

darstellen dürften, daß sie die Anwendung von Kulturmaßnahmen für die Saatgutproduktion erschweren, daß sie weiter die Einschätzung der genetischen Qualität des Saatgutes sehr erschweren und es schließlich zu einer sehr schwierigen Aufgabe machen, sehr viel Züchtungsfortschritt durch negative Auslese in Species zu erreichen, die große erbliche Variation in verschiedenen wirtschaftlich wichtigen Merkmalen zeigen. Auch wird darauf hingewiesen, daß bei der Bestimmung der Zusammenhänge zwischen Merkmalen junger und alter Bäume bei *Pinus elliottii* und bei der Einschätzung des Genotyps von Bäumen bei der für das Konzept der Sämlings-Samenplantage charakteristischen Durchforstung wichtige Probleme noch ungelöst sind. Es wird geschlossen, daß heute Klonsamenplantagen verschiedene Vorteile gegenüber Sämlings-Samenplantagen besitzen, daß aber kein Plantagentyp für alle Situationen und Species ganz (befriedigend) dürfte.

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Tree Distribution in a Seedling Seed Orchard Following Between and Within Family Selection

By R. E. GODDARD

The possibility of substantial economic gain through use of genetically improved forest planting stock has been shown by numerous studies throughout the world. In areas of intensive forest management and large scale artificial reforestation, there has developed among forest managers a sense of urgency in obtaining improved planting stock in the shortest period possible. Among the many methods of obtaining genetic improvement, perhaps the most widely adopted other than use of correct geographic sources, has been individual tree selection. It is obviously impossible to obtain sufficient seed from the few truly outstanding individual trees selected to regenerate the thousands of acres planted annually. Thus, the situation demands, simultaneously, mass seed production and substantial genetic improvement.

In the southern United States, the breeding technique most widely adopted has been vegetative reproduction of selected individuals and establishment of clonal seed orchards. It is stated, or at least implied, that each clone so established will be progeny tested so that clones not producing a desired level of improvement may be eliminated from the orchards. To date, approximately 2500 acres of such clonal orchards have been established in the southern states. Alternative methods have been suggested (for example, GODDARD and BROWN, 1961) whereby sexual progeny of the same selected trees would be used for mass production of improved seed. Variations of this method have received limited application. While there are several reasons for this, most important is probably the less vigorous development and promotion of seedling orchards by those in charge of the southern tree improvement programs. As progeny tests must be conducted in conjunction with established clonal orchards and there is strong probability that these orchards will not produce sufficient seed for all

future needs, especially if direct seeding is expanded, seedling orchards developed from progeny tests offer a potential source of a vastly increased supply of improved seed. The purpose of this paper is to explore one possible procedure for the conversion of a progeny test into a seedling seed orchard. The discussion deals primarily with southern pines but should apply to other species which flower at a relatively early age.

Some Comparisons Between Clonal and Seedling Orchards

There can be little doubt that both clonal and seedling seed orchards can result in a substantial improvement of the genetic quality of planting stock. The theoretical gains to be obtained by several variations of both general types have been thoroughly discussed by WRIGHT (1959, 1960). As experimental evidence of actual gains achieved through application of any of the proposed methods is not available for many tree characteristics, there is little to be gained by a repetition of theoretical calculations. It is sufficient to say that selection of the best individuals within the best families should achieve genetic improvement in the following generation at least equal to and probably superior to the progeny of a clonal seed orchard. This is particularly true with moderate heritabilities and a substantial portion of the genetic variance attributed to additive effects. If most genetic variance is due to epistasis, neither multi-clone orchards nor first generation seedling orchards should be expected to be very effective.

The costs of establishing a clonal orchard by grafting, as is required with southern pines, were briefly discussed by GODDARD and BROWN (1961). Since that paper was prepared, the cost of grafting has no doubt been reduced because of increased efficiency and wider experience in this type of work. Also, seedlings produced as a result of controlled

pollinations are not inexpensive, particularly, if scattered selected parent trees must be repeatedly climbed for this purpose. However, even with extensive culling within families and assuming that the entire family lines to be removed would be the same as entire clones removed in a clonal orchard, the seedling orchard still has a substantial advantage in terms of the cost of each plant retained.

Actually, however, there are advantages to the use of clonal and seedling orchards in conjunction with one another. Controlled pollination, and all of the activities implied by the term, is much more easily accomplished in an orchard than in scattered wild trees. Also, progeny tests, either with open- or controlled-pollinated progenies, are essential to the achievement of the highest gains for clonal orchards. Therefore, the expansion of existing clonal orchards with the progeny from these orchards and the use of supplemental progeny tests as an aid in the roguing of both appears to offer many advantages. In addition, highly desirable individuals selected in progeny tests may be vegetatively propagated to fill in excessive blanks created by roguing in orchards of either type.

There is little doubt that, with the southern pines, grafts of older trees will flower earlier on the average than seedlings. However, cone production in less than 10 years is not sufficient to have an appreciable impact on planting programs involving a million or more trees annually. A few highly productive slash and loblolly pine clones produce 100 or more cones per plant annually after approximately the fifth year, but cone production of the average grafted plant is much lower than this. For example, in one slash pine breeding orchard seven years after establishment¹⁾, 38 per cent of the grafts had not flowered and the average cone production per flowering graft was 11.5 cones. Because seedling plantations are rarely arranged to promote maximum flowering, comparable figures for cone production on seedlings are scarce. Although occasional precocious slash pine seedlings flower at two or three years of age (GREEN and PORTERFIELD, 1962), a fully stocked stand will produce relatively few cones even at 30 years. The most common age for first flowering on open-grown slash and loblolly pines appears to be approximately 5 to 7 years (RIGHTER, 1939). One example demonstrative of comparable flowering on grafted and seedling loblolly pines exists in an experimental area established by the Texas Forest Service (1961). On one area are loblolly pine grafts used in an experiment involving fertilization and other cultural practices. In an adjacent area a loblolly pine planting was heavily thinned at five years of age and various top pruning treatments were applied. The comparison of flowering on check trees in both experiments is very interesting. In this area seven year old grafts averaged 5-25 female strobili per tree, the larger production in cultivated plots. On the adjacent area, unpruned and uncultivated loblolly pines of seedling origin and comparable age produced 11.7 female strobili per tree. HOEKSTRA and MERGEN (1957) and MERGEN (1961) have shown that fertilization and other treatments will increase flowering in young pines. Thus, it appears that seedling seed orchards of southern pines properly treated would produce some cones at least during the second five years after their establishment. Although the overall production of cones during the first 10 years will probably be somewhat heavier in grafted orchards, without substantiating data it is only possible to theorize that, after this period, cone production should be similar in orchards of both types.

¹⁾ Unpublished data from University of Florida.

Converting a Progeny Test to a Seedling Orchard

Slash and loblolly pine clonal orchards are established in the South with as few as 20 clones to well over 100 clones per orchard. Using a moderate figure, perhaps 40-50 selections would be a satisfactory number of parents for a seedling orchard. No progeny tests available to the author involving this number of parents are established and developed to a stage suitable for conversion to a seedling orchard. However, for purpose of this discussion, a small test established on the school forest of the University of Florida has been chosen. This study illustrates the procedures involved and demonstrates the practicability of the technique even though only a few progenies are included and the parents were not highly selected.

The planting discussed here included crosses and self-pollinations among slash pines selected for apparent vigor, open-pollinated lots from the same and other trees, and a control lot obtained from the Florida Forest Service from seed used in their regular nursery program. Considering each lot individually, there were 15 progeny groups in total. Nine replications of 16-plot blocks were established, each replication consisting of one 4-tree plot of each progeny group and two plots of control seedlings. Significant differences among lots in height growth and other characteristics have been previously reported (PETERS and GONDARD, 1961).

The trees in this study are now in their eighth growing season. As indicated in *Figure 1*, the trees originally planted at a spacing of 6 x 6 feet are well advanced into crown competition and lower limbs are already dead. Although a few cones have already been produced in this planting, satisfactory quantities cannot be anticipated without thinning. Thus, if substantial cone production is desired in as short a period as possible, the stage has been reached in this test at which conversion to an orchard should be started.

All trees were remeasured in June, 1963 — mean heights are given in *Table 1*. There have been slight shifts in ranking based on total heights since fifth year measurements, but no lots that would be rejected on the basis of the earlier measurement would be retained on the basis of present means. The low mean heights of lots L and M which are



Figure 1. — Slash pine progeny test planting on the school forest of the University of Florida illustrating the effects of crown competition in the eighth growing season.

Table 1. — Mean height at 8 years and relative ranking of 15 slash pine progenies.

Lot	Rank	Mean Ht. (ft.)
F	1	19.90
H	2	19.37
D	3	18.34
G	4	18.15
E	5	17.99
K	6	17.51
I	7	17.45
P	8	16.80
J	9	16.36
O	10	16.28
A	11	16.19
C	12	15.64
B	13	15.32
L	14	9.50
M	15	8.18

self-pollinated progenies exaggerate the differences. However, differences nearly as large as this have been observed between cross pollinated progenies in other studies.

Although the progenies included in this study are of mixed nature, for purpose of this discussion all were considered as if they were one-parent progenies. To determine which lines should be entirely removed, the mean performance of the control, Lot C, was used as a guide. All lots with lower or only slightly better mean height than Lot C would be cut. The removal of Lots A, B, C, L and M would reduce stocking from 1210 to 756 trees per acre. Lots O, J and P with nearly significantly better height growth than Lot C would be retained for the present if supplementary unthinned tests were available by which later performance of these lines could be checked.

On each of the remaining plots in each block, only the largest tree would be retained — a removal of 75 per cent of the trees in the better lines. In the occasional case in which no trees in a plot were as large as the block average, all trees in that plot would be removed. Height and diameter measurements of trees in Block II are given in Table 2 with trees to be retained indicated by an x. Trees to be kept in other blocks were selected in a similar man-

Table 2. — Height in feet and d. b. h. in inches of trees in Block II, measured June, 1963.

Lot C		Lot C		Lot G		Lot L	
16.2	11.3	12.0		16.3	x16.3	8.1	8.1
2.3	1.7	1.6		2.3	2.5	1.1	0.9
11.3	14.7	13.2	12.8	13.7	15.8		11.2
1.7	1.8	1.8	2.0	2.1	2.2		1.4
Lot P		Lot K		Lot A		Lot H	
12.2	13.4	14.6	14.8	8.3	16.4	16.7	x19.6
2.0	2.0	2.3	2.6	1.2	2.5	2.4	2.8
12.3	x13.8	x16.7	12.8	17.0	17.6	19.0	
2.0	2.1	2.4	1.9	2.4	3.0	3.2	
Lot E		Lot F		Lot D		Lot O	
11.7	10.5	x17.7		19.5	18.2	x18.0	16.0
1.2	1.4	2.6		2.7	2.7	3.2	1.9
x14.6	13.8	16.1			x20.3	17.9	13.7
2.6	2.0	2.4			3.1	2.5	1.3
Lot B		Lot I		Lot M		Lot J	
17.4	16.0	20.1	14.6	8.2	16.5		14.0
2.4	2.7	2.0	2.4	0.7	2.1		2.0
18.6	18.1	21.8	x23.0	7.3	3.0	x15.9	13.0
2.9	2.7	3.0	3.4	0.7		2.5	1.7

ner. Both within line and between line selection in this example served to reduce stocking to 189 trees per acre, an average spacing of approximately 15 feet between trees. Approximately 15 per cent of the original stand would be retained. The average height of remaining trees would be 20.50 feet in contrast to the mean height of 15.64 feet for controls, a 28 per cent increase. The plot arrangement and distribution of the trees selected for retention are shown in Figures 2 and 3. It may be noted that, because of random assignment of lots to block locations, two trees of the same line are occasionally in close proximity to one another, for example, trees of line H in blocks 1 and 3. To avoid inbreeding it would be desirable to eliminate the poorer individual in such cases.

A very drastic thinning applied in this manner would allow the remaining trees to develop nearly as open grown for several years. During this period the application of fertilizer and cultivation should aid in the production of appreciable cone crops. After five or more years a second thinning would likely prove advisable. At that time remaining trees in families of borderline desirability might be removed along with other individuals that do not maintain adequate growth or quality. If 40 or more highly selected parents were used initially, sufficient genetic diversity would be maintained with only half of the families retained after the second thinning. With the necessity of very early thinning, no doubt an occasional family will be eliminated because of poor initial performance which would have proven desirable on the basis of later development. Errors of the opposite type, i. e., retention of inadequate families, can be corrected in the second or later thinnings.

The purpose of this discussion of thinning for seedling orchard establishment on the basis of total tree height is simply to illustrate with actual data a method of choosing the best trees in a test planting and retaining a fairly adequate distribution of trees over the test area. Other selection criteria could, of course, be employed if desired. A more complete evaluation of each tree, such as grading methods used in original selections, could be employed. The best tree in each plot could be selected on the basis of some composite evaluation. Nor is the method restricted to the 4-tree plot employed in this study. A test using, for example, 10-tree row plots could be used. After removal of entire lines of less than acceptable average performance, the best single tree in each half of each remaining plot could be retained — thus keeping the better 20% of the better families. If original spacing were 6 × 6 feet, the two trees retained in each plot would be 6-56 feet apart. To avoid inbreeding it would be desirable to eliminate one tree in cases where the two were less than 30 feet apart. This would serve to increase selection intensity but probably over 100 fairly well distributed trees per acre would be retained. The seedling orchard can be expanded to any size desired by adding replications of the basic block which includes all progeny groups, assuming that sufficient seedlings are available.

Summary

The seedling seed orchard offers a method of mass production of improved seed, the genetic gain from which should be at least equivalent to that of a clonal orchard from the same parental stock. Seedling orchards adopted from progeny tests are especially applicable to the expansion of previously established clonal orchards. The conversion of a progeny test into a seedling orchard was illustrated with a test planting of slash pine involving 15

	I	III	V	VII
	A A P P J J M M	G G A A I I D D	C C J J C C G G	F F E E G G L L
	A A P P J J M M	G G A A I I D D	C C J J C C G G	F F E E G G L L
	O O L L E E C C	C C C C B B P P	P P O O A A E E	C C I I C C H H
	O O L L E E C C	C C C C B B P P	P P O O A A E E	C C I I C C H H
	I I C C D D G G	F F K K J J L L	D D B B M M K K	D D B B A A K K
	I I C C D D G G	F F K K J J L L	D D B B M M K K	D D B B A A K K
	B B K K F F H H	H H M M E E O O	I I M M F F H H	O O M M P P J J
	B B K K F F H H	H H M M E E O O	I I M M F F H H	O O M M P P J J
II	C C C C G G L L	B B C C J J H H	C C C C F F J J	I I K K L L J J
	C C C C G G L L	B B C C J J H H	C C C C F F J J	I I K K L L J J
	P P K K A A H H	L L D D E E F F	D D K K H H P P	C C C C B B H H
	P P K K A A H H	L L D D E E F F	D D K K H H P P	C C C C B B H H
	E E F F D D O O	C C O O I I K K	B B E E L L I I	F F D D P P G G
	E E F F D D O O	C C O O I I K K	B B E E L L I I	F F D D P P G G
IX	B B I I M M J J	A A P P G G M M	M M A A G G O O	A A O O M M E E
	B B I I M M J J	A A P P G G M M	M M A A G G O O	A A O O M M E E
	E E L L K K H H	C C P P C C O O	I I J J A A B B	G G D D M M F F
	E E L L K K H H	C C P P C C O O	I I J J A A B B	G G D D M M F F

Figure 2. — Arrangement of 15 progeny groups in 9 replications at time of test establishment in 1956. Each letter represents an individual tree. Check lot "C" is represented by duplicate plots in each block.

	I	III	V	VII
	P J	G D	J G	F E
		I		G
	E		P O	I H
	D G	K P	E K	D K
	I	F J	D I	O P
	K H	E O	F H	J
	F	H		
II	G		J	I
		J H	F	K J
	H	D E F	K H P	H
	P K	O K	D	G
	F	I	E I	F D P
	O	P	G O	O E
E				
	I J	G		
IX	E	P O	I J	F
	K H		G D	

Figure 3. — The arrangement of the test planting as it would appear after between and within family (progeny group) selection in 1963.

seed lots. Using tree height at 8 years as a selection criterion, all trees in lines with poor mean height growth and 75 per cent of the trees in better lines were rejected. By this procedure the original stocking of 1210 trees per acre would be reduced to 189 trees per acre. — 15 per cent of the original stand. The mean height of trees retained was 20.05 feet in comparison to 15.64 feet for a control lot. Some of the trees have already produced a few cones. Very thoroughly released in this manner, the trees should very rapidly increase their rate of cone production if fertilizer and other cultural treatments are applied.

Résumé

Titre de l'article: *Répartition des arbres dans un verger à graines de semis à la suite d'une sélection entre et à l'intérieur des familles.*

Le verger à graines de semis constitue une méthode de production en masse de graines améliorées, dont le gain génétique devrait être au moins équivalent à celui d'un verger de clones obtenu à partir des mêmes parents. Les vergers de semis constitués à partir des tests de descendance permettent en particulier de franchir une deuxième

étape après les vergers de clones. La conversion d'un test de descendance en un verger de semis a été illustrée par une plantation comparative de *Pinus elliotii* comportant 15 lots de graines. En prenant comme critère de sélection la hauteur des arbres à l'âge de 8 ans, on a éliminé tous les arbres des familles dont la croissance en hauteur moyenne était faible et 75% des arbres des meilleures familles. En procédant de cette manière, on réduirait le nombre primitif d'arbres à l'acre de 1210 à 189, soit 15% du peuplement primitif. La hauteur moyenne des arbres conservés était de 20,05 pieds (env. 6 m) pour 15,64 pieds (env. 4,75 m) dans un lot témoin. Certains arbres ont déjà produit quelques cônes. Si l'on dégage bien les arbres de cette manière, leur production de cônes doit augmenter très rapidement après application d'engrais et autres traitement culturaux.

Zusammenfassung

Titel der Arbeit: *Baumverteilung in einer Sämlings-Samenplantage nach Auslese zwischen und in Familien.*

Die Sämlings-Samenplantage stellt eine Methode der Massenerzeugung züchterisch verbesserten Saatguts dar, deren Züchtungsfortschritt dem einer Klonsamenplantage vom gleichen Elternmaterial zumindest gleich sein sollte. Sämlings-Samenplantagen aus Nachkommenschaftsprüfungen eignen sich besonders zur Erweiterung früher angelegter Klonsamenplantagen. Die Überführung einer Nachkommenschaftsprüfung in eine Sämlings-Samenplantage wird an einer Versuchsfläche mit 15 Sorten von *Pinus elliotii* erläutert. Als Auslesekriterium diente die Baumhöhe im Alter von 8 Jahren. In Sorten mit geringem middle-

rem Höhenwachstum wurden alle Bäume, in den besseren Sorten 75% der Bäume verworfen. Durch diese Maßnahme wäre die ursprüngliche Bestockung von 1210 Bäumen pro acre (2990 Bäumen pro ha) verringert auf 189 Bäume pro acre (465 Bäume pro ha) oder etwa 15% des ursprünglichen Bestandes. Die Mittelhöhe der beibehaltenen Bäume war 20,05 Fuß (etwa 6 m) im Vergleich zu 15,64 Fuß (4,75 m) für eine Kontrollsorte. Einige Bäume haben schon einige Zapfen getragen. Nachdem die Bäume auf diese Weise völlig freigestellt sind, sollten sie bei Anwendung von Düngung und anderen Kulturmaßnahmen sehr schnell ihre Zapfenproduktion erhöhen.

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Flowering Age of Clonal and Seedling Trees as a Factor in Choice of Breeding System

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A scion collected from an old tree and grafted on a young seedling often continues to behave as if it were still a part of the old tree. This phenomenon, known as "topophysis" has been studied intensively by MUCKADELL (1959) in Denmark. It includes such things as continued prostrate growth habit on the part of cuttings taken from the lower branches of some trees, continued thornlessness of grafts made from thornless branches of a thorny tree, early or late leaf fall according to whether scion wood is taken from leaf-dropping or leaf-retaining portions of a tree crown, and persistent growth-rate differences of root-cuttings taken from various portions of a tree crown.

Topophysis also includes the ability of a scion taken from the upper, fruiting portion of a tree crown to continue flowering after being grafted on a young rootstock. This precociousness on the part of grafted trees is a very useful property to tree breeders because it permits the assemblage of flowering material of many scattered clones in a compact breeding arboretum where control-pollination is convenient. It also hastens the time at which seed orchards can be brought into commercial seed-bearing.

The amount by which grafting hastens flower production varies considerably. Seedlings of some northern species do not flower much before their 40th year whereas grafts may bear commercial quantities of seed by the 10th to 15th

year. At the other extreme are forest trees which reach sexual maturity before their 5th year and in which recourse to grafting might slow down seed production. Also, there are trees in which flower production seems to be controlled by general vigor and in which grafting has the same effect as would cultivation or fertilization.

The importance to be placed on early fruiting also varies. Breeders working with very late-blooming species may set early seed harvest as their primary goal. They are justified in ignoring cost and genetic gain considerations. On the other hand, a breeder may wish to achieve the greatest possible genetic improvement over a period of time such as 50 years. In doing so he may consider age of fruiting as less important than heritability or cost.

The present paper is a brief summary of available knowledge on the flowering ages of clones and seedlings, and of the use of such data when choosing a breeding system.

Experimental Evidence on Age of Flowering

Pine (Pinus)

RIGHTER (1939) compiled a list of minimum flowering ages for 57 pine species or varieties propagated by seed at the Institute of Forest Genetics in California. The minimum