Crown Character Differences Between Well-pruned and Poorly-pruned Virginia Pine Trees and Their Progeny[1])

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Introduction

Virginia pine (Pinus virginiana Mill.) is now being utilized with greater frequency throughout its commercial range because of its desirable wood properties, its natural regeneration potential, rapid growth rates, and high yield per hectare on average and marginal sites. In Virginia, it comprises approximately 28% of the softwood growing stock (Sternitzke and Nelson, 1970) and nearly 41% of the total softwood acreage in the state (Knight and McClure, 1967).

Several southern state agencies and industrial concerns are actively engaged in selection programs for superior phenotypes and are establishing P. virginiana clonal seed orchards. Despite these applied improvement programs, only studies by Genys (1966) and Evans (1971) have been directed toward analysis of the genetic variability in P. virginiana.

P. virginiana generally exhibits the undesirable characteristic of retaining dead branches the entire length of its stem for long periods of time. This characteristic limits its use as a major sawtimber species (Fibldng, 1960) and increases harvest costs for pulpwood (Zobel and Haught, 1962; Ehrenberg, 1970).

Naturally occurring well-pruned P. virginiana have been found growing in proximity to poorly-pruned individuals. Because of uniform environmental conditions under which these trees occurred, Bramlett[3]) suggested the pruning phenomenon is under some degree of genetic control.

The objectives of this study were to: (1) determine if significant crown differences exist between progeny from well-pruned and poorly-pruned parent trees and (2) to determine the degree of genetic control of crown characteristics. A secondary objective was to quantify dead branch differences among the well-pruned and poorly-pruned parent trees.

Literature Review

Natural Pruning Ability

Published studies report pruning ability to be under genetic control (Ehrenberg, 1970). Barber (1964) estimated narrow sense heritability for self-pruning in slash pine (Pinus elliottii Engelm.) to range from .36 to .64. Inherent variation of pruning ability has also been reported for European larch (Larix decidua L.) (Vyskot, 1966) and for eastern cottonwood (Populus deltoides) (Wilcox and Farmer, 1967). Vezina and Paille (1967) attempted to assess natural pruning in black spruce (Picea mariana Mill.) and balsam fir (*Abies* balsamea (L.) Mill.) by multiple regression analysis of stand and crown variables. Their results indicated this approach to be of little value. Chang (1962) discussed natural pruning ability of P. virginiana in terms of stand density, but his observations did not indicate any hastening of natural branch removal even at dense spacing.

Crown *Characteristics*

Several investigations of branching traits of gymnosperms have been completed in the past few years. Particular interest has been directed toward the interrelations among crown traits and relations between crown traits and economically important stem characteristics. Crown development has been manipulated by the silvicultural technique of spacing. Future demand for increased quantity and quality of wood fiber may not be accommomodated by this technique exclusively, but rather by the concerted efforts of both cultural and breeding programs.

Most branching characteristics have been found to be under moderate to strong genetic control (Barber, 1964; Ehreberg, 1963; Strickland and Goddard, 1965; and Trousdell et al., 1965). The only crown trait heritability values published on P. virginiana have been calculated on two-year-old half-sib progeny (Evans, 1971).

The "ideal" tree exhibiting a well formed crown is characterized by short, small diameter, flat angle branches and low branch frequency. These traits have been studied in relationship to growth rates (Ehrenberg, 1963; Holst and Teich, 1969), stem volume (Campbell, 1963) and multinodal growth (Tepper, 1963). Observations have also been made on the influence of branching traits on anatomical stem characteristics of loblolly pine (P. taeda) (Zobel and Haught, 1962) and the influence of these traits on gum yields of P. elliottii (Gansel, 1966).

Materials and Methods

Parent Trec Selection *and* Progeny Outplanting

Forty-eight P. virginiana trees representing well-pruned and poorly-pruned populations were selected in natural stands on the Lee Experimental Forest during the winter of 1962—1963. The Lee Experimental Forest is approximately 1,090 hectares in size and is located in Buckingham County, Virginia. To minimize environmental differences between well-pruned and poorly-pruned populations, the selection procedure used involved selection of a well-pruned individual (a rare occurance in stands used for selection) and a poorly-pruned individual within the same stand. Selected trees were similar in diameter, height, and age but varied in the number and size of dead branches. Table 1 lists the characteristics analyzed in parent trees. Branch measurements were made between a stem height of 2.22M and 5.27M to avoid branches that may have been broken by early grazing (in some stands) and to avoid inclusion of any live branches. All branches measured within this interval were dead and in varying states of decay. Branch angles were measured from individual tree photographs.

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Table 1. — Crown means of well-pruned and poorly-pruned *P. virginiana* parent trees and statistical comparisons between means.

Character	Poorly-Pruned parents			Well-Pruned parents			Statistical Significance[1])
	N	$\bar{X}$	SE	N	$\bar{X}$	SE	
D.B.H. (cm)	15	20.85	±0.61	15	19.53	±0.74	ns
Age (years)	15	35.80	±1.12	15	36.20	±1.17	ns
Height (meters)	15	16.91	±0.37	15	18.10	±0.39	*
Branch number	15	40.53	±1.28	15	29.20	±1.92	**
Branch diameter (cm)	15	1.98	±0.08	15	1.24	±0.05	**
Branch angle (degrees)	15	60.56	±1.89	15	61.81	±2.00	ns

[1]) ns = not significant
* = significant at 5 percent level of probability
** = significant at 1 percent level of probability

Seed of open-pollinated origin were collected from the parent trees in September, 1963 and sown in May, 1964, in nursery beds located on the Lee Experimental Forest. Two progeny outplantings were established in May, 1965. The outplanting used here was a completely randomized design containing progeny from fifteen pairs of selected trees. Absent selected trees were not represented in the outplanting because of problems associated with seed yield and seedling survival in the nursery. Seedlings were planted at an 8 × 8 foot spacing.

Measurements of Progeny Crown Characteristics

Measurements of progeny crown characteristics were taken during the winter of 1971—1972 to determine if significant branch habit differences could be detected between the poorly- and well-pruned progeny groups. Branch traits measured were:

1. Branch diameter (Measurements were taken 0.65 cm. from the point of branch attachment and recorded to the nearest 0.025 cm. Branches smaller than 0.65 cm. in diameter were excluded.)
2. Branch angle (angle to the nearest degree) from the vertical axis of the stem to the lateral branch.
3. Number of branches.
4. Number of nodes (node defined as point of attachment of one or more branches).
5. Number of branches per node (number of branches/number of nodes).

Branch traits were measured for the 1968 growth; all branches within this growth interval were alive. This portion of the crown appeared to exhibit an intermediate form relative to upper crown branches (Snyder, 1961). Trees exhibiting deformities such as stunted growth, basal forking, or other anomalies resulting from obvious environmental conditions were not measured.

Statistical Analysis

Parent tree measurements were analyzed using a simple one-way analysis of variance. Crown trait means for individual progeny were analyzed by a two-level pure model II nested analysis of variance (Sokal and Rolf, 1969) to test for significant differences between the well-pruned and poorly- pruned progeny groups. The model employed in the analysis was:

$$Y_{ijk} = \mu + A_i + B_{ij} + E_{ijk}$$

where μ = parametric mean of population.
A_i = random contribution of the poorly-pruned and well-pruned groups; i = 1, 2.
B_{ij} = random contribution among families within groups; j = 1, 2, 3, ... 15.
E_{ijk} = error; k = 1, 2, 3, ... 10.
Y_{ijk} = crown measurement of the kth tree within the jth family of the ith treatment.

Correlation coefficients for measured traits were calculated using mean individual tree values and were calculated using data from both the well-pruned and poorly-pruned groups.

Genetic evaluation of calculated variance components for each trait was made using data from progeny derived from both well-pruned and poorly-pruned trees. A one-way analysis of variance was employed for estimation of genetic parameters (Becker, 1967). The model used in the analysis was:

$$Y_{ij} = \mu + A_i + E_{ij}$$

where μ = parametric mean of population.
A_i = random effects of families; i = 1, 2, 3, ... n.
E_{ij} = Error; j = 1, 2, 3, ... 10.
Y_{ij} = crown measurement of the jth tree within the ith family.

The assumptions listed by Stonecypher (1966) were made when estimating the genetic components of variance. For characters demonstrating significant among family differences (as judged by the F test), narrow sense heritability values and standard errors for individual progeny crown traits were calculated by the formula:

$$h^2 = \frac{4\,\sigma^2_F}{\sigma^2_F + \sigma^2_W} \pm \frac{4\sqrt{2(N-1)\,(1-t^2)\,[1+(k-1)t]^2}}{(\frac{1}{F})^2\,(N-F)\,(F-1)\,(\frac{N-\sum n_i^2}{N})}$$

(Becker, 1967)

where σ^2_F = among family variation.
σ^2_W = within family variation.
N = number of progeny analyzed.
n_i = number of progeny in each family (i).
F = number of families analyzed.
t = intraclass correlation.

Corresponding genotypic correlations were calculated by means of a nested analysis of covariance (Becker, 1967) as follows:

$$r_g = 4\,cov_F \,/\, \sqrt{[4\,\sigma^2_{F(x)}] \cdot [4\,\sigma^2_{F(y)}]}$$

where cov_F = family covariance for individual traits.
$\sigma^2_{F(x)}$ = family variance for trait x.
$\sigma^2_{F(y)}$ = family variance for trait y.

Results

Parent Tree Measurements

Mean values and statistical comparisons for poorly-pruned and well-pruned trees are listed in *Table 1*. Dia-

meter at breast height and age variables were not significantly different between parent groups but the well-pruned parent trees were significantly greater in height than the poorly-pruned parent trees. The poorly-pruned trees had a significantly greater number of dead branches and larger branch diameters than the well-pruned trees. Branch angle was not significantly different between the well-pruned and poorly-pruned select trees.

Progeny Measurements

Branch character comparisons among progeny derived from the well-pruned and poorly-pruned trees are listed in *Table 2*. Branch length was significantly greater in the progeny derived from the poorly-pruned parent trees than in progeny from the well-pruned parent trees. Average branch diameter was larger for the progeny derived from poorly-pruned trees; however the difference was not statistically significant at the 5% level of probability. No other crown characteristics were found to differ significantly between progeny of the well-pruned and poorly-pruned groups.

Heritability values (narrow sense), listed in *Table 3*, are similar to those reported by SCHRUM and GERHOLD (1969), HATTEMER (1963), STRICKLAND and GODDARD (1965) and EHRENBERG (1963). Of the eight crown traits measured, most had moderate to high heritability values. Number of branches per node was the only variable showing nonsignificant among family differences.

The phenotypic correlations among crown characteristics of progeny from both groups are listed in *Table 4*. The negative correlations of branch angle with branch diameter and length were highly significant. Branch diameter was observed to be significantly correlated with branch length. These particular crown trait relationships have been previously reported for other species by BARBER (1964), CAMPBELL (1961), and STRICKLAND and GODDARD (1965). Branch angle was found to be significantly correlated with number of branches per node and number of nodes. Branch length and diameter were not found to be correlated with number of branches, number of branches per node or number of nodes. Number of branches per node, number of nodes and number of branches were all significantly correlated with one another with the exception of number of nodes × number of branches per node.

Comparisons of phenotypic and genotypic correlations are listed in *Table 4*. Calculated genotypic correlations of 1.03 and 1.00 for branch angle × number of branches and number of branches × number of nodes respectively indicate that sample size or assumptions were inappropriate for these two calculations.

Table 2. — Mean values of crown characteristics of progeny derived from well-pruned and poorly-pruned *P. virginiana* parents and statistical comparisons between means.

Character	Poorly-pruned progeny			Well-pruned progeny			Statistical Significance[1])
	N	$\bar{X}$	SE	N	$\bar{X}$	SE	
Branch angle (degrees)	145	63.53	±0.53	143	62.99	±0.54	ns
Branch diameter (cm)	145	1.73	±0.03	143	1.65	±0.03	$.1 > P > .05$
Branch length (meters)	145	1.45	±0.02	143	1.38	±0.02	$0.05 > P > 0.01$
Number of branches	145	12.26	±0.32	143	12.12	±0.33	ns
Number of branches per node	145	3.14	±0.05	143	3.05	±0.06	ns
Number of nodes	145	3.90	±0.08	143	3.98	±0.09	ns

[1]) ns = not significant

Table 3. — Heritability values of crown characteristics in progeny derived from well-pruned and poorly-pruned *P. virginiana* parent trees.

Character	h^2	Std. Error
Branch angle	0.75	±0.24
Branch diameter	0.29	±0.17
Branch length	0.42	±0.20
Number of branches	0.21	±0.16
Number of branches per node	[a]—	—
Number of nodes	0.32	±0.18

[a] Heritability values not calculated because of nonsignificant variation among families.

Discussion

Parent Tree Measurements

Genetic control of natural pruning ability can only be inferred from the significantly different crown characteristics of the poorly- and well-pruned parent populations *(Table 1)*. Analyses of tree crown characteristics indicated that the observed pruning phenomenon of the two select populations was not influenced exclusively by environmental factors. If branch size is correlated with pruning ability, the possibility of breeding *P. virginiana* for small branch diameters may be feasible since the heritability value of this trait was observed to be moderate ($h^2 = 0.29$; *Table 3)*. The well-pruned parent group was observed to have significantly greater height and a statistically significant smaller number of dead branches than the poorly-pruned trees. Well-pruned trees had a tendency toward small diameter branches indicating that well-pruned trees may distribute proportionately more photosynthate into the stem than the poorly-pruned trees.

Progeny Measurements

Branch length was the only crown characteristic found to be significantly different between the progeny groups *(Table 2)*. The small branch diameter differences between progeny derived from the poorly- and well-pruned trees suggests that branch diameter may be an important crown trait involved in natural pruning. Failure to detect additional crown trait differences between progeny groups may be attributed to the following factors:

1. No biological differences existed.
2. Inefficiency of the experimental design.
3. Juvenility of material measured.

GODDARD *et al.* (1959) and WOESSNER (1965) considered the above factors as influential in progeny test evaluations.

Heritability values listed in *Table 3* provide evidence that most crown traits are under moderate to strong ge-

Table 4. — Phenotypic and genotypic crown characteristic correlations of progeny (n = 288) derived from well-pruned and poorly-pruned *P. virginiana* parent trees.[1])

		Branch Diameter	Branch Length	Number of Branches	Number of branches per node	Number of nodes
Branch angle	P	—0.28**	—0.26**	0.25**	0.25**	0.13*
	G	—0.42	—0.27	1.03	—b	0.89
Branch diameter	P		0.83**	0.03 ns	0.03 ns	0.03 ns
	G		0.59	—0.82	—b	—0.41
Branch length	P			—0.02 ns	0.03 ns	—0.03 ns
	G			—0.51	—b	—0.39
Number of branches	P				0.59**	0.79**
	G				—b	1.00
Number of branches per node	P					—0.01 ns
	G					—b

[1]) P = phenotypic correlations
G = genotypic correlations

** = significant at .01 level of probability
* = significant at .05 level of probability
ns = not significant
b = correlation not calculated because of nonsignificant among family differences and negative variance component.

netic control, indicating that it is feasible to genetically modify crown traits of *P. virginiana*. Phenotypic and genetic correlations *(Table 4)* suggest that a successful selection program for developing *P. virginiana* with flat angled, short and small diameter branches is possible. This particular breeding scheme has been recommended by Strickland and Goddard (1965) and Ehrenberg (1970). Although selection for small diameter branches may be accompanied by increases in number of branches, number of nodes and number of branches per node, pruning ability may be enhanced by breeding for many small diameter branches as durable branch heartwood would be kept to a minimum. Fungal decay of suppressed branches may therefore be accelerated.

Abstract

Fifteen pairs of well-pruned and poorly-pruned mature *Pinus virginiana* (Mill.) trees were selected in 1962 on the Lee Experimental Forest near Buckingham, Virginia. The two populations were selected on the basis of dead branch retention. Crown trait comparisons of dead branches of the tow select populations revealed that branch number and diameter were significantly greater for the poorly-pruned trees than for the well-pruned trees.

Live branch length was observed to be significantly greater in progeny derived from the poorly-pruned parents than the well-pruned parents. Number of live branches, number of nodes and number of branches per node were not found to be significantly different between progeny from the well-pruned and poorly-pruned select trees. A strong degree of genetic control was observed for branch angle and branch length. Branch diameter, number of branches and number of branch nodes exhibited moderate heritability values. Phenotypic and genotypic correlations among crown traits were also calculated.

Key words: Pinus virginiana (Mill.), heritability, crown characters, pruning.

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Extractive contents and fungal degradation of branches from well-pruned and poorly-pruned mature Virginia pine[1])

A Note

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Introduction

Natural pruning ability of forest tree species has generally been considered a function of stand density (SMITH, 1962). Canopy development of full-stocked stands gradually decreases levels of solar energy needed to support the photosynthetic activity of lower crown branches causing their gradual suppression and ultimate death. Dead and dying branches are subsequently attacked by fungal agents weakening their attachment to the tree bole. The structurally-weakened branches are then sloughed from the stem by gravitational and wind forces.

The retention time of branches after death may be influenced by branch diameter or by qualitative and/or quantitative antifungal extractive elements within the branch tissue. Fungal agents probably require longer time intervals to structurally weaken large diameter branches than small branches. The fungitoxic capacity of extractive elements or specific chemical compounds contained in branchwood extractives may be additional factors responsible for natural pruning characteristics. If chemical properties of branch extractives and branch size are indeed important factors related to natural pruning ability, elucidation of the genetic control of these characters would be important for genetic improvement of selected forest tree species. Investigation of pruning in terms of retained dead branch susceptibility to wood decaying fungi, although implied in the literature (CHANG, 1962; SLOCUM and MILLER, 1953), has not been previously considered.

Pinus virginiana (MILL.) normally exhibits poor natural pruning characteristics even in densely stocked stands. Retention of dead branches for extended periods has been attributed to the large amounts of durable branch heartwood (SLOCUM and MILLER, 1953). Presumably, the chemical components in the wood complemented by branch size provides resistance to fungal degration.

Genetic variation for natural pruning in *P. virginiana* was found on the Lee Experimental Forest[3]) by BAILEY *et al.* (1974). Adjacent well-pruned and poorly-pruned mature *P. virginiana* were observed growing (under similar environmental conditions) at various locations on the forest.

The primary objectives of this study were to compare rates of fungal degradation of dead retained branches from the two selected populations and to compare the percentage and phenolic composition of ethanol-benzene extractives in dead branches of the two select populations.

Literature Review

Natural Wood Durability

Wood durability of living and harvested timber is of considerable interest to plant pathologists. Research has focused primarily on host-saprophyte- and -parasite relationships involved in natural fungal inoculation and rates of cellulolytic degradation (HART and HILLIS, 1972; HANOVER and HOFF, 1966; JORGENSEN, 1961; LI *et al.*, 1969; LOWMAN, 1970 a; LOWMAN, 1970 b; RUDMAN, 1963; and SHRIMPTON and WHITNEY, 1968). Due to the unique chemical composition of pine extractives (MIROV, 1961) a substantial amount of research has been attempted to determine the importance of these extractives as factors responsible for natural resistance to wood decay (JORGENSEN, 1961; LOWMAN, 1970 b; SHRIMPTON and WHITNEY, 1968; and THIELGES, 1968).

Much of the research attempting to determine the fungitoxic effects of extractives employ *in vitro* procedures. RUDMAN (1962, 1963) believes erroneous results may be obtained from such techniques and the use of natural substrates in their original form provides results more comparable to natural conditions. Extrapolation of *in vitro* techniques may be complicated by antagonistic or synergistic effects of host extractive compounds (LI *et al.*, 1969; LI *et al.*, 1972). Despite the complexities encountered when assessing the inhibitory effects of extractives on fungal growth by *in vitro* techniques, such methods do provide valuable information concerning the possible mechanisms responsible for maintaining wood integrity.

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