GENETIC VARIATION IN THE HEIGHT-DIAMETER RATIO IN SCOTCH PINE

Jonanthan W. Wright[1/]

ABSTRACT.--A range-wide provenance test including seed from 110 parts of the species' natural range was established in 1961 in three Michigan plantations. The trees were measured in 1973-1974, shortly after crown closure. At that time the plantation in the Upper Peninsula averaged 12.7 ft. tall and 3.3 in. diameter-at-l-foot; the two plantations in the Lower Peninsula averaged 23.9 and 23.2 ft. tall and 6.0 and 6.2 in. diameter, respectively. The average height/diameter ratio (feet/feet) was 54:1 in all three plantations. The six tallest seedlots (30 percent taller than average) were from Belgium, northern France, West Germany, and eastern Czechoslovakia. Their height/diameter ratio varied from 50:1 to 54:1 (differences not significant); all six were among the eight largest in diameter. Thus, selection for rapid volume growth can be done on the basis of either height or diameter. Trees from the north (northern Sweden, Siberia, and the Ural Mountains) grew at very slow to moderate rates (40 to 90 percent of average). Such trees were more slender than average, having height/diameter ratios of 56:1 to 58:1. The stockiest trees (i.e., lowest height/diameter ratios) were from Spain, Greece, Turkey, and northern Italy (average height/diameter ratios of 44:1, 49:1, 50:1, and 50:1, respectively). Those races grew at moderate rates (80 to 100 percent of average) and are among the best for Christmas tree production from the standpoints of foliage color and needle length.

Traditionally in genetic experiments either height or diameter have been measured and separately reported. Sometimes both have been used as the basis for volume estimates but rarely has there been a critical analysis to show the exact relation between the two. This relation concerns the general question of whether growth is controlled by general "growth rate" genes, by specific genes for height growth and for diameter growth, or by a combination of the two types. The

1/ Professor of Forestry, Forestry Department, Michigan State University, East Lansing, Michigan.

objective of the study is to answer this important question.

If "growth rate" genes predominate, tree breeding efficiency would improve in several ways: (1) selection of plus-trees for high yield would be simplified; (2) roguing of progeny test seedling seed orchards would be made easier; (3) measurements when trees are taller would be much less costly because only diameters would need to be measured, and (4) the prediction of future genetic differences would be more accurate.

PREVIOUS WORK

A few generalizations can be made from the extensive silvicultural research on diameter growth and stem form. Diameter growth is usually greatest in young trees, primarily because they suffer the least severe competition. In humid regions, rate of diameter growth may be nearly constant until crown closure and then decrease rapidly. It may then increase after thinning, to decrease again as growing space becomes limiting. In young trees the rate of diameter growth is approximately the same at different heights, resulting in a conical bole. With increasing age, diameter growth tends to be greatest near the base of the live crown. Hence, in old forest-grown trees the lower bole may be almost cylindrical.

Genetically, height and/or diameter have been measured more frequently than any other trait. Large differences among seedlots have been found in both traits, but the degree of independence between them has rarely been investigated. One exception is La Farge 2/ who worked with 10 to 12-year-old provenance and with half-sib progeny tests., The average ratio of total height to diameter-breast-high varied from 25:1 to 29:1 (ft/ft) in ponderosa pine, 67:1 to 73:1 in eastern white pine, and 36:1 to 38:1 in Scotch pine. In all three species most of the variation was associated with region of origin, little with differences among stands located a few miles from each other or with differences among the offspring of different trees within the same stand. In ponderosa and eastern white pines the fattest trees (i.e., the lowest ratios) were of southern origin; in Scotch pine the fattest trees were of northern origin. La Farge also studied the ratio between diameter at midheight to that at breastheight. Particularly in ponderosa pine, there were interesting differences in this ratio. It varied from 0.53 to 0.58 (conical stem form) in trees from the interior, and from 0.62 to 0.65 (cylindrical lower boles) in western trees.

2/ La Farge, Timothy. 1971. Inheritance and evolution of stem form in three northern species. Michigan State University Ph.D. thesis, 332 p.

Although much smaller than the differences in either height or diameter, the differences in these ratios were statistically significant and large enough to be of practical importance. La Farge interpreted some of the ratio-differences to be due to differences in cold hardiness; in the northern test area extreme winter cold may have affected height growth more than diameter growth with the result that the least hardy southern trees had the fattest stems. Some he interpreted as due to the presence of separate genes for height and diameter growth.

MATERIAL AND METHODS

The present study is based upon three provenance-test plantations established with 2-0 stock in 1961 as part of the NC-99 regional tree improvement project. The total experiment includes 122 seedlots representing 106 natural stands well distributed over the species' natural range in Eurasia. In the three plantations, 72, 108, and 110 of the seedlots were represented.

The seedlings were planted at a spacing of 8 by 8 ft, with 4-tree plots and 7 to 10 replications per plantation. Necessary weed control was practiced the first 2 years. Survival averaged 90+ percent at each site, but growth was much inferior in northern Michigan (table 1).

Table 1.--Mean heights, diameters, and height/diameter ratios in three Michigan test plantings of Scotch pine

Plantation location	Year measured	Average Height	Average Diameter at 1 ft	Average Height/diameter ratio
		ft	inches	ft/ft
Kellogg Forest,southern Michigan	1974	23.9	6.0	54.6
Rose Lake, central Michigan	1974	23.2	6.4	53.4
Dunbar Forest, northern Michigan	1973	12.7	3.3	53.6

Crowns closed between 1971 and 1973 in the two fastest growing southern Michigan plantations. These plantations were thinned in the winter of 1973-1974 to leave the three best (tallest and/or straightest trees per plot and the trees were pruned to leave six whorls per tree. Crowns have not closed in the northern Michigan plantation, which has been pruned but not thinned.

Total height and diameter, as well as other traits, were measured in the summers of 1973 and 1974 on the two tallest trees per plot. These were generally straight-stemmed trees in which growth rate had not been affected by insect or bird damage. Measurement of the two tallest trees per plot results in inflated estimates of height and diameter but the values of one seedlot to another are rarely affected by more than 1 percent. Diameter was measured at a height of 1 foot above the ground (or 15 inches if there was a branch whorl). Diameter measurements near the ground were better for biological purposes than diameter measurements at breast height because one plantation was twice as tall as another, and some seedlots were four times as tall as others in the same plantation.

Wright _et al_.[3/] describe variation in other traits and give general recommendations for the choice of Scotch pine planting stock.

An analysis of variance was performed on the height, diameter, and height/diameter ratio separately for each plantation and for all plantations combined,

RESULTS

Mortality averaged less than 10 percent in each of the three plantations. Most deaths occurred the first 2 years after field planting, primarily because of poor planting or weed competition.

The growth data are summarized by variety in table 2. In most varieties, both height and diameter were 70 to 100 percent greater the Lower Peninsula than in the Upper Peninsula plantation.

Varieties _haguenensis_ and _carpatica_ from north-central Europe grew fastest at all locations. In the Lower Peninsula they averaged 28 ft tall 13 years after planting and grew at the rate of 2.5 ft per year during the previous 5 years. The six fastest growing seedlots, all from the same two varieties, grew 2.6 ft per year. Thus, they compare favorably with native pine species.

Varieties from northern Eurasia grew only 50 to 80 percent as fast, whether planted in the Upper or Lower Peninsula. Because of their slow growth and because they turn yellow during the winter, they are not planted extensively for either timber or Christmas trees.

Western and southern varieties are preferred for Christmas tree planting because they remain green during the winter and have short needles (table 2). Most grew 75 to 90 percent as fast as the timber varieties. Var. _iberica_ from Spain, which remains the greenest during winter and is the favorite of many southern Michigan growers, suffered severe winter injury and consequently grew very slowly in the Upper Peninsula.

3/ Wright, Jonathan W., W. A. Lemmien, J. N. Bright, M. W. Day, and R. L. Sajdak. 1975. Scotch pine varieties for Christmas tree and forest planting in Michigan. Michigan Agric. Exp. Stn. Res. Rep. (In press.)

Table 2.--Height, diameter, and height/diameter ratios of 18 Scotch pine varieties grown in 3 Michigan plantations (data from the 2 Lower Michigan plantations were similar so they were combined)

Variety and place of origin 1/	Height L.P. 2/	Height U.P.	Diameter L.P.	Diameter U.P.	Height/diameter ratio L.P.	Height/diameter ratio U.P.
	Feet		Inches		Feet	
VARIETIES FROM NORTHERN EURASIA						
lapponica N SWE N FIN	14.1	6.7	3.4	1.9	56	45
septentrionalis SWE	19.9	10.5	4.8	2.8	55	50
rigensis S SWE LAT	22.9	14.1	5.8	3.5	55	54
mongolica SIB	20.9	12.2	4.7	2.7	57	53
uralensis URA	23.9	12.3	5.4	3.2	58	55
VARIETIES FROM CENTRAL EUROPE						
polonica POL	27.4	15.5	7.0	3.7	54	55
hercynica W GER W CZE E GER	27.1	15.6	6.7	3.9	54	54
carpatica E CZE	27.6	16.2	6.9	4.0	54	55
haguenensis BEL N FRA W GER	28.3	15.8	7.4	4.0	51	53
pannonica HUN	26.4	12.6	7.1	3.3	51	51
VARIETIES FROM WESTERN AND SOUTHERN EURASIA						
"E. Anglia' ENG	27.1	15.7	7.1	3.8	52	56
scotica SCO	22.7	11.5	5.9	3.0	52	52
iberica SPA	21.6	6.0	6.3	2.1	46	42
aquitana S FRA	22.9	11.6	5.9	3.1	53	54
subillyrica N ITA	24.2	12.4	5.9	3.8	50	51
illyrica YUG	25.3	13.2	6.3	3.4	54	51
rhodopaea GRE	24.0	12.8	6.3	3.3	50	47
armena TUR GEO	24.5	11.9	6.2	3.2	50	51

1/ BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GREece, GERmany, HUNgary, ITAly, LATvian SSR, POLand, SCOtland, SIBeria, SPAin, SWEden, TURkey, URAl Mountains, YUGoslavia.

2/ L.P. = Lower Peninsula, Michigan; U.P. = Upper Peninsula, Michigan.

Despite the large differences in growth rate between the Upper and Lower Peninsula plantations, bole form was similar. The height/ diameter ratio averaged 54 ft/ft at all three test sites. Northern varieties were the most cylindrical, i.e., had the highest height/ diameter ratios. Southern varieties were generally the most conical, having the lowest ratios. Spanish var. iberica was especially noteworthy, with ratios of 46 and 42 in the Lower and Upper Peninsula plantations, respectively. The very low ratio of 42 in the Upper Peninsula plantation was related to the severe winter injury suffered by Spanish trees there. Because of repeated top dieback, they made little height growth but continued diameter growth.

In both height and diameter, differences among varieties accounted for three-fourths of the total genetic variance (table 3). Interactions accounted for most of the remainder. Much of the interaction was caused by the very different performances of var. iberica and var. lapponica in the northern and southern test sites.

Table 3.--Statistical significance of the differences in height, diameter, and height diameter ratio

Source of variation	Degrees of freedom	Trait: Height	Diameter	Height/ diameter ratio
		Mean squares		
Variety	16	16,564**	6,482**	6,546**
Seedlot within variety	92	215	137**	667**
Variety x plantation	32	720**	416**	1,983**
Seedlot within variety x plantation	150	184**	68	301
Replication within plantation	14	2,086**	864**	1,526**
Error (= seedlot within variety x replication within plantation)	1,271	94	58	259
		Variance components, as percent of total genetic variance		
Variety		79	74	32
Seedlot within variety		1	6	21
Variety x plantation		9	12	40
Seedlot within variety x plantation		10	8	7

** = statistically significant at 1 percent level.

In the height/diameter ratio, differences among varieties were important but not overwhelming. About 20 percent of the total genetic variance was due to differences among seedlots within the same variety. For example, this ratio varied from 49 to 54 within the, fastest growing variety, _haguenensis_, and from 53 to 56 within the second fastest growing variety, _carpatica_. Also, there was some interaction in the ratio, due primarily to the different behavior of the slow growing var. _lapponica_ and the cold sensitive var. _iberica_ in the two peninsulas.

POSSIBLE CAUSES OF DIFFERENCES IN HEIGHT/DIAMETER RATIOS

Measurement Technique

For the best estimates of a tree's productivity, measure diameter at ground level and total height. Measuring diameter at a higher point will result in an increase in height/diameter ratios and the effect will be much larger for small than for large trees.

The present data are based upon diameters measured 1 foot above the ground, thus eliminating butt swell. The 1 foot was an appreciable portion of total height only for the slowest growing seedlots planted in the Upper Peninsula. The fact that height/diameter ratios were low indicates that the results were not influenced appreciably by measurement technique.

Competition

The measurements were timed to provide information on bole form of trees grown under competition-free conditions. Actually, crown closure in the two Lower Peninsula plantations had begun in 1971 and was practically complete by the time the measurements were made. Thus, there was some opportunity for competition-induced inflation of height/diameter ratios. However, judging from the stumps of trees cut in thinning and by the similarity of ratios between the plantations which differed markedly in growth rate, competition had not affected rate of diameter growth appreciably at the time of measurement.

Winter Hardiness

Lack of cold hardiness had a demonstrable effect on the height/diameter ratio of var. _iberica_ in the Dunbar Forest plantation. Nearly every winter most trees of this variety suffered dieback of branches or main stem and as a consequence grew little in height. However, most retained live branches below the snow line and continued diameter growth.

Other southern varieties did not suffer visible winter injury in Michigan, but in European experiments have not withstood extreme winter cold. There is a possibility that their growth processes are upset during Michigan winters, and that this upset is apparent only in a slight reduction in rate of height growth the subsequent season. However, this cannot be demonstrated by a difference in ratio for most southern varieties grown in the Upper versus the Lower Peninsula.

Separate Genes for Height and Diameter Growth

The main purpose of this experiment was to determine whether there are general genes for growth rate or separate genes for height growth and for diameter growth. The results indicate that both types of genes are present. A strong correlation exists between height and diameter, indicating that some genes influence both. But differences in the height/diameter ratio sufficient to cause 10 percent differences in diameter growth among varieties having the same rates of height growth indicate that some genes affect mainly height growth or mainly diameter growth.

PRACTICAL SIGNIFICANCE

Timber Production

Good stem form and high volume production are the primary considerations in timber production. The ideal Scotch pines are those that grow most rapidly in height and in diameter. From the practical standpoint, the most important data on height/diameter ratios are those that concern the fastest growing seedlots. The height/diameter ratio did not differ enough among these seedlots to be of practical importance at the present time. The fastest growing variety, haguenensis, was tallest and had the largest diameter and would, therefore, be selected for planting no matter what the criterion. Of the 122 individual seedlots, those which ranked 1, 2, 3, 4, 5, and 6 in rate of height growth ranked 7, 3, 1, 8, 2, and 6 in rate of diameter growth; they did not differ significantly in either height or diameter. Having both height and diameter data would improve the estimates of genetic gain in volume production, but would not materially change the amount of such genetic gain.

Christmas Tree Production

Christmas tree growers are interested primarily in Scotch pines that retain green foliage color during the winter, have short needles, and grow slowly enough to require a minimum of shearing. For those reasons, southern and western varieties are preferred.

The height/diameter ratio is also of interest to growers who ship long distances, because shipping costs are highest for heavy-boled trees. Several growers have reported that their shipping costs were extraordinarily high for Spanish trees. The present data show that this is true because the Spanish var. iberica has the lowest height/diameter ratio. For trees of equal height, bole diameter is 10 percent greater and bole volume is 20 percent greater for Spanish than for most other Christmas tree varieties.

Volume Production

Some data on volume production of Scotch pine over long rotations in Michigan are already available. They are based on 30- to 40-year-old plantations, probably of German (var. hercynica) origin. For estimates of volume production with genetically improved trees, we must rely on comparatively young experiments such as described here.

To do so requires extrapolation. Under Lower Peninsula conditions, the six fastest growing seedlots (var. haguenensis and carpatica) averaged 29.1 ft tall and are growing at the rate of 2.6 ft per year; 11 percent superior to var. hercynica. Up to age 14 there has been very little change in growth rates of various seedlots, and it is safe to assume that the long term genetic gain in rate of height growth is 11 percent.

For those six seedlots the present genetic gain in diameter growth is also 11 percent or 0.7 inches. However, future diameter growth will be governed more by spacing than by genetic potential because crowns have closed. If these six seedlots were planted for saw logs and subjected to frequent thinning, a continuation of the 11 percent advantage in rate of height growth and rate of diameter growth could be assumed, at least until age 25 or 30. In that case, there would be an approximate 37 percent gain in rate of volume production per tree. If, however, plantations of the improved stock were managed so as to maintain a closed crown canopy, the 0.7 in. diameter advantage by age 14 would be maintained, but future rate of diameter growth would be similar to that already found for plantations of var. hercynica. In that case, volume estimates for the improved Scotch pine should assume 11 percent greater height and 0.7 in. greater diameter for all trees after age 14.

Future Measurement of Test Plantations

The three test plantations described here are easy to walk through. They have been pruned, and diameter measurements are easily made. Early height measurements were not much of a problem but those made at age 14 were time consuming. By age 20, the tallest varieties will exceed 40 ft and individual trees will be 50 ft tall.

Yet such experiments as this must be maintained and may produce their most valuable information after age 20. Growth data will be an important part of that information. The easiest solution will be to measure diameter only and to assume a constant height-diameter relation. That would be moderately satisfactory as regards choosing those seedlots with the greatest average growth rates but would be totally unsatisfactory in comparing future growth rates of northern and southern varieties, in view of the large racial differences in the height/diameter ratio.