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Introgressive Hybridization between two Minnesota Birdies[1]

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Introduction

Natural interspecific hybridization in the genus *Betula* is relatively common, with numerous examples on record. Some of the earliest hybrids were described by Regel (1865), who also pointed out that since F_1 hybrids often have sterile pollen, they are more likely to be pollinated by either of the parents. He realized that such backcross progenies rather than being intermediate between the parental species, tend to resemble the recurrent parent more closely.

In spite of the many recorded instances of hybridization between members of the genus, few cases of introgression have been demonstrated. The European white birches, *Betula verrucosa* Ehrh. (B. *pendula* Roth) and B. pubescens Ehrh. have previously been regarded as one species, B. alba L. Recently the similarity between these species has been interpreted as resulting from introgressive hybridization between them by Yurkevich and Gel'tman (1956) in Russia, Jentys-Szaferowa (1950) in Poland, Stern (1959) and Natho (1959) in Germany. Natho also showed that B. *humilis* Schrank was introgressing into B. verrucosa and B. pubescens. In the United States, Froiland (1952) found evidence of introgression of B. occidentalis Hook. (B. *fontinalis* Sarg.) into B. papyrifera Marsh. in a hybrid swarm near Boulder, Colorado.

This paper deals with a case of introgressive hybridization between bog birch, B. pumila var. glandulifera Regel and paper birch, B. papyrifera Marsh. According to the classification of the genus by Winkler (1904), both species belong to the section Eubetula Regel. B. pumila L., together with all the other shrubby birches, is a member of the subsection *Nanae* Regel, while B. papyrifera and most other white-barked tree birches belong to the subsection Albae Regel. The major distinctions between the two species are their habit and bark characteristics. B. pumila is

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a low, many-stemmed shrub with reddish-brown, non-peeling bark; *B. papyrifera* is a tree with one or few stems, having white, exfoliating bark. The two species also differ in chromosome numbers. *B. pumila* is a tetraploid species (2n = 56), and *B. papyrifera* is either pentaploid (2n = 70) or hexaploid (2n = 84). Both species have a wide geographic distribution. The northern boundary of typical *B. pumila,* according to FERNALD (1950), reaches from Newfoundland and Labrador in the east to Ontario in the west. The southern limit of the species extends from Wisconsin through northern Indiana and Ohio to northern New Jersey and New England. The variety *glandulifera* is distributed from western Quebec to eastern British Columbia and southward to Montana, eastern North Dakota, central Minnesota, southeastern Wisconsin, northern Illinois, Indiana and New York. Only *B. pumila* var. *glandulifera* occurs in Minnesota, but for the sake of brevity this taxon will be referred to as *B. pumila* in this paper. *B. papyrifera* (including its five named botanical varieties) occurs as far north as Newfoundland and Labrador in the east and Alaska in the west, while its southern boundary extends from northeastern Washington through northern Idaho, Montana, Wyoming, Nebraska, Iowa, Illinois and Indiana eastward to north-central Pennsylvania and New York. The two species are, therefore, sympatric over the greater part of their ranges. The natural hybrid between these birches *(B.* × *sandbergii* BRITT.), first discovered in Minnesota in 1890 (ROSENDAHL, 1916), has only been found in southeastern North Dakota, Minnesota, Wisconsin, and Michigan, indicating that hybridization is more common near the southern limit of the parental ranges. Increasing frequency of hybrids from north to south within Minnesota supports this hypothesis (CLAUSEN, 1959).

History and Description of Study Area

The birch population studied is located about 10 miles north of St. Paul, Ramsey County, Minnesota (Long. 93° 09' W, Lat. 45° 06' N) in a bog just east of Lexington Avenue and north of County Road I *(Figure 1).* The soil in this area, derived from a yellowish-brown calcareous till, is overlain by muck in the boggy part. Except in severe drought periods, there is usually standing water in the lowest part of the bog, indicating a fairly high ground water table, probably due to the presence of Turtle Lake about 150 meters south of the area. The average precipitation in this vicinity is 26.8 inches, most of which falls during the period April through September (based on the 38-year record of St. Paul Weather Bureau Station). The average length of the growing season is 170 days.

The vegetation on the upland in the northwestern part of the study area is a relatively undisturbed open oak stand. Prior to cutting, the boggy lowland was covered with a dense tamarack *(Larix laricina* [DU ROI] K. KOCH) swamp with scattered paper birches. When cut in 1905, the trees ranged up to 30 cm in diameter. Following stump removal, the land was seeded with grass and used as a hay meadow until 1935, disturbed only by plowing and reseeding in 1925. After 1935, when the area was converted into a pasture, various shrubs began invading. Cattle were kept in the pasture until 1948. Since that time the land has been unused. Although it is common practice to burn old pastures in the spring in this region, the study area has not been exposed to fire. In 1923 the laying of a conduit, 6 feet in diameter, for transport of water to the city of St. Paul created considerable disturbance of the area immediately north of County Road I. In the following years a fairly dense growth of birches and various shrubs became established in a narrow strip on either side of the conduit. Among the birches were 23 individuals of the *B. pumila* × *B. papyrifera* hybrid, most of which unfortunately were lost in 1959 when a new conduit was installed north of the old one. Eight of these hybrid individuals, from which sufficient data and specimens had been collected before their destruction, were included in the study, together with 39 additional hybrids still present in the population.

The map *(Figure 1)* shows the major types of woody vegetation as well as the location of these 39 birch hybrids. Due to the recent disturbance, a 55 meter wide strip of the bog just north of County Road I was excluded form the map.

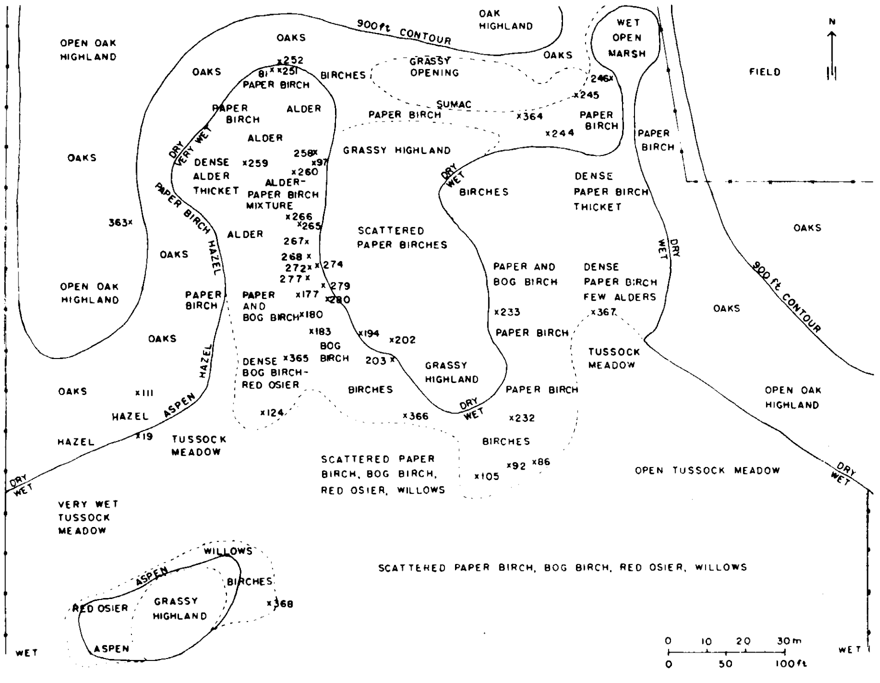

Figure 1. — Map of study area showing location of hybrids (X81, X86, etc.). The dashed lines indicate boundaries of dense vegetation.

Methods of Data Collection

The data for this study were obtained from 347 of the birches in the population. In addition to the 47 birches showing hybrid characteristics 150 individuals of each parental species were included. The parental groups comprised all of the *B. pumila* present in the population and a randomly selected sample of about 20% of the *B. papyrifera* individuals. A number of characteristics were measured or scored and the values punched on 40 column IBM cards in the field. This information was later transferred by machine to 80 column IBM cards on which all laboratory measurements were punched also. All data punched on the cards were then tabulated on an IBM machine. The 12 characteristics measured are listed below:

1. Length of male catkin
2. Length of female catkin
3. Length of female catkin peduncle
4. Pairs of lateral leaf veins
5. Number of teeth between 2nd and 3rd lateral veins above base
6. Length of leaf blade (AC)
7. Length of leaf petiole
8. Distance from leaf apex to widest part (AB)
9. Position of maximum leaf width (AB/AC)
10. Basal leaf angle
11. Leaf weight
12. Width of leaf blade

The mean of five measurements per individual was used for each catkin characteristic. The leaf measurements represented the mean of ten randomly selected spur-shoot leaves; these were used since they tend to vary less than long-shoot leaves. The leaves, taken from dried specimens collected in the beginning of August, were placed on graph paper (millimeter) and traced with a sharp pencil. Thus a permanent record was obtained and measurements could be read directly. The ratio AB/AC was calculated, because in *Populus* clones this characteristic has been found to vary little throughout the growing season (Broekhuizen, 1961). The basal leaf angle was measured as suggested by Woodson (1947), but due to the asymmetry of occasional leaves, the mean value of both leaf halves was used.

Six characteristics were assigned scores on a scale from 0 to 4. In all cases individuals resembling *B. papyrifera* received scores of 0, and those resembling *B. pumila* were scored as 4. The meaning of the scores is explained in *Table 1.*

Pollen viability was estimated in 32 *B. pumila*, 33 hybrids, and 31 *B. papyrifera*. The pollen was stained with a vital stain containing methyl green and phloxin (Worsley, 1959), and about 500 grains from each plant were examined. Grains having fully expanded red cytoplasm and green pollen wall were classified as viable, and green grains with collapsed cytoplasm or slightly expanded cytoplasm stained a mottled red color were considered aborted.

A hybrid index based on the 12 measured morphological characteristics was developed. This index differs from that of Anderson (1936) in being based on actual measurements, rather than on scores from an arbitrary scale. Greater objectivity was expected of this type of index. For each characteristic a mean between the parental groups was calculated, and all individual values of the characteristic were converted to percentages of this mean. In this way differences due to varying units of measurement were eliminated and all characteristics received equal weight in the index. To avoid large numbers the mean rather than the sum of the converted values of the 12 characteristics was used as the hybrid index value of an individual. Hybrid index values were computed for all 347 birches included in this study.

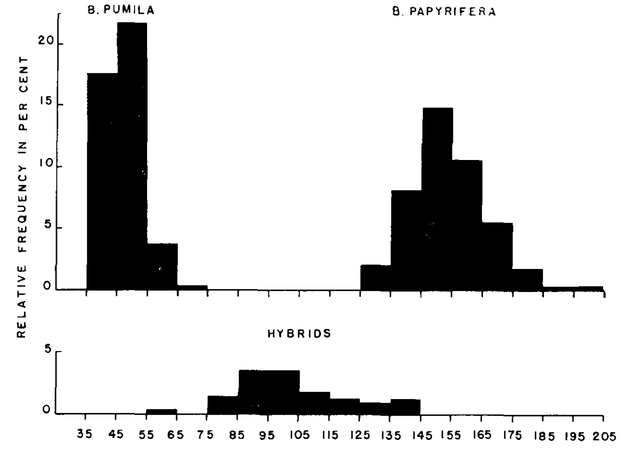

Figure 2. — Histograms of hybrid index values of *B. pumila*, hybrids, and *B. papyrifera*.

Alcohol extracts were made from the inner bark of samples of *B. pumila*, *B. papyrifera* and 35 hybrids. Aliquots of the concentrated extracts were spotted on Whatman No. 1 filter paper and placed in a chromatographing cabinet previously equilibrated with ammonium hydroxide, secondary butyl alcohol and water. The chromatograms were developed by descending irrigation for 24 hours, using secondary butyl alcohol equilibrated with water as the irrigating solvent. The dried chromatograms were sprayed with a 2% aqueous solution of sodium carbonate and again dried. The treatment with sodium carbonate caused fluorescent spots to appear on the chromatograms when these were viewed under ultraviolet light.

Results

The *B. pumila* and *B. papyrifera* individuals had hybrid index (H. I.) values separating the two taxa clearly from each other, but the *B. papyrifera* sample had much more variation in H. I. values than the *B. pumila* sample *(Figure 2)*. Most of the hybrids received intermediate H. I. values, indicating that these individuals probably are F_1 hybrids. A number of putative hybrids were clearly inside the distributions of H. I. values of the parental groups *(Figure*

Table 1. — Meaning of scores assigned to six morphological characteristics.

Characteristic	Scores				
	0	1	2	3	4
Bark color	White	Yellowish or grayish-white	Tan	Light reddish-brown	Dark reddish brown
Bark exfoliation	Extensive	Some	Little	Few strips	None
Position of ♂ catkins	Terminal	—	Terminal and axillary	—	Axillary
Position of ♀ catkins at maturity	Pendent	—	Intermediate	—	Erect
Size of fruit wings	Wider than nutlet	—	As wide as nutlet	—	Narrower than nutlet
Shape of fruit bract	Lateral lobes divergent	—	Lateral lobes truncated	—	Lateral lobes ascending

2) and may not be F_1's. They may be F_2's or they may have been derived from backcrosses to either of the parental species. Since hybrid pollen is highly sterile, F_2's would not be expected. Only one hybrid, No. 183, fell inside the frequency distribution of *B. pumila*, suggesting a backcross to this taxon. Seven hybrids had H. I. values within the range of *B. papyrifera;* these may have resulted from backcrosses to this parent. The larger number of putative backcrosses to *B. papyrifera* indicates an introgression in this direction.

An index value which is the mean of 12 characteristics may of course obscure some of the variation in each hybrid individual since divergent tendencies, if present, will tend to counteract each other. A hybrid could thus resemble one parent in half of the characteristics and the other parent in the other half of the characteristics and still receive an intermediate H. I. value. It is therefore of interest to compare the interactions of the 12 characteristics in the 47 hybrid individuals. The polygonal graph employed in this work is one method of portraying and comparing several variables simultaneously (Davidson, 1947).

The polygons *(Figures 3 and 4)* graphically demonstrate that the average *B. papyrifera* had higher values than the average *B. pumila* in all characteristics, while most of the hybrids, as expected, were nearly intermediate between the parental groups. Although many of the hybrids resembled each other closely, as evidenced by the similarity in size and shape of the polygons, some variation in different characteristics was of course present. The length of the male catkin and the female catkin and its peduncle appeared more variable than most of the leaf characteristics. In general, individuals having intermediate H. I. values tended to be intermediate in most characteristics. This was particularly true of hybrids No. 124 through 105 *(Figures 3 and 4).*

Hybrid No. 183 approached *B. pumila* in all characteristics, differing mainly in its longer catkin peduncle. The similarity between the two polygons suggests that this individual probably was derived from a backcross to *B. pumila.* Since hybrids No. 92, 364, 232, 233, and 19 approached *B. papyrifera* in all 12 characteristics, their polygons resemble each other and that of *B. papyrifera.* Hybrid No. 244 resembled *B. papyrifera* in all characteristics except leaf weight and leaf width; for these characters it had values about intermediate between the parental groups. Individual No. 81, except for the smaller leaf weight and the longer female catkin, approached *B. papyrefera* in all characteristics. These differences are reflected in the respective polygons in *Figure 4.* The general appearance of these seven polygons suggests the close affinity of these hybrids to *B. papyrifera* and the probability that they have been derived from backcrosses to this taxon.

The coefficients of correlation demonstrate that most of the 12 characteristics are positively correlated in the hybrids *(Table 2).* Since 9 of the characteristics are leaf attributes, this result is not surprising. The correlations indicate that certain characteristics tend to be associated with each other, but the nature of the study material does not permit investigation of possible linkage.

A pictorialized scatter diagram (Anderson, 1949) was prepared as an additional method of displaying character association. Two strongly correlated characteristics used in the hybrid index, male catkin length and position of maximum leaf width, served as coordinates, and each individual in the population was plotted on these axes *(Figure 5).* The two areas enclosed by the dashed lines in Figure 5 represent the distribution of the parental groups. The six scored morphological characteristics of the mean *B. pumila*, the mean *B. papyrifera*, and of each hybrid individual are indicated by symbols. Five of these characteristics, bark color, bark exfoliation, male catkin position, female catkin position and shape of fruit bracts, appeared to be qualitative traits. The sixth characteristic, size of the fruit wings, probably is a quantitative trait, but was scored instead of measured.

The ranges of variation in position of maximum leaf width were about equal in the parents, while the *B. papyrifera* sample varied much more in male catkin length than the *B. pumila* sample. The mean *B. pumila* had 3.3 mm-long axillary male catkins, erect female catkins, fruit wings narrower than the nutlet, and fruit bracts with ascending lateral lobes. The bark was dark reddish-brown and tight, and the widest part of the leaf was the upper half (a value of less than 0.50 on the ordinate). The mean *B. papyrifera*, on the other hand, had 26.6 mm-long terminal male catkins, pendent female catkins, fruit wings wider than the nutlets, and fruit bracts with divergent lateral lobes. The extensively-peeling *B. papyrifera* bark was white, and the widest part of the leaf was the lower half (value of more than 0.50 on the ordinate).

The pictorialized scatter diagram *(Figure 5)*, like the hybrid index, placed 39 of the hybrids between and completely outside the ranges of the parental species. In this group, male catkin length ranged from 6 to 16 mm, and the ratio measuring position of maximum leaf width varied from 0.47 to 0.65. Since most of the hybrids clustered around a ratio of 0.55, their leaves were widest slightly below the middle. Valid chi-square tests of independence

Table 2. — Correlation coefficients of 12 hybrid index characteristics in hybrids.

Char.1) No.	1	2	3	4	5	6	7	8	9	10	11
2	.625**										
3	.247	.352*									
4	.797**	.288*	.279								
5	.612**	.505**	.192	.771**							
6	.630**	.414**	.179	.577**	.533**						
7	.617**	.464**	.304*	.476**	.401**	.814**					
8	.704**	.411**	.193	.710**	.673**	.925**	.779**				
9	.518**	.194	.106	.645**	.645**	.411**	.377**	.719**			
10	.653**	.311**	.147	.783**	.755**	.442**	.378**	.766**	.745**		
11	.559**	.226	.242	.400**	.299*	.799**	.794**	.710**	.242	.379**	
12	.635**	.334**	.138	.609**	.587**	.885**	.698**	.834**	.409**	.633**	.727**

1) Characteristics numbered as on page 144

* = significant at the 5% level

** = significant at the 1% level

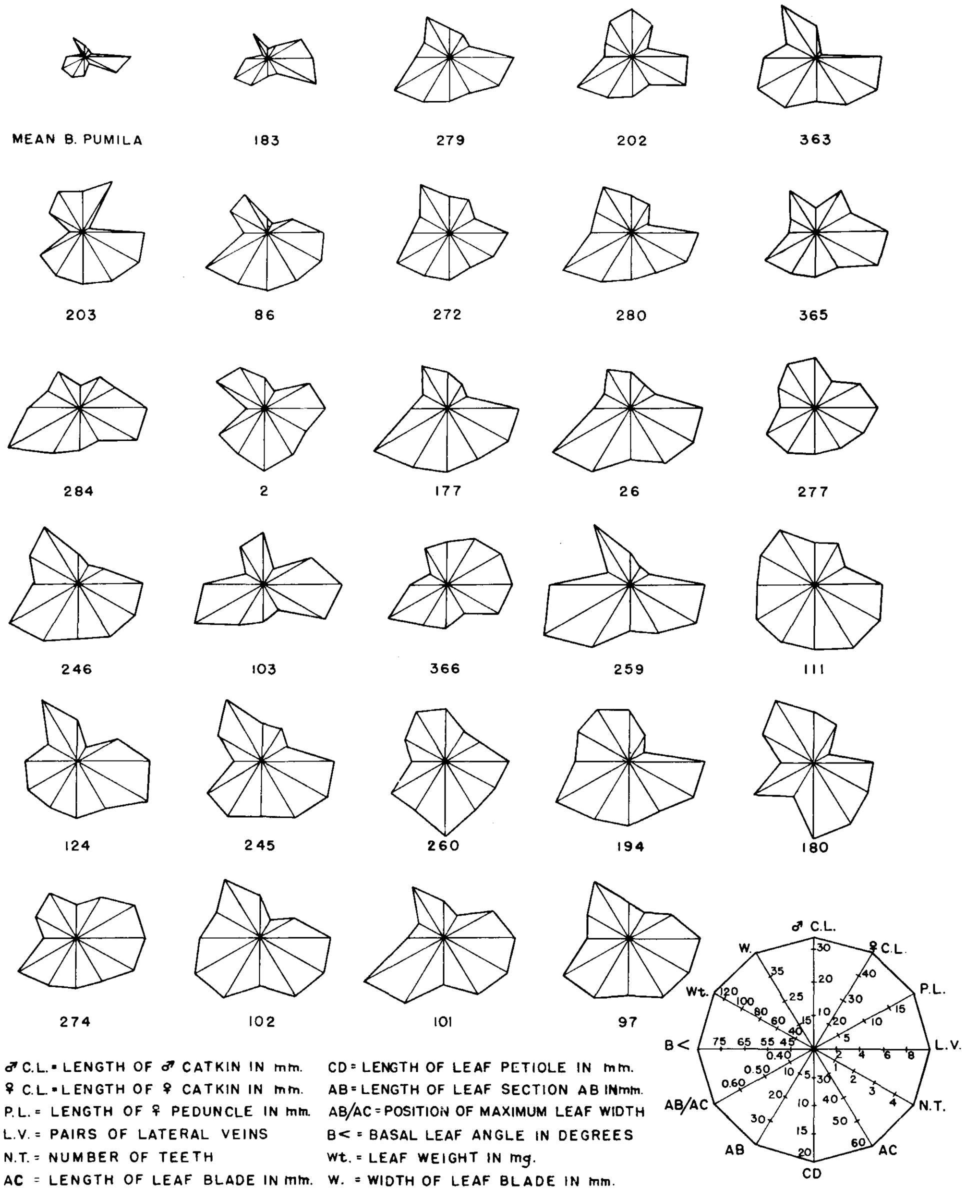

Figure 3. — Polygonal graphs showing expressions of 12 morphological characteristics in the mean *B. pumila* and in 28 hybrids. Numbers (183, 279, etc.) are individual plant numbers.

between the six scored morphological characteristics could not be made, but certain traits seemed to be associated. The strongest association appeared to be between size of fruit wings and shape of fruit bracts, indicating that these characteristics, which are good taxonomic criteria in the birches, possibly are genetically linked. Characteristics showing weaker association were position of male and female catkins and the color and exfoliation of the bark.

Plant No. 183, the putative offspring of a backcross to *B. pumila*, again fell inside the range of this species and differed from the mean *B. pumila* only in having a slightly smaller male catkin and the widest part of the leaf slightly lower down in the leaf. Seven putative backcrosses to *B. papyrifera* fell within the range of the recurrent parent, and all resembled the mean *B. papyrifera* to greater or lesser degree. However, the H. I. value of one of these individuals (No. 368) was not inside the range of *B. papyrifera*, while No. 244, whose H. I. value was inside the range, fell outside in the scatter diagram. Probably both individuals should be considered as progeny of backcrosses to *B. papyrifera*.

Viability of pollen samples of the three taxa is presented in *Table 3*. Individual plants of *B. pumila* had from 77.4 to 99.5% viable pollen, while the mean for the species was 94.1%. *B. papyrifera* plants ranged from 71.6 to 100%, with a mean pollen viability of 91.0%. Both parental species thus had normal pollen, while most of the hybrids had a high proportion of inviable pollen. Individual hybrids ranged from 28.1 to 94.5% stainable pollen; the mean for this taxon being 58.0%. Two hybrids, No. 233 and No. 232, which were classified as progeny of backcrosses to *B. papyrifera*, had 91.7 and 94.5% viable pollen respectively. Since pollen fertility tends to increase with backcrossing, the normal pollen found in these individuals substantiates their backcross origin. Pollen of other putative backcrosses was not available for testing.

The paper chromatograms showed that certain colored spots were characteristic of each species. Since the perti-

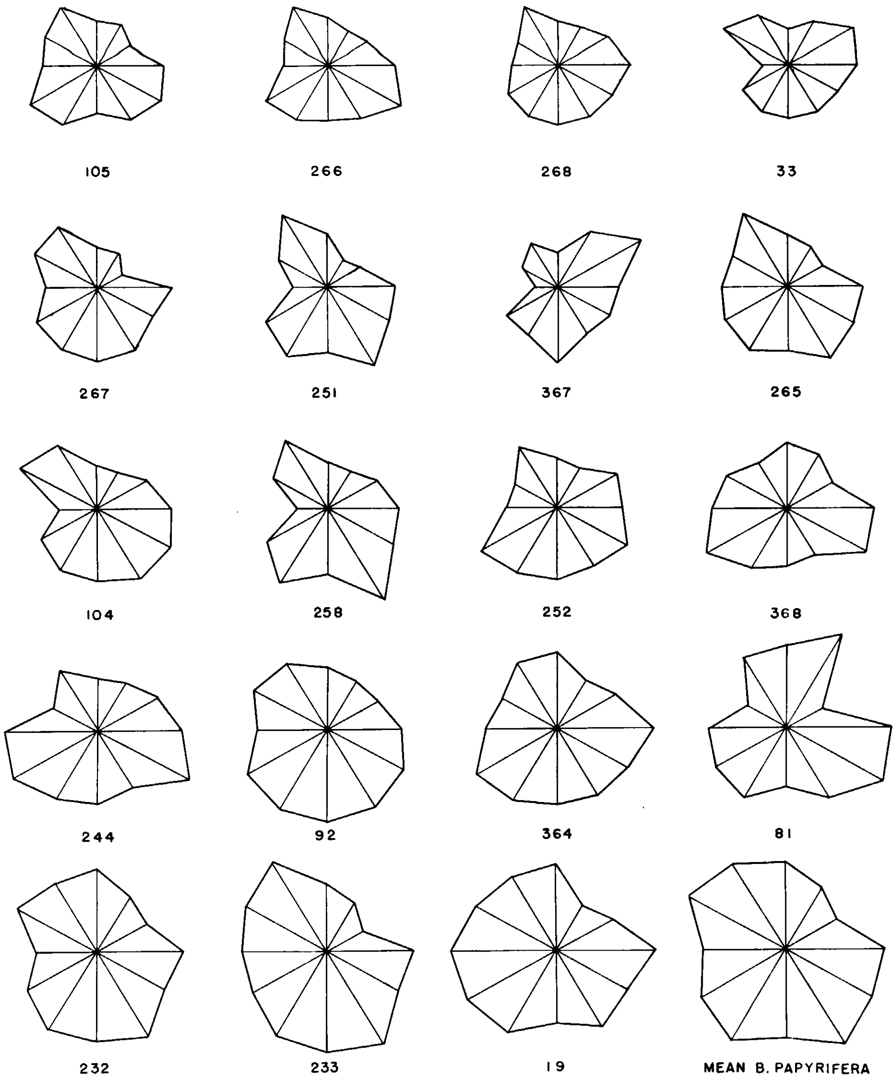

Figure 4. — Polygonal graphs showing expressions of 12 morphological characteristics in 19 hybrids and in the mean *B. papyrifera*. Numbers (105, 266, etc.) are individual plant numbers.

nent spots were invisible in daylight, the color designations in the following refer to their fluorescence under ultraviolet light. Chromatograms of *B. pumila* extract typically had three small purple spots of about equal size, while the typical *B. papyrifera* chromatograms had one larger bright blue spot. There were no clear-cut interactions of these colors in the hybrids. Eight of the hybrids resembled paper birch in having one large bright blue spot, while one individual (No. 268) had one light blue spot and another individual (No. 180) had one light purple spot. Fifteen hybrids had two spots in various combinations of bright blue, light blue, bluish purple, light purple, or purple. The 10 hybrids having three spots had combinations of two or three colors, and none resembled bog birch in having three purple spots with the possible exception of hybrid No. 363, which had one light purple and two purple spots. The compounds responsible for the spots were not identified.

Table 3. — Frequency distribution of pollen viability.

Viability Classes (Per Cent)	Number of Individuals		
	B. pumila	Hybrids	*B. papyrifera*
21- 30	-	2	-
31- 40	-	4	-
41- 50	-	4	-
51- 60	-	10	-
61- 70	-	5	-
71- 80	3	5	5
81- 90	6	1	7
91-100	23	2	10
Total	32	33	31

Discussion

The hybrid index and the pictorialized scatter diagram provide evidence that introgressive hybridization has taken place in this birch population. Since only one hybrid was found which appeared to be a backcross to *B. pumila*, backcrossing to this taxon probably is rare. The fact that all *B. pumila* and individuals resembling this taxon in the population were examined, precludes any possibility that other putative backcrosses in this direction were overlooked.

The objection may of course be raised that the hybrid index, while capable of separating most of the hybrids from either parent, may fail to distinguish the putative backcrosses, so that other more subjective criteria must be used in conjunction with it. Fruit characteristics are generally considered good taxonomic criteria, and in the

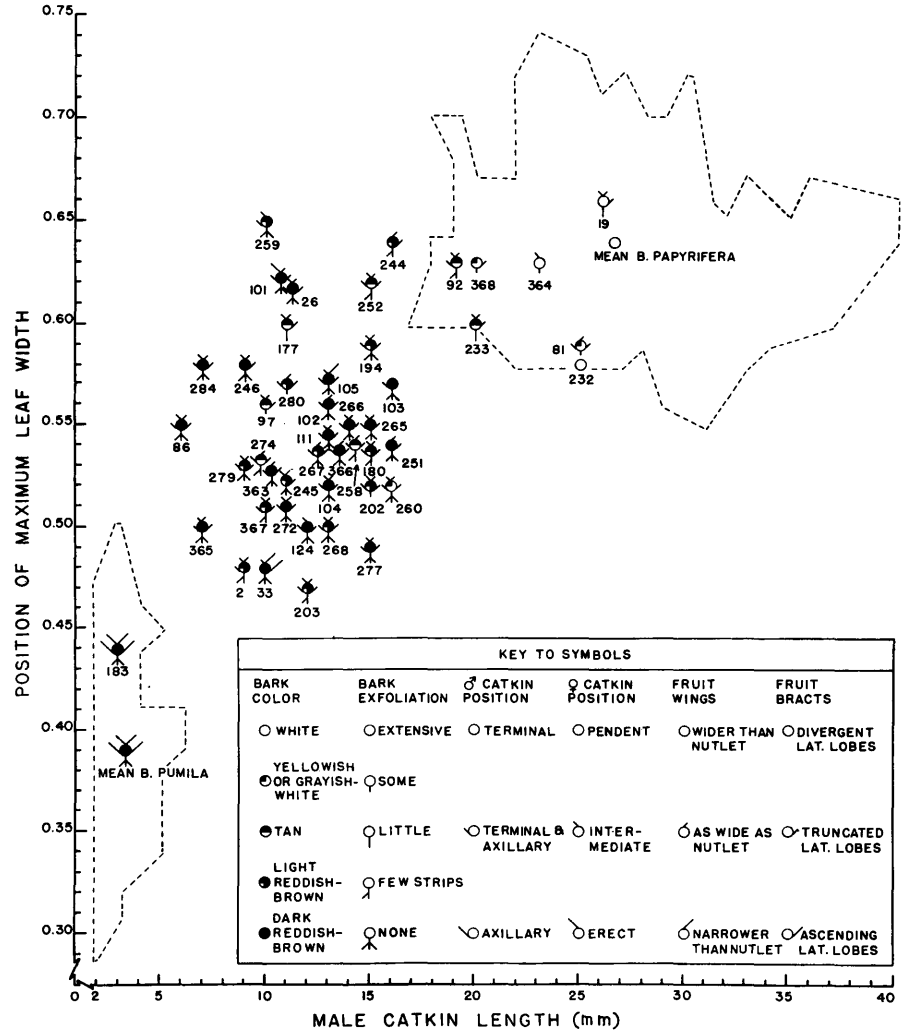

Figure 5. — Pictorialized scatter diagram showing combinations of eight morphological characteristics in the mean *B. pumila*, in 47 numbered hybrids, and in the mean *B. papyrifera*. The dashed lines enclose the distributions of the parental groups.

birches they appear to provide reliable means of recognizing hybrids and hybrid segregates. Paper chromatography of substances present in the inner bark in this case was not an infallible taxonomic tool, but the technique proved to be of value in providing substantiating evidence. In four individuals which were classified as hybrids (Nos. 364, 233, 232, and 19), but resembled *B. papyrifera* closely, the presence of the compound typical of *B. pumila* gave evidence that these individuals were not misclassified, but were probably backcrosses to *B. papyrifera*. The presence of the *B. pumila* compound no doubt reflects the introgression of *B. pumila* genes into *B. papyrifera*. The fact that two of these backcross hybrids, No. 232 and 233, had pollen of as high fertility as the average for the parental species also substantiates the classification of these individuals as progeny derived from backcrosses to *B. papyrifera*.

The presence of eight backcrosses to *B. papyrifera* strongly suggests that the gene flow has been from *B. pumila* into *B. papyrifera*. In this population *B. papyrifera* also has more variation in both the individual characteristics and in hybrid index values than *B. pumila*. This could be the result of repeated backcrossing in the past which has introduced *B. pumila* genes into the *B. papyrifera* population. Such previous introgression would not be easily recognized, but could account for increased variation in a group of plants. Since only 20% of the individuals in the study population resembling *B. papyrifera* was examined, it is possible that additional backcrosses to *B. papyrifera* were present in the population, but were not detected in this study.

The conclusion that the introgression has been in the direction from the shrubby parent into the tree-sized parent is similar to the conclusions reached in other studies of introgressive hybridization in *Betula*. Froiland (1952) found evidence of introgression of the shrub, *B. occidentalis*, into *B. papyrifera* in a hybrid swarm in Colorado, and Natho (1959) in Germany, showed that the shrubby *B. humilis* was introgressing into two species of trees, *B. verrucosa* and *B. pubescens*. Two of these examples of introgression also resemble the present case in that gene flow was from a species of lower ploidy into a species of higher ploidy. Thus in one case, *B. occidentalis* is a diploid, while *B. papyrifera* is pentaploid or hexaploid, and in the other case *B. humilis* is diploid and *B. pubescens* tetraploid. In the third case both parents, *B. humilis* and *B. verrucosa*, are diploid species. Several European authors (Yurkevich and Gel'tman, 1956; Jentys-Szaferowa, 1950; Stern, 1959; Natho, 1959) have also reported introgressive hybridization between the diploid *B. verrucosa* and the tetraploid *B.*

pubescens. Although some backcrossing to *B. verrucosa* is considered likely, most authors agree that most of the introgression is from *B. verrucosa* into *B. pubescens.* In *Betula,* when the parents differ in chromosome number, the direction of the introgression thus seems to be from the species of lower ploidy into the species of higher ploidy; in the present case from a tetraploid into a pentaploid or hexaploid.

ANDERSON (1948) developed the hypothesis that the occurrence of hybrid swarms was limited to areas where nature or man had disturbed the habitat. Several published accounts of introgression in herbaceous species have supported this viewpoint. In trees fewer cases of introgressive hybridization are known, but SILLIMAN and LEISNER (1958) stated that hybrids between *Quercus alba* L. and *Q. prinus* L., showing introgression of the former into the latter, were only found in disturbed habitats. PRYOR (1953) in Australia concluded that hybrids between species of *Eucalyptus* normally occupying different ecological niches had arisen in overlapping areas of distribution when the balance of the plant communities had been upset by fire and clearing by man. An earlier study of the distribution of the hybrid *(B. pumila* var. *glandulifera* × *B. papyrifera)* in Minnesota (CLAUSEN, 1959) revealed that most hybrid individuals occurred along roadsides and ditches and in other areas where the environmental conditions had been disturbed.

The present study lends further support to ANDERSON's hypothesis. The study area, as mentioned previously, had been subjected to considerable disturbance by man's activities, chiefly logging, stump removal, and plowing. The fact that a total of 62 hybrids had become established in the relatively small area studied, indicates the importance of site disturbance in the establishment of natural hybrids and their segregates. The occurrence of 23 hybrids in the area along the water conduit suggests that increased habitat disturbances favor a high frequency of hybrid establishment.

The map of the study area *(Figure 1)* shows that the majority of the hybrids grew in the transition zone between the wet boggy part of the area and the slightly higher upland. Only a few were found in the very wet places where *B. pumila* was common and fewer occurred on the highland. Most of the hybrids thus appeared to occupy habitats intermediate in soil moisture conditions between those of the parental species, indicating that physiological characteristics, such as site requirements, are under genetic control in the birches. Since introgressive hybridization leads to the establishment of populations containing a few genes or chromosomal segments of one species on the genetic background of another (ANDERSON, 1949), the visible effects of the introgression may only be an apparent modification and amplification of the variation pattern of the recurrent species. However, since hybrids and their segregates may differ from either parent in less obvious physiological characteristics, they may be better suited to new ecological niches created by disturbances of the habitat. The selective advantage possessed by the hybrids and their offspring may thus allow them to spread and multiply in the new environment to which they are adapted. Introgression may thus play an important part in the development of populations adapted to specific environmental conditions and the consequent evolution of ecotypes. Since interspecific hybridization under favorable circumstances may lead to introgression, this type of gene exchange, as pointed out by STEBBINS (1959) is thus not necessarily a "blind alley" of evolution.

In addition to the discussed cases in the genus *Betula,* introgression has been demonstrated in *Acer* (DANSEREAU and DESMARAIS, 1947; PADDOCK, 1961), *Aesculus* (HARDIN, 1957), *Juniperus* (HALL, 1952), *Picea* (GARMAN, 1957; HEIMBURGER, 1958; HORTON, 1959), *Pinus* (ZOBEL, 1951; BANNISTER, 1958; HALLER 1959; NEWCOMB, 1959), and *Quercus* (STEBBINS, MATZKE and EPLING, 1947; COOPERRIDER, 1957; BRAY, 1960; TUCKER and HASKELL, 1960; MULLER, 1961). This indicates that introgression is an important phenomenon in forest trees and should be recognized as such. Thus, in studies of racial variation, samples collected from areas where two species of the same genus are sympatric may contain unexpected hidden variation due to introgression. Furthermore if an introgressed individual, which can be almost indistinguishable from the recurrent species, is used as a mother tree or pollen source in artificial hybridizations, undesired characteristics of the donor parent may be transmitted to the progeny. Forest geneticists and persons engaged in forest tree improvement should, therefore, be aware of introgression and take it into account not only in the planning and establishment of studies but also in the analysis and interpretation of experimental results.

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Summary

A Minnesota population consisting of 150 shrubby individuals of *Betula pumila* var. *glandulifera,* 150 trees of *B. papyrifera* and 47 natural hybrids between these species has been studied. A hybrid index based on 12 morphological characteristics disclosed the presence of one backcross to *B. pumila* and seven backcrosses to *B. papyrifera.* An additional backcross to *B. papyrifera* was identified using a pictorialized scatter diagram, which demonstrated interactions of two of the hybrid index characteristics with six additional morphological characteristics. The higher number of backcrosses to *B. papyrifera* and the larger range of variation of this species suggests an introgression of *B. pumila* into *B. papyrifera.* The identification of four hybrids as backcrosses was verified with the aid of paper chromatography. An unidentified compound typically present in the inner bark of *B. pumila* was found in these individuals, which otherwise resembled *B. papyrifera* very closely. Two of these backcrosses also had normal pollen, while most hybrids had pollen with much lowered viability. Most of the hybrids occurred in areas intermediate in soil moisture content between those of the parental species. Known disturbances of the habitat by man no doubt created the new ecological niches necessary for the establishment of the F_1 hybrids and their segregates.

Zusammenfassung

Titel der Arbeit: *Introgressive Hybridisation zwischen zwei Birken in Minnesota.*

Eine Population aus Minnesota, die aus 150 strauchigen Individuen von *Betula pumila* var. *glandulifera,* 150 Bäumen von *B. papyrifera* und 47 natürlichen Bastarden zwi-

schen diesen beiden Arten bestand, ist untersucht worden. Der angewandte Bastard-Index, der auf 12 morphologischen Merkmalen aufgebaut war, klärte das Vorhandensein von 1 Rückkreuzung zu *B. pumila* und von 7 Rückkreuzungen zu *B. papyrifera* auf. Eine weitere Rückkreuzung zu *B. papyrifera* wurde anhand eines gezeichneten Streuungsdiagrammes identifiziert, das Interaktionen von 2 im Bastard-Index verwandten Merkmalen mit 6 zusätzlichen morphologischen Charakteren aufzeigte. Die höhere Zahl der Rückkreuzungen mit *B. papyrifera* und die größere Variationsbreite dieser Spezies deuten auf eine Introgression von der *B. pumila* in die *B. papyrifera* hin. Die Identifikation von 4 Bastarden als Rückkreuzungen war mit Hilfe der Papierchromatographie verifiziert worden. Eine nicht näher identifizierte Komponente, die sonst für die innere Rinde von *B. pumila* typisch war, wurde bei diesen Individuen gefunden, die im übrigen der *B. papyrifera* sehr stark ähnelten. Zwei von diesen Rückkreuzungen besaßen auch normalen Pollen, während sonst die meisten Hybriden nur Pollen von stark verminderter Lebensfähigkeit aufwiesen. Die meisten dieser Hybriden fanden sich in Gebieten mit einer intermediären Bodenfeuchte zu denen der beiden Eltern-Arten. Die durch den Menschen verursachten Veränderungen in der natürlichen Verbreitung ergaben zweifellos diese neuen ökologischen Nischen, die für eine solche F_1-Entstehung und ihre Aufspaltungen erforderlich gewesen waren.

Résumé

Titre de l'article: *Hybridation introgressive entre deux bouleaux du Minnesota.*

On a étudié une population du Minnesota comprenant 150 individus buissonnants de *Betula pumila* var. *glandulifera,* 150 arbres de *B. papyrifera* et 47 hybrides naturels entre ces deux espèces. Un index d'hybridation basé sur 12 caractères morphologiques a permis de mettre en évidence la présence d'un croisement en retour vers *B. pumila* et 7 croisements en retour vers *B. papyrifera.* On a pu identifier un autre croisement en retour vers *B. papyrifera* en employant un diagramme de dispersion qui a révélé des interactions entre deux des caractéristiques de l'index d'hybridation et six caractères morphologiques supplémentaires. Le nombre plus élevé de croisements en retour vers *B. papyrifera* et la variabilité plus large de cette espèce suggèrent une introgression de *B. pumila* dans *B. papyrifera.* L'identification de quatre hybrides comme des croisements en retour a été vérifiée par chromatographie sur papier. Un corps non identifié, présent dans l'écorce intérieure de *B. pumila,* a été trouvé dans ces individus, qui, par leurs autres caractères, ressemblent beaucoup à *B. papyrifera.* Deux de ces croisements en retour ont aussi un pollen normal alors que la plupart des hybrides ont un pollen avec une viabilité très affaiblie. La plupart des hybrides se trouvent dans des zones intermédiaires en ce qui concerne la teneur en eau du sol entre les zones habitées par les espèces parentes. La perturbation par l'homme des habitats naturels a sans aucun doute créé les nouvelles «niches écologiques» nécessaires pour que s'installent les hybrides F_1 et leurs descendants.

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