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Heritability and expected Gain Estimates for Traits of Black Locust in Michigan¹⁾

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(Received 18th February 1988)

Summary

Open-pollinated progeny from 434 families from the natural and naturalized range of black locust were tested at two sites in Michigan. Observations of height, dieback, the number of dominant leaders, length of thorns, borer attack, time of bud-break (opening of wood plates to show green material), and time of leaf initiation (appearance of leaves) were made after one growing season. The analysis of variance showed significant family, block, and site differences for all traits from the combined data. There were no apparent geographic patterns in variation for any of the traits. Single tree heritabilities for length of thorns, time of bud-break, and time of leaf initiation were higher than family heritabilities from the combined data. Estimated genetic gains from combined selection for height, dieback, number of dominant leaders, length of thorns, time of bud-break, and time of leaf initiation were 45%, 46%, 18%, 52%, 32%, and 55%, respectively, when the best 20 individuals from the best 20 families were selected. The data were corrected for block and site effects for genetic gain estimations.

Key words: selection, genetic correlations, genetic variation, half-sib progeny, breeding.

Introduction

Black locust (*Robinia pseudocacia* L.) is used for lumber, poles, beekeeping, fuelwood, land reclamation, forage, and wood fiber. In the United States, it has been widely planted outside its natural range which is limited to the Ozark Plateau and the Appalachian mountains of eastern United States. Very little genetic improvement has been done on the species in the U.S., and literature on the estimated genetic parameters for growth or other traits is lacking.

In Hungary, a black locust breeding program for fast growth, stem straightness, frost resistance, increased nectar yields, and prolonged flowering period was started in 1930 (KERESZTESI, 1983). Selections were made from stands established with materials imported from the United States between 1710 and 1720. The improvement work included induced polyploidy, crossbreeding, and cloning. A half-century's improvement has resulted in the development of many registered cultivars for specific uses.

¹⁾ Michigan Agricultural Experiment Station Report No. 12415

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In 1978, a species trial consisting of many pines and hardwoods including black locust, was established at various locations in Michigan (MILLER *et al.*, 1987). Even though the survival of black locust was not impressive due to harsh site conditions, it was the fastest growing species in the test. In another species trial its growth was comparable to that of hybrid poplar (MILLER *et al.*, 1987). This observation revealed the potential of black locust as a fast-growing biomass plantation tree.

A provenance test of black locust, done by the University of Georgia (KENNEDY, 1983), showed that the variation in height, diameter, spine length, rachis length, number of pinnae, time of leaf initiation, and time of bud-break of one-year-old seedlings was substantial within the populations tested; there were no apparent geographical trends. KENNEDY suggested the need for progeny tests to select the best families for improvement of the species.

Based on the results, and on the need for high yielding biomass trees in Michigan, a long term breeding plan was initiated by Michigan State University. This paper presents data on the extent of genetic variation present in black locust from half-sib progeny tests of the base population. Heritabilities, genetic gains, genetic correlations, and Spearman correlations are summarized for height, dieback, length of thorns, number of leaders, time of bud-break, and time of leaf initiation.

Materials and Methods

Between 1982 and 1983, open-pollinated seeds were collected from 434 trees, covering the natural and naturalized range of black locust in the Eastern United States and Canada. The seeds were treated with sulfuric acid and sown in the nursery at the Tree Research Center, Michigan State University, East Lansing, Michigan, in the spring of 1984. The seedlings were planted in the spring of 1985 at four sites in Michigan: East Lansing (Ingham County), Kellogg Forest (Kalamazoo County), Tawas (Iosco County), and Brampton (Delta County). The experimental design was a randomized complete block, with four blocks and three tree plots. Blocking was done by soil series at the East Lansing site, but the other three sites were composed of a single soil series. All sites were characterized by good internal soil drainage except for localized pockets.

In March of 1985, all four sites were mowed, and Round-up was applied to reduce weed competition (prior to plant-

ing). Planting was done by machine at a spacing of 2.4 m × 1.8 m. In July of 1985, all four sites were mowed and sport sprayed with Simazine.

Measurement of tree characteristics was done after one growing season at the East Lansing and Kellogg sites. The trees in the Tawas and Brampton sites were severely browsed by deer and were not measured.

In the winter of 1986 (January to March), the following variables were measured on each tree:

- i — Total height in centimeters (along the main leader)
- ii — The length of dieback due to cold damage, in centimeters
- iii — The number of dominant leaders
- iv — The length of thorns (scored on a scale of 0 = no thorns, 1 = small, 2 = medium, and 3 = large thorns)
- v — the presence or absence of the locust twig borer (*Ecdytophla insiticiana*) attack.

Beginning the first week of April 1986, the following observations were made twice a week:

- i — Time of bud-break, defined as the day at which at least 50% of the buds in the current year's growth break their woody plate to show a green material.
- ii — Time of leaf initiation, defined as the day at which at least 50% of the buds have expanded to show a single leaf.

To reduce the large amount of time required to do the observation on bud-break and leaf initiation on individual trees, a limited number of families were randomly selected to represent the entire range of the collection. Observations were made on 150 families in two blocks in the Kellogg site and in three blocks in the East Lansing site.

Analysis

The bud-break and leaf initiation data (in dates) were converted to growing degree-days (GDD) for accurate comparison among measurements which will be done in later years. Growing degree-days were defined as (maximum daily temperature + minimum daily temperature)/2 - 7.2° C (BAKER, 1975). Daily GDD were accumulated beginning the first day with positive GDD.

Plot means instead of individual tree measurements were used in the analysis to reduce the data to a manageable size. To reduce the amount of missing data, the analysis was performed on 287 families which occurred in at least six of the eight blocks. Analysis of variance (AOV) using a SPSS (version 9.0) statistical package was done for each site and for the combined data from the two sites.

Narrow sense family and single tree heritabilities and their standard deviation were calculated using the variance components generated from the analyses of variance. The formulae used to estimate the heritabilities were (WRIGHT, 1976):

For Combined AOV:

$$h^2_T = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_{fs} + \sigma^2_e} \quad (1)$$

$$h^2_F = \frac{\sigma^2_f}{\sigma^2_e/S_B + \sigma^2_{fs/S} + \sigma^2_f} \quad (2)$$

For each site:

$$h^2_T = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_e} \quad (3)$$

$$h^2_F = \frac{\sigma^2_F}{\sigma^2_e/B + \sigma^2_f} \quad (4)$$

where

F = the number of families.

S = the number of sites.

B = the number of blocks.

σ^2_f = variance due to differences among families.

σ^2_e = variance due to sampling error, block × family interaction.

σ^2_{sf} = variance due to interaction of families and sites.

h^2_T = Narrow sense single tree heritability.

h^2_F = Narrow sense family heritability.

The standard errors of the heritability estimates were calculated using the formulae in WRIGHT (1976).

Since plot means rather than single tree values were used in the analysis, within family source of variation was not included in the AOV. Omission of this source of variation might result in slightly higher estimation of single tree heritability (WRIGHT, 1976).

Genetic correlations between all traits except for borer attack were calculated from analysis of covariance. The equation used to estimate genetic correlations was:

$$r_A = \frac{\text{COV}_{xy}}{\sqrt{(\text{COV}_{xx})(\text{COV}_{yy})}} \quad (5)$$

where:

r_A = the additive genetic correlation coefficient.

COV_{xy} = the half-sib family component of covariance between traits X and Y.

COV_{xx} = the half-sib family component of covariance of trait x with itself which is equal to the variance component in an AOV.

COV_{yy} = the half-sib family component of the covariance of trait y with itself which is equal to the variance component in an AOV.

The equation used to calculate expected genetic gain was (FALCONER, 1981):

$$G = ih^2\sigma_p \quad (6)$$

where:

i = intensity of selection

h^2 = narrow sense heritability.

σ_p = phenotypic standard deviation of the trait.

Genetic gains were calculated on a single tree (mass), family, and combined selection (NEBGEN and LOWE, 1982) basis. For combined selection the best individuals in the best families were selected.

Results and Discussion

Mean Performance

Survival of seedlings was 85% at East Lansing and 78% at the Kellogg Forest. The mean height at age 1 over all the plantations was 126.5 cm with a range of 34 cm to 290 cm. The shortest family was only 50% of the mean, and the tallest family was 64% greater than the mean. About 6% of the trees in East Lansing and 2% in Kellogg were more than 200 cm tall. In general height growth at East Lansing was better than the Kellogg site. The relatively lower height growth at Kellogg could have been due to more weed competition and different soil types. Black locust does not grow well on heavy soils or in water logged areas (KERESZTESI, 1983), and this was evident from the shorter heights and mortality of a block of trees in the East Lansing plantation which was located on relatively wet ground.

The amount of dieback is a measure of susceptibility to cold damage. It is an important trait to consider in breeding programs for three main reasons: 1) reduced total height of a tree, the magnitude of its effect will be great when accumulated over the rotation age (KERESZTESI, 1980); 2) formation of multiple leaders the next growing season (WRIGHT, 1944); and 3) the importance in predicting the northern growing limit of a family.

The mean dieback in East Lansing was 8.7 cm and 4.6 cm in Kellogg, ranging at each site from 0 to more than 100 cms. Higher dieback in East Lansing was due to colder temperatures. The dieback evaluation was confounded by the twig borer effect. Some trees died back above the swell created by the twig borer attack. Other trees with the same swell size showed little or no dieback, beyond the swell. The dieback observed in some trees was from a combined effect of the cold damage and the borer attack. This phenomenon was much more frequent at the Kellogg site.

Thorns supposedly serve as mechanisms of defense against browsing animals, but this was not the case in the Brampton and the Tawas plantations where heavy deer browsing prevented collection of meaningful data. Results from the Kellogg and East Lansing plantations indicated that all of the trees browsed probably had thorns. Thorns do not provide much protection the first year because they do not fully develop until the end of the growing season. The range of thorn length was from 1 mm to 26 mm.

Very few trees died because of the locust twig borer even though dieback occurs above the swell. Rather, its effect was a predisposing one to breakage. Borer attacks occur anywhere in the tree, but preferred areas seem to be those exposed to direct sunlight. Attack is usually initiated on the southern side of the trees. Almost all trees in the East Lansing site were attacked by the borer, but the damage varied from a speck to a swell as large as 2.5 cm in diameter. At Kellogg, 59% of the trees were attacked.

The number of dominant leaders varied from one to nine, the mean over the two plantations was 2. Dieback and borer attack could influence the number of leaders.

The mean growing-degree days (GDD) required for bud-break and leaf initiation in East Lansing was twice that of Kellogg. Some trees in both plantations started bud-break on the same date (the first day of observation). The temperature at Kellogg was normal for the season. At East Lansing, there were periods of freezing days alternated by one- or two-day periods of warm temperatures, resulting in frost damage. Because of the repeated frost damage, the East Lansing trees did not break bud until

April 21. On April 26, temperatures suddenly rose to the lower 20's (°C) and about 50% of the trees broke bud on April 28. The difference between the means of the two sites for bud break and leaf initiation was due to this phenomenon.

Variation

The F-values for among family differences from the analysis of variance at each site and the combined data are presented in *Table 1*. Analysis of variance was not performed for borer attack since the data do not satisfy the requirements of the assumptions. The analysis of variance for combined data indicated significant family differences (.01 probability level) for all six traits. There was also a significant family difference at each site except for dieback at Kellogg. Site differences were highly significant for all traits. The proportion of total variation due to family differences was small in all cases (< 10%).

Family \times site interaction is a source of variation which directs subsequent selection methods and breeding programs. A significant family \times site interaction means that a family's performance is variable in different site conditions relative to others. Family \times site interactions were non-significant for all traits except dieback. There was a highly significant family \times site interaction (.01 probability level) for dieback when data were analyzed either using the actual measurements or when dieback was expressed as a percent of total height.

Heritabilities

Family and single tree narrow-sense heritabilities along with their standard deviations for all traits are presented in *Table 1*. Negative variance components were considered zero for heritability estimation. Family heritability for height from the combined data was relatively higher and close to estimates made for other tree species (BONGARTEN and HANOVER, 1986; NIENSTADT, 1985; LINK, 1984). Single tree heritability for height was as high as the family heritability, but was inflated because the within plot variance component was not included in the denominator of heritability estimates. Both family and single tree heritabilities were low for dieback. Family heritabilities for bud-break, length of thorns, and leaf-initiation and single tree heritabilities for bud-break and length of thorns were relatively high (> .56). Single tree heritability for leaf initiation was greater than 1, a phenomenon sometimes encountered in statistical analysis of juvenile trees (ADAMS and JOLY, 1977; HICKS *et al.*, 1977; RINK, 1984). This phenomenon could have resulted from exclusion of the block and site variance components during heritability estimation and partly due to closer relatedness than the expected half-sib relationship assumed. There was a moderate heritability (0.31 and 0.40 for single-tree and family, respectively) for number of dominant leaders.

The results from our study are consistent with those of BONGARTEN and HANOVER (1986) who reported that family heritabilities from combined data were higher than the heritabilities estimated from individual plantation data because family \times site interactions were negligible or absent. The family heritabilities from the combined data were higher than those from individual plantation data in those cases where family \times site interactions were non-significant (*Table 1*). This pattern was not true for single tree heritabilities. Family heritability for dieback in the Kellogg site was 0 because there was no significant family difference.

Table 1. — F-values for among family differences and heritabilities with their standard deviations (σ).

Trait		Height	Dieback	Number of Leaders	Length of Thorns	Bud-Break	Leaf Initiation
F-value for	Kellogg	1.53**	0.95NS	1.17**	1.92**	1.36**	1.73**
among family difference	E. Lansing	1.90**	1.6**	1.31**	2.65**	1.48**	1.57**
	Combined	2.23**	1.24**	1.77**	3.18**	3.57**	4.57**
Individual Tree		-----Heritability $\pm \sigma$ -----					
	Kellogg	.46 \pm .027	0	.17 \pm .023	.74 \pm .03	.62 \pm .064	1.07 \pm .065
	E. Lansing	.74 \pm .03	.52 \pm .028	.29 \pm .025	1.16 \pm .032	.55 \pm .047	.64 \pm .048
	Combined	.56 \pm .019	.13 \pm .013	.31 \pm .016	.89 \pm .023	.83 \pm .038	1.11 \pm .04
Family							
	Kellogg	.34 \pm .065	0	.15 \pm .057	.48 \pm .063	.27 \pm .092	.42 \pm .088
	E. Lansing	.48 \pm .063	.38 \pm .065	.24 \pm .062	.62 \pm .055	.33 \pm .069	.36 \pm .069
	Combined	.55 \pm .072	.22 \pm .063	.40 \pm .075	.69 \pm .060	.57 \pm .086	1.11 \pm .076

NS Not significant at the 5 percent level

* Significant at the 5 percent level

** Significant at the 1 percent level

Single-tree heritabilities for length of thorns, bud-break and leaf initiation were higher than family heritabilities. This is contrary to WRIGHT's (1976) conclusion that family heritabilities are always higher than single-tree heritabilities. The contradiction cannot be fully explained by the overestimation of the single tree heritabilities mentioned earlier, because some of the traits had little within family variation from observations made during measurement, and the differences between single-tree and family heritabilities are much bigger. Part of the explanation for this discrepancy may be due to closer relatedness than the expected half-sib relationship assumed.

The heritability estimates were made assuming the progenies were half-sibs. Open-pollinated families may be a mixture of selfs, half-sibs, and full sibs; consequently, heritabilities would be over- or underestimated depending on the proportion of selfs and full-sibs (KHALIL, 1985; RINK, 1984). Heritability estimates done on other tree species (RINK, 1984; KEDHARNATH, 1982; SOLANKI *et al.*, 1984; NIENSTAEDE, 1985) showed changes over time because of changes in genetic control and the external environment with age (NAMKOONG *et al.*, 1972; NAMKOONG and CONKLE, 1976). Therefore, estimates must be done again in later years.

Correlations

Genetic and phenotypic correlations among the traits and with latitude and longitude are presented in Table 2. Phenotypic correlations between the geographical parameters (latitude and longitude) and the tree traits were

very low. In the highest correlation, only 7.6% of the variation in borer attack was explained by latitude. Phenotypic correlations among the traits were also low, with the exception of bud-break and leaf initiation, which was 0.55, and explained 30% of the variation. Many of the correlation coefficients were small but significant due to the large degrees of freedom.

Since the analysis of variance showed a highly significant block effect for all traits, the data were adjusted for block effects before correlation computations. The correlations changed little. The families included in the test were from the natural and naturalized range. To remove some doubt that the correlations could have been confounded by widespread planting of the species, the correlations were calculated for trees only within the natural range. The correlation coefficients remained low.

Genetic correlations of height with number of dominant leaders, length of thorns, and bud-break were high and positive (Table 2). Selection and breeding for rapid height growth will result in trees with many leaders, large thorns, and late bud-breaking. Late bud emergence could be advantageous, since such trees will suffer less from early spring frosts. Leaf initiation is highly correlated with number of dominant leaders, length of thorns, and bud-break. All correlations were positive, and selection for delayed leaf initiation will increase the other traits in the same direction. Bud-break was also highly correlated with number of dominant leaders and length of thorns. The other genetic correlation coefficients were low.

Table 2. — Phenotypic (lower diagonal) and genetic (upper diagonal) correlations.

	Lati- tude	Longi- tude	Height	Dieback	# of leaders	Length of Thorns	Borer Attack	Time of Bud- break	Time of Leaf ini- tiation
Lati- tude									
Longi- tude									
Height	-.051**	-.005		-.15	.53	.73		.97	.17
Die- back	-.083**	-.025	.011		-.42	-.37		.28	.34
# of leaders	.019	-.049**	.007	.037*		.24		.75	.88
Length of thorns	.027	.031	-.004	.016	.012			1.22	.60
Borer attack	.066**	.138**	.013	-.063**	-.029	.276**			1.19
Time of bud- break	-.111**	-.020	-.028	.050	-.007	.204**	-.023		
Time of leaf initi- ation	-.151**	.020	-.002	.186**	-.025	.055	-.021	.550**	

* Significant at the 5 percent level

** Significant at the 1 percent level

Expected Genetic Gains

Expected genetic gains for each trait using different selection schemes are presented in Table 3. For comparison purposes the genetic gains were estimated for different selection intensities. Because of the significant block and site effects, selection were made by correcting the phenotypic measurements as suggested by COTTERILL (1987). Gains from single tree selections for bud-break and leaf initiation are omitted because the values were unusually high for the same reasons described above.

Since our main objective is breeding black locust for higher biomass and bolewood production, height is the

most important trait to consider. Selection for rapid height growth will increase the mean of the number of leaders, length of thorns, and bud-break, because of the high and positive genetic correlations. Delayed bud-break is desired to avoid early spring frost damage, whereas increased length of thorns and number of dominant leaders do not have much effect on biomass production. The number of leaders can be controlled by cultural methods such as pruning.

Dieback is the trait which directly reduces height growth, but the genetic correlation with height was very low and

Table 3. — Predicted genetic gains (%) from different selection schemes under different selection intensities.

	Type of select.	Height	Length of thorns	# of leaders	dieback	bud- break	leaf initiat.
BEST 10 TREES	tree	61	46	18	52		
	combin.	47	46	18	52	42	81
	family	19	27	18	38	16	19
BEST 20 TREES	tree	56	46	18	52	80	84
	combin.	45	46	18	52	32	55
	family	16	24	16	35	12	14
BEST 40 TREES	tree	51	46	18	52	58	63
	combin.	41	46	18	52	31	51
	family	13	20	14	31	9	10

negative. It will not be difficult to select for fast growth with little or no dieback.

The expected genetic gain estimated for height from mass selection was the highest compared to family and combined selection. Since single-tree selection could result in many trees from relatively few families, this scheme was not recommended. On the other hand, combined selection will provide slightly less gain than mass selection, while providing a broader genetic base for future breeding programs (NEBGEN and LOWE, 1982). About 47% of the mean height can be gained from combined selection, and this is relatively high compared to gains estimated for other species (NEBGEN and LOWE, 1982; RINK, 1984; FARMER *et al.*, 1983; FOSTER and LESTER, 1983). Predicted genetic gains from combined and mass selection for length of thorns, bud-break, and leaf initiation were also high.

Acknowledgements

The authors acknowledge the assistance of TOM STADT and KARL GRUBER in making measurements, and Dr. RAY MILLER and PAUL BLOESE for data analysis.

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Isozyme Polymorphisms in Silver Fir (*Abies alba* Mill.)

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(Received 22nd February 1988)

Abstract

Data of isozyme analyses are reported for 4 enzyme systems in silver fir. The studies were based on single tree seed lots. Megagametophyte as well as embryo tissue was studied. SKDH is found to be monomorph. GDH shows two variants, two alleles may be involved. 6-PGD is under the control of two loci with two and two or three alleles respectively. IDH is coded for by two loci and five alleles as well. A further IDH-B allele is supposed. IDH-B enzymes seem to have a dimeric subunit structure. The IDH and 6-PGD loci act independently from each other, linkage tests gave no significant results. In bud tissue the same banding patterns as in seeds were found.

Key words: *Abies alba*, isozymes, linkage.

Zusammenfassung

Die an vier Enzymsystemen der Weißtanne beobachteten genetischen Polymorphismen werden beschrieben. An Einzelbaumabsaaten wurde sowohl Megagametophyten- als auch Embryogewebe untersucht. SKDH zeigte keine Variation. Bei GDH wurden zwei Varianten beobachtet, möglicherweise liegen zwei Allele vor. 6-PGD wird von zwei

Genorten mit je zwei bzw. zwei bis drei Allelen gesteuert. Auch bei IDH konnten zwei Loci mit insgesamt fünf Allelen nachgewiesen werden. Das Vorliegen eines weiteren IDH-B-Allels wird vermutet. Aktive Enzyme des Genorts IDH-B liegen als Dimere vor. Eine Kopplung zwischen den hier beschriebenen Genorten der Enzyme IDH und 6-PGD wurde nicht gefunden. Knospengewebe zeigte dieselben Bandenmuster wie Samengewebe.

Introduction

The species *Abies alba* MILL. is found to have its natural range throughout Central and Southern Europe. Being, besides Norway spruce, the most common conifer species in the south of Western Germany it is of considerable ecological and economic importance. However, knowledge regarding the genetic differentiation of this species to date is very poor (GÜRTH, 1982; LARSEN, 1986).

In view of this efforts should also concentrate on an elucidation of basic genetic features of this species. For this purpose single tree seed collections were utilized to study the genetic control of isozyme systems.