

Model Relating Levels of Genetic Variance To Stand Development of Four North American Conifers

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Summary

Rate of genetic improvement over time of any long-lived organism can be increased to some degree by early testing and selection if genetic correlations in juvenile-mature traits are strong and positive. Through the use of path coefficients, the required relationships were illustrated. Most genetic analyses of juvenile-mature relationships in growth traits such as height and volume have been based on estimates of phenotypic rather than genotypic correlations. Predictions about genetic gains based on phenotypic correlations are accurate only insofar as associated environmental correlations are negligible. Only in the recent past has analysis of long-term data on families of forest trees provided for recognition of the impact of stand development on the expression of genetic variance. From published data on Douglas-fir and ponderosa pine, a hypothetical model interpreting the expression of genetic and environmental variances in height growth was proposed. The model permits the comparison of the magnitude of genetic versus environmental variances at various stages of stand development. Under the model, stand development was divided into juvenile-genotypic, mature-genotypic, and codominance-suppression phases. Data on loblolly and slash pines were fitted to the model; all four sets of data showed good agreement on phase changes relative to expression of additive genetic variance. The most important recommendation based on the model is that selection for gain in height and volume with conifers grown at conventional spacings should be deferred at least until half rotation age.

Key words: Juvenile-mature correlation, progeny testing, genetic gain, environmental correlation, genetic selection, juvenile testing.

Zusammenfassung

Die Rate der genetischen Verbesserung eines jeden langlebigen Organismus lässt sich in der Zeit durch Frühtest und Selektion in hohem Maße steigern, wenn die genetische Korrelation zwischen Jugend- und Altersmerkmalen streng und positiv ist. Durch den Gebrauch von Wegekoeffizienten wurde die geforderte Beziehung veranschaulicht. Die meisten der genetischen Analysen der Jugend-Reife-Beziehung in bezug auf Wachstumsmerkmale, wie Höhe und Volumen, basieren eher auf Schätzungen phänotypischer als genotypischer Korrelationen. Vorhersagen über genetische Gewinne die auf phänotypischen Korrelationen basieren, sind nur insofern genau, als assoziierte Umweltkorrelationen unbedeutend sind. Nur in jüngster Vergangenheit sind Analysen langfristiger Daten von Waldbaum-Familien für die Erkennung des Ansatzes der Bestandesentwicklung als Ausdruck genetischer Varianz in Erwägung gezogen worden. Anhand veröffentlichter Daten von *Pseudotsuga menziesii* und *Pinus ponderosa* wurde ein hypothetisches Modell vorgeschlagen, das die Bedeutung der genetischen und umweltbedingten Varianzen des Höhenwachstums herausstellt. Das Modell erlaubt den Vergleich des Umfangs der genetischen und der umweltbedingten Varianzen zu verschiedenen Zeitpunkten der Bestandesentwicklung. Im Modell wurde die Bestandesentwicklung in Jugend-genotypische, Reife-genotypische sowie die Coherrschafts-Unterdrückungs-

Phase unterteilt. Daten von *Pinus taeda* und *Pinus elliotii* wurden in das Modell eingesetzt, alle vier Datengruppen zeigten eine gute Übereinstimmung im Phasenwechsel in Beziehung zur additiven genetischen Varianz. Die wichtigste Empfehlung aus diesem Modell ist die, daß eine Selektion auf Höhe und Volumen von Koniferen, die in konventionellem Abstand aufgewachsen sind, mindestens bis zum halben Rotationsalter aufgeschoben werden sollte.

Introduction

Rate of genetic improvement of any long-lived organism can be increased by early testing and selection if certain genetic relationships exist between juvenile and mature phases. Woody perennials, especially forest trees, are among the most extreme in longevity and developmental complexity of both individuals and stands (ZIMMERMAN, 1976). Therefore, tree breeders often resort to early testing in an attempt to increase the rate of genetic gain over time. Increasing amounts of data are becoming available to describe and quantify juvenile-mature relationships in commercially important forest tree species.

Until recently, most genetic analyses of juvenile-mature relationships in growth traits such as height and volume were based on estimates of phenotypic correlations of provenance or family means. Correlations have generally been high or at least positive, leading to the conclusion that selection based on juvenile traits is effective in obtaining genetic gain in mature traits (cf. SQUILLACE and GANSEL, 1974). However, the magnitude of genetic versus environmental effects and the timing of their maximum impacts during stand development were largely ignored until two recent publications on variation in the relative strength of environmental and genetic causal factors (NAMKOONG *et al.*, 1972; NAMKOONG and CONKLE, 1976). This type of data offers new opportunities to understand the complex interrelationships between changing internal and external environments of trees, families, and provenances. Their results show extremely large changes in the relative magnitude of genetic and environmental effects on height growth during stand development. These changes may be caused by the onset of competition in stands and thus related to factors of environment such as site quality and stocking (FORD 1975, 1976).

In this paper I present a review of fundamental theory related to selection gain based on juvenile-mature correlations, as well as a hypothetical model to explain long-term trends in genetic and environmental variances observed in studies of four major timber species in the United States.

Quantitative Genetic Relationships

The fundamental basis for the general conclusion that early testing and selection will result in genetic gains in mature populations is based on a relatively simple model (FRANKLIN, In Press). For analytical purposes, juvenile and mature measurements of a trait such as height may be considered as two different traits, say J and M. The quantitative genetic model for correlated responses is then the same as that for two traits such as height and cold-hardiness meas-

ured at the same age (FALCONER 1960, p. 318). In this context, the juvenile-mature correlation is the phenotypic correlation between the juvenile trait (J) and the mature trait (M). The cause-effect model for this correlation may be derived with path coefficients (Figure 1) according to the following equation from FALCONER (1960, p. 315):

$$r_P = h_J h_M r_G + e_J e_M r_E \quad (1)$$

where r_P = juvenile-mature correlation between phenotypes,
 h_J = square root of heritability for juvenile trait,
 h_M = square root of heritability for mature trait,
 r_G = juvenile-mature correlation between genotypes,
 e_J = square root of the environmental intraclass correlation for juvenile trait, $(\sqrt{1 - h_J^2})$,
 e_M = square root of the environmental intraclass correlation for mature trait, $(\sqrt{1 - h_M^2})$,
 r_E = juvenile-mature correlation between environments

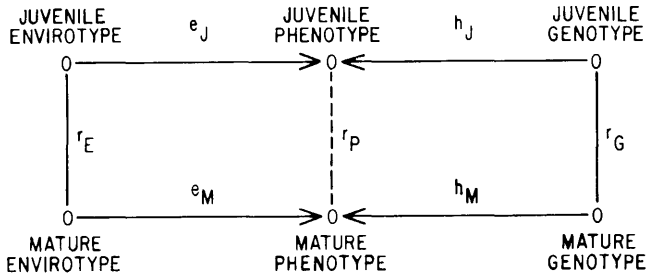


Figure 1. — Path coefficients of the genetic and environmental causes for relationships between a juvenile and a mature trait such that $r_P = h_J h_M r_G + e_J e_M r_E$. (Symbols defined in the text).

Note that $h_J^2 + e_J^2 = 1$, and $h_M^2 + e_M^2 = 1$, symbolically reflecting the total determination of the phenotype as the sum of genetic and environmental causes (NANSON, 1967). Unless genetic and environmental analyses are based on clonal data (broad-sense heritability, etc.), r_E will usually contain some or all of the non-additive genetic effects (FALCONER 1960, p. 314). I have not considered the effects of genotype by environmental interaction, which a more thorough treatment would include (NANSON, 1967).

The tree breeder's first question is, "If I can make a certain gain (G_J) in a juvenile trait, what gain can be expected in the mature trait?" The answer can be estimated by this equation adapted from FALCONER (1960, p. 318):

$$G_{M/J} = i_J h_J r_G h_M \sigma_{PM} \quad (2)$$

where $G_{M/J}$ = gain in mature trait as a correlated response to selection in juvenile trait,

i_J = selection intensity for the juvenile trait,

σ_{PM} = square root of phenotypic variance of the mature trait, and

h_J, r_G, h_M are as defined above.

Note that $h_J r_G h_M$ is the product of the genetic path coefficients from the juvenile to the mature phenotype (Figure 1). From equation (1), $h_J h_M r_G = r_P - e_J e_M r_E$. Substituting this expression into equation (2) gives:

$$G_{M/J} = i_J (r_P - e_J e_M r_E) \sigma_{PM} \quad (3)$$

where all terms are defined above.

It is usually assumed that $e_J e_M r_E$, the product of the environmental path coefficients from the juvenile to the mature

phenotype (Figure 1), is negligibly small. When this assumption is correct, equation (3) simplifies to:

$$G_{M/J} = i_J r_P \sigma_{PM} \quad (4)$$

This equation implies that the genetic gain from the correlated response can be estimated solely on the basis of phenotypic parameters, and it is the basis for most of the literature on the subject. Unfortunately, the assumption that the product of the environmental path coefficients is negligible must be critically reconsidered, especially as it relates to the expression for correlated juvenile-mature selection response (equation 3). The limited range of environmental variation sampled by experiments in only one location, by family row plots with few replications, and by repeated measurements on the same tree over time all increase probabilities that sampling bias in estimating environmental and genetic parameters will be large and difficult or impossible to adjust. Research is needed to specify field designs and analytical methods that are statistically and economically efficient for short-term progeny testing. The hypothetical model presented below is offered as an interpretive aid for the data presented and as a rationale for studies to further clarify the practical use of juvenile testing in applied tree breeding programs.

The Model

On the basis of the total determination of the variance of the phenotype being the linear sum of genetic and environmental variances, the simplest of equations was used to re-analyze data on Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] (NAMKOONG *et al.*, 1972) and ponderosa pine (*Pinus ponderosa* LAWS.) (NAMKOONG and CONKLE, 1976). The equation is:

$$\sigma_P^2 = \sigma_A^2 + \sigma_E^2 \quad (5)$$

where σ_P^2 = phenotypic variance,

σ_A^2 = additive genetic variance, and

σ_E^2 = environmental variance.¹⁾

In terms of this equation, the efficiency of selection, *i. e.*, heritability (h^2), is defined as:

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

These parameters were estimated and plotted for the data sets on Douglas-fir (Figure 2) and ponderosa pine (Figure 3). Comparison of these charts revealed strikingly similar patterns of change in population variances over time. With each species, the additive genetic variance remained at a very low level approximately until the time of stand closure, at which time there was an abrupt increase. Additive genetic variance continued to increase in the case of Douglas-fir to about age 40. Between ages 40 and 53, a marked decrease in additive variance was observed. Data for similarly advanced ages of ponderosa pine were not available. For each species, heritability reached a rather high level during early stand development and then decreased markedly, declining to its lowest point in each case in the same year that the additive genetic variance began its marked increase, about the time of stand closure. For height of Douglas-fir, heritability reached a maximum at approximately age 23. It then began a gradual and then more rapid decline to age 53.

A hypothetical model based on the Douglas-fir data was developed to aid in the interpretation of these results. Stand

¹⁾ Non-additive genetic variance is included with environmental variance in this type of analysis; such inclusion is standard for simple mass, family, and combined selection models.

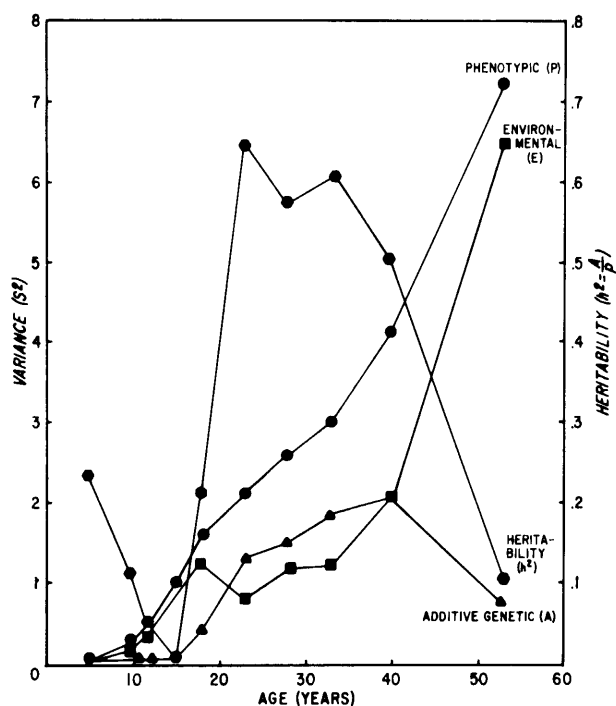


Figure 2. — Trends in variances and heritability of height in a Douglas-fir family trial through 53 years of growth. Data on Wind River population from NAMKOONG *et al.* (1972).

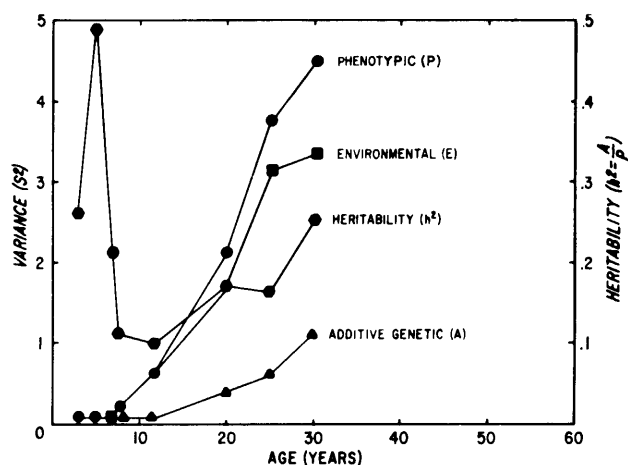


Figure 3. — Trends in variances and heritability of height in a ponderosa pine family trial through 30 years of growth. Data from NAMKOONG and CONKLE (1976).

development was divided into three phases: (1) juvenile-genotypic, (2) mature-genotypic, and (3) codominance-suppression (Figure 4). Locations of boundaries between phases were based exclusively on trends in additive genetic variance. Corresponding levels of heritability during the three phases were also shown. Juvenile-genetic and mature-genetic culmination points are defined as the highest levels of heritability (selection efficiency) that could be obtained within the phase.

Shortly after the development of this model, a data set²⁾ was analyzed which contained 25-year measurements of 30 families of loblolly pine (*Pinus taeda* L.) grown in a progeny plantation in a randomized complete-block design. Parent trees were open-pollinated and selected for various crown

characteristics. When the data were analyzed, trends in variance components over time were similar to those already observed in the other two species (Figure 5). From ages 3 to 5, the additive genetic variance was quite low. At age 5, about the time of crown closure at a spacing of 8×8 feet, there was a marked increase in additive genetic variance. Through age 20, additive genetic variance increased, but declined sharply from ages 20 to 25, corresponding to the trends from ages 40 to 53 in Douglas-fir. Correspondingly, heritability went from a relatively high level at age 3 to a low at age 5, and then abruptly increased to a high at age 10. It then dropped to an unexpectedly low level at age 15, then substantially increased to age 20. From ages 20 to 25, there were sharp drops in both heritability and additive variance. These data on loblolly pine closely fit the genetic-phase model developed for the Douglas-fir and ponderosa pine populations (Figure 6). The boundary for the transition from the mature-genotypic to the codominance-suppression phase is clearly marked by the sharp drop in additive genetic variance, as is the boundary between juvenile- and mature-genotypic phases by the sharp upturn in additive genetic variance. The pattern for volume is similar, but the boundary between the juvenile- and mature-genotypic phases is age 15 instead of age 5 (Figure 7).

The similarity between the data sets for Douglas-fir and ponderosa and loblolly pines stimulated an interest in analyzing a data set on slash pine (*Pinus elliottii* ENGELM.) containing both control- and wind-pollinated offspring.³⁾ Results for wind- and control-pollinated families were similar; therefore, only the results on wind-pollination are reported here. Patterns for height and volume resembled those already outlined (Figure 8). Additive genetic variance remained relatively low to age 8, at which time it showed a sharp increase and continued to increase to age 30. Herita-

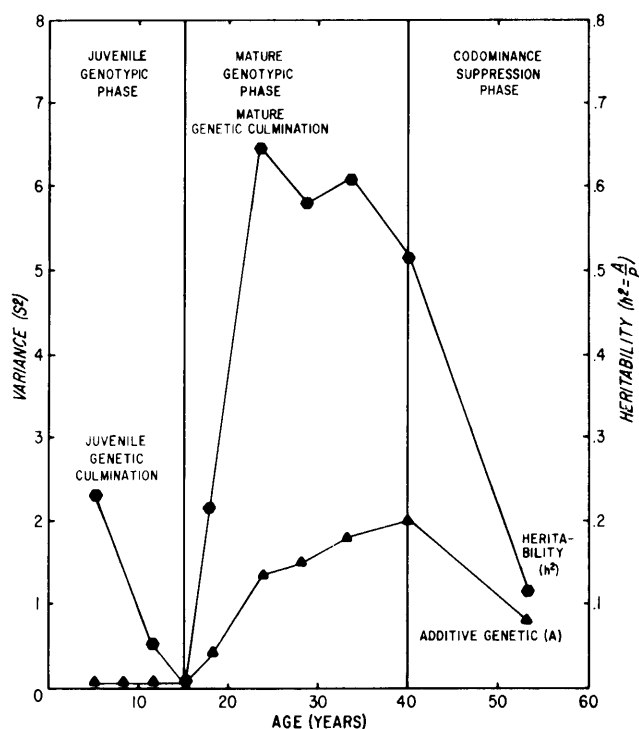


Figure 4. — Genetic phases of stand development interpreted for height in a Douglas-fir family trial. Data on Wind River population from NAMKOONG *et al.* (1972).

²⁾ Study NCP-45 after Trousdell, this laboratory.

bility was high at age 1, but decreased markedly from ages 1 to 3. At age 8 it began a sharp increase which continued through age 25. A sharp decrease in heritability from ages 25 to 30 may be signaling the transition into the codominance-suppression phase in the next 5-year period. This transition will be later than in the loblolly pine probably because the slash plantation was grown at 20×20 ft. spacing. With reference to the model, the data on height of slash pine fit the juvenile-mature transition model very well.

Similarly, the variances for volume in slash pine follow the pattern previously observed for loblolly pine volume but on a somewhat extended time frame presumably because of the wide spacing (Figure 9). Additive genetic variance began a rapid increase around age 14, which continued through age 30. Heritability has also increased through age 30. How soon drops in additive genetic variance and heritability might be seen cannot be predicted now.

Interpretation of Developmental Phases

The genotypic response of seedlings soon after plantation establishment is one of adapting to a number of varying microsites in addition to competing with herbaceous and woody vegetation that comes in after establishment. Seedlings that are genetically superior in this phase of develop-

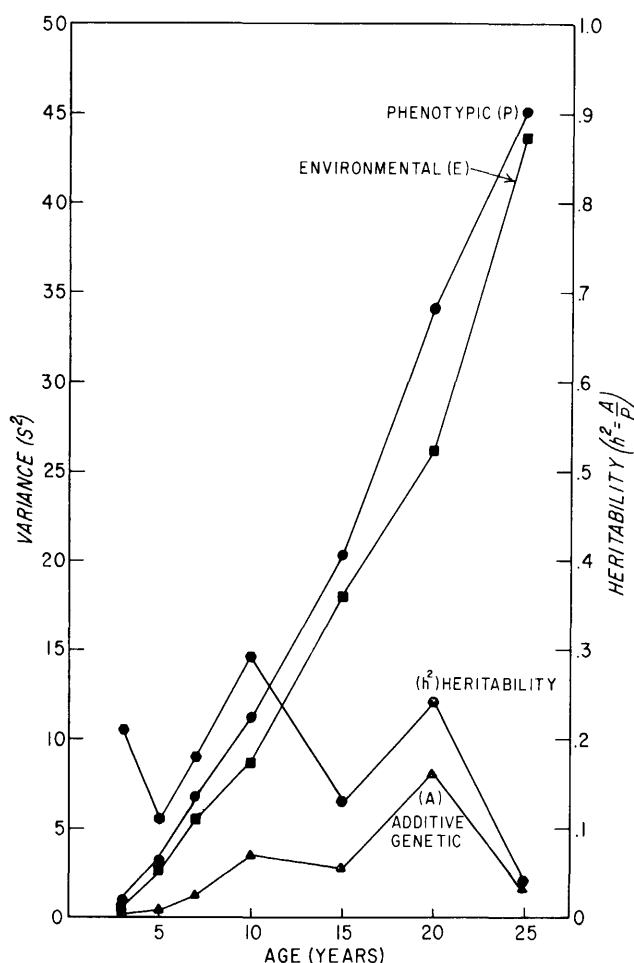


Figure 5. — Trends in variances and heritability of height in a loblolly pine family trial through 25 years of growth. Data from unpublished study NCP-45 by TROUSDELL.

³⁾ Study 0—116 after SQUILLACE and GANSEL (1974).

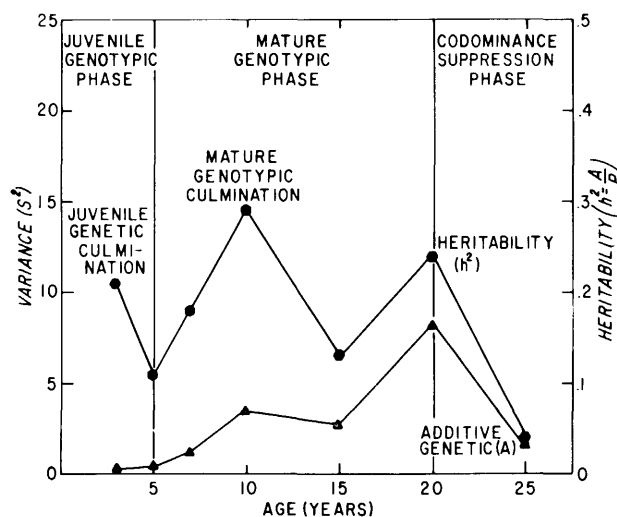


Figure 6. — Genetic phases of stand development interpreted for height in a loblolly pine family trial. Data from unpublished study NCP-45 by TROUSDELL.

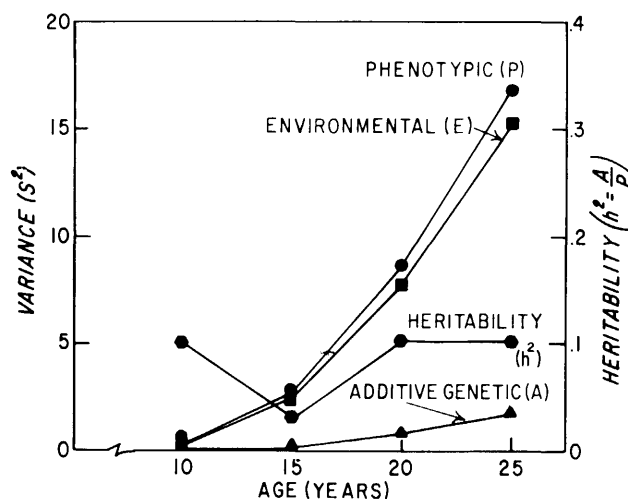


Figure 7. — Trends in variances and heritability of volume in a loblolly pine family trial through 25 years of growth. Data from unpublished study NCP-45 by TROUSDELL.

ment rapidly capture their microsites and enter into a period of comparatively free growth. Seedlings that are less well adapted lag behind, the maximum lag being at the period of maximum genetic variance. Increases followed by decreases in additive genetic variance were found in the juvenile genetic phase in both Douglas-fir and slash pine. As the more slowly developing seedlings capture their sites, the stand becomes one of uniformly growing young seedlings and saplings, a transition period in which very little genetic variation is observed. Although this is a plausible explanation for the relatively high heritabilities observed in the juvenile phase, the numerical relationship between the rapidly increasing phenotypic variance and the static additive genetic variance accounts for most of the dramatic drop in heritability during the juvenile phase.

The transition into the mature genotypic phase seems to coincide roughly with the intensification of inter-tree competition, as suggested by NAMKOONG and CONKLE (1976). With close spacing on a good site, there was a rapid increase in additive genetic variance and heritability with the Douglas-

fir and loblolly pine populations. With wider spacing or a poor site or both, increases in additive genetic variance and heritability were less rapid, as seen in ponderosa and slash pine. There is little doubt that crown competition has a marked effect on this phenomenon, but the data on slash pine at 20 × 20 foot spacing demonstrated that crown competition is not essential in the development of the phenomenon, i. e., root competition or internal physiological changes would seem to be sufficient to bring about the phase change.

The transition into the codominance-suppression phase is similar in many respects to the transition into the mature genotypic phase; in both, rapidly developing phenotypes

are slowing while less rapidly developing phenotypes are catching up. Eventually, a uniformly developed stand of dominants and codominants plus suppressed and dying trees reflects very low levels of genetic variances as the stand approaches what might be called genetic maturity. For example, between ages 15 and 25 in the loblolly pine plantation, 82 trees (18 percent) died, almost all because of suppression. At wide spacings, such as that in the slash pine plantation, a delay in the transition into a codominance-suppression phase was noted.

Implications of the Model for Genetic Selection

Significant amounts of genetic gain in a mature trait can be obtained by selection on a juvenile trait only if the product $h_j h_M r_G$ is relatively large, as shown in equation (2) and illustrated in figure 1. There must be strong heritabilities in the juvenile and mature phases of stand development, and the genetic correlation between phases must also be high, reflecting the effects of the same genes in the juvenile and mature phases. With reference to genetic correlations, it is illustrative to refer to tables 1 and 2, which show genetic correlations within and between juvenile and mature phases in the data on Douglas-fir and ponderosa pine. The trend of correlations appears strongly positive and high within phases and generally weak or negative between phases, indicating that little or no genetic gain could be obtained by juvenile selection in these populations. Similar genetic correlations were found in the loblolly population (Table 3). The abrupt increase in genetic correlations for heights and volumes at age 15 with age 25 clearly indicates the need to avoid selection until the middle of the mature-genotypic phase. Slash pine results shown with phenotypic correlations were similar (SQUILLAGE and GANSEL, 1974). Correlations for heights, diameters, and volumes between ages 14 and 25 were markedly higher than those at younger ages with age 25. The pattern of correlations in all four species strongly suggests that juvenile and mature genotypes are quite different even for the same trait, and therefore under typical stand conditions selection should be deferred until about half of the rotation age.

Ways to Improve Juvenile Testing

In most species we can ill-afford to wait for the mature-genotypic phase to obtain progeny test results or to make selections. This is especially true when considering volume which may not reach genetic culmination until 20 or 25 years of age. The need is to hasten the onset of the mature-genotypic phase by inducing fast growth at close spacing and perhaps by manipulating other environmental factors. The

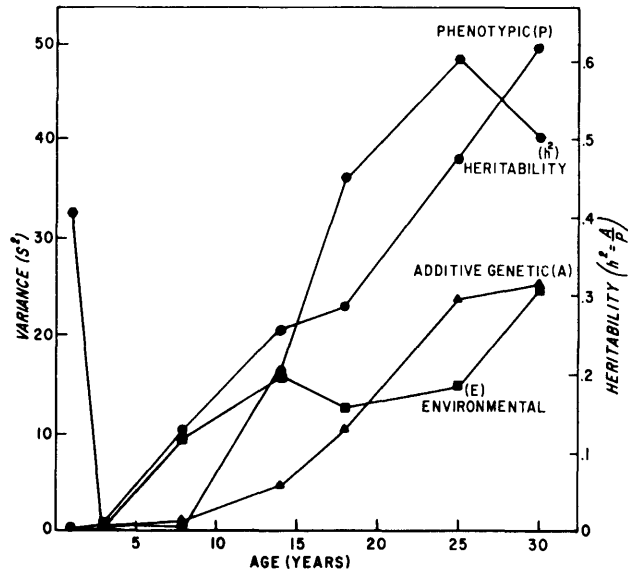


Figure 8. — Trends in variances and heritability of height in a slash pine family trial through 30 years. Data on wind-pollinated offspring from SQUILLAGE and GANSEL (1974).

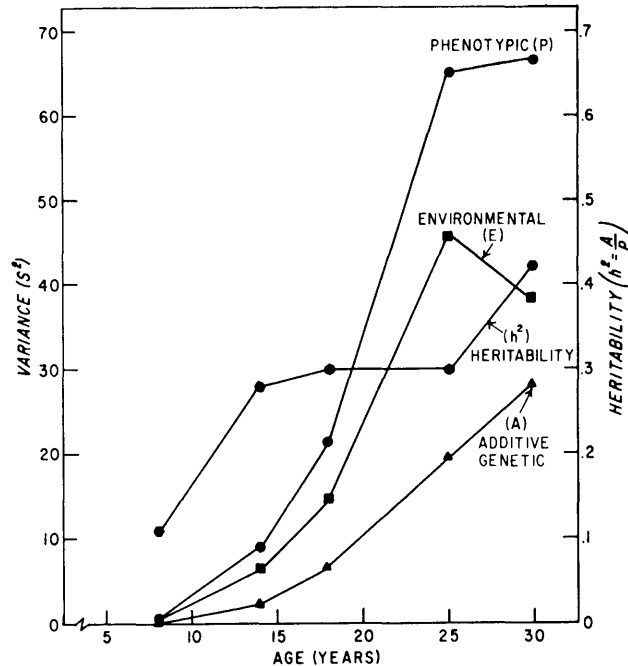


Figure 9. — Trends in variances and heritability of volume in a slash pine family trial through 30 years. Data on wind-pollinated offspring from SQUILLAGE and GANSEL (1974).

Table 1. — Correlations for average heights of families over the indicated range of ages for Douglas-fir at Wind River for ages 5 through 33 (after NAMKOONG, et al. 1972). Triangles emphasize the generally high correlations within groups of measurements at younger and at older ages.

	Correlations for height at ages--						
Years	10	12	15	18	23	28	33
5	.60	.14	-.07	-.23	-.20	-.44	-.57
10		.60	-.01	-.01	0.14	-.58	-.74
12			-.11	-.21	-.37	-.91	-1.00
15				1.00	.64	.26	.24
18					.85	.77	.93
23						.95	.97
28							.96

Table 2. — Correlations for average heights of families over the indicated range of ages of ponderosa pine (after NAMKOONG and CONKLE, 1976). Triangles emphasize the generally high correlations within groups of measurements at younger and at older ages.

Years	Correlations for height at ages--						
	5	7	8	12	20	25	29
3	.67	1.00+	.77	-.47	-.38	-.19	.05
5		1.00+	.93	-.52	.58	.28	.19
7			.88	.05	.00	-.52	-.47
8				.14	.13	-.61	-.60
12					1.00+	.63	.64
20						.82	.85
25							1.00+

Table 3. — Genetic correlations in the loblolly pine population between heights and volumes at various ages (data from study NCP-45 by TROUSDELL). Triangles emphasize the generally high correlations within groups of measurements at younger and at older ages.

Age	Correlations for height at ages--						
	3	5	7	10	15	20	25
3		.93	.84	.66	.41	.07	.17
5			.93	.76	.50	.19	.34
7				.86	.60	.34	.40
10					.62	.49	.47
15						.88	.88
20							.67

	Correlations for volume		
	10	15	20
		.91	.84
			.97
			.93
			.96

procedures would simply eliminate, as much as possible, the juvenile phase and concentrate on thorough and intense between-tree competition to elicit the mature-genotypic response. Reliable results obtained with short-term progeny testing in slash pine (FRANKLIN and SQUILLACE, 1973) illustrated the efficacy of this procedure, although at that time the causal mechanisms were not suggested. A strikingly high offspring-parent correlation for height was obtained by comparing 3-year-old offspring grown under accelerated, highly intensive culture with heights of their 25-year-old parents grown in a widely spaced plantation (Figure 10). Similarly high correlations were also found for other traits.

Further Research

Further research is needed (1) to determine if genetically superior families grown at very close spacings and at relatively fast rates will rapidly undergo the stand development phases of the model as expressed by trends over time in phenotypic, environmental, and additive genetic components of variance, and (2) to evaluate the utility of this procedure as a method for identifying genetically superior families and individual trees. Some of this research is now underway at this and other laboratories in the Southeastern United States.

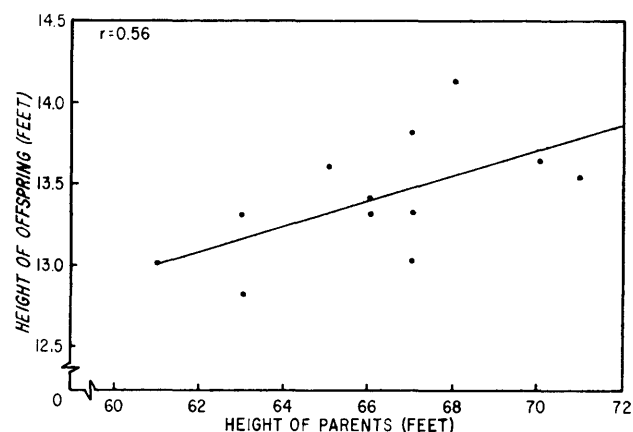


Figure 10. — Correlation of tree heights in 25-year-old slash pine parents and their 3-year-old offspring. Data from FRANKLIN and SQUILLACE (1973).

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