Genetic Variability of Photosynthetic Efficiency and Dry-Matter Accumulation in Seedling Douglas-Fir

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Introduction

DECKER (1953), RICHARDSON (1960), and KOZLOWSKI (1963) have suggested that strains of forest trees with superior growth can be built by selecting parent trees on the basis of relative photosynthetic capability. DECKER's idea presupposes that a tree increases in dry matter (accumulates carbon) directly as photosynthesis exceeds respiration, and accordingly, that a tree with superior photosynthetic capability would have superior capacity to utilize its growing space for wood production. HUBER (1950) has adapted and used the infra-red gas analyzer to provide a rapid and inexpensive method for measüring photosynthetic rate. This makes selection for photosynthetic capability economically possible, but breeding feasibility also depends on the trait's genetic structure. Relative amounts of genetic and environmental variance, relative importance of the contribution of types of gene action to genetic variance, and relation of photosynthesis to growth will dictate, in large part, the breeding scheme to be used, and its practicability.

In forest tree species, genetic variability has been demonstrated for two basically different measures of photosynthetic capability. One measure estimates relative photosynthetic efficiency of nesdle tissue (P.E.) by determining CO_2 absorbed per unit leaf weight, volume, or surface area, per unit time. The other estimates relative photosynthetic capacity (P.C.) of an entire plant by determining CO, absorbed per plant per unit time. Both are measures of net photosynthesis (rate of gross photosynthesis minus rate of respiration).

Genetic variability in P.E. has been shown among 16 clones of Populus (HUBER and POLSTER 1955). Most clones represented separate species and their hybrids within the sections Aigeiros and *Tacamahaca*. However, in two comparisons, differences were also shown among clones representing varieties within species.

Slight racial variability in P.E. has been reported in *Pinus* strobus (BORDEAU 1963) and in Douglas-fir (KRUEGER 1933) (SORENSEN 1964). Differences did not show up as main effects, but appeared in the interaction of races with measurement temperatures (BORDEAU, SORENSEN), or with premeasurement temperatures and seedling age (SORENSEN). Loblolly pine seedlings from Georgia source had higher P.C. than seedlings from Florida, but differences were caused by greater amounts of foliage on Georgia seedlings (MCGREGOR, et al., 1961); within-species variability in P.E. was not discovered. REINES (1962) and WYATT and BEERS (1964) demonstrated significant ~differencesin P.C. among seedling families in slash pine. REINES concluded that both relative efficiency of needles and amount of functional green tissue per plant may have contributed to variability.

The genetic relationship between photosynthetic efficiency and plant growth is not clear. WATSON (1952), after an extensive review of crop-plant literature, concluded that yield is primarily increased by enlarged photosynthetic surface rather than by increased P.E. The works of MCGREGOR et al. (1961) and SORENSEN (1964) support WATSON'S conclusions. MCGREGOR et al. reportsd a strong correlation of seedling size with P.C., but concluded that the correlation results because larger seedlings have more foliage. SORENSEN could find no association between average P.E. of Douglas-fir races and dry-matter accumulation. On the other hand, HUBER and POLSTER (1955) found that plant size was strongly correlated to both P.C. and P.E. (Table 12 b, page 405). The above studies, including those reviewed by WATSON, deal with phenotypic correlations between various measures of photosynthetic capability and yield. LERNER (1958, page 149), FALCONER (1961, page 351), and several others have noted that phenotypic correlation is not necessarily closely related to genetic correlation.

Photosynthetic efficiency, as opposed to photosynthetic capacity, is likely to be of more interest to tree breeders. Photosynthetic capacity can theoretically be increased by improving P.E., by enlarging the photosynthetic factory (foliage), or by doing both. In the latter two cases, branchiness may be expected to increase directly as foliage increases — with detrimental effects on wood quality and growing-space requirements. On the other hand, if P.E. is improved, efficiency with which a tree uses growing space is also improved. This greater efficiency can be utilized to enhance wood production per acre, or to provide higher quality wood at present volumes by minimizing branchiness.

Primary objectives of this study have been: (1) to estimate additive and dominance genetic components of variance for P.E. and total dry weight, and (2) to estimate genetic correlations between P.E. and total dry weight. These estimates are obtained from measurements of full- and half-sib families, which are not available in Douglas-fir of near-rotation age. Consequently, the study is proceeding in two parts. Results of Part I tests on seedling families are reported in this paper. In Part II, results of seedling studies will be correlated with tests of P.E. and growth made on the parent trees.

Materials and Methods

Full- and half-sib families were obtained from crosses made following design B/A (COCKERHAM 1963) which is genetically equivalent to design I by ROBINSON, et al. (1949). Each of ten trees used as a female was crossed to ten trees used as males, all males and females being different trees. Parents were selected randomly from reproductive trees in a young, naturally regenerated, pure stand of Douglas-fir in Pack Demonstration Forest near La Grande, Washington. All parents were located within a circular area of one kilometer diameter on a gravelly, glacial outwash plain.

A 2-replicated simple lattice design (COCHRAN and Cox 1950, page 280) was used. Each family plot consisted of a quart plastic container in which five seeds were sown and, at the time of measurement, every plot contained from one to five seedlings. After seedlings had passed one growing season in the greenhouse and were from 8 to 15 cm high, they were transferred (25 Oct. 1963) in the original con-

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tainers to a controlled environment chamber, where they remained until tests were concluded (23 April 1964). A consistent regime designed to keep seedlings dormant was maintained in the chamber throughout the run. Day and night dry-bulb temperatures were 20° C and 16.5° C, respectively, with corresponding relative humidities of 74 and 76 percent. Sylvania Grolux fluorescent lights provided 1200 foot-candles to seedling crowns for a 10-hour day. Soil moisture was maintained near field capacity.

The experimental design called for measuring two seedlings per replication, from each family plot, making a total of 400 seedlings to be tested from 100 families. The order in which seedlings were to be measured was based on the lattice design. This was necessary to provide for some measure of the bias that could result from the extended period needed to run the complete experiment. Consequently, tests on seedlings were run plot by plot within consecutive blocks, within each replicate of the design. This confounds possible time-of-measurement effects with blocks within replications, thus making time-effects to some extent measurable.

The method used for determining CO_2 absorption was a modification of one described by DECKER (1959). Two average seedlings in each container were chosen for measurement. The crown of one intact potted seedling was sealed in a cylindrical cuvette with modeling clay and maintained at an illumination of 1500 ft-c at 15° C (dry bulb) throughout the measurement period. The cuvette was attached in a 2.065-liter closed system to a BECKMAN Model 15A infrared gas analyzer coupled to an Esterline-Angus, 50-milliampere recorder. The analyzer gave a continuous reading of CO_2 concentration in the system. At the start of each measurement, CO_2 was added to increase CO_2 concentration to between 400 and 500 ppm, and the subsequent decrease of CO_2 in the system was recorded. Decrease was considered to show amounts of CO_2 absorbed by the seedling (net photosynthesis). Rate of CO_2 absorption was computed from the slope of a line drawn tangent to the point on the recorder tracing where the system reached 300 ppm. (See DECKER 1959, Fig. 1, for method). The procedure was repeated immediately for the second of the seedlings chosen for measurement. Following this, fresh and dry weights of needles, and dry weights of stems and roots, separately, were obtained for each seedling. P. E. data were reported as $\mu gmCO_2$ fixed/min/gm dry leaf material.

Two seedlings from each family plot per replication were measured with three exceptions, caused by lack of two measurable seedlings in the plots. Rather than use averaging or missing plot techniques, seven additional families were randomly eliminated from the genetic component analysis. In this way, a balanced statistical design was retained. The design chosen was that of KEMPTHORNE (1957, page 458; see for derivations and computation details). The analysis permits the partition of error into two portions and clearly indicates the source of each. Between- and within-plot variances were analyzed in two steps as given in *Table 1, a and b*. For this study there were $m = 10$ maternal parents each mated to $p = 9$ different sires with $n = 2$ full-sib progeny in each of $r = 2$ replications.

Genetic- and environmental-component estimates are obtained as in *Table 2* by equating observed mean squares to expectations. Assuming no maternal effects, no inbreed-

Table 1. — Variance analysis appropriate to Design B/A.

a. Plot means

Source	d. f.	M. S.	Expectation of Mean Square[1])
Replicates	r-1		
Maternal	(m-1)	M	$\frac{1}{n}\sigma_1^2 + (\sigma_2^2 - \text{Cov FS}) + r\,(\text{Cov FS} - \text{Cov HS}) + rp\,(\text{Cov HS})$
Paternal within maternal	m (p-1)	P	$\frac{1}{n}\sigma_1^2 + (\sigma_2^2 - \text{Cov FS}) + r\,(\text{Cov FS} - \text{Cov HS})$
Maternal-paternal by replicates	(pm-1) (r-1)	I	$\frac{1}{n}\sigma_1^2 + (\sigma_2^2 - \text{Cov FS})$

b. Between and within plots

Source	d. f.	M. S.	Expectation of Mean Square[1])
Between plots	pmr-1		
Within plots	pmr	E	σ_1^2
Total	pmrn		

[1]) Cov FS = Covariance of full sibs

Cov HS = Covariance of half sibs

r = 2, p = 9, m = 10, n = 2

$\sigma_1^2 = \sigma_c^2 + \sigma_G^2 - \text{Cov FS}$

$\sigma_2^2 = \sigma_e^2 + \text{Cov FS}$

Where:

σ_e^2 = portion of error common to all individuals of the same plot — the "plot error" of plot environment and family interaction components.

σ_c^2 = portion of error specific to each individual — the "within-plot" error of environment and interaction components.

σ_G^2 = Genotypic variance of original random mating population.

Table 2. — Components estimated from Table 1.

Component for:[1])	Estimated from Mean Square[1])
σ_1^2	E
Cov HS	$\frac{1}{rp}$ (M-P)
Cov FS - Cov HS	$\frac{1}{r}$ (P-I)
Cov FS	$\frac{1}{r}$ (P-I) + $\frac{1}{rp}$ (M-P)
σ_e^2	$I - \frac{1}{n}$ E
$\sigma_c^2 + \sigma_G^2$	E + $\frac{1}{r}$ (P-I) + $\frac{1}{rp}$ (M-P)

[1]) Symbols as in *Table 1.*

ing, no epistasis, and no linkage effects, the progeny variance among maternal families (Cov HS) estimates ¼ of the additive genetic variance; progeny variance among paternal families (Cov FS − Cov HS) estimates ¼ of the additive genetic variance plus ¼ of the dominance variance. Additive genetic variance, σ_A^2, is thus 4 (Cov HS) and dominance variance, σ_D^2, is 4 (Cov FS − 2 Cov HS).

As KEMPTHORNE points out (1957, page 464), with the analysis used here, two or more measures of narrow-sense heritability are possible because two environmental variances, σ_e^2 and σ_c^2, are estimated. In the present case, two measures of heritability were calculated: one, estimated by $\sigma_A^2/(\sigma_G^2 + \sigma_c^2)$, uses the environmental variance specific to individuals within plots; the other, $\sigma_A^2/(\sigma_G^2 + \sigma_c^2 + \sigma_e^2)$, uses a composite of environmental variance common to individuals in plots plus environmental variance specific to individuals.

Genetic correlation estimates were obtained from components of covariance. Analysis of covariance took exactly the form described above for analyses of variance *(Table 1 a.)*. For traits X and Y, the general equation for genetic correlation is, 4 (component of covariance between X and Y), ÷ $\left[(\sigma_A^2 \text{ for X})\ (\sigma_A^2 \text{ for Y})\right]^{1/2}$.

Results

Interpretation of results is based on mean squares from five analyses of variance *(Table 3)*, each of which was further partitioned into genetic and environmental components *(Table 4)*.

Genetic variability

Additive and dominance genetic coefficients of variation indicate that a moderate amount of genetic variability exists in each of the five traits *(Table 5)*. Additive variance appears as a major contributing source of variability only for P. E.: dominance variance is estimated as being larger than additive variance for all traits (see ratio σ_D^2/σ_A^2 — *Table 5)*.

Variance components from which the above estimates have been derived are not equally reliable. This can be seen by examining results of F tests applied to maternal and paternal mean squares *(Table 3)*. There is little question that

Table 3. — Analysis of variance for five seedling traits in Douglas-fir.

Source	d. f.	Mean squares				
		P. E.	Seedling dry wt.	Dry wt. needles	Dry wt. needles + stem	Fresh wt. needles
Replicates	1	16,986	0.39555	0.01955	0.05927	0.07426
Maternal	9	8,441 (.05)[1])	0.06499 (.20)	0.00403 (.22)	0.00785 (.25)	0.02174 (.40)
Paternal in maternal	80	4,275 (.07)	0.04595 (.05)	0.00297 (.22)	0.00612 (.08)	0.01944 (.22)
Maternal-paternal × replicates	89	3,036	0.03111	0.00254	0.00447	0.01666
Between plots	179	7,877	0.08296	0.00581	0.01136	0.03700
Within Plots	180	893	0.01873	0.00188	0.00342	0.01069
Total	359					

[1]) Probability of sample having larger variance ratio (F) due to chance.

Table 4. — Components of variance for five seedling traits in Douglas-fir.

Parameter[1])	Component estimate				
	P. E.	Seedling dry wt.	Dry wt. needles	Dry wt. needles + stem	Fresh wt. needles
$\sigma_1^2 = \sigma_c^2 + \sigma_G^2$ — Cov FS =	893	0.01873	0.001884	0.00342	0.01069
Cov HS =	231 (203)[2])	0.00106 (.00159)	0.000059 (.000099)	0.000095 (.000193)	0.00013 (.00054)
Cov FS — Cov HS =	619 (201)	0.00742 (.00213)	0.000215 (.000133)	0.000824 (.000290)	0.00142 (.00098)
Cov FS =	851	0.00847	0.000273	0.000920	0.00154
$\sigma_e^2 = \sigma_2^2$ — Cov FS =	2,590	0.02175	0.001602	0.002755	0.01131
$\sigma_c^2 + \sigma_G^2$ =	1,744	0.02720	0.002157	0.004344	0.01223

[1]) Symbols as in *Table 1.*
[2]) Standard error (computed as in SNEDECOR 1956, page 262) in parenthesis pertains to component above.

Table 5. — Estimates of means, dominance and additive genetic variances and their ratios, genetic coefficients of variation, and heritabilities for five seedling traits in Douglas-fir.

Parameter[1])	Traits				
	P. E. (μ gm Co_2/ min/gm dry leaf)	Seedling dry wt. (gms)	Dry wt. needles (gms)	Dry wt. needles + stems (gms)	Fresh wt. needles (gms)
Seedling mean ($\bar{x}$)	168.0	0.6185	0.1608	0.2111	0.3767
$\sigma_A^2 = 4$ (Cov HS)	925.7	0.00423	0.00023	0.00039	0.00050
σ_A	30.4	0.065	0.015	0.020	0.022
$\sigma_A/\bar{x}$	.18	.10	.10	.09	.06
$\sigma_D^2 = 4$ (Cov FS — 2 Cov HS)	1,551.5	0.02543	0.00062	0.00291	0.00517
σ_D	39.4	0.159	0.025	0.054	0.072
$\sigma_D/\bar{x}$	.23	.26	.15	.25	.19
σ_D^2/σ_A^2	1.68	6.01	2.67	7.57	10.33
$h_1^2 = \sigma_A^2/\sigma_c^2 + \sigma_G^2$	.53	.15	.11	.08	.04
$h_2^2 = \sigma_A^2/\sigma_c^2 + \sigma_e^2 + \sigma_G^2$	.21	.09	.06	.05	.02

[1]) σ_A^2 = additive genetic variance.

σ_D^2 = dominance genetic variance.

$\sigma_A/\bar{x}$ = additive genetic coefficient of variation.

$\sigma_D/\bar{x}$ = dominance genetic coefficient of variation.

h_1^2 = narrow-sense heritability where environmental variability is specific to individuals within plots.

h_2^2 = narrow-sense heritability where environmental variability is that of entire experiment.

Other symbols as in *Table 1.*

genetic variance is exhibited in both maternal and paternal components for P. E., and in the paternal components for seedling dry weight and for dry weight of stem plus needles. It is also apparent that the experiment was not large enough to give conclusive evidence either for or against the presence of genetic variance in other traits. In any case, the five traits, which all represent aspects of seedling vigor, are under weak additive genetic control in the environment common to the whole experiment (see h_2^2, *Table 5*); and additive genetic control is moderate to weak even under environmental conditions specific to individuals within quart-sized planting containers (h_1^2, *Table 5*). Both estimates of narrow-sense heritability are higher for P. E. than for other traits, which apparently is an effect of the greater additive genetic variance for P. E.

Environmental Variability

Although P. E. measurements were made from January through March 1964, no consistent effect of this extended measurement period could be shown. Measurements were made according to a simple lattice design with the object of confounding time-of-measurement and block effects. An analysis of P. E. measurement data based on this lattice design had a relative efficiency of 102 percent compared to analysis of the data based on a randomized block design. From this, the conclusion was that there were no block-to-block effects which could be attributed to time of measurement. On the other hand, the two replicates were significantly different in each of the analyses of variance from which genetic components were computed for the individual traits *(Table 3)*. One explanation for this is that the two replicates were kept separate while in the greenhouse by insetting all plots (containers) of each replication into a stainless steel tray. This may have contributed to replication differences by facilitating development of distinctive environments for the replications, particularly in the water regime.

Genetic Correlation

Estimates of genetic correlation are consistently strong and positive among the traits P. E., seedling dry weight,

Table 6. — Analyses of covariance, components of covariance, and genetic correlations among photosynthetic efficiency, total seedling weight, and dry weight needles.

Source	d. f.	Mean Products		
		P. E. × seedling wt.	P. E. × d. wt. needles	Seedling wt. × d. wt needles
Replicates	1	81.9672	18.2256	.0879
Maternal	9	13.7538	1.4105	.0125
Paternal in maternal	80	7.5171	1.1892	.0101
Maternal-paternal × replicates	89	2.3294	0.8261	.0105
Maternal component of covariance		0.3465	0.01230	.00013
Paternal component of covariance		2.5939	0.18154	.00035
Genetic correlations based on:				
maternal components		0.70	1.06	0.53
paternal components		0.35	.50	—0.25

and dry weight of needles. Analyses of covariance, the components derived therefrom, and additive genetic correlations among the traits are presented in *Table 6*. Two estimates of genetic correlation have been made for each trait: one is based on the maternal component and one on the paternal. Each is valid to the extent that the component estimates ¼ of the additive genetic covariance between traits. Since there is considerable evidence for dominance variance in P. E. and seedling dry weight, and dominance is strongly represented in the paternal component, genetic correlations calculated from maternal components are more likely to describe the additive genetic situation in the population studied.

Discussion

Assumptions

Several assumptions have had to be made to permit genetic interpretation of components resulting from analyses of variance. If assumptions are in large part true, interpretation has not been unduly biased and evidence for the following three items has been strengthened: (1) there is a moderate amount of within-population genetic variability in P. E., (2) dominance genetic variance is relatively more important than additive genetic variance, and (3) seedling dry weight and P. E are strongly correlated, genetically. The first and third items afford reasonable evidence that plant dry weight can be improved by selecting for P. E. The second item bears strongly on a choice of mating scheme that would permit the most rapid improvement rate. It therefore seems pertinent to examine the more important assumptions regarding the traits being studied: (1) coupling and repulsion linkage phases are at equilibrium in the parent population, (2) there is no epistasis, (3) there are no maternal effects, and (4) parents and progenies are not inbred.

Linkage

Linkage between genes that condition the expression of a trait affects covariance estimates only when coupling and repulsion phases of linked genes are not in equilibrium. With non-equilibrium, in mating design B/A, contributions of the two phases may be expected to be equivalent and compensating in their effect on the maternal (Cov HS) covariance component. This is not the case for the paternal (Cov FS − Cov HS) component. Here, linkage may be expected to increase covariance, if the linked genes are those that affect vigor or yield (Robinson and Comstock, 1955). Therefore, linkage disequilibrium effects cause paternal genetic components to be overestimated relative to maternal components, in design B/A. This, in turn, causes upward bias in estimates of σ^2_D/σ^2_A. On the other hand, linkages in equilibrium contribute neither to covariance nor to bias unless epistatic variances exist. Random-mating populations that have not resulted from recent mixture of strains are expected to be in equilibrium (Falconer 1961, p. 20). Families studied here resulted from random crossings in a small, naturally regenerated Douglas-fir stand, and linkage disequilibrium bias is therefore not likely to be a factor in the present study.

Epistasis

If epistasis is present, epistatic variance is contained in both maternal and paternal components, as Comstock (1955) has shown. Although epistasis adds to both components, the paternal (Cov FS − Cov HS) component is relatively more affected, in design B/A. This is because additive epistatic effects are more strongly represented, and dominance epistatic effects are exclusively represented, in the paternal variance component. This can be seen in the following partition of covariances by Cockerham (1956), which assumes that parents are not inbred:

$$\text{Cov HS} = {}^1/_4\,\sigma^2_{10} + {}^1/_{16}\,\sigma^2_{20} + {}^1/_{64}\,\sigma^2_{30} + {}^1/_{256}\,\sigma^2_{40} + \ldots .$$

$$\text{Cov FS} = {}^1/_2\,\sigma^2_{10} + {}^1/_4\,\sigma^2_{01} + {}^1/_4\,\sigma^2_{20} + {}^1/_8\,\sigma^2_{11} + {}^1/_{16}\,\sigma^2_{02} + {}^1/_8\,\sigma^2_{30} + {}^1/_{16}\,\sigma^2_{21} + {}^1/_{32}\,\sigma^2_{12} + {}^1/_{64}\,\sigma^2_{03} + \ldots$$

Where σ^2_{10} = additive genetic variance

σ^2_{20} = additive × additive epistatic variance, etc.

σ^2_{01} = dominance variance

σ^2_{02} = dominance × dominance variance, etc.

σ^2_{11} = additive × dominance epistatic variance, etc.

Therefore, σ^2_D, as estimated by 4 (Cov FS − 2 Cov HS), includes $\sigma^2_{01} + {}^1/_2\,\sigma^2_{20} + {}^1/_2\,\sigma^2_{11} + {}^1/_2\,\sigma^2_{02} + {}^{12}/_{32}\,\sigma^2_{30}$, disregarding higher order interactions with negligible coefficients. In comparison, σ^2_A, estimated by 4 (Cov HS), includes $\sigma^2_{10} + {}^1/_4\,\sigma^2_{20} + {}^1/_{16}\,\sigma^2_{30}$. It can be seen that σ^2_D/σ^2_A ratios can be appreciably biased in cases where additive × additive or additive × dominance epistasis adds greatly to genetic variance. However, for this to occur, each of the epistatic classes would have to contribute about 50 percent as much variance as the main effects of dominance or additiveness. Robinson and Comstock (1955) thought it unlikely that bias due to epistasis would seriously affect covariance estimates in open-pollinated varieties of corn. There appears to be little reason to think differently for open-pollinated forest tree species.

Maternal effects

With the B/A mating design, maternal effects would be expected to contribute to half-sib covariances through seed weight and seed nutrition effects. In this study, mean full-sib family seed weight could not be shown to be significantly correlated to mean family P. E. ($r = 0.10$) or to seedling dry weight ($r = 0.04$). Lavender (1958) also found that Douglas-fir seed weight did not affect seedling size or weight. Still, the connection between seed weight and seedling vigor traits has been demonstrated on sufficient occasions with other species (Righter 1945, Fowells 1953, Mergen and Voight 1960, Burgar 1964) to make it likely that the same exists in Douglas-fir. Maternal effects would inflate estimates of σ^2_A upward, consequently biasing σ^2_D/σ^2_A downward.

Inbreeding

No general solution is possible for effects of within-line inbreeding on variances where dominance is present. Effects are in large part dependent on initial gene frequencies. Robertson (1952) has worked out a special case in which recessive genes are at low frequencies and dominance is complete at the relevant loci. This may be the situation if recessive genes deleteriously affect fitness of an individual to survive, although Lerner (1954) considers that intermediate gene frequencies and overdominance are more likely. At any rate, traits in the present study can be reasonably assumed to be closely related to adaptive fitness, and Robertson's conclusions may apply. If so, and under

slow inbreeding, within-line variance is relatively greater at intermediate inbreeding levels than it is at either low or high levels. ROBERTSON's treatment also suggests that with low inbreeding levels, dominance variance contributes more to within-line variance than does additive, whereas, with intermediate levels, additive variance contributes proportionally more. The advantage is not great in either case.

The parental stand for this study has a regeneration history that would appear to facilitate low levels of inbreeding. This is true in many naturally regenerated stands in the Douglas-fir region where large populations may originate from a few trees remaining after logging or fire. Slight inbreeding is not likely to contribute to bias — even if ROBERTSON's conditions apply. As seen above, neither dominance nor additive variances are increased disproportionately by slow inbreeding. Furthermore, in practice the total increase in within-line variance is probably not detectable, except in very large experiments.

Reliability of Estimates

Very large experiments are necessary to obtain reasonably close estimates of variance and covariance components. Available growth-chamber space limited the size of the present experiment. This limitation is undoubtedly reflected in the large standard errors of maternal and paternal components *(Table 4)* and in the generally low probabilities shown by the F tests of mean-square-ratios *(Table 3)*. Clearly the sampling variances of σ^2_A and σ^2_D are large. It therefore must be stressed that any given estimate has poor reliability, based as it is on variance components that have been measured inexactly because of the small experiment size. But, in view of this, the general agreement among the five traits in sign and magnitude of estimate for genetic variances and their ratio, and for genetic correlation, is striking. The conclusion is that estimates are meaningful, at least in respect to the general trends indicated by the five vigor-related traits.

In summary, several inferences may be made concerning effects of the parent population's genetic structure on interpretation of study results:

1) Where gene frequencies and gene interaction complexities are unknown, as in wild plant populations, no estimate can be made of the bias likely to result from linkage, epistasis and inbreeding.
2) Both additive and dominance variances have probably been inflated by epistasis, if it is present, and additive variance probably by maternal effects.
3) Maternal effects have tended to decrease the σ^2_D/σ^2_A ratio. Epistatic and linkage effects are not likely to have affected variances here, but if present they would tend to increase the ratio. Therefore biases may be to large extent compensating.

Level of Dominance

Interpretation of σ^2_D/σ^2_A estimates in regard to level of dominance has been discussed by ROBINSON, COMSTOCK, and HARVEY (1955) and ROBINSON and COMSTOCK (1955). Exact interpretation is not possible, in any case, in open-pollinated material with unknown gene frequencies at the relevant loci. ROBINSON *et al.* detoured this problem by reasoning from expected values of σ^2_D/σ^2_A for various levels of dominance and gene frequencies. From their *Table 5* (in either of above papers), the five estimates of σ^2_D/σ^2_A for the vigor-related traits studied here *(Table 5)* are in the range of complete dominance to overdominance. Ratio magnitudes can be explained by assuming complete dominance at all loci, but this requires the further hypothesis that frequencies of favorable alleles average 0.75 or better. Or, if medium to high levels of overdominance are assumed, the ratios could be expected in populations with average gene frequencies ranging from approximately 0.5 to 0.95. Unfortunately, there is no reasonable basis for choosing a probable average gene frequency; if complete dominance exists at all loci, the frequency of adaptively advantageous genes would be expected to be near unity; if overdominance is the mode, heterozygote superiority leads to equilibrium frequencies near 0.5. Consequently, results obtained here can be attributed with equal validity either to complete dominance or to overdominance.

The problem of whether overdominance exists remains an open question, as FALCONER (1961, page 283) has recently pointed out. ROBINSON and COMSTOCK (1955) and MATHER (1955) have questioned results purporting to demonstrate its existence. On the other hand, LERNER (1954) argued from a comprehensive literature review, with convincing logic, that those complex characters of an organism that are connected with adaptive fitness will exhibit overdominance. Traits such as total dry-weight, P. E. and needle weight are undoubtedly controlled by complex physiological mechanisms; it is therefore not unlikely that their genetic bases are equally complex. Since there is also little doubt that these traits are basic to "fitness" for seedlings, it would not be surprising to find that they exhibit overdominance, in the light of LERNER's hypothesis.

Relation of P. E. to Dry-matter Accumulation

Phenotypic correlation studies reported by WATSON's review (1952) and by others indicate that little relationship exists between P. E. and various measures for yield, whereas a strong genetic correlation of $r_A = 0.70$ between P. E. and seedling dry-weight is reported here *(Table 6)*. Either of two reasons may explain the apparent discrepancy. First, the estimate of genetic correlation is admittedly based on scanty data, and its attendant error is therefore large. Second, different measures of correlation are used in the two cases. Phenotypic correlation is compounded of associations arising from genetic and environmental sources of covariance. Genetic correlation is the correlation of breeding values and results from covariance of additive genetic variation in the related traits. Since traits may be affected through different physiological mechanisms by environment and genes, phenotypic correlation is not necessarily closely related to genetic correlation.

The concordance of phenotypic and genetic correlation can be expected to be especially poor where trait heritability is low (FALCONER 1961, page 315), and heritability of P. E. is likely to be low except under conditions of precise environmental control. This is because P. E. is particularly susceptible to environmental modification: for example, almost all major factors of environment such as light, temperature, soil moisture and mineral nutrition strongly affect photosynthetic rate (KRAMER and KOZLOWSKI 1960), and the photochemical, diffusion and biochemical processes of photosynthesis are apparently affected differentially (GAASTRA 1963).

As estimated here, the genetic relationship between P. E. and amount of foliage is very close *(Table 6,* $r_A = 1.06$), and in turn, amount of foliage is related to seedling weight *(Ta-*

ble 6, $r_A = 0.53$). This strong and positive relationship is reasonable: increase in P. E. will cause additions to foliage as well as to root and stem, and this increase in foliage represents an increase in the total photosynthetic factory. Furthermore, it is not unreasonable to expect that the increased plant size will affect P. E., in view of the recognized influence of moisture, temperature and nutrition on photosynthetic rate.

The above interrelationships suggest the difficulty of designating "cause and effect" within the system. This may explain the debatable success of previous attempts (WATSON, 1952) to determine relative contributions to yield by P. E. versus foliage amounts.

Relevancy to Breeding

The practical objective of this paper is to examine the feasibility of selecting for P. E. with the goal of producing strains of trees with superior growth characteristics. Portions of the results can be used to judge the effect of selection for P. E. in older trees. Unfortunately, results indicate that selection for P. E. in near-mature trees would be less efficient than selection for the desired growth traits themselves. This is because selection for P. E. is an indirect selection for growth, and because benefits can be derived only from the correlated response of growth resulting from selection for P. E. Under this circumstance, P. E. selection in mature trees can more efficiently produce faster growing strains only if P. E. and growth are highly correlated, genetically and if heritability of P. E. is substantially higher than for growth (FALCONER 1961, page 320). Furthermore, this presupposes equal selection intensities for both traits whereas, in fact, selection intensity for growth is likely to be higher than for P. E. because growth measurements are less expensive than P. E. measurements in older trees. The genetic correlation between seedling P. E. and growth apparently is high, and this high correlation may be maintained in older populations. On the other hand, heritability of P. E. in seedling populations is only moderate *(Table 5,* $h_2^2 = 0.21$), except under special environmental conditions common to very small plots; P. E. heritability can be expected to be even lower in stands of older trees where environment is likely to be more variable. In older trees, therefore, there is little chance that heritability of P. E. will be significantly greater than heritability of growth traits. For example, compare P. E. heritability estimates *(Table 5)* with estimated narrow-sense heritabilities of .18 to .35 for stem-volume growth of slash pine 14 years of age (SQUILLACE and BENGTSON 1961).

The conclusion is that selection for P. E. is desirable and feasible only if seedling values are strongly correlated to mature-tree growth. If so, the breeder could take advantage of the shorter breeding generation interval that can be obtained by early family testing. Also, seedling P. E. heritability could be increased substantially by growing seedlings in controlled environment, as demonstrated by the high heritability obtained in environments specific to plots *(Table 5,* $h_1^2 = 0.53$). With heritabilities of this magnitude, genotypes are strongly correlated with phenotypes, and selection of parents on the basis of progeny means is very effective.

The possibility that a large proportion of genetic variance is dominance variance could have considerable practical significance. If this trend holds for vigor traits (e. g., height growth and yield) in older trees, it has definite implications regarding choice of breeding systems. With dominance variance being of moment, one of several selection methods for specific combining ability is indicated.

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Summary

The feasibility of building strains of forest trees with superior growth by selecting parent trees on the basis of relative photosynthetic capability was examined. To do this, relative amounts of additive and dominance genetic variance, and the genetic correlation of photosynthetic efficiency (P. E.) with dry-matter accumulation, were estimated in 90 seedling families of Douglas-fir. Within-population genetic variation is indicated for P. E., seedling total dry weight, and dry weight of needles plus stem. Dominance variance makes up the larger proportion of genetic variance. Genetic correlation estimates were strong and positive among P. E. and dry-weight traits. Narrow-sense heritability estimates were moderate to low except for P. E. where heritability was high in the environment specific to small plots. Results indicate that selection for P. E. in near-mature trees would be less efficient than selection for the desired growth traits themselves. Selection for P. E. in seedlings may be feasible if seedling values are strongly correlated with mature-tree growth.

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Geographic Variation in Virginia Pine

Results of the First Trial in Pennsylvania, Maryland and Tennessee[1])

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1. Introduction

Virginia pine (*Pinus virginiana* MILL.), distributed over a large range in the eastern United States, is highly valued for pulpwood. Therefore, it is worth consideration for planting and more intensive study.

As a pioneer species on a variety of sites, Virginia pine occurs from sea level to elevations of 2,500 feet in the Appalachian Mountains (*Fig. 1*). It grows naturally in 16 states from Long Island (New York) and central Pennsylvania to northern Mississippi, Alabama and South Carolina but is not found on the Coastal Plain south of Virginia. The western range consists of isolated stands in southeastern Indiana and western Tennessee.

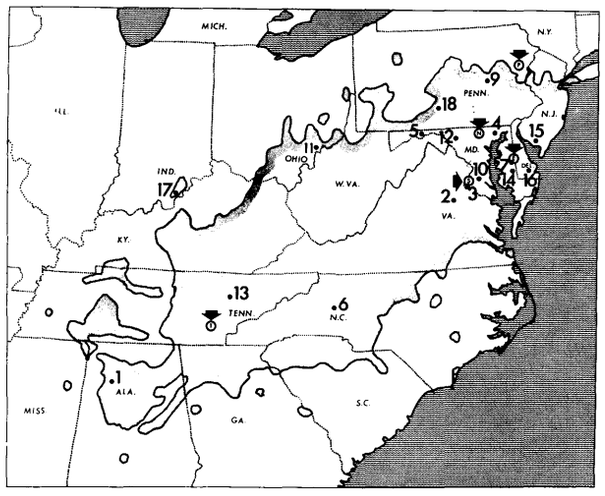

Figure 1. — Natural distribution of Virginia pine, locations of collection areas (numbered dots) and locations of test areas (letters in circles, devoted by arrows).

Virginia pine is placed in the series *Insignes*. It has two (sometimes three) needles per fascicle which are 1.5 to 3.5 inches long, pale green, usually twisted, rigid, and sharp-pointed. Cones are two to three inches long, reddish brown at maturity, conic-ovoid to oblong, symmetrical, persistent and are found in all portions of crown. Cone scales are thin, flat, terminating in a prickle.

The bark is dark brown. Under forestry conditions Virginia pine reaches heights of 80 feet and more, but open-grown trees are stunted and scrubby.

This species has only recently become a commercially important tree with the growth of the southern pulp industry. Consequently, there is no large backlog of silvicultural, growth and genetic information for Virginia pine as exists for many other species in the region (NELSON *et al.*, 1951; GENYS *et al.*, 1964). Several attempts have been made to cross Virginia pine with other species (especially of *Insignes*), but only the cross of *P. virginiana* × *P. clausa* was a certain success. Some superior tree selection has been made followed by grafting and establishment of seed orchards but there are no published data on individual tree inheritance. THOR (1964) studied the phenotypic range in wood properties of Virginia pine in Kentucky and Tennessee. He found variations of .49 to .55 in specific gravity and 3.5 to 4.2 millimeters in tracheid lengths.

2. Objectives, Materials and Methods

This study was started in 1955 by CRAIG D. WHITESELL, then employed by the Maryland Department of Research and Education (WHITESELL, 1958). The objectives were to (1) determine the range and pattern of genetic diversity, (2) provide practical information on the best seed sources for immediate reforestation needs, and (3) provide basic information for future, more intensive improvement programs.

Two trials were started. This is a report on Trial No. 1, which includes data on a total of 17 provenances from 10 states, grown in permanent test plantations in three states (*Fig. 1*). Two plantations in Maryland were nearly complete

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