Survival, Growth, and Flowering of yellow birch Progenies in an open-field Test

By K. E. CLAUSEN*)

North Central Forest Experiment Station,
Forestry Sciences Laboratory,
Carbondale, Illinois.

(Received September 1979 / June 1980)

Summary

Survival of 147 yellow birch families from 21 stands after 5 years in a northern Wisconsin plantation ranged from 14 to 100% and varied greatly among families within stands. Although survival was not directly related to seed origin, some northern families appeared to survive better than southern ones. The stands which earlier differed in both tree height and diameter now differed only in diameter. However, in agreement with earlier results, within-stand variation was shown to be much more important than among-stand variation. When 382 plots of 80 families from 14 stands were analyzed, less than one-third of the stands had significant family differences for any one variable.
Within-stand differences were found for height and diameter in 3 stands each and for crown length, diameter, volume, and surface area in 4 stands each. Seven stands originating from a narrow latitudinal band along the northern limit of the species accounted for all significant family differences—each stand varied in at least 2 characteristics. The range between extreme families varied greatly among stands and the 4 crown characteristics were more variable than tree height or diameter. None of the characteristics measured was related to seed origin. Female flowering began at age 6 and male flowering at age 8 and increased with time. By age 9, 60% of the families had females and 50% produced pollen. The number of catkins per tree increased with age and exceeded 1,000 in some trees.

Key words: provenances, variation, correlations, stress, crown size.

Zusammenfassung

Titel der Arbeit: Überlebensfähigkeit, Wachstum und Blühverhalten von *Betula alleghaniensis* Nachkommenschaften in einem Feldversuch.

Die Überlebensfähigkeit von 147 Gelbbirken-Familien aus 21 Beständen reichte nach 5 Jahren in einer Pflanzung im nördlichen Wisconsin von 14 bis 100% und variierte stark zwischen den Familien eines Bestandes. Obwohl das Überlebensprozent nicht direkt mit der Saatgutherkunft in Beziehung stand, schienen einige Familien nördlicher Herkunft besser als die südlicher Herkunft zu überleben. Die Bestände, die früher sowohl in der Baumhöhe als auch im Durchmesser differierten, unterschieden sich jetzt nur noch im Durchmesser. Wie auch immer, in Übereinstimmung mit früheren Resultaten wurde gezeigt, daß die Variation innerhalb eines Bestandes sehr viel bedeutender war, als die zwischen Beständen. Als 382 Parz. mit 80 Familien aus 14 Beständen analysiert wurden, zeigten weniger als ein Drittel der Bestände signifikante Familienunterschiede für jede einzelne Variable. Differenzen innerhalb eines Bestandes wurden für Höhe und Durchmesser für jeweils 3 Bestände und für Kronenumfang, -durchmesser, -volumen sowie Oberfläche für jeweils vier Bestände festgestellt. Sieben Bestände, die, mit relativ geringen Unterschieden in den Breitengraden, aus dem nördlichen Grenzgebiet der Verbreitung der Art stammten, erklärten alle signifikanten Familienunterschiede. Jeder Bestand variierte in mindestens 2 Merkmalen. Der Unterschied zwischen den extremen Familien variierte stark zwischen den Beständen und die vier Kronenmerkmale variierten stärker, als Baumhöhe oder Durchmesser. Keines der untersuchten Merkmale stand mit der Saatgutherkunft in Beziehung. Die ersten weiblichen Blüten zeigten sich im Alter von 6 Jahren, die ersten männlichen im Alter von 8. Ihre Anzahl erhöhte sich mit zunehmendem Baumalter. Im Alter von 9 Jahren hatten 60% der Familien weibliche Blüten und 50% produzierten Pollen. Die Anzahl der Kätzchen je Baum erhöhte sich mit zunehmendem Baumalter und überstieg bei einigen Bäumen die Zahl 1000.

Abstract

Progenies of 147 yellow birch from 21 stands were tested in northern Wisconsin. Survival after 5 years in the field ranged from 14 to 100% and varied greatly among families within stands. Some northern families appeared to survive better than southern ones. The trees averaged 1.83 m tall and 1.07 cm d.b.h. and showed greater within-stand variation than among-stand variation in these characteristics as well as in crown size. Seven stands originating near the northern limit of the species accounted for all significant family differences. The range between extreme families varied greatly among stands. Length, diameter, volume, and surface area of the crown were more variable than tree height and stem diameter. None of the characteristics measured was related to seed origin. Female flowering began at age 6 and male flowering at age 8. At age 9, 11% of the trees had female flowers, 5% had male flowers, and 4% had both male and female flowers. However, by this time 60% of the families had some trees with females and 50% had some pollen-bearing trees. Number of catkins per tree increased with tree age and exceeded 1,000 in some trees.

Introduction

Yellow birch (*Betula alleghaniensis* BRITT.) was previously found to exhibit clinal variation in shoot growth initiation and cessation but height and diameter growth of the 55 provenances tested showed no clear geographic pattern of variation (CLAUSEN, 1973a). Because the seed lots used for the provenance study were mixtures from an average of 10 trees per stand, a progeny test was begun in 1968 in order to assess the genetic variability due to individual parent trees. The seedlings for this test were grown in a nursery at Rhinelander, Wisconsin, for 4 years from open-pollinated seed of 10 average-or-better trees from each of 21 stands of a wide geographic range (*Fig. 1*). As previously reported, the 198 families included had excellent but variable growth in the nursery and families usually

*)Principal Plant Geneticist,

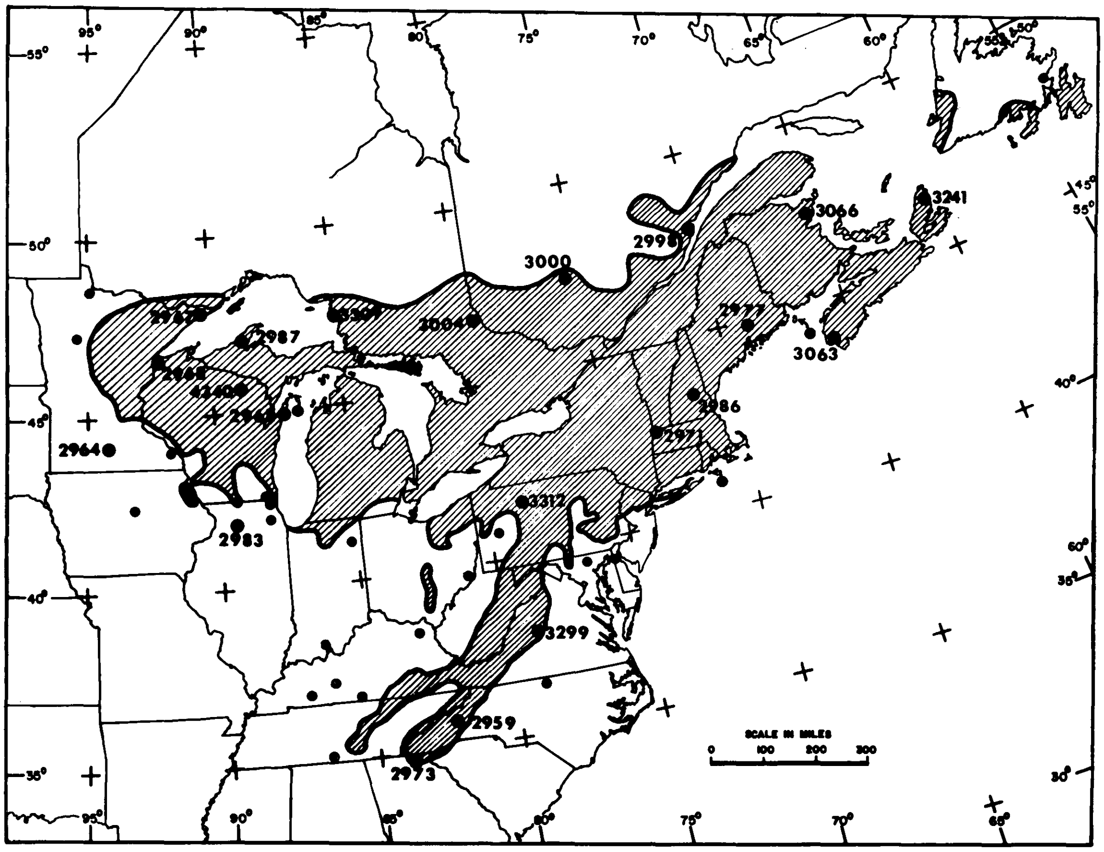

Figure 1. — Natural range of yellow birch and location of stands providing seed for this test.

accounted for more of the variation than provenances (CLAUSEN, 1973b). Results presented in this article corroborate the earlier findings and provide information on survival and growth after 5 years in the field, and on early flowering and seed production.

Methods

In the spring of 1972 the seedlings were planted in the field near Lake Tomahawk in Oneida County, north-central Wisconsin. The test site, a former potato field and pasture on Padus sandy loam was kept cleancultivated through the summer of 1975 and later mowed. The plantation originally contained 147 progenies *(Table 1)* in a split-plot design with 4-tree plots and 6 or 8 replications. Spacing was 8×8 ft (2.4 × 2.4 m).

Many seedlings died the first year due to the combined effects of heat, drought, unseasonable frost, and disease. Therefore, in the spring of 1973 the surviving plants were consolidated into 4 blocks and supplemented with replacement plants that had been kept in reserve in the nursery. Additional plants were replaced in the spring of 1974. Survival was checked each fall thereafter. All surviving trees were measured in 1976 at the end of their fifth growing season in the field. Measurements included: tree height, stem diameter at d.b.h. (1.3 m), crown length, and crown diameter. Crown length was taken as the distance from the lowest live branch to the top of the tree. Crown diameter was recorded as the average of two measurements taken at right angles to each other at the widest part of the crown. In addition, crown volume was calculated as a simple cone and crown surface as two opposing cones with heights of 2/3 and 1/3 crown length, respectively (CLAUSEN, 1979). Preformed male catkins and fruiting catkins were counted each autumn from 1974 through 1976 and all

Table 1. — Origin of 21 yellow birch stands and number of open-pollinated families included in progeny test

Stand No.	State or Province	Location Lat.	Location Long.	Number of families
		deg.	deg.	
3241	Nova Scotia	46.6	60.5	8
3063	Nova Scotia	44.1	65.8	7
3066	New Brunswick	47.4	65.2	6
2998	Quebec	48.2	70.2	9
3000	Quebec	47.5	75.0	9
3004	Ontario	46.7	79.6	8
3309	Ontario	47.5	84.8	8
2977	Maine	44.8	68.6	7
2986	New Hampshire	43.5	71.4	4
2971	Massachusetts	42.7	73.2	5
3312	Pennsylvania	41.6	78.7	5
3299	Virginia	37.8	79.1	5
2959	North Carolina	35.7	82.3	3
2973	Georgia	34.8	83.8	5
2983	Illinois	41.9	89.4	9
2962	Wisconsin	44.9	87.2	6
4340	Wisconsin	45.6	88.6	8
2968	Wisconsin	46.5	92.1	9
2987	Michigan	47.0	88.7	9
2967	Minnesota	47.8	90.2	8
2964	Minnesota	44.2	94.1	9
Total				147

flowering catkins were counted in spring 1976 and spring 1977.

Data analysis was complicated by differential survival of various families and stands, by block differences, by unequal numbers of families per stand, and by unequal numbers of plots per family in different replications. The data from blocks 1 and 4 were adjusted because they consistently had lower and higher values, respectively, than blocks 2 and 3. The adjustment factor for each characteristic was calculated as the average of the means for blocks 2 and 3 divided by the mean for block 1 or 4. The survival data reported in the following refer to all families and stands. However, the analyses of growth were based on various numbers of stands and families. The stands with few survivors (2959, 2971, 2973, 2986, 3066, 3299, and 3312) were not included in any of the statistical analyses. Three different analyses were performed:

1. Analysis of variance among stands based on family means and limited to 14 stands having at least 18 plots in the 4 blocks and to families that were present in at least 3 blocks in the fall of 1976. This analysis is approximate because the unequal number of plots per family was ignored.
2. Balanced analysis of variance among families and stands based on data from eight stands with five families in each of the four blocks. When more families or plots were present, those included in the analysis were randomly selected from the available material.
3. Unbalanced analysis of variance for each stand that had at least two families in at least three of the four blocks. The analysis included all usable plots of a family and was based on family means per block weighted by the number of plots. This comprehensive analysis included 382 plots of 80 families from 14 stands.

The Newman-Keuls range test was used in comparisons among stands and families but due to the unequal number of plots per family it is only approximate.

Results

Survival

Following the spring 1974 replacement planting, 17 % of the trees in the plantation were from the original 1972 planting, 59 % were 1973 replacements, and 24 % were 1974 replacements. Survival at the end of the 1974 growing season averaged 92 % and was high for all stands (family groups) except Massachusetts' stand 2971 (*Table 2*). The families varied considerably in how well they survived and stand 2971 not only had the family with the poorest survival but also showed the most variation among families within a stand. The trees planted in 1972 and 1973 survived equally well but those planted in 1974 had about 4% poorer survival. By fall 1975 stand survival ranged from 50 to 95 % and had declined to an average of 83 %. The increased variation among stands was accompanied by an even greater increase in the range of family means. Again, stand 2971 had the most within-stand variation but New Brunswick stand 3066 was also highly variable. The trees planted in 1972 and 1973 again survived equally well while the trees planted in 1974 averaged 11 % poorer survival.

Following a prolonged drought during the summer and fall of 1976 survival declined to an average of 63 % with a range among stands from 39 % for Georgia stand 2973 to 78 % for Wisconsin stand 2962.

Concurrently, the variation among families within stands increased greatly. For example, one of the 8 families from stand 4340 had only 14 % survival while another family had 93 % survival. Although 11 families still had 100 % survival, most of them originally contained only few trees and may, therefore, not be representative. One family each from stands 2971 and 4340 had the poorest survival (14 %) and 21 other families had less than 50 % survival. By 1976, the trees planted in 1972 averaged 77 % survival compared with 67 % for the trees planted in 1973 and 43 % for the trees planted in 1974.

Growth

Early results showed that the growth trends reported from the nursery continued for at least the first 3 years in the field (Clausen, 1975a). Tree height after 5 years in the field ranged from 1.54 m to 2.07 m and averaged 1.83 m for the 21 stands (*Table 3*). When heterogeneity of variance was considered, Analysis 1 gave a significant F value but according to the Newman-Keuls range test, none of the 14 stands analyzed differed from any other in height. Stem diameter varied from 0.92 to 1.26 cm and averaged 1.07 cm. The range test showed that stand 3063 had a significantly

Table 2. — Survival of 147 yellow birch families from 21 stands after 3, 4, and 5 years in the field

Stand No.	State or Province	Fall 1974 Stand mean	Fall 1974 Range of family means	Fall 1975 Stand mean	Fall 1975 Range of family means	Fall 1976 Stand mean	Fall 1976 Range of family means
		Percent					
3241	NS	99	92-100	86	60-100	67	50- 70
3063	NS	93	50-100	83	50-100	52	49-100
3066	NB	90	86-100	81	43-100	55	28-100
2998	PQ	95	67-100	93	67-100	71	44-100
3000	PQ	93	78-100	83	71- 92	61	51- 72
3004	ON	95	80-100	92	80-100	73	40-100
3309	ON	98	86-100	95	86-100	73	40- 91
2977	ME	93	67-100	84	70- 90	61	33- 80
2986	NH	97	88-100	85	71-100	67	38- 89
2971	MA	65	43-100	59	28-100	53	14-100
3312	PA	84	57-100	68	54-100	48	41- 62
3299	VA	84	78- 93	68	44- 86	47	19- 78
2959	NC	94	75-100	88	75-100	67	64- 75
2973	GA	78	73-100	50	33- 80	39	25- 80
2983	IL	96	75-100	92	75-100	76	25- 89
2962	WI	96	83-100	90	83-100	78	43-100
4340	WI	93	86-100	88	71-100	70	14- 93
2968	WI	95	86-100	88	71-100	63	25-100
2987	MI	96	88-100	85	78-100	62	43-100
2967	MN	98	80-100	91	82- 97	67	53- 82
2964	MN	94	85-100	91	82-100	76	64- 89
Mean		92		83		63	

Table 3. — Tree height, diameter, and crown size of 110 yellow birch families from 21 stands after 5 years in the field[1]

Stand No.	State or Province	Height		Diameter		Crown length		Crown diameter		Crown volume		Crown surface	
		Stand mean	Family means	Stand mean	Family means	Stand mean	Family means	Stand mean	Family means	Stand mean	Family means	Stand mean	Family means
		m	range	cm	range	m	range	m	range	m^3	range	m^2	range
3241	NS	1.72	91-110	1.05	96-108	1.49	87-109	0.94	86-114	0.38	68-128	2.79	82-122
3063	NS	1.66	92-108	.92	93-108	1.45	94-104	.84	90-118	.31	82-144	2.44	89-125
3066	NB[2]	1.63	83-116	.94	87-120	1.37	78-114	.89	84-125	.32	61-175	2.50	70-142
2998	PQ	1.79	84-110	1.01	82-110	1.48	76-113	.79	72-116	.26	36-142	2.22	54-130
3000	PQ	1.77	91-111	.98	87-117	1.55	88-117	.90	81-132	.37	54-176	2.76	68-148
3004	ON	2.06	96-103	1.06	96-103	1.80	92-108	1.00	86-114	.56	58-141	3.52	75-124
3309	ON	1.86	75-115	1.04	84-111	1.60	68-114	.99	58-125	.43	23-154	3.22	38-132
2977	ME	1.94	96-107	1.09	93-109	1.55	93-108	.90	89-113	.35	79-121	2.70	86-115
2986	NH[2]	1.72	92-108	1.07	88-110	1.41	95-104	.83	94-117	.30	60-138	2.36	75-121
2971	MA[2]	1.86	78-117	.99	86-113	1.56	74-115	1.21	87-130	.42	53-124	3.02	66-118
3312	PA[2]	2.07	92-106	1.26	86-114	1.59	89-112	.95	80-115	.41	61-144	2.96	73-130
3299	VA[2]	1.78	88-105	1.13	96-107	1.39	58-114	.92	96-116	.35	70-114	2.67	79-110
2959	NC[2]	1.77	95-103	1.03	90-109	1.45	90-107	.76	86-110	.23	64-119	2.20	73-120
2973	GA[2]	1.54	79-112	1.10	83-119	1.36	78-112	.91	65-119	.32	30-120	2.53	48-126
2983	IL	1.79	94-114	1.20	91-108	1.46	95-111	1.06	90-122	.51	69-174	3.26	83-140
2962	WI	2.01	86-113	1.19	84-107	1.72	82-118	1.07	81-124	.56	48-171	3.62	65-143
4340	WI	1.97	88-106	1.13	91-109	1.55	84-111	.93	86-110	.39	86-121	2.88	83-116
2968	WI	1.98	77-122	1.09	83-113	1.73	83-129	1.13	77-138	.73	38-230	4.00	59-178
2987	MI	1.74	84-110	1.20	89-110	1.46	93-106	.87	82-115	.32	56-136	2.50	73-118
2967	MN	1.85	86-125	1.07	82-133	1.62	87-123	.96	84-118	.45	63-158	3.02	76-130
2964	MN	1.89	88-118	1.15	87-123	1.62	84-119	1.21	71-152	.69	38-253	4.08	56-186
Mean of 21		1.83		1.07		1.53		.96		.41		2.92	
Mean of 14		1.86		1.08		1.57		.98		.46		3.11	

[1] Family means are expressed as percent of stand means.
[2] Stand not included in statistical analysis.

smaller diameter than the three top-ranking stands (2983, 2962, 2964) and that the diameter for stand 3000 was significantly smaller than those of stands 2983 und 2962. Average crown size for the 14 stands analyzed was slightly larger than for all 21 stands, but the stands did not differ significantly in any of the four crown characteristics.

Although the differences among stands in tree size and crown size were small, family differences were large (*Table 3*). The results of the balanced ANOVA (Analysis 2) showed that tree and crown characteristics were not significantly different among stands 2964, 2967, 2983, 2987, 2998, 3000, 3309, and 4340 (*Table 4*). However, families within stands were significantly different in tree height and in crown length, diameter, and surface area.

The results of the unbalanced ANOVA (Analysis 3) showed that there were significant family differences for any one variable in less than a third of the stands. Families differed for tree height and stem diameter in three of the stands, and they differed within stands for the four crown variables in four stands (*Table 5*). Seven stands accounted for all the family differences. Of these, stands 3000, 3309, and 2968 each showed variation in two traits, 2962 differed in three traits, 2967 and 2964 varied in four traits each, and 2998 had family differences in five of the six characteristics measured. In the analysis af variance, stands 2962 and 2964 had significant family differences in crown length but no differences among families were apparent according to the Newman-Keuls multiple-range test. Similarly, stand 3000 had a significant F value for crown surface but showed no family differences in the range test.

Although only one-half of the stands exhibited statistically significant family differences, much variation was, in fact, present. The differences between the tallest and the shortest family was up to 45 % of the stand mean in stand 2968 from northwestern Wisconsin. In addition, within-

Table 4. — Results of balanced analysis of variance for 8 stands with 5 families each

Characteristic	Significance of F[1]		
	Blocks	Stands	Families in stands
Tree height	NS	NS	*
Stem diameter	NS	NS	NS
Crown length	NS	NS	*
Crown diameter	*	NS	*
Crown volume	NS	NS	NS
Crown surface	*	NS	*

[1] * = significant at 0.05 level
NS = not significant

stand variation was greater than the range of stand means in seven of the stands. The height difference between extremes of all 80 families was 73 %. Similarly, the range between extreme family means in stem diameter was as high as 51 % in stand 2967 from northeastern Minnesota. Within-stand variation in d.b.h. exceeded the range of stand means in seven of the stands and the best family had 84 % greater diameter than the poorest one.

Family variation was even greater for the four crown characteristics. Extreme family ranges (in percent of stand means) were 56 for crown length, 81 for crown diameter, 215 for crown volume, and 130 for crown surface (*Table 3*). The number of stands in which within-stand variation was greater than the range of stand means was 10 for crown length, 6 for crown diameter, and 5 for both crown volume and crown surface.

Other indications of the variability present in this material were the large residual standard deviations observed

Table 5. — Stands with family differences in tree and crown size according to unbalanced analysis of variance[1]

Stand No.	Families	Plots	Tree height	Stem diameter	Crown Length	Crown Diameter	Crown Volume	Crown Surface	No. of traits with family differences
2998	5	29	NS	*	*	*	*	*	5
3000	8	39	NS	NS	NS	*	*	S	2
3309	7	31	*	NS	*	NS	NS	NS	2
2962	5	26	NS	NS	S	**	**	**	3
2968	6	24	**	NS	*	NS	NS	NS	2
2967	6	26	**	**	**	NS	NS	*	4
2964	8	39	NS	*	S	**	**	**	4
No. of stands with family differences			3	3	4	4	4	4	

[1] ** = significant at the 0.01 level
* = significant at the 0.05 level
S = significant F value but no difference in range test
NS = not significant

for each variable and for most stands. The residual standard deviation is an expression of the family × block interaction and thus a measure of the variation among individual plots of a family. Significant interactions were recorded for the following stands and variables: 2964—crown volume; 3309—crown volume and crown surface; 2968—crown diameter, crown volume, and crown surface; 2983—all variables except crown diameter. Of these, all but 2983 were stands with significant family differences. Another source of variation was the difference among trees within a plot. Considerable within-plot variation was observed but could not be quantified due to the small number of replications and the differential survival.

Flowering

Any tree having one or more catkins was counted as flowering or fruiting. Female flowering began in the spring of 1974 when the trees were 6 years old from seed (Clausen, 1977). By the following autumn <1 % of the trees had fruiting catkins but the percentage of seed-bearing trees increased to about 4 in 1975 and 1976 (*Table 6*). By the spring of 1977 14 % had female flowers.

Male flowering did not begin until the fall of 1975. As the trees grew older the percentage of trees with male catkins increased from 1 % in 1975 to 7 in 1976 and 8 % in the spring of 1977. Similarly, trees having both male and female catkins increased from <1 % in the fall of 1975 to 4 % in the spring of 1977 (*Table 6*).

Trees of northern origin began to bear seed and to produce pollen at an earlier age than those of southern origin (Clausen, 1977). This trend continued through the spring of 1977 when the 12 northern stands (latitude 44.5° N or above) had an average of 11.8 female-flowering trees per stand compared with 9.8 trees for the 9 southern stands. Similarly, the number of trees per stand with male catkins by this time averaged 6.9 for the northern stands and 5.7 for the southern stands. By the fall of 1975 at least one tree from each of the 21 stands had borne seed and all but New Brunswick stand 3066 had produced male catkins.

The number of fruiting families increased from 12 in 1974 to 45 or almost one-third of the families in 1976 (*Table 6*). About 60 % of the families had female flowers in the spring of 1977. The number of families with male catkins increased from 13 in 1975 to 73 in 1976. Thus, by age 9 one-half of the families were producing pollen.

The number of flowering or fruiting trees per family varied with years, stands, and families, but generally increased with increasing age of the trees (*Fig. 2*). Certain families tended to be more prolific producers of both seed

Table 6. — Incidence of flowering and fruiting by year and season

Season	Trees with catkins[1] ♂	Trees with catkins[1] ♀	Trees with catkins[1] ♂ + ♀	Families with catkins ♂	Families with catkins ♀	Families with catkins ♂ + ♀
	- - Percent - -			- - Number - - -		
Fall 1974	-	<1	-	-	12	-
Fall 1975	<1	4	<1	13	51	5
Spring 1976	<1	3	<1	13	48	7
Fall 1976	6	2	2	73	45	30
Spring 1977	5	11	4	73	89	43

[1] Trees in columns 1 and 2 had male or female catkins only and are not included in column 3.

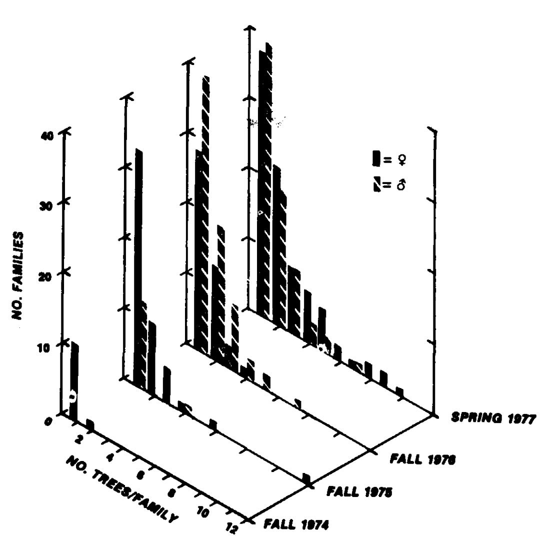

Figure 2. — Frequency distribution of families with flowering or fruiting trees.

and pollen than others (CLAUSEN, 1977). Number of fruiting catkins per tree varied greatly, increased with time, and approached a maximum of 200 catkins in both 1975 and 1976. The number of female catkins per tree in the spring reached 429 in 1976 and exceeded 1,000 in 1977; due to abortion the number of fruiting catkins the next fall was usually lower. Of the 230 trees with female catkins in the spring of 1977, 24% had more than 100 catkins per tree. Number of male catkins per tree increased markedly from a maximum of 57 in the fall of 1975 to 1,379 in 1976 when 27% of the flowering trees had more than 100 catkins per tree.

Discussion

Survival after 5 years in the field was not closely related to seed origin in this test—families from the northern stands (latitude 44.5° N or above) averaged 68% survival while those from the southern stands averaged 64%. However, only 19% of the 95 northern families had poor survival (50% or less) compared with 31% of the 52 southern families. Furthermore, 11 of the 15 families with 91 to 100% survival were of northern origin. Thus, northern families tended to survive better than southern ones but the large variation among families within stands and the replacements obscured any definite trends.

The amount of among-family variation in survival was unrelated to the average stand survival. For example, Minnesota stand 2964 and Illinois stand 2983 both averaged 75% survival but the range between the best and the poorest family was 23 in stand 2964 and 64 in stand 2983. Large as well as small family ranges were as common in northern stands as in southern stands. The apparent absence of association between seed origin and survival may be due partly to the small number of stands tested. In a previous study of 55 provenances, including 20 of the stands in the current study, 5-year survival was closely related to latitude of origin ($r = 0.74$) (CLAUSEN, 1975b).

Some of the 5-year results for tree height are in contrast to previous results. Stand differences were highly significant both in the nursery and after 3 years in the field (CLAUSEN, 1975a) but were not significant after 5 years according to the ANOVA. One possible reason is that only 14 stands were included in the ANOVA (Analysis 1) compared with 19 and 18 in the previous analyses. However, the balanced analysis showed highly significant within-stand differences after 5 years, which agrees with nursery and 3-year results.

Stand differences in stem diameter were not significant in the nursery (CLAUSEN, 1975a) but were highly significant after 3 and 5 years in the field. Families within stands, on the other hand, differed significantly on all three occasions. Thus, the results of the three analyses agreed reasonably well.

The seven stands with significant family differences always differed in more than one characteristic. The number per stand ranged from 2 to 5 of the 6 characteristics measured but did not follow any definite pattern. These stands all came from a 4-degree-wide latitudinal band along the northern limit of the species. Four of the stands were also concentrated in the western one-fourth of the range. Why family differentiation should only be apparent in these populations has no obvious explanation, and the results could conceivably have been different at another test location.

The amount of within-stand variation in tree height and diameter rarely remained the same from one measurement period to the next. Some stands showed a large decrease in family range between nursery and 3-year analyses but little change thereafter. Other stands decreased in range between the nursery and 3-year measurements and increased after 5 years. Only a few stands changed little in family range from the nursery through the 5-year results. These fluctuations in within-stand variation, though often substantial, did not follow any patterns and are probably not of genetic origin. Instead, they may be random changes caused by the severe stress to which these plants were exposed.

Tree height was essentially uncorrelated with latitude and longitude of stand origin. Diameter showed a similar lack of correlation with latitude but tended to increase slightly with increasing longitude. Thus, neither height nor diameter growth of the stands in this plantation were closely related to their origin. This agrees with previous work on yellow birch (CLAUSEN, 1973a, 1975b).

Variation between and within populations in portions of the range may be more important than variation between widely separated populations. For example, trees from the three Wisconsin stands and the two Minnesota stands had heights and diameters up to 11% greater than the plantation mean. Furthermore, 50 to 83% of the families from these five stands exceeded the plantation means for height and diameter. Although the best family from one of these stands (4340) was only 6% above the stand mean, it was 14% taller than the plantation average. Similarly, the tallest family from another one of these stands (2968) exceeded the stand and plantation means by 22 and 32%, respectively. The best families from the other three stands were from 22 to 26% taller than average. Thus, within the stands of this region, which performed well as a group, there were families with substantially better than average or even superior growth. Similarly, WEARSTLER and BARNES (1977) found significant differences between and within physiographic regions of Michigan in several characters of yellow birch. Therefore,the greatest gain in growth of the species will probably come by selecting the fastest growing families from limited geographic regions such as the Lake States.

The survival and growth data presented above should be interpreted with caution for the following reasons: (1) the results are from only one plantation; (2) the plantation suffered severe environmental stress which led to inconsistent responses by the families and undoubtedly increased the variation; (3) data analysis was less precise and, hence, less reliable than under normal circumstances due to the way the plant material was handled and its irregular performance; and (4) the families were tested on an open-field site, which may not provide as good conditions for production of high-quality yellow birch as growing them under an overstory would have (CLAUSEN, 1975b).

The finding that yellow birch trees can produce viable seed during their seventh growing season and male flowers during the eighth, indicates that seedling seed orchards should work well with this species. It also means that second generation selection and testing ca begin soon after an improvement program has been initiated.

The fact that 60% of the families had female flowers and one-half of the families produced pollen by age 9 suggests that trees less than 10 years old are capable of producing substantial seed crops. Of the fruiting trees in 1976, 53 % had 100 to 200 seeds per catkin and 3 % had more than 300 seeds per catkin. Thus, a tree with 100 catkins can easily produce between 10,000 and 30,000 seeds. Because certain families and trees tend to flower earlier and more prolifically than others, excellent opportunities exist for selecting for high seed production at an early stage in an improvement program.

Selection for early flowering in *Betula* should, however, be approached with caution. Thus, STERN (1963) found the correlation between growth and early, prolific flowering in *Betula verrucosa* EHRH. to be positive in some families but negative in others. For this reason, 265 flowering trees in this study were each compared with a non-flowering tree from the same plot. A t-test showed that the flowering trees tended to be taller and to have bigger crowns than the non-flowering ones (CLAUSEN, 1979). Thus, early and prolific flowering did not have an adverse effect on growth of these yellow birch families.

Literature Cited

CLAUSEN, K. E.: Genetics of yellow birch. U. S. Dep. Agric. For. Serv., Res. Pap. WO-18, 28 p. (1973 a). — CLAUSEN, K. E.: Within-provenance variation in yellow birch. Northeast. For. Tree Improv. Conf. Proc. 20: 90—98 (1973 b). — CLAUSEN, K. E.: Early results of a yellow birch progeny test. IUFRO Working Party on Progeny Testing S2.04.3 Meeting on Progeny Testing of Hardwoods. Nov. 1974. Proc. p. 16—24. Southeast. For. Exp. Stn., Asheville, NC. (1975 a). — CLAUSEN, K. E.: Variation in early growth and survival of yellow birch provenances. Northeast. For. Tree Improv. Conf. Proc. 22: 138—148 (1975 b). — CLAUSEN, K. E.: Early flowering and seed production in a yellow birch progeny test. Cent. States For. Tree Improv. Conf. Proc. 10: 9—19 (1977). — CLAUSEN, K. E.: The relation between tree size and flowering in yellow birch saplings. IUFRO Symposium: Flowering and Seed Development in Trees, Starkville, Mississippi, May 1978 Proc. p. 77—82 (1979). — STERN, K: Über die Abhängigkeit des Blühens der Sandbirke von Erbgut und Umwelt. Silv. Genet. 12: 26—31 (1963). — WEARSTLER, K. A., Jr., and B. V. BARNES.: Genetic diversity of yellow birch seedlings in Michigan. Can. J. Bot. 55: 2778—2788 (1977).

Genetic Heterozygosity and Radial Growth Variability in Pinus contorta

By P. KNOWLES and J. B. MITTON

Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA

(Received October 1979 / February 1980)

Summary

The relationship between heterozygosity level and stability in the phenotypic character, annual radial growth, was examined within a population of *Pinus contorta*. Needle tissue was sampled from 152 lodgepole pines in the subalpine region of the Front Range in Colorado. Heterozygosity levels were determined from four electrophoretically detectable enzymes from the needle tissue. Each tree was cored, ages were estimated, and ring widths were measured. The coefficient of variation, a measure of dispersion in growth increment, was calculated for each tree and related to the level of heterozygosity. The results indicate that trees with overall high levels of heterozygosity have significantly less growth variability than trees with low levels of heterozygosity. When the loci are examined seperately, however, there are no significant differences between the genotypic groups. This suggests a complex interaction among the four loci involved. Although the mechanism linking overall heterozygosity level to phenotypic variability remains unknown, these results add to the increasing evidence that a strong relationship exists between heterozygosity and phenotypic variability.

Key words: heterozygosity, lodgepole pine, developmental homeostasis, growth variability, isozyme variation

Zusammenfassung

In der Population von *Pinus contorta* wurde die Beziehung zwischen Heterozygotiegrad und der Stabilität des phänotypischen Merkmals Jahrringbreite untersucht. Stichproben des Nadelgewebes wurden von 152 Kiefern in der subalpinen Zone des Front Range Gebietes in Colorado (U. S. A.) entnommen. Der Heterozygotiegrad wurde jeweils an 4 elektrophoretisch nachweisbaren Enzymen des Nadelgewebes bestimmt. An Bohrproben jedes Baumes wurde das Alter geschätzt und die Jahrringbreite gemessen.

Der Variationskoeffizient wurde als Maß für die Streuung des Zuwachses für jeden Baum berechnet und zum Heterozygotiegrad in Beziehung gesetzt. Die Ergebnisse zeigen, daß Bäume mit insgesamt hohem Heterozygotiegrad eine signifikant geringere Variabilität des Wachstums aufweisen als Bäume mit geringerem Heterozygotiegrad. Werden die Loci jedoch getrennt untersucht, ergeben sich keine signifikanten Unterschiede zwischen den Genotypgruppen. Dies deutet auf eine komplexe Interaktion zwischen den vier betreffenden Loci hin. Obwohl der Mechanismus des Zusammenhangs zwischen Gesamtheterozygotiegrad und phänotypischer Variation unbekannt bleibt, tragen die Ergebnisse zur steigenden Evidenz einer engen Beziehung zwischen Heterozygotie und phänotypischer Variation bei.

Introduction

The relationship between protein variation and morphological variation in natural populations is poorly understood. One aspect of this issue which has received some em-