Natural Variation and Hybridization of Yellow Birch and Bog Birch in Southeastern Michigan[1]

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Introduction

Yellow birch is an important component in the forest communities of the northeastern United States and adjacent Canada, yet very little is known of its natural variation, adaptation patterns, and the extent and significance of hybridization with other birches (CLAUSEN 1968 a). Yellow birch, a hexaploid ($2n = 84$), was originally described and named ***Betula lutea*** by MICHAUX (1812). This name is now considered illegitimate (LITTLE 1953, and BRAYSHAW 1966 a), and the name ***B. alleghaniensis*** BRITTON is generally accepted.

In 1964 and subsequent years populations of yellow birches containing many individuals with dark bark were found in southeastern Michigan. Trees having similar forms have been reported by numerous authorities (DANCIK 1969). One objective of the study was to investigate the variability of various characters in one such population and attempt to determine the relationship of these trees to the classically described yellow birch. The second objective was to study the extent of hybridization, backcrossing, and introgression of yellow birch and bog birch ***(B. pumila*** L.) in this population. Hybridization was of particular interest because it frequently has been reported in the birches and because some of the variation and unusual forms of yellow birch might be due to hybridization.

Bog birch, a tetraploid ($2n = 56$), is a common member of swamp and bog communities in the Lake States. A natural hybrid between yellow and bog birch, first discovered by PURPUS at Clark Lake, Michigan, was described and named ***B.*** X ***purpusii*** SCHNEIDER (SCHNEIDER 1906). This hybrid has been reported from Michigan (HANES and HANES 1947), Wisconsin (CURTIS 1959), Minnesota (ROSENDAHL 1916), Illinois (JONES and FULLER 1955), Indiana (DEAM 1921), and Ohio (BRAUN 1961). Bog birch is also known to have hybridized and backcrossed with paper birch ***(B. papyrifera*** MARSH.) in Minnesota (CLAUSEN 1962 b).

Study Area and Methods

An unusual birch population was discovered at Walsh (Welch) Lake, 42° 21' N latitude, 84° 05' W longitude, at about 965 feet (294 m) elevation, Washtenaw County, Michigan ***(Fig.*** 1). The yellow birches occurred within 200 feet of the lake in a low, wet zone having vegetation characteristic of a lowland forest community.[3] The population consisted of 3 general strata. Most of the birches were 40 to 45 years old, a few wolf trees and suppressed individuals were 50 to 65 years old, and several saplings appeared to have originated within the last 10 to 15 years. Bog birches grew primarily in the adjacent, relatively open marsh or on the border between the stand and the marsh. Most of the putative hybrids were in the stand; one was on the border between the stand and the marsh. The soil on the area, Houghton muck, is a well decomposed, moderate-to-slightly-acid muck, developed from the remains of non-woody plants (VEATCH *et al.* 1930). The water table was at or within 1 foot of the soil surface during most of the growing season.

The area has a continental climate with a mean annual temperature of 48° F, a January mean of 24° F, and a July mean of 73° F. The mean annual precipitation is 31 in., of which 18 in. are received from April through September (U.S. Department of Commerce 1964).

All of the birches along the western third of the lake, 112 yellow birches, 39 bog birches, and 8 putative hybrids, were numbered, tagged, and mapped. The diameter at breast height (DBH) and total height were measured and the number of stems per individual recorded. The ages at 4½ feet above the ground of 7 trees were determined by increment borings.

In late April and early May, before flowering, branches bearing closed staminate catkins were collected from all flowering individuals and forced to flower. Pollen was collected and permanently mounted in glycerine jelly. The percentage of malformed, rollapsed, and empty grains in a 200-grain sample of each individual was determined. The diameters of 25 of 50 grains were measured, the lower number if the particular sample appeared uniform. The length and width of discharged male flowers and unpollinated female flowers were measured.

From August 19 to 28, 1966, staminate catkins that appeared to be undergoing meiosis were collected from a subsample of the population and immediately fixed in NEW-

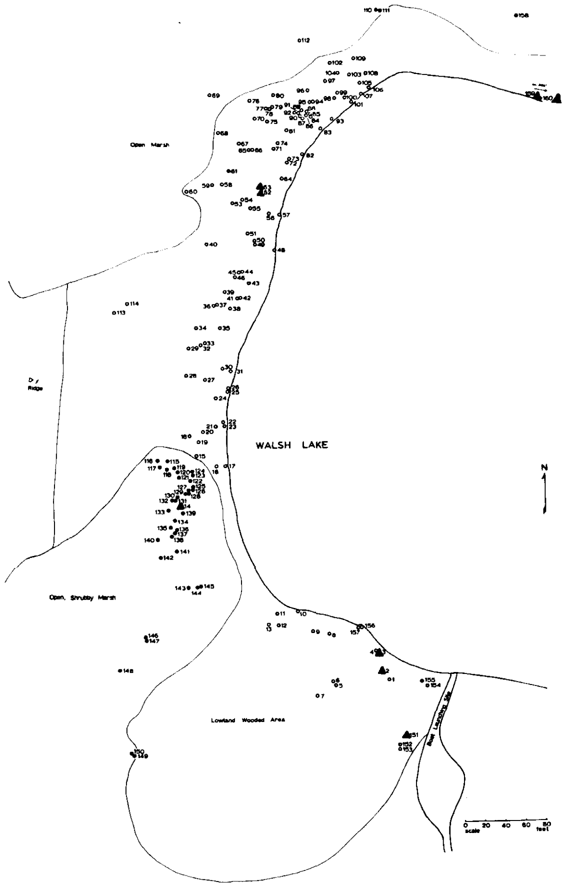

Fig. 1. — The Walsh Lake study area. Waterloo Recreating Area, Washtenaw Co., Michigan. Yellow birch — o; bog birch — •; hybrid — ▲.

[1]) Based on a thesis submitted to the University of Michigan, School of Natural Resources in partial fulfillment of the requirements of the Master of Forestry degree.

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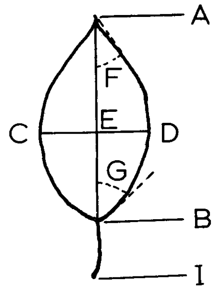
[3]) DANCIK, BRUCE P. 1967. A population study of the birches, Betula alleghaniensis, B. pumila, and their hybrid. M. F. Thesis, University of Michigan, 89 pp.



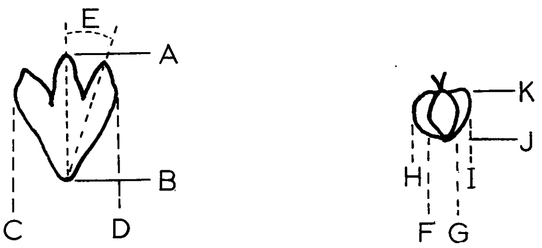


Fig. 2. — Outline of birch leaf illustrating the characteristics measured. — (a) total blade length in mm. (AB). — (b) maximum blade width in mm. (CD). — (c) point of max. blade width (BE/AB). — (d) petiole length in mm. (BI). — (e) number of teeth on one side of blade. — (f) number of pairs of veins. — (g) apical angle (F). — (h) basal angle (G). — *Fig. 3.* — Outline of pistillate bract and samara illustrating the 6 characteristics measured. — (a) bract length (AB). — (b) bract width (CD). — (c) lobe angle (E). — (d) samara width (HI). — (e) seed width (FG). — (f) samara length (KJ).

COMER's and CARNOY's solutions. The anthers were squashed in acetocarmine stain, and cells undergoing meiosis examined.

Mature pistillate catkins were collected from all fertile individuals in late August 1966. One bract and 1 samara were picked from the central portion of each of 2 randomly selected pistillate catkins of each individual, and several measurements made *(Fig. 3).* The total lengths of the axes of the pistillate catkins were measured.

Leaves were collected from all individuals in the first 2 weeks of August 1966. Spur-shoot shade leaves were collected from the lower-inside crown of each plant. Twelve undamaged spur-shoot leaves of each individual were chosen, 8 characteristics measured *(Fig. 2),* and selected leaves mounted.

Leaves of 56 yellow birch, 13 bog birch, and 8 hybrids were cleared in a solution of 5% sodium hydroxide at 140° F for several days, bleached, stained by the tannic acid-ferric chloride method, and mounted on microscope slides in diaphane. Ten randomly selected stomata in the lower epidermis of each leaf were measured.

A computer program was written to compare the taxa by the hybrid-index method of ANDERSON (1949). The bog birch individual having the extreme form of a character was assigned a value of 0 while the yellow birch at the other extreme was rated 10. All other individuals were given proportional values between 0 and 10. The range between the smallest bog birch index and the largest yellow birch index was divided into 30 equal intervals. The frequency of individuals in each interval was then determined for each taxon. The program was developed to place a line-file description of coordinate information for frequency distribution of hybrid index into a file, from which the graphs were generated by a Calcomp Plotter. Three graphs were constructed using 19, 15, and 8 characters. Similarly, a pictorialized scatter diagram (ANDERSON 1949) was constructed to compare the taxa.

Results

Gross Observation

Obvious differences in stem size and form were used to separate the 3 taxa *(Table 1).* The bog birch had a uniform, almost black, smooth bark. The bark of the hybrid was dark red to black, smooth, and sparsely exfoliating. The bark of yellow birch, however, was extremely variable. The color ranged from a deep reddish-black through brown and gray to a very light yellow. Bark types ranged from smooth to highly exfoliating *(Fig. 4).* Five of the 7 bored trees, diameter 6.9 to 13.6 in., were 33 to 37 years old. Bark types of these trees ranged from smooth to heavily exfoliating. Two trees were 45 and 55 years old. The 55-year-old tree and a 33-year-old tree, diameters 7.6 and 7.7 in., had remarkably similar bark.

Fig. 4. — Bark of representative yellow birches in the Walsh Lake population (No. 1, left; No. 19, right).

Chromosomes

Meiosis proceeded from the base toward the tip of the staminate catkin. An abrupt transition was usually found between cells that had not initiated meiosis and those that had completed meiosis. Chromosome figures of pollen

Table 1. — Gross characteristics of bog birch, yellow birch, and their hybrid.

	Total no. indiv.	DBH Mean (in.)	DBH Range (in.)	Total height Mean (ft.)	Total height Range (ft.)	Number of stems per individual Mean	Number of stems per individual Range
Bog birch	39	0.3	0.1 — 0.5	6.6	4.5 — 8.5	11.0	1 — 24
Hybrid	8	0.9	0.3 — 2.4	18.4	13 — 25	8.5	4 — 14
Yellow birch[1])	95	8.1	4.4 — 18.8	48.0	35 — 60	1.1	1 — 3

[1]) Trees 4 in. DBH and larger.

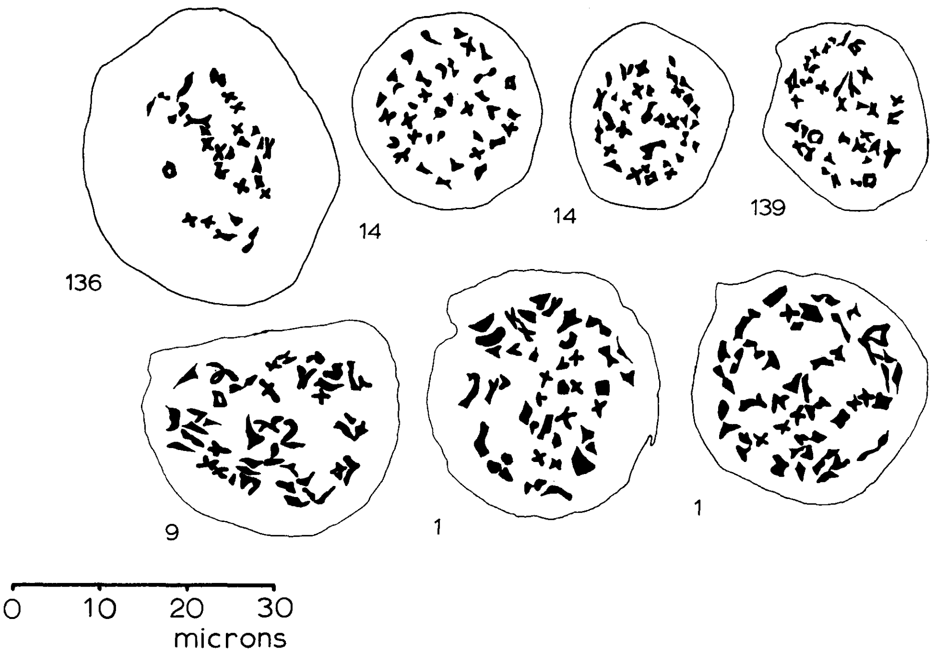


Fig. 5. — Camera lucida drawings of chromosome complements at metaphase I of meiosis. Bog birch 136 (28 units), hybrid 14 (33—36 units), plant 139 (35 units), yellow birches 1 and 9 (42 units).

mother cells were obtained from 2 yellow birches (1, 9), 1 hybrid (14), and 2 bog birches (136, 139) *(Fig. 5)*. Although pollen mother cells of many other plants were examined, we were unable to get good figures at the proper stage for definitive chromosome counts.

Yellow birches 1 and 9 and bog birch 136 showed normal meiosis and cell division. The number of chromosome units was equal or very close to the expected hexaploid (42) or tetraploid (28) numbers (Woodworth, 1929 and 1930), indicating that all units were probably bivalents. Putative hybrid 14 and plant 139, along with the other hybrids for which accurate counts could not be made, exhibited erratic pairing of chromosomes and lagging univalents on the spindle during anaphase I. The 2 figures for putative hybrid 14 indicated about 33 and 36 units of indistinguishable valency, close to the 35 bivalents (pentaploid) one would expect if normal pairing occurred. Woodworth (1930) reported that he could distinguish 28 bivalents and 14 univalents in the pollen mother cells of the bog × yellow birch hybrid. The figure of plant 139 had 35 units whose valency could not be accurately interpreted. Meiosis was irregular with lagging chromosomes on the spindle at anaphase I.

Pollen Viability and Morphology

On the average, there were over 10 times as many aborted grains in the hybrids as in the parent species *(Table 2)*. Differences between all pairs of taxa were significant at $P < .001$. In addition, the anthers of the hybrids did

Table 2. — Pollen abortion of bog birch, yellow birch, and their hybrid.[1])

Taxon	No. of trees	% Aborted Grains		
		Mean	Range	Standard Deviation
Bog Birch	37	0.6	0.0 — 2.0	0.59
Hybrid	7	23.5	6.0 — 42.0	13.90
Yellow birch	70	2.1	0.0 — 8.5	1.67

[1]) Based on 200 grains per individual.

Table 3. — Pollen size of bog birch, yellow birch, and their hybrid.[1])

Taxon	No. of Trees	Pollen Diameter (μ)		
		Mean	Range	Standard Deviation
Bog birch	37	21.5	19.8 — 24.1	0.80
Hybrid	7	26.4	24.1 — 30.0	2.18
Yellow birch	70	27.1	24.2 — 30.3	1.10

[1]) Based on 25 or 50 grains per individual.

not freely dehisce. We have noted in many plants putatively identified as birch hybrids that the anthers do not completely open, and pollen is not released freely.

The pollen of bog birch had a mean diameter of 21.5 microns *(Table 3)*, which is within the range of sizes reported for the species by Clausen (1962 a) and Leopold (1956). The pollen of yellow birch had a mean diameter of 27.1 microns, close to the size reported for the same species by Leopold (1956) and Wodehouse (1935). The hybrid pollen had a mean diameter of 26.4 microns not significantly different ($P > .1$) from that of yellow birch, but with much greater size variation than either parent. The differences between the pollen diameter of bog birch and the other 2 taxa are significant ($P < .001$).

The pollen of bog birch was uniformly tri-porate. Many yellow birches had a few polyporate pollen grains. All of the hybrids had some polyporate pollen grains. Numerous tetraporate, several pentaporate, and a few septaporate grains were observed in yellow birch and the hybrid but the frequency was much lower in the yellow birch pollen. Erdtman (1943) and Wodehouse (1935) also noted the presence of polyporate grains in yellow birch. Clausen (1962 a) and Dugle (1966) reported polyporate pollen in several hybrid birches.

Phenology

Pollen shedding of bog birch began up to 4 days before anthesis in any yellow birch, and reached its peak 5 days before yellow birch. However, overlapping did occur so pollen exchange between the 2 species was possible. Pollen-shedding of the hybrids primarily overlapped that of yellow birch. The pistilate catkins appeared to be receptive 1 to 2 days before pollen discharge on the same plant. Sarvas (1952) reported a similar condition in *B. verrucosa* Ehrh. and *B. pubescens* Ehrh. in Finland.

In all taxa, active shedding in any individual lasted from 1 to 3 days, and about 80% or more of an individual's pollen was shed during this period. Sarvas (1952) similarly reported that at least 70% of the pollen of individual trees of *B. pubescens* and *B. verrucosa* was released within a 3 day period. Examination of individual catkins indicated that another dehiscence proceeded from the central region to either end and from the side exposed to sunlight to the protected side.

Morphology

Flowers:

Differences in the size of inflorescences between the taxa were marked *(Table 4)*.

Leaves:

The 3 taxa could be easily separated by visual inspection of leaf characteristics *(Fig. 6* and *Table 5)*. In addition the bog birch had relatively few spur-shoot leaves in comparison to yellow birch and the hybrid. Generally, the early leaf of bog birch was spatulate to obovate or orbicular with a crenate margin. Yellow birch had an ovate leaf with a singly or doubly serrate margin. The hybrid had an oval to ovate leaf with a dentate margin. Leaves of any one individual varied considerably in size, but shape, tooth number, and number of lateral veins remained relatively constant. Many individuals of yellow birch could be distinguished from one another by leaf characters; the same is true for bog birch. However, the hybrids were more uniform and could be individually distinguished only with difficulty. The hybrids exhibited smaller coefficients of variation than either parent in most characteristics *(Table 5)*. Coefficients of variation were somewhat greater for the bog birch than the yellow birch in most leaf characteristics. The yellow birches exhibited a range of margin types from a regular, single serration to a pronounced double serration, while the bog birches were all crenate.

Table 4. — Size of inflorescences of bog birch. yellow birch, and their hybrid forced in late April, 1966.

Taxon	No. of Trees	Mean catkin dimensions (mm).			
		Male		Female	
		length	width	length	width
Bog birch	35	12.3	3.9	9.5	2.1
Hybrid	7	39.6	4.8	13.8	2.9
Yellow birch	70	55.9	6.5	14.4	3.6

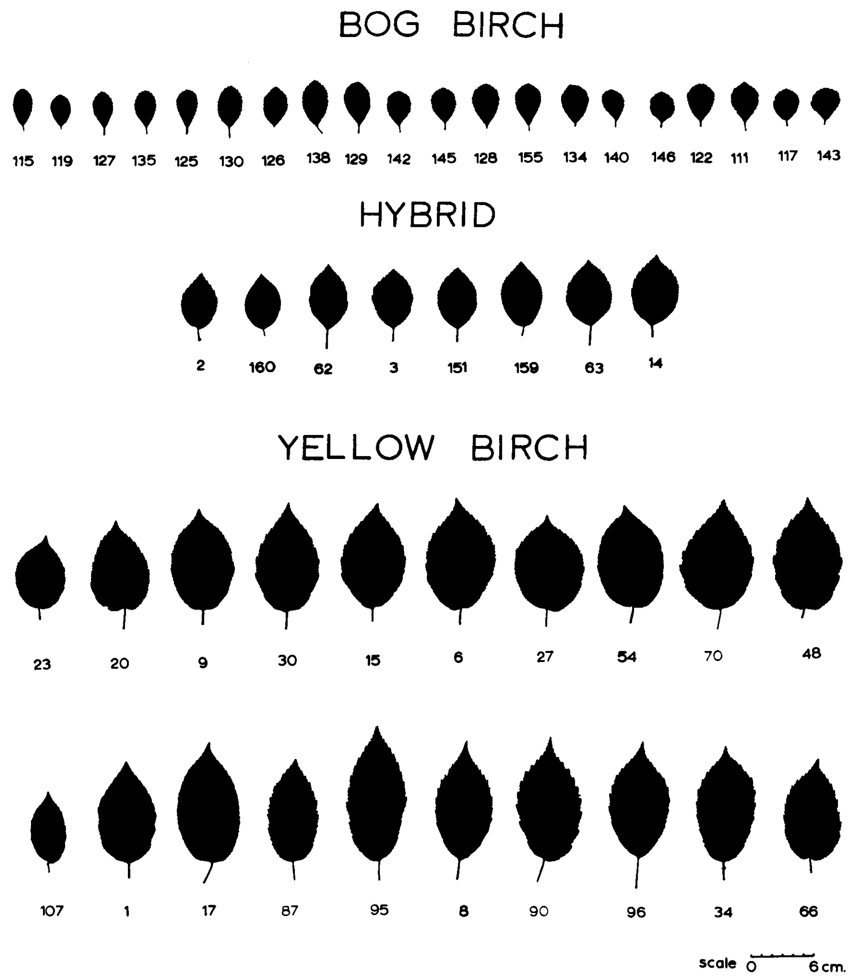


Fig. 6. — Leaf silhouettes of representative individuals in the Walsh Lake population.

Table 5. — Means and coefficients of variation of leaf characters of bog birch, yellow birch, and their hybrid.

Character	Bog Birch Mean	Bog Birch C. V.	Hybrid Mean	Hybrid C. V.	Yellow Birch Mean	Yellow Birch C. V.
1	32.7	18.6%	57.4	5.6%	97.5	11.0%
2	20.9	15.3	38.8	7.2	55.0	11.8
3	0.61	19.7	0.51	3.9	0.44	9.1
4	6.0	21.7	12.5	30.4[1])	16.5	10.3
5	11.7	15.4	26.2	10.7	47.7	14.0
6	4.6	10.2	7.5	13.3	11.0	8.2
7	33.7	19.9	60.0	13.3	83.4	18.3
8	53.6	9.3	44.7	4.9	34.8	11.8

Characters:
1 = length of leaf blade in mm.
2 = width of leaf blade in mm.
3 = point of maximum width (BE/AB, Fig. 2)
4 = petiole length in mm.
5 = number of teeth on one side of the leaf
6 = number of pairs of veins
7 = basal angle in degrees (G in Fig. 2)
8 = apical angle in degrees (F in Fig. 2)

[1]) This high coefficient of variation is probably due to the extreme values of hybrids 62 and 63. If these two plants are excluded, the coefficient of variation is 13.4%.

The yellow birches also had a variety of leaf-base types including cuneate, truncate, rounded, and sub-cordate, while the bog birches all had cuneate bases.

Of the 8 characteristics, only blade length, number of pairs of veins, and number of teeth *(Fig. 7a)* of the hybrids did not overlap with those of the parents. Blade width *(Fig. 7b)*, position of the point of maximum blade width, and basal leaf angle of the hybrids and yellow birches overlapped. The hybrids and bog birches overlapped in apical leaf angles *(Fig. 7c)*. Petiole lengths of all 3 taxa overlapped *(Fig. 7d)*.

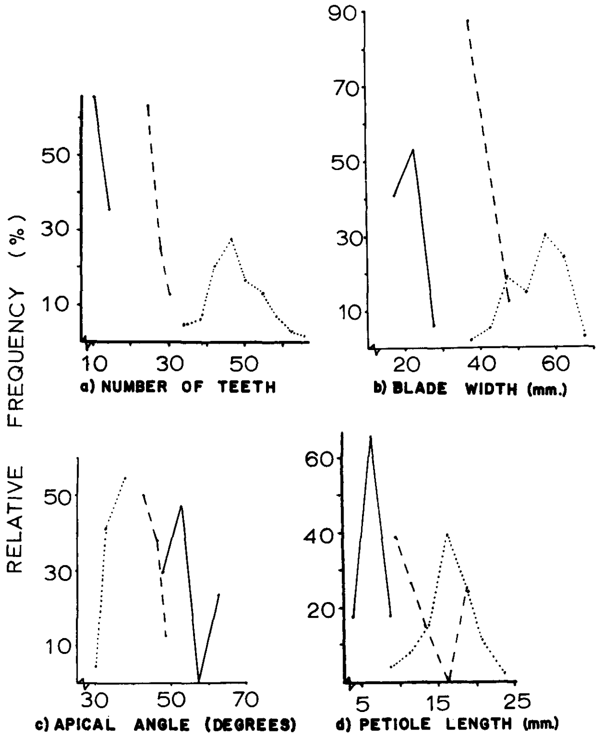


Fig. 7. — Frequency distributions of four leaf characters. Bog birch: ———, yellow birch: . . . . ., hybrid: - - - - -.

Plants 15 and 23, putatively identified as yellow birches, had fewer teeth, 33.4 and 34.6, than any of the other yelow birches, very close to the range (22—31) of the hybrids. Tree 23 also had smaller and more leathery leaves than the yellow birches.

Pistillate Bracts, Samaras, and Catkins:

In general, differences in bract size allowed easy separation of the taxa *(Fig. 8* and *Table 6)*. The shapes of the bracts of the yellow birches showed marked variation. They ranged from the cruciform types of trees 35, 51, and 76 to the extended, ternate forms of trees 8 and 22. Clausen (1968 b) also noted a marked variation in bracts of yellow birch in his rangewide variation study. Plant 139, putatively identified as a bog birch because of its leaves and form, had much larger, ternate bracts than those of the typical bog birch. Bracts of most of the yellow birches at Walsh Lake had much less pubescence and fewer cilia than yellow birches from northern Michigan (numbers 501 and 503 in *Fig. 8)*. Bracts of bog birch were glabrous.

The bracts of yellow birch generally were tardily deciduous. Those of bog birch were persistent. Those of the hybrids were persistent to tardily deciduous, except for those of 62 and 63, which were strongly deciduous.

Samaras of the hybrids were relatively intermediate in size between those of the 2 parents *(Table 6)*. The wide wing of the samaras of 2 hybrids (62 and 63) closely resembled the very wide wing of paper birch samaras. The lengths of the axes of the pistillate catkins of the taxa overlapped completely. The catkins of hybrids 62 and 63 were much longer than those of the other hybrids and slightly longer than the longest catkins of yellow birch.

Stomata:

The stomata of yellow birch, bog birch, and the hybrid averaged 33.6, 42.8, and 34.4 microns, respectively. A t-test indicated that the differences in size were highly significant between bog birch and the other 2 taxa ($P < .001$), but not between the hybrid and yellow birch ($P > .4$).

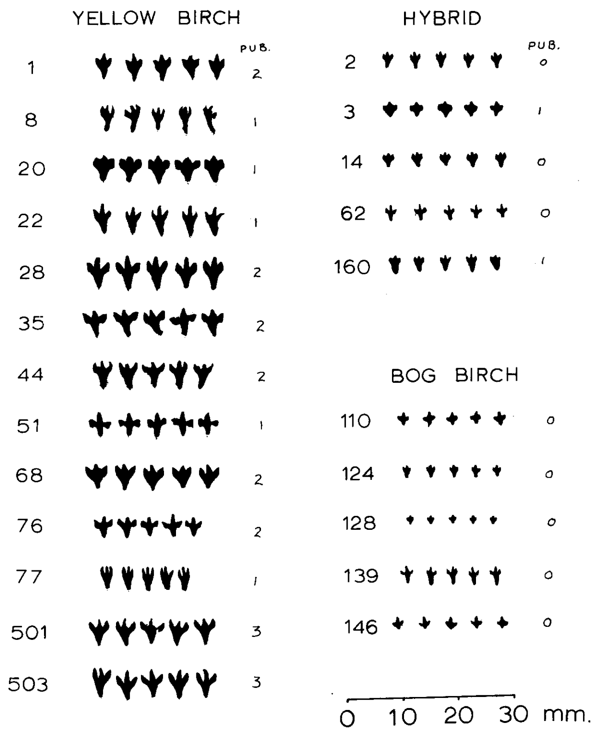


Fig. 8. — Silhouettes of pistillate bracts of several Walsh Lake birches. Yellow birches 501 and 503 are from northern Michigan. Pubescence ratings are also indicated on the scale: 0 = glabrous, 1 = slightly pubescent and ciliate, 2 = moderately pubescent and ciliate, 3 = very pubescent and ciliate.

Groupings of Characters

The hybrid index method of Anderson (1949) frequently has been used to analyze hybrid plant populations, including birches (Brayshaw 1966 b, Clausen 1962 b and 1963 a, Dieterich 1963, and Dugle 1966). Of the 3 graphs of frequency distribution of hybrid index that were constructed, the 1 using 8 characters best represented the relationship of this hybrid to its parents (*Fig. 9*); graphs using 15 and 19 characters were similar. The 8 characters were chosen on the bases that adequate and reliable data were available for each character, that the major groups of characters were all represented, and that each character separated the parent species reasonably well.[4])

Table 6. — Mean values of fruit characteristics of bog birch, yelow birch, and their hybrid.[1])

	Character						
Taxon	1	2	3	4	5	6	7
Bog birch	13.3	4.0	3.4	43.5	1.7	1.3	2.3
Hybrid	23.3	5.8	4.3	36.4	2.8	1.3	2.9
Yellow birch	21.3	9.0	6.7	27.8	3.6	1.6	3.3

Characters:
1 = Length of the axis of the pistillate catkin in mm.
2 = Length of the pistillate bract in mm. (AB in Fig. 3)
3 = Width of the pistillate bract in mm. (CD in Fig. 3)
4 = Lobe angle of the pistillate bract in degrees (E in Fig. 3)
5 = Length of the samara in mm. (JK in Fig. 3)
6 = Width (without wing) of the seed in mm. (FG in Fig. 3)
7 = Width of the samara (with wing) in mm. (HI in Fig. 3)

[1]) Basis: 25 bog birch, 66 yellow birch, and 8 hybrids.

[4]) Characters: 1) stomatal size, 2) pollen diameter, 3) leaf petiole length, 4) seed length, 5) number of teeth per leaf side, 6) staminate catkin length, 7) leaf base angle, and 8) pistillate bract width.

The hybrid population was found to be closer to the yellow birch population in the pictorialized scatter diagram (*Fig. 10*). Trees 15 and 23, putatively identified as yellow birches, appeared intermediate between the yellow birch and hybrid groups.

Discussion

Variability

The bog birches and yellow birches exhibited marked variability of most morphological characteristics measured. The bog birch appeared to be more uniform than yellow birch in some characteristics, such as pollen abortion, bark color and exfoliation, leaf margin types, bract pubescence and persistence, and leaf shape. Bract forms similar to those of sweet birch (*B. lenta* L.), paper birch (*B. papyrifera*), and river birch (*B. nigra* L.) were found among the yellow birches. This is significant because it suggests that bract form, traditionally used to distinguish birch taxa, must be used with greater discrimination. Although the bracts of bog birch are variable in shape, their small size prevented them from being confused with those of other native birches. Individuals of bog birch exhibited markedly uniform pollen with low abortion percentage. Pollen of yellow birch had a significantly greater amount of aborted and polyporate grains than that of bog birch. In marked contrast to the 2 parent species, the hybrids were relatively uniform in the leaf characteristics studied.

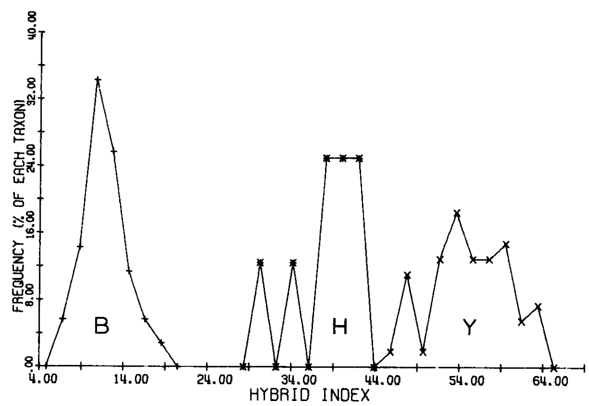


FIG. 9.— GRAPH OF FREQUENCY DISTRIBUTION OF HYBRID INDEX USING 8 CHARACTERS. BOG BIRCH (+) - 35 PLANTS, YELLOW BIRCH (X) - 54 PLANTS, AND HYBRID (*) - 8 PLANTS. MEAN HYBRID INDICES: BB = 11.6, H = 38.1, YB = 55.2.

The variability of the 2 species could be a result of 1) genetic differences due to recombination within and among different genomes of the respective species, 2) environmental modifications, or 3) hybridization and gene flow from other species.

The Walsh Lake yellow birches differed from classically described yellow birches in 3 respects:

1) some individuals had a dark and tight bark, very different from the yellow, silver, or bronze and highly exfoliating type reported for yellow birch (Gleason and Cronquist 1963, and Fernald 1950); 2) pistillate bracts were less pubescent and ciliate; and 3) the shapes of the pistillate bracts were quite variable and not consistently the ternate shape reported for yellow birch. The bark difference led many authors to confuse the dark and tight-barked birch with other birch taxa and hybrids (Dancik 1969). The similarity of many morphological characteristics and chromosome number of this yellow birch population to typical

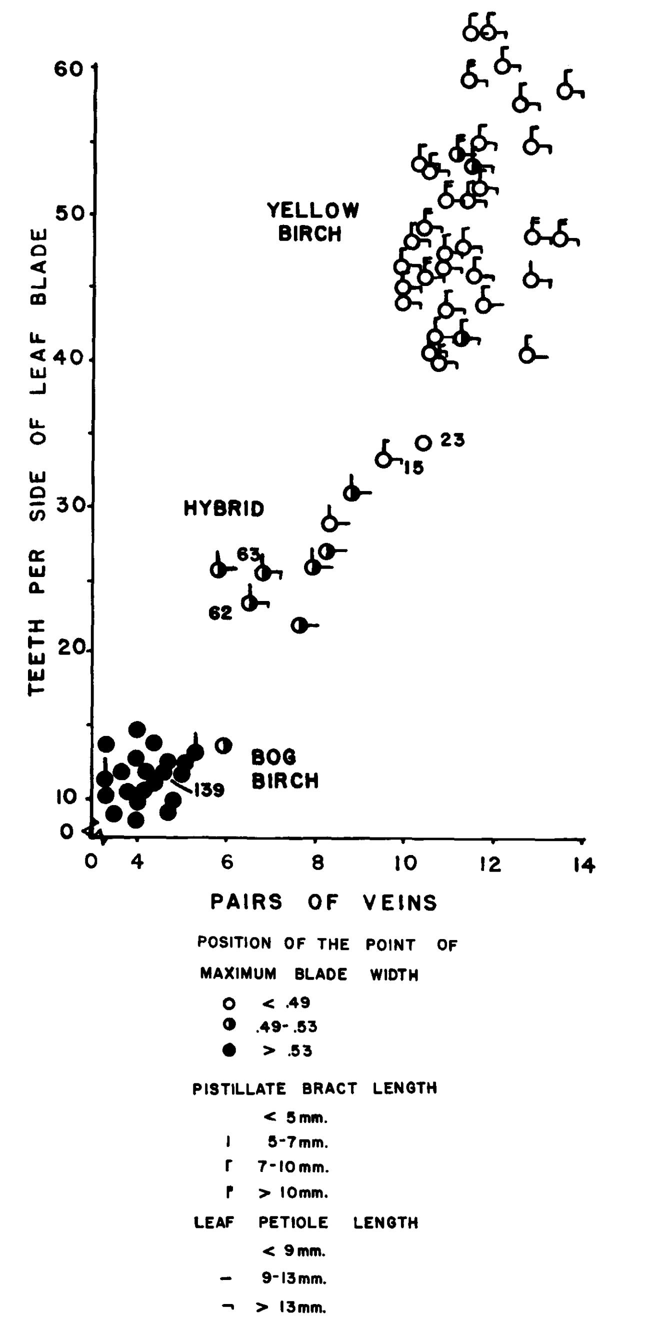


Fig. 10. — Pictorialized scatter diagram comparing 22 bog birches, 8 hybrids, and 37 yellow birches on the basis of 5 characters. (Tree 23 was incompletely plotted due to a lack of pistillate bracts).

yellow birch indicates a close relationship between the 2. There may even be no genetic differences — environmental modification alone may have caused the phenotypic differences. More likely, genecological differentiation has occurred, and a distinct race or clinodeme has been formed. Less likely, gene flow from bog birch may account for the differences.

Several individuals among the 3 taxa deserve special mention. Trees 15 and 23, initially identified as yellow birches, may be backcrosses of the hybrid to yellow birch. When compared with the other yellow birches, they had the most leathery leaves and the fewest teeth and veins of all. Pollen of 15 had the highest percentage of abortion of the yellow birches (23 had no pollen).

Plant 139, tentatively identified as a bog birch, may be a backcross of the hybrid to bog birch. Its leaves were larger than all but one of the bog birches, and its pistillate bracts were much larger and more linear than any of the bog birches. It had irregular meiosis and a chromosome number of approximately $n = 35$.

Hybridization and Introgression

On the basis of their morphological characteristics, abnormal cytological behavior, intermediate chromosome number, variability of pollen size, and high pollen abortion percentage, the 8 intermediate plants were considered F_1 hybrids between yellow birch and bog birch. Yellow birch was probably the seed parent of the hybrid plants. Bog birch generally flowered before yellow birch, and female flowers on any plant were receptive 1 or 2 days before pollen discharge on the same plant. Therefore, female flowers of the early flowering yellow birches would be receptive to bog birch pollen before yellow birch pollen was available. Sufficient flowering overlap did occur for bog birch pistillate flowers to be pollinated by yellow birch pollen, but presence of large amounts of bog birch pollen makes fertilization and development of hybrid seed less likely. Clausen (1961) reported the reverse situation for the parents of *B.* × *sandbergii* Britton in Minnesota, where the flowering sequence of the tree species, paper birch, and the bog birch was reversed.

The similarity of many characters of the hybrids to those of the yellow birches was probably due to the greater number of chromosomes and genes contributed by yellow birch. Thus, the intermediate plants were apparently F_1 hybrids and not backcrosses or introgressants. Theoretically the hybrid should receive 50% more chromosomes from yellow birch (42) than from bog birch (28). Assuming quantitative inheritance and predominantly additive gene action, the average hybrid index value of the F_1 population might be expected to fall 42/70 or 60% of the way between the 2. The average hybrid index for the hybrid population using 15 and 8 characters was 57% and 61%, respectively, of the distance between the parental means. Evidence from controlled crosses in *Betula* documents this interpretation. Dietrich (1963) reported that foliage characters of hybrids produced by controlled crosses between *B. pendula* Roth ($2n = 28$) and *B. pubescens* ($2n = 56$) were much closer to those of *B. pubescens*, the parent of higher ploidy.

Introgression is an increasingly common explanation given when intermediate plants resemble one of the parents in certain traits. We feel it is a term that is loosely used; introgression is often claimed without being demonstrated. Recently, negative evidence of introgression has been reported involving 2 of the classical examples of this concept (Randolph *et al.* 1967, Turner 1969). Introgression is the gradual infiltration of the germplasm of 1 species into that of another, or as explained by Anderson (1949), an increased variability in the participating species derived through repeated backcrossing of hybrids to 1 or both parents. Stebbins (1959) and Davis and Heywood (1963) have called attention to its 3 phases: hybridization, backcrossing, and natural selection of favorable recombinant types. Because of the attractiveness and possible evolutionary significance of this concept we believe authors (ourselves included) are prone to interpret results as introgression and overlook other explanations. Such explanations pertinent to this paper would be misidentifying F_1 hybrids and first generation backcrosses as introgressants. Because of the unequal chromosome contributions, introgressants in *Betula* would be expected to resemble very closely the parent of higher ploidy and would be unlikely to occur among those identified as F_1 hybrids. The only indication of introgression in our yellow birch population was the persistent amount of pollen abortion. However, this could be due to other factors, e. g., meiotic irregularities in the hexaploid yellow birch.

Recent studies of hybrid birch populations have emphasized introgression, but these conclusions are open to question for the above reasons. CLAUSEN (1962 b and 1963 b) concluded that introgression was evident in a population of paper birch, bog birch, and their natural hybrid. The finding that CLAUSEN's hybrid population overlapped that of paper birch, the parent of higher ploidy, would, in light of DIETRICH's work, suggests that the hybrids were F_1 individuals and not introgressants. The larger number of paper birch chromosomes could be responsible for the position of the intermediate plants nearer paper birch.

DUGLE (1966) reported numerous examples of introgression in several populations of birches. She reported that introgression in the hybrid populations of *B. glandulifera* REGEL × *B. resinifera* BRITT., *B. glandulosa* MICHX. × *B. glandulifera, B. fontinalis* SARG. × *B. papyrifera,* and *B. papyrifera* × *B.* × *sargentii* DUGLE was toward the parent of higher ploidy. DUGLE stated:

> No case among previous papers on introgression has come to my attention where the taxon with larger chromosome number introgresses the taxon with smaller chromosome number. The evidence would seem to point to the fact that in *Betula,* when other factors are equal, the species with the lower degree of ploidy introgresses the species with higher degree of ploidy.

What is almost always interpreted as introgression toward the taxon of higher ploidy, alternatively, may only be hybridization — the F_1 individuals resemble the parent of higher ploidy because it contributes more genes.

A questionable interpretation of introgression is evident in DUGLE's *B.* × *eastwoodae* SARG., a hybrid between 2 species of equal ploidy ($2n = 28$), *B. fontinalis* and *B. glandulosa.* The hybrid was midway between the parents in numerous traits and DUGLE reported that introgression proceeded equally toward both parents. However, the intermediate population might be only a group of F_1 hybrids whose range of phenotypic variation overlaps somewhat the ranges of the parents. This also seems possible since the hybrids alone were collected over an enormous range — from Saskatchewan to the Yukon territory.

Thus, in diverse birch populations, including our own, we question whether introgression has, in fact, occurred. To establish the existence of introgression, the range of variability of parents in populations not subject to hybridization should be determined along with the range of variability of F_1 hybrids and backcross generations produced by controlled pollinations. And, difficult as it is, considerable cytogenetic study must be employed before the extent and significance of hybridization and introgression in birches can be adequately resolved.

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Summary

A natural population of 112 unusual yellow birch, 39 bog birch, and 8 putative natural hybrids at Walsh Lake, Washtenaw Co., Michigan, U.S.A., was studied to determine 1) the variability of various characters of these taxa, 2) the relationship of this population of yellow birches to the classically described yellow birch; and 3) the extent and importance of hybridization and introgression. Studies of phenology, morphology, cytology, and pollen indicated that the intermediate plants were F_1 hybrids between bog birch and yellow birch. Haploid chromosome counts indicated $n = 28$ in the bog birch and $n = 42$ in the yellow birch; the hybrid was intermediate with $n = 35$.

Enough overlap in time of pollen discharge and female receptivity of the presumed parents occurred to allow hybridization. Yellow birch was probably the seed parent. Most morphological characters and groupings of characters of the hybrid plants were not midway between parental characteristics, but closer to those of the yellow birch. Assuming quantitative inheritance of most of the traits, these results were expected due to the fact that yellow birch ($n = 42$) contributes more chromosomes to the hybrid ($2n = 70$) than bog birch ($n = 28$). Two of the plants originally identified as yellow birch and 1 identified as bog birch were thought to be backcrosses.

Both bog and yellow birch exhibited a marked variation of all characters. The similarity of many of the characteristics of the Walsh Lake yellow birches to that of typical yellow birch indicated that they are closely related. Some individuals had a very dark and tight bark unlike the silvery-yellow, exfoliating bark typical of yellow birch. Pistillate bracts were less pubescent and ciliate and were not consistently the ternate form described for the species. The variability of yellow birch and these differences may be due to non-genetic environmental modifications, genetic differences caused by adaptation to local site conditions, gene flow from bog birch, or a combination of these possibilities. A combination of the first 2 seems the most plausible explanation at this time.

Compelling evidence of introgression was lacking. Although a few putative backcrosses were found, they could not be verified due to lack of knowledge of the range of variability in yellow birch and the F_1 hybrid. The widespread acceptance of introgression in birch populations was questioned. In most of these cases, natural hybrids were reported from species of unequal ploidy. The fact that individuals resembling the parent of higher ploidy are found does not necessarily indicate that they are backcrosses or that introgression has occurred. Rather they may be F_1 hybrids and, assuming quantitative inheritance and negligible dominance and environmental effects, resemble the parent of higher ploidy due to that parent's greater chromosome contribution to the hybrid. Clearly, studies of natural variation of parental species and the variation of F_1's and backcrosses from controlled pollination are needed before introgression can be accepted to have occurred or be important in natural populations of birches.

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Variation in Habit Forms of Scots Pine (Pinus silvestris L.) on the Area of Poland

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The presented paper presents one of segments of the complex research in native forms of Scots pine, carried out by the Forest Research Institute in Warsaw.

The main purpose of studies provided: 1) identification of characteristic types of habit forms in pine from selected seed producing stands, and 2) determination of their differentiating characters as criteria for preliminary evaluation of these forms for needs connected with the planned selection of native ecotypes of this species.

Such an approach determined the main direction of studies. It was expressed by the desire to know the population variations in the species on the background of identified geobotanical regions and plant associations, in which pine presents a fundamental or one of main forest-forming elements.

Studies were carried out during years 1961—1965 on the area of the whole country except of mountain and highland regions, where the Scots pine occurs in entirely different, when compared with lowlands, environmental conditions and where its quantitative share in specific composition of stands is rather low.

The distribution and quantity of study areas were conditioned by the previous selection of pine seed producing stands (TYSZKIEWICZ 1960). These areas are least numerous in central provinces, while more numerous in peripheral ones, what results from the higher forest area percentage in these regions.

Study method and area

Carrying out studies on so vast area brings about the necessity of the use of classification arranging changeable geographic and natural elements of the region with the consideration to their mutual relations.

In the present work there was accepted the division of Poland into geobotanical units proposed by Prof. W. SZAFER (1959).

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This division, considering relations existing between terrain sculpture, climate, and soil on the one hand, and plant associations on the other, is based on rather universal criteria for the evaluation of differentiation in vegetation conditions. Basing on the knowledge of natural geographical distribution of important trees and shrubs, natural variation of plant associations, and the history of plant cover development SZAFER identified on the area of Poland four geobotanical units of Ist order — "sections", and within "sections" units of lower order „subsections", "geographical regions", and, finally, "geobotanical districts".

The work included the area of two sections occupying the overwhelming portion of the country, namely: Baltic and Northern.

The Baltic Section occupies the whole lowland Poland and the major portion of highlands reaching Carpathians and Sudety. This area remains under the climatic influence of sea, which is less pronounced towards the east.

The Northern Section includes the eastern part of Mazurian Lake District and the north-eastern part of Mazowsze lowland. This section is distinguished by a more severe thermal climate, which contributed to the withdraw of few tree species from this area: beech, durmast oak, sycamore maple. Spruce is dominant in forest associations of this area.

Due to the unequal distribution of seed-producing stands on the area of country, the differentiation of habit characters in pine has been discussed for regions in order to avoid the excessive dispersion of experimental material. It is only within the Northern Section, where the analysis of differences within geobotanical districts was possible.

The seed-producing stands, in which measurements were taken, revealed optimal adaptation to local site conditions and, at the same time, distinguished themselves with a high quality of produced wood raw material. During measurement works they revealed a small differentiation in taxation features: tree cover and density was contained within