GENETIC VARIATION OF SEED AND SEEDLING CHARACTERISTICS OF PAPER BIRCH (BETULA PAPYRIFERA) AND EUROPEAN WHITE BIRCH (BETULA VERRUCOSA)

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ABSTRACT

GENETIC VARIATION OF SEED AND SEEDLINGS CHARACTERISTICS OF PAPER (BETULA PAPYRIFERA) AND EUROPEAN WHITE (BETULA VERRUCOSA) BIRCH

By

Michael Francis Sohasky

The key to the improvement of paper birch (*Betula papyrifera*) is a knowledge of how much genetic variation present in the species. Because of the growing importance of paper birch as a timber producing tree and its potential for artificial regeneration, information on geographic variation patterns in growth rate and other desirable traits is an important first step towards its improvement.

The objectives of this study was to investigate the amount and pattern of genetic variation in paper birch through the measurement of 1) germination capacity and germinative energies of the seed, 2) growth rates, and 3) developmental and morphological characters of juvenile seedlings.

Variation patterns in the germination characteristics of paper birch seed were investigated on 219 half-sib families collected in Michigan, and 25 seedlots of Finnish birch. Studies of growth rates, and developmental and

morphological characters were done on container-grown seedlings grown under greenhouse conditions.

Temperature and geographic origin each had a significant effect on the germination capacity and germinative energy of paper birch seed. Seed from the Upper Peninsula (UP) of Michigan revealed a wider range of temperatures optimum for germination, and increased germinative energy, in comparison with seed from the Lower Peninsula (LP). There were distinct differences in the initiation phase of seed germination, with UP families beginning first.

There was also genetic variation between- and within-populations of paper birch in germination capacity and germinative energy. Seed from populations in the western UP began germination sooner, proceeded more rapidly, and reached optimum levels earlier than populations in the eastern UP and LP.

Genetic variation in juvenile height growth of container-grown paper birch seedlings grown under greenhouse conditions was essentially random with respect to major geographical gradients. Most of the variation in height growth of 4- and 5-month-old greenhouse grown seedlings was due to within-population differences (87%). Thus variation between half-sib families was greater than differences among widely separated populations. The amount of variation in growth between families differed among the populations sampled but the maximum variation between any

two populations was small (20%) compared to the maximum variation observed between two families (68%).

Comparative analysis between paper birch and European white birch (<u>Betula verrucosa</u>) from Finland, grown under greenhouse conditions, revealed the height superiority of the Finnish sources of birch. If this superiority holds true in test plantations it would indicate a possible use of European white birch for reforestation purposes in Michigan.

Variation in 26 developmental and morphological characters measured was essentially random over the natural range of paper birch, following no geographical or clinal pattern. Significant genetic variation was found in a number of characters, including number of lateral branches, stem pubescence, leaf number, leaf area, leaf length, and leaf shape. Variability in these characters exists both between widely separated populations of paper birch, and between paper birch and European white birch.

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By

Michael Francis Sohasky

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CHAPTER I

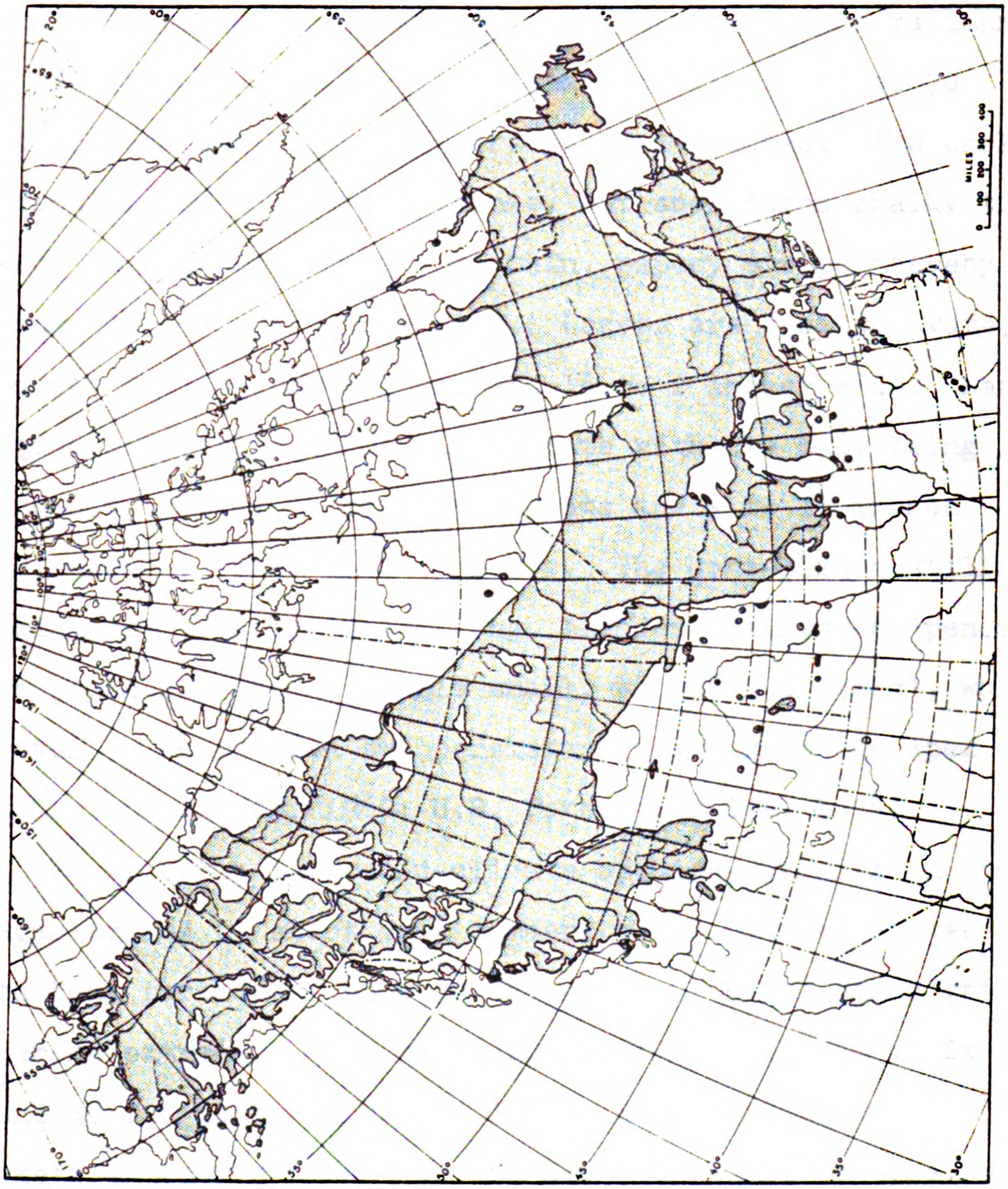
INTRODUCTION

Species Description

Paper birch (*Betula papyrifera* Marsh.), also known as white or canoe birch, is one of the 40 species of trees and shrubs that comprise the genus *Betula*. Paper birch has a transcontinental range, extending northward almost to the absolute limit of tree growth in the Boreal Forest Region of Canada and Alaska (Figure 1-1). It extends continuously across Canada from Newfoundland to Alaska, and penetrates the United States in the Northeast, southward to Pennsylvania, in the Lake States, and in northern Idaho and Montana. Outliers occur as far south as North Carolina, West Virginia, Iowa, Nebraska, in the Dakotas, and Colorado. Paper birch reaches its best development in the northern New England area (Hutnik and Cunningham, 1961; Fowells, 1965).

In eastern North America, paper birch shares the cooler part of its range with *B. cordifolia*, and in the warmer parts its range overlaps with *B. populifolia*. In the northern prairies and British Columbia paper birch is sympatric with *B. neoalaskana* and overlaps in Alberta and British Columbia with *B. fontinalis*, with which it sometimes hybridizes (Dugle, 1966; Grant and Thompson, 1975).

Figure 1-1. The range of paper birch.



The range of paper birch.

In paper birch, Brittain and Grant (1966, 1967) have found somatic chromosome numbers of 56, 70, and 84, possibly attributed to hybridization.

Paper birch is a short-lived, fast growing tree. Trees reach maturity as early as 60 years of age, with a maximum age of about 140 years. It attains heights of 50 to 70 feet and average stem diameters of 12-24 inches. The bark at first is dark brown or bronze, but soon turns chalky to creamy white, separating into thin, papery strips thereby giving it its distinctive name. Leaves are oval to ovate, commonly 2 to 3 inches long, and 1½ to 2 inches wide. Leaf margins are singly to doubly serrate with the base being rounded or obtuse. Staminate aments are ½ to 1¼ inches long, usually borne in 2's or 3's. The cone-like pistillate catkins are 1 to 1¼ inches long, slender-stalked and pendant each scale may bear a single small, winged nut (seed), which is oval in shape with two persistent stigmas at the apex (Harlow and Harrar, 1969; U.S. Forest Service, 1974).

Paper birch is a cold-climate species, growing in areas characterized by short cool summers and long cold winters with long periods of snow on the ground. Paper birch grows under an extremely wide range of habitat conditions. It is found as far north as the 55°F July isotherm, with out-pockets extending almost to the absolute limit of tree growth (Halliday and Brown, 1943). It seldom occurs naturally where the average July isotherm exceeds 70°F (Fowells, 1965). It occurs in areas where killing frosts can occur in the spring as late as the first week in June, and in the fall as early as the first week in September (Marquis et al., 1969). In view of its transcontinental range, paper birch can tolerate wide variations in the patterns and amounts of precipitation. The average annual precipitation within the commercial range varies from 25 to 45 inches, with about half occurring as snow.

Paper birch is confined largely to soils of the Spodosol region. However, it occurs on gray-brown and brown podzolic soils. Within these groups, numerous soil series and soil types are satisfactory for the growth of paper birch. Maximum development is reached on well-drained sandy loams. It is common on shallow stony soils and even occurs on wet bog and peat soils. The soils range from acid to highly calcareous, with the optimum pH in the range of 4.5-6.0.

For the most part, paper birch occurs at all elevations, and on all aspects and slopes. It is one of the few hardwoods found near timberline on the highest mountains in New England and New York. However, in the southern part of its range, it occurs only on the cooler sites--at higher elevations and on steep north- and east-facing slopes (Fowells, 1965).

Paper birch is an intolerant tree, occurring as a scattered tree in the mixed coniferous-hardwood forests of the north. They are less tolerant than their common forest associates--principally sugar maple, beech, yellow birch, red spruce, white spruce, and balsam fir. For this reason paper birch generally disappears from a stand after one generation, leaving only the more tolerant species. In some localities, especially the northern Lake States, paper birch together with white spruce and balsam fir, comprises a large portion of the forest (Hyvarinen, 1968).

Fire plays an important role in the regeneration of paper birch. After fire, paper birch often seeds in large areas where mineral soil has been exposed, especially on moist sites where it may form nearly pure stands. In this respect, paper birch is similar to the aspens and is commonly found in mixture with them on old burns (Harlow and Harrar, 1969). Reproduction is mostly from seed, although moderate stump sprouting can occur, especially after cutting or fire.

Paper birch growing stock volume in North America is estimated to be about 36 billion cubic feet. Of this, about one-fifth is in the U.S. and four-fifths in Canada. Twenty-seven percent of the 7 billion cubic feet of growing stock in the U.S. is located in the Lake States, 43 percent in Alaska, 29 percent in the Northeastern States, and 1 percent in the Pacific Northwest (Quigley and Babcock, 1969). The approximately 1.6 billion cubic feet represents about one-fourth the amount of the aspen volume in the Lake States (Hyvarinen, 1968).

Pulpwood is the most substantial use for paper birch in the Lake States. In 1965 pulpwood production was around 55,000 cords (Horn, 1966). In 1974 however, 184,000 cords of paper birch pulpwood was cut in this region (Blyth and Hahn, 1974).

Fuelwood is the second most important use of paper birch, especially for small-sized sticks. The largest paper birch trees are cut into sawlogs and veneer logs, with the highest quality logs used for veneer. The wood of paper birch is light, strong, smooth textured, and straight grained. A considerable quantity of paper birch is used for miscellaneous turning products, especially in New England (Hyvarinen, 1968).

Paper birch is also a valuable tree aesthetically. Its showy bark makes paper birch an important tourist attraction in the northern landscape, where recreation is rapidly growing.

Paper birch has a number of important disease and insect pests that cause widespread economic losses. The agents most damaging economically to paper birch are micro-organisms that cause discoloration and decay. The principle pathogens are Torula ligniperda causing red heart, Fomes igniarius and Poria obliqua associated with heart rot (Hepting, 1971).

Major insect pests associated with paper birch include the bronze birch borer, Agrilus anxius, birch leaf miner, Fenusa pusilla, and the forest tent caterpillar, Malacosoma disstria (Conklin, 1969).

In the 1940's and early 50's widespread and serious decline of birch, known as "birch dieback", occurred in the

Northeast and Canada. Paper birch is also susceptable to a condition known as post-logging decadence, where paper birches have been exposed by opening the stands (Fowells, 1965).

Objectives

Because of its rapid growth, high value wood, and aesthetic value, the demand for paper birch will continue to increase, especially high-quality veneer and sawlogs. To help meet this increase in demand, the establishment of plantations containing genetically improved progeny superior in growth rate, quality, and form is essential.

To effectively meet this demand by tree improvement, the extent of genetic variation must be estimated. While this information is known for many important commercial trees such as eastern white pine, jack pine, red pine, and white spruce, research on paper birch is scanty.

The objective of this study was to investigate the amount and pattern of genetic variation of paper birch (*Betula papyrifera*). In addition, European white birch (*Betula verrucosa*) was included for comparative analysis between the two species in:

1. Germination capacity
2. Germinative energy (rate)
3. Growth rates of seedlings
4. Developmental and morphological characters of seedlings

CHAPTER II

GEOGRAPHIC VARIATION IN GERMINATION OF BIRCH SEEDS

Paper birch (*Betula papyrifera*) seed ripens from early August till mid-September. Seed dispersal begins soon after ripening and continues throughout the winter months. The seeds are wind-disseminated, and because of their light weight they can be carried long distances. However, most seeds fall within a few hundred feet of the parent tree (Marquis et al., 1969). Due to their very small size, birch seeds are very sensitive to the light, moisture, and temperature conditions at the time of germination.

The effect of light and temperature on paper birch seed germination has been demonstrated by many workers. Vaartaja (1952) and McDermott (1953) found that the germinating capacity of *Betula pubescens* and *B. nigra* seeds is clearly stronger in light than in darkness. Studies by Black and Wareing (1954, 1955) show that the germination capacity of unchilled *B. pubescens* seeds depends on both the light period and temperature. Under long daylengths and a temperature of 15°C, germination is high (90%), whereas it is low under short-day conditions (25%). At 20°C, the photoperiodic response disappears and the percentage of germination is high under both long- and short-day conditions. Cold treated _B_. _pubescens_ seeds do not have any light requirement for germination (Black and Wareing, 1954).

Vaartaja (1959) has shown photoperiodism with respect to the germination of _B_. _pubescens_ seeds, and also suggested that the response of birch seed germination to light does not vary greatly among seedlots of different origins.

Probably the most crucial factor in determining germination of birch seeds in the soil is a suitable temperature. As seeds are the principle means of propagating the species, their germination should occur at a time when it will favor the survival of the young seedlings. In many species, including paper birch, this time does not coincide with its dispersal. Despite the fact that moisture is often present when the seeds are shed, the seeds may not germinate. Paper birch seeds may have a minimum temperature requirement which delays germination. The value of such a temperature requirement is obvious. Due to the large variations in climatic conditions found within the natural range of paper birch, it is possible that geographic variation patterns in germination capacity and germinative energy have evolved in relation to the temperature conditions at their origins.

Reports of variation in germination of seeds from different geographic origins in response to temperature has been contradictory for a number of species. McNaughton (1966) reported that Typha populations from southern origins germinated at lower temperatures. Fraser (1971) observed just the opposite effect with white spruce provenances, i.e., northern provenances of white spruce germinated at lower temperatures than those from warmer more southerly provenances. Mergen (1963) reported that seed of eastern white pine from northern sources germinated more rapidly than southern ones. More recently, Winstead (1971) reported that northern U.S. populations of sweetgum require the longest time to reach peak germination at all temperatures, whereas Mexico seedlots showed earliest peak germination. In white spruce, Fraser (1971) again found just the reverse, with northern provenances germinating sooner and ranking higher than southern provenances at temperatures up to and including 60°F.

In birch, Govorukha and Mamaev (1971) were the first to study the effect of geographic origin on the germination of _B_. _verrucosa_ and _B_. _pubescens_ at various temperatures. The germination of birch seeds at various temperatures, collected in the steppe, S. tiaga, and N. tiaga zones of Russia, revealed a clear relationship to geographic origin.

Seeds of both birch species from the more southern (steppe zone) origin, were found to have a wider temperature range and optimum, as well as increased germinative energy in comparison with birch seed from the more northern (N. tiaga) origin. Higher temperatures were required for the germination of seeds from the northern origin. Germination of seeds of northern origin also decreased sharply with an increase in temperature. Germinative energy or speed of germination varied from 95 percent germination in 5 days at 30°C for the southern origin to 95 percent germination in seven days for the more northern origin. At temperatures of 20° and 35°C, even wider differences in germinative energy were observed.

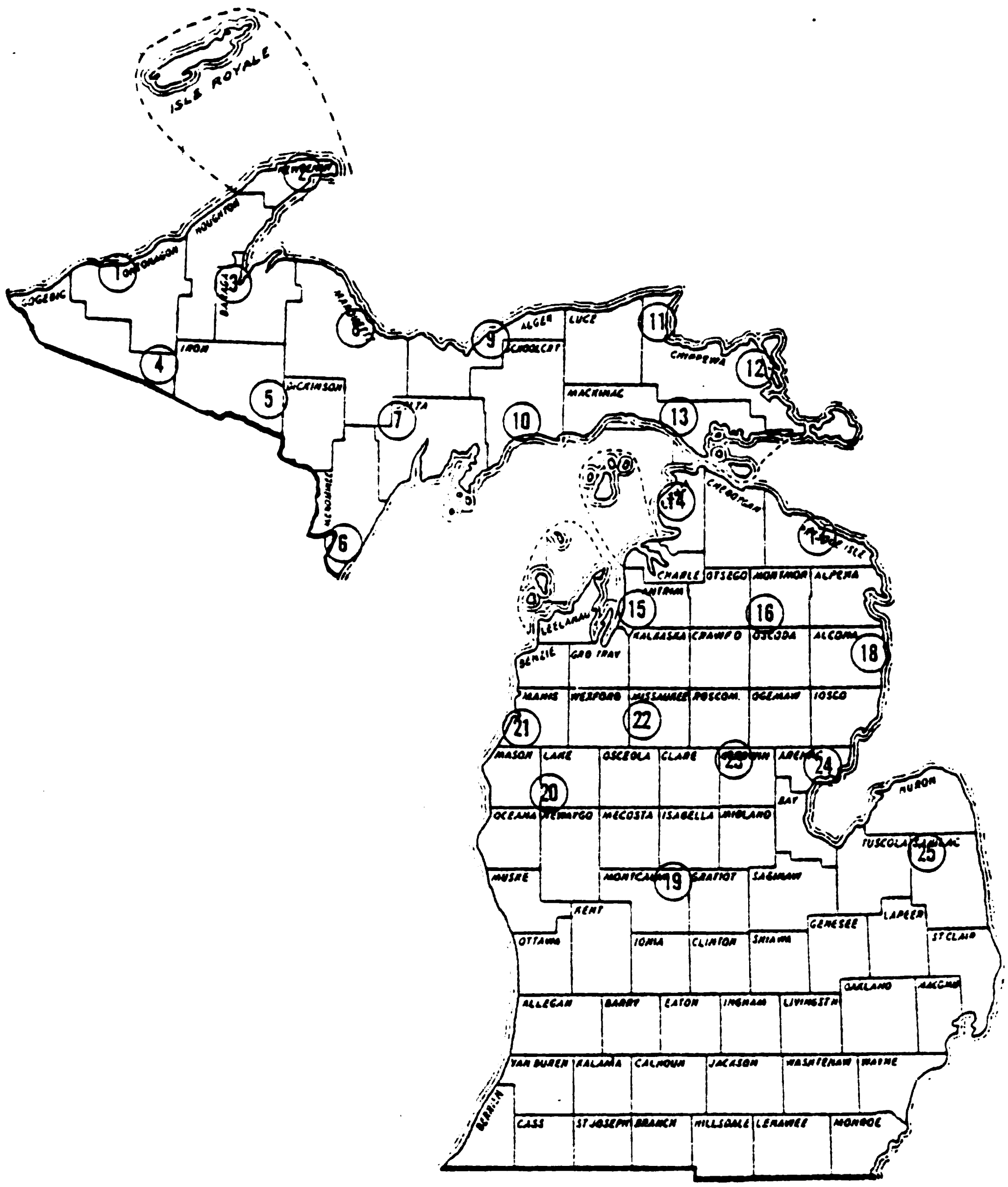
Knowledge of geographic variation in seed germination of paper birch provenances in response to varying temperatures is non-existent in paper birch. The objective of this study therefore was to measure the variation in germination characteristics of different seed sources of paper birch in response to temperature.

Materials and Methods

The seeds used in this study originated from a statewide collection of fruiting catkins (strobili) of paper birch during September, 1975. Collections began in the western portion of Michigan's Upper Peninsula (UP) on September 3rd and ended on September 25th in southern Michigan (LP). The seed sources used here are part of a larger collection described later.

Collection areas (populations) were uniformly distributed over the State of Michigan. Twenty-five different populations were collected (Figure 2-1). In each population, encompassing about a hectare in size, seeds were collected from 5 to 11 parent trees (seedlots), with an average seedlot per population of 9. Thirteen populations and 124 seedlots in the UP and 12 populations and 95 seedlots in

Figure 2-1. Location and population numbers of the 25 paper birch populations.


ISLE ROYALE
GOGEBIC
ONTONAGON
HOUGHTON
BARAGA
IRON
DICKINSON
ALGER
LUCE
SCHOOLCRAFT
MACKINAC
CHIPPEWA
CHEBOYGAN
CHARLE
OTSEGO
ALPENA
ANTRIM
LEELANAU
KALKASKA
OSCODA
ALCONA
BENZIE
GRD TRAV
WEXFORD
OGEMAW
IOSCO
MASON
LAKE
OSCEOLA
CLARE
ARENAC
BAY
HURON
OCEANA
NEWAYGO
MECOSTA
ISABELLA
MIDLAND
TUSCOLA
MONTCALM
GRATIOT
SAGINAW
KENT
GENESEE
LAPEER
OTTAWA
IONIA
CLINTON
SHIAWA
ST CLAIR
OAKLAND
ALLEGAN
BARRY
EATON
INGHAM
VAN BUREN
KALAMA
CALHOUN
JACKSON
WASHTENAW
WAYNE
BERRIEN
CASS
ST JOSEPH
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the LP were collected. Each parent tree was identified and assigned a Michigan State University accession number.

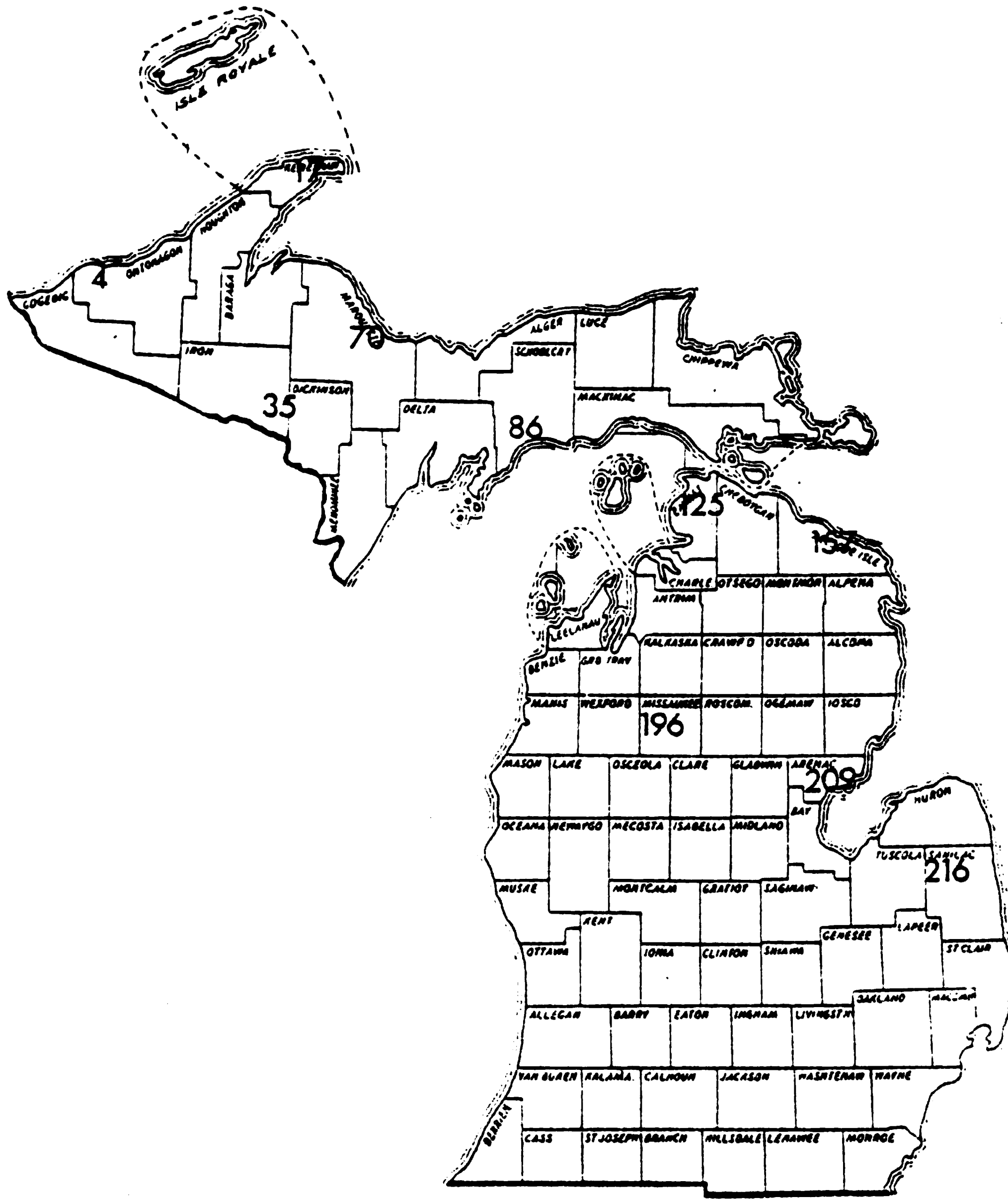
The number of catkins collected depended on the size of the seed crop. For each tree, green catkins were put into paper sacks, numbered, and allowed to dry at room temperature for approximately ten days to a moisture content of four percent. Seeds, bracts, and a small amount of drierite were then placed in sealed zip-lock plastic sandwich bags, labeled and placed in cold storage (4^oC).

Experiment I

To study germination in response to different temperatures, ten widely scattered populations were chosen, five from the UP and five from the LP. A seedlot was randomly selected from each of these populations. The locations and identification numbers of the selected seedlots are shown in Figure 2-2.

On October 9, 1975, the seeds were placed into covered Petri dishes containing one layer of white Whatman 9.0 cm filter paper. Distilled water was added to moisten the filter paper and was periodically applied as necessary. The dishes were placed in small illuminated, forced-draft, constant-temperature Sherer model CEL-25-7-HL growth chambers. Continuous illumination was provided by a mixture of cool-white flourescent tubes and 25 watt incadescent bulbs providing 800 ft-candles of light.

Figure 2-2. Location and identification numbers of the ten seedlots (families) used in Experiment I.


ISLE ROYALE
KEWEENAW
HOUGHTON
ONTONAGON
GOGEBIC
BARAGA
IRON
MARQUETTE
DICKINSON
MENOMINEE
DELTA
ALGER
LUCE
SCHOOLCRAFT
MACKINAC
CHIPPEWA
CHEBOYGAN
PRESQUE ISLE
CHARLEVOIX
ANTRIM
OTSEGO
MONTMORENCY
ALPENA
LEELANAU
BENZIE
GRAND TRAVERSE
KALKASKA
CRAWFORD
OSCODA
ALCONA
MANISTEE
WEXFORD
MISSAUKEE
ROSCOMMON
OGEMAW
IOSCO
MASON
LAKE
OSCEOLA
CLARE
GLADWIN
ARENAC
BAY
HURON
OCEANA
NEWAYGO
MECOSTA
ISABELLA
MIDLAND
TUSCOLA
SANILAC
MUSKEGON
MONTCALM
GRATIOT
SAGINAW
KENT
OTTAWA
IONIA
CLINTON
SHIAWASSEE
GENESEE
LAPEER
ST CLAIR
ALLEGAN
BARRY
EATON
INGHAM
LIVINGSTON
OAKLAND
MACOMB
VAN BUREN
KALAMAZOO
CALHOUN
JACKSON
WASHTENAW
WAYNE
BERRIEN
CASS
ST JOSEPH
BRANCH
HILLSDALE
LENAWEE
MONROE
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The experimental design consisted of three replications of approximately 60-75 seeds from each of the ten seedlots, in each of the four temperature treatments: 10°, 21°, 32°, and 43°C.

The germinated seeds were counted daily throughout a period of 21 days. Most germination had taken place at the end of 21 days except a few seed from a southern seedlot which germinated up to 35 days. A seed was considered germinated when the radicle protruded 1 mm or more from the seed coat.

The seeds were not stratified before treatment and were not subjected to any cold storage. Immediately after the initial drying phase the seeds were placed into the temperature treatments.

Percent germination data were transformed to degrees by the arc sine (arc sine$\sqrt{\text{percent germination}}$) method to normalize the data, and they were then subjected to analysis of variance. Duncan's (1955) multiple range test was used to test significance of treatment and seedlot means in germination capacity. Seed germination capacity was calculated as the percent of seed germinating after 21 days. Germinative energy was calculated as the number of days required for 75 percent of the seeds to germinate.

Experiment II

To further study germination responses to temperature, a much narrower range of temperatures was selected. Rather than using all the seedlots in Experiment I, three of the seedlots that revealed poor germination were excluded, leaving seven seedlots, three from the UP and four from the LP. The location and identification numbers are represented in Figure 2-3.

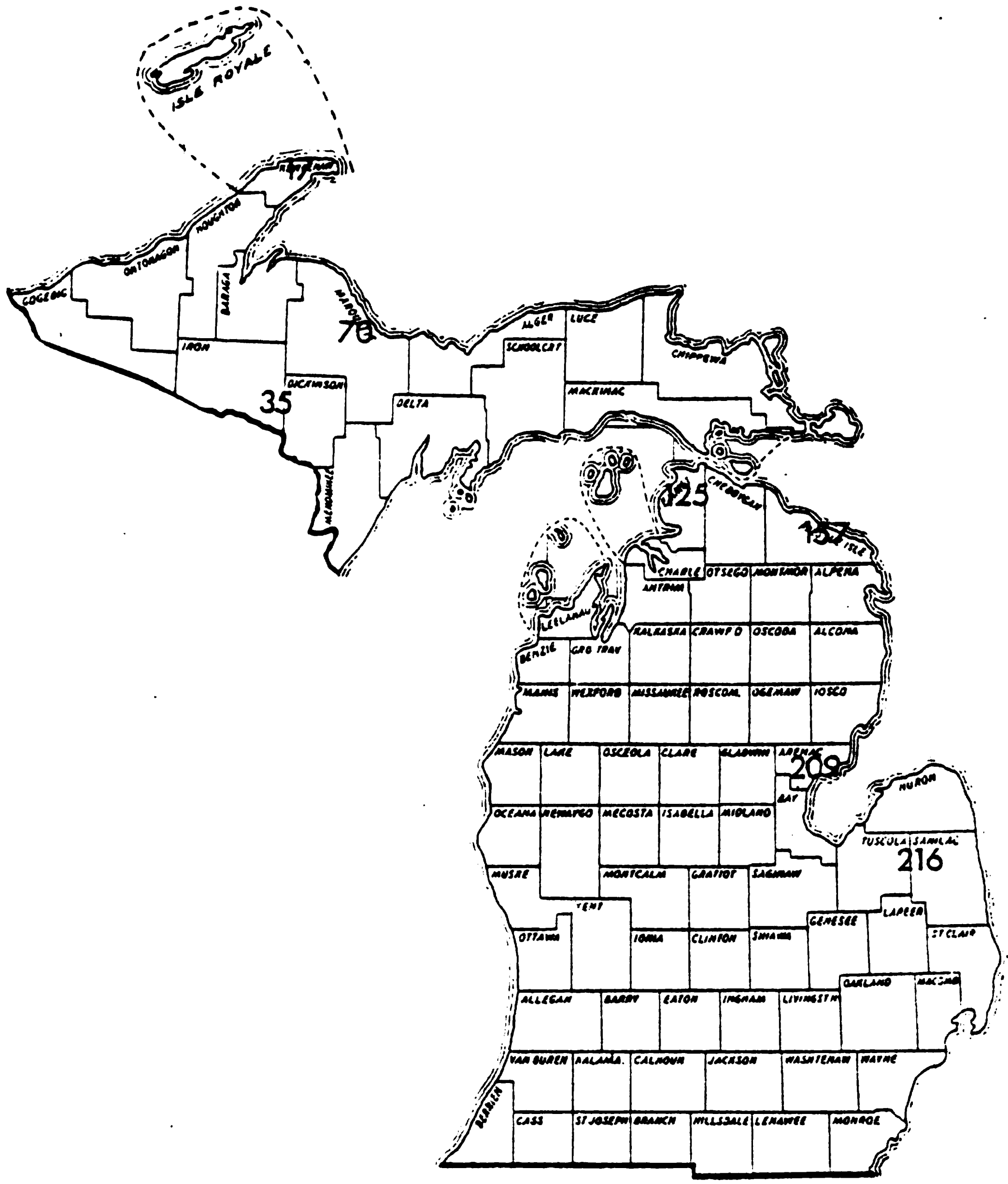
On October 28, 1975 the birch seeds were removed from the cold room ($4^{o}C$) after storage in dry sandwich bags for three weeks, and subjected to the same method of germination and experimental design as used in Experiment I. Four temperature treatments used were 27^{o}, 29^{o}, 32^{o}, and $35^{o}C$.

The germinated seeds were counted daily throughout the 21 day period. Analysis of variance was performed on transformed percent germination data.

Experiment III

Materials for this study consisted of all 219 seedlots from the 25 populations of paper birch. In addition, three different groups of birch seed from Finland were used, through the cooperation of Martti Lepistö of the Foundation for Forest Tree Breeding, Helsinki, Finland. The three groups consisted of 1) ten seedlots from a commercial seed orchard of *B. verrucosa* originating from southern and central Finland, 2) five seedlots from their greenhouse intraspecific hybrids of *B. verrucosa*, and 3) ten interspecific hybrids between *B. verrucosa* and other species of birch.

Figure 2-3. Location and identification numbers of the seven seedlots (families) used in <u>Experiment II</u>.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CHIPPEWA
MACKINAC
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CHEBOYGAN
OTSEGO
ALPENA
ANTRIM
LEELANAU
BENZIE
GRD TRAV
KALKASKA
OSCODA
ALCONA
WEXFORD
MISSAUKEE
ROSCOM
OGEMAW
IOSCO
MASON
LAKE
OSCEOLA
CLARE
ARENAC
209
BAY
HURON
OCEANA
NEWAYGO
MECOSTA
ISABELLA
MIDLAND
TUSCOLA
SANILAC
216
MONTCALM
GRATIOT
SAGINAW
GENESEE
LAPEER
ST CLAIR
OTTAWA
IONIA
CLINTON
SHIAWA
OAKLAND
ALLEGAN
BARRY
EATON
INGHAM
VAN BUREN
CALHOUN
JACKSON
WASHTENAW
WAYNE
CASS
ST JOSEPH
BRANCH
HILLSDALE
LENAWEE
MONROE
BERRIEN

This experiment was carried out at a constant temperature (30°C) for all 219 seedlots and was designed to test seedlot differences.

On November 7, 1975 the birch seed was removed from cold storage (4°C) after storage in dry plastic sandwich bags for 4 weeks, and placed into covered Petri dishes in a growth chamber (model CEL 512-37) with lighting as in the previous experiments. Each germination dish contained 100-175 seeds.

The germination period extended to 42 days. Germinated seeds were counted from the day germination started. This counting was done every day the first three days, and then periodically every 2, 3, and 4 days as time progressed. At each observation the counted seeds were removed.

Germination capacity was calculated as the percent of seed germinating in 42 days. Germinative energy was expressed as the number of days to a certain percentage of the total germination.

Results

Experiment I

Analysis of variance of the transformed percent germination data shows that temperature and seedlot each have a significant effect on the germination of *Betula papyrifera* seeds (Table 2-1). The interaction of temperature x seedlot suggests that the response of birch germination to

Table 2-1. Analysis of variance between ten seedlots of paper birch in response to four temperature treatments.

Source of variation	d.f.	M.S.	F-value
Temperature	3	1770.6	17.9**
Seedlot	9	548.0	5.6**
Temperature x seedlot	27	98.8	10.4**
Error	80	9.5	
Total	119		

** $P<0.01$

temperature varies greatly among different seedlots.

Germination capacity is significantly affected by temperature, as shown in Table 2-2. The optimum temperature of 32°C produced an average germination percent of 31.3. At the lowest temperature treatment of 10°C, germination capacity was significantly reduced, averaging 6.9 percent. The UP seedlots had germination in all five seedlots, whereas the LP seedlots had only two with any germination at all. Conversely, at the maximum temperature of 43°C, the LP seedlots had no germination, but in the UP two seedlots showed some germination.

At 21°C the 16 percent germination percentage is markedly less than the 29 percent germination at 32°C in all five seedlots from the LP. The UP seedlots showed nearly identical germination capacity at temperatures of 21°C and 32°C. Therefore, it appears that LP seedlots have a much narrower range of temperatures optimum for germination.

Table 2-2. Influence of temperature and seedlot on the germination of *Betula papyrifera* seeds after 21 days.

Seedlot No.	Michigan County	Temperature °C 10°	21°	32°	43°	Seedlot Means
		- - - - - - percent - - - - - -				
Upper Peninsula:						
4- 4	Ontonagon	0.7	8.0	9.3	0.0	4.5ef 1/
-17	Keweenaw	48.1	95.1	92.4	0.7	59.1a
-35	Iron	3.1	15.2	24.3	0.0	10.7cd
-70	Marquette	8.8	35.7	34.7	0.0	19.8b
-86	Schoolcraft	3.2	9.2	7.5	2.3	5.6de
Mean		12.8	32.6	33.6	0.6	19.9
Lower Peninsula:						
4-125	Emmet	0.0	6.1	8.4	0.0	3.6ef
-157	Presque Isle	1.2	29.3	44.6	0.0	18.8bc
-196	Missaukee	0.0	0.7	3.8	0.0	1.0f
-209	Arenac	0.0	1.7	29.7	0.0	7.9ef
-216	Sanilac	3.4	42.1	58.6	0.0	26.0b
Mean		1.0	16.0	29.0	0.0	11.5
Combined means:		6.9a	24.3b	31.3c	0.3d	

1/ Any two means with the same letter are not significantly different ($P<0.05$) by Duncan's Multiple Range Test.

Table 2-2 also illustrates the broad variation in germination capacity of each individual seedlot. Overall germination percent of the seedlots ranged from 59.1 percent for seedlot 4-17 to 1.0 percent for seedlot 4-196. Within a seedlot, increasing temperatures up to 32°C generally increased germination, especially in the LP where it occurred in all seedlots. There was no significant decrease in germination response of northern origins (UP) at 32°C as reported for _B. pubescens_ by Govorukha and Manaev (1971). They reported that a temperature of 33-35°C was optimum for seed germination of _B. pubescens_ from the southern steppe zone of Russia, whereas the more northern origins showed a noticeable decrease in germination capacity.

The influence of temperature on the rate of germination or germinative energy of the ten seedlots is evident in Table 2-3. As temperature increased rate of germination increased. At a temperature of 32°C all the seedlots showed maximum germinative energy. Germination began soonest proceeded at a more rapid rate, and reached optimum levels soonest at that temperature.

At the lowest temperature (10°C) not only was germinative energy significantly reduced, but germination was delayed. Germination began later and proceeded at a much lower rate than at the other temperatures.

This experiment revealed that germinative energy of birch seeds from the northern populations (UP) was much faster than southern populations (LP) at 21°C and at the

Table 2-3. Number of days required for *Betula papyrifera* seeds to reach 75 percent germination (germinative energy) at various temperatures.

Seedlot No.	Michigan County	Temperature °C			
		10°	21°	32°	43°
		- - - - - - - No. days - - - - -			
Upper Peninsula:					
4- 4	Ontonagon	12.0	13.4	11.8	- 1/
-17	Keweenaw	12.5	7.5	6.6	9.0
-35	Iron	14.3	8.7	5.6	-
-70	Marquette	15.3	12.6	7.4	-
-86	Schoolcraft	10.6	8.1	4.9	8.0
Lower Peninsula:					
4-125	Emmet	-	13.8	7.6	-
-157	Presque Isle	13.0	15.2	9.9	-
-196	Missaukee	-	17.0	-	-
-209	Arenac	-	11.4	12.9	-
-216	Sanilac	10.3	15.6	12.8	-
UP combined		12.2	10.1	7.5	8.6*
LP combined		16.0*	14.3	11.4	-

1/ No germination occurred.

* Represented by only two seedlots.

optimum temperature of 32°C (Figure 2-4). Thus, the combined UP seedlot means show that at the optimum temperature, 75 percent germination was obtained in just 7.5 days, whereas the LP combined seedlot means reached 75 percent germination in 11.4 days, a difference of 3.9 days.

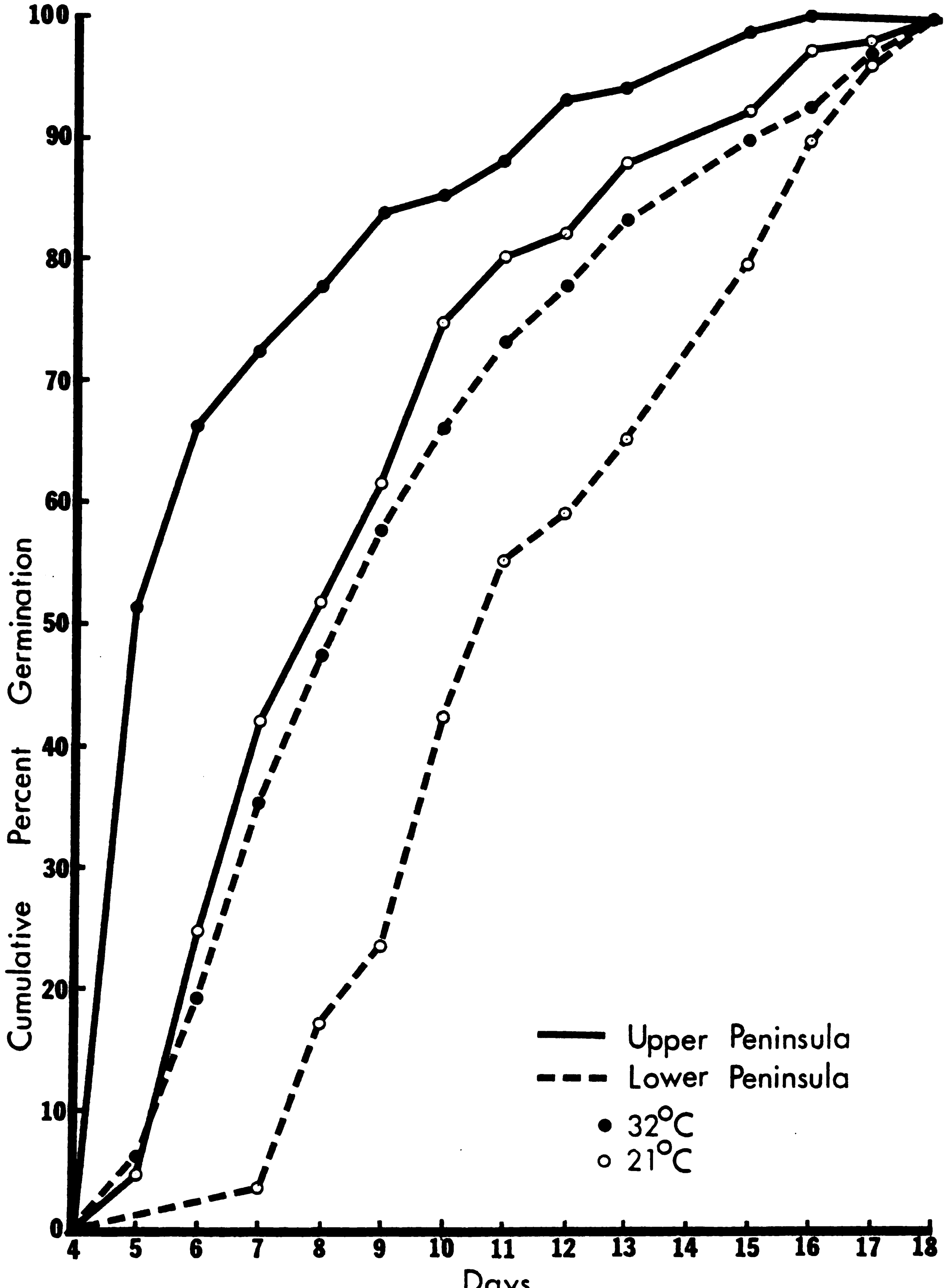
Seedlots from the UP showed a much faster initial rate of germination. For example, at 32°C the germinative energy of birch seeds from the UP was 51 percent in 5 days, while in the LP, it was only 6 percent. At the cooler temperature of 21°C, the LP had no seed germination until the 7th day, whereas the UP seedlots had begun germination by the 5th day.

Experiment II

This experiment was similar to Experiment I, except that a much narrower range of temperature treatments was selected to determine the optimum germination temperature for paper birch seeds, and to obtain any further insights into variation patterns of germination capacity and germinative energy.

Analysis of variance of the percent germination data presented in Table 2-4 revealed that temperature and seedlot each have a significant effect on the germination of paper birch seeds. The significant interaction of temperature x seedlot again suggests that the response of birch seed germination to temperature varies among different seedlots.

Figure 2-4. Cumulative percent germination of ten combined seedlots of paper birch from the Upper Peninsula (UP) and Lower Peninsula (LP) of Michigan, at temperatures of 21° and 32°C.



100
90
80
70
60
50
40
30
20
10
0
Cumulative Percent Germination
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Days
Upper Peninsula
Lower Peninsula
32°C
21°C

Table 2-4. Analysis of variance between seven seedlots of paper birch in germination response to four temperature treatments.

Source of variation	d.f.	M.S.	F-value
Temperature	3	1043.7	18.10**
Seedlot	6	590.9	10.25**
Temperature x seedlot	18	57.7	3.02**
Error	56	19.1	
Total	83		

** $P<0.01$

The results from this experiment are shown in Table 2-5. The optimum temperature for germination ranges from 27° to 32°C, combined over all seven seedlot means. No significant differences existed between the three temperature treatments of 27°, 29°, and 32° using combined seedlot means, but the optimum temperature for the more southerly (LP) was shifted in the direction of the lower temperature. At the maximum temperature of 35°C, the LP seedlots revealed almost no germination, with only one seedlot germinating at a much reduced capacity. Conversely, the more northerly (UP) seedlots all showed more germination than the LP seedlots at 35°C, but this temperature still gave lower germination than the other three temperatures. This is exactly the opposite the findings of Govorukha and Manaev (1971) on _B_. _pubescens_ who reported that more southerly population had 90 percent germination at 35°C and the more northerly population showed a decrease in germination to 60 percent.

Table 2-5. Influence of temperature and seedlot on the germination percentage of *Betula papyrifera* seeds after 21 days.

Seedlot No.	Michigan County	Temperature °C 27°	29°	32°	35°	Seedlot Means
		- - - - - -	percent	- - - - -		
Upper Peninsula:						
4-17	Keweenaw	94.6	95.7	96.5	32.0	79.7a 1/
-35	Iron	19.4	19.6	22.7	19.3	20.3de
-70	Marquette	35.9	40.6	34.5	18.4	32.4c
Mean		49.9	52.0	51.2	23.2	44.1
Lower Peninsula:						
4-125	Emmet	14.2	8.6	6.8	0.0	7.4f
-157	Presque Isle	35.7	39.8	43.3	3.5	30.6cd
-209	Arenac	39.8	22.2	17.8	0.0	20.0e
-216	Sanilac	63.2	69.4	59.5	0.0	48.0b
Mean		38.2	35.0	31.9	0.9	26.5
Combined means:		43.3a	42.3a	40.2a	10.5b	

1/ Any two means with the same letter are not significantly different ($P<0.05$) by Duncan's Multiple Range Test.

As indicated in Experiment I, Table 2-5 also illustrates the broad variation in germination capacity of each individual seedlot. Final mean germination capacity ranged from 79.7 to 7.4 percent, for seedlots 4-17 and 4-125, respectively. Within a seedlot, increasing the temperature at these closely spaced temperatures did not significantly increase the germination. Some seedlots increased slightly with increasing temperatures, while others decreased.

Germinative energy, or rate of germination, of paper birch seeds showed variation due to seedlot, temperature, and peninsula. The influence of temperature on the rate of germination of the seven seedlots is evident in Table 2-6. In contrast to Experiment I, increasing temperatures at these closely spaced treatments did not necessarily increase the germinative energy of the seedlots. Within a seedlot or peninsula the differences are small and quite variable, with no observable patterns except for 35°C where germinative energy was significantly reduced.

Between the two peninsula's, substantial differences are observed in germinative energy. Germinative energies of birch seed from the UP were much faster than the LP seedlots at all temperatures (Table 2-6). At 32°C the combined UP seedlot means revealed that 75 percent of the germination was obtained in 6.9 days, whereas the LP combined seedlot means reached the same level of germination in 13.0 days, a difference of 6.1 days.

Table 2-6. Number of days required for *Betula papyrifera* seeds to reach 75 percent germination at various temperatures.

Seedlot No.	Michigan County	Temperature °C				Combined Temp. Tmts.
		27°	29°	32°	35°	
		- - - - - - - No. days - - - - -				
Upper Peninsula:						
4-17	Keweenaw	6.0	6.0	6.5	11.5	
-35	Iron	6.0	9.0	7.0	8.0	
-70	Marquette	8.0	7.0	9.0	11.0	
Lower Peninsula:						
4-125	Emmet	11.0	8.0	11.0	-1/	
-157	Presque Isle	12.0	9.0	13.0	15.0	
-209	Arenac	13.0	13.0	15.0	-	
-216	Sanilac	11.0	11.0	13.0	-	
UP combined		6.1	7.5	6.9	9.8	6.8
LP combined		12.2	10.8	13.0	-	12.3

1/ No germination occurred.

Figure 2-5 graphically illustrates the relationship in germinative energy between the UP and LP at the various temperatures. At the lowest temperature of 27°C, the germinative energy of the birch seeds from the combined UP seedlots was 74 percent in 6 days, while for the combined LP seedlots, germination was only 14 percent for the identical length of time. When data from temperatures of 27°, 29°, and 32°C are pooled, all the seedlots from the UP showed a much faster rate of germination than seedlots from the LP (Figure 2-6). Variation within a peninsula was small, whereas variation between the two peninsulas is readily apparent. The UP combined seedlot means reached 75 percent germination in 6.8 days, whereas the LP combined seedlot means took 12.3 days to reach 75 percent of its germination.

Experiment III

The results from this experiment which included all paper birch and European white birch seedlots revealed a wide pattern of genetic variation in both germination capacity and germinative energy in relation to their geographic origins.

Germination capacity varied both within a population and between populations. Variations in germination capacity ranged from 0.0 to 90.3 percent for all 219 seedlots. Within an individual population (stand located in a Michigan county), germination varied widely. In many populations, single trees (seedlots) within 30 feet of each

Figure 2-5. Cumulative percent germination of seven combined seedlots of paper birch from the UP and LP of Michigan, at temperatures of 27°, 29°, 32°, and 35°C.

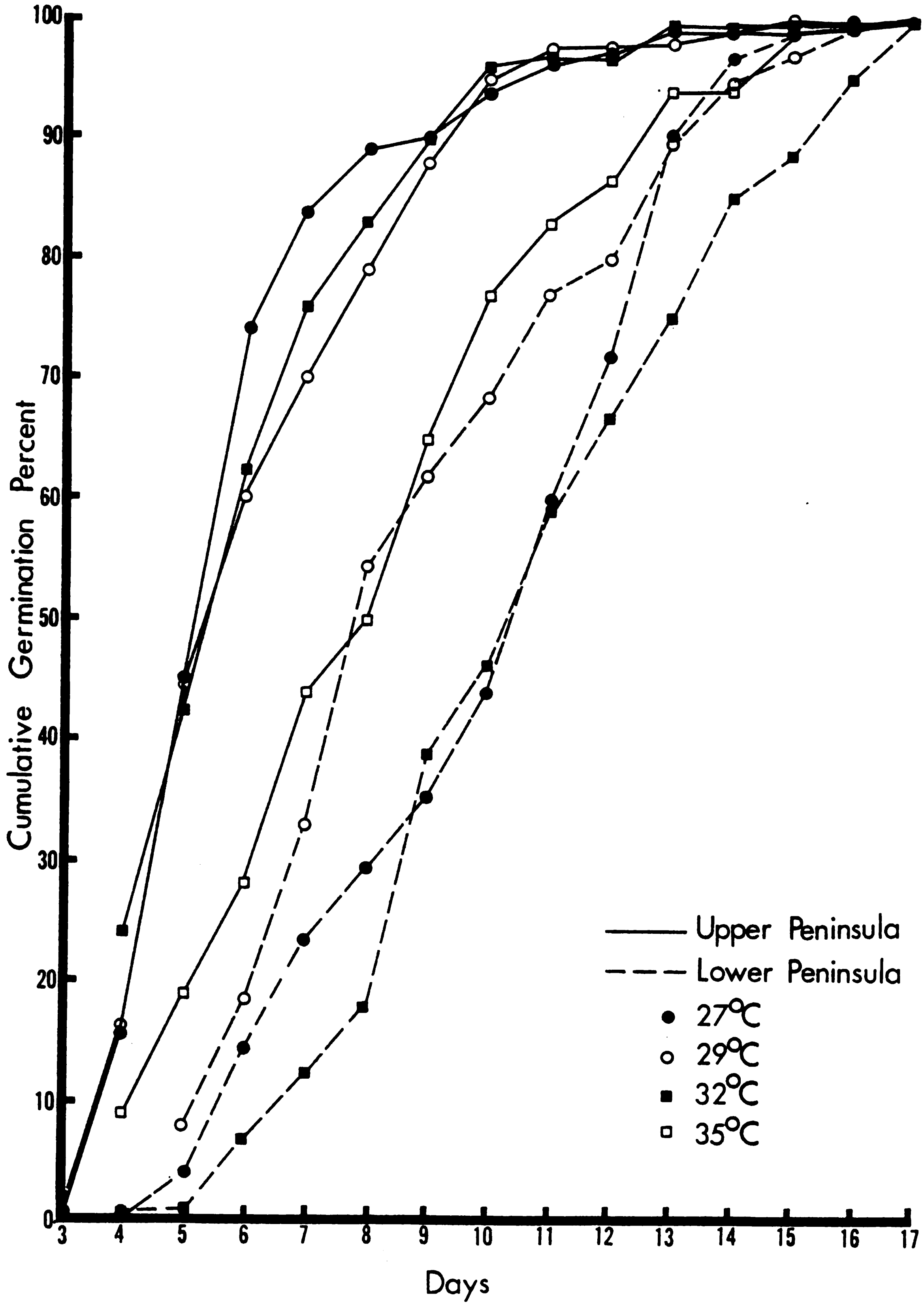
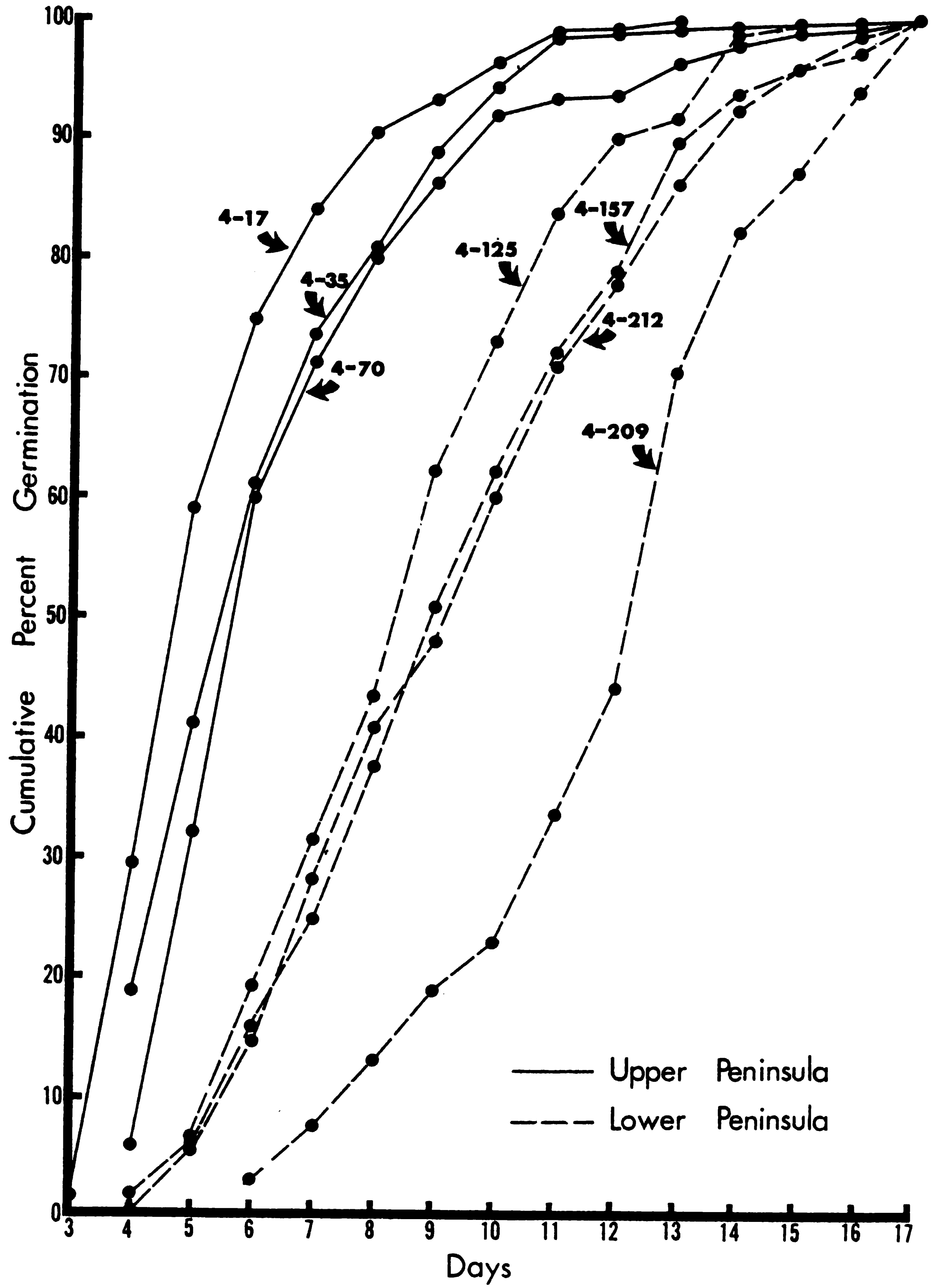

100
90
80
70
60
50
40
30
20
10
0
Cumulative Germination Percent
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Days
Upper Peninsula
Lower Peninsula
27°C
29°C
32°C
35°C

Figure 2-6. Cumulative percent germination of all seven individual seedlots of paper birch, averaged over all three temperatures of 27°, 29°, and 32°C.


Cumulative Percent Germination
100
90
80
70
60
50
40
30
20
10
0
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Days
4-17
4-35
4-70
4-125
4-157
4-212
4-209
Upper Peninsula
Lower Peninsula

other differed by over 42 percent (4-19 and 4-20), and others within 50 yards often differed by over 63 percent (4-8 and 4-10). Therefore single trees within a population have substantial differences in their germination capacities.

Substantial variation also exists between populations as evident in Table 2-7. Variations in germination capacity range from a high of 59.1 percent for population #2, located in Keweenaw county in the UP, to only 1.7 percent for population #16, located in Montmorency county in the LP. Poorest germination occurred primarily in the western and north-central areas of the LP. The average percent germination of the seven populations in this region was 4.8 percent. In the eastern portion of the LP the average percent germination for the five populations was much higher at 33.5 percent. Patterns in germination capacities in the UP are less conspicuous, except for an average germination capacity of 38.9 percent for all six populations bordering the southern shoreline of Lake Superior in the northern portion of the UP.

Table 2-7 also shows the germination capacities of the three groups of birch seed from Finland. The first group contains seed of B. verrucosa selected from a seed orchard. The average germination capacity was 41 percent, with much less variation within the group, ranging from 29.0 to 55.0 percent. As stated previously, paper birch populations from Michigan varied more than European white birch.

Table 2-7. Average percent germination, and the range of germination means, of 25 populations of Betula papyrifera seeds from Michigan, and three groups of Finnish sources of birch, after 42 days.

Species	Population No.	Origin	Number of families	Percent germ.	Range of means
				- - -percent - -	
Betula papyrifera		Michigan County			
Upper Peninsula:	1	Ontonagon	7	35.0	17-62
	2	Keweenaw	10	59.1	16-90
	3	Baraga	10	32.7	6-66
	4	Gogebic	7	8.7	3-13
	5	Iron	10	22.4	8-44
	6	Menominee	10	4.4	1-15
	7	Delta	10	45.4	4-78
	8	Marquette	10	22.4	2-72
	9	Alger	10	37.1	13-72
	10	Schoolcraft	11	13.6	1-58
	11	Chippewa(W)	9	47.0	14-73
	12	Chippewa(E)	10	28.3	3-53
	13	Mackinac	10	10.7	3-28
		UP mean		28.4	
Lower Peninsula:	14	Emmet	10	6.2	0-12
	15	Antrim	5	5.3	0-10
	16	Montmorency	10	1.7	0- 5
	17	Presque Is.	10	32.8	6-51
	18	Alcona	10	16.5	0-32
	19	Montcalm	4	9.2	3-17
	20	Lake-Mason	5	5.1	2- 8
	21	Manistee	8	2.6	1- 4
	22	Missaukee	10	3.4	0- 7
	23	Gladwin	9	28.7	1-61
	24	Arenac	9	37.7	18-66
	25	Sanilac	5	51.6	43-61
		LP mean		17.9	
	Overall mean:			24.1	
Finnish sources:					
	#1	Seed orchards	10	41.0	29-55
	#2	Intraspecific hybrids	5	1.2	0- 6
	#3	Interspecific hybrids	10	3.6	0-16

The second Finnish group consists of seed collected from their intraspecific provenance hybrids. Germination was very low, ranging from 0.0 to 6.0 percnet, with an average of only 1.2 percent (Table 2-7).

Group three consists of seed collected from their interspecific hybrids of various species of *Betula* with *B. verrucosa*. The average germination capacity was 3.6 percent, with a range of 0.0 to 16.0 percent. The hybrid of *B. papyrifera* x *B. verrucosa* the highest germination capacity of the group at 16.0 percent.

Thus, both the intra- and interspecific hybrids revealed low female fertility, except for the cross of *B. papyrifera* x *B. verrucosa*. The reciprocal cross of *B. verrucosa* x *B. papyrifera* was found to have surprisingly good female fertility, with 8.0 percent germination (Johnsson, 1945).

Wide variations in germinative energy between the populations of paper birch also was found (Table 2-8). Each value in the table represents the combined cumulative germination of all the seedlots in that population. Individual seedlots within a population varied in their germinative energies, but to a lesser extent than between populations. They were therefore bulked into their respective populations.

Marked differences in germinative energy between the UP and LP exists (Table 2-8). Thus, 63 percent of the birch seed from the UP germinated in 7 days, whereas birch seed from the LP showed 66 percent germination only after 13 days. In addition, germination began sooner and proceeded

Table 2-8. Cumulative percent germination over time for Betula papyrifera and three groups of Finnish birch seed.

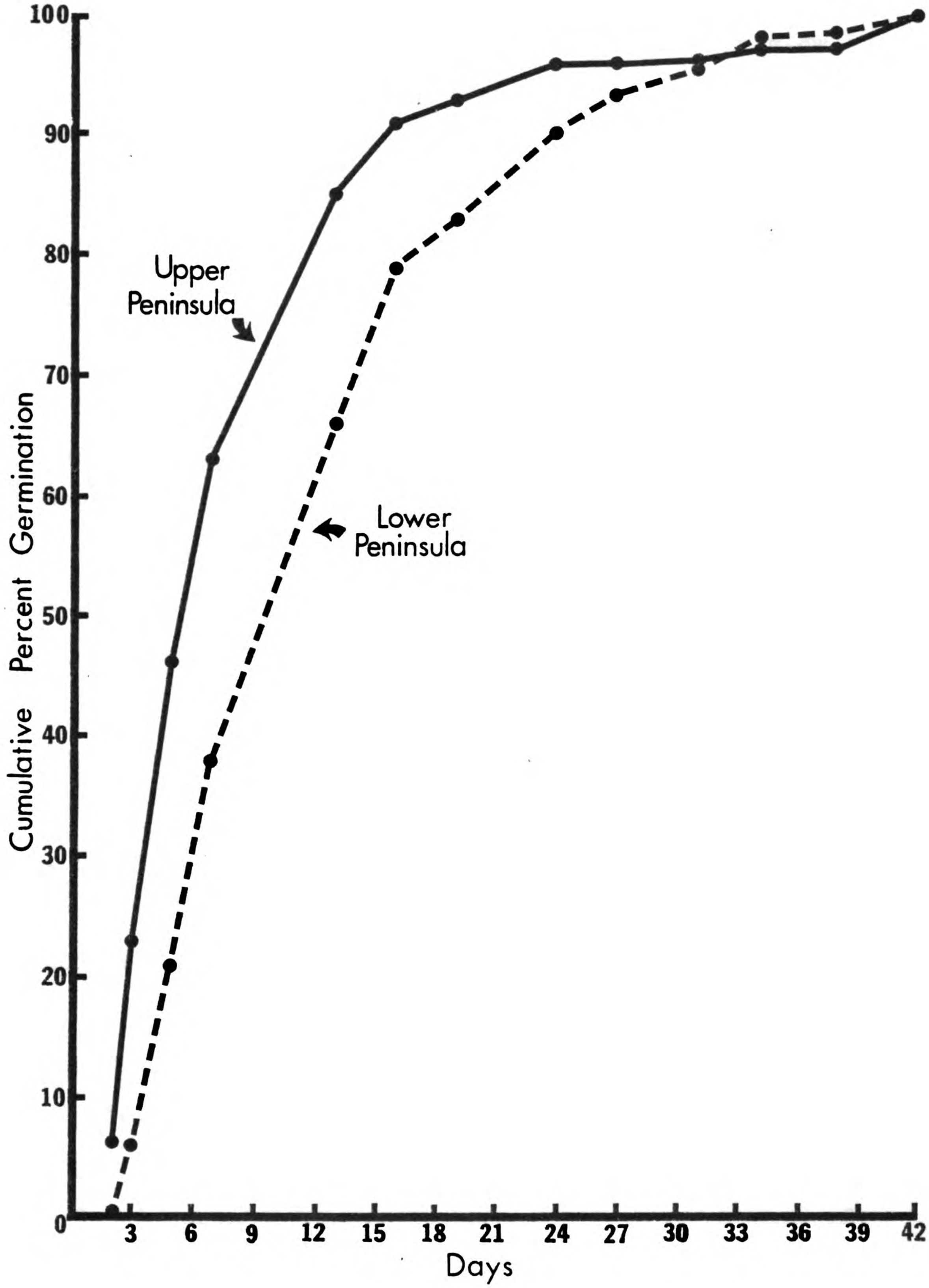
Population No.	Michigan County	Days from start of experiment					
		2	3	5	7	13	19
Betula papyrifera		- - - -	- - - -	- percent	- - - -	- - - -	- - - -
Upper Peninsula:							
1	Ontonagon	1	11	29	51	69	88
2	Keweenaw	18	43	72	87	97	99
3	Baraga	9	30	50	64	85	95
4	Gogebic	5	15	20	42	71	92
5	Iron	4	23	48	63	87	94
6	Menominee	0	6	14	26	66	94
7	Delta	8	29	52	67	84	94
8	Marquette	10	26	51	71	91	98
9	Alger	2	16	42	67	92	98
10	Schoolcraft	0	9	25	38	70	89
11	Chippewa(W)	1	9	33	41	73	78
12	Chippewa(E)	3	17	48	69	88	94
13	Mackinac	0	4	13	46	82	92
Lower Peninsula:							
14	Emmet	0	3	18	48	83	100
15	Antrim	0	0	45	68	77	81
16	Montmorency	7	27	27	55	89	100
17	Presque Isle	1	13	36	56	65	91
18	Alcona	0	6	32	51	73	90
19	Montcalm	0	10	20	29	49	71
20	Lake-Mason	0	0	0	11	56	75
21	Manistee	0	0	14	23	72	86
22	Missaukee	0	0	8	25	74	88
23	Gladwin	0	2	9	24	55	72
24	Arenac	0	1	13	25	55	75
25	Sanilac	0	11	25	42	65	89
UP combined		6.6	22.7	46.2	63.0	84.5	93.1
LP combined		0.4	6.1	21.0	38.4	66.0	83.1
Finnish sources:							
#1	Seed Orchards	51	72	88	97	100	100
#2	Intraspecific hybrids	0	41	41	82	100	100
#3	Interspecific hybrids	19	63	93	96	100	100

more rapidly in the UP, with 6.6 percent of the seeds germinating in the first two days, while only 0.4 percent of the seeds from the LP germinated in the same period of time. Figure 2-7 shows graphically the combined UP and LP cumulative percent germination over the 42 day period.

Variations between the 25 individual populations are evident in Table 2-8. Population #2 from Keweenaw county in the UP, gave the highest rate of germination, with 72 percent of the seed germinating in just 5 days. The slowest rate of germination was for population #20, from Lake county in the LP, showing no germination in 5 days and only 11 percent after 7 days.

Several patterns of variation are apparent from Table 2-8. The 25 paper birch populations are arranged in decreasing latitude and proceed from the western UP to eastern UP, through the northern and central LP (Figure 2-1). It is evident that the western UP populations (#1-5,7,8) as a group all began germinating very early and proceeded at a much faster rate than the other populations as a group. The eastern UP and northern-most LP populations (#9-18) as a group show intermediate results. Generally, they began germinating early but at a lesser rate than the first group, and are intermediate in germinative energy, averaging 12 percent germination in 3 days, whereas the western UP group averaged 30 percent germination after 3 days. Within this intermediate group, all ten populations show wide variations.

Figure 2-7. Cumulative percent germination of UP and LP combined populations over a 42 day period.



Upper Peninsula
Lower Peninsula
Cumulative Percent Germination
Days
0
10
20
30
40
50
60
70
80
90
100
3
6
9
12
15
18
21
24
27
30
33
36
39
42

The third discernible group is the south-central LP populations (#19-25). This group shows extremely slow early germination and a much lower germinative energy, with only 4 percent germination in 3 days. At 7 days, only 29 of the seeds had germinated in this group, whereas group one and two already completed 70 and 54 percent of their total germination, respectively. The third group, and especially the southern-most populations (#19,20,23-25) have their germination extended over a very long period of time, reaching 77 percent of their total germination after 19 days.

Also included in Table 2-8 is the cumulative germination percents of the Finnish seed and hybrids. The single trees that comprise the seed orchard group initiated germination very early, and proceeded at a very fast rate. Twenty-four hours after the beginning of the experiment, 2 percent of the seeds already germinated. By the second day, 51 percent of the seeds had germinated, showing the maximum germinative energy of both species of birch. It should be understood that European white birch seed is from selected parents and not comprised of wild populations as paper birch. Groups two and three had very few seed germinate, and the results are similar to some populations of paper birch.

One important difference between the two species of birch is that *B. verrucosa* had no germination past the 13th day, unlike *B. papyrifera*, which required at least 42 days in a number of seedlots.

Discussion

In addition to determining the optimum temperatures for the germination of paper birch seed, the present study also demonstrated significant differences in germination capacity and germinative energy in response to temperature and geographic origins.

The response of birch germination to temperature varies greatly among different seedlots. Generally, as temperature is increased germination capacity and energy is increased. Seedlots from the UP all showed a much wider optimum temperature range as well as increased germinative energy in comparison with seedlots from the LP.

The optimum temperature range for paper birch seed germination percentage and rate is between 27^{o}- $32^{o}C$.

Germination occurred from 10^{o} to $43^{o}C$ in the UP seed, revealing extreme plasticity, whereas the LP seedlots showed much reduced germination at 10^{o} and $35^{o}C$ with $43^{o}C$ being lethal. The UP seedlots had an extremely wide range of temperatures optimum for germination (21^{o}-$32^{o}C$), with no significant differences existing between 21^{o} to $32^{o}C$, whereas the LP seedlots had a much narrower range of optimum temperatures (27^{o}-$29^{o}C$).

These findings are contradictory to those reported by Govorukha and Manaev (1971) for _B_. _pubescens_ and _B_. _verrucosa_, in which seeds from more southern latitudes had a wider range of optimum temperatures, and northern origins required higher temperatures. The work reported by Fraser (1971) on white spruce provenances in Canada is in general agreement with these findings, with northern provenances germinating at lower temperatures.

There are several possible reasons for the wide range of germination temperatures in the UP seed. Natural shedding of seeds takes place from late fall to early spring. During the winter months, the seed remains in an environment unfavorable for germination. In the UP, seed dispersal coincides with the arrival of consistently cooler temperatures, whereas in the LP, dispersed seed is subjected to wide fluctuations in temperatures. Sources in the LP may have adapted to safeguard the species from germinating in the late-fall when temperatures may reach 10°C or greater for extended periods of time. These warm periods are often followed by cold periods severe enough to kill any newly emerged paper birch seedlings. It is possible therefore that ecotypes producing seeds that germinate with a wide range of temperatures allowing germination would tend to be eliminated to a greater extent in the southern LP than in the northern latitudes of the UP. Those seed produced in the UP would be subjected to less deviation in the fall temperatures, thereby allowing a wider range of germination temperatures.

A similar situation exists with regard to spring temperatures. The LP frequently experiences late winter thaws where temperatures reach 10°C for extended periods of time, followed by a return to freezing temperatures that would kill any newly emerged seed. This would be less likely to occur in the UP where the growing seasons are short and where frozen soils, protective during the winter, warm up slowly.

Another possibility may be a requirement of LP seedlots to accumulate a certain "heat sum" before triggering germination. Thus, at 10°C, the LP seedlots may require a large number of degree-hours, before reaching the triggering "heat sum" or the temperature may be too low to even begin accumulating degree-hours.

Phillips (1922) noted that fruit trees apparently required more heat before blooming in the South than in the North. Boyer (1972) found that longleaf pine from North Carolina required fewer degree-hours for peak pollen shedding, than those in southwestern Alabama.

Experiments I and II also revealed differences in the initiation phase of seed germination. At temperatures ranging from 10°-29°C, LP seedlots did not initiate germination until 48 hours after the UP seedlots had already begun germination. At temperatures of 32°C, germination was initiated on the same day for all seedlots from both peninsulas.

Rapidity of germination can have an important bearing upon seedling survival and establishment. Experiments I and II revealed significant differences in germinative energy due to seedlot origin and temperature. Generally, as temperature was increased, germinative energy was increased.

High and consistent germinative energy for seedlots in the UP occurred from 27°-32°C. The optimum temperature for the LP seedlots ranged from 27°-32°C, with 29°C providing the highest germination rate (Figure 2-5). The two experiments revealed that, at all temperatures, UP seedlots began germination sooner, proceeded more rapidly, and reached optimum levels sooner than LP seedlots.

Experiment III was designed to elucidate the specific pattern of geographic variation found in the previous two experiments, but on a much larger scale. The results confirm the pattern of variation found in the previous two experiments. Variation exists within a population, between populations, and between upper and lower Michigan in both germination capacity and germinative energy.

Germination between all seedlots ranged from 0.0 to 90.3 percent. Within an individual population, encompassing about a hectare in size, differences ranged from 16 to 90 percent. Significant differences between population in germinative energy occurred, varying by a maximum of 54.7 percent. One population in Presque Isle county (#17), for example, averaged 32.8 percent germination while another population 40 miles away averaged only 1.7 percent.

Variability in germination capacity can be due to a number of factors. Seed viability depends greatly on local weather conditions during pollination, fertilization, and subsequent seed development. Quality of seed varies from year to year, and is usually good in years with a heavy seed crop, but poor when the seed crop is light (marquis, 1969). A study of germination capacity of paper birch seed in Maine through 1958-1960 revealed germination of 77 percent during a heavy seed year, versus germination of 13 and 24 percent during the two previously poorer seed years (Bjorkbom et al., 1965).

Results here indicate that size of the seed crop of the parent tree has little influence on germination capacity. Each parent tree was assigned a number relating to the size of the seed crop: 1=light, 2=medium, and 3=heavy. Correlation analysis was used on all 219 seedlots to determine if a relationship existed between the seed crop of the parent trees with percent germination of the seedlots. A non-significant correlation (r) of 0.06 was found. In many cases trees with a very light seed crop had very high germination capacities. Within a population, seed crops varied from light to very heavy. In some populations the ten or so single trees varied only between the ranges of light-medium, or medium-heavy. No single population had all single trees with the same seed crop rating. For the 25 populations, correlation between average seed crop and percent germination also were non-significant (r=0.03)

Germinative energy, or rate of germination, revealed wide variations, with several observable patterns. The combined UP populations reached 63 percent germination in 7 days, whereas the combined LP populations took nearly 13 days to reach the same level. The most distinctive difference is between the western UP and the south-central LP populations. When grouping populations in these larger areas, the western UP group revealed very high germinative energy, beginning germination very early and prodeeding at a much faster rate than the south-central LP populations. For example, 70 percent of the birch seed from the western UP germinated in 7 days, whereas birch seed from the south-central LP showed only 29 percent in the same time period. A large amount of variation also existed between the 25 individual populations of paper birch.

Bjorkbom (1971), studying paper birch seed germination in Maine, reported that germinative energy reached higher levels in the better seed years, with germination beginning sooner and proceeding more rapidly than in less productive seed years. Results reported here tend to disagree with the above findings, although this analysis was on seeds collected in a single seed year and on a population basis, each comprised of individual trees. Correlation analysis was performed on the 25 populations of paper birch to relate the average parental seed crop of the population to cumulative percent germination occurring after 5 days. No correlation was found (r=-0.09), indicating that germinative energy is not related to size of the paper birch parental seed crop.

Since germinative energy expresses how rapidly germination proceeds, it is better than germination capacity as a practical measure of the average viability and quality of a seed crop. For artificial regeneration, high germinative energy is an important requirement. The practical advantage to a greenhouse and nursery manager is the ability of the seedlings to get off to a prompt and even start, producing uniform growing stock responsive to favorable growing conditions.

Ecologically, rapidity of germination has an important bearing upon early seedling survival and subsequent establishment. The more rapid rate of germination for the UP seedlots may have a considerable survival value for these northern seedlots, i.e., their high rate of germination allows the fragile seedlings to quickly take advantage of warm growing days in the spring and therefore make better use of the shorter growing season. In addition, seedlings will have a maximum length of time to become established before subjected to summer drought and high temperatures.

During this investigation of the germination behavior of paper birch seed, a few seed showed abnormal germination. In studying 10,000 yellow birch seed, Maini and Wang (1967) reported the occurrence of "twin seedlings" at a frequency of 0.12 percent, and in a few other seedlings the cotyledons emerged from the pericarp before the radicle. Of the approximately 34,000 seeds handled in these experiments, the emergence of "twin seedlings" was encountered in four seeds, giving a frequency of 0.012 percent. About 10-15 seeds showed reversed germination or early cotyledon emergence.

Summary and Conclusions

This study appears to have revealed some important variation patterns in the germination of paper birch seeds. Temperature and geographic origin each had a significant effect on germination capacity and germinative energy. Seedlots from the UP of Michigan showed a much wider range of temperatures optimum for germination, as well as increased germinative energy, in comparison with LP seedlots of Michigan. Distinct differences were also observed in the initiation of seed germination, with the UP seedlots beginning first. Germination capacity and germinative energy were not correlated with the size of the parental seed crop.

Genetic variation exists both between and within populations of paper birch in germination capacity and germinative energy. Populations in the western UP were characterized by germination beginning much sooner, proceeding more rapidly, and reaching optimum levels earlier than populations located in the south-central LP.

If these observations made in a controlled environment are indicative of the actual responses occurring in natural environments, UP and LP seedlots each have adapted to their local environments, providing continual renewal of the species.

European white birch initiates seed germination very early, and proceeds at a much faster rate than the paper birch seedlots. In addition, European white birch ended germination after 13 days, whereas paper birch extended germination for a period of 42 days.

CHAPTER III

GEOGRAPHIC VARIATION IN THE GROWTH RATES OF SEEDLINGS

Introduction

Variation within a species creates opportunities for locating superior types. Without variation there would be nothing to improve upon. Species with a very large natural range, such as paper birch, contain considerable genetic variation and diversity. Variation is the result of the interaction of two forces: first and most important is the genetic make-up of the individuals, and secondly, the influence of the local environment. This variation may be either clinal, as shown by gradual transitions following environmental changes, or ecotypical and composed of fairly distinct subdivisions or ecotypes. To determine the presence and amount of geographic variation in any species, large numbers of seedlings from a range of geographic regions need to be tested under similar conditions and distributed throughout its range over a variety of climatic and edaphic conditions.

A prerequisite to the improvement of a particular species is the need to know how much genetic variation is present. While this information is known for many important commercial trees such as eastern white pine, jack pine, red pine, white spruce, Douglas-fir, etc., research on paper birch has been scanty.

Geographic origin studies on paper birch have been absent. The past geographic variation studies in birch has been limited mainly to Betula alleghaniensis, yellow birch.

Clausen (1968a) found that catkin and fruit characteristics of yellow birch vary in an apparently random manner over its natural range and differ among individual trees within the stands. Morphological variation in characters such as leaf size and shape, catkins, and seed is believed due to natural hybridization and introgression (Clausen, 1962; Dugle, 1966; Dancik and Barnes, 1972).

In some species of birch this variation is believed to be due in part to differences in the chromosome numbers. In paper birch, Brittain and Grant (1966, 1967) have shown that chromosome counts of 56, 70, and 84 with 56 and 70 most prevalent in eastern Canada, and 84 more common in northwest Canada.

In terms of growth characteristics, wide variations has been demonstrated for yellow birch. Clausen (1968b) reported that second-year nursery height growth of 55 seed sources of yellow birch, comprising approximately 10 trees per stand, varied greatly but essentially in a random manner. Height was not correlated with latitude, longitude, growing season, average January or July temperatures, or annual precipitation. In contrast to the random variation in height growth, the study demonstrated that yellow birch exhibits clinal variation in growth cessation.

Clausen and Garrett (1969) reported the one-year results from a 199 single tree progeny test to determine whether the large height variability observed in the 55 seed-source study might be due to the fact that the seedlots used were a mixture from an average of 10 trees per stand. After the first growing season , seedling height was significantly different not only among the 21 sources but also among the trees within each source.

The results reported after 4 years showed that certain provenances were much more variable than others, and the amount of variation in a particular provenance frequently differed from year-to-year. Within-provenance variation in 4-year heights of yellow birch seedlings was often greater than differences among the 21 widely separated provenances. It was concluded that due to the large amount of individual tree variation present in yellow birch a selection program should focus on single tree selection (Clausen, 1972).

Because of the growing importance of paper birch as a timber producing tree and potential for artificial regeneration, information on geographic variation in growth rate, along with other desirable traits, is an improtant first step towards its improvement.

Due to the apparent ample geographic variation and the large amount of individual tree variation in yellow birch, the same possibilities may exist in paper birch. Therefore, this initial study was undertaken to investigate the genetic variation patterns present in this species.

Materials and Methods

The seed used for these studies originated from the state-wide collections of fruiting catkins during September of 1975. Details of the collection procedure and locations were described in Chapter II.

This study consisted of three separate experiments:
Experiment I included all 219 seedlots (single half-sib families) of *B. papyrifera* and 25 seedlots of Finnish birch.
Experiment II consists of 42 seedlots (populations) of paper birch distributed over its natural range.
Experiment III consisted of essentially a re-analysis, in part, of the previous two experiments. Included was a total of 74 seedlots, of which 48 were single families of paper birch from the Michigan state-wide test, 11 single families re-collected in September of 1976, 9 single families from the rangewide test, 4 seedlots of *B. verrucosa*, and two miscellaneous species of birch.

Experiment I

This initial experiment on variations in juvenile height growth of the seedling progeny contained all 219 single families, representing 25 distinct populations, collected in Michigan in Fall of 1975. Exact location of the 25 populations are shown in Figure 3-1. In addition

Figure 3-1. Location and population numbers of the 25 paper birch populations used in <u>Experiment I</u>.

25 seedlots of birch seed from Finland, consisting of three groups, as discussed in Chapter II, are included in the study.

On January 6, 1976 all 219 seedlots of paper birch and the 25 seedlots of European white birch were sown in a greenhouse progeny test at Michigan State University's Tree Research Center. The seeds were sown in polycoated (Zeiset) paper plant bands 5cm x 5cm x 28cm deep, containing a soil mixture of peat-vermiculite (Redi-Earth, manfactured by Terra Lite). The paper plant bands were packed in milk cases, each containing 36 bands. The number of seeds sowed ranged from 3 to 150 depending on the percent germination of that seedlot. The seeds were not covered but were watered frequently during the germination phase.

Greenhouse temperatures during germination was increased to approximately 27°C to promote rapid and uniform germination.

Transplanting and thinning of the seedlings took place one month after sowing when the seedlings were 0.5-1.0cm in height. At this time they were thinned down to the three most vigorous seedlings. After two more weeks they were finally thinned to the most vigorous seedling in each band.

Fertilization began with Peters 20-20-20, two weeks after sowing, and was applied with a hozon injector (12:1) throughout the observation period. A fungicide (Benlate) was applied to control fungus. No damping-off was observed.

Continuous light was provided by high-output (HO), cool white, 8 foot fluorescent lights which were placed 7 feet above the cases. The lights provided approximately 120 ft-candles at the soil surface, and were operated during the night.

Temperatures in the greenhouse was maintained at approximately the 23-27^{o}C range, both day and night throughout the 4-month growth period.

The experimental design consists of a randomized complete block with 5 replications. Each replicate contained one row of six seedlings per seedlot, for 234 seedlots. Each replication contained 39 cases, of which each case contained 6 randomly chosen seedlots, with each seedlot being represented by a single row of six seedlings, giving a total of 36 trees per case.

In May 1976, 4 months after sowing, the containerized seedlings were measured and moved outside to the nursery to condition them for field planting.

Analysis of variance was made on growth rate of the seedlings at age 4-months, prior to their removal from the greenhouse. The LSD test was employed to determine the significance of height differences between seedlots, populations, and peninsulas. The tallest three trees per plot were measured and seedlot means were used as items.

Experiment II

The objectives of this experiment on the variations in juvenile height growth of paper birch seedlings is identical to the previous experiment. The only major difference is the materials used are not part of the state-wide collection made in 1975, but instead include seed from over the entire range of paper birch.

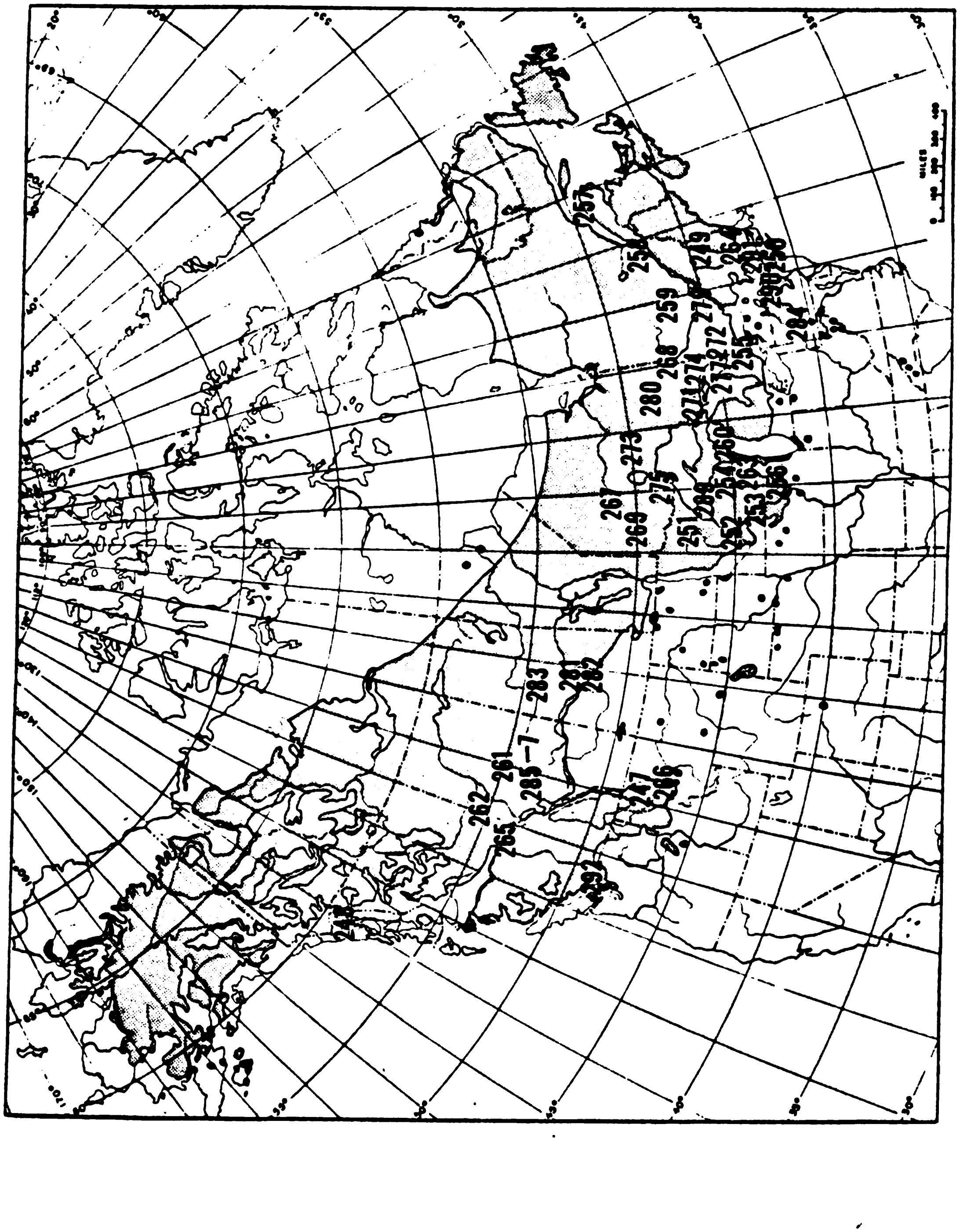
In the Fall of 1975, David S. Canavera, Assistant Professor, University of Maine, initiated a rangewide collection of various seed origins of paper birch through the cooperation of various private and governmental agencies. The seed used here is a portion of those seed sources.

Seeds from a given locality were collected from each of about ten average trees per stand. Catkins collected within a local area were separated into two groups. Some seedlots were identified by ten single tree seedlots and others were bulked into one seedlot comprising ten individual trees. Seedlots used in this study are comprised of the latter, a bulking of about ten trees per stand. Seedlots were accompanied by data on latitude, longitude, elevation, and collection date.

Exact locations of the 42 seedlots used in this study are shown in Figure 3-2. The origins and pertinent climatic data are presented in Table 3-5.

On March 24, 1976 the 42 seedlots (populations) from throughout the range of paper birch were sown in a greenhouse at M.S.U.'s Tree Research Center. Details of the method of sowing, handling, and growing conditions, are identical to those described in this Chapter under Experiment I.

Figure 3-2. Location and population numbers of the 42 paper birch populations used in _Experiment II_.



The range of paper birch.

Experimental design consists of a randomized complete block with 6 replications.

In August 1976, 5-months after sowing, the containerized seedlings were measured and moved outside to the nursery to condition them for field planting.

Analysis of variance was made on growth rates of the seedlings at age 5-months, prior to removal from the greenhouse. Measurements were made on the tallest three trees in each 6-tree plot. LSD was used to determine the significance of height differences between the seedlots. Seedlots means were used as items. Simple correlations, using seedlot means as items, were calculated between latitude, longitude, and length of the growing season at place of seed origin, and juvenile height growth of 5-month old seedlings.

Experiment III

This final study was designed to measure variation in the juvenile height growth rates of seedlings. The major difference is that this is essentially a re-analysis, in part, of the two previous experiments. The objective is to compare the results observed in the previous two experiments.

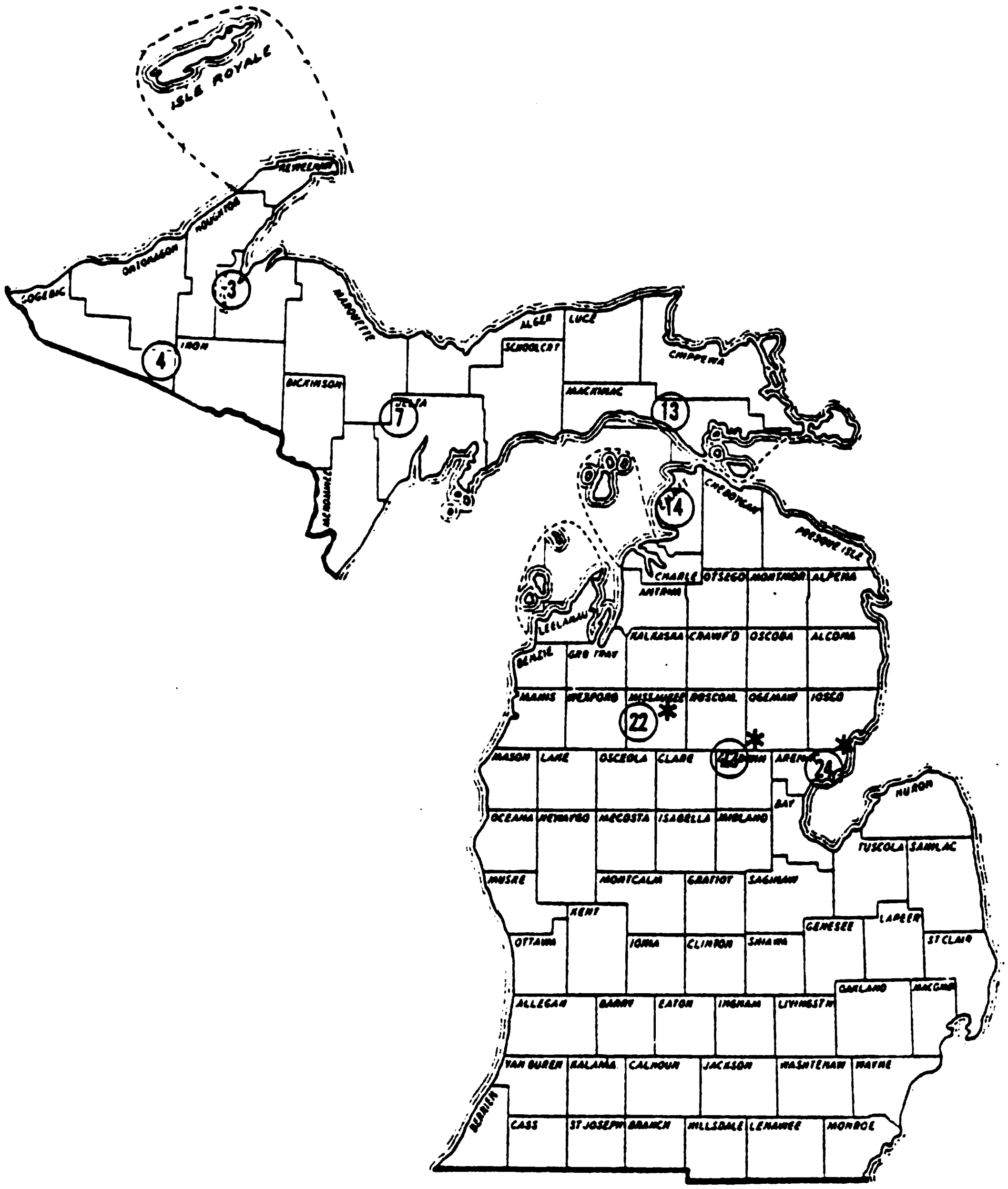
Materials used in this study are a part of those previously used, but not all the seedlots were used for both. This progeny test contained a total of 74 seedlots of which 48 were single tree families, contained in 8

Michigan populations, collected in 1975. In addition, 11 single families originally collected in 1975 were re-collected in 1976. This means that 11 seedlots out of the 48 original seedlots have both 1975 and 1976 seed represented. Also included are 9 single tree families from the range-wide test collected from three geographic areas; 4 seedlots of Finnish origin; and two miscellaneous species of birch. The exact location of the 8 Michigan populations are represented in Figure 3-3.

The seedlots for this experiment were selected to cover a wide range of climatic conditions and were based upon previous results of the juvenile height growth data. Two populations were selected in each climatic area of Michigan; the western UP, eastern UP, northern LP, and southern LP. Within each area, the fastest and slowest populations were selected on the basis of the results of Experiment I. Within each population, the three fastest and the three slowest individual families were selected. Therefore, there were 8 populations, 6 families per population, and a total of 48 seedlots. The 11 re-collected families are from three LP populations, located in three counties: Missaukee, Gladwin, and Arenac.

In Experiment II, seedlots included a bulked sample of ten average trees per stand. In this experiment, nine individual families were randomly chosen, three families from each of three widely separated areas: Montana, Quebec, and Alberta.

Figure 3-3. Location and population numbers of the 8 paper birch populations from Michigan used in <u>Experiment III</u>. Populations marked with a asterisk are represented by seed collected in 1975 and 1976.


ISLE ROYALE
KEWEENAW
HOUGHTON
ONTONAGON
GOGEBIC
IRON
MARQUETTE
DICKINSON
ALGER
LUCE
SCHOOLCRT
CHIPPEWA
MACKINAC
CHEBOYGAN
PRESQUE ISLE
LEELANAU
BENZIE
CHARLE
ANTRIM
OTSEGO
MONTMOR
ALPENA
KALKASAA
CRAWF'D
OSCODA
ALCONA
GRD TRAV
MANIS
WEXFORD
ROSCOM
OGEMAW
IOSCO
MASON
LAKE
OSCEOLA
CLARE
ARENAC
BAY
HURON
OCEANA
NEWAYGO
MECOSTA
ISABELLA
MIDLAND
TUSCOLA
SANILAC
MUSKE
MONTCALM
GRATIOT
SAGINAW
KENT
GENESEE
LAPEER
OTTAWA
IONIA
CLINTON
SHIAWA
ST CLAIR
OAKLAND
MACOMB
ALLEGAN
BARRY
EATON
INGHAM
LIVINGST'N
VAN BUREN
KALAMA
CALHOUN
JACKSON
WASHTENAW
WAYNE
BERRIEN
CASS
ST JOSEPH
BRANCH
HILLSDALE
LENAWEE
MONROE
3
4
7
13
14
22
24
*

The four seedlots of Finnish origin represented wide areas of Finland. Three are B. verrucosa individual tree families selected from a seed orchard, and the other is a B. verrucosa interspecific hybrid.

On October 20, 1976 all 74 seedlots were sown in a greenhouse progeny test at M.S.U.'s Tree Research Center. The seeds were sown in polycoated (Zeiset) paper plant bands 7.5cm x 7.5cm x 28cm deep, containing a soil mixture of peat, perlite, and vermiculite (1:1:1). The plant bands were packed in milk cases, each containing 16 bands. Seed was sown in proportion to the germination percentage of the seedlot.

Fertilization with Peters 20-19-18 (Peat-lite special) began two weeks after sowing and was applied with a hozon injector (12:1) throughout the observation period. Benlate was applied periodically to inhibit fungus growth.

Supplimental light were used as described in Experiment I.

The experimental design consisted of randomized complete blocks with four replications. Each replication contained one row of four seedlings per seedlot (family), randomly distributed, for all 74 seedlots.

On March 1, 1977, 4-months after sowing, the final of the four periodic measurements were made. Three weeks later, the containerized seedlings were cut-off 3-4" from the root collar. Re-sprouting ability was periodically observed.

Analysis of variance was made on growth rates of the seedlings at ages 2½, 3, 3½, and 4-months. LSD was used to determine the significance of height differences between families, populations, families within-populations, and between peninsulas. Seedlot means were used as items. Simple correlations, using family and population means as items, were calculated between 4-month juvenile height growth and latitude, longitude, length of the growing season, 2½- and 3-month height growth.

Results and Discussion

Under the conditions of greenhouse culture and 24-hours continuous light (long-days), variation in seedling height growth and leaf morphology were observed. It should be noted that these results are observed on seedlings subjected to an unnatural artificial environment of continuous light, and controlled temperatures. Early evaluations of the results reported here should be correlated with the performance of similar materials grown under natural field conditions. Juvenile-mature correlations of future height growth of these seedlings, established in future plantations, will give an indication of the reliability and usefulness of such early observations in a genetic improvement program.

Experiment I

Due to cultural difficulties encountered during the initial growth period of the seedlings, statistical analysis was impossible. These cultural problems originated from both the variability of the soil mix and watering. A definite "case effect" was observed, with some cases showing very slow growth common to all six seedlots in that case. The reasons are thought to be due to uneven packing of the soil mix (Redi-Earth) and overwatering. If a case had been packed too tightly, the soil water-holding capacity was greatly increased and waterlogging occurred. Results observed indicate that this phenomenon occurs as a result of the physical nature of the soil mix itself. Due to the initial dry form and the 28cm depth of the soil column, wetting was difficult, and once wet, drying was impossible and waterlogging occurred.

The present study was undertaken to determine how much of the variation in juvenile growth rates can be ascribed to differences both within- and between-populations of paper birch.

Results obtained under these growing conditions reveal that within a population (stand) of paper birch, large variation exists in juvenile height growth (Table 3-1). Certain populations were much more variable in height growth than others, but the within-population (family) variation was greater than differences among populations.

The average 4-month height of the study was 59.2cm, with a range between the two extreme populations of just 19 percent. Only one individual population, in Antrim county population (#15), with a range of 10 percent of its mean, had less within-population (family) variation than

Table 3-1. Four-month relative heights of 25 paper birch seed sources expressed as percent of the overall mean (Experiment I).

Michigan Peninsula	Population No.	Michigan County	Number of families	4-month relative heights	Range of family means 1/
				- - - - percent	- - - -
Upper:	1	Ontonagon	7	96	84-114
	2	Keweenaw	10	105	79-119
	3	Baraga	10	108	80-116
	4	Gogebic	7	98	83-119
	5	Iron	10	108	84-120
	6	Menominee	10	100	88-108
	7	Delta	10	108	92-117
	8	Marquette	10	96	88-123
	9	Alger	10	98	86-116
	10	Schoolcraft	11	101	92-112
	11	Chippewa(W)	9	95	86-121
	12	Chippewa(E)	10	100	90-115
	13	Mackinac	10	98	84-109
Lower:	14	Emmet	10	95	84-116
	15	Antrim	5	93	95-105
	16	Montmorency	10	98	83-116
	17	Presque Is.	10	96	82-114
	18	Alcona	10	101	88-113
	19	Montcalm	4	96	86-114
	20	Lake-Mason	5	105	84-113
	21	Manistee	8	91	87-128
	22	Missaukee	10	106	86-108
	23	Gladwin	9	103	84-113
	24	Arenac	9	100	85-115
	25	Sanilac	5	98	81-116
			219		
	Overall mean:			59.2cm	
Upper Peninsula, combined				101	
Lower Peninsula, combined				98	

1/ Expressed as percent of population means.

the overall difference among the populations of 19 percent. All other populations had a greater amount of within-population variation, with the maximum of 41 percent of the mean for the population in Manistee county (#21) in northwest lower Michigan (Table 3-1).

Maximum individual family variation in height growth ranged from a high of 77cm (130% of the overall mean) for family (35) located in Iron county, to 47cm (79% of the overall mean) for family (129) located in Emmet county in the LP. Thus, the Iron county family grew 61 percent as much as the Emmet county family, which was poorest.

Population differences after combining the families within each population are small. Two populations, Baraga and Manistee, separated by a range gap of about four miles between the two peninsulas of Michigan, and a distance of over 300 miles, differed only by 19 percent. Other populations with the same distribution had nearly identical 4-month heights.

When family means for the UP and LP of Michigan were combined, the differences between the two peninsulas was only 1.6cm (Table 3-1).

Family evaluation after only 4-months would be highly speculative. However, 4-month results indicate family differences in juvenile height growth are substantial. Sixty-six families that were present in all 5 replications were averaged to locate the six best and six poorest families (Table 3-2). Averaged across all 5 replicates,

Table 3-2. Four-month height of the six best and six poorest families of all 66 families represented in all five replicates.

Six families	Seedlot No.	Michigan County	4-month heights	Mean
			------ cm	------
Best:	64	Delta	75	
	18	Baraga	74	
	34	Gogebic	69	
	42	Iron	69	
	62	Delta	68	
	98	Chippewa (W)	68	
				70.6
Poorest:	185	Manistee	47	
	31	Gogebic	48	
	78	Alger	50	
	65	Marquette	51	
	66	Marquette	51	
	184	Manistee	51	49.7
Mean of the six best families:			70.6	
Overall mean of all 66 families:			59.5	
Mean of the six poorest families:			49.7	
Percent improvement over the overall mean:				16.0%

the six best families averaged 70.6cm in total height after 4-months of accelerated growth. The six poorest families averaged 49.7cm in total height. An improvement of 16 percent is obtained when the six best families are compared to the overall mean of the 66 families.

Results also revealed wide variations in the juvenile growth rates of the 25 seedlots of European white birch included in the progeny test of paper birch. The 25 seedlots of birch seed, consisting of three separate groups, also showed wide variation in growth rates under these conditions.

Maximum individual seedlot variation in height growth ranged for 86cm (145% of the overall mean) for seedlot number 1459 located in southern Finland, to 44cm (74% of the overall mean) for seedlot number 1456 also located in southern Finland, a difference of 95 percent.

Taken as a group, the ten interspecific hybrids performed the best, averaging 110 percent of the mean. The B. papyrifera x B. verrucosa hybrid averaged 68cm in total height, 15 percent over the overall study mean of paper birch, and 9 percent over the mean for European white birch.

Due to the diversity of the cases in terms of moisture, a comparative analysis of the two birches is difficult. It was readily observed however, that when the European birch occurred in a optimum case, it outgrew the paper birch seedlings.

After only 4-months continuous growth, some individual progeny of both birches reached 115cm in height.

Experiment II

Seedlots included in this experiment consisted of seed collected from about ten individual trees per stand, bulked together to make a seedlot. The seedlots used in Experiment I, differ from those used here which are single tree families and not populations.

Cultural problems encountered in Experiment I were virtually eliminated, and statistical analysis was therefore possible.

Results obtained under these growing conditions revealed wide variation in juvenile height growth of the 42 populations of paper birch distributed over its natural range. The average 5-month height of the populations was 81.6cm, with a range between the two extreme populations, Minnesota (251) at 98cm (120% of the overall mean) and British Columbia (265) at 62cm (76% of the overall mean), of 36cm, or 58 percent taller than the poorest population (Table 3-3).

For comparison, Clausen (1969) reported for 55 seedsources of yellow birch, the best provenances was 117 percent taller than the poorest provenance after three years in the nursery, averaging 47.8cm.

Analysis of variance revealed that variations in the growth rates of seedlings of paper birch, grown under accelerated conditions, to be significant (Table 3-4).

Differences between populations were significant at the 5-percent level and highly significant differences

Table 3-3. Five-month relative height growth and origin data of 42 paper birch populations, expressed as percent of the overall mean.

Geographic Area	Pop. No.	State or Province	Degrees of- N. Lat.	Degrees of- W. Long.	Elev.	Growing Season 1/	No. of families 2/	5-month relative heights	Relative heights of geog. area
					-ft-	-days-		- - - percent - - -	
N.W. U.S. and Canada:	248	Alaska	59.2	135.4	250	122	4	82	
	265	Brit. Col.	53.7	120.8	2200	100	10	76	
	292	Brit. Col.	49.3	121.5	100	200	10	108	
	247	Montana	48.0	114.0	3150	149	10	99	
	266	Montana	47.7	113.8	3800	138	10	103	94
Western Plains:	261	Alberta	55.2	114.6	2200	90	10	99	
	262	Alberta	55.0	114.6	1750	85	10	98	
	285	Alberta	54.1	115.8	3350	90	2	98	
	286	Alberta	54.1	115.8	3350	90	5	104	
	287	Alberta	54.1	115.8	3350	90	7	103	100
Central Plains:	281	Saskatch.	52.0	105.0	1500	70	-	114	
	282	Saskatch.	52.0	105.0	1700	80	-	94	
	283	Saskatch.	53.5	106.0	1950	70	-	113	107
Northern Lake States	269	Ontario	49.5	93.0	1200	108	10	98	
	267	Ontario	49.9	92.3	1300	100	10	114	
	273	Ontario	49.8	86.7	1100	75	10	113	
	275	Ontario	48.3	89.2	620	95	10	115	110
Western Lake States	251	Minnesota	47.5	93.0	1450	111	10	120	
	252	Minnesota	44.9	93.6	945	139	10	115	
	253	Minnesota	44.0	91.5	1250	158	12	71	
	254	Wisconsin	45.5	89.5	-	127	10	107	
	256	Wisconsin	43.2	90.2	850	146	9	92	
	260	Wisconsin	44.8	88.5	-	126	10	93	
	263	Wisconsin	44.5	89.5	1100	130	7	118	
	289	Wisconsin	47.0	91.0	830	116	10	96	101
N.E. Lake States	271	Ontario	46.3	83.4	700	110	10	102	
	274	Ontario	46.7	80.6	-	100	10	113	
	280	Ontario	48.1	83.5	1400	80	10	78	
	268	Ontario	47.1	79.8	950	90	10	99	98
S.E. Lake States	277	Ontario	44.8	81.1	590	145	10	83	
	255	Ontario	44.3	80.0	700	140	12	91	
	272	Ontario	45.0	80.3	600	140	5	91	88
N.E. New England and Canada	279	Ontario	45.5	77.0	-	125	10	104	
	259	Quebec	46.9	76.1	1100	175	10	92	
	258	Quebec	47.0	71.5	700	175	7	96	
	257	Quebec	49.2	66.4	1200	150	6	102	
	249	Vermont	44.5	72.9	900	95	10	118	102
Eastern U.S.	264	Mass.	42.7	73.2	1760	144	10	107	
	291	Mass.	42.6	73.0	1980	156	10	107	
	250	Conn.	41.9	73.3	1300	131	6	98	
	284	Pennsyl.	40.8	78.0	1500	150	6	86	
	290	Pennsyl.	41.3	75.6	1600	160	3	91	98
Overall mean								81.6cm	
LSD (0.05) of a population mean								25.7 percent	

1/ Average number of days without a killing frost.
2/ Number of individual trees collected per population.

Table 3-4. Analysis of variance of juvenile height growth of 42 paper birch seedlots 5-months from seed.1/

Source of variation	d.f.	M.S.	F-value
Between blocks	5	643.03	1.86**
Between seedlots (Pops.)	41	559.18	1.62*
Between geographic areas	8	415.47	0.70
Between seedlots w/areas	33	594.10	1.72**
Error	205	345.38	-

1/ The analysis is based on plot means. Tallest three trees per plot.
* Significant at the 5-percent level.
** Significant at the 1-percent level.

existed between the geographic areas.

Correlation analyses showed that height growth of 5-month-old seedlings grown under accelerated conditions is not correlated with latitude or longitude, and appears to vary in a random manner (Table 3-5).

Table 3-5. Correlation between juvenile height growth of 42 paper birch seedlots and environmental variables of the seedlots.

Environmental variable	Height growth
	r value
Latitude	0.01
Longitude	-0.07
Length of growing season	-0.41*1/

* Significant at the 5-percent level.
1/ Based on 24 origins with reliable data on the length of the growing season. Includes all origins from Minnesota, Wisconsin, Quebec, Ontario, and Vermont.

Correlation analysis revealed a weak correlation of 5-month height with length of the growing season. Of interest is the fact that the correlation coefficient is negative, meaning that under conditions of continuous light those populations from areas with a shorter growing season tended to grow the fastest. The same negative trend was also apparent in Experiment I, with a non-significant r=-0.39.

A possible explanation for this effect could be due to the fact that under conditions of continuous light, populations in areas with a short growing season take full advantage of the season's length, and subsequently grow at a faster rate. Likewise, populations in areas with a longer growing season have evolved mechanisms to extend the growth phase through a longer period of time, and therefore, not be as responsive to continuous light.

The data not only revealed differences in juvenile height growth but also in leaf morphology, leaf number, branching, and stem pubescence.

Variation in stem pubescence ranged from densely pubescent to a sticky glandular exudate. All the seedlings from the Saskatchewan and Alberta provinces of Canada were absent of any stem pubescence and produced a glandular exudate, which appeared warty in nature. These warts appear as white flecks or scabs on the stems. Brittain and Grant (1975) reported similar observations on young paper birch seedlings collected from Prince Edward Island and the

Rocky Mountain area of Alberta.

In addition, all seedlings from the Sasketchewan and Alberta area produced a large number of leaves and a prolific branching habit. In terms of growth rate all the seedlings from these areas ranked equal to or above the overall mean (Table 3-3). Seedlings from these areas initiated growth earlier in the spring than any other seed-lots of paper birch when observed the following year.

It is possible due to its overlapping range with a small tree or shrub, _B. fontinalis_, that these trees are natural hybrids. Dugle (1966) reports these two species sometimes hybridize, which may account for the warty condition of the seedlings, common on the twigs of western red birch (_B. fontinalis_)

Wartiness also appeared in a more random manner on two widely separated populations. Population (258), located in Quebec exhibited the condition. In addition, population (249) from Vermont produced about one-half the seedlings pubescent and the other half glandular, revealing additional variation within a particular stand of ten trees.

Additional morphological variation was observed to be associated within individual populations. An Ontario population (280) exhibited an unusual pattern of leaf venation, shape, and serrations on all seedlings. Population (275), located on the north shore of Lake Superior in Ontario characteristically produced larger leaves than other populations of paper birch.

It is revelant to point out that the populations used are distributed over a wide geographic area. They are comprised of individuals from varying age groups, diverse sites, and a wide range of climatic conditions. No taxonomic attempt was made to measure and catagorize the morphological variability present. Instead, some of the more observable characters were mentioned. Obviously considerable morphological variability exists between different populations of paper birch, which in part reflects its wide geographic range, overlapping with many other species of birch, and the diverse ecological sites occupied by this species.

Chapter IV examines in more details the developmental and morphological variability observed in certain characters of seedlings.

Experiment III

Unlike the two previous experiments, this experiment is basically a re-analysis of the results observed in the previous two experiments on juvenile height growth of paper birch seedlings. Cultural problems encountered in the past experiments were eliminated entirely, and statistical analysis was possible.

Only relative comparisons will be given between this experiment and the previous two. Major differences included a different soil mixture, larger plant bands ($7.5cm^2$ x 28cm versus $5cm^2$ x 28cm), the experiment was initiated at a different time of the year, and there was very good control of watering and cultural conditions.

Results obtained under these growing conditions again revealed wide variation in juvenile height growth as reported in Experiment I.

Table 3-6 gives the relative growth rates of the paper birch and European white birch populations used in this study. The material consisted of 8 populations from Michigan, collected in 1975, with each population represented by six individual families. In addition, 3 populations re-collected in 1976 are included. Also three widely separated populations from the rangewide study, each containing three individual families. Seedlots of Finnish origin are included, represented by *B. verrucosa* seed orchard material (3 seedlots) and one interspecific hybrids. Two miscellaneous species of birch are included, thereby giving a total of 74 seedlots in the study.

Analysis of the results are presented in two ways: the first, analysis contains only the 48 single families collected in Michigan in 1975, and the second analysis included all 74 seedlots.

Analysis of the 48 individual families from Michigan at 4-months show that certain populations were much more variable in height growth than others, and within-population (family) variation was greater than differences among populations (Table 3-6).

Table 3-6. Species, origin, and 4-month relative height growth expressed as percent of the overall mean for 8 populations of paper birch collected in 1975, 3 populations re-collected in 1976, three range-wide populations, and two other species of birch (Experiment III).

Species	Population No.	Origin	Number of families	4-month relative heights	Range of family means 1/
				- - - percent - -	
Betula papyrifera					
1975 Collections:		Michigan County			
	3	Baraga	6	107b 2/	82-121
	4	Gogebic	6	95bc	80-111
	7	Delta	6	102b	87-121
	13	Mackinac	6	89c	78-100
	14	Emmet	6	98bc	87-109
	22	Missaukee	6	101bc	91-109
	23	Gladwin	6	92c	72-114
	24	Arenac	6	93c	78-107
1976 Re-collections:					
	22	Missaukee II	4	95bc	91- 98
	23	Gladwin II	3	97bc	92-105
	24	Arenac II	4	94bc	82-101
Range-wide collections:		State & Provinces			
	247	Montana	3	101bc	83-116
	259	Quebec	3	105b	103-109
	285	Alberta	3	106b	94-120
Betula verrucosa		Finland			
	Seed orchards		3	143a	143-145
	Species hybrids		1	134a	-
Betula spp.					
	Mongolian birch		1	94bc	-
	Van's Seed Orchard		1	101bc	-
			Overall mean	55.2cm	

1/ Expressed as percent of population means.

2/ Any two valuse with the same letter are not significantly different (P 0.05) by LSD.

The average 4-month height growth of the 48 families was 53.5cm. Individual families, not separately identified in Table 3-6, varied from a low of 40cm (72% of the overall mean) to a high of 67cm (121% of the overall mean). Thus, the Baraga county family (19) and the Delta county family (56) grew almost 68 percent as much as the Gladwin county family (197), which was poorest. Relationships found in <u>Experiment I</u> are similar to those found in this re-analysis study.

The differences between families were highly significant (Table 3-7).

Table 3-7. Analysis of variance of juvenile height growth of 48 paper birch families 4-months from seed.1/

Source of variation	d.f.	M.S.	F-value
Between blocks	3	313.60	5.55**
Between families	47	173.95	3.08**
Between populations	7	251.08	1.56
Families within populations	40	160.45	2.84**
Between peninsulas	1	84.00	0.48
Error	141	56.48	-

1/ The analysis is based on plot means, measurements made on four trees per plot.
** Significant at the 1-percent level.

Differences between populations (counties) after combining the six individual family means into a population mean were small, and statistically non-significant (Table 3-7). Thus, the Baraga county population in the UP, at only

107 percent of the mean grew only 20 percent as much as the Mackinac county population at 89 percent of the overall mean. Again the relationships found here support the results found in Experiment I, in that the variation between two populations is small compared to the variation between families.

When family means for the upper and lower Peninsulas of Michigan were combined, the difference between them was only 2.4cm or 4.6 percent.

Of interest is the amount of genetic variation that exists within a population. No population had less within-population (family) variation than the maximum difference (20%) of the two extreme populations of Baraga and Mackinac counties. Thus, all populations had a greater amount of within-population variation, up to 58 percent for population number 23 in Gladwin county (Table 3-6). The Baraga county population has a 49 percent height difference between the six individual families. In addition, families 26 and 27 differed by 40 percent, with the parent trees in that stand within 50 yards of each other.

Analysis of variance shows that families within populations are highly significant and thus accounts for 87.3 percent of the total amount of genetic variation, whereas, differences between populations and peninsulas are non-significant (Table 3-7).

The results observed for all 74 seedlots are also presented in Table 3-6. The average 4-month height growth of the 74 seedlots was 55.2cm. Analysis of variance revealed highly significant differences between seedlots, between populations, and between seedlots within the populations (Table 3-8).

Table 3-8. Analysis of variance of juvenile height growth of 74 seedlots of birch 4-months from seed. 1/

Source of variation	d.f.	M.S.	F-value
Between blocks	3	276.88	4.36**
Between seedlots	73	260.89	4.12**
Between populations	17	652.48	4.59**
Seedlots within populations	56	142.01	2.24**
Error	219	63.37	-

1/ The analysis is based on plot means, measurments made on four trees per plot.
** Significant at the 1-percent level.

Seedlots within a population accounted for 41.4 percent of the total genetic variation and populations accounted for 58.6 percent. This is due primarily to the fact that this analysis included all 74 seedlots, including the Finnish sources, which grew significantly faster than all the paper birch seedlots. When only the 48 single families from Michigan are analyzed separately, populations account for only 12.7 percent of the total genetic variation.

Table 3-6 reveals the large height superiority of the Finnish sources of birch. The three _B. verrucosa_ seedlots averaged 79.0cm or 143 percent of the overall mean of the study. Thus, under supplemental light, all three

Finnish seedlots grew almost twice as much as the source from Gladwin county (197), indicating that B. verrucosa may be more responsive to supplemental light than B. papyrifera. Krizek (1972) reported that B. papyrifera may be more responsive to light than B. verrucosa, opposite the tendency found in this study. It is entirely possible though that the seedlots of European white birch, obtained from a seed orchard, have been selected for growth rate.

The other two species of birch, Mongolian birch and Van's Pines seed orchard stock remained near the overall mean.

Included in this analysis are the three widely scattered paper birch population, of which three individual seedlots (families) were grown. These populations also revealed wide variations within the populations, with the Alberta seedlots 1133 and 1136 differing by 27 percent. The Quebec population on the other hand had a maximum family difference of only 5 percent, and could be due to the use of only three seedlots per population (Table 3-6).

In order to test the amount of variation in half-sib progenies from year-to-year, eleven families originally collected in 1975 were re-collected again in the fall of 1976. Variations in juvenile growth between the two successive years is essentially random. Overall mean height within these populations ranged up to 19 percent between families 207A and 208A in Arenac county.

Between the two successive years, four 1975 families increased in height, one remained unchanged, and six decreased in height. The largest difference between the two years was for the Gladwin county families (202 and 202A), which grew an average of 9.0cm (17 percent) faster in 1975 than the 1976 re-collection, but this difference was not statistically significant. Correlation analysis of the 4-month seedling height with the 1975 and 1976 collections resulted in a non-significant correlation coefficient (r) of 0.41.

Correlation analyses of all paper birch families revealed that height growth under the conditions of continuous light and controlled temperatures is apparently not correlated with latitude, longitude, and length of the growing season (Table 3-9).

Table 3-9. Correlation analysis between juvenile height growth of paper birch progeny and environmental variables at the seed origin.

Environmental variable	Height growth	
	r 1/	r 2/
Latitude	0.44	0.60*
Longitude	0.59	0.37
Length of growing season	-0.04	-0.05

1/ Based on 8 populations, including 48 Michigan families.
2/ Based on 14 populations, including all 68 paper birch families.
* Significant at the 5-percent level.

Weak correlation of height with latitude exists when the three populations of Montana, Alberta, and Quebec are added to the analysis. The unusual aspect of this is that the correlation coefficient is positive, meaning that as latitude is increased from south to north, height is increased. This is opposite of most geographical variation patterns found in many species, including yellow birch (Clausen, 1968b), and may be due to the effect of continuous light.

Age-age correlations were performed to determine how early genetic superiority was established. Measurements were taken at ages of 2½-, 3-, 3½-, and 4-months from seed averaging 7.2, 20.2, 39.5, and 55.2cm in height, respectively. As early as 2½-months from seed at an average height of only 7.2cm, a highly significant correlation coefficient (r) of 0.84 was obtained. At 3-months of age r=0.88.

Under the conditions of continuous optimum growth, remarkable growth rates are obtained. After 5-months from seed some individual seedling progeny of paper birch and European white birch, growing continuously, attained over 150cm heights.

Although some of the variation between families seem to be due to differences in growth rates, these differences do not follow any consistent geographical pattern. Whether the pattern of variation, if any, in height growth in paper birch is actually random should become clearer with long-term observations and future plantation measurements.

Summary and Conclusions

The individual parent-progeny data obtained in this study allows an assessment of the amount of genetic variation that exists between- and within-populations of paper birch. This information is valuable because it gives the tree breeder an idea as how to implement a selection program to improve paper birch.

The results of this study have shown that within-population variation in height of 4- and 5-month-old seedlings of paper birch is greater than differences among widely separated populations. Some populations exhibited more family variation than others.

Height differences between Michigan populations accounted for approximately 13 percent of the total genetic variation, whereas within-population (family) variation accounted for 87 percent. Thus, the maximum variation in height growth between any two populations is small (20%) compared to the maximum variation observed between two families (68%).

Comparative analysis between paper birch and European white birch revealed the height superiority of the Finnish sources of birch. In the re-analysis section, the four sources, randomly chosen, averaged 143 percent of the overall mean, growing significantly faster than any families of paper birch, and growing twice as much as the poorest Michigan family (197). Continued observations of European white birch in our established plantations may result in recommendations for its use for reforestation purposes in Michigan.

Considerable morphological variability in leaf size, shape, number, and stem pubescence was observed both between- and within-populations of paper birch, which in part reflects its wide geographic range overlapping with many other species of birch. No attempt was made to measure the variation here, but the following chapter will study the characters in more detail.

This study provides no evidence of clinal variation in height growth of paper birch. Under greenhouse conditions, no height superiority is established for sources of southern origin, in contrast to the general pattern for many conifer and hardwood tree species of North America (Wright, 1976).

Certain seedlots grew much better than others, but the variation appears to be essentially random, with much local variation. Although the variation between seedlots seems to be due mainly to differences in growth rates, these differences seem to follow no geographic pattern.

Correlation analyses showed that height growth of 4- to 5-month-old seedlings grown under greenhouse conditions apparently are not correlated with latitude, longitude, or length of the growing season. Whether any pattern of variation in height growth is actually random should become clearer after long-term observations in test plantations.

From a practical standpoint, maximum genetic improvement for height growth would be most efficient by practicing family selection. Results from the between- and within-population analysis show there are large amounts of variation in height within populations to make individual tree selection worthwile, and demonstrates the importance of progeny testing all paper birches to be used in an improvement program. Thus, much potential growth may be lost if a slow-growing seed source is used for reforestation purposes.

CHAPTER IV

DEVELOPMENTAL AND MORPHOLOGICAL CHARACTERS OF SEEDLINGS

Introduction

During the study of genetic variation in growth rates of seedlings of paper birch (*Betula papyrifera*) reported in the previous chapter, a wide range of morphological variability was observed in the seedlings. Since variation in a species is a key prerequisite to its improvement, we must know how much genetic variation is present, and whether or not this variation fits any geographic pattern.

As reviewed earlier, several variation studies have been done in yellow birch (*Betula alleghaniensis*). Morphological variation has been studied in characters such as leaf size and shape, catkin, and fruit characters (Clausen, 1968a; Dugle, 1966; Dancik and Barnes, 1972). Some morphological studies have been done on paper birch by Brittain and Grant (1966, 1967) reporting their observations of Canadian white-barked species of birch.

In their work they examined ten morphological characters of leaves, catkins, bracts, seed, and guard cell length. Their major objective was to define a "typical" white birch.

In the past, Fernald (1945) recognized a number of varieties. In trying to classify these variants they found they did not invariably correspond to the definition of any named variety. Thus, Brittain and Grant established an arboretum, where a comparison of juvenile characters, growth, and development could be carried out.

Results of Brittain and Grant's work indicate that considerable variability exist in paper birch due to its wide geographical distribution and occupancy of so many diverse sites. Geographical variants were noted but these were not sufficiently distinct to warrant taxonomic delineation. A number of hybrids were detected between *B. papyrifera* x *B. populifolia*, x *B. cordifolia*, and x *B. fontinalis*.

The purpose of this study is to elucidate the patterns of variation in leaf morphology and developmental characters between individual populations of paper birch and seedlots of European white birch. The reson for seeking knowledge of the patterns and underlying causes of this variation, is to relate morphological and developmental characters of the seedlings to the geographic location of the seed source. Thus, some of these differences may reflect a physiological adaptation to a specific geographical area or location.

Materials and Methods

Materials used for this morphological and developmental study were randomly selected from the previous collections of paper birch and European white birch, and were described in the previous chapters.

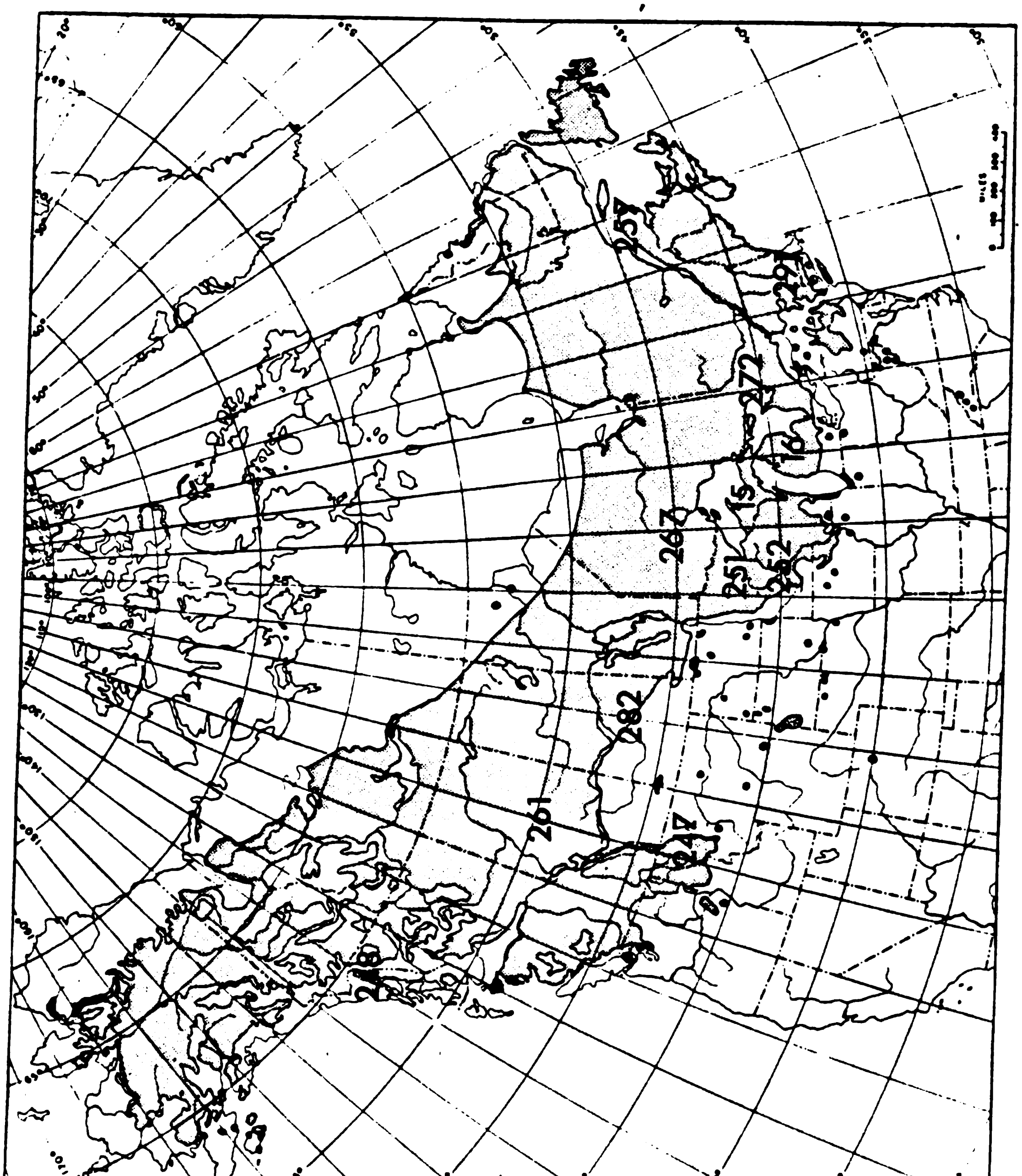
A total of 16 seedlots of birch were studied. These included 12 populations randomly selected from 12 widely separated geographic areas over the range of paper birch. Each population consisted of a bulked sample of 6-10 trees per population (stand). In addition, 2 seedlots of *B. verrucosa* seed orchard material of Finnish origin,and 2 birch hybrids *B. papyrifera* x *B. verrucosa* (#14) and *B. verrucosa* x *B. verrucosa* (#13) were included in the study. Exact locations of the paper birch populations are given in Figure 4-1.

The material was grown from seed. On June 25, 1976 all 16 seedlots of birch were sown in our greenhouse at M.S.U.'s Tree Research Center. The seeds were sown in polycoated (Zieset) paper plant bands 7.5cm x 7.5cm x 28cm deep containing a soil mixture of 3-parts peat-vermiculite (Redi-Earth) and 1-part coarse perlite. The plant bands were packed in milk cases, each case containing 16 bands. Greenhouse temperatures were maintained in the 21°- 27°C range, both day and night throughout the 3½-month growth period.

Details of the cultural treatments and handling are identical to those discussed in Chapter III.

Seedlings were grown under continuous supplemental light provided by high-output (HO), cool white, 8 foot fluorescent light which produced approximately 120 ft-

Figure 4-1. Location and population number of the 12 paper birch populations used for this study.



The range of paper birch.

candles at the soil surface.

The experimental design consisted of a 4x4 square lattice, with 5 replications, 4 blocks, and 5 arrangements. Each population is therefore represented by 4 trees per replication with 5 replications, giving a total of 20 trees per population that measurements were made on.

Eighteen characters, encompassing growth parameters, stems, and leaves were measured for each individual seedling grown in the greenhouse study. Eight additional variables (8,9,10,16,17,24,25,26) were generated as ratios of other measured characters, giving a total of 26 characters as listed below:

<u>Growth Parameters</u>

1. Height growth
2. Diameter
3. Stem dry weight
4. Root " "
5. Leaf " "
6. Shoot " "
7. Total " "
8. Root/Shoot ratio
9. LWR (leaf weight ratio) = Leaf weight/Total plant D.W.
10. RWR (root weight ratio) = Root D.W./Total plant D.W.

<u>Stem characters</u>

11. Number of lateral branches
12. Number of internodes

<u>Leaf characters</u>

13. Number of leaves on main shoot
14. Total number of leaves
15. Total leaf area
16. Average total leaf area (Total leaf area/Total number of leaves)
17. LAR (leaf area ratio) = Total leaf area/Total plant D.W.
18. Average area of a single leaf
19. Total leaf length
20. Blade length
21. Petiole length
22. Point of maximum leaf width (W)

23. Distance from leaf apex to point of max. leaf width (A).
24. Attenuation factor = A/M ratio
25. Blade length/blade width
26. Number of serrations/average area of a single leaf

On October 6, 1976, 13-weeks after sowing, each containerized seedling was measured for height, diameter, number of lateral branches, internodes, and leaves. The plant bands and growth medium was then carefully washed free of the roots. The stems and roots were collected separately, and packed for oven-dry weight determinations. The leaves of each seedling were measured for leaf area, before oven-drying, with a Lambda Portable Leaf Area Meter Model LI-3000. Individual measurements of leaf characters was performed on a single leaf of each seedling, selected on the basis of the leaf with the largest area per seedling. Actual linear leaf measurements were obtained according to Figure 4-2.

Analysis of variance was used to determine the significance of the 26 characters observed between the 16 seedlots of birch. Characters were analyzed on Michigan State University's CDC 6500 digital computer, using a square lattice program.

Figure 4-2. Diagrammatic sketch of a leaf showing the linear measurement numbers.

Results and Discussion

Results under the conditions of continuous growth revealed wide variations between the populations of paper birch distributed over its entire natural range. They indicate that few discernible geographic patterns exist for any of the 26 characters measured. It appears that paper birch populations vary essentially in a random manner over the natural range of the species, and follow no set pattern. Roth (1970), working on river birch (*B. nigra*), was also unable to detect any significant clinal variation in leaf width, leaf length, leaf area, or petiole length on either latitude or longitude.

Data on all measured developmental and morphological characters are presented in Table 4-1. Due to some cultural difficulties encountered in the initial watering of the soil mix, the ten growth parameters showed wide variability but no significant differences. All dry weights measured are directly linked to growth rate of the plant. Thus, any patterns that appear related to height will not be considered further.

Of more practical importance are the morphological and developmental characters which are less dependent on growth rate. Statistically significant differences were found for many stem and leaf characters (Table 4-1).

Extremely wide variability exists between widely separated populations of paper birch, between paper birch

Table 4-1. Developmental and morphological characters measured on 16 seedlots of paper and European white birch. Each value is a mean of 20 seedlings.

Seed-lot No.	Origin	No. lateral branches	No. inter-nodes	No. leaves on main shoot	Total No. leaves	Total leaf area	Ave. total leaf area
						- - -cm²	- - -
Paper birch							
248	Alaska	1.6	15.9	10.9	13.3	319	21.4
247	Montana	4.7	20.7	15.0	20.8	550	20.8
261	Alberta	5.4	17.7	12.5	19.2	314	19.2
282	Saskatchewan	7.1	19.8	15.1	25.1	314	12.1
267	W. Ontario	2.3	17.7	13.0	14.2	326	19.7
251	N. Minnesota	1.6	15.9	11.1	12.7	262	18.0
252	S. Minnesota	2.0	14.4	9.7	13.1	293	16.5
15	Michigan(UP)	2.4	15.1	11.2	14.0	399	26.1
16	Michigan(LP)	3.5	16.6	11.8	13.5	237	18.9
272	E. Ontario	2.4	15.1	11.1	13.8	388	23.8
257	Quebec	2.2	14.6	10.2	12.3	234	19.9
291	Mass.	2.0	16.1	9.9	11.3	261	23.0
	mean ($\bar{x}$)	3.1	16.6	11.8	15.3	325	19.9
European white birch							
1459	Finland	6.2	20.3	14.4	19.1	347	16.7
1482	Finland	2.8	21.7	15.4	18.0	370	18.3
8001	Finland	1.1	23.1	16.9	19.1	317	15.5
9530	Finland	4.8	20.0	14.5	17.4	348	19.0
	mean ($\bar{x}$)	3.7	21.3	15.3	18.4	345	17.4
Overall mean ($\bar{x}$)		3.3	17.8	12.7	16.1	330	19.2
F-value	.05=1.90 .01=2.47	2.57**	4.31**	3.49**	2.33*	1.28	2.54**
LSD (0.05)		3.2	3.8	3.4	7.1	191	6.6

Table 4-1. Continued....

Seed-lot No.	Origin	LAR	Ave. single leaf area	Total leaf length	Blade length	Petiole length
			-cm^2-	- - - - - - -	cm	- - - - - - -
Paper birch						
248	Alaska	284	54.2	12.8	9.8	3.0
247	Montana	219	52.9	12.3	9.6	2.7
261	Alberta	266	36.6	10.4	7.8	2.6
282	Sask.	182	30.0	9.3	7.2	2.1
267	W. Ontario	209	49.4	12.1	9.2	2.8
251	N. Minn.	252	44.9	11.9	9.1	2.8
252	S. Minn.	300	42.2	10.7	8.2	2.6
15	Mich. (UP)	211	60.3	13.6	10.7	2.9
16	Mich. (LP)	250	54.1	12.5	10.0	2.5
272	E. Ontario	266	61.2	14.2	11.0	3.1
257	Quebec	231	47.6	12.2	9.4	2.8
291	Mass.	301	50.3	12.9	9.8	3.1
	mean ($\bar{x}$)	248	48.6	12.1	9.3	2.8
European white birch						
1459	Finland	200	44.6	11.6	8.5	3.1
1482	Finland	198	45.3	12.0	9.2	2.8
8001	Finland	167	35.0	9.7	7.4	2.3
9530	Finland	199	43.5	11.5	8.6	2.9
	mean ($\bar{x}$)	191	42.1	11.2	8.4	2.8
Overall mean ($\bar{x}$)		234	47.0	11.9	9.1	2.8
F-value	.05=1.90 .01=2.47	2.31*	3.36**	5.88**	5.27**	3.17**
LSD (0.05)		78	13.4	1.5	1.3	0.46

Table 4-1. Continued....

Seed-lot No.	Origin	Point of maximum leaf width(M)	Length from leaf apex to point of max. width. (A)	Attenuation factor (A/M)	Blade length /width	No. serrations/ ave.leaf area
		- - - - - - cm	- - - - - -		- cm -	
Paper birch						
248	Alaska	7.9	7.3	0.92	1.24	6.6
247	Montana	7.5	7.5	0.99	1.27	7.8
261	Alberta	6.6	6.0	0.90	1.18	9.0
282	Sask.	6.1	5.4	0.88	1.19	9.1
267	W. Ontario	7.3	7.4	1.00	1.25	7.1
251	N. Minn.	7.1	7.0	0.98	1.28	7.1
252	S. Minn.	7.0	6.2	0.89	1.18	7.3
15	Mich. (UP)	7.8	8.3	1.05	1.37	7.7
16	Mich. (LP)	7.5	7.8	1.04	1.34	6.4
272	E. Ontario	8.1	8.4	1.04	1.36	6.7
257	Quebec	7.2	7.0	0.98	1.31	7.7
291	Mass.	7.4	7.5	1.01	1.35	7.8
	mean ($\bar{x}$)	7.3	7.2	0.97	1.28	7.5
European white birch						
1459	Finland	7.8	6.4	0.82	1.09	7.4
1482	Finland	7.6	6.9	0.89	1.19	8.1
8001	Finland	7.0	5.4	0.77	1.05	9.0
9530	Finland	8.0	6.3	0.78	1.08	8.1
	mean ($\bar{x}$)	7.6	6.3	0.82	1.10	8.2
Overall mean ($\bar{x}$)		7.4	6.9	0.94	1.23	7.7
F-value	.05=1.90 .01=2.47	1.82	4.42**	10.64**	12.70**	1.77
LSD (0.05)		1.1	1.2	0.08	0.08	1.8

and European white birch, and between the seedlots of European white birch.

As stated previously, the paper birch characters studied varied in an apparently random manner, following no general geographic pattern. Of interest though are a few distinct relationships between some of the populations. The most distinctive, is the close relationship of the two paper birch populations from the Canadian Provinces of Alberta (261) and Saskatchewan (282). These two populations, as a group, show many morphological characters significantly different from the other ten paper birch populations. For example they differ in the number of internodes, number of leaves per main stem, total number of leaves per seedling, and the highest number of serrations per average area of a single leaf (Table 4-1).

The Alberta (261) and Saskatchewan (282) populations, particularly the latter, exhibit the lowest average area of a single leaf of all the seedlots (Table 4-1). Also, they developed the shortest total leaf length, blade length, petiole length, and the narrowest leaf width (M) and the shortest distance from the leaf apex to the point of maximum leaf width (A). Subsequently the leaf attenuation factor, referred to as the A/M ratio (Brayshaw, 1966), was smallest due to the small length of the leaf (A) in comparison to (M). Thus, in comparison with the other paper birch populations, these populations had a wider leaf width than leaf length, measured from the apex to the point of maximum leaf width (A).

These two populations from the northern plains closely resembled B. verrucosa in many developmental respects, such as lateral branching, number of internodes, number of leaves per main stem, and total number of leaves per seedling. In addition, at this early age, they appear similar in stem form, leaf color, and pubescence. Of unique consequence is the complete absence of stem pubescence. The seedlings from these two populations had no stem pubescence, but rather produced a glandular exudate, which appeared warty in nature. Brittain and Grant (1975) reported similar observations on young paper birch seedlings from the Rocky Mountain area of Alberta. It is possible that these seedlings are natural hybrids with the small tree or shrub B. fontinalis, which overlapps the range of paper birch in that area. Dugle (1966) has reported that these two species due in fact sometimes hybridize, which may account for the seedlings warty condition, commonly found on the twigs of B. fontinalis.

The only other evidence of geographic variability in the paper birch populations is shown by the three populations from the central Lake States, including populations from Michigan (15 and 16) and eastern Ontario (272). These three are as closely related as any of the populations, especially the UP (15) and eastern Ontario (272) populations. In terms of stem characters no significant differences exist between them and the other paper birch populations. In terms of morphological characters of the leaves however, the three central Lake States populations stand out. These three populations had extremely large leaves, averaging 58.5 square centimeters per leaf, with the eastern Ontario (272) population averaging 61.2 cm^2 or over twice the size of the Saskatchewan population (282) which was 30.0 cm^2 (Table 4-1).

Due to the large leaf size, measurements of blade and petiole length were also larger. To account for this effect, a leaf attenuation factor (A/M) was determined. It is believed that leaf shape is more strongly controlled genetically than leaf size (Crane and Lewis, 1949). Even though the central Lake States populations had wider leaves (M) and a longer distance from the apex to the point of maximum leaf width (A) than other populations, the A/M ratio was consistently large. This indicates that the leaves were proportionately longer than wide. Thus, the Lake States populations had very large leaves in terms of area and they were long and narrow in shape.

Research on yellow birch has revealed results similar to those reported here on paper birch. Variation studies of branch and leaf characters showed significant provenance differences, but the variation was small and appeared to be random in most cases. An exception was leaf shape, which appeared to show clinal variation with southern provenances having narrower leaves than northern ones (Clausen, 1973). Dancik (1971) also found Appalachian Mountain trees had narrower leaves than those from the western Great Lakes region.

The results of my work on paper birch do not substantiate the trend found in yellow birch. The most southerly source (252) from southern Minnesota had next to the lowest A/M ratio and the lowest ratio of blade length to width of all twelve paper birch populations (Table 4-1). Two of the more northerly populations from the northern plains of Canada (261 and 282) had the lowest A/M and leaf length/width ratios, supporting the observations on yellow birch. The group with the narrowest leaves were the three populations from the central Lake States.

This initial study was designed to provide information on broad geographical variation patterns using a relatively small number of seed sources so that only major types of variation could be detected. An intensive study of a smaller geographic area including many more populations and individual families within these populations is needed to test regional and local variation in a number of characters. This would bring to light any geographic patterns that may actually be present.

Included in this study were four seedlots of Finnish origin, two of which (1459 and 1482) are European white birch (B. verrucosa) from southern Finland. The other two seedlots are controlled crosses, one is a seedlot obtained from the hybridization of two B. verrucosa provenances (8001), and the second, is a hybrid of B. papyrifera x B. verrucosa (9530).

The lower portion of Table 4-1 includes the four Finnish seedlots and their respective means for each character. Some of the important differences within the Finnish seedlots and between them and the paper birch populations will be discussed.

As may be expected, wide variations exist within the four seedlots due to the inclusion of the hybrids. One interesting observation involves the amount of variation in number of lateral branches between the two European white birch provenances, 1459 and 1482, which are within 35 miles of each other in southern Finland. Seedlot 1459 produced over twice the number of lateral branches per seedling as seedlot 1482, significant at the 5-percent level (Table 4-1). The two seedlots were similar in all the other chacters except the leaf shape ratios, A/M and blade/width.

The provenance hybrid (8001) showed extreme developmental and morphological variability. Compared with all other seedlots this one exhibited very little branching (1.1 branches per seedling), the highest number of internodes, largest number of leaves per main stem, lowest LAR, shortest length from leaf apex to the point of maximum width (A), and the lowest A/M and blade length/width ratios (Table 4-1).

The most distinguishing characters of the Finnish seedlots as a group compared with paper birch populations as a group, are the larger number of internodes, larger number of leaves per main stem, lower LAR, and the smaller leaf shape ratios (Table 4-1). In many characters, overlapping frequently occurred, especially with the Alberta (261) and Saskatchewan (282) population. The Finnish source 1482 was comparable in many characters to paper birch, including number of lateral branches per seedling, average total leaf area, average area of a single leaf, and all the morphological leaf measurements (Table 4-1).

In comparison the paper birch populations and the hybrid B. papyrifera x B. verrucosa, very few significant differences exist. This hybrid seems intermediate in most characters, including average total leaf area, average area of a single leaf, total leaf length, blade length and width, petiole length, and number of serrations per single leaf based on area. Large differences do exist between the hybrid and most of the paper birch populations in number of internodes and the leaf shape ratios. The hybrid leaves are noticeably wider and shorter than paper birch leaves, very characteristic of B. verrucosa. Thus, the leaf shape is the only character that is significantly different from all the paper birch seedlots.

A comparison of the hybrid birch with the two B. verrucosa seedlots reveals no significant differences in any character measured. The hybrid appears to resemble European white birch more than paper birch. Johnsson (1949) studied morphological characters of birch hybrids and found that the hybrid B. verrucosa x B. papyrifera is intermediate in leaf size. It is possible that my results do not show the intermediate relationship because I used only two _B_. _verrucosa_ seedlots. The use of more seedlots of the species and hybrid birch might show the hybrid to be intermediate.

Casual observations were made on stem pubescence but it was not measured. It appears that stem pubescence varies also in an apparently random manner. The stem of paper birch is usually densely pubescent beginning in the early seedling stage. Some of the paper birch populations differ from others, but four populations had seedlings which varied in pubescence within the population. The Alaskan source (248) differed from other populations in developing only slight pubescence. In addition, variation also existed within this population, with about 25 percent of the seedlings developing a glandular condition on the stem and complete absence of pubescence.

This same trend with respect to stem pubescence occurred on populations from western Ontario (267), northern Minnesota (251), and eastern Ontario (272). The reason for this variation is probably because the species occupies such diverse sites and has a wide geographic range. Its range is sympatric with _B_. _neoalaskana_, _B_. _cordifolia_, and _B_. _populifolia_ all of which exhibit the glandular exudate at an early age. This probably allows numerous varieties of paper birch to develop through hybridization. It is interesting to note that within a population, consisting of about ten trees bulked together, variation in stem pubescence also exists between individual parent trees in a stand differ in stem pubescence. Further studies of other morphological and anatomical characters of individual trees in a stand are needed to clearly illustrate the exact nature of inherited variation.

Two populations that show extreme differences in stem pubescence in all its progeny are the Alberta (261) and Saskatchewan (282) populations was entirely lacking stem pubescence, and produced a glandular exudate. The cause of this variation can possibly be ascribed to hybridization with _B. fontinalis_.

Dense pubescence on the other hand occurred consistently in three populations of paper birch, including both Michigan populations (15 and 16) and the southern Minnesota population (252). Only slight variations in pubescence were observed within these populations.

Pubescence was also variable on the Finnish seedlots of birch. European white birch developed a moderate pubescence whereas the birch hybrid (8001) showed a wide range of variability from moderately pubescent to a slight glandular state. Suprisingly, the _B. verrucosa_ x _B. papyrifera_ hybrid (9530) had moderate pubescence consistently on most of the seedlings.

Summary and Conclusions

Variation in 26 developmental and morphological characters was essentially random with respect to geographical gradients over the natural range of paper birch.

Significant differences between seed sources were observed for many stem and leaf characters in seedlings of paper birch, European white birch, and the hybrids between them. Extreme variation was found in two populations occurring in the northern plains of Canada, especially in stem pubescence, number of lateral branches, average area of a single leaf, and leaf shape ratios. Paper birch populations from the central Lake States developed very large leaves in terms of area, and the leaves were long and narrow in shape.

Two European white birch seedlots overlapped in many foliar characters with paper birch, differing significantly only in producing larger number of internodes, larger numbers of leaves, and lower leaf shape ratios. The hybrid *B. papyrifera* x *B. verrucosa* was intermediate in many morphological characters except for leaf shape which closely resembled European white birch.

Stem pubescence was also variable and ranged from a glandular form to densely pubescent. No geographical patterns were observed except for the distinctness of the two populations in the northern plains. It is entirely possible that much of the variation in pubescence may be due to natural hybridization of paper birch and other birches with sympatric ranges.

No significant clinal variation associated with latitude or longitude was found in any of the developmental and morphological characters measured.

There was an absence of large morphological and developmental differences between the Alaskan population (248) located the farthest north and west, and the other populations further east and south. For example, the Quebec (257) and Alaskan populations are separated by over 2,000 miles but did not differ significantly in any character measured. In addition, the most southern source, located in southern Michigan (16), differed significantly from the Alaskan population in only the two leaf shape characters.

Although this rangewide study on widely separated populations provided information on gross geographic patterns in morphology and development, it also brought out the need for further research on local variation patterns within an individual population. Variations in stem pubescence and juvenile height growth, as demonstrated in Chapter III illustrate the need for intensive studies over small geographic areas. These studies should include many more populations with data on progeny performance of families selected within these populations.

Information on local variation patterns for a number of characters within a population could reveal the relative amount of variation due to gene action and a complex of environmental variables. Thus further investigations of paper birch are needed in order to better understand the causes of the intraspecific variability found in this research.

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

Paper birch seed and seedlings revealed a large amount of geographic variation which was not related to any environmental gradients.

Seed germination

The germination capacity and germinative energy of paper birch seed was significantly affected by temperature of the test conditions and geographic origin.

Seed from the Upper Peninsula (UP) of Michigan had a wider range of temperatures optimum for germination, and increased germinative energy, in comparison with seed from the Lower Peninsula (LP) of Michigan. In addition, the UP seed revealed much plasticity in its ability to germinate at very low ($10^{o}C$) and high ($43^{o}C$) temperatures.

Seed from the UP initiated seed germination earlier than seed from the LP, especially at lower temperatures.

Germination capacity was found to vary significantly both within- and between-populations of paper birch. Within a population, individual families occassionally differed by 70 percent or more in percent germination.

The amount of seed borne by the parent tree, or seed crop, showed no correlation with percent germination of the seedlot, and seed crop varied both within- and between-populations. One population with the lowest average seed crop rating of the parent trees had one of the highest germination percentages.

Variation in seed germinative energy was also related to geographical origin. The combined UP populations reached 63 percent germination in 7 days, whereas the combined populations from the LP took nearly 13 days to obtain the same percent germination.

The most distinctive difference in seed germination was noted between the western UP and south-central LP populations. Seed from populations in the western UP began germination sooner, proceeded more rapidly, and reached optimum levels earlier than populations in the south-central LP.

The rapidity of germination or germinative energy was not correlated with size of the parental seed crop.

Growth

Variation in height growth of 4- and 5-month-old greenhouse-grown seedlings of paper birch, was due mostly (87%) to within-population differences. In other words variation between half-sib families was greater than differences among widely separated populations. The amount of variation in growth between families differed among the populations sampled, but the maximum variation between any two populations was small (20%) compared to the maximum variation observed between two families (68%).

Genetic variation in juvenile height growth of container-grown paper birch seedlings grown under greenhouse conditions was essentially random, with respect to environmental gradients. Long-term observations in plantations should show whether or not height growth is actually random under natural conditions and over longer periods of time.

European white birch from Finland was superior to paper birch in height growth. If this superiority holds true in test plantations it would indicate a possible use of European white birch for reforestation purposes in Michigan.

Morphology

Considerable morphological variability in leaf size, shape, number, and stem pubescence was observed both between- and within-populations of paper birch.

Variation in 26 developmental and morphological characters measured was essentially random over the natural range of paper birch, following no geographic or clinal pattern.

Significant amounts of genetic variation were found in a number of characters, including number of lateral branches, stem pubescence, leaf number, leaf area, leaf length, and leaf shape. Variability in the above characters exists both between widely separated populations of paper birch, and between paper and European white birch.

Two distinct ecotypes were found in the range-wide morphological study of paper birch. The populations from the northern plains of Canada (Saskatchewan and Alberta) and from the central Lake States as a group, showed similarities within groups in many of the characters examined, separating them from the other populations.

The two European white birch seedlots overlapped with paper birch in many foliar characteristics, but differed significantly in production of larger numbers of internodes, larger number of leaves, and low leaf shape ratios.

Recommendations

This study of widely separated paper birch populations provided information on broad geographic variation patterns in germination characteristics, juvenile height growth, and morphology and development. It also brought out the need for further research on local variation patterns within an individual population. Variations in stem pubescence and juvenile height growth illustrate the need for intensive studies within small geographic areas. These studies should include many more populations with data on progeny performance of families selected within these populations.

Further genetic studies of paper birch are required to learn more about intraspecific variability, in order to serve as a basis for future breeding strategy. There is also a need to establish correlations between juvenile and mature physiological and morphological characteristics of paper birch.

Information is needed on juvenile height growth of half-sib progenies grown under lights versus natural photoperiods in a greenhouse environment. Such studies would determine the effect of supplemental light on the performance of the seedlings, and the residual effects of these treatments on the trees in test plantations.

Growth rate, branching, and branch angle are important characters for the improvement of tree quality and increasing the financial return of plantation-grown paper birch. The considerable amount of genetic variation in these characters revealed in this study indicate a potential for their improvement.

Observations of European white birch should be continued in our established plantations because they could result in recommendations for its use for reforestation in Michigan.

From a practical standpoint, maximum genetic improvement for height growth would be accomplished most efficiently by practicing individual tree (family) selection, due to the large amounts of within-population (family) variation present. Results indicate the importance of progeny testing all paper birches to be used in an improvement program, without progeny testing much potential growth improvement may be lost if slow-growing seed sources are used for reforestation purposes.

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