The hybrid Betula lutea, sect. Costatae x Betula occidentalis, sect. Albae

By HELGE JOHNSSON[1])

(Received November 1973)

The two tall-growing North-American Betula species, B. lutea and B. occidentalis, differ conspicuously from each other in a number of characteristics. B. lutea is put into the section Costatae, which is distinguished by the narrow samara wings, not as broad as the nutlet, and B. *occidentalis* into the section Albae, which have samara wings broader than the nutlet (cee fig. 8). B. lutea has serrate oblong-ovate leaves, B. occidentalis more or less distinctly doubly serrate ovate leaves (fig. 6). The most striking difference is seen in the strobiles, which in B. lutea are ovate, subsessile and erect, in B. occidentalis cylindric, slender-stalked and pendulous (figs. 2—3). B. lutea has considerably larger bracts than B. occidentalis and also longer nutlets (figs. 8—9). B. lutea occurs in Eastern North-America, B. occidentalis in the western part. Possibly the two areas of distribution touch each other south of Lake Winnipeg. Both species are hexaploid — n = 14 — (WOODWORTH 1931) in contrast to related species that are for the most part diploid or tetraploid.

Material

The material dealt with in this paper originates in a cross made in the spring of 1945 in greenhouse on a bottle-grafted twig of B. lutea (*fig.* 1). Both parents are cultivated,

Fig. 1. — Bottle-grafted twig of ***Betula lutea,*** used in hybridizing experiments.

one in the botanical garden in Uppsala, the other in the botanical garden in Lund. Thus, their exact provenances are unknown. However, they are typical for their species as regards morphology as well as chromosome number. The cross gave 6 mature strobiles, from which 20 seedlings could be raised. As a strobile contains approximately 350 seeds, it implies a germinability of about 1%. The chromosome numbers were stated for 15 seedlings, which were all hexaploid. In the spring of 1955 some of the young trees flowered. The pollen grains were examined for 7 trees. The percentually, morphologically good grains varied from 86.7 to 97.8. Corresponding values for B. lutea and B. occidentalis were 98.1 resp. 98.2. The average grain diameters varied between 10.7 and 11.5 units for the progeny as compared with 11.5 units for B. lutea and 11.3 for B. occidentalis. The size variation of the grains was not greater in the progeny than in the parent species. Three crosses with 5 trees involved were made with seed yields as below:

Combination	Number of seeds	Seeds with embryo %
No. 15 X No. 8	9,780	2.3
No. 14 X No. 11	504	54.0
No. 10 X No. 14	4,074	5.4

All progenies grow on Ekebo research station.

Habit and strobiles

Both generations have now grown up to a height of 10—12 meters, which indicates a rather slow growth rate. The form of the stems is relatively good. The bark is lead-grey with a reddish tint. The foliage recalls B. lutea but the strobiles immediately reveal that the first generation is really hybridous, as they are cylindric like the father species, pendulous or pointing laterally, never erect, and the petioles are intermediate in length (fig. 4).

In habit, vitality and growth rate the second generation is not more variable than the first one.

The leaves

Even if the foliage in its intirety resembles B. lutea in both generations, characteristic deviations are shown between the hybrids and the parent species on closer examination. By measuring length and width of 20 leaves from each of 5 F_1-trees, of 10 F_1-trees and of both the parents, the mean values presented in Table 1 have been obtained.

Fig. 2. — Strobiles of B. ***lutea,*** shortly before maturity.

[1]) The Institute for Forest Improvement, Ekebo, Svalöv, Sweden.

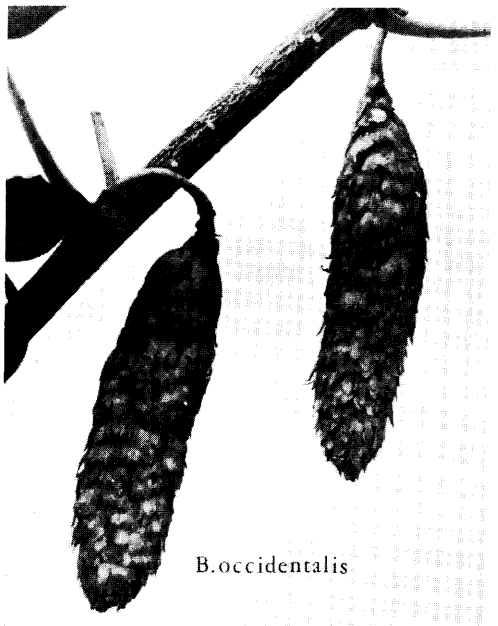

Fig. 3. — Strobiles of *B. occidentalis*, shortly before maturity.

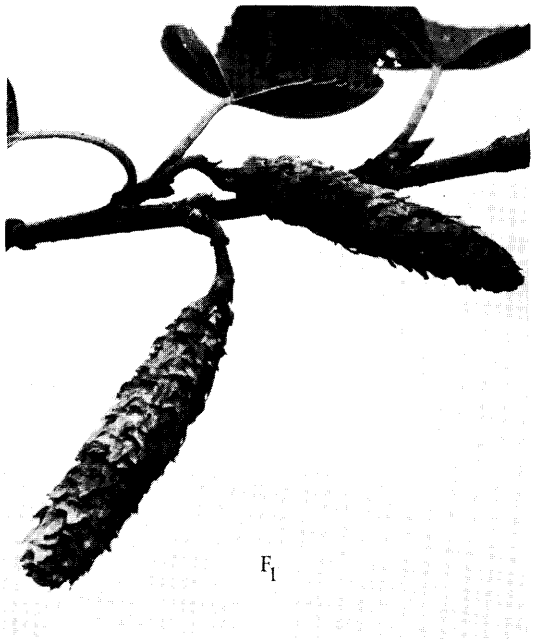

Fig. 4. — Strobiles of F_1 *B. lutea* × *occidentalis*, shortly before maturity.

When measuring, leaves from short shoots in the upper half of the crowns have been used. The main difference between the parent species is shown by the length of the leaves, *B. lutea* having 49% longer leaves than *B. occidentalis*, 98.8 mm as against 66.3 mm. The difference in width is only 7%. Consequently, the length/width ratio amounts to 1.94 for *B. lutea*, compared with 1.40 for *B. occidentalis*. The averages for the F_1-trees are almost exactly intermediate. The analysis of variance reveals only one significant difference between the five F_1-trees, tree No. 3 having narrower leaves than the other ones. The margins of the leaves are somewhat influenced by *B. occidentalis*, and this they show by a more or less marked tendency to double serration *(fig. 6)*. The averages for the F_2-trees do not differ significantly from F_1. However, between the F_2-individuals there exist some differences. Thus, tree No. 5 has longer

Fig. 5. — Strobiles of F_2 *B. lutea* × *occidentalis*, shortly before maturity.

leaves than its sibs, numerically even longer than *B. lutea*, 103.7 mm as against 98.8. No. 1 has significantly narrower leaves than Nos. 3, 5, 6, 8 and 10. The trees Nos. 2, 3 and 10 have lower length/width ratio than Nos. 1, 4 and 5. In other words, the variation in F_2 is increased to some extent in comparison with F_1, which is shown more exactly in *Table 2*, where the limits for the individual means in F_1 and F_2 are given. As expressions for the variability, the coefficient of variation, v, and the heritability, h^2, have

Table 1. — Leaf measurements

Species and hybrids	Number of trees	Length mm	Width mm	Length/ width
B. lutea	1	98.8	51.2	1.94
F_1	5	83.1	48.7	1.71
F_2	10	85.8	51.9	1.67
B. occidentalis	1	66.3	47.7	1.40

Table 2. — Individual variation in the hybrid generation

Gene-ration	Number of trees	Length of leaves mm	v	h^2	Width of leaves mm	v	h^2	Length/width ratio	v	h^2
F_1	5	76.4— 88.1	0.23	0.26	45.8—54.5	0.18	0.07	1.60—1.80	0.21	0.28
F_2	10	78.6—103.7	0.39	0.54	43.2—56.8	0.34	0.33	1.48—1.91	0.42	0.58

v = coefficient of variation
h^2 = heritability (broad sense)

been calculated. v = the standard deviation/generation mean, $h^2 = \frac{\sigma^2_g}{\sigma^2_p}$, i. e. the heritability in broad sense (genotypical heritability) is calculated in the usual way from the components of the mean squares. The genotypical influences on length and length/width ratio are twice as great in F_2 as in F_1, and as regards width almost five times as strong. Also the tendency to double serration varies perceptibly in F_2 *(fig. 7)*.

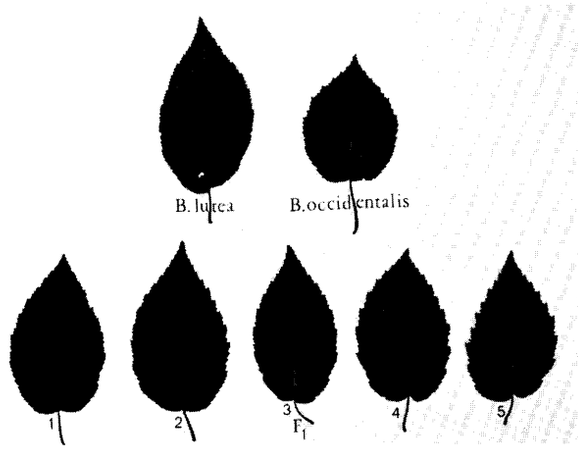

Fig. 6. — Leaves of *B. lutea, B. occidentalis* and of five F_1-trees.

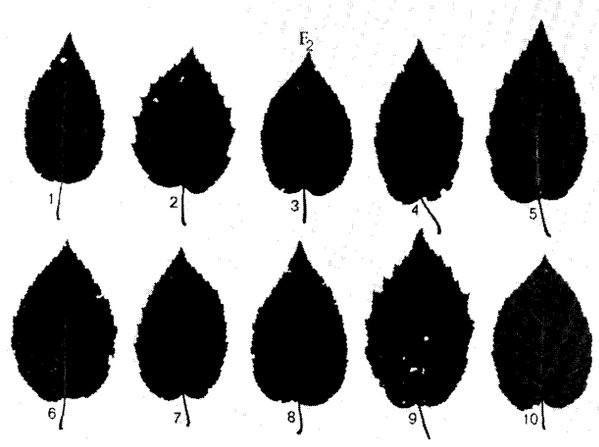

Fig. 7. — Leaves of ten F_2-trees.

Samaras and bracts

Besides the parents, strobiles, have been available from two F_1 trees and only from one F_2-tree. The length and the width of the nutlets as well as the width of the samara wings have been measured on 60 samaras from each tree. The individual means are collected in *Table 3*. The length of the nutlets from the hybridous trees is almost intermediate, whereas the width coincides with *B. lutea*. Consequently, the length/width ratio, which is the same in the parent species, receives considerably lower values in the hybrids than in the parents. The width of the samara wings in relation to the width of the nutlets is for one of the F_1-individuals higher than for *B. lutea*, for the other one as for the F_2-individual much the same. Under all circumstances, with this ratio as decisive characteristic, the hybrids should be placed in the section Costatae. The form of the samaras must be described as specific for the hybrids with the wings low down on the nutlets. Thus, the

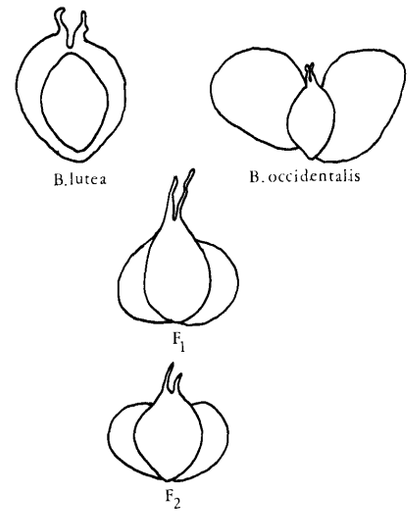

Fig. 8. — Samaras of *B. lutea, B. occidentalis,* F_1- and F_2-hybrids.

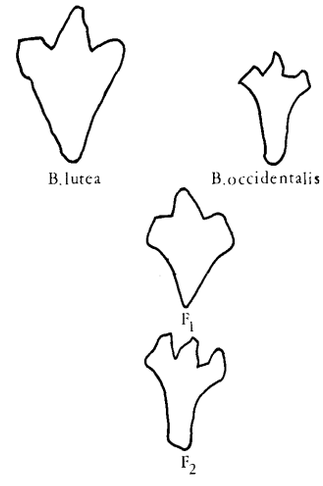

Fig. 9. — Bracts of *B. lutea, B. occidentalis,* F_1- and F_2-hybrids.

Table 3. — Samara measurements

Species and hybrids	Nutlets Length	Nutlets Width	Length/ width	Width of wings/ width of nutlets
B. lutea	27.1	15.8	1.72	0.31
F_1—1	22.3	16.4	1.36	0.49
F_1—2	21.1	15.7	1.35	0.27
F_2	23.4	17.4	1.35	0.31
B. occid.	17.2	9.9	1.75	1.41
Error	0.21	0.14	0.017	0.018

1 unit = 0.12 mm

Table 4. — Bract measurements

Species and hybrids	Length	Width	Length/ width
B. lutea	57.0	37.6	1.52
F_1—1	40.4	36.8	1.10
F_1—2	40.7	31.9	1.28
F_2	40.5	26.5	1.53
B. occid.	45.9	24.5	1.88
Error	0.65	0.41	0.029

1 unit = 0.15 mm

fusion between the wing margins and the stigma, characterizing *B. lutea*, does not recur in the hybrids *(fig. 8)*.

Corresponding measures have been taken on 40 bracts of each tree. The results are summarized in *Table 4*. The length of the bracts for the tree hybrids corresponds closely but is significantly shorter than for either of the parent species. Their width occupies positions between the parents, the F_1-trees closer to *B. lutea*, the F_2-tree closer to *B. occidentalis*. The length/width ratio for F_1 is significantly less than in the parent species, for F_2 it coincides with *B. lutea*. In view of the bracts, also, the form in F_1 must be considered as specific, whereas in the only F_2-individual traits can be seen which recall of *B. occidentalis (fig. 9)*.

Discussion

Thus, the F_1-generation appears as a mosaic of *lutea*-like, *occidentalis*-like, intermediate and specific characteristics:

lutea-like: the width of the nutlets, the ratio samara wings/widths of the nutlets, the width of the bracts;

occidentalis-like: the form of the strobiles;

intermediate: the position of the strobiles, the length, width and length/width ratio of the leaves, the length of the nutlets;

specific: the ratio length/width of nutlets and bracts, the length of the bracts and the forms of nutlets and bracts.

The variation in morphology and size of the pollen-grains for the F_1-individuals is not greater than for the parent species, indicating that no serious meiosis disturbances occur. Also the fertility of crosses between F_1- individuals has been shown to be fairly good. In one combination as much as 54% seeds with embryos was obtained, which is a high value even for an intraspecific cross within the genus *Betula*.

In respect of vitality and form of growth the F_2-families do not display greater variability than any *Betula*-family. On an average the leaves of the F_2-generation coincide rather well with F_1, but the individual variation is somewhat broader. The question is whether the variation is really broader than what is usual for a *Betula*-species. In any case it is quite clear that the F_1-hybrid between *B. lutea* sect. Costatae and *B. occidentalis* sect. Albae has fairly good fertility and gives rise to progenies not showing any obviously great variability. To formulate a hypothesis about the cytological background to this behaviour is simple. Assume that two *lutea*-genomes pair autosyndetically, that two *occidentalis*-genomes act in the same way and that the two remaining genomes pair allosyndetically. The result will be a regular meiosis. In fact, on account of the high polyploidy-level, small deviations in chromosome number will probably not cause drastic effects either for gametes, embryos or adults. Unfortunately, detailed meiosis studies are very difficult to pursue in these high polyploid plants with their small chromosomes.

That embryos are formed when *B. lutea* is pollinated with *B. occidentalis* was reported by WOODWORTH (1931). CLAUSEN (1970) has performed a great number of crossing experiments between and within sections of *Betula* and recorded the germinability of the resulting seeds. He has also stated that germinable seed can be obtained from the cross *B. alleghaniensis* × *B. papyrifera*, 4—6 x. *B. alleghaniensis* is probably used by him as a synonym for *B. lutea* and *B. papyrifera*, 6 x, must be thought to be the same as *B. occidentalis*. As a generic judgement CLAUSEN advances that crosses with a Costatae-species as female and Albae-species as male have higher compatibility than crosses between species of the same section. The question whether the boundaries between the sections are really of a higher rank than the boundaries between species of the same section must, however, to be on the safe side be left open for the time being. Doubtless complications must be taken into consideration such as differences in polyploidy level between the species and conspicuous individual variation in compatibility, which might be connected with the occurrence of one-locus S allele incompatibility systems within the species (HAGMAN 1971). Also, the posibility of apomictic seed formation, released by foreign pollen, must not be overlooked, why progenies in hybridization experiments should be tentatively identified as hybrids by means of morphological comparisons or other studies.

Summary

The F_1-hybrid between the two hexaploid *Betula* species *B. lutea* and *B. occidentalis* display a mosaic of *lutea*-like, *occidentalis*-like, intermediate and specific characteristics. The rate of growth is moderate. The pollen grains have no visible defects and their size is not more variable than that of the parents. The fertility of crosses between F_1-idividuals is different but can be rather high.

The vitality and form of growth in the F_2 generation do not show broader variation than in any other *Betula* family. Up to the present, the morphology of the leaves has only been studied in detail. Even if the individual variation is broader in F_2 than in F_1, it may be doubted whether it is more conspicuous than in any other *Betula* species.

Key words: *Betula* species, chromosome numbers, compatibility, pollen grains, habit, leaf-morphology, samaras, bracts, boundaries between sections and species.

Zusammenfassung

Die F_1-Hybriden zwischen den beiden hexaploiden *Betula*-Arten, *B. lutea* Sect. Costatae und *B. occidentalis*, Sect. Albae wiesen ein Mosaik von *lutea*-ähnlichen, *occidentalis*-ähnlichen, intermediären und spezifischen Merkmalen auf. Die Zuwachsstärke ist mäßig. Die Pollenkörner sind dem Aussehen nach normal und variieren nicht mehr in der Größe als die der Eltern. Die Fertilität bei Kreuzungen zwischen F_1-Individuen ist wechselnd, kann aber hoch sein.

Die F_2-Generation ist nicht mehr variierend in Vitalität und Schaftform als jede *Betula*-Familie. Mehr eingehende Untersuchungen liegen nur für die Blattmorphologie vor. Auch wenn die individuelle Variation in der F_2 größer ist als in der F_1, ist es fraglich, ob sie größer ist als bei jeder *Betula*-Art.

References

CLAUSEN, K. E.: Interspecific Crossability Tests in *Betula*. Report IUFRO, Working Group Meeting on the Sexual Reproduction of Forest Trees, Varparanta, Finland, 1970. — HAGMAN, M.: On Self- and Cross-Incompatibility shown by *Betula verrucosa*, EHRH. and *Betula pubescens*, EHRH. — Commun. Inst. Forest. Fenn. 73, 1971. — WOODWORTH, R. H.: Polyploidy in the *Betulaceae*. — Journ. Arn. Arb. XII, 1931.