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ABSTRACT

INHERITANCE AND EVOLUTION OF STEM FORM IN THREE NORTHERN PINE SPECIES

By

Timothy La Farge

The height/diameter ratio, the correlation between height and diameter, and taper (= diameter/diameter ratio) were measured at ages 10 to 13 in replicated plantations in Michigan to obtain information on stem form inheritance and evolution.

In a range-wide provenance test of 55 ponderosa pine (Pinus ponderosa) seedlots, correlations between height and diameter were high despite significant differences in the height/diameter ratio. That ratio was considerably higher for northern ecotypes (2.47) than for southern ones (2.14), due both to differences in hardiness and to different growth patterns.

Taper (= ratio of mid- to basal diameter, mid-diameter being measured at the mid-point of the 4th internode from the top) differed strongly between varieties. The Pacific Coast var. ponderosa, which is native to a region with summer drought and heavy wet snow, was most nearly cylindrical with an average taper of 0.64. The Interior

var. scopulorum was more conical (average taper = 0.56). The taper difference corresponds most strongly to the July-August/annual precipitation ratio, but the adaptive significance of this correlation is not clear.

In a range-wide provenance test of 15 eastern white pine (Pinus strobus) seedlots, there was significant variation for height, diameter, volume and the height/diameter ratio, but not for taper. The height/diameter ratio, which varied from 5.55 in a southern source to 6.46 in a northern one, was strongly correlated with north latitude and January temperature.

In a Scotch pine (Pinus sylvestris) provenance test of 12 origins replicated at each of two locations, varieties accounted for most of the variation in height, diameter and taper. Trees of Scandinavian varieties lapponica and septentrionalis had more cylindrical stems (average taper = 0.74) than did trees of German varieties borussica and hercynica (average taper = 0.66). The height/diameter ratio was lower in the northern var. lapponica (3.14) than in the southern var. hercynica (3.60), contrary to the trend found in ponderosa and eastern white pines.

Two Scotch pine open-pollinated progeny tests were also studied. One consisted of 9 Norwegian families grown at two sites; the other included 80 East German families grown at three sites. High genetic correlations ($r_G = 0.68$ to 0.97) were obtained between height and diameter,

suggesting that most growth-rate genes control both height and diameter together, the remainder controlling height and diameter separately. With such high genetic correlations, gains in volume were the same whether selection was for height, diameter or volume.

Taper was not a useful selection criterion to improve volume growth. Sources with the greatest height and diameter growth had the greatest volumes even when they had the least cylindrical stems.

These trees were 7 to 19 feet tall when measured, and the crowns had not yet closed. Forecasting future volume production after crown closure depends on assumptions made about relative height and diameter growth rates between genotypes. If there is an upper ecological limit to volume production, the diameter growth rate differences between slow- and fast-growing genotypes decrease to compensate for differences maintained in height growth, so that volume growth becomes the same. Or, with an upper limit in volume, basal area growth rates may be the same after closure, so that differences in volume production between genotypes are proportional to height growth only. If there is no upper limit, the diameter growth rate differences continue to increase, so that fast-growing genotypes maintain or increase their advantage in yield.

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IN THREE NORTHERN PINE SPECIES

By

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To Fran and Jason

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CHAPTER I

INTRODUCTION

An important objective in most forest tree improvement programs is to select and breed geographic races and/or individual trees for superior growth. Height and diameter are usually measured, and basal areas and volumes are derived from these variables as in standard management practice. However, stem form may also be heritable. Numerous investigations have studied genetic variation in total height and/or diameter at breast height (d.b.h.), but few have studied the inheritance of stem form traits.

Height/diameter ratios, correlations between height and diameter and diameter/diameter ratios may provide information on the heritable growth relationships between height and diameter. This information may be useful for both practical and theoretical considerations. In practice, high genetic correlations between height and diameter mean that selection in tree breeding programs can be simplified and costs lowered by restricting measurement to only one trait. For example, in very young progeny or provenance tests, height is easier to measure than diameter, since branches may reduce the accessibility of the stem. Conversely, in

merchantable plantations, d.b.h. is much less costly to measure than total height. Special volume tables could be developed for such plantations, so that selection within them could be based on diameter alone. Moreover, the degree to which selection for one trait (d.b.h. in this case) results in the response of another correlated trait (total height) can be determined for a given intensity of selection (Falconer, 1960). Animal breeders utilize the correlated response to selection.

These relationships are also of theoretical interest, because with more information we may be able to formulate better hypotheses relating gene action to growth. By combining analyses of variance of height/diameter ratios with correlations between height and diameter, we may be able to determine the feasibility of breeding for growth improvement by means of selection for one trait only. To test the feasibility of one-trait selection, it is desirable to consider three possible relationships between height and diameter.

The first possibility is that, if height varies genetically but diameter does not (or vice-versa), the height/diameter ratio will vary among genotypes. In this case there is no need to measure any variable other than the genetically variable one when we make selections. Instead, if only height varies genetically, we should assume

an average diameter and develop volumes based on the variability in height.

A second possibility might be that both height and diameter growth are highly correlated because they are controlled by the same genes, in which case the height/diameter ratio would not vary greatly. In this case as in the first, it is only necessary to measure one variable, height or diameter, at any given age or site.

Finally, the third possibility is that height and diameter are each genetically controlled but not by the same genes, so that their genetic correlation is low. In this situation, the measurement of both height and diameter should be included in any breeding program. Moreover, the height/diameter ratio will probably vary genetically.

Aside from the practical desirability of reducing volume determination to the measurement of a single parameter, the height/diameter ratio is an indicator of stem form or taper: the greater the height/diameter ratio, the less conical is the stem as a whole. However, the height/diameter ratio does not reflect variations in the rate of taper in the branch-free bole or within the crown. In order to detect these variations it is necessary to measure two or more diameters at different heights on the stem. Although some workers have used height/diameter ratios as estimates of taper (Nilsson, 1968; Johnsson, 1960; Callaham and Liddicoet, 1961; Squillace and Silen, 1962), in the present

study the height/diameter ratio and taper (= diameter/diameter ratio) will be considered as separate traits.

It is generally considered desirable to grow trees that have thin branches and little taper (Johnsson, 1960; Larson, 1963). These attributes are desirable whether the trees are to be grown for sawtimber or pulpwood. The reduced tapering results in a more cylindrical stem, so that there is more usable wood volume in each tree having any given height and diameter. Moreover, thin branches produce smaller knots and lead to earlier natural pruning.

The height/diameter ratio may also be an indicator of adaptation, especially to winter hardiness. When trees are moved northward, winter injury or dying back of the terminal leaders often results. If diameter growth is not so inhibited, low height/diameter ratios result. It may be that diameter growth is the truest indicator of the genetic potential for growth which such trees would have when planted at lower latitudes.

Adaptive trends may have evolutionary significance. Stem form variations may reflect adaptations to such climatic factors as wind or snow. Present geographic barriers may reflect former geologic or climatic disturbances. Hence, stem form differences in presently separated populations may provide clues to adaptations to ancient climatic trends.

CHAPTER II

CONCEPTS OF STEM FORM VARIATION

An examination of the genetic control of height/diameter ratios in temperate zone trees cannot be adequately undertaken without some consideration of the factors affecting the development of stem form in general.

Larson (1963) reviewed the physiological, environmental and genetic factors affecting stem form development in forest trees. He defined stem form "as the relative rate of change in stem diameter with increasing tree height. . . ." The rate of change of stem taper is correlated with crown size and the length of the branch-free bole. Within the crown, the stem tapers strongly because of the cumulative contribution to stem growth of the increasing number of branches downward from the top. As the clear bole lengthens upward due to natural pruning, the lower stem becomes more cylindrical, the principal factor being a tendency for growth to be concentrated near the crown base.

Since dominant and codominant trees tend to have larger crowns than intermediate and suppressed trees in natural stands, they also tend to be more conical. Generally, favorable conditions tend to shift growth lower on

the stem. Hence, stem form or taper is largely subject to manipulation by silvicultural methods, especially thinning and pruning. Thinning favors a conical bole, since the resultant wider spacing retards natural pruning. Artificial pruning favors a cylindrical stem by shifting the crown base upward.

As responsive as stem form is to environmental effects and cultural practices, Larson concluded that a tree's heredity predetermines it to a basic form which can only be modified by environment and silviculture. This basic form was defined by Duff and Nolan (1953), who devised a stem analysis technique which distinguishes three growth sequences of ring width: (1) from pith to bark; (2) in the same annual ring at different heights; and (3) at the same number of rings from the pith at different heights.

In a study of red pine (Pinus resinosa Ait.), ring width was found to vary independently of age or position on the tree when the samples were removed from successive internodes in a vertical sequence up the stem at a constant number of annual rings from the pith. Thus the annual ring corresponding to each added annual increment was sampled at a different height on the tree. Chronological age increases in this sequence; physiological age, which is probably a more important cause of variation in ring width, is held constant. Ring width also varied systematically when sampled in any single annual ring at successively higher

internodes. It varied from pith to bark when sampled in successive annual rings within a given internode. Duff and Nolan demonstrated by means of stem analyses of trees on different sites and in varying stand densities that the up-and-down and horizontal sequences conform to a basic pattern which is fundamentally determined by the hereditary potential of the tree.

Pederick (1970) explored the genetic control of stem form or taper in loblolly pine (Pinus taeda L.). There was very little variation among half- and full-sib families in progeny tests. He found statistically significant differences among families in form class, but these differences had little effect on volume determinations. There was, however, considerable genetic variability in bark thickness in 6- to 10-year-old loblolly plantations. Heritability based on single trees was found to be about 0.65. Pederick recommended selection for diameter growth and bark thickness simultaneously in order to maximize gains.

Johnsson (1960) cited a 1958 study by Nilsson of Pinus sylvestris L. and Picea abies (L.) Karst., in which the height/diameter ratios of mother trees were significantly correlated with the same ratios in their 10-20 year-old progenies ($r = +0.28$). Johnsson suggested that tapering, as measured by the height/diameter ratio, was less dependent on the environment and was controlled by fewer genes than growth rate. However, in a more recent study of Scotch pine,

Nilsson (1968) obtained negative correlations between parents and their half-sib progenies for the same traits ($r = -0.25$ and -0.24 for studies involving 18 and 34 families respectively).

Callaham and Liddicoet (1961) found height/diameter ratios of ponderosa pine (Pinus ponderosa Laws.) and Jeffrey pine (P. jeffreyi Grev. & Balf.) in California to be highly correlated with elevation at the seed source. The stockiest origins came from the highest elevations in two of the three plantations in which they were tested, and the slimmest sources were from low or middle elevations. The plantation in which the height/diameter ratios were relatively constant was located at the highest elevation (5,650 feet). The environment at this site rendered all origins about equally stocky.

Squillace and Silen (1962), in a similar but older study of ponderosa pine in northern Idaho, showed that the absolute values of the height/diameter ratios changed over a 20-year period. The relative rankings of the origins remained the same, however. The origins with the slimmest trees were derived from the middle or lower elevations and the stockiest from the highest. Similarly, Nilsson (1968) found that northern provenances of Scotch pine tended to have low height/diameter ratios.

CHAPTER III

OBJECTIVES

The objectives of this study were: (1) to determine the degree of genetic control of height and diameter growth and of relative diameter growth at different heights on the stem; (2) to suggest the evolutionary and physiological causes of variation in the height/diameter ratio and stem taper; (3) to determine the relevance of genetic variation in stem form to accepted measurements of growth in tree improvement research and in commercial practice, where volume data are important; and (4) to determine the extent to which measurements of either height or diameter can be substituted for measurements of both.

To accomplish these objectives, I measured two different kinds of experiments in three pine species, hoping thereby to learn how conclusions based on one species can be applied to others.

CHAPTER IV

MATERIALS AND METHODS

This work involved analysis of data from three pine species located in ten plantations at three Michigan State University experimental forests in Michigan.

Material

All plantations were established as randomized complete-block experiments, with 8 X 8 foot spacing. Intensive weed control was practiced at each plantation for 1 to 3 years after planting, with the result that survivals have been high and growth good. Most of the plantations have been studied by others. The most pertinent details about the individual experiments are given below.

Ponderosa Pine

(Pinus ponderosa Laws.), range-wide provenance test at W. K. Kellogg Forest in southwestern Michigan, 55 seedlots, established in 1962 with 2-0 stock, 7 replicates, 6 trees per plot; site nearly level, with a sandy loam soil in corn the year before planting; measured at age 10 from seed; previously reported on by Wells (1964a, 1964b) and Wright et al. (1969).

Eastern White Pine

(Pinus strobus L.), range-wide provenance test at Kellogg Forest, 15 seedlots, established in 1960 with 2-1 stock, 10 replicates, 4 trees per plot; site nearly level, with a fertile loam soil in corn in the year prior to planting; measured at age 13 from seed; previously reported on by Wright et al. (1963) and Wright (1970).

Scotch Pine

(Pinus sylvestris L.), two kinds of experiments.

Provenance test: 12 seedlots of four varieties from Scandinavia, Germany and Czechoslovakia, established in 1961 at Kellogg and Fred Russ Forests, both in southwestern Michigan, with 2-1 stock, 10 replicates per plantation, 4-tree plots; Kellogg site variable, hilly and flat with loamy sands and sandy loams; Russ site flat, loamy, in corn the year before planting; measured at age 11 from seed; previously reported on by Wright et al. (1966).

Progeny tests: 9 Norwegian open-pollinated families, established in 1961 at the Kellogg Forest with 2-1 stock, 4 replicates on each of two sites, 4-tree plots; one site an Oshtemo loamy sand and hilly, the other a Hillsdale sandy loam and flat; measured at age 11 from seed; previously reported on by Wright (1963).

Eighty East German open-pollinated families, established in 1961 at the Kellogg, Russ and Dunbar Forests, the

Dunbar Forest located in the Upper Peninsula, 5 replicates per site, except for Kellogg with 7 replicates, 4-tree plots; soils loamy sands and sandy loams at Kellogg and Russ, loamy at Dunbar; Dunbar site very wet at certain months.

The Kellogg and Russ Forests are within 60 miles of each other in southwestern Michigan and have similar climates. January temperature averages about 24^o F and average annual precipitation is about 32 to 34 inches. The Dunbar Forest is located near the eastern tip of the Upper Peninsula. It has an average January temperature of about 15^o F, and the annual precipitation averages 28 inches.

The seed for the ponderosa pine experiment was obtained by O. O. Wells with the permission of R. Z. Callaham of the U.S. Forest Service, who arranged for its collection. This material was the basis for Wells' Ph.D. dissertation, which considered traits that had been measured in the nursery. The eastern white pine seed was collected by the U.S. Forest Service in 1956 and was sown by that agency in 1957. All of these experiments, including the Scotch pine studies, were done as part of the NC-51 regional tree improvement project titled "Improvement of Forest Trees Through Selection and Breeding," which was supported in part by the U.S. Department of Agriculture.

The height and diameter data for the Scotch pine progeny tests were donated by G. E. Howe, who studied the genetic variability of a number of traits in Scotch pine for his doctoral dissertation.

General Status of the Plantations

In all plantations, survival and growth were average or better-than-average in comparison with plantations of the same species on similar sites in Michigan. Crown closure had not yet occurred in any plantation, so that competition was not a factor.

The ponderosa pine plantation at the W. K. Kellogg Forest had an average total height of 7.3 feet. The crowns were so vigorous that it was not possible to see someone five rows away.

The eastern white pine plantation had exceptional growth. Total height averaged 18.6 feet, and the trees were on the verge of crown closure.

Although the Scotch pine plantations differ in site quality, all have good growth and low mortality. Average total height at different sites varied from 8.3 feet at the Dunbar Forest to 13.7 feet at the Fred Russ Forest.

Measurements

Five traits were measured: (1) total height; (2) 5-year height growth (= height growth of last five years); (3) basal diameter, measured six inches above ground level; (4) d.b.h.; and (5) mid-diameter. I defined "mid-diameter" as the mid-point of the fourth internode from the top in ponderosa pine, as the mid-point of the sixth internode from the top in eastern white pine, and as the mid-point of the

fifth internode from the top in Scotch pine. These are uninodal species with one growth flush per year.

All traits were not measured on every species. Five-year height growth was not measured in ponderosa or eastern white pine, and basal diameters were not measured in the Scotch pine progeny test material. D.b.h. was measured in the eastern white pine plantation only.

All diameter measurements were done to the nearest 10th inch with wooden calipers. Also, at every measuring point on every tree, two measurements were made perpendicular to each other and averaged. Total height was measured to the nearest quarter of a foot. All data were recorded by individual trees, and all trees were measured in every plot.

Calculation Procedures

Height/diameter ratios, taper and volume were calculated from the basic measurements. Taper was calculated as the mid-diameter/basal diameter ratio.

Volume was calculated directly from the height and diameter data. In the ponderosa pine data the volume was calculated as:

$$V = \frac{\pi (D_b^2) h}{4} \cdot (D_m/D_b) = \frac{\pi (D_b) (D_m) h}{4} , \quad (1)$$

where V = volume, D_b = basal diameter, D_m = mid-diameter, and h = total height. To convert to volume in cubic feet,

the denominator was multiplied by $12^2 = 144$. Also, this equation was multiplied by $\frac{1}{2}$ to give a standard correction for taper. Hence, the final equation was:

$$V = \frac{\pi(D_b)(D_m)h(\frac{1}{2})}{4(144)} = \frac{\pi(D_b)(D_m)h}{1152} \quad (2)$$

Since taper was included as a variable, inclusion of the constant of $\frac{1}{2}$ probably caused an underestimate of actual volume but did not affect relative volumes.

In the eastern white pine data volume was determined as:

$$V = \frac{\pi(D_{bh}^2)h(D_m/D_b)}{1152} \quad (3)$$

where D_{bh} = diameter at breast height.

In the Scotch pine provenance test data, volume was determined by the summation of the volumes of two tree sections as follows:

$$V = \frac{(\pi D_b^2 + \pi D_m^2)h_1}{1152} + \frac{\pi(D_m^2)h_2}{1152} \quad (4)$$

where h_1 = the height from the tree base to the fifth whorl from the top, and h_2 = the length of stem from the fifth whorl to the top.

In the Scotch pine progeny-test data for the nine Norwegian families, the volume calculation was:

$$V = \frac{\pi(D_m^2)h}{1152} \quad (5)$$

Volumes were not determined from the data for the progeny test of 80 East German families.

The three derived variables were calculated from the single-tree data for most analyses. However, in the analyses of 80 East German families, the height/diameter ratios were calculated from plot means. There was very little difference between height/diameter ratios calculated from plot means and those calculated from individual trees.

Statistical Methods

Since all plantations were established as randomized complete-block designs, the standard analysis of variance (two-way classification) was applied to the data from each experiment. Additionally, in the ponderosa pine data a two-level nested analysis of variance with unequal subclass numbers was performed to detect the amount of variation among varieties and among ecotypes within varieties. Origin means were used as items.

In the Scotch pine provenance test, a one-level nested analysis of variance, with unequal numbers of origins per variety, was performed to determine the significance of differences among the four varieties. Tukey's "hsd" test was employed as a test of significance of differences among origins within varieties.

In the half-sib progeny tests of Scotch pine, also established as randomized complete-block designs, more refined procedures were used. The progeny test of nine

Norwegian families was analyzed on the basis of data obtained from two sites (plantations 2-61 and 4-61) at the W. K. Kellogg Forest. This combined analysis was performed to measure genotype X environment interactions. One site was hilly, the other flat.

The primary objective of this progeny test was to obtain genetic correlations between height and diameter. Precise determinations of genetic correlations require large numbers of observations. Therefore, the data in this test were analyzed with individual trees within plots as experimental units.

Because many plots at both sites had missing trees, two trees per plot were randomly selected. Hence, since the design included four replications per site, the total number of observations was 144. The model for the degrees of freedom and expected mean squares obtained from this analysis is presented in Table 1.

The primary reason for studying the Scotch pine progeny test of 80 East German families was that its large size favored precise estimates of the genetic correlations. Since this experiment was large, plot means as items provided an adequate number of observations.

This progeny test was analyzed twice. In one analysis, only the material planted at the W. K. Kellogg Forest was considered. There were seven replications, but only the families from each stand were replicated together,

Table 1. The expected mean squares or cross products used in the analyses of variance and covariance of the half-sib progeny test of nine Norwegian Scotch pine families

Source	Degrees of Freedom	Expected mean squares ^a
Family	$f-1$	$\text{Var } (e) + n \text{ Var } (FR(S))$ $+ nr \text{ Var } (FS) + nsr \text{ Var } (F)$
Site	$s-1$	$\text{Var } (e) + n \text{ Var } (FR(S))$ $+ nr \text{ Var } (R(S))$ $+ nr \text{ Var } (FS)$
Replication within site	$s(r-1)$	$\text{Var } (e) + n \text{ Var } (FR(S))$ $+ nf \text{ Var } (R(S))$
Family X site	$(f-1)(s-1)$	$\text{Var } (e) + n \text{ Var } (FR(S))$ $+ nr \text{ Var } (FS)$
Family X replication within site	$s(f-1)(r-1)$	$\text{Var } (e) + n \text{ Var } (FR(S))$
Error	$fsr(n-1)$	$\text{Var } (e)$
Total	$fsrn-1$	

^aVar = variance.

so that stands were not replicated. Hence, comparisons could only be made among families within stands. There were 560 plot means. The analysis of variance model is given in Table 2.

Table 2. The expected mean squares or cross products used in the analyses of variance and covariance of the half-sib progeny test of 80 East German Scotch pine families from five stands tested at the W. K. Kellogg Forest

Source	Degrees of Freedom	Expected mean squares ^a
Stand	s-1	Var (e) + r Var (F(S)) + f Var (R(S)) + fr Var (S)
Family within stand	s(f-1)	Var (e) + r Var (F(S))
Replication within stand	s(r-1)	Var (e) + f Var (R(S))
Error	s(f-1)(r-1)	Var (e)
Total	sfr-1	

^aVar = variance.

In the second analysis, the data from the W. K. Kellogg, Fred Russ and Dunbar Forests were combined. Since stands were replicated at three locations, inferences about the genetic variation among stands could be made. The number of replications was five, the number available at every

location, and there are 1200 observations. The model for this analysis of variance and its expected mean squares is presented in Table 3.

In both progeny tests, these analyses were structured as random model analyses of variance. In this model, families were assumed to be random, since the mother trees were known to have been selected at random in their respective stands in Norway and East Germany.

The genetic correlation, as discussed by Falconer (1960) and Becker (1967), was calculated as:

$$r_G = \frac{\text{Cov } A_{xy}}{\sqrt{(\text{Var } A_x)(\text{Var } A_y)}} \quad (6)$$

where $\text{Cov } A_{xy}$ and $\text{Var } A$ represent the additive or family covariance and variance respectively, and x and y represent the two different traits to be correlated. These variance components were obtained from the expected mean squares of the analyses of variance mentioned above. Phenotypic correlations were obtained in a similar manner but with the inclusion of the appropriate variances and covariances for error and for the genotype X replicate and X site interactions. The approximate standard error of each genetic correlation was obtained from the mean squares and variance components as outlined by Becker (1967).

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Table 3. The expected mean squares or cross products used in the analyses of variance and covariance of the half-sib progeny test of 80 East German Scotch pine families from five stands tested at the W. K. Kellogg, Fred Russ and Dunbar Forests

Source	Degrees of freedom	Expected mean squares ^a
Stand	s-1	Var (e) + fr Var (SP) + pr Var (F(S)) + r Var (PF(S)) + f Var (R(SP)) + pfr Var (S)
Place (= forest)	p-1	Var (e) fr Var (SP) + r Var (PF(S)) + f Var (R(SP)) + sfr Var (P)
Stand X place	(s-1) (p-1)	Var (e) + r Var (PF(S)) + f Var (R(SP)) + fr Var (SP)
Family X place in stand	s(p-1) (f-1)	Var (e) + r Var (PF(S))
Replication in stand X place	sp(r-1)	Var (e) + f Var (R(SP))
Error	sp(f-1) (r-1)	Var (e)
Total	spfr-1	

^aVar = variance.

In both progeny tests, correlated responses to selection were determined (Falconer, 1960). The responses calculated were the correlated response in total height to selection for diameter, the correlated response in diameter to selection for total height, and the correlated response in volume to selection for total height or diameter. The correlated responses were compared with the direct responses for each trait. Family selection was assumed for all response calculations.

Plot heritabilities were derived from the variance components in the analyses of variance. Family heritabilities were calculated according to methods and assumptions given by Comstock and Robinson (1952), Hanson, Robinson and Comstock (1956), and Namkoong, Snyder and Stonecypher (1966).

In addition to analyses of variance, correlation and regression methods were employed to determine certain relationships among variables. For every plantation, simple correlations, based on provenance or family means as items, were calculated among all combinations of variables.

Regression analyses were also performed. Volume was the dependent variable, and various combinations of height, diameter and taper were treated as independent variables to evaluate the contribution of each trait to the total genetic variability of volume growth. The following associated statistics were also obtained from these analyses: (1) the regression coefficients for each independent variable;

(2) the F ratio attributable to each independent variable; (3) the partial correlation coefficient between each independent variable and the dependent variable, when all other independent variables were held constant; and (4) the coefficient of determination (R^2), which is a measure of the contribution of the independent variables to the total variability of volume growth. Presumably most of this variation is genetic, since the units of data are family means obtained from a randomized complete-block design.

In the three provenance tests, simple correlations were also obtained between the height/diameter ratios and taper versus several geographic and/or climatic variables. The geographic and climatic variables that were correlated will be specified in those sections in which they are discussed.

Most statistical operations were performed on the CDC 3600 computer at Michigan State University. Canned programs obtainable from the STAT Series of the Michigan State University Agricultural Experiment Station were used. However, missing plot calculations, heritabilities, responses to selection, nested analyses of variance and many of the calculations needed to determine genetic or phenotypic correlations and their standard errors were performed on a desk calculator or slide rule.

CHAPTER V

VARIETAL AND ECOTYPIC DIFFERENCES OF
STEM FORM IN PONDEROSA PINE

The ponderosa pine plantation at the W. K. Kellogg Forest contains trees grown from seed collected in 55 different places. The collections sampled the greater portion of the species range in the western United States. Hence, the seedlots analyzed in this experiment provided a good opportunity to determine varietal and ecotypic differences in growth and stem form.

Climatic and geographic data were available for all seedlots. Therefore it was also possible to determine to what extent certain regional geographic and climatic factors may have influenced the evolution of stem form and other traits. Hence, my study objectives were: (1) to determine if there were significant differences in taper, height, diameter and the height/diameter ratio among varieties and ecotypes within varieties; (2) to determine what climatic or geographic factors were strongly correlated with these differences and might be selective forces in their evolution; and (3) to determine the contribution of taper to genetic variation in volume growth.

Varietal Differences in Taper

The two varieties of ponderosa pine, Pacific Coast var. ponderosa and Interior var. scopulorum, may be delineated in Figure 1 if a line is drawn from western Montana to southern California.

Taper was defined as the mid-diameter/basal diameter ratio. As indicated in Table 4, the higher taper values of the Pacific Coast var. ponderosa mean that it is the most nearly cylindrical or bullet-shaped. In contrast, the Interior var. scopulorum was relatively conical. By far the greatest portion of the variance in taper was due to the differences among varieties (Table 5). This strong difference was true despite considerable variation in height and diameter growth within each variety. For example, fast-growing and hardy seedlots from Montana had the same taper as slow-growing trees from southern California that were susceptible to winter injury. No other growth trait measured showed such a difference between varieties.

Varietal Differences in Other Traits

Strong differences between varieties have also been observed for other traits in the same experiment. These differences, as reported by Wells (1964a), Wright et al. (1969) and Read (1971) are summarized in Table 6. The concentration of each of the five foliar mineral elements which showed varietal differences was highest in the Pacific

Figure 1. Natural distribution of ponderosa pine, including the origins of 55 seedlots comprising the provenance test at the W. K. Kellogg Forest. This figure was taken from Wells (1964a).



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Table 4. Variety and ecotype means for basal diameter, mid-diameter and taper in ponderosa pine

Variety and ecotype	Diameter		Taper (= ratio of mid- to basal diameter)	
	Basal	Mid		
	<u>Inches</u>	<u>Inches</u>	<u>Inches/inches</u>	
<u>ponderosa</u>				
Nor. Plateau	3.8	2.4	0.619	
Coastal Oregon	3.4	2.1	0.638	
Nevada	3.2	2.0	0.638	
Nor. Calif.	3.0	2.0	0.653	
Sou. Calif.	2.8	1.8	0.646	
Average	3.2	2.0	0.636	
<u>scopulorum</u>				
Nor. Interior	3.5	1.9	0.536	
Colorado	3.0	1.7	0.588	
Utah	3.0	1.7	0.578	
Utah--north. New Mexico	3.7	2.1	0.553	
Ariz.--south. New Mexico	3.6	2.0	0.559	
Average	3.4	1.9	0.560	
Tukey's hsd: ^a	5% level	0.6	0.3	0.045
	1% level	0.7	0.4	0.055

^aEach hsd applies only to comparisons among ecotype means, not to variety means.

Table 5. Percentages of total variance in both diameters and taper accounted for by differences among varieties, ecotypes and seedlots of ponderosa pine

Source of variation	Variances as percents of total variance		
	Diameter		Taper (= ratio of mid- to basal diameter)
	Basal	Mid	
Variety	0	0	77***
Ecotype within variety	56***	51***	4
Seedlot within ecotype	44	49	19
Total	100	100	100

***Significant at the 0.1% probability level, using an analysis of variance with 1, 8 and 45 degrees of freedom for variety, ecotype and seedlot respectively.

Table 6. Major sources of variation--whether between varieties, ecotypes or seedlots--in ponderosa pine traits measured by Wells (1964a) and Wright et al. (1969)

Trait	Variety	Ecotype within variety	Seedlot within ecotype	Remarks
Winter injury	--	*	--	Injury greatest on trees from Calif., W. Oreg., Ariz., and New Mex.
Lammas growth	--	**	--	Most in southern origins
Bloom on twigs	--	**	--	Most on Southern Interior ecotypes
Rabbit browsing	**	--	--	Most on var. <u>ponderosa</u>
Bud color	**	--	--	Reddest on var. <u>ponderosa</u>
Bud scale appression	**	--	--	Most appressed on var. <u>ponderosa</u>
Foliar concentration of:				
N	**	--	--	Highest in var. <u>ponderosa</u>
P	**	--	--	
K	**	--	--	
B	**	--	--	
Ca	*	--	*	
Mg	--	--	**	
Mn, Fe, Cu	--	--	**	

* $\geq$ 40% of the variation for that trait.

** $\geq$ 50% of the variation for that trait.

Coast var. ponderosa. These differences may have adaptive significance, since it seems likely that the accumulations of the major elements are important to the survival and growth of the trees.

Regional Climatic Differences

Ponderosa pine occurs mostly within the arid transition zone of the West. This transition zone includes a range of climatic types designated as: (1) humid; (2) moist subhumid; (3) dry subhumid; (4) semiarid; and (5) arid (Yearbook of Agriculture: Climate and Man, 1941). The regions occupied by ponderosa pine contain the greatest climatic variation per unit of area in the United States.

The most striking differences between the regions occupied by the two varieties is in the ratio of July-August to annual precipitation (Table 7). The Pacific Coast var. ponderosa occupies a summer-dry region with only 1 to 8 percent of the total annual precipitation occurring during July and August. The Interior var. scopulorum occupies a summer-moist region, in which 14 to 34 percent of the total annual precipitation occurs during the two summer months.

The region occupied by the Pacific Coast var. ponderosa has a generally greater total annual precipitation than falls on the Interior var. scopulorum. However, there is considerable variation in total annual rainfall within each of the two regions. The difference between regions is

Table 7. Major climatic differences between regions occupied by the varieties of ponderosa pine and variation within those regions

Region occupied by variety and ecotype	<u>July-August</u> annual precipitation ratio	Annual precip- itation	January temper- ature
	<u>%</u>	<u>Inches</u>	<u>°F</u>
<u>ponderosa</u>			
Nor. Plateau	8	18	22
Coastal Oregon	2	41	39
Nevada	4	21	23
Nor. Calif.	1	46	33
Sou. Calif.	1	40	38
Average	3	35	32
<u>scopulorum</u>			
Nor. Interior	21	19	22
Colorado	26	31	22
Utah	14	23	17
Utah--north.			
New Mexico	24	19	22
Ariz.--south.			
New Mexico	34	23	30
Average	25	21	24
Sources of variation	Variances as percents of total variance		
Region	80	35	29
Ecotype within region	10	23	45
Station within ecotype	10	42	26
Total	100	100	100

not so striking as was the case for the seasonal distribution of precipitation.

There is also a difference in the average January temperature. In the mountains of California and the Pacific Northwest, the mean January temperature varies from 22° F to 39° F, whereas in the Interior it varies from 17° F to 30° F.

Other factors which might differ between the Pacific Coast and Interior regions are: (1) wetness of snow; (2) wind velocity; and (3) fire. Each of these factors could exert strong selection pressures on stem taper if they differ between regions.

Evolution and Adaptation of Taper

Seasonal rainfall distribution: The July-August/annual precipitation ratio is the most puzzling environmental factor to relate to the adaptation of stem taper. It is the only observed factor which varies strongly between the variety regions in a manner that parallels the taper difference between varieties. However, there is no clear reason why stem taper should be adapted to different moisture regimes.

One possible explanation is that the surface-to-volume ratio is lower in cylindrical stems than in conical stems. To the extent that a lower surface-to-volume ratio might reduce transpiration, this could be a selective trait.

S. N. Stephenson told me that he has observed similar variations in the surface-to-volume ratios of species of Cactaceae and Bursera in Baja, California. However, by far the major portion of the transpiration in pines probably occurs through the stomata in the needles, not through the bark. Hence, the surface-to-volume ratio would not seem to be an important selective advantage against moisture deficits.

Although the selective advantage of a cylindrical stem in a summer-dry environment is not clear, it is reasonable to assume that, if stem taper responds in some way to water stress, water deficits occurring during July and August would exert the greatest selection pressure. Stem taper is a function of variations in radial growth, and radial growth occurs later in the growing season, whereas most height growth occurs in the spring (Larson, 1963). It follows that stem-form variations are most apt to be controlled by differences in summer rainfall which affect the controls of radial growth.

Foliar mineral content: The observations by Wright et al. (1969) of varietal differences in the foliar content of five mineral elements indicate a similar paradox (Table 6). They suggested that the Pacific Coast var. ponderosa may have developed a high uptake mechanism, since the soils in the more moist Pacific Coast region are more leached than those in the relatively dry Interior region. If such an

uptake mechanism should exist, it might affect the radial distribution of stem growth indirectly. Such a mechanism is not known.

Mean annual precipitation: Annual precipitation may be directly related to foliar mineral content. An uptake mechanism which evolves in response to excessive leaching is probably an adaptation to annual rainfall. However, unless foliar mineral nutrient levels are related to taper, the relationship of annual precipitation to taper is not apparent.

Mean January temperature: The relevance of January temperature to taper is not clear.

Wetness of snow: An environmental factor which is a function of both moisture and temperature regimes is the wetness of snow. The Pacific Coast region, being warmer and more moist in winter, has a much greater frequency of wet snow than the Interior.

Selection for resistance to breakage of stems and branches by wet snow could also affect stem form. It could be direct in that a more cylindrical stem would seem to be structurally more resistant to breakage in its upper portion than would a conical stem.

Indirect selection for a more cylindrical stem might result from the fact that heavy snow favors smaller branches and a larger, narrower and more spruce-like crown. Such an intimate relationship between crown form and stem form has

been observed in many instances in the past (Larson, 1963). In areas of heavy snow, slender crowns permit maximum crown vigor while providing smaller branches which retain less snow. Several investigators have observed more cylindrical stem form with increasing latitude and elevation in Scotch pine and have attributed this trend to resistance to snow-breakage (Larson, 1963).

Wind velocity: Another possible explanation of varietal differences is that a conical stem taper bestows a selective advantage for resistance to wind. Larson (1963) reviewed literature devoted to the importance of stem form in determining resistance to wind. Generally, tree boles in windy situations are most conical. The conical boles of the Interior var. scopulorum sources are best adapted to the stresses of a wind-swept existence. However, for this factor to be important, the trees of the Interior var. scopulorum must be frequently exposed to more severe winds than are the trees of the Pacific Coast var. ponderosa.

Data obtained from the U.S. Department of Commerce (Local Climatological Data: Annual Summary with Comparative Data, 1969) revealed a slight difference in average wind speed between the Pacific Coast and Interior regions. Average wind velocity, based on data from 11 stations in the Pacific Coast region, was 8.2 mph. The corresponding figure from the Interior region, based on data from 16 stations,

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was 9.9 mph. However, there was so much difference within regions that the difference between regions was not significant.

It seems questionable whether an average difference in wind velocity of 1.7 mph is a strong enough selection differential between varieties when the plasticity of tree stem responses is considered. Jacobs (1954) showed that the diameter growth of pine trees in Australia prevented from swaying by guy wires was so reduced that they were no longer able to support themselves when the wires were removed.

It is possible that differences in wind speed were much greater at some former geologic time. Geographic separation may have maintained adaptive differences in stem form after much of the selection pressure had ceased to exist.

Exposure to wind does vary with stand density, which differs between the two varieties. The higher annual precipitation of the Pacific Coast region favors relatively dense stands. Ponderosa pine typically grows in open, park-like stands in the Interior. Trees growing in dense stands are less exposed to wind stress than are trees growing in open stands. Hence, the trees of the Interior var. scopulorum might have developed a conical stem from an adaptation to growth in open situations.

Fire: Fire is another factor which could affect stem taper. It is possible that trees adapted to survival

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in regions of frequent burning develop thicker bark on the lower portions of their stems. Such a bark distribution would contribute to a more conical stem.

Since bark thickness was not measured, the effect of fire could not be evaluated. However, if fire is an important factor, there must be a greater difference in fire occurrence between variety regions than within regions. According to the records, this does not appear to be the case.

Curtis and Lynch (1965) reported that fire was common in many Pacific Coast and Interior portions of the range of ponderosa pine before the advent of white man. Fire has occurred at 8- to 10-year intervals since the 16th Century in the ponderosa pine forests of California, Oregon and Washington.

Fire has also occurred in the Interior region. Pine stands in Arizona have been frequently burned. The Great Plains, including those regions occupied by ponderosa pine forests or stands, have a history of fire as an ecological factor in the regeneration of grasslands. Hence, there appears to be no difference in fire occurrence between the two regions.

Adaptation versus genetic drift: Finally, the possibility remains that taper evolved as a non-adaptive trait. Isolation and restricted population sizes during glacial advances could have resulted in random genetic drift. An

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examination of geological events of the last three epochs may help to clarify this point.

Crustal uplift and the formation of the Great Basin in the early and middle Miocene (Dunbar, 1960) may have been the initial geological event separating the two varieties. However, it seems more likely that the species was not divided into two populations until either the late Pliocene or middle Pleistocene time. According to Dunbar (1960), the greatest crustal upheaval in California occurred in the middle Pleistocene.

Once crustal uplift had rendered the terrain and climate of western North America sufficiently diverse, the environment of the Great Basin could no longer support ponderosa pine. The species was forced to migrate to slightly moister sites at higher elevations both east and west of the Great Basin. Hence, two populations were created.

The Pleistocene is distinguished from the Pliocene by the occurrence of four major glaciations. The Great Basin was a non-glaciated region. However, Flint and Gale (1958) reported evidence of pluvial periods corresponding to the two most recent glaciations. Stratigraphic columns and radiocarbon dates from Lake Searles, California indicate that the earliest pluvial period began about 46,000 years ago. Further, Roosma (1958) found juniper pollen in the mud portions of the column and sagebrush pollen from the saline section. Pine pollen was not found.

Woodbury (1947) reported that a juniper-pinyon community in northern Arizona and Utah lies mainly within the 10-15 inch annual precipitation belt. In contrast, the lower limit for submontane shrubs and ponderosa pine is about 15 inches. From this evidence it appears that the climate within the Great Basin did not get sufficiently moist during pluvial periods for ponderosa pine to reoccupy the region. Hence, the two varieties were possibly separated as early as the Miocene and no later than the middle Pleistocene.

In the context of this geologic sequence, it seems unlikely that the varietal differences are non-adaptive. Small populations no doubt were separated from the rest of the species by geographic barriers in several portions of the range. However, glacial advance was very limited in the western United States (Flint, 1957), so that the sizes of the major populations could not have been sufficiently decimated for genetic drift to occur. Hence, it seems most likely that differentiation between the two varieties as a whole is the result of adaptation to climatic changes that have been developing since the middle or early Pleistocene.

Variation Within Varieties in
the Height/Diameter Ratio

In sharp contrast to the difference between varieties in stem taper, total height, diameter and the height/diameter ratio varied among ecotypes within varieties, but not between varieties (Tables 8 and 9). There is also an apparent correlation between total height and the height/diameter ratios. An analysis of origin means as items showed that total height was correlated with the total height/basal diameter ratio ($r = 0.59$) and the total height/mid-diameter ratio ($r = 0.64$). Both correlations are significant at the 1 percent probability level.

The highly significant differences obtained among ecotypes (Table 9) are due to the fact that the North Plateau and Northern Interior trees were the tallest and had the largest height/diameter ratios. The two northernmost ecotypes also had the lowest percentages of winter injury. It follows that the slower growth of the southern ecotypes may be due to either winter injury or to a general lack of winter hardiness in southern Michigan.

An analysis of total height and the two height/diameter ratios with winter injury as a covariate revealed that winter injury cannot fully explain the ecotypic differences for these traits (Table 10). The variability for these traits was not significantly altered by the effect of winter injury.

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Table 8. Variety and ecotype means for total height and the height/diameter ratios in ponderosa pine

Variety and ecotype	Total height	<u>Total height</u> Basal diameter	<u>Total height</u> Mid-diameter
		ratio	ratio
	<u>Feet</u>	<u>Feet/inches</u>	<u>Feet/inches</u>
<u>ponderosa</u>			
Nor. Plateau	9.2	2.39	3.88
Coastal Oregon	7.6	2.27	3.55
Nevada	6.5	2.04	3.19
Nor. Calif.	6.7	2.19	3.35
Sou. Calif.	5.9	2.13	3.35
Average	7.0	2.21	3.48
<u>scopulorum</u>			
Nor. Interior	8.6	2.47	4.62
Colorado	6.8	2.30	3.91
Utah	6.4	2.12	3.67
Utah--north. New Mexico	7.8	2.08	3.78
Ariz.--south. New Mexico	7.6	2.14	3.84
Average	7.6	2.22	3.97
Tukey's hsd: ^a			
5% level	1.4	0.15	0.39
1% level	1.6	0.19	0.47

^aEach hsd applies only to comparisons among ecotype means, not to variety means.

Table 9. Percentage of total variance in height, the height/diameter ratios and winter injury accounted for by differences among varieties, ecotypes and seedlots of ponderosa pine

Source of variation	Variances as percents of total variance			
	Total height	<u>Total height</u> Basal diameter ratio	<u>Total height</u> Mid-diameter ratio	Winter injury, 1964-65
Variety	0	0	38	36
Ecotype within variety	68***	73***	41***	40***
Seedlot within ecotype	32	27	21	24
Total	100	100	100	100

***Significant at the 0.1% probability level, using an analysis of variance with 1, 8, and 45 degrees of freedom for variety, ecotype and seedlot respectively.

Table 10. Percentages of total variance in height and the height/diameter ratios accounted for by differences among varieties, ecotypes and seedlots of ponderosa pine after the effect of winter injury as a covariate has been removed

Source of variation	Variances as percents of total variance		
	Total height	<u>Total height</u> Basal diameter ratio	<u>Total height</u> Mid-diameter ratio
Variety	0	14	0
Ecotype within variety	59***	53***	54***
Seedlot within ecotype	41	33	46
Total	100	100	100

***Significant at the 0.1% probability level, using an analysis of variance with 1, 8, and 45 degrees of freedom for variety, ecotype and seedlot respectively.

Although winter injury appears to explain little of the variation in the growth traits, the correlations between winter injury and the height/diameter ratios were quite strong (Table 11). These correlations differed little whether they were based on the whole species or on each variety alone.

Table 11. Simple correlation coefficients (r) between winter injury and the height/diameter ratios in ponderosa pine and its two varieties

Characters to which correlation applies	<u>Pinus ponderosa</u>	Pacific Coast var. <u>ponderosa</u>	Interior var. <u>scopulorum</u>
Winter injury versus:			
<u>Total height</u> Basal diameter ratio	-0.48**	-0.53**	-0.60**
<u>Total height</u> Mid-diameter ratio	-0.67**	-0.56**	-0.54**

**Significant at the 1% probability level.

A careful examination of Table 8 shows why winter injury did not account for more of the variation in the height/diameter ratios. The Nevada and Utah sources, which have been completely hardy in Michigan, had as low height/diameter ratios as the California sources. Also, the

Coastal Oregon sources, which were not hardy, had much better growth and height/diameter ratios than the California origins. However, differences in height growth and the height/diameter ratios between the hardy North Plateau origins and the non-hardy California origins were probably due to the effect of winter injury.

Climatic Differences Within Regions

Climatic trends are approximately indicated by the three climatic variables summarized in Table 7. In the Pacific Coast region, there is a tendency for the percentage of summer rainfall to increase with north latitude. This correlation is $r = 0.74$ and is highly significant. Conversely, in the Interior the correlation between the July-August/annual precipitation ratio and north latitude is $r = -0.63$, and it is also highly significant.

The elevation at the seed source tends to increase with decreasing latitude in both regions. However, in spite of this trend, the southernmost origins have the highest mean January temperature in both regions. Hence, the increase in seed source elevation toward the south does not completely compensate for the most southerly latitudes.

In both regions, there is a decrease in the average annual number of clear days with north latitude (Yearbook of Agriculture, Climate and Man, 1941). Hence, there is a corresponding decrease in solar radiation.

Evolution and Adaptation of the Height/Diameter Ratio

Seasonal rainfall distribution: The height/diameter ratio is not an adaptation to the seasonal distribution of rainfall. The main evidence for this is that strong correlations were obtained between the height/diameter ratios and the July-August/annual precipitation ratios in both regions, but they were of opposite sign. Although the height/diameter ratios increased with north latitude in both regions, the July-August/annual precipitation ratio increased with north latitude in the Pacific Coast region and decreased with north latitude in the Interior. Such correlations must be biologically meaningless.

Annual precipitation: The mean annual precipitation was not strongly correlated with the height/diameter ratios. The ecotype means also indicated that there was no meaningful relationship between these variables.

Mean January temperatures: The mean January temperature was only weakly correlated with the height/diameter ratios in the Pacific Coast region ($r = -0.40$ and -0.37), and it was not correlated with them in the Interior ($r = -0.04$ and 0.11). These correlations might have been stronger if they had not been confounded by the tendency for elevation at the seed source to increase with decreasing latitude. Partial correlation analyses resulted in somewhat stronger correlations between January temperature and the

height/diameter ratios in the Pacific Coast region when elevation was held constant. However, the corresponding partial correlations for the Interior region remained non-significant.

Such inconsistent correlations indicate that adaptation to severe temperatures is not the only factor affecting the height/diameter ratio throughout the range of ponderosa pine. The ecotype means of total height and the two height/diameter ratios in Table 8 indicate that the only consistently strong differences are those between the northernmost ecotype and the four remaining ecotypes within each variety.

Wells (1964b) noted that some characters which show adaptive trends are weakly correlated with climatic variables in certain ecotypes because of reproductive isolation. This could be the case in the Interior. In Colorado, New Mexico and Utah, mountain ranges and deserts result in discontinuous and isolated ponderosa pine populations. In such situations random genetic drift could have resulted in variations in the height/diameter ratio. This kind of random variation can affect adaptive and non-adaptive traits alike.

Glaciation: In the western United States, glaciation was restricted mostly to the higher elevations of the highest mountain ranges, such as the California Sierra Nevada (Flint, 1957). Hence, many of the habitats presently occupied by ponderosa pine were never glaciated. However, the glacial advances probably did force this species to

retreat to somewhat lower latitudes and elevations. Moreover, because of a steeper climatic gradient between the glaciated and tropical zones, the total range of ponderosa pine was probably more restricted than it is now. Since the Great Basin was not glaciated and was subject to pluvial conditions (Flint, 1957), it would appear that the four southernmost ecotypes within each variety region were not greatly displaced from their present latitudes. However, the North Plateau and Northern Interior ecotypes were probably forced to migrate southward during the glaciations because of the colder climate. Or, if they were not displaced, they became better adapted to the colder climate. In either case, selection was for greater winter hardiness. Hence recent glacial history may be the primary reason for the superior cold hardiness of these two ecotypes in southern Michigan.

Volume Correlated With Height,
Diameter and Taper

Since volume calculations were based on total height, basal diameter and taper, the contribution of each variable to the total variability of volume was of interest. Taper may have had a significant effect on differences in volume, since the varietal difference in taper was so strong.

Correlations were performed between total height, basal diameter, taper and volume (Table 12). Moreover, volume was regressed on total height and basal diameter,

Table 12. Simple correlations between each combination of total height, basal diameter, taper and volume in ponderosa pine

	Total height	Basal diameter	Taper (= ratio of mid- to basal diameter)
Basal diameter	0.92**		
Taper	-0.43**	-0.43**	
Volume	0.95**	0.95**	-0.27*

*, **Significant at the 5% and 1% probability levels respectively.

and then on total height, basal diameter and taper. For all calculations, origin means were used as items. The very high simple correlations of volume versus total height and basal diameter suggest that these two variables were the most important. When volume was regressed on total height and basal diameter, the resulting equation accounted for 94 percent of the total variability in volume. However, total height and basal diameter each accounted for 90 percent of the variability in volume. Hence, there appears to be little gained by measuring both height and diameter when making selections.

When taper was included as an independent variable with height and diameter in the regression equation, R^2 became 0.97. All three independent variables had highly

significant F ratios. Hence, taper contributed almost as much to the total genetic variability of volume as did height or diameter.

This effect of taper does not necessarily mean that taper should be measured and evaluated on an origin basis when selections are made to improve yield. However, it may mean that, if the variety differences in taper are real, the variety with the most favorable taper for maximum volume should be favored. The variety indicated by the taper data (Table 4) is the cylindrical Pacific Coast var. ponderosa.

Differences in taper, however, could be due to variations in bark thickness. Pederick (1970) analyzed the differences between "measured volume," which was the actual volume of wood inside the bark of young loblolly pine trees, and the "expected volume" estimated by the use of height and d.b.h. measurements outside bark as given in a volume table. This analysis determined the significance of the effect of the deviations in stem taper on the volume of half- and full-sib families. Taper had a significant effect on the volume variation, but this effect was erased after bark thickness was removed as a covariate. Pederick concluded that height and diameter are quite adequate for predicting volume growth, so long as an adjustment is made for bark thickness. However, he also noted that only 1 in 20 families had sufficiently thick or thin bark to over- or underestimate volume by as much as 2.8 percent.

The possibility exists that bark thickness is the primary cause of the strong differences among varieties. However, it seems doubtful that bark thickness could vary sufficiently on these young trees to account for the large differences obtained between variety means. For example, the difference between variety means for taper is $0.636 - 0.560 = 0.076$, which is $100(0.076)/0.636 = 12$ percent of the mean of the most cylindrical variety. Since it can be assumed that the effect on the volume difference would be even greater, a reduction of 2.8 percent resulting from an overestimate of volume because of thick bark seems unimportant. The genetic variation of bark thickness in ponderosa pine would have to be at least four times as great as that obtained in loblolly pine to account for the difference in taper between varieties.

Conclusion

In summary, taper differed strongly between varieties, the Pacific Coast var. ponderosa being the most cylindrical, whereas the Interior var. scopulorum was conical. The Pacific Coast is a region of greater annual precipitation but drier summers than the Interior region. The regional difference in the July-August/annual precipitation ratio corresponds most strongly to the difference in taper, but the adaptive significance of this correlation is not explainable with the existing data.

In contrast, the height/diameter ratios differed strongly among ecotypes within varieties but not between varieties. These differences were correlated with latitude, the ratios being higher for northern than for southern ecotypes. These differences appeared to be due both to hardiness in Michigan and to different growth patterns.

Although taper accounted for a high percentage of the variation in estimates of the volume growth of different seedlots, the data did not indicate that taper was essential for accurate prediction. Height and/or diameter data were sufficient.

CHAPTER VI

GEOGRAPHIC VARIATION IN STEM FORM
OF EASTERN WHITE PINE

The 15 origins of eastern white pine planted at the W. K. Kellogg Forest provided an opportunity to observe trends in growth, the height/diameter ratio and stem taper as the result of racial variation over a large portion of eastern North America. The objectives specific to the study of eastern white pine were: (1) to determine if there were significant differences in height, diameter, the height/diameter ratio and stem taper among origins; (2) to determine which climatic factors were strongly correlated with the observed differences; and (3) to determine if taper is an important component contributing to the genetic variation in volume growth.

Regional Climatic Variation

Eastern white pine occurs within the cool and humid portions of eastern North America (Figure 2). This range includes a superhumid zone in the Appalachian Mountains and a moist sub-humid portion in Iowa and Minnesota.

Figure 2. The origins of the 15 seedlots comprising the provenance test of eastern white pine at the W. K. Kellogg Forest (from Wright et al., 1963).

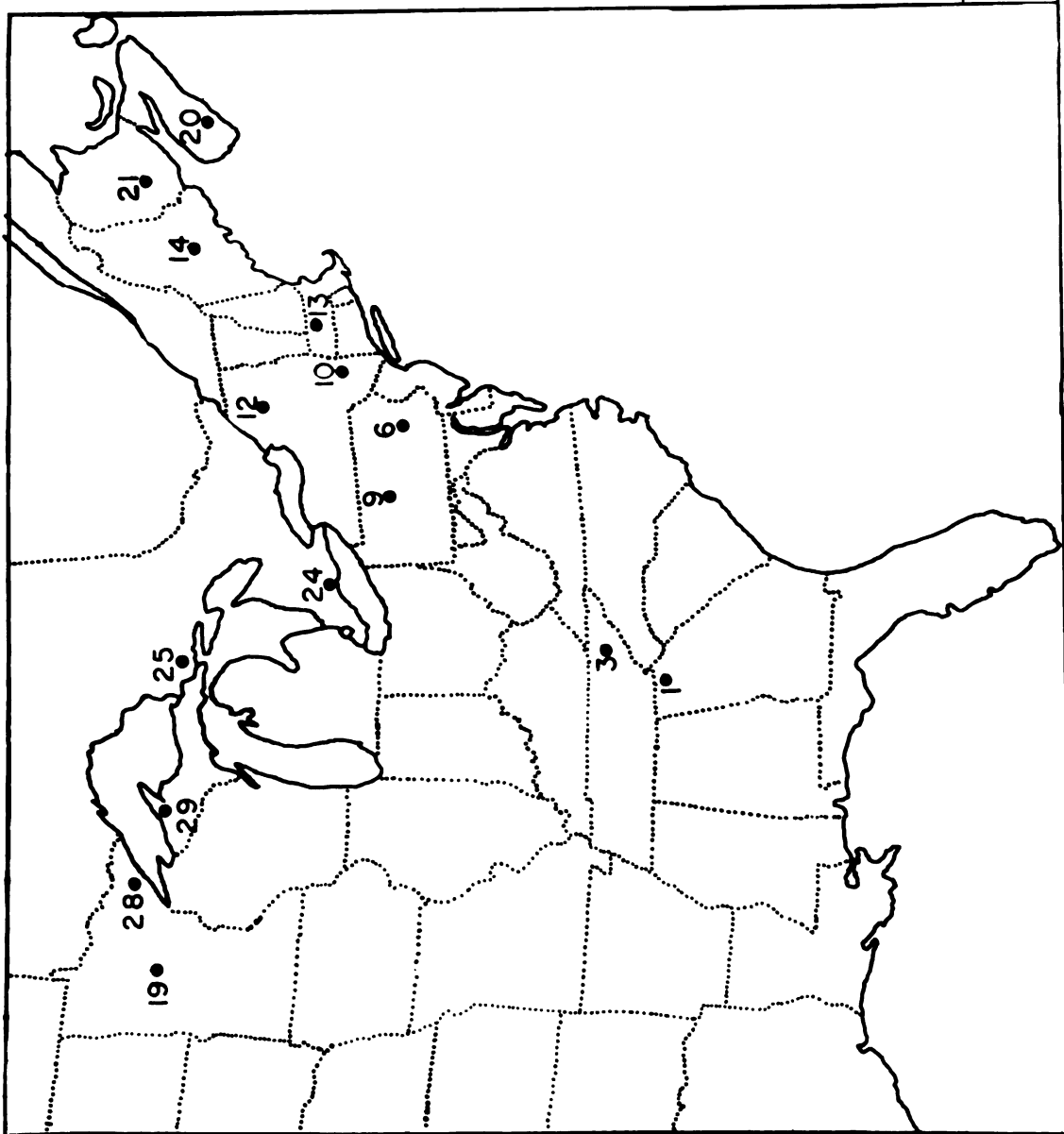


Figure 2

Annual precipitation varies from about 71 inches in northern Georgia to 22 inches in Minnesota (Table 13). Because precipitation is about 1 to $1\frac{1}{2}$ times the evaporation from free water surfaces, there is no moisture deficit in any season (Wilson and McQuilkin, 1965).

Mean January temperature varies from 7° F in Minnesota to 40° F in Georgia. Its range is approximately delimited by a zone in which the mean July temperature varies between 62° F and 70° F. However, the western part of its range is bordered by the prairies, which suggests that moisture is a limiting factor in Minnesota and Iowa.

Geographic Trends

No ecotypes, varieties or races have been defined for eastern white pine, and no ecotype boundaries were indicated by the data. However, there were significant differences among geographic origins for height, diameter, volume and the height/diameter ratio (Table 14).

The relatively weak significance levels of the F ratios for the three height/diameter ratios compared with those for height and diameter indicate that the pattern of variation for stem form was not very clear. According to the lack of significance for taper, stem form is not heritable. The results suggest that height and diameter respond to selection pressures in a parallel manner.

Table 13. Geographic origins and major climatic differences among origins of eastern white pine

Seedlot number and state or province of origin	North latitude	West longitude	January temper- ature	Annual precipi- tation
	<u>Degree</u>	<u>Degree</u>	<u>°F</u>	<u>Inches</u>
1 GEORGIA	34.8	84.0	40	71
3 TENNESSEE	36.0	82.8	39	42
6 PENNSYLVANIA	41.1	75.4	24	49
9 PENNSYLVANIA	40.8	78.5	28	44
10 N YORK	42.0	74.0	25	39
12 N YORK	44.4	74.2	16	37
13 MASSACHUSETTS	42.3	72.4	22	43
14 MAINE	44.9	68.6	18	40
19 MINNESOTA	49.4	94.7	7	22
20 N SCOTIA	44.6	64.6	20	55
21 N BRUNSWICK	45.9	66.8	18	40
24 ONTARIO	42.7	80.5	24	32
25 ONTARIO	46.2	82.6	10	30
28 MINNESOTA	48.1	91.3	13	26
29 MICHIGAN	44.3	84.8	15	28

Table 14. Significance of differences in height, diameter, volume, the height/diameter ratio and taper in eastern white pine

<u>Variable</u>	<u>F ratio</u>
Total height	8.94***
Basal diameter	7.16***
Mid-diameter	6.74***
D.b.h.	9.38***
Volume	9.99***
$\frac{\text{Total height}}{\text{Basal diameter}}$ ratio	3.83***
$\frac{\text{Total height}}{\text{Mid-diameter}}$ ratio	1.87*
$\frac{\text{Total height}}{\text{d.b.h.}}$ ratio	4.46***
Taper (= $\frac{\text{mid-diameter}}{\text{basal diameter}}$ ratio)	1.21

*, ***Significant at the 5% and 0.1% probability levels respectively.

The height/diameter ratio was correlated only with north latitude and January temperature; these correlations were quite strong (Table 15). Taper showed no geographic or climatic trends. Although the height/diameter ratio was not related to winter injury, the correlations strongly implicate some form of winter hardiness. The low correlation of the height/diameter ratio with annual precipitation was to be expected, since it was not a limiting factor.

Table 15. Simple correlation coefficients (r) of the total height/d.b.h. ratio and taper versus each of five geographic or climatic variables for eastern white pine

Geographic or climatic variable	<u>Total height</u> D.b.h. ratio	Taper (= ratio of mid- to basal diameter)
North latitude	0.76**	0.12
West longitude	-0.13	-0.47
Mean January temperature	-0.66**	-0.05
Winter injury	-0.29	-0.45
Average annual precipitation	-0.36	0.01

**Significant at the 1% probability level.

The relationship between the height/diameter ratio and winter hardiness is illustrated by the origin means in Table 16. The Georgia and Tennessee origins, which sampled the southernmost portion of the natural range of eastern white pine, had two of the lowest height/d.b.h. ratios.

Wright (1970) noted changes in relative growth rate with age of these origins. An analysis of relative growth rate revealed a declining variability. The height superiority of the Georgia and Tennessee origins was considerable soon after they were outplanted, but it has been declining ever since. It is reasonable to expect such growth rate changes to affect the height/diameter ratio as well.

It can also be seen from Table 16 that there were three strong exceptions to the tendency for northern origins to have the slowest growth and the greatest height/diameter ratios. These origins were 13-MASS, 24-ONT and 25-ONT. Since these seedlots would not seem to suffer from deficiencies in winter hardiness, the environmental factors which might select for lower height/diameter ratios are not entirely accounted for. Perhaps January temperature and north latitude do not represent the selective factors which determine this kind of adaptation. Or perhaps there is no adaptation.

Table 16. Origin means for height, diameter, volume, the height/diameter ratio and taper in eastern white pine

Seedlot number and state or province of origin	Total ht.	D.b.h.	Volume	$\frac{\text{Tot. ht.}}{\text{D.b.h.}}$ ratio	Taper (= ratio of mid- to basal diameter)
	<u>Feet</u>	<u>Inches</u>	<u>Cu ft</u>	<u>Ft/in</u>	<u>In/in</u>
1 GEORGIA	19.5	3.4	0.41	5.77	0.665
3 TENNESSEE	21.0	3.8	0.55	5.55	0.659
6 PENNSYLVANIA	19.9	3.5	0.45	5.70	0.658
9 PENNSYLVANIA	19.5	3.4	0.41	5.85	0.662
10 N YORK	19.8	3.3	0.41	6.01	0.671
12 N YORK	18.1	2.9	0.30	6.19	0.689
13 MASSACHUSETTS	19.0	3.4	0.40	5.69	0.659
14 MAINE	17.5	2.8	0.26	6.46	0.677
19 MINNESOTA	16.6	2.6	0.21	6.33	0.650
20 N SCOTIA	17.7	2.8	0.26	6.45	0.676
21 N BRUNSWICK	17.0	2.7	0.24	6.26	0.678
24 ONTARIO	20.3	3.4	0.47	6.07	0.688
25 ONTARIO	19.1	3.3	0.37	5.90	0.660
28 MINNESOTA	17.2	2.7	0.24	6.34	0.670
29 MICHIGAN	16.6	2.7	0.23	6.14	0.668
Tukey's hsd:					
5% level	2.3	0.6	0.16	0.68	0.050
1% level	2.7	0.7	0.19	0.78	0.057

Volume Correlated With Height
and Diameter

Wright (1970) noted significant differences among origins for the height/diameter ratio in the same white pine plantation. He stated that this may mean that height growth and diameter growth are inherited separately, so that both should be measured when selecting provenances for commercial planting.

Two methods, correlation and regression, were utilized to test for separate inheritance of height and diameter growth. Correlations were obtained among the following variables: total height, basal diameter, mid-diameter, d.b.h. and taper (Table 17).

Table 17. Simple correlations between each combination of total height, basal diameter, mid-diameter, d.b.h., volume and taper in eastern white pine

	Total height	Basal diameter	Mid- diameter	D.b.h.	Volume
Basal diameter	0.89**				
Mid-diameter	0.95**	0.98**			
D.b.h.	0.97**	0.96**	0.99**		
Volume	0.98**	0.93**	0.97**	0.99**	
Taper (= ratio of mid- to basal diameter)	-0.11	-0.49	-0.31	-0.29	-0.20

**Significant at the 1% probability level.

Regressions of volume on height and d.b.h., and on each variable independently were obtained as well. Taper was not included because it was not a significant independent variable in any combination with height and/or diameter.

The very high correlations between each combination of variables, except for those involving taper, suggest that the measurement of either total height or d.b.h. will adequately predict volume. The somewhat lower correlations of basal diameter with height and with volume may be due to a high variability in the rough bark on the stem surface near the base. Some trees had started to develop bark fissures, others had not.

The regressions indicate that either height or d.b.h. predict a high percentage of the variation among white pine provenances in this plantation, but d.b.h. predicts the highest percentage with the lowest standard error of estimate. The prediction equations for volume follow:

$$\hat{Y}_{VOL} = -1.496 + 0.125X_{HT},$$

for which $R^2 = 0.93$ and $s_{y \cdot x} = 0.019$.

$$\hat{Y}_{VOL} = -1.438 + 0.462X_{DBH},$$

for which $R^2 = 0.96$ and $s_{y \cdot x} = 0.012$.

These equations compare favorably with the following prediction equation based on total height and d.b.h.:

$$Y_{VOL} = -1.590 + 0.057X_{HT} + 0.275X_{DBH},$$

for which $R^2 = 1.00$ and $s_{y.x} = 0.012$.

Since d.b.h. is the quickest and easiest parameter to measure on trees of commercial size, it appears to be the most useful for making selections among provenances. However, an inspection of the provenance means will make this point clear (Table 16).

The seedlot with the best total height (best 1 of 15 = 1.74 standard deviations above the mean) also had the largest d.b.h. and the greatest volume. This seedlot is 3-TENN. If we also select the origin with the second best total height, 24-ONT, its volume is 0.47 cubic feet, which is second best and is not significantly different from 3-TENN, which had 0.55 cubic feet. Further, it is significantly greater than seven other provenances ($0.47 - 0.16 = 0.31$ cubic feet).

Conversely, if we select the origin with the second best d.b.h., 6-PENN, the volume is 0.45 cubic feet, which is third best. It is not significantly different from the best, and it has significantly greater volume than six seedlots ($0.45 - 0.16 = 0.29$ cubic feet).

In conclusion, it appears that there is very little error in making selections on the basis of height or diameter alone. Contrary to Wright's (1970) conclusion, these data suggest that height and diameter are inherited together, not separately, despite the varying height/diameter ratio.

CHAPTER VII

VARIETAL TRENDS IN STEM FORM OF SCOTCH PINE

The test of four Scotch pine varieties, located in plantations at the Fred Russ and W. K. Kellogg Forests, samples a very limited portion of the Scotch pine range. Therefore, inferences cannot be made about the patterns of variation in height, diameter or stem taper for the species as a whole. Many previous experiments have demonstrated considerable variation among varieties of this species (e.g., Ruby, 1964; Wright and Bull, 1963; Wright et al., 1966). Nevertheless, trends observed in this material may be comparable with trends observed in ponderosa pine or in eastern white pine.

Specific objectives in studying the Scotch pine provenance test were: (1) to detect significant differences in the height/diameter ratio and taper among provenance and variety means; (2) to determine what percentages of the variation are attributable to varieties and to provenances within varieties; and (3) to determine the significance of the contribution of taper to volume growth.

Regional Climatic Variation

Climatic data specific to the 12 provenances (Figure 3) that were studied were not available. However, general information about the regional climates to which the four varieties were adapted were obtained from the Yearbook of Agriculture: Climate and Man (1941). These data are summarized in Table 18.

Table 18. Major climatic differences between regions occupied by four north European varieties of Scotch pine

Variety	Elevations at which seedlots were collected	January temperature	Annual precipitation
	<u>Feet</u>	<u>°F</u>	<u>Inches</u>
<u>hercynica</u>	960-1620	28	36
<u>borussica</u>	350-400	31	23-29
<u>septentrionalis</u>	600-750	24-27	19-23
<u>lapponica</u>	1350	< 20	≥ 23

It is apparent that the climates in which these varieties grow are not very different. Though somewhat variable between regions, precipitation does not seem to be limiting. However, the range of January temperatures characteristic of the regions occupied by these varieties was not fully sampled by the origins represented.

Figure 3. Natural distribution of Scotch pine in Europe, including the origins of seedlot numbers 202, 210, 273, 274, 525, 527-529, and 543-546 comprising the provenance test at the Fred Russ and W. K. Kellogg Forests, and the origin of seedlot numbers 275-283 comprising the test of 9 Norwegian half-sib families at the W. K. Kellogg Forest (from Wright and Bull, 1963).

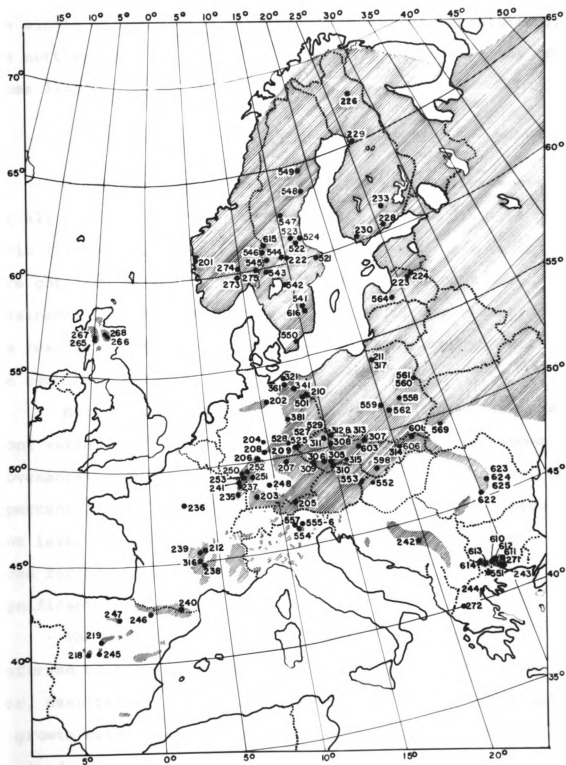


Figure 3

The range of var. lapponica extends much further north than the single origin tested in this study. The temperatures in the northernmost regions are considerably lower than any of those listed.

Variation Among and Within Varieties

There was considerable variation among provenances for all variables except the total height/basal diameter ratio (Table 19). Significant differences for this ratio were obtained at the W. K. Kellogg Forest, but none were obtained at the Fred Russ Forest. For all other variables the results for each location agreed closely with those of the combined analysis.

Most of the racial variation was due to differences among varieties (Table 20). Significant differences among provenances within var. septentrionalis were obtained at the 5 percent level for 5-year height growth and at the 1 percent level for total height and mid-diameter. No differences for any variable within any other variety were significant.

The differences in growth rate between varieties conformed to those observed by Wright et al. (1966). However, despite very considerable differences among varieties in growth rate, the two height/diameter ratios and taper remained relatively stable.

7

Table 19. Significance of differences among provenances in height, diameter, volume, the height/diameter ratio and taper in Scotch pine

<u>Variable</u>	<u>F ratio</u>
Total height	147.98***
5-year height growth	95.70***
Basal diameter	24.45***
Mid-diameter	43.53***
Volume	39.22***
$\frac{\text{Total height}}{\text{Basal diameter}}$ ratio	1.06
$\frac{\text{5-year height growth}}{\text{Mid-diameter}}$ ratio	5.24**
Taper (= $\frac{\text{mid-diameter}}{\text{basal diameter}}$ ratio)	9.98***

, *Significant at the 1% and 0.1% probability levels respectively.

Table 20. Percentages of total variance in height, diameter, the height/diameter ratio and taper accounted for by differences among varieties and origins of Scotch pine

	Variances as percents of total variance			
	Total height	5-year height growth	Basal diameter	Mid-diameter
Variety	92***	90***	88***	90***
Seedlot within variety	8	10	10	10
Total	100	100	100	100
	Taper (= mid-diameter basal diameter ratio)			
	$\frac{\text{Total height}}{\text{Basal diameter}}$ ratio	$\frac{\text{5-year height growth}}{\text{Mid-diameter}}$ ratio	$\frac{\text{mid-diameter}}{\text{basal diameter}}$ ratio	
Variety	10	65**	64**	
Seedlot within variety	90	35	36	
Total	100	100	100	

, *Significant at the 1% and 0.1% probability levels respectively, using an analysis of variance with 3 and 8 degrees of freedom for variety and seedlot respectively.

Geographic Variation in Taper

The varietal means given in Table 21 indicate a strong tendency for stem taper to become more cylindrical with north latitude. The correlation between stem taper and north latitude is $r = 0.91$ and is highly significant.

The cylindrical bole form of northern European origins of Scotch pine has been previously observed by Wright and Bull (1963). Larson's (1963) review of literature on stem form indicates considerable interest among European authors in the tendency of Scotch pine crowns and stems to become more cylindrical with increasing latitude and elevation. The generally accepted adaptive reason for this is that narrow crowns with small lateral branches are less subject to breakage because they retain less snow. For several possible reasons discussed in Chapter V, there is a strong tendency for trees with cylindrical crowns to have cylindrical stems.

It is also possible that the type of root system influences stem and crown form. Wright and Bull (1963) noted that var. lapponica has a very shallow but fibrous and "hard-to-pull" root system, whereas origins from more southern latitudes, such as var. hercynica, can be lifted very easily. Presumably the root system of var. lapponica is an adaptation to permafrost conditions.

Table 21. Variety means for height, diameter, the height/diameter ratio and taper in Scotch pine

Variety	Total height		5-year height growth		Basal diameter		Mid-diameter	
	<u>Feet</u>		<u>Feet</u>		<u>Inches</u>		<u>Inches</u>	
<u>lapponica</u>	5.6		4.3		1.9		1.4	
<u>septentrionalis</u>	8.4		6.3		2.7		2.0	
<u>borussica</u>	13.6		10.0		4.3		2.8	
<u>hercynica</u>	13.8		10.0		4.3		2.8	
Tukey's hsd: 5% level								
	2.5		1.8		0.9		0.4	
1% level								
	3.3		2.4		1.2		0.6	
Variety	<u>Total height</u>		<u>5-year height growth</u>		<u>Basal diameter</u>		<u>Mid-diameter</u>	
	<u>Basal diameter</u>	ratio	<u>Mid-diameter</u>	ratio	<u>ratio</u>		<u>ratio</u>	<u>Taper (= mid-diameter basal diameter ratio)</u>
<u>lapponica</u>	3.07		3.14				0.744	
<u>septentrionalis</u>	3.11		3.22				0.735	
<u>borussica</u>	3.20		3.52				0.664	
<u>hercynica</u>	3.25		3.60				0.654	
Tukey's hsd: 5% level								
	0.35		0.36				0.076	
1% level								
	0.46		0.47				0.101	

Pleistocene Evolution

Wright and Bull (1963) indicated the probable evolutionary trends of Scotch pine differentiation during the Pleistocene glaciations of northern Europe. They suggested that remnants survived in highlands within the glaciated areas or in areas south of the ice.

The differentiation of varieties lapponica and septentrionalis might be postulated more specifically. The tenacious root system, slow growth and cylindrical stem form of var. lapponica may have evolved rather rapidly during glaciation to a very severe existence on nunataks in the Scandinavian mountains. Flint (1957) noted the presence of such rocky outcrops, which were inferred from botanical and geological evidence.

Flint also cited evidence that glaciation had resulted in a lower sea level to the extent that the North Sea floor was at least partially emerged during the last glaciation. Such a habitat might have been temporarily suitable for the occupation of var. septentrionalis until it could re-occupy its present habitats in southern Scandinavia.

Varieties borussica and hercynica presently grow in areas of central Europe that have been relatively unglaciated. Hence, their relative displacements during glaciation need not have been so great as those of the two northern varieties.

Geographic Variation in the Height/Diameter Ratio

It is not clear from the data presented in Tables 20 and 21 that the height/diameter ratio can be distinguished from stem taper for the purpose of interpreting adaptive trends. In contrast to the ponderosa pine and eastern white pine experiments, in Scotch pine the total height/basal diameter ratio and the 5-year height growth/mid-diameter ratio were negatively correlated with north latitude ($r = -0.63$ and -0.91 respectively, significant at the 5 percent and 1 percent levels respectively). Hence, a lack of winter hardiness cannot explain differences in the height/diameter ratio on the basis of the relative retardation of terminal growth. Further, these four varieties do not suffer winter injury in Michigan.

The 5-year height growth/mid-diameter ratio, which is the only one of the two measurements that varied significantly, has a variation pattern almost identical with that of stem taper (Table 20). It seems that this variable parallels the variations in stem taper for the same biological reasons that stem taper varies. Hence, the northern origins have lower height/diameter ratios because their mid-diameters are fatter than are those of southern origins. Since the biological and evolutionary reasoning applied to stem taper may be extended to the 5-year height growth/mid-diameter ratio, no further discussion is needed.

Volume Correlated With Height,
Diameter and Taper

The correlations between every combination of height, diameter, volume and taper in Table 22 indicate that any variable measured alone in the four Scotch pine varieties tested will account for most of the racial variation in volume. Either height or diameter alone will account for 98 percent of the variation.

Table 22. Simple correlations between each combination of total height, 5-year height growth, basal diameter, mid-diameter, volume and taper in Scotch pine

	Total height	5-year height growth	Basal diameter	Mid- diameter	Volume
Five-year height growth	1.00**				
Basal diameter	1.00**	0.99**			
Mid-diameter	0.99**	0.99**	0.99**		
Volume	0.99**	0.98**	0.99**	0.97**	
Taper (= ratio of mid- to basal diameter)	-0.94**	-0.93**	-0.95**	-0.91**	-0.96**

**Significant at the 1% probability level.

In this material we would only select among varieties, since there was relatively little variation within varieties. According to Wright et al. (1966), varieties hercynica and borussica are among the fastest growing of any Scotch pine varieties. This superiority holds at all plantations tested, and it is confirmed by this analysis. No significant differences between or within these two varieties were detected for height, diameter or volume growth.

To include stem taper as a selection criterion is meaningless for these four varieties. The variety with the most cylindrical and desirable stem form, var. lapponica, is by far the slowest growing, and there is no significant difference between varieties hercynica and borussica for taper.

CHAPTER VIII

SELECTION FOR HEIGHT AND/OR DIAMETER IN SCOTCH PINE HALF-SIB FAMILIES

Half-sib progeny tests provide bases for assumptions and methods of estimation of certain genetic relationships which cannot be tested by means of provenance tests. In each of the previous three chapters, I have made some attempt to determine the genetic variation between height and diameter. The present chapter will explore this relationship by means of different methods.

The objectives for studying the two Scotch pine half-sib progeny tests were: (1) to determine if there was genetic variation in the height/diameter ratios among individual trees within stands; (2) to obtain genetic correlations between height and diameter; (3) to determine the correlated response in height to selection for diameter (and vice-versa); and (4) to compare the correlated response with the direct response to selection of each variable itself. These objectives were all aimed at one question: is selection for both height and diameter necessary?

Genetic Correlations

If the height/diameter ratio varies significantly among families, we would not expect a high correlation between height and diameter. Conversely, we might attribute a lack of variation in the height/diameter ratio to a high correlation between height and diameter.

In the F ratios in Table 23, there was little agreement between the progeny tests. In the test of nine Norwegian families, there were large differences among families for the height/diameter ratio but not for height or diameter. On the other hand, in the test of 80 East German families, the strong differences among families were for height and diameter, not for the height/diameter ratios. Such comparisons make it clear that the tests of significance of the genetic variability of the height/diameter ratio do not indicate very precisely what the genetic relationship between height and diameter is. Progeny tests make it possible to obtain the desired genetic correlations.

The genetic correlations between height and diameter were high in both progeny tests (Table 24). Also, there was very close agreement between all correlations based on total height and those based on 5-year height growth. Such agreement provides a check on the reliability of the correlations.

Table 23. Significance of between-family differences in height, diameter, their ratios and volume in two half-sib progeny tests of Scotch pine

Variable	F ratio ^a		
	9 Norwegian families tested at Kellogg	80 East German families ^b tested at:	
		Kellogg	Kellogg, Russ & Dunbar
Total height	1.20	1.79**	1.66***
5-year height growth	1.10	1.94***	1.63***
Mid-diameter	2.06	1.99***	1.50*
$\frac{\text{Total height}}{\text{Mid-diameter}}$ ratio	4.18*	1.17	1.54*
$\frac{\text{5-year ht. growth}}{\text{Mid-diameter}}$ ratio	6.86**	1.18	1.31*
Volume	1.78	--	--

*, **, ***Significant at the 5%, 1% and 0.1% probability levels respectively.

^aF ratio applies to between-family variance.

^bThe seedlot (MSFG) numbers of the 80 East German families are: 321-336; 341-345, 347-351, 354-359; 362-367, 369-378; 381-396; 501-502, 504-512, 514-518.

Table 24. Genetic, phenotypic and simple correlations among three variables derived from analyses of two Scotch pine half-sib progeny tests

		Total height	5-year height growth
Progeny test I		9 Norwegian families on two sites at the W. K. Kellogg Forest ^a	
Mid-diameter	Genetic	0.97 ± 0.37	0.91 ± 0.97
	Phenotypic	0.61	0.58
	Simple	0.89	0.84
Progeny test II		80 East German families tested at the W. K. Kellogg Forest ^b	
Mid-diameter	Genetic	0.95 ± 0.05	0.94 ± 0.05
	Phenotypic	0.79	0.78
	Simple	0.79	0.79
		80 East German families tested at the Kellogg, Russ and Dunbar Forests ^c	
Mid-diameter	Genetic	0.70 ± 0.14	0.68 ± 0.16
	Phenotypic	0.72	0.70
	Simple	0.81	0.81

^aGenetic correlations based on 144 observations.

^bGenetic correlations based on 560 observations.

^cGenetic correlations based on 1200 observations.

Despite the F-ratio differences between the two progeny tests, there was a very close agreement between the genetic correlations in both progeny tests when they were conducted at the W. K. Kellogg Forest.

There was a considerable difference between progeny tests in the magnitudes of the standard errors of the genetic correlations. The relatively low standard errors of the genetic correlations obtained from the test of 80 East German families indicate that the size of that experiment was sufficient. The numbers of observations were $N = 560$ for the W. K. Kellogg Forest data and $N = 1200$ for the analysis of data from the W. K. Kellogg, Fred Russ and Dunbar Forests combined.

In the progeny test of East German families, the relationship between the height/diameter ratios and the genetic correlations was consistent with expectations. At the W. K. Kellogg Forest alone, the height/diameter ratios were not significant (Table 23), and the genetic correlations between height and diameter were high (Table 24). At all three locations, the height/diameter ratios varied significantly, and the genetic correlations were considerably lower.

The relatively smaller genetic correlations obtained from the analysis of data from the Kellogg, Russ and Dunbar Forests suggest that genotype X environment interactions were affecting the genetic correlations. However, the

family X location interactions were not significant for any variable ($F \leq 1.00$).

There was no consistent relationship between the genetic, phenotypic and simple correlations compared in Table 24. The phenotypic correlations were much lower than the genetic correlations in both progeny tests at the W. K. Kellogg Forest but not different from them when the data from the Kellogg, Russ and Dunbar Forests were analyzed together.

The simple correlations, which were based on family means as items, underestimated the genetic correlations in both progeny tests at the W. K. Kellogg Forest but overestimated them in the test of 80 East German families at three locations.

The tendency for the phenotypic correlations to be equal to or lower than either the genetic or simple correlations may mean that environmental factors inhibit inherent similarities between height and diameter growth.

A Polygenic Model

The genetic correlations of $r_G = 0.68$ to 0.97 between height and diameter are high. However, they are low enough to allow for the occurrence of some genetic variation in the height/diameter ratios (Table 23). In fact, they would probably have to be very close to unity for the height/diameter ratio not to vary genetically.

On the basis of such high genetic correlations, we can postulate a model for genetic control of tree growth in Scotch pine. If growth is controlled by many genes, most genes which affect growth control height and diameter growth in the same manner. The remaining growth genes control either height or diameter increment separately.

Correlated and Direct Responses to Selection

All genetic correlations between height and diameter in both progeny tests were high. However, we may wish to know how much genetic gain we might obtain in one trait if we select for improvement only in the other trait. Such correlated responses to selection were obtained by the method given by Falconer (1960).

The correlated responses obtained in these experiments were based on heritabilities of family means for each variable (Table 25) and on the genetic correlations between height and diameter presented above (Table 24). The correlated and direct responses to selection are presented together for comparison in Table 26. The direct response is the genetic gain obtained in a given trait when selection is for improvement in that trait alone.

Table 25. Heritabilities of family means for height, diameter, volume and the height/diameter ratio in two Scotch pine half-sib progeny tests

Variable	Heritabilities of family means		
	9 Norwegian families tested at Kellogg	80 East German families tested at	
		Kellogg	Kellogg, Russ & Dunbar
Total height	0.36	0.76	0.70
5-year height growth	0.22	0.79	0.67
Mid-diameter	0.73	0.80	0.67
Volume	0.66	--	--
$\frac{\text{Total height}}{\text{Mid-diameter}}$ ratio	0.85	0.40	0.61
$\frac{\text{5-year ht. growth}}{\text{Mid-diameter}}$ ratio	0.86	0.42	0.47

Table 26. Correlated and direct responses to selection for height or diameter in two half-sib progeny tests of Scotch pine^a

Progeny test and analysis	Total height		Diameter	
	Correlated response to selection for diameter	Direct response to selection for height	Correlated response to selection for height	Direct response to selection for diameter
	%	%	%	%
<u>Progeny test I</u>				
Best one of 9 Norwegian families tested at the Kellogg Forest	7	5	11	16
<u>Progeny test II</u>				
Best one of 16 East German families in each of 5 stands tested at the Kellogg Forest	12	12	10	11
Best of 4 of 80 East German families in all 5 stands tested at the Kellogg, Russ and Dunbar Forests	6	8	6	8

^aThe responses are expressed as percentages of their respective progeny test means.

Nine Norwegian Families

Strictly speaking, family selection cannot be practiced in the test of nine Norwegian families, since significant differences were not obtained among families for height, diameter or volume. However, this test is the only one in which volumes were calculated. Hence, the correlated responses in volume growth to selection for height or diameter may be demonstrated even if such selections would not be feasible in actual practice.

In this progeny test, the heritability for diameter was much higher than it was for height (Table 25). Hence, the correlated response in height to selection for diameter is actually greater than is the direct response to selection for height.

The advantage of selection for diameter growth is also suggested by the correlated response in volume growth to selection for diameter or height. The correlated response is compared with the direct response in the following tabulation:

<u>Increase in</u> <u>volume growth</u>	<u>Following</u>
%	
32	Direct selection for volume
33	Indirect selection for diameter
23	Indirect selection for height

The response in volume growth was actually greater when selection was for diameter alone than it was when both

diameter and height were measured in order to determine the direct response to selection for volume.

The correlated response can be seen more clearly if we compare the rankings of the family means of the correlated traits. For example, the tallest of the 9 Norwegian families also had the best average diameter and therefore the greatest volume. Hence, the correlated response to the selection of the best one of 9 families for diameter was the same as it was for height. However, in practice we would wish to select more than one family to avoid inbreeding depression.

Eighty East German Families

In the progeny test of East German families, it makes very little difference whether selection is for height or diameter, since their correlated responses were almost equal (Table 26). In the analysis based on data from the Kellogg, Russ and Dunbar Forests, the direct response was somewhat greater than the correlated response. However, in the analysis of data from the Kellogg Forest alone, there was almost no difference between the correlated and direct responses. This difference between the two analyses was probably due to the lower genetic correlations between height and diameter obtained in the combined analysis than correlations obtained from the analysis of the data from the Kellogg Forest alone. Since volumes were not determined in the progeny test of East German families, inferences about

the correlated response to selection for both height and diameter could not be made.

In this progeny test it may be questioned whether it is necessary to select the best families on the basis of their performances at all three locations, since the family X site interactions were so weak. It would be simpler and cheaper in the future to make selections on the basis of their performance at one location only, such as the W. K. Kellogg Forest. Further, the higher genetic correlations between height and diameter for the Kellogg Forest data mean that the correlated responses to selection for one trait should be higher than they would be if based on selections made at all three locations.

However, there is one major advantage to the selection of families on the basis of their performances at all three locations. The experimental design is such that all families can be compared only when tested at all three sites. At each location the stands are replicated in separate groups, so that family means from one stand are not directly comparable with family means in another stand. Hence, in the analysis of the data from the Kellogg Forest alone, there were significant differences among stands, but there was no way of determining to what extent these differences were genetic and to what extent environmental. Genotype was confounded with environment. Only families replicated within stands could be genetically compared.

When the stands and families within stands were tested at all three locations, the environmental effects at each location were to some extent averaged out. Hence, in this analysis there was a valid basis for comparing genetic differences among stands.

Stand differences were highly significant for most variables when tested at the W. K. Kellogg Forest alone. However, stand differences were not significant for any variable when tested at all three locations. Therefore, stand performances at any one location should not be considered when making selections. If selection is to be practiced for growing improved stock at the W. K. Kellogg Forest, the responses to selection predicted on the basis of data obtained from that location should be used as the selection criterion (Table 26). However, the lack of significant differences between stands at all locations means that the best families from each stand should be selected for planting at the Kellogg Forest, not just the best families in the best stand.

Genetic Versus Simple Correlations

In a replicated progeny test, genetic and phenotypic correlations may be derived from variance components. Simple correlations based on family means as items serve the same purpose as genetic correlations, since the environmental effects have been largely averaged out by replication.

However, simple correlations are much simpler to calculate. The only question is the degree of precision with which they estimate the true genetic correlation. The phenotypic correlation is not useful for this purpose, since it is obtained from variance components which account for both genetic and environmental effects.

In Table 24, the simple correlations underestimated the genetic correlations in two analyses but overestimated them in the test of East German families at three locations. The magnitude of these errors can be tested by substitution of the simple correlations for the genetic correlations in the formula determining the correlated response to selection. For example, if the simple correlation between total height and mid-diameter of 0.81 is substituted for $r_G = 0.70$ in the calculation of the correlated response in total height to selection for diameter (Table 24), the response is $CR_H = 0.77$ foot. When rounded to the nearest whole percent, this is 6 percent of the progeny test mean which is no different from the 6 percent obtained by the use of the genetic correlation (Table 26). Similarly, the correlated response in diameter to selection for height becomes $CR_D = 0.15$ inch. This is also 6 percent of the progeny test mean and is not different from the 6 percent obtained by means of the genetic correlation when rounded to the nearest whole percent.

The genetic correlation is very cumbersome and time-consuming to obtain. Moreover, a large number of observations are needed to attain an acceptable level of precision. Calculation of the genetic correlation requires the calculation of the analysis of covariance between the two traits in question as well as of the analysis of variance of each.

Simple correlations based on family means as items are relatively easy to determine in any replicated experiment. Hence, the close agreement between simple and genetic correlations in these progeny tests indicates that simple correlations, based on family means as items, are sufficiently accurate and precise for most practical applications.

CHAPTER IX

DISCUSSION

There appears to be genetic variation for stem form in some pine species, but this variability is of little practical consequence. However, the genetic control of stem form has theoretical implications which may be useful for understanding the inheritance of growth in general.

Practical Implications

In the three species studied, there was some evidence that measurements of either height or diameter will adequately predict genetic variation in volume growth. Applied to practical tree improvement programs, this means that time and money can be saved if selections are made on the basis of only one trait. For short-term studies and very young plantations, height is the quickest and easiest growth trait to measure. When trees reach pulpwood or pole size, diameter measurements are the most efficient.

Although taper is under genetic control in two of the three species studied, the results of these experiments do not indicate that stem form should be a criterion in the selection and breeding of trees for improved volume production.

Forecasting Future Volume Growth from Juvenile Data

How well do juvenile growth data forecast future volumes? The upper limit of site productivity may be approached soon after crown closure is achieved. Differences among genotypes in their ability to utilize site productivity or to photosynthesize efficiently may change their relative growth rates. Young plantations do not test these conditions.

Zobel et al. (1971) found gains of up to 53 percent in progeny tests of loblolly pine at age 4 when the best 25 percent of the crosses were compared with commercial check lots. Corresponding gains for height and diameter were 18 and 12 percent respectively. In the progeny test of nine Norwegian families, discussed in Chapter VIII, a genetic gain of 32 percent was obtained for volume growth, the gains for height and diameter being 5 and 16 percent respectively (Table 26). If there is an upper limit to the dry matter production on a given site after crown closure, such gains in volume growth may be diminished.

Three possible models may be postulated, as in Figure 4. In Model I, an upper limit to the volume production attainable on a given site is assumed. Since height growth is not affected over a wide range of stand densities (Smith, 1962), the diameter growth of the initially faster-growing Genotype A is necessarily more adversely affected by crown closure than the diameter of Genotype B. Hence, in

Figure 4. Three hypothetical models portraying the effect of crown closure on two genotypes of forest trees. In Model I, the diameter growth difference converges to compensate for a difference in height growth, since an upper limit to volume production is assumed. In Model II, the upper limit of volume is also assumed, but the diameter growth trends are parallel, so that the difference in volume is proportional to height growth after closure. In Model III, no upper limit is assumed, and diameter growth trends continue to diverge.

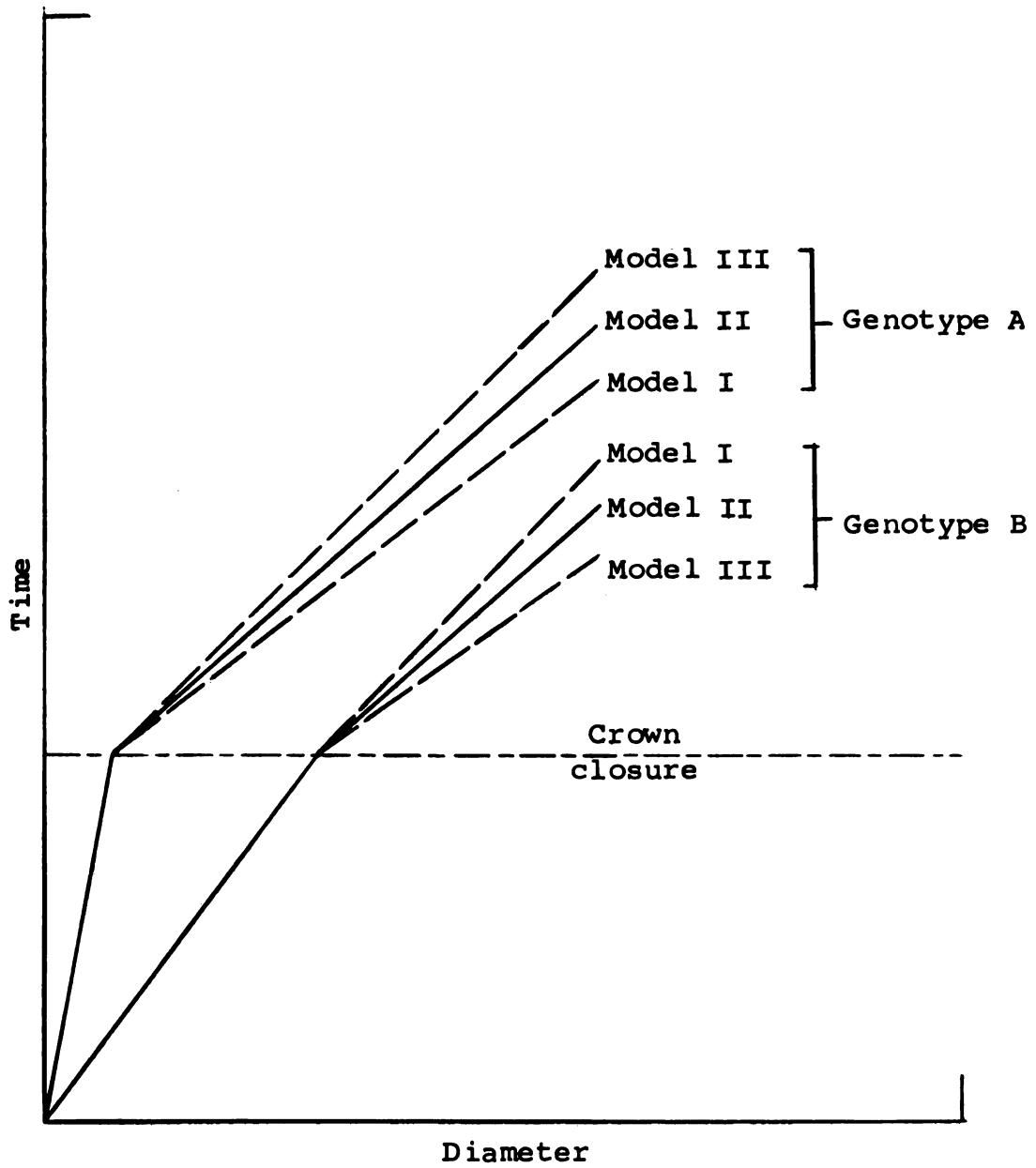


Figure 4

Figure 4 the diameter growth trends converge to compensate for the difference in height that is unaffected by crown closure. The net effect is that there is no difference between genotypes in volume growth after the productivity limit of the site has been attained. This occurs soon after crown closure.

In Model II, differences between genotypes in volume production result from the initial differences obtained before crown closure. A slow-growing genotype attains crown closure at a later age than a fast-growing genotype, but with equal spacing it will have the same height and diameter at closure. As the upper limit of site productivity is approached, the height-growth difference is maintained as in Model I. However, basal area growth rate will be diminished until it reaches the same plateau for both genotypes. Hence, the volume growth difference between genotypes varies in proportion to height, not to basal area.

For example, if Genotypes A and B differ by one cord per acre at age 5, they will differ by one cord per acre by age 50. This means that in percentage terms the genetic gain will be declining. The initial divergent trends between genotypes in diameter growth, followed by parallel trends after closure (Figure 4), will be negated in older trees, since the first five years of diameter growth will account for a declining percentage of total volume.

Applied to Zobel's data (1971), this means that the volume growth response of 53 percent at age 4 will decline toward the presently estimated height growth response of 18 percent at age 40. Likewise, in our progeny test of 9 Norwegian families, the presently deduced volume growth response of 32 percent (direct selection) will decline to the presently estimated 5 percent response for height.

In Model III, there is no limit to growth at any known stand density. The growth rate trends continue to diverge after crown closure, though at a reduced rate, so that genotypic differences in volume remain. This is essentially the model found by Baskerville (1965) to apply to shade-tolerant spruce and fir stands (Picea and Abies spp.).

These trends are summarized in the following tabulation:

<u>If the volume growth superiority of Genotype A before crown closure is:</u>	<u>At age 50 volume growth superiority of Genotype A is as follows in Model:</u>		
	<u>I</u>	<u>II</u>	<u>III</u>
53%	$\geq 0\%$	$\geq 18\%$	$> 53\%$
33%	$\geq 0\%$	$\geq 5\%$	$> 33\%$

Which one of these models applies to particular silvicultural situations depends on the species involved and the management goals. Generally, Model II would seem to be the most reasonable. Most forest stands probably do

have an upper limit to productivity, and it is unlikely that the rates of diameter growth of different genotypes converge after closure.

When thinning is practiced, Model III is pertinent, since the upper limit of site productivity is effectively moved out of reach. The practical implication of Model III is, therefore, that genetic gains can be optimized by intensive silviculture. Cultural methods, such as thinning, favor maximum genotypic expression under minimum environmental restrictions.

In commercial practice, it is likely that some combination of Models II and III would apply. Intensive silviculture is the exception rather than the rule in the United States. Hence, Model II applies until a thinning is performed, at which time the growth pattern conforms to Model III. At the recurrence of crown closure, the situation reverts to Model II.

Theoretical Implications

In all three species, variations in taper showed little or no correspondence with variations of the height/diameter ratio. This difference is pertinent to future studies of stem form. Experiments which estimate the genetic control of stem form variation by means of height/diameter ratio measurements (e.g., Callaham and Liddicoet, 1962; Nilsson, 1968) are not directly comparable with

studies which evaluate stem form differences based on stem section methods or diameter/diameter ratios (e.g., Pederick, 1970).

For the purpose of studying racial variation, or for evolutionary considerations, the height/diameter ratio and stem taper may both be useful. The fact that these traits were not strongly correlated suggests that they are controlled by different genes. Such uncorrelated traits are useful in studies of phylogeny and numerical taxonomy, in which multivariate statistical techniques are enhanced by the incorporation of many uncorrelated traits.

Genetic Control of Growth Processes

The genetic correlations between height and diameter and the variations in stem taper suggest a number of avenues of inquiry for the physiological geneticist.

For example, it is not known if there is genetic variation in the quantity of auxin synthesized by any plant species, let alone members of the genus Pinus.

Other growth regulators are no doubt involved. Differences in growth or taper may arise from a genetically monitored interaction or balance between auxins, gibberellins and cytokinins.

Genes may not only regulate the synthesis of different relative amounts of growth hormones, but translocation of such substances through plant tissues may also be genetically controlled. For example, the rate at which auxin is

translocated down the stems of trees after the first flush of growth may be inherited.

The auxin theory can also help to explain how height and diameter growth may be controlled by many of the same genes and yet occur at different times. For example, basic growth processes, such as cell elongation and division, may be controlled by the same genes regardless of tissue location or time in the growing season. These processes, however, may be triggered by growth regulators.

According to this model, the growth regulators are controlled by genes which differ with time of season and tissue location. Some genes affect apical or primary growth by stimulating auxin synthesis at a particular time in response to external stimuli, such as temperature or photoperiod. Other genes control the rate of auxin translocation downward in the stem, so that radial growth is induced. The radial growth process is further developed by genes which determine the time of synthesis and translocation of cytokinins, so the cell division occurs.

The net effect on growth is that height and diameter are affected in the same manner by those genes which simply set the pace of cell elongation and division. They are affected differently by those genes which determine the time of auxin synthesis in particular tissues and its rate of translocation.

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