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Inheritance of Needle and Bud Characteristics of Slash Pine

By FRANK C. SORENSEN

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The purpose of this investigation was to analyze the extent of gene control of several variable needle and bud characteristics in slash pine (*Pinus elliotii* ENGELM.). Variation in needle and bud characteristics, particularly needle length, has often been used as a tool in investigations of geographic variation and of interspecific hybridization in pine species. Only rarely, however, have the observations and studies included determination of an approximate degree of genetic control of variation, or compared different characteristics on this basis.

Review of Literature

DENGLER (1938), in studying a number of pines, found that different races still varied in needle length in the second generation. In another European investigation, BURGER (1941) found that Scots pines (*P. sylvestris* L.) of different origins, but grown on the same site, required different amounts of needles to produce the same wood volume increment.

Three pertinent observations have been made in ponderosa pine (*P. ponderosa* LAWS.) in this country. LORENZ (1949), in a seed source study, reported major differences in color and texture of needles of trees of different sources when grown on the same site. In a similar study, MUNGER (1947) noted that progeny from some seed sources were bushier than others and that variation existed in needle color, duration of needle retention, and angle of the needle with the twig. Average needle length ranged from 4 inches for one source to 7½ inches for another. WEIDMAN (1939) showed that 22- to 26-year-old ponderosa pine progenies from different geographic sources differed in the number of needles per fascicle, length of needles, and general appearance of foliage. These differences corresponded to differences between trees of the various parent localities, and the conclusion was drawn that the characteristics were strongly inherited.

Several needle characteristics of slash pine and some of its hybrids were investigated by MERGEN (1958). The number of resin ducts per needle and the number of stomata

per millimeter of length showed a pattern which could be correlated with the geographic distribution of the species. The number of teeth on the needle margin, however, did not appear to be so correlated.

Procedure

Description of Material

The plant materials used in this study were: 1) 15-year-old rooted cuttings obtained from a group of slash pine trees selected for their high gum-yielding ability, and 2) 15-year-old progenies produced by controlled pollinations among the same high-gum-yielding selections. Both of the plantations were situated near Olustee, Florida. The material was made available to the author by the Lake City Research Center of the U. S. Forest Service.

The clones were growing in an informal plantation about ¾ acre in size, containing varying numbers of ramets from each clone. The ramets of some clones were planted in unreplicated row plots while those of other clones were located more or less at random. Five of the clones were chosen for study (Table 1).

The progeny plantation was about 6 acres in size. In it, varying numbers of trees of most progenies were planted randomly within seven blocks. A few progenies were represented only in replacement blocks where the trees were planted in unreplicated row plots. Seven of the progeny

Table 1. — Clonal and progeny averages for all traits measured.

Clone or progeny	Trees per clone or progeny	Needle length	Needle-bundle volume	Needles per bundle	Fascicle sheath length	Needle divergence	Bud scale length
CLONES							
G-1	6	263	.785	2.17	14.1	11.4	14.1
G-2	8	239	.520	2.04	10.5	15.2	11.5
G-3	2	248	.667	2.00	13.5	5.7	13.1
G-4	6	264	.632	2.05	16.0	17.8	15.2
G-7	1	297	.786	2.30	17.0	9.9	— ¹⁾
PROGENIES							
1 × 2	14	244	.515	2.13	11.6	16.3	— ¹⁾
1 × 7	14	248	.509	2.14	13.3	14.9	— ¹⁾
3 × 2	14	227	.472	2.04	11.2	12.6	14.0
4 × 1	14	252	.557	2.31	13.0	19.6	15.7
2 × 7 ²⁾	7	252	.505	2.12	— ¹⁾	15.8	— ¹⁾
3 × 4 ²⁾	7	— ¹⁾	— ¹⁾	2.14	— ¹⁾	16.9	15.9
4 × 2 ²⁾	4	240	.454	2.05	12.3	17.3	— ¹⁾

¹⁾ Not measured.

²⁾ Progenies represented in the replacement blocks only.

¹⁾ Based upon a thesis presented by the author in partial fulfillment of the degree of Master of Science in Forestry at the University of Florida, 1960. The investigation was conducted in cooperation with the Southeastern Forest Experiment Station, Lake City, Florida, which supplied the plant material. Acknowledgements are due to Dr. T. O. PERRY for suggesting the problem and to Mr. A. E. SQUILLACE for much helpful advice. Further acknowledgements are made to Drs. R. R. SILEN and H. IRGENS-MÖLLER for reviewing the paper. The author is presently a Research Forester with the Pacific Northwest Forest & Range Experiment Station at Corvallis, Oregon, USA.

groups were chosen for study. Of these, four were within the replicated blocks while three were within replacement blocks (Table 1).

Foliage and bud collections were made in late January and early February, 1959. At this time the terminal vegetative buds of the upper 2 or 3 whorls of primary branches were about 3 to 5 centimeters long. Visible elongation of the new needles had not yet begun. A total of 10 needle bundles were taken from each tree. Five of these were selected from branches in the middle one-third of the crown and five from branches in the lower one-third. The selection of bundles was restricted to 1- and 2-year-old wood only. Vegetative bud samples were taken from the extreme upper portions of the crown. Two buds of vigorous appearance were taken randomly from the top two whorls of each tree.

After collection the needles and buds were placed in polyethylene bags containing a small amount of water and stored in a refrigerator at about 40° F. until measurement. Measurements were then begun and completed within about 6 weeks. The traits measured are listed below.

Needle length was measured from the base of the needle bundle to the tip of the needles.

Needle-bundle volume was measured by water displacement and expressed in relative terms. The bundles were immersed in a narrow glass tube containing water and the length of displacement of the column of water was measured. All needles were measured within 2 weeks after storage. Through a "uniformity trial" the effect of length of storage time upon clonal or progeny differences was shown to be not greater than 3 percent.

Fascicle sheath length was measured from the base of the needle bundle to the tip of the sheath.

Needle "divergence" as used here, refers to the separation of needles as they extend out from a single fascicle sheath. The distance between needles of the same bundle was measured in millimeters at a point 10 centimeters from the base of the fascicle sheath.

Bud scale length was measured on scales located approximately 1 centimeter back from the tip of the bud. Two scales were plucked from opposite sides of the bud at this point.

Statistical Analysis

Because the materials were growing in two plantations and represented two different types of propagation, the presence of genetic effect could be tested through: 1) variance of individuals and clones in the clonal plantation, 2) variance of progenies in the progeny plantation. 3) correlation between parents (represented by clones) and progenies.

Variance of the clones was analyzed according to a hierarchical classification model (SNEDECOR, 1956). The main samples were clones. The clones were composed of sub-samples of ramets which in turn were composed of sub-samples of needle bundles. These classifications were used for all traits except needles per bundle, which could only be classified into clones and ramets. The sources of variation and the estimated variance parameters were:

Source of variation	Parameters estimated
Clones	$\sigma^2 + n\sigma_T^2 + bn\sigma_C^2$
Trees in clones	$\sigma^2 + n\sigma_T^2$
Bundles in trees in clones	σ^2

where:

σ^2 is the component of variance due to bundles of the same tree,

σ_T^2 is the component of variance due to trees of the same clone,

σ_C^2 is the component of variance due to clones,

n is the number of bundles (buds) on which the individual tree average is based (10 for needle traits and 2 for the bud traits),

b is the number of trees on which the clonal mean is based (4.22 for needle characteristics, and 5.21 for the bud trait). Because the clones contain different numbers of ramets, the averages were computed using the following formula for unequal sample sizes (SNEDECOR, 1956):

$$b = \frac{1}{a-1} \left(c - \frac{\sum b_i^2}{c} \right)$$

where:

a is the number of clones,

c is the total number of trees in all clones,

b_i is the number of ramets in each clone.

The components of variance for clones and trees within clones were then determined.

Because trees of the different clones have different genotypes, it can be said that there is genetic control of the variation of a particular trait if the component of variance contributed by clones is significant.

Data from the randomized block design of the progeny plantation were subjected to the typical analysis of variance. The sources of variation and the estimated parameters were:

Sources of variation	Parameters estimated
Blocks	$\sigma^2 + ak_B^2$
Crosses	$\sigma^2 + ck_C^2$
Remainder	σ^2

where:

σ^2 is the component of variance due to trees of the same cross or parentage,

k_C^2 is the component of variance due to crosses,

k_B^2 is the component of variance due to blocks,

a is the number of crosses on which the block estimate is based (4 for needle traits and 2 for bud traits),

c is the number of blocks on which the cross estimate is based (7).

If genetic influence is measurable, trees of the same parentage on the average should resemble each other more than they resemble individuals of other parentages. The evidence in the analysis for this is a significant component of variance due to crosses.

Parent-progeny correlations were determined between the clones and their progenies. The progeny value for each comparison was estimated by the average value of all trees of the progeny. The parental value for each comparison was estimated by the mid-point value of the parents making up the cross. Each parental value was estimated by the average of the ramets which represented it in the clonal plantation. In terms of this analysis then, genetic effect is present if the parents and their progeny show positive correlation. Regressions of the offspring on the mid-point of the parents were also determined.

Table 2. — Analyses of variance for all traits measured in the clonal plantation

Characteristic	Degrees of freedom			Mean squares			Estimated variance components			Clone contribution ¹⁾	
	Clones	Trees	Needles	Clones	Trees	Needles	Clones	Trees	Needles	Percent	Percent
Needle length	4	18	207	11,950**	517.6*	291.0	270.9	22.66	291.0	84	84
Bundle volume	4	18	207	4,407**	67.80	74.64	102.8	Negative ¹⁾	74.64	94	94
Needle divergence	4	18	207	722.0**	27.82	19.74	16.45	.808	19.74	86	86
Fascicle sheath length	4	18	207	307.8**	2.528	1.652	7.234	.0866	1.652	97	97
Needles per bundle	4	18	— ²⁾	.0300*	.00833	—	.00691	.00833	—	45	45
Bud scale length	3	18	22	36 10**	1.415	1.732	3.329	Negative ¹⁾	1.732	82	82

1) If the variance component was estimated as a negative value, it was treated as zero for determining the estimated clone contribution.

2) Estimate of individual needles was not possible.

3) Clone contributions obtained by the formula, $\frac{n\sigma_c^2}{\sigma_e^2 + n\sigma_t^2 + n\sigma_c^2}$ in which "n" is the number of needles on which the tree average is based, and the variances are those due to error, trees, and clones as shown by the subscripts.

** Significant at the .01 level of confidence.

* Significant at the .05 level of confidence.

Results

Analyses of variance of clones: The clones significantly differed for all traits (Table 2). For all characteristics except needles per bundle, the genetic, or clone, contribution was greater than 80 percent of total tree variance. The estimated clonal component for needles per bundle was significant, but relatively small compared to the measure-

ment traits. Analysis of only one characteristic, needle length, showed significant differences between trees of the same clone.

In these analyses, as well as in those of the subsequent two paragraphs, the calculations for genetic contributions to variance were the same as those normally used for "heritability" estimates. However, because the genotypes

Table 3. — Analyses of variance for all traits measured in the progeny plantation

Characteristic	Degrees of freedom			Mean squares			Estimated variance components			Cross contribution ¹⁾	
	Crosses	Blocks	Remainder	Crosses	Blocks	Remainder	Crosses	Blocks	Remainder	Percent	Percent
Needle length	3	6	18	855.5**	127.1	75.74	114.4	13.86	75.64	60	60
Bundle volume	3	6	18	56.12*	13.42	12.40	6.25	.255	12.40	34	34
Needle divergence	3	6	18	57.96**	8.208	8.608	7.05	Negative	8.608	45	45
Fascicle sheath length	3	6	18	7.699**	.3155	.4777	1.03	Negative	.4777	68	68
Needles per bundle	3	6	18	.0446	.0569	.0240	.00294	.00822	.0240	11	11
Bud scale length	1	6	6	10.81*	1.738	1.408	1.34	.166	1.408	49	49

1) Cross contribution obtained by dividing the cross component by the sum of the cross plus remainder components.

** Significant at the .01 level of confidence.

* Significant at the .05 level of confidence.

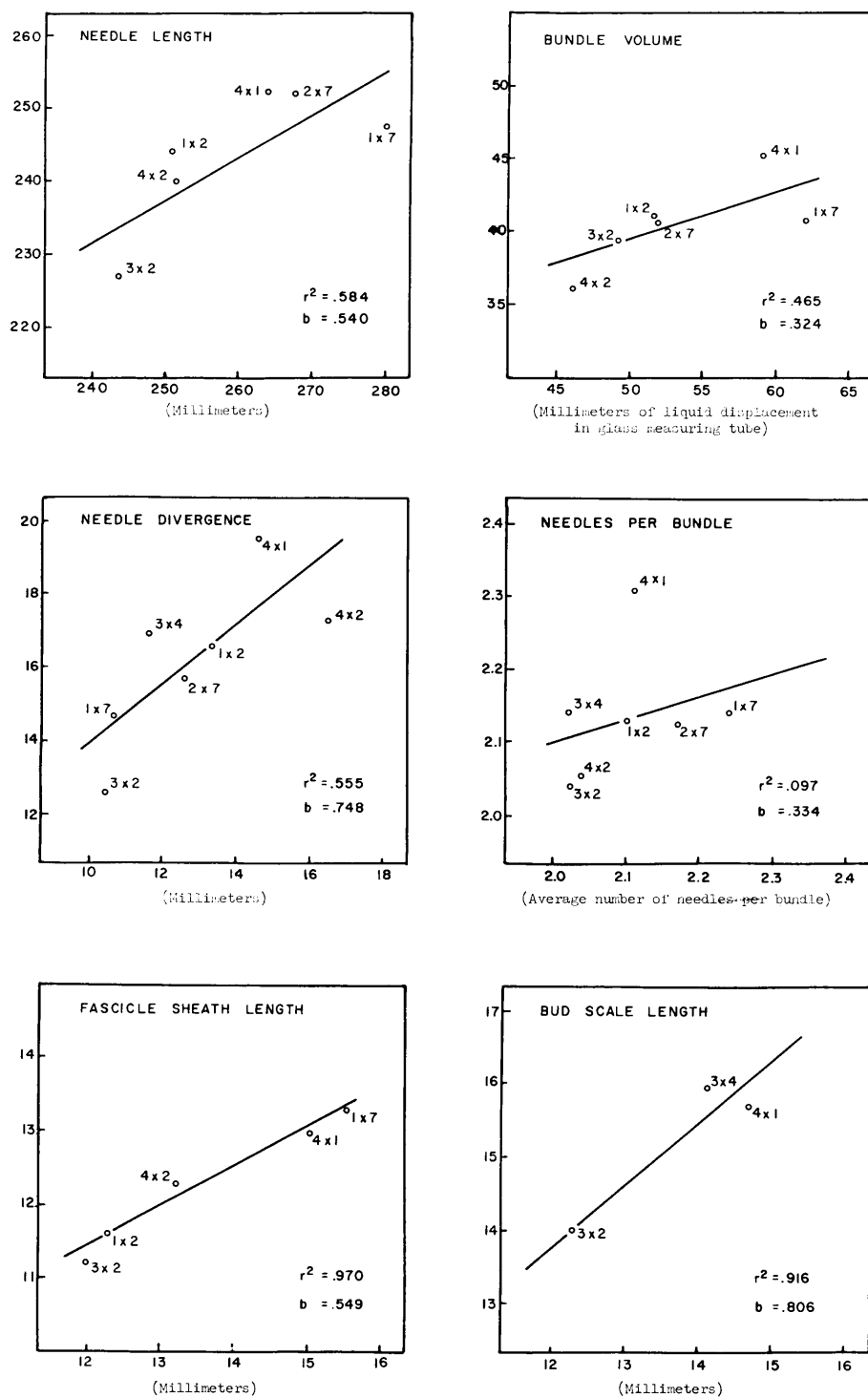


Figure 1. — Scatter diagrams and regressions of progeny on parents for the various traits. The ordinates are scaled for the progeny values; the abscissae are scaled for the parental values. See text for further description of traits and measurement techniques.

were not randomly selected, the term “heritability” has not been used.

Analyses of variance of progeny: The crosses varied significantly for all measurement traits but not for needles per bundle (Table 3). Because the variance of trees within a cross is greater than the variance of ramets within a clone, the genetic contributions were lower than in the clonal analyses. Except for needles per bundle they still

ranged from 34 to 68 percent of the cross plus remainder components.

Parent-progeny correlation analyses: Because few degrees of freedom were available, an extremely high correlation was necessary to achieve statistical significance. Only one trait, fascicle sheath length, attained this significance. The squares of the correlation coefficients showed the estimated additive parental contributions to the proge-

ny performances. They ranged from 10 percent for needles per bundle to 97 percent for fascicle sheath length (Table 4 and Figure 1).

Table 4. — Parent-progeny correlation coefficients and regression coefficients for various traits.

Characteristic	Degrees of freedom	r ²	r	b
Needle length	4	0.584	0.764	0.540**
Bundle volume	4	.465	.682	.324**
Needle divergence	5	.555	.745	.748**
Fascicle sheath length	3	.970	.985**	.549**
Needles per bundle	5	.097	.312	.334
Bud scale length	1	.916	.957	.806**

** Significant at the .01 level of confidence.

Correlations between traits: It is often of value to know, particularly in selection work, if traits are negatively or positively correlated. Although the characteristics examined in the present study are not economically important, their relationships were determined using the material in the clonal plantation (Table 5). The following formula was applied to correct for unequal numbers of individuals within the clones³⁾.

$$r = \frac{\sum n_i \cdot (x_i - \bar{x}) (y_i - \bar{y})}{\left[\sum n_i (x_i - \bar{x})^2 \right] \left[\sum n_i (y_i - \bar{y})^2 \right]}$$

Table 5. — Between trait correlation coefficients

	Needles per bundle	Bundle volume	Fascicle sheath length	Bud scale length
Needle length	.696	.777	.904*	.968*
Needles per bundle	—	.792	.405	.349
Bundle volume	—	—	.665	.658
Fascicle sheath length	—	—	—	.995**

* Significant at the .05 level of confidence.

** Significant at the .01 level of confidence.

Discussion

All traits except needles per bundle behaved in a manner consistent with a high degree of genetic control. Based on the results of all analyses, fascicle sheath length seems to be the most strongly inherited, followed by bud scale length.

Needle length is subject to considerable variation within the genotype as shown by the significant within clone difference and by the high estimated component of variance due to needles of the same tree (Table 2). The high variance of the latter possibly explains the former. Probably this trait is somewhat more susceptible to environmental influences such as position on the branch, position on the tree, age of needle, etc., than are the other traits. If this is true, and small samples (10 bundles) are taken, the effect of the within tree influence could easily be estimated differently in one ramet than in another. A larger sample, or greater restrictions on sampling, should decrease the within tree and remainder variance terms.

The same reasoning applies to bundle volume, at least to the extent that volume is dependent upon length. Although this trait shows no significant difference between trees of the same clone, the component of variance due to needles is fairly high (Table 2). Also, the remainder component for crosses (Table 3) is higher than that of any other measurement trait.

Needle "divergence" has a high genetic component of variance, but it also has one complicating feature involved

in its measurement and inheritance. The extent of "divergence" apparently depends primarily on relative growth rate of certain parts of the needle, and the relative growth rate of these parts can be modified by other needle structure characteristics. For example, one clone (No. 2) had twisted needles and all the progeny which had that clone as a parent ranked lower on the "divergence" scale (see Figure 1) than was predicted. (The predicted value was based on the trend established by progeny which did not have "twisted" as a parent.) Therefore, some clones and progeny groups are remarkably uniform in needle "divergence", but in general, considerable between tree variation exists, particularly in the progeny plantation.

Needles per bundle has a significant, but relatively small, genetic component in the clonal test, and a nonsignificant genetic effect in the other two analyses. The reason for this is the extreme variability among individuals in some of the clones. That is, the ramets of one clone are exclusively two-needled; the ramets of another clone vary from entirely two-needled to 40 percent three-needled. In the progeny plantation the variability is even more striking. The 14 offspring in one progeny group are made up of 5 trees having 90 percent 2-needle bundles and 9 trees having 100 percent 2-needle bundles. In contrast, the 14 offspring of another mating include one tree which is 100 percent 3-needled, 3 trees which are 60 to 80 percent 3-needled, 7 trees 10 to 30 percent 3-needled, and 3 trees 100 percent 2-needled. Thus, it appears that some gene combinations exert strong control over number of needles per bundle, but that others are less effective.

Generally, the parent-progeny correlation and regression results are quite compatible with results from the analyses of variance. The main exception is bud scale length. It appears to be under considerably more genetic control when parents and progeny are compared (Table 4) than when the progeny alone are analyzed (Table 3).

In conclusion, the limits of variation of all the traits except needles per bundle are under strong genetic control. This conclusion is based on (1) the cross contribution to the variation in the progeny plantation and (2) the correlation and regression coefficients from the parent-progeny correlations. Fascicle sheath length and bud scale length are found to be the most strongly inherited, needle length and needle divergence are second, and bundle volume third.

Summary

Fifteen-year-old slash pine, growing in a clonal and in a progeny plantation were investigated to determine if, and to what extent, several characters of needles and buds were inherited. The characters were needle length, needle bundle volume, fascicle sheath length, needle "divergence", number of needles per bundle, and bud scale length. Three statistical analyses were applied: the variances of the clones and ramets were analyzed, the variances of the progenies were analyzed, and parent-progeny correlations were determined. All traits except number of needles per bundle were found to be strongly controlled by the genotype; the genetic control of the latter, although significant in one analysis, was relatively slight.

Résumé

Titre de l'article: *Hérédité des caractères d'aiguilles et de bourgeons chez Pinus elliottii*.

On a étudié des *Pinus elliottii* de 15 ans, poussant dans un parc à clones et dans un test de descendance, afin de

³⁾ Personal communication from Mr. K. W. DORMAN.

déterminer si et dans quelle mesure plusieurs caractères d'aiguilles et de bourgeons sont héréditaires. Ces caractères étaient: la longueur des aiguilles, le volume des fascicules d'aiguilles, la longueur de la gaine, la «divergence» des aiguilles, le nombre d'aiguilles par fascicule, et la longueur de l'écaille du bourgeon. Les trois analyses statistiques suivantes ont été effectuées: variance des clones et des ramets, variance des descendances, et corrélations parent-descendant. Tous ces caractères, excepté le nombre d'aiguilles par fascicule, se sont révélés fortement contrôlés par le génotype; le contrôle génétique du dernier caractère, bien que significatif dans une des analyses, est relativement faible.

Zusammenfassung

Titel der Arbeit: *Über die Vererbung von Nadel- und Knospenmerkmalen bei Pinus elliotii.*

15jährige Kiefern aus Klonplantagen und Nachkommenschaftsanbauten wurden untersucht, um festzustellen, ob und in welchem Umfang einige Nadel- und Knospenmerkmale vererbt werden. Untersucht wurden die Nadellänge, Größe des Nadelbündels, Länge der Faszikelscheide, die

Nadel-, „Divergenz“, die Anzahl der Nadeln je Bündel und die Länge der Knospenschuppen. Drei statistische Analysen wurden angewandt: Die Varianzen der Klone und Klonglieder wurden analysiert, ebenso die Varianzen der Nachkommenschaften und die Eltern-Nachkommenschafts-Korrelationen bestimmt. Alle Merkmale, ausgenommen die Nadellänge je Bündel, wurden durch den Genotyp stark kontrolliert; die genetische Verankerung der Nadellänge je Bündel war mit einer Ausnahme nur relativ schwach.

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Inheritance of Yellow Oleoresin and Virescent Foliage in Slash Pine

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Simply inherited, qualitative traits, although often not of economic importance, can be valuable aids in studies of reproductive systems, cytogenetical analyses, population studies, and others. Such “gene markers” have been used extensively in animal and crop plant genetics, and results of these studies have been basic to breeding work. In forest trees, where life spans are relatively long, qualitative traits are especially useful when their expression occurs early in the life of the plant.

The occurrence of two such characters in slash pine (*Pinus elliotii* ENGELM.) are described in this report. One of these is yellow oleoresin, and the other is a type of chlorophyll deficiency, “virescent foliage”. They were found incidentally in a program designed to breed for high oleoresin yield (MITCHELL *et al.*, 1942). A third qualitative character occurring in slash pine, albinism, was reported upon earlier (SQUILLACE and KRAUS, 1963).

Yellow Oleoresin

Normal slash pines yield an oleoresin that is transparent and colorless when fresh. Occasionally deviants from this type have been found. One, identified as tree 29, yields a golden yellow oleoresin. Analysis of the turpentine fraction of this oleoresin by gas chromatography has revealed no difference in chemical composition which would account for the unusual color. However, the β -phellandrene content was unusually high, 40.5 percent in contrast to 7 percent or less in commercial turpentine reported by FISHER *et al.* (1957). Turpentine yield as a percent of the oleoresin weight was relatively low, 15 percent, compared with the normal yield of about 22 percent given by MIROV (1961)².

¹) Research Foresters, stationed at the Naval Stores and Timber Production Laboratory, Southeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Olustee, Florida.

Crosses were made in the spring of 1960 (table 1). At the time of cone collection, cones pollinated by windborne pollen also were collected. Seed were extracted, and wings removed. Sound and unsound seed were separated in an air column seed separator. Seed were sown in the spring of 1962 in row plots randomized and replicated three times.

In November 1962 a narrow strip of bark and wood approximately 1 inch long was cut from the stem of each seedling. Within 2 hours enough oleoresin had exuded from the wounded surface to permit discrimination of oleoresin color.

Table 1. — Results of crosses on slash pine 29 producing yellow oleoresin.

Mating	Seedlings producing yellow oleoresin	Total seedlings examined
<i>N u m b e r</i>		
29 × 29	15	15
29 × 1960 mix ¹)	0	271
29 × wind	1	140

¹) The “1960 mix” consisted of equal volumes of pollen from 21 trees.

All of the selfed seedlings produced yellow oleoresin. All of those from outcrosses produced normal colorless oleoresin (table 1). One seedling among the wind-pollinated progeny produced yellow oleoresin. This probably resulted from natural self-pollination.

These results indicate that tree 29 is homozygous for a recessive gene or genes governing production of yellow oleoresin. Further breeding by selfing or crossing trees

²) Thanks are due Mr. GORDON S. FISHER of the U. S. D. A. Agricultural Research Service, Naval Stores Laboratory, Olustee, Florida, for his analysis and interpretation of the oleoresin composition.