HEIGHT AND SEASONAL GROWTH PATTERN OF JACK PINE FULL-SIB FAMILIES

Don E. Riemenschneider [1]

Abstract.--Total tree height, seasonal shoot elongation, dates of growth initiation and cessation, and mean daily growth rate were measured and analyzed for a population of jack pine full-sib families derived from inter-provenance crosses. Parental provenance had no effect on these variables although this may have been due to small sample size. Progenies differed significantly for all characteristics and little detectable dominance variance. Total tree height and total seasonal growth were more strongly related to mean daily growth rate than to the date of growth cessation, which was a measure of growth duration.

Additional keywords. Growth rate, growth initiation, growth cessation, genotype correlation, heritability, dominance.

The importance of seasonal growth patterns in jack pine (*Pinus banksiana* Lamb.) in regard to latewood formation (Kennedy 1968), frost hardiness (Yeatman 1966), and resistance to eastern pineshoot borer attack (Jeffers 1978) has been noted. Teich and Hoist (1969) in a study of rangewide collections of jack pine provenances found a significant positive correlation between total seasonal growth and date of growth cessation and speculated that selection for height would delay the average date of growth cessation, reduce the percentage of latewood formed and enhance susceptibility to early fall frosts.

The applicability of provenance test data may be limited to an applied breeding program however. The magnitude of genotypic covariances is partly dependent on the reference population of genotypes, and it is unlikely that a single breeding program would include the wide range of sources found in provenance experiments (Comstock and Moll 1964).

The objectives of this study were (1) to estimate phenotypic and genotypic variances and heritability for tree height, date of growth initiation, date of growth cessation, mean daily growth rate, and total shoot elongation; and (2) to estimate the phenotypic and genotypic correlations between these traits in a more geographically restricted population of jack pine.

MATERIAL AND METHODS

The Experimental Population

The population consisted of 69 full-sib families of jack pine that resulted from a series of controlled pollinations in an incomplete factorial design among

---

[1] Plant Geneticist, North Central Forest Experiment Station, Forest Service, Forestry Sciences Laboratory, Rhinelander, Wisconsin.

22 females and 6 males. The parents were selected in a Lake States jack pine seed source test and represented Minnesota, Wisconsin, and Michigan (table 1).

Table 1.--Source of male and female parents used to produce the jack pine full-sib families

Provenance Number	Provenance Location	Female parent number	Male parent number
1589	Cass Co., MN	3642	4814
		3643	
		3644	
1606	Forest Co., WI	3645	4816
		3646	
		3647	
		3648	
1616	Manistee Co., MI	3650	4811
		3651	
		3652	
1604	Douglas Co., WI	3653	4813
		3655	
		3656	
1609	Marinette Co., WI	3657	4815
		3659	
		3660	
1611	Wood Co., WI	3661	4812
		3662	
		3664	

Pollinations were made in 1968 and 1969. Seed was sown in the greenhouse at Rhinelander, Wisconsin, in December 1970, and the seedlings were transplanted to the nursery the following spring. In May 1973 the seedlings were field planted in a randomized complete block design at two locations in northern Wisconsin and one location in northern Minnesota. The plantation at the Harshaw Experimental Farm near Harshaw, Oneida County, Wisconsin (Lat. 45.5° N) was selected for use in this study because more families were established at this site than any other. Of the original families, 69 were still found in all 10 blocks by 1975 and were the subject of detailed growth measurements taken during the 1975 growing season. All 6 of the male parents but only 19 of the female parents were represented by the 69 full-sib families (table 2). Even though patterns of seasonal growth vary between years, observation for a single growing season was deemed sufficient because the differences among genotypes are the same in species with determinant growth (Cannell *et al*. 1976).

Table 2.--The mating design used to produce the 69 jack pine full-sib families.

Female parent No.	Male parent No.					
	4814	4816	4811	4813	4815	4816
3642	X	X	X	X	X	X
3643	X	X	X			X
3644	X	X	X		X	X
3645	X	X	X	X	X	X
3646	X		X	X		X
3647	X		X			X
3648	X		X		X	X
3650	X		X	X	X	X
3651	X	X	X			
3652			X			X
3653	X	X	X	X	X	X
3655	X	X	X	X	X	X
3656			X			X
3657			X			X
3659			X		X	X
3660			X			
3661			X			X
3662			X			X
3664	X		X	X	X	

Measurements

Shoot elongation was measured to the nearest mm on one tree per 4-tree plot in each of 10 replications and 69 families beginning on May 13, 1975, when the trees were beginning their fifth growing season. This measurement was repeated weekly until September 3 when no further elongation could be observed, for a total of 17 measurements. From these data the dates when 5% (initiation) and 95% (cessation) of growth was completed were determined by interpolation or extrapolation (Worrall 1973; Rehfeldt and Lester 1966; Hanover 1963). The duration of growth is not discussed here since it was highly correlated with the date of growth cessation (r = .90 on a family mean basis) and would provide little additional information. Mean daily growth rate for each tree was determined by dividing the elongation between the 5% and 95% days by the number of days it took to complete this phase of growth. Total tree height was measured to the nearest cm on October 20. Temperature during the entire season was recorded using a hydrothermograph located adjacent to the experimental population.

Analysis of Data

Variation at the provenance level was investigated with analyses of variance. A one-way analysis was used with parental provenance combinations as treatments and family means as entries. The provenance mean square would thus contain variance due to the average breeding value of each provenance plus any variance due to provenance x provenance interaction. The within-provenance combination mean square used as the denominator in the F test would be the residual, among-progeny variation after accounting for provenance effects.

The division of family variance into that due to males, females, and the male x female interaction was more complex because the mating design was not complete. A least squares analysis (Snedecor and Cochran 1967), which provides a powerful test of the null hypothesis of no males x females interaction, was used to estimate variation due to these sources. Genetic covariances were estimated from analysis of covariance.

Heritability for all traits was estimated on both an individual and family basis using the variance component method. Standard errors for variance component and heritability estimates were computed as functions of independent mean squares (Namkoong 1979). Standard errors for genotypic correlations were computed using the method of Tallis (1959) for full-sib progenies. Because the exact sampling distribution of the genotypic correlation is unknown, it is difficult to determine levels of significance. The "t" statistic was used to test the null hypothesis of the genotypic correlation equal to zero. A correlation was declared significant at the .95 probability level if $t > 1.99$ and at the .99 probability level if $t > 2.65$.

The combined effect of mean daily growth rate and date of growth cessation on total seasonal growth and total tree height was investigated using multiple regression analysis.

RESULTS

The average date of growth initiation was May 13 and family means ranged from May 11 to May 15. The average date of growth cessation was July 6 and the range was much larger -- from June 30 to July 14. Mean height was 1.71 m and families ranged from 1.45 to 1.88 m. A mean shoot elongation during the 1975 growing season of 58.9 cm accounted for an average 34% of the total tree height. Mean daily growth rate between the 5% and 95% days was 10.1 mm.

Although no significant provenance variance was evident for any trait, differences among progenies were significant for all traits measured (Table 3). The magnitude of variation due to males, females, and males x females, however, depended on the specific trait. For both tree height and total shoot elongation, differences due to both males and females were significant. Differences due to females were significant for mean daily growth rate and the date of growth cessation. Differences due to males were significant for the date of growth initiation. In no case was the males x females interaction significant. The fact that for some variables, variation was detectable due to females and not males and vice versa is difficult to explain because both components of variation estimate the same genetic parameter, namely 1/4 of the additive genetic variation. This is probably due to the small number of parents involved in the crossing scheme and the resultant low precision. Because of this, and also because the test of the male x female interaction indicated lack of dominance variance, additive genetic variation was estimated as $2(\sigma^2FS)$, where σ^2FS is the variance among full-sib progenies.

The failure to detect dominance variance for growth variables in this population was somewhat unexpected, because inbreeding deptression for several traits is known to occur in jack pine (Rudolph 1976).

Heritability was higher for total tree height ($h_1^2 = .22$) than for the seasonal growth variables (Table 4). It was also higher than previous estimates in other populations (Yeatman 1974; Riemenschneider 1979). Heritability on an individual basis ranged from .30 to .15 for the seasonal growth variables. Because heritability estimates for these traits have not been made before in jack pine, it is impossible to judge whether or not these values are typical. The estimates do indicate that all characteristics measured in this study could be modified by selection.

Phenotypic and genotypic correlation coefficients were estimated from analyses of covariance (Table 5). In the covariance analysis, additive genetic covariance was estimated as $2(\sigma FS_{xy})$, where σFS_{xy} is the covariance between traits due to full-sib progenies. This estimate is unbiased in the absence of dominance and epistatic covariance. Because estimates of dominance variance were nonsignificant it is reasonable to suspect that dominance covariance and subsequent bias from this source would be small. Epistatic effects remain unestimated and are beyond the scope of this study; however, it is assumed that they are not important.

Tree height, total seasonal growth, and mean daily growth rate were all positively correlated with the exception of the genotypic correlation of tree height and mean growth rate, which was less than twice the standard error. Although the methods of Tallis (1959) indicate that this correlation is not significant, the strong phenotypic correlation between the two traits (Table 5), and the genotypic relation between height and shoot elongation, and shoot elongation and growth rate indicate that a real relation may exist. On the basis of this evidence and the fact that the significant test is inexact, the genetic correlation between tree height and mean growth rate (r = .298) might be

Table 3.--Analyses of variance for tree height and seasonal growth variables from 69 full-sib families of jack pine.

Source	Tree height df	Tree height MS	Date of growth initiation MS	Date of growth cessation MS	Shoot elongation MS	Mean daily growth rate MS
Replications	9	$.07353^{ns\,1/}$	$8.870^{**\,3/}$	137.99^{ns}	$215.8^{*\,2/}$	8.918^{*}
Progenies	68	$.08956^{**}$	3.561^{**}	135.98^{**}	192.8^{**}	7.600^{**}
Females	18	$.16717^{**}$	4.209^{ns}	289.92^{**}	240.2^{*}	13.910^{**}
Males	5	$.18552^{**}$	7.128^{*}	73.66^{ns}	576.8^{**}	7.281^{ns}
Females x Males	45	$.03369^{ns}$	2.560^{ns}	73.95^{ns}	116.6^{ns}	4.838^{ns}
Pooled error	612	.03959	1.953	79.19	108.5	4.240

1/ ns = not significant

2/ * = significant at P >.95

3/ ** = significant at P >.99

Table 4.--Variance component and heritability estimates for tree height and and seasonal growth variables. (Standard errors are given in parentheses)

	Tree height	Date of growth initiation	Date of growth cessation	Shoot elongation	Mean daily growth rate
σ_R^2	0.00049 (.00046)	0.100 (.055)	0.852 (.855)	1.55 (1.34)	0.068 (.055)
σ_{FS}^2	0.00500 (.00153	0.161 (.061)	5.679 (2.342)	8.43 (3.32)	0.336 (.131)
σ_E^2	0.03959 (.00226)	1.953 (.111)	79.194 (4.520)	108.50 (6.19)	4.240 (.242)
σ_A^2	0.01000 (.00306)	0.322 (.124)	11.357 (4.684)	16.86 (6.64)	0.672 (.261)
σ_P^2	0.04459 (.00254)	2.114 (.117)	84.873 (4.672)	116.93 (6.46)	4.576 (2.53)
$\sigma_{\bar{P}}^2$	0.00896 (.00151)	0.3561 (.0602)	13.598 (2.298)	19.28 (3.26)	0.760 (.128)
h_I^2	.22 (.06)	.15 (.06)	.13 (.05)	.14 (.04)	.15 (.05)
h_F^2	.56 (.08)	.45 (.10)	.42 (.10)	.44 (.10)	.44 (.10)

σ_R^2 = variance among replications

σ_{FS}^2 = variance among full-sib families

σ_E^2 = error variance

σ_A^2 = additive genetic variance = $2\ \sigma_{FS}^2$ assuming no dominance

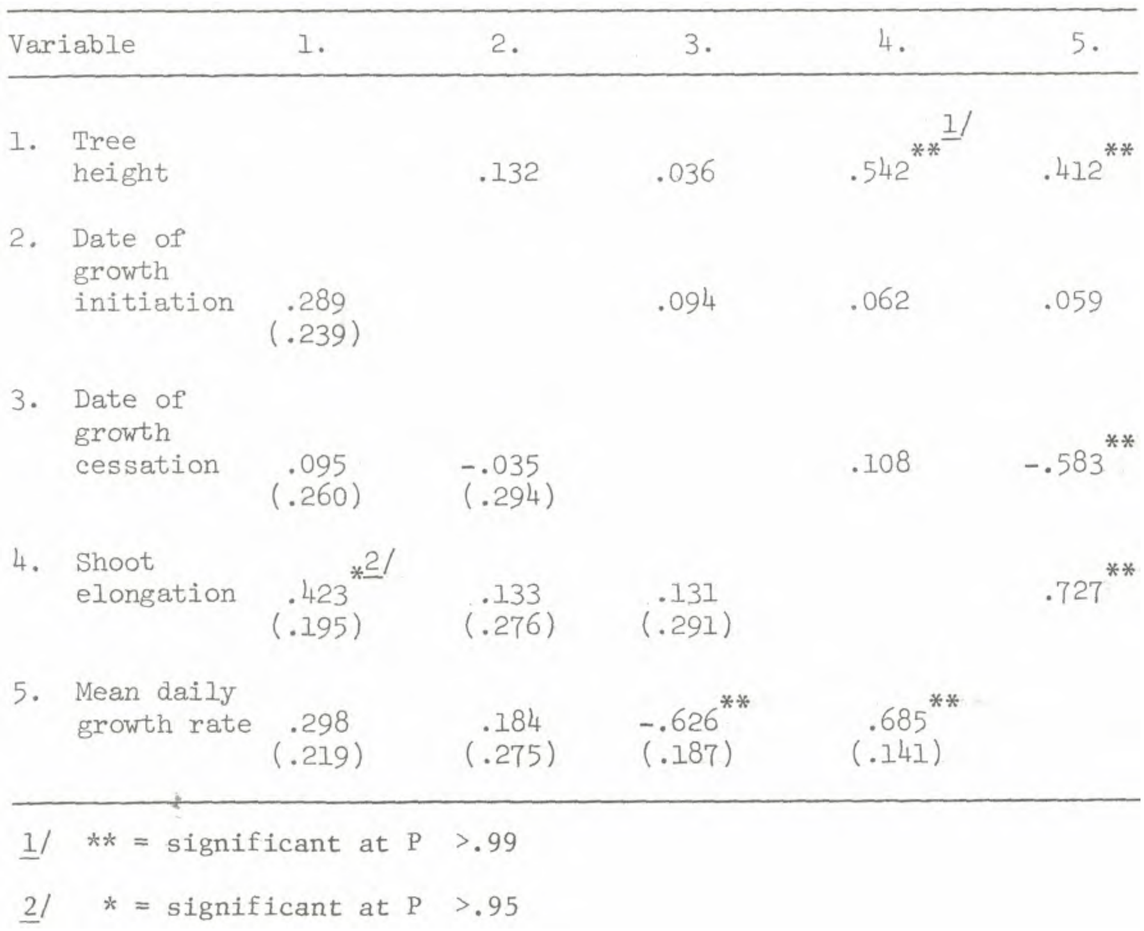
σ_P^2 = phenotypic variance among individuals
$= \sigma_E^2 + \sigma_{FS}^2$

$\sigma_{\bar{P}}^2$ = phenotypic variance among full-sib families
$= \sigma_E^2/_{10} + \sigma_{FS}^2$

h_I^2 = heritability on an individual basis = σ_A^2 / σ_P^2

h_F^2 = heritability on a family basis = $\frac{1}{2}\ \sigma_A^2 / \sigma_{\bar{P}}^2$

Table 5.--Phenotypic (above diagonal) and genotypic (below diagonal) correlation coefficients between growth variables. Standard errors for genotypic correlations are given in parentheses. The genotypic correlation between mean daily growth rate and tree height was considered significant for reasons given in the text.



Variable	1.	2.	3.	4.	5.
1. Tree height		.132	.036	.542**1/	.412**
2. Date of growth initiation	.289 (.239)		.094	.062	.059
3. Date of growth cessation	.095 (.260)	-.035 (.294)		.108	-.583**
4. Shoot elongation	.423*2/ (.195)	.133 (.276)	.131 (.291)		.727**
5. Mean daily growth rate	.298 (.219)	.184 (.275)	-.626** (.187)	.685** (.141)	

1/ ** = significant at P >.99

2/ * = significant at P >.95

considered biologically important even though it was not statistically significant.

Contrary to the results of Teich and Holst (1969), the date of growth cessation was not correlated with either tree height or total seasonal growth (table 5, fig. 1). The date of growth cessation was negatively related both phenotypically and genotypically to mean daily growth rate (fig. 1). Those families that grew most rapidly during the linear period of growth also completed their growth earliest.

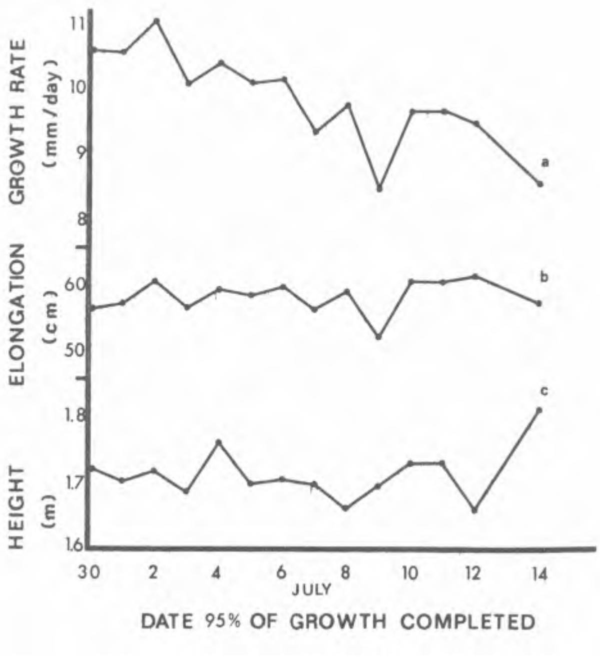


Figure 1.--The relation between mean daily growth rate (a), total seasonal elongation (b), and total tree height (c) and the date at which 95% of seasonal growth was completed. Points represent the means of all families that stopped growth on each date. The only significant relation was between mean daily growth and 95% day (a).

The combined effects of growth rate and date of cessation was investigated by multiple regression analysis. with both factors as independent variables, the date of growth cessation added significantly to regressions on total seasonal elongation and total tree height (Table 6). As expected, the 2 independent variables accounted for less variation in total tree height ($R^2 = .26$) than they did for the current year's growth ($R^2 = .94$) where the model more adequately explained variation in the dependent variable. In this case, the standardized regression coefficients were .78 for date of growth cessation and 1.18 for mean daily growth rate. Again, growth rate appears to be the more important causal factor.

Table 6.--Standardized partial regression coefficients for the regression of mean daily growth rate and date of growth cessation on total tree height and seasonal elongation

Independent variable	Dependent variable	
	Total tree height	Seasonal elongation
Mean daily growth rate	.63	1.18
Date of growth cessation	.69	.78
R^2	26%	94%

The relation between tree height, growth rate, and date of growth cessation was investigated further by closely examining two families representing extreme growth rates. A comparison of the fastest and slowest growing families shows that the growth patterns are similar in shape (fig. 2). The family from cross 3648 x 4814 had the highest mean daily growth rate (12.29 mm/day) and ranked 8th for mean total tree height. Cross 3642 x 4811 produced trees with the slowest mean daily growth rate (8.23 mm/day) and ranked 66th for total tree height. The rankings of these two families for total height and growth rate again demonstrate the relation between the two characteristics. Daily height increment in jack pine partly depends on daily temperature (Rudolph 1964). Early in the growing season both families responded similarly to the high daily temperatures with increased growth rate indicating little genotype x temperature interaction during this period. The fastest growing family (cross 3648 x 4814) maintained a roughly constant superiority in growth rate until June 23. At that time its growth rate slowed while trees from cross 3642 x 4811 continued to respond to high late June temperatures. Even though the slower growing trees (cross 3642 x 4811) had a faster growth rate late in the season, it was not enough to offset their poor early performance. After about July 15, neither family responded to daily temperature.

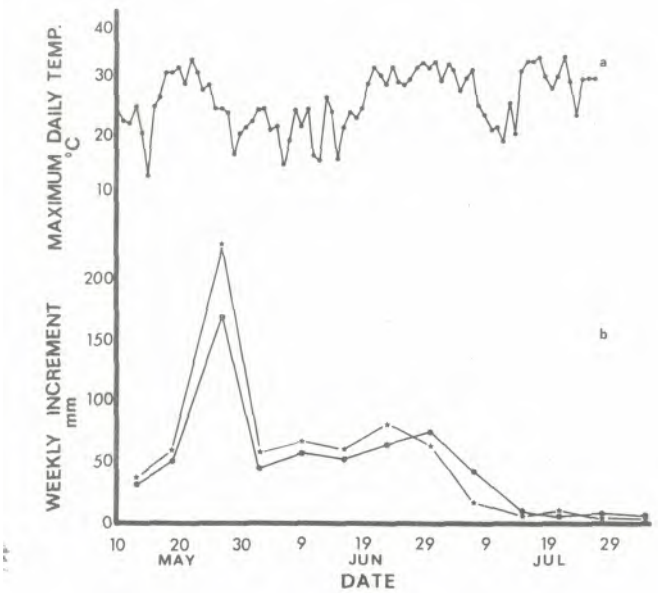


Figure 2. Mean weekly height increment (b) of the two families with the fastest mean daily growth rate (* , cross 3648 x 4814) and slowest mean daily growth rate (• , cross 3642 x 4811) in relation to daily maximum temperature (a).

A negative relation between growth rate and duration of growth (highly related to date of growth cessation in this study) has been reported in ponderosa pine (Hanover 1963) and red pine (Rehfeldt and Lester 1966). The sign of the relation indicates that even though height and date of growth cessation are unrelated, recurrent selection for height could lead to an earlier date of growth cessation and shorten the duration of growth if mean daily growth rate was used as an indirect selection criterion.

SUMMARY AND CONCLUSIONS

Numerous studies have shown that the seasonal growth pattern generally varies among provenances of temperate climate species (Cannell *et al*. 1976) and also among families of *Pinus taeda* L. (Cannell *et al*. 1978). The results of this study show that such variability also exists in a population of jack pine families. Although the limitations of the mating design precluded highly precise estimates of additive and dominance genetic variance, the data indicated that dominance variance is relatively unimportant for total tree height and several seasonal growth variables. This result combined with the nonzero heritability estimates for all characteristics shows that simple selection schemes concentrating on intrapopulation improvement would be successful.

The relations between variables were not similar to those found in a provenance test study. Teich and Holst (1969) found a positive relation between tree height and date of growth cessation (r = .92) and noted the possible effects of selection for height on such factors as wood quality and cold hardiness. In this study tree height and total seasonal growth appeared to be more closely related to mean daily growth rate while the date of growth cessation was less important. The data show that it would be possible to select for increased tree height while shortening the length of the growing period as suggested by Worrall (1973) for *Picea abies* (L.) Karst. The heritable nature of the variables studied here and the success with which growth curves have been modified in laboratory organisms (for example, see McCarthy and Bakker 1979) using such techniques as the restricted selection index (Kempthorne and Nordskog 1959; Cunningham *et al*. 1970), suggest that many combinations of characteristics can be achieved.

ACKNOWLEDGMENTS

The author would like to acknowledge the efforts of Mr. Richard Jeffers in initiating the study and Mr. Werner Bigalke in collecting and summarizing the data.

LITERATURE CITED

Cannell, M. G. R., Thompson, S., and Lines, R. 1976. An analysis of inherent differences in shoot growth within some north temperature conifers. *In* M. G. R. Cannell and F. T. Last (eds.) Tree physiology and yield improvement. p. 173-205, N.Y. Academic Press.

Cannell, M. G. R., Bridgewater, F. E., and Greenwood, M. S. 1978. Seedling growth rates, water stress responses and root-shoot relationships related to eight-year volumes among families of *Pinus taeda* L. Silvae Genetica 27: 237-248.

Comstock, R. E., and Moll, R. H. 1964. Genotype x environment interactions. In Statistical genetics and plant breeding. p. 164-194.

Cunningham, E. D., Moen, R. A., and Gjedrem, T. 1970. Restriction of selection indexes. Biometrics 26: 67-74.

Hanover, J. W. 1963. Geographic variation in ponderosa pine leader growth. Forest Sci. 9: 86-95.

Jeffers, R. M. 1978. Seed source-related eastern pineshoot borer incidence in jack pine. Silvae Genetica 27: 211-214.

Kempthorne, 0., and Nordskog, A. W. 1959. Restricted selection indices. Biometrics 15: 10-19.

Kennedy, R. W. 1968. Wood formation in jack pine seedlings of various provenances. Proc. of the Eleventh Meet, of the Committee on Forest Tree Breed. in Canada. p. 101-110,

McCarthy, J. C., and Bakker, H. 1979. The effects of selection for different combinations of weights at two ages on the growth curve of mice. Theoretical and Applied Genetics 55: 57-64.

Namkoong, G. 1979. Introduction to quantitative genetics in forestry. U.S. Dept. of Agriculture, Forest Service, Tech. Bull. No. 1588. 342 pp.

Rehfeldt, G. E., and Lester, D. T. 1966. Variation in shoot elongation of Pinus resinosa Ait. Can. J. Bot. 44: 1457-1469.

Riemenschneider, D. E. 1979. Genetic variation and predicted response to selection for height in a north-central Minnesota population of jack pine (Pinus banksiana Lamb.). Ph.D. Thesis, Univ. of Minnesota, Dec. 1979.

Rudolph, T. D. 1964. Lammas growth and prolepsis in jack pine in the Lake States. For. Sci. Monog. 6. 70 p.

Rudolph, T. D. 1976. Cone set, seed yield, seed quality, and early seedling development in S_2 generation jack pine. Proc. Tenth Cent. States For. Tree Improv. Conf., p. 42-60.

Snedecor, G. W., and Cochran, W. G. 1967. Statistical methods. The Iowa University Press, Ames.

Tallis, G. M. 1959. Sampling errors of genetic correlation co-efficients calculated from analyses of variance and covariance. Australian J. of Statistics 1: 35-43.

Teich, A. H., and Holst, M. J. 1969. Breeding for height growth of Pinus banksiana Lamb. Proc. Second World Consultation on Forest Tree Breeding. Vol. 1, p. 129-138.

Worrall, J. 1973. Seasonal, daily, and hourly growth of height and radius in Norway spruce. Can. J. For. Res. 3: 501-511.

Yeatman, C. W. 1966. Geographic variation in jack pine (Pinus banksiana Lamb.) seedlings. Ph.D. Thesis. Yale University.

Yeatman, C. W. 1974. A progeny test of Ottawa Valley jack pine - 6-year results. Proc. Ninth Cent. States For. Tree Improv. Conf., p. 71-84.