and letter designations, (4) the average total height in feet (for all sites) of each seed source. Boundaries of the range of slash pine and its South Florida variety are from Little and Dorman (1954).

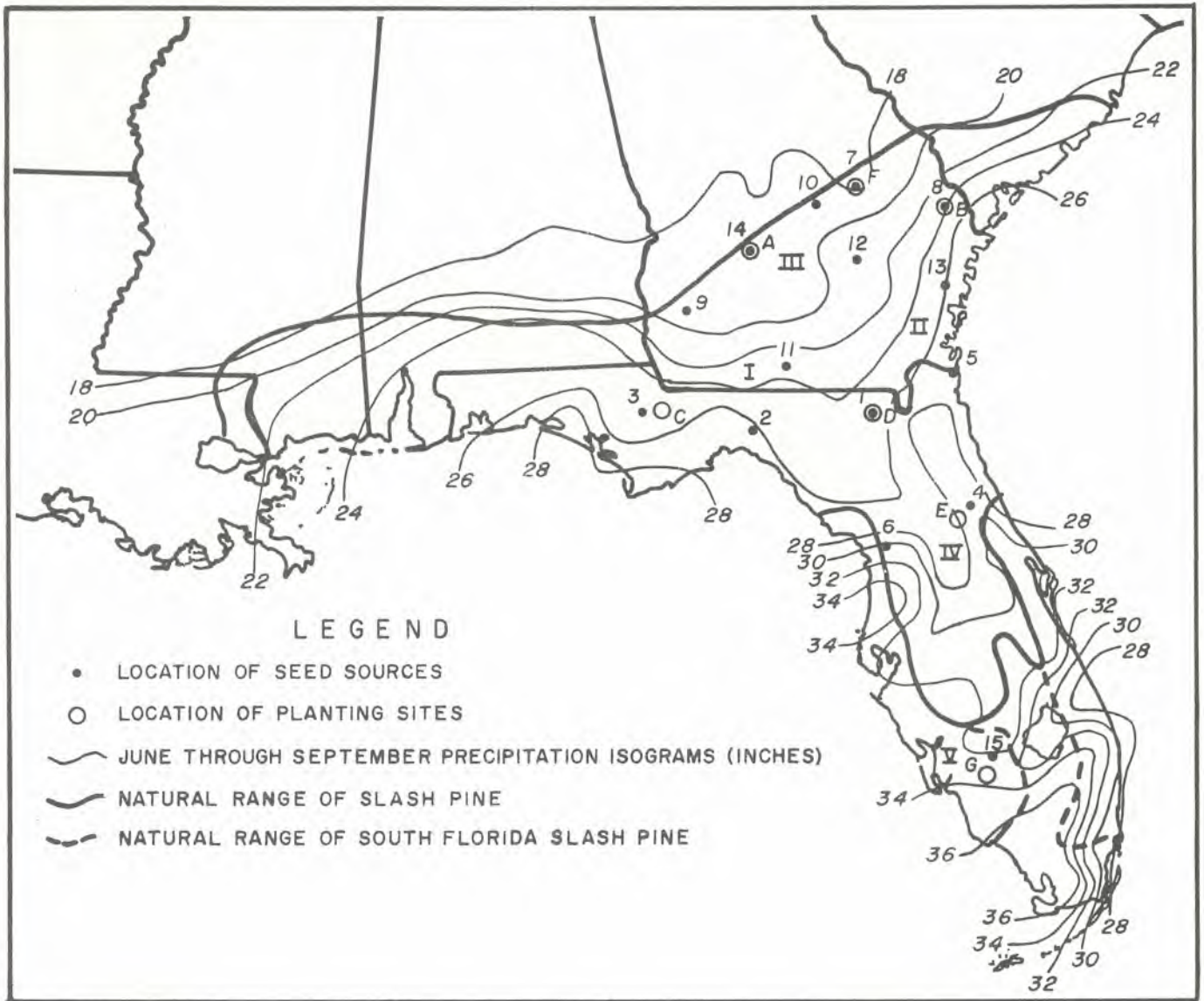


Figure 2.—A portion of Southeastern United States showing (1) the pattern of late-season rainfall, (2) approximate location of climatic zones (Roman numerals) discussed in text, and (3) the location of seed sources and planting sites with their respective number and letter designations. Boundaries of the range of slash pine and its South Florida variety are from Little and Dorman (1954).

Table 1. Average total heights of trees as of the winter of 1957-58 (4 years from seed) by seed source and planting site 1/

Seed source number and locations	Complete planting sites					Average A thru E	Incomplete planting sites		Average A thru G
	Dooly Co., Ga.	Effing- ham Co. Ga.	Liberty Co., Fla.	Baker Co., Fla.	Lake Co., Fla.		Emanuel Co., Ga.	Collier Co., Fla.	
	(A)	(B)	(C)	(D)	(E)		(F)	(G)	
	- - - - - Feet - - - - -								
1 Baker Co., Fla.	3.22	4.70	3.32	3.18	2.14	3.31	(3.91)	2.37	3.26
2 Taylor Co., Fla.	3.41	4.85	3.60	3.21	2.20	3.45	3.98	3.03	3.47
3 Calhoun Co., Fla.	3.69	5.20	3.35	3.28	2.12	3.53	(4.17)	(2.68)	3.50
4 Volusia Co., Fla.	3.24	4.39	3.03	2.68	2.18	3.10	(3.66)	2.42	3.08
5 Nassau Co., Fla.	4.10	4.68	3.12	2.77	2.48	3.43	4.00	(2.60)	3.39
6 Citrus Co., Fla.	3.50	4.51	2.72	2.54	1.95	3.04	(3.59)	(2.31)	3.02
7 Emanuel Co., Ga.	3.44	4.32	3.74	3.18	2.16	3.37	3.86	(2.56)	3.32
8 Effingham Co., Ga.	3.42	4.87	2.96	3.46	2.30	3.40	(4.01)	(2.58)	3.37
9 Calhoun Co., Ga.	3.46	4.81	3.04	2.72	2.22	3.25	4.16	(2.47)	3.27
10 Laurens Co., Ga.	3.20	4.56	2.81	2.77	2.14	3.10	(3.66)	(2.35)	3.07
11 Brooks & Lowndes Co., Ga.	3.29	5.62	3.51	3.40	2.12	3.59	4.34	(2.72)	3.57
12 Jeff-Davis Co., Ga.	3.38	4.94	3.14	3.34	2.34	3.43	(4.05)	(2.60)	3.40
13 McIntosh Co., Ga.	3.13	4.53	3.16	3.23	1.98	3.21	(3.79)	2.56	3.20
14 Dooly Co., Ga.	3.00	4.94	2.65	3.06	1.93	3.12	3.52	1.92	3.00
15 Hendry Co., Fla. ^{2/}	--	--	--	--	--	--	--	1.08 ^{3/}	(1.41)
Average	3.39	4.78	3.15	3.06	2.16	3.31	(3.91)	(2.51)	3.28

1/ Values in parenthesis are estimates made mainly to prevent bias in computing all-plantation averages.

The estimated value for Calhoun Co., Fla. under Emanuel Co., Ga., for example, was computed as follows:

Average of all sources actually planted at Emanuel Co., Ga. = 3.98

Average of all planting sites for same sources planted in the first five plantations listed = 3.37

Estimated average for Emanuel Co., Ga. site = $3.31/3.37 \times 3.98 = 3.91$

Estimated value for Calhoun Co., Fla. source = $3.53/3.31 \times 3.91 = 4.17$

Seed source numbers and planting site letter designations (A thru G) correspond to those shown in figures 1, 2, and 3.

2/ South Florida slash pine, not included in averages.

3/ $3.28/2.51 \times 1.08 = 1.41$.

percent faster at all plantations than the latter. Some seed sources grew fast at some sites and slowly at others this "interaction effect" was significant at the 5-percent level. However, variation due to seed source was significantly greater. (5-percent level) than variation due to interaction.

Note the large growth differences between plantations. These, unlike the differences between seed sources, cannot be interpreted with any degree of reliability. They may have been caused by effects of climate and soil, but also by such extraneous factors as differences in site preparation, ensuing competition, and others.

Highly significant differences in survival occurred among seed sources, with a rather high degree of consistency among all plantations (table 2). Trees native to the northernmost portion of the range of slash pine generally survived better than those from the southern portion.

Earlier reports of the study included differences in other traits that were attributed to seed sources. Mergen and Hoekstra (1954) noted variation in germination percent. Foliage of seedlings in the nursery possessed differences in number of resin ducts, stomates per millimeter, and marginal teeth per millimeter (Mergen, 1958). Langdon (1958) showed differences in insect attack in addition to growth and survival among trees from the five slash pine sources planted at Collier County, Florida.

Climate

Our analysis of weather records showed that seasonal distribution of rainfall and the length of growing season are two outstanding features of the climate within the test area. In contrast to annual rainfall, which varies little over the area in question, the seasonal distribution of rainfall not only varies greatly but the variation also follows a definite pattern (figs. 1 and 2). In the analysis we used (1) the average total rainfall occurring from January through April, which we shall call "early-season rainfall" and (2) average total rainfall occurring from June through September, which we shall call "late-season rainfall". All climatic data were obtained from Weather Bureau records and were usually based upon averages for the period 1921-1950.

Note in figure 1, that early-season rainfall increases in going from the southwest tip of Florida northward and also westward from the Atlantic coast through north Florida, and south Georgia. The pattern of late-season rainfall is similarly pronounced but increases in the opposite direction. Within the range of typical slash pine there may be as little as 10 inches of early-season rain combined with 32 inches of late-season rain in south Florida and as much as 18 inches of early-season rain with only 19 inches of late-season rain in central Georgia. In some parts of the range of South Florida slash pine there may be as little as 7 to 8 inches of early-season rain with 36 inches of late-season rain.

Table 2. Average percent survival of trees as of the winter of 1957-58 (4 years from seed) by seed source and planting site 1/

Seed source number and locations	Complete planting sites					Average A thru E	Incomplete planting sites		Average A thru G
	Dooly Co., Ga. (A)	Effingham Co., Ga. (B)	Liberty Co., Fla. (C)	Baker Co., Fla. (D)	Lake Co., Fla. (E)		Emanuel Co., Ga. (F)	Collier Co., Fla. (G)	
1 Baker Co., Fla.	43.0	48.4	77.0	76.6	36.7	56.3	(49.9)	77.3	58.4
2 Taylor Co., Fla.	53.9	41.8	77.0	76.2	56.2	61.0	51.2	86.7	63.3
3 Calhoun Co., Fla.	43.4	52.7	68.0	82.0	44.1	58.0	(51.4)	(72.3)	59.1
4 Volusia Co., Fla.	23.8	34.4	59.8	55.1	35.2	41.7	(37.0)	44.5	41.4
5 Nassau Co., Fla.	59.8	37.5	69.1	87.1	55.1	61.7	57.4	(76.9)	63.3
6 Citrus Co., Fla.	42.6	46.1	71.5	69.5	55.2	57.0	(50.5)	(71.0)	58.0
7 Emanuel Co., Ga.	58.2	47.3	78.5	84.0	64.4	66.5	59.8	(82.9)	67.9
8 Effingham Co., Ga.	51.2	47.3	75.8	82.4	50.0	61.3	(54.4)	(76.4)	62.5
9 Calhoun Co., Ga.	50.4	50.0	74.6	79.3	43.7	59.6	62.9	(74.3)	62.2
10 Laurens Co., Ga.	55.1	54.7	72.6	79.7	53.9	63.2	(56.1)	(78.8)	64.4
11 Brooks & Lowndes Co., Ga.	40.6	40.6	71.9	78.9	48.0	56.0	52.3	(69.8)	57.4
12 Jeff-Davis Co., Ga.	51.2	42.2	69.9	86.3	48.8	59.7	(52.9)	(74.4)	60.8
13 McIntosh Co., Ga.	44.5	45.3	74.2	75.4	44.9	56.9	(50.5)	71.9	58.1
14 Dooly Co., Ga.	49.6	59.8	71.1	86.7	57.8	65.0	44.1	69.5	62.6
15 Hendry Co., Fla. ^{2/}	--	--	--	--	--	--	--	42.2 ^{3/}	(34.5)
Average	47.7	46.3	72.2	78.5	49.6	58.8	(52.2)	(73.3)	60.0

1/ Values in parenthesis are estimates, made mainly to prevent bias in computing all-plantation averages. See footnote 1, table 1, for method of computation.

Seed source numbers and planting site letter designations (A thru G) correspond to those shown in figures 1, 2, and 3.

2/ South Florida slash pine, not included in averages.

3/ $60.0/73.3 \times 42.2 = 34.5$.

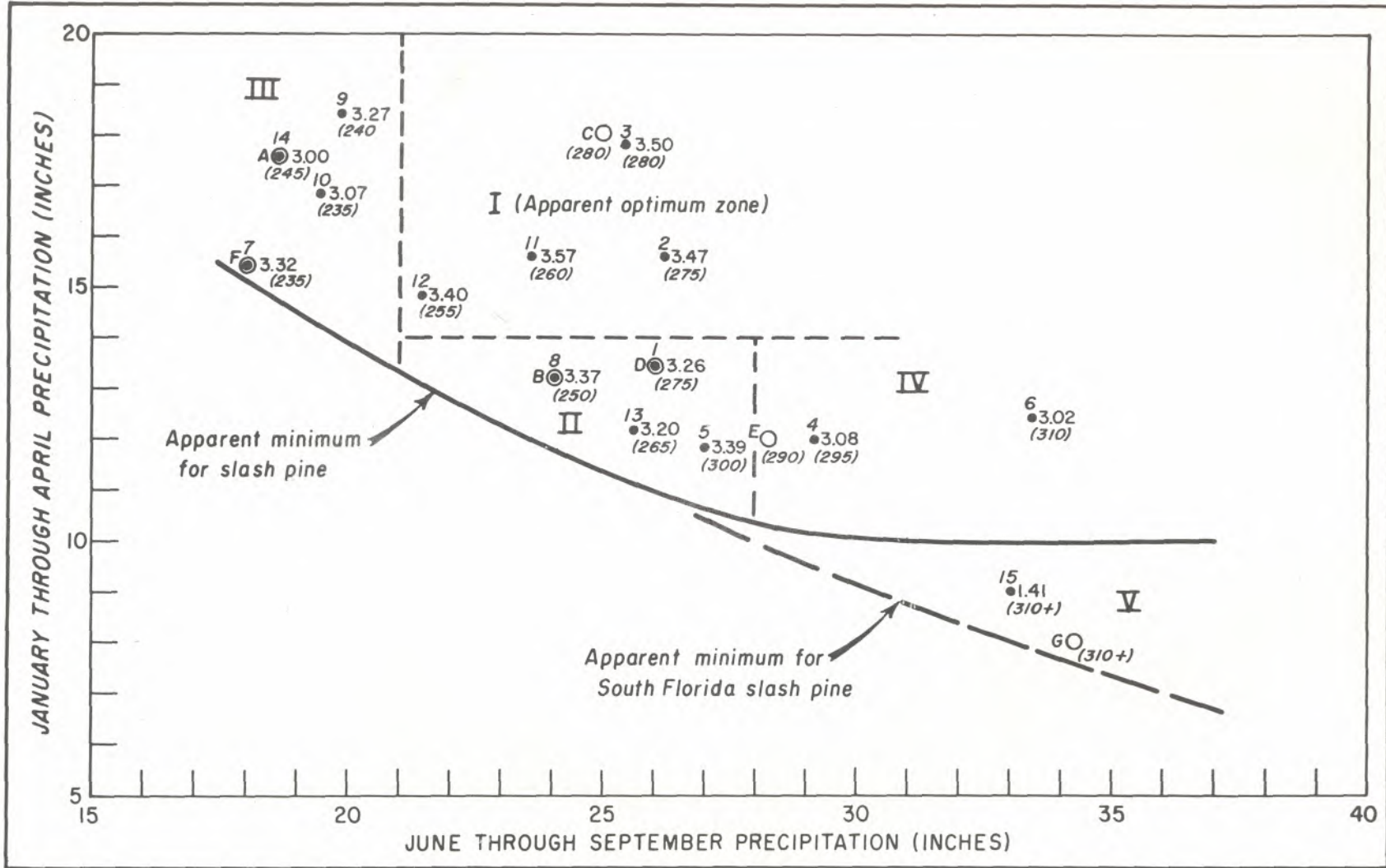


Figure 3.—Early-season rainfall plotted over late-season rainfall for each of the seed sources (dots) and planting sites (circles). At each point the following are also shown: (1) number and letter designation for seed source and planting site, respectively, (2) the length of growing season (figure in parentheses, days), and (3) average total height in feet (for all sites) of each seed source.

Any of a number of temperature factors could be related to racial variation in slash pine. Although summer temperatures vary little, such factors as length of growing season (frost-free periods), average winter temperatures, minimum winter temperatures, and others are highly variable within the species range. Without studying each of these thoroughly we decided to use the length of growing season in our analysis of growth on the assumption that it is a combined expression of temperature factors. The approximate length of growing season for the localities of seed origin and planting sites is shown in figure 3 (Anonymous, 1941). Mean January temperature was also used in the analysis of survival data.

Climate and Clinal Variation

How are growth rate and the climatic variables related? It is, very possible that seasonal distribution of rain and length of growing season were instrumental in causing the apparent inherent variation found in growth rate. Note in figure 1 that trees usually growing the fastest originated from the north-central part of Florida (Calhoun and Taylor Counties) and the south-central portion of Georgia (Brooks and Lowndes Counties). The area encompassed by these seed sources may well be an optimum climatic zone. Trees originating from areas to the north, east, and south of this supposed optimum zone generally grew more slowly in our tests. Unfortunately no sources from areas west of this zone were included in the study. Within the optimum zone early-season rainfall varies from about 14 to 18 inches and late-season rainfall from 21 to 28 inches, and length of growing season is more than 250 days (figs. 1, 2, and 3). To the north the growing season is shorter and late-season rainfall is less. To the east and south early-season rains decrease. To the west rainfall remains generally within the supposed optimum, but length of growing season varies from as much as 290 days in parts of the southern portion to less than 230 days in parts of the northern portion.

Because of this apparent relation of growth rate to climatic factors, we decided to group the seed sources and planting sites according to similarities in climate. Figure 3 shows the basis for the grouping and delineation of climatic zones. We do not wish to imply here that the zones represent different ecotypes. Conversely, our results indicate that the inherent variation is clinal as will be discussed later. Grouping of the data and delineation of climatic zones was done merely to facilitate further interpretation of the results.

Note that trees originating from south-central Georgia and north-central Florida (zone I), representing the apparent optimum climatic area and the "heart" of the slash pine range, generally grew tallest of all areas (table 3). The growth differences were greatest when trees were planted in areas which appear to be the best sites from the climatic viewpoint. Trees from southeast Georgia and northeast Florida (zone II), which has high late-season rain but low early-season rain, were generally second best in growth rate. Those

Table 3. Average total heights and survival of trees, as of the winter of 1957-58 (4 years from seed) by climatic zones 1/ of seed sources and planting sites.

Climatic zone of seed source	Climatic zone of planting site				
	I	II	III	IV	V
- - - - - Average height in feet - - - - -					
I	3.40	4.23	3.79	2.20	2.76
II	3.14	3.93	3.70	2.22	2.53
III	3.06	3.80	3.54	2.11	2.32
IV	2.88	3.53	3.50	2.06	2.36
V	--	--	--	--	1.08
- - - - - Average survival in percent - - - - -					
I	71.7	62.6	49.6	49.3	75.8
II	74.0	62.5	51.3	46.7	75.6
III	74.2	67.7	54.5	55.0	76.4
IV	65.6	51.3	38.5	45.2	57.8
V	--	--	--	--	42.2

1/ See text and figure 3 for description of climatic zones.

from the northern extremities (zone III), with high early-season rain, low late-season rain, and short growing seasons, were third best. Those from central Florida (zone IV) were fourth best. "Central Florida" was kept distinct from "southeast Georgia and northeast Florida" partly on the basis of latitude. The former gets more late-season rain than the latter, and early-season rains are about equal. However, early season temperatures in central Florida are higher and hence less moisture is likely available to plants at this apparently critical period. Trees of the single South Florida slash-pine source, representing very low early season rain and very high late-season rain, grew very slowly at the single plantation representing its native climate (zone V). Thus, the results imply that growth decreases to the north of the apparent optimum zone with decreasing length of growing season and late-season rains. Similarly, growth decreases to the east and south of the optimum zone with decreasing early-season rains.

Survival data is again shown in table 30. Note that trees from the northern extremities (zone III) generally survived best of all plantations while those from central and south Florida (zones IV and V) survived poorest. The differences between sources from zone I, II, and III were, however, usually not great.

In a correlation analysis survival was found to be inversely related to mean January temperatures of the localities of seed origin ($r = -.86$, highly significant). Thus, clinal variation, associated with climate, is established for survival. From this relationship we might assume that natural selection among trees growing in the colder climates has favored resistance to frost or other winter damage.

The fact that trees of the northern sources (from zones I, II, and III) survived better than those of the central and south Florida sources (from zones IV and V), even when planted in the latter areas, was surprising. However, in considering this fact from the standpoint of the evolution of racial variation, we must remember that the trees were planted rather than established by seeding. If the seeds were sown under natural growing conditions, results may have been different. Under natural conditions in south Florida, time of germination and also seedling development may be adapted to low early-season rain. Planting of seedlings obscures inherent adaptation of this sort.

Some attempts were made to obtain statistical proof of the apparent clinal variation in growth rate. However, the association of the climatic variables appears to be too complicated and the number of sources too few for a thorough regression or correlation analysis. For example, the apparent effect of late-season rains is likely curvilinear, since there is undoubtedly a threshold beyond which additional rain has no further beneficial effect. The same may be true with early-season rain and length of growing season. Other factors, such as soil differences, which were not studied, may further complicate the picture. Thus, statistical proof of the exact nature of the growth rate variation found will have to await further study.

For the purposes of future studies we might hypothesize that slash pine trees native to that portion of the species range where the climate is optimum are inherently superior in growth rate. This could come about by a natural selection over a period of many years. Assuming a heterogeneous population, the more rapidly growing trees will on the average survive in greatest numbers to produce the next crop, eventually resulting in trees which are inherently superior in growth rate. At points progressively further away from this optimum zone, the climate may favor some other trait, at the expense of rapid growth. For example, in progressing northward from an optimum point, colder winters may cause more rigid selection for resistance to frost, with less stringent selection for rapid growth. The same could be true for rainfall at critical periods. The hypothesis, then, implies clinal variation deviating away from what may be the "heart" of a species range.

Whether or not growth rate is inherently good in the western portion of the range (southern Alabama and Mississippi and southeastern Louisiana) is unknown. The Southwide Pine Seed Source Study may eventually provide the answer and we can only speculate now. As seen in figures 1 and 2, the

seasonal distribution of rainfall seems to be fully as favorable as the supposed optimum zone in south Georgia and north Florida. The length of the growing season in the approximate southern half of the western portion is also apparently optimum but it is considerably less in the northern half.

As mentioned earlier, Mergen (1958) presented evidence of clinal variation in stomatal frequency. Using earlier data in the Lake City test Mergen showed that trees originating from the eastern portion of the species range had more stomata per unit of needle length than those from the west. We suspected that this longitudinal relationship may have been caused by early-season rain, which, as noted earlier, follows an east-west pattern over much of the species range. Hence, we computed the correlation coefficient between his stomatal data and early-season rainfall and found it to be highly significant (-.76). Stomatal frequency tended to be high where early-season rainfall was low and vice versa, Miller (1938), citing the work of several authors, pointed out that this same relationship was found with a number of other plant species. The exact cause of the association was not determined but some authors noted that plants grown under optimum moisture had larger epidermal cells and hence greater spaces between stomata. In any event it appears that stomatal frequency may be a useful tool for further genetic investigation of slash pine.

Larson (1957) showed that percentage of summerwood and specific gravity of slash pines growing in their native habitats increased with increasing June plus July rainfall and decreased with increasing January plus February rain. Thus, apparently trees in localities with light early-season rain and heavy late-season rain grew mostly in summer. Conversely, under heavy early-season rain and light late-season rain relatively more growth occurred in spring. On first thought this would seem to be strictly an environmental effect. However, it could well be that these same environmental factors, operating as natural selection forces, could have caused genetic variation in summerwood percent and specific gravity. For example, trees which inherently start growth early in the season could conceivably often succumb to drought in those areas where early-season rains are deficient. Natural selection in those areas, then, may have favored those trees which inherently postpone their grand period of growth until summer. As soon as the trees in the Lake City test become of age we will be able to check this hypothesis by measuring summerwood percent and specific gravity along with phenology of growth.

Practical Application of Results

Results of the test suggest that inherent variation in growth rate exists and that use of local seed may not always be the best policy, Seed collected from an apparently optimum climatic zone seems to be moderately superior even when planted in other climates with no great loss in survival. These early results may change as the test trees grow older and new trials may

give different results. But if these results hold we may in the future be able to deviate somewhat from the usual "local seed rule" to obtain a modest or even large genetic improvement in slash pine by wise choice of seed sources. Meanwhile, if possible, we should continue to avoid moving seed over great distances.

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