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**Heritability and genetic correlations for volume, foxtails, and other
characteristics of Caribbean pine in Puerto Rico**

By F. TH. LEDIG and J. L. WHITMORE



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in collaboration with

W. H. G. Barrett
Fiplasto Forestal
Maipú 942 - Piso 21
1340 Buenos Aires
Argentina

J. Burley
University of Oxford
Department of Forestry
Commonwealth Forestry Institute
South Parks Road
Oxford OX1 3RB
England

W. G. Dyson
Centro Agronomico Tropical de
Investigación y Enseñanza
(C.A.T.I.E.)
Turrialba
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D. P. Fowler
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Canadian Forestry Service
Tree Improvement
P. O. Box 4000
Fredericton, N. B. E3B 5P7
Canada

M. Giertych
Instytut Dendrologii
Polskiej Akademii Nauk
63-120 Kórnik
ul. Parkowa 5
Poland

M. Hagman
Metsäntutkimuslaitos
The Finnish Forest Research Institute
Unioninkatu 40 A
SF-00170
Helsinki 17
Finland

M. Hühn
Institut für Pflanzenbau und
Pflanzenzüchtung der Universität
Kiel
Neue Universität/Haus 41
Olshausenstraße 40—60
2300 Kiel
Bundesrepublik Deutschland

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Bundesforschungsanstalt für Forst- und
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unter Mitwirkung von

R. C. KELLISON
School of Forest Resources
North Carolina State University
Department of Forestry
Box 5488
Raleigh, N. C. 27607
U. S. A.

T. N. Khoshoo
National Botanical Research Institute
Lucknow - 226001
India

J. F. Lacaze
Centre de Recherches Forestières
d'Orléans
Station d'Amélioration
des Arbres Forestiers
Ardon
45160 Olivet
France

J. D. Matthews
University of Aberdeen
Department of Forestry
St. Machar Drive
Old Aberdeen AB9 2UU
Scotland

G. H. Melchior
Institut für Forstgenetik
und Forstpflanzenzüchtung
Siekerlandstraße 2
2070 Großhansdorf 2 — Schmalenbeck
Bundesrepublik Deutschland

G. Namkoong
Department of Genetics
North Carolina State University
Box 5487
Raleigh, North Carolina 27607
U. S. A.

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Bundesforschungsanstalt für Forst- und
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avec la coopération de

D. G. Nikles
Department of Forestry
P. O. Box 5
Brisbane, Roma Street
Brisbane 4000
Australia

K. Ohba
Forestry and Forest Products
Research Institute
P. O. Box 16, Tsukuba Norin Kenkyu
Danchi - nai
Ibaraki, 305 Japan

M. Quijada R.
Universidad de los Andes
Facultad de Ciencias Forestales
Instituto de Silvicultura
Apartado No. 305
Mérida
Venezuela

C. J. A. Shelbourne
Forest Research Institute
Private Bag
Rotorua
New Zealand

F. Stettler
University of Washington
College of Forest Resources
Seattle, Washington 98195
U. S. A.

L. Szöny
MEM ESZ Póstaflók 10
H 1355 Budapest
Hungary

J. W. Wright
Michigan State University
Department of Forestry
East Lansing, Michigan 48824
U. S. A.

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Heritability and genetic correlations for volume, foxtails, and other characteristics of Caribbean pine in Puerto Rico

By F. TH. LEDIG¹⁾ and J. L. WHITMORE²⁾

Institute of Tropical Forestry, Southern Forest Experiment
Station, Forest Service, U. S. Department of Agriculture,
Rio Piedras, P. R.

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Summary

Caribbean pine is an important exotic being bred throughout the tropics, but published estimates are lacking for heritability of economically important traits and the genetic correlations between them. Based on a Puerto Rican trial of 16 open-pollinated parents of var. *hondurensis* selected in Belize, heritabilities for a number of characteristics ranged from 0.04 to 0.53. Volume had a moderate heritability of 0.11 while bark thickness had a high heritability of 0.53. These values are similar to those for southern pines, and indicate the potential for substantial gains from selection of individuals within Puerto Rican plantations. Family variation within provenance for foxtail growth form, a subject of much speculation, was tested and found to be 0.17, a value indicating that selection against foxtails could also be effective. Phenotypic correlations between traits were weak, but additive genetic correlations appeared stronger, so selection for one characteristic must consider correlated responses for others.

Key words: *Pinus caribaea*, progeny tests, bark thickness, stem form, branching characteristics.

Zusammenfassung

Pinus caribaea MORELET ist eine wichtige Exotenbaumart, die überall in den Tropen gezüchtet wird, aber veröffentlichte Schätzwerte für die Heritabilität ökonomisch wichtiger Merkmale und ihrer genetischen Korrelationen fehlen. Die Heritabilitäten einiger Merkmale wurden aufgrund eines puertoricanischen Versuches mit 16 frei abgeblühten Eltern der Varietät *hondurensis*, die in Belize selektiert worden waren, geschätzt und lagen zwischen 0,04 und 0,53. Das Volumen hat eine mäßige Heritabilität von 0,11, während die Rindendicke mit 0,53 eine hohe Heritabilität hat. Die Werte gleichen denen südlicher Kiefernarten und verdeutlichen das Potential wesentlicher Selektionsgewinne bei Individuen in puertoricanischen Pflanzungen. Die Variation von Familien innerhalb von Provenienzen mit Fuchsschwanz-Wuchsform, einem Merkmal, über das viel spekuliert wird, wurde untersucht und festgestellt, daß diese mit 0,17 einen Wert anzeigt, der eine Selektion gegen Fuchsschwanz-Wuchs effektiv erscheinen läßt. Die phänotypische Korrelation zwischen den Merkmalen war gering, aber die additiven genetischen Korrelationen waren stärker. Daher muß bei der Selektion auf ein bestimmtes Merkmal auch die Korrelation mit anderen Merkmalen berücksichtigt werden.

Introduction

Caribbean pine (*Pinus caribaea* MORELET) is becoming one of the most important exotics in tropical and subtropical forestry (e.g. articles in BURLEY and NIKLES, 1972). Its rate of growth is often excellent, occasionally over 50 m³/ha/year to age 12 in Puerto Rico (WHITMORE and LIEGEL, 1980), but there is substantial variation in volume production and form. In the moist tropics, var. *hondurensis* BARRETT and GOLFARI outgrows var. *bahamensis* BARRETT and GOLFARI and var. *caribaea*, but the slower growing vars. *caribaea* and *bahamensis* have superior form (eg. MUSALEM and ROSERO, 1973; WIERSUM, 1973). Within var. *hondurensis* there are differences among provenances. It is likely that both growth and form can be improved by selection and breeding of variety, provenance, and trees within provenance. However, there is little information on heritability of economically important traits from which to estimate potential gains from selection. Nor is there quantitative data on the

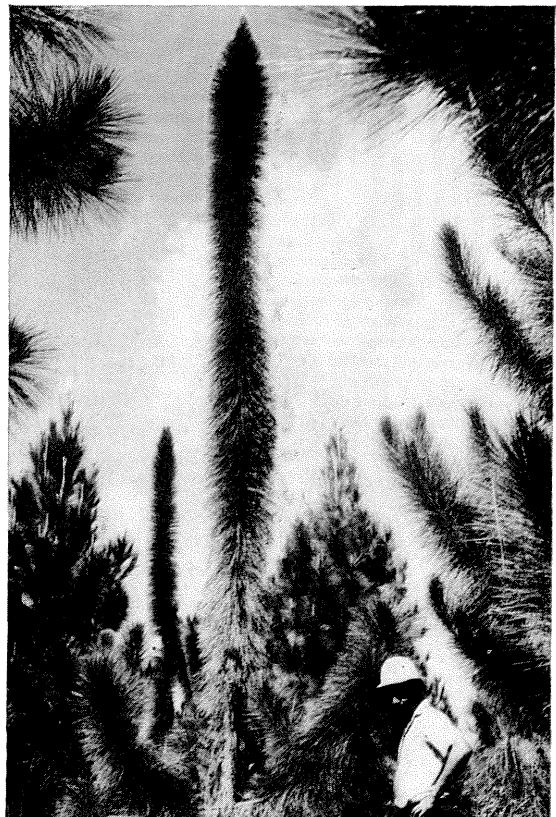


Fig. 1. — Two Caribbean pines in foxtail growth stage. Branched pines in the background are a Mexican species (*P. oocarpa* SCHIEDT).

¹⁾ Present address: Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, P. O. Box 245, Berkeley, CA 94701, U.S.A.

²⁾ Present address: International Forestry Staff, Forest Service, U. S. Department of Agriculture, P. O. Box 2417, Washington, D. C. 20013, U.S.A.

relationship between form and growth rate necessary to design multi-trait improvement programs.

In particular, the magnitude of the genetic component for foxtail growth form in Caribbean or other tropical pines is unknown, and whether foxtailing is genetically linked with volume growth is uncertain. Foxtails are a particularly undesirable stem form. They occur on pines grown where there is no pronounced dry season, and are characterized by uninterrupted apical elongation and formation of needle fascicles without the production of branch primordia (Fig. 1; LANNER, 1965, 1972). When buds are finally set, the resulting branch cluster is usually dense, producing a "basket" effect (Fig. 2) and creating a weak point in the stem; apical dominance may be lost, resulting in permanent forking, and breakage of the whip-like stem may be a problem.

The relationship of foxtails to vigor is unclear. The slower growing varieties of Caribbean pine produce almost no foxtails, but between two provenances of var. *hondurensis* planted in Costa Rica, the slower-growing one from Nicaragua had a greater proportion of foxtails than the faster-growing Belizian provenance at 2.5 and 4 years of age (WIERSUM, 1973; MUSALEM and ROSERO, 1973). Within a seed source, foxtail Caribbean pine on some sites in Malaysia were superior to non-foxtail trees in height and diameter at six years of age, but on other sites were slightly smaller in diameter (IBRAHIM and GREATHOUSE, 1972). In plantations of the closely related slash pine (*P. elliottii* ENGELM.) in Florida, trees with foxtails were taller and of larger diameter and height than those with normal growth (PETER and SQUILLACE, 1978).

We report heritabilities and character correlations estimated from an open-pollinated progeny test of 16 families raised from superior phenotypes selected on Mountain Pine Ridge, Belize. The *P. caribaea* var. *hondurensis* of Mountain Pine Ridge is a common source of seed for Caribbean pine planting in Puerto Rico and many other tropical countries. We use the estimates of genetic parameters to calculate the gain from selection within planted stands of Caribbean pine in Puerto Rico.

Materials and Methods

The 16 open-pollinated families represented in the test were progeny of trees selected on Mountain Pine Ridge, Belize by A. F. A. LAMB (LAMB and BURLEY, 1972). According to communication with IAN NAPIER³⁾, selection for large size may be ineffective in increasing growth because these stands were established after fire, and large trees may represent early colonists or even remnants of the old stand rather than rapid-growers. Major emphasis in selection was placed on stem and crown form. Most trees were located close to roads, so apparently, accessibility was important. Because there is no foxtailing in the natural stands, it was not a criterion for selection. It is likely that the selected families represent a nearly random sample in relation to growth and foxtailing under Puerto Rican conditions, but may have a narrowed base for stem and crown form.

Families were planted in December 1971 in row plots of four trees, replicated in 12 blocks, on one site. Containerized seedlings and a 3- × 3-m spacing were used. The site is in the subtropical moist forest life zone (HOLDRIGE, 1947; EWEL and WHITMORE, 1973), on Pandura (Typic Eutro-

Table 1. — Form of the analyses of variance and covariance.

Source	d.f.	Expected Mean Squares ¹⁾	Expected Mean Products ²⁾
Blocks	11		
Families	15	$\sigma^2_w/3.05 + \sigma^2_e + 12\sigma^2_f$	$\sigma_{w_1w_2}/3.05 + \sigma_{e_1e_2} + 12\sigma_{f_1f_2}$
Residual	164	$\sigma^2_w/3.05 + \sigma^2_e$	$\sigma_{w_1w_2}/3.05 + \sigma_{e_1e_2}$
Within plot	449	σ^2_w	$\sigma_{w_1w_2}$

1) Components of variance: $\sigma^2_f = 1/4 \sigma^2_{hs}$, the variance among half-sib families; σ^2_e , the residual or plot to plot variance; σ^2_w , the variance within plots.

2) Components of covariance between traits 1 and 2: $\sigma_{f_1f_2}$, the family covariance; $\sigma_{e_1e_2}$, the residual of plot-to-plot covariance; $\sigma_{w_1w_2}$, the covariance within plots.

pept) and Mayo (Typic Dystropept) soils near Yabucoa, Puerto Rico. The altitude is 50 m and annual precipitation is about 2000 mm.

Measurements reported here were recorded in May 1978 when the plantation was 6.5 years-old (7 years from seed). Survival was 83% and did not vary significantly among families. Height was measured to the nearest 0.5 m with a Haga altimeter and diameter at breast height (dbh) was measured to 0.1 cm with a diameter tape. Height averaged 11.2 m and dbh 16.0 cm. Volume was calculated as total overbark volume with the equations developed for Tanzania by ACKHURST and MICSKI (1971), the commonly used volume table in Puerto Rico. The plantation average was 0.117 m³ per tree. Maturing cones were counted from one viewing point and multiplied by three to estimate total cone crop; the method has not been calibrated and values can be considered only relative. Bark thickness was recorded in inches as the average of three measurements made with a bark gauge around the bole at breast height. Other characteristics were scored subjectively from 0 to 2: foxtailing—0 for none, 1 for a foxtail resulting in no defect such as the loss of apical dominance associated with the "basket of branches" that often terminates foxtails, and 2 for repeated foxtailing and foxtailing resulting in loss of leader dominance; forking—0 for none, 1 for forking where one leader eventually assumed dominance, 2 for repeated or permanent forking; branch angle—0 for near horizontal (0° to 30°) 1 for average (30° to 45°) 2 for steeply ascending branches (45°); branch diameter—0 for fine, 1 for average, 2 for heavy; stem straightness—0 for perfectly straight, 1 for slight deviation but no serious degrade, 2 for crooked; interwhorl length, the distance between branch whorls exclusive of foxtail segments—0 for close, 1 for average, 2 for long segments.

Data were analyzed on a plot mean basis by analysis of variance and covariance, with families a random effect. Because of a shortage of seedlings, one family was omitted from block XII, so values for analysis were estimated by missing plot techniques (SNEDECOR, 1956). Within-plot variance was calculated separately. Components of variance and covariance were derived using the expected mean squares and products in Table 1.

The family component of variance, σ^2_f , was assumed to represent 1/4 σ^2_a , the additive variance attributed to differences among half-sib families. Family covariance between traits was taken as 1/4 $\sigma_{a_1a_2}$. If selective pollination or fertilization occurs, the family components may be larger

³⁾ Forest Department, Belize.

than half-sib variances and covariances, and estimates of additive variance and covariance will be inflated. However, in pines it is likely that open-pollinated families closely approach half-sib families unless parents are isolated. Heritability (h^2) on an individual basis was estimated as:

$$h^2 = 4 \sigma_f^2 / (\sigma_f^2 + \sigma_e^2 + \sigma_w^2), \tag{1}$$

and heritability (h_p^2) on a plot mean basis was:

$$h_p^2 = \sigma_f^2 / (\sigma_f^2 + \sigma_e^2 / 12 + \sigma_w^2 / 48), \tag{2}$$

where symbols are defined as in Table 1.

Results

Most traits differed significantly among families. The single exception was branch angle, which did not vary among families at the 0.05 level of probability. Estimates of family variation for height and volume were smaller than those for dbh, number of cones, foxtailing, forking, branch thickness, or bark thickness.

Variance components were used to estimate narrow sense heritability on an individual tree and plot mean basis (Table 2). Individual heritability ranged from low values of 0.04 for branch angle and 0.10 for height, to a maximum of 0.53 for bark thickness. For half-sib family selection within a plantation of 4-tree plots and 12 replicates, heritabilities would be much higher (Table 2).

Because of the large number of observations ($N = 639$), many phenotypic correlations among traits were statistically significant, although relatively weak and ineffective as predictors of covariation (Table 3). Only the correlations between volume and height or dbh were high, which is to be expected because volume is calculated from dbh and height. Height and dbh were moderately correlated ($r = 0.66$), as were dbh and bark thickness ($r = 0.50$) and volume and bark thickness ($r = 0.42$).

By contrast, genetic correlations among traits were generally stronger (Table 4), but must be used cautiously because standard errors for genetic correlation are notoriously large, in general, and range from 0.042 to 0.580 for our estimates. The correlation between foxtailing and vigor i.e., dbh or height) was particularly interesting. There was a weak genetic association between foxtails and dbh, but between foxtails and height the correlation was almost zero. Cone crop was negatively associated with dbh, interwhorl length, and foxtails, but positively associated with

Table 2. —Variance components and heritabilities for growth and form.

Trait	Variance Components			Heritability	
	Family	Plot-to-Plot	Within Plot	Individual	Plot1)
Volume	0.00006	0.00027	0.00192	0.11	0.49
Height	0.07958	0.57787	2.57998	0.10	0.44
Dbh	0.38720	0.72318	6.98051	0.19	0.65
Foxtails	0.01429	0.01240	0.31594	0.17	0.65
Cones	58.060	38.152	607.33	0.33	0.79
Forking	0.03075	0.03294	0.43387	0.25	0.72
Branch angle	0.00277	0.01798	0.28069	0.04	0.27
Straightness	0.00882	0.02065	0.23400	0.13	0.57
Branch diameter	0.02432	0.01889	0.23131	0.35	0.79
Interwhorl length	0.01075	0.01690	0.24507	0.16	0.62
Bark thickness	0.00340	0.0	0.02201	0.53	0.88

1) For 12 replications of 4 trees per plot.

Table 3. — Half-matrix of phenotypic correlations among growth and form traits.1)

Trait	Height	Dbh	Foxtails	Cones	Forking	Branch angle	Straightness	Branch diam.	Interwhorl length	Bark thickness
Volume	0.81	0.93	-0.03	0.16	-0.02	-0.11	-0.08	0.12	-0.13	0.42
Height		0.66	0.08	0.15	-0.01	-0.17	-0.12	0.01	-0.22	0.22
Dbh			-0.06	0.15	-0.02	-0.03	-0.06	0.18	-0.08	0.50
Foxtails				-0.16	0.12	0.00	0.10	0.17	-0.15	-0.03
Cones					-0.03	0.00	-0.07	-0.00	0.07	-0.00
Forking						0.02	0.10	0.03	-0.08	-0.00
Branch angle							-0.02	0.20	-0.02	-0.14
Straightness								0.08	-0.00	0.04
Branch diameter									-0.21	0.08
Interwhorl length										0.01

1) Correlation of ± 0.08 required for significance at 0.05 level of probability.

Table 4. — Genetic correlations among growth and form traits.1)

	Dbh	Foxtails	Cones	Forking	Branch angle	Straightness	Branch diam.	Interwhorl length	Bark thickness
Volume	0.95	0.28	-0.07	0.13	1.08	0.47	0.28	0.23	0.40
Height	-0.33	0.07	1.00	0.01	-1.11	0.40	-0.71	-0.27	-0.39
Dbh		0.35	-0.35	0.20	1.40	0.24	0.52	0.29	0.47
Foxtails			-0.42	0.49	0.34	-0.09	0.44	-0.94	-0.05
Cones				0.20	-0.47	0.17	-0.10	-0.42	-0.29
Forking					0.54	0.57	0.56	-0.86	0.06
Branch angle						-0.24	1.05	0.53	-0.03
Straightness							-0.26	-0.04	0.23
Branch diam.								-0.29	-0.22
Interwhorl length									0.09

1) Absolute values greater than one are arithmetically possible, but are meaningless, and in the table largely reflect the large standard error associated with the component of variance for branch angle.

height. Perhaps as should be expected, large diameter branches were positively related to dbh. Forking was associated with both large diameter branches and foxtails; the former because steeply ascending branches, or forks, are in a position to compete for dominance and achieve larger size, and the latter because foxtails are often terminated by a cluster of coequal branches. The high correlations of branch angle with several other variables probably resulted from the low level of genetic variation in branch angle and the resulting high standard error.

Discussion

Heritability is peculiar to the population for which it is estimated, in the present case var. *hondurensis* from Mountain Pine Ridge, Belize, the common seed source used in Puerto Rico. In addition, the narrow-sense heritabilities estimated here strictly apply only to the progeny test site. Because of the failure to take into account family $\times$ environment interactions, which could be estimated only by replication of the trial on different sites, our statistics would overestimate heritabilities if applied over a wider area. Therefore, heritabilities in Table 1 must be considered upper limits. The progeny test values can not be applied to selection in natural stands because heritability in natural stands would be lower due to the heterogeneous conditions

of establishment, spacing, and competition. However, the estimates of heritability are applicable for countries like Puerto Rico where Caribbean pine is not native and selection is carried out in commercial plantings, similar in character to progeny test environments. Estimates of heritability presented here are among the few available for Caribbean pine, and their relative magnitude is likely to be similar for other populations and trials. The general trends will be valuable in planning breeding programs for this species.

In the nursery phase of this test GEARY and de BARROS (1973) found that family mean height at 21 weeks was correlated with percent germination, vigor as expressed by the inverse of days to 50% germination, and number of full seeds collected from the parent tree, considered a measure of parental environment ($r = 0.32$ to 0.64). We found no significant correlations between volume at 7 years and these variables. Neither was family mean volume at 7 years predicted by nursery height ($r = 0.11$ n.s.). Thus, influence of parental or nursery environment has apparently disappeared since outplanting and should have no effect on the heritabilities reported here.

Unless family $\times$ environment interactions are large, gains from selection in plantations should be rewarding and gains from family selection in progeny tests, substantial. For example, LEDIG and WHITMORE (in preparation) selected 36 trees for volume from among ca. 95,550 plantation-grown Caribbean pine in Puerto Rico. The selection differential, S was 0.524 m^3 . With a heritability of 0.11 for volume, predicted gain is:

$$\begin{aligned} G &= h^2 S \\ &= (0.11) (0.524) \\ &= 0.058 \text{ m}^3. \end{aligned} \quad (3)$$

On the basis of a mean volume of 0.324 m^3 at 16 years (LEDIG and WHITMORE, in preparation) a gain of 0.058 m^3 represents an improvement of 18% over present volume of Caribbean pine in plantations. Even allowing for an inflated estimate of heritability, tree improvement in Caribbean pine is promising, but these data must be interpreted with caution. The calculated gain refers to volume of individual trees, and it is questionable whether volume growth per acre can be increased to the same extent, unless grown under spacing regimes that take advantage of rapid growth rates. Large-plot trials would be necessary to determine whether competition among and within superior families would reduce gains expected from trials in which rapidly growing and slowly growing types are randomly interspersed.

Heritabilities reported here are similar to those in southern pines. For example, bark thickness was one of the most strongly inherited characteristics in several loblolly pine (*P. taeda* L.) progeny tests, in the southern United States, ranging from 0.5 to 0.7 (PEDERICK, 1970) compared to 0.53 for Caribbean pine in Puerto Rico. The heritability of 0.17 for foxtailing is the only estimate we know, and indicates that substantial reduction in the incidence of foxtails could be achieved by selection. Because foxtailing is a threshold character (i.e., either present or absent), selection will be most effective if conducted in environments highly favorable to the production of foxtails, in climates characterized by ample rainfall, evenly distributed throughout the year (see FALCONER, 1960).

Genetic correlations suggest that selection for volume growth will tend to increase crookedness because poor stem



Fig. 2. — Caribbean pine that terminated a stage of foxtail growth with a dense branch cluster ("basket"), making it susceptible to bending and wind breakage.

form is linked positively with height, dbh, and volume. Therefore, any improvement program for volume should maintain selection pressure for stem straightness as well. Likewise, negative aspects of crown form, such as large diameter branches, are positively correlated with dbh and volume, and must be considered in selection for the latter to prevent further deterioration of crown form. The high positive correlations of dbh and volume with branch angle are not significant because the genetic component of variation in branch angle is small.

Foxtails, forking, and branch diameter are positively associated. The positive associations of foxtailing with forking and branch diameter arise from the tendency toward loss of apical dominance and proliferation of a "basket" of heavy branches following a phase of foxtail growth (Fig. 2). Forked trees are ones which produce steeply angled branches, which grow to large diameter because of their tendency to retain a favored position in the canopy. The reason for a negative association between distance between branch whorls and foxtailing was not immediately apparent because both traits would seem to represent a continuum in the frequency with which branch whorls are produced.

It may be important to note that the genetic correlation of cone crop with height was positive, but that with dbh was negative. Obviously, cone production of suppressed or intermediate trees would be restricted, while taller, dominant trees would produce more cones, explaining the positive correlation of cone crop and height. Taller trees also tend to have larger dbh, because the tree is in a favored position for growth, and hence the positive phenotypic

correlation between height and dbh. But, the negative genetic correlation of cone crop with dbh suggests that within size classes there must be competition for photosynthate between cambial growth and reproduction. Cone production was also low in foxtail trees and those with long interwhorls that have fewer branches and therefore fewer sites for cone production.

Finally, the positive correlation between bark thickness and volume or dbh has potential value. In an analysis of loblolly pine progeny tests, PEDERICK (1970) found that selection for double-bark thickness would result in more effective gains in dbh than direct selection for dbh itself. Gain from indirect selection depends on the product of the heritabilities for the correlated characters and their genetic correlation. The formula for correlated volume gain (CG_v) to selection for bark thickness is:

$$CG_v = ih_v h_b r_{g_{vb}} \sigma_{p_v} \tag{4}$$

where i is selection intensity, h_v and h_b are the square roots of heritability for volume and bark thickness, respectively, $r_{g_{vb}}$ is the additive genetic correlation between volume and bark thickness, and σ_{p_v} is the phenotypic standard deviation for volume. In this case:

$$CG_v = i (0.33) \cdot (0.73) \cdot (0.4) \cdot (0.04743) = 0.0046i \text{ m}^3. \tag{5}$$

For direct selection on volume, gain is:

$$\begin{aligned} G_v &= ih_v^2 \sigma_{p_v} \\ &= i (0.11) \cdot (0.004743) = 0.0052i \text{ m}^3. \end{aligned} \tag{6}$$

The ratio of G_v/CG_v is 1.13. Thus, direct selection for volume is slightly more effective than indirect selection based on bark thickness, despite the much higher herita-

bility for bark thickness. However, bark thickness might be valuable as an aid to volume selection in a selection index. It is also important in demonstrating the errors that can be made using overbark volume tables. Because bark thickness varies among families, volume will necessarily be overestimated in some cases and underestimated in others.

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Formulae 1. — Mathematical formulae as numbered in text.

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Untersuchungen über die Jugendentwicklung von Douglasienprovenienzen in Hessen

Von M. JESTAEDT

Mitteilungen der Hessischen Landesforstverwaltung,

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Vor fast genau 150 Jahren sind die ersten Douglasien in Mitteleuropa angebaut worden. Seit dieser Zeit hat der Anteil an der Bestockung langsam aber kontinuierlich zugenommen, so daß die Einbürgerung dieser Art zur Bereicherung des in der Eiszeit verarmten Baumartenspektrums beigetragen hat.

Um jedoch Risiken zu vermeiden, welche durch den Import von Herkünften mit unbefriedigenden Wuchs- und Resistenzeigenschaften entstehen können, muß versucht werden, die Forstbetriebe mit Saat- und Pflanzgut zu versorgen, welches den hiesigen standörtlichen Verhältnissen wegehend angepaßt ist.

Um das Variationsmuster der Baumart zu erkunden und um geeignete Erntebetriebe in Nordamerika abgrenzen zu können, wurde vom Institut für Forstpflanzenzüchtung der Hess. Forstlichen Versuchsanstalt ein umfangreicher Douglasien-Provenienzversuch (Ernte der IUFRO) begründet. Daneben sind in 6 Douglasien-Beständen in der Eifel Einzelbäume

beerntet worden; das Saatgut wurde zu einem Parallelversuch verwendet, um die einheimischen Bestände auf ihre Erbeigenschaften durch Nachkommenschaftstests zu überprüfen.

Neben umfangreichen Kampfaufnahmen werden die Auswertungsergebnisse von den zahlreichen Versuchsflächen bis zum Alter von 8 Jahren dargestellt. Diese stimmen sehr gut mit den Ergebnissen überein, welche aus anderen Versuchen und aus der waldbaulichen Praxis gewonnen werden konnten. Aus diesem Grunde ist es recht gut möglich, für Douglasienstandorte in Hessen und vergleichbaren Bereichen geeignete Erntegebiete in Nordamerika abzugrenzen.

Aus dem Versuchsmaterial aus einheimischen Beständen wird deutlich, daß sich hier möglicherweise ein Schritt zu einer ‚Landrasse‘ vollzogen hat, die besser an die hiesigen Verhältnisse angepaßt ist.

J. D. SAUERLÄNDER'S VERLAG, FRANKFURT A. M.