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Analiza zbiorowego gatunku Betula alba L. na podstawie pomiarów liści

Część II: Betula pubescens Ehrh., B. tortuosa Ledeb., B.carpatica Waldst. et Kit.

Analysis of the collective species Betula alba L. on the basis of leaf measurements.

Part II: Betula pubescens Ehrh., B. tortuosa Ledeb., B. carpatica Waldst. et Kit.

Mémoire

de M^me^ *J. JENTYS-SZAFEROWA*

présenté le 6 Fevrier 1950 par M. W. Szafer m. t.

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The method applied by the author in the analysis of the collective species *Betula alba* L. was described by her in detail in Part I (1949) of her work. Therefore, without repeating the description, the author proceeds at once to present the results of her studies concerning the three above-mentioned birch species.

I. Betula pubescens Ehrh.

In her investigations of *B. pubescens* the author adopted as a comparative unit the arithmetic means from a sample concerning 100 leaves from 50 trees from a large part of the European distributional area of the latter species. Their distribution is shown in

Fig. 1. Therefore, the above-mentioned unit is analogical to the sample of *B. verrucosa*, used by the author as a comparative unit in Part I of her work. From outside of Europe the author had but two leaves from a single tree from the vicinity of Tomsk.

The same as in Part I, here also the author first asked herself the question whether a sample including 100 leaves from 50 trees is sufficiently large for the purpose of characterizing the shape

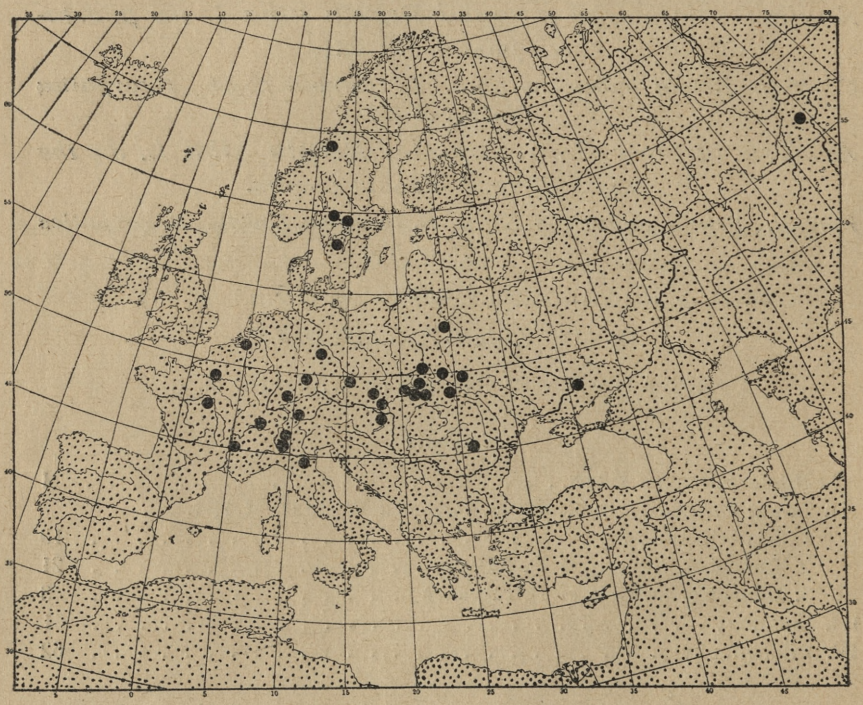

Fig. 1. Map of distribution of trees of *B. pubescens* whence the leaves have been taken for study.

of leaves of *B. pubescens*. With this object in view the author compared with the arithmetic means of the latter sample the means of a sample comprising 1000 leaves from 500 trees in Europe, with a preponderance of trees from Poland and adjacent countries, inasmuch as she had only such material at her disposal. The numerical differences between the above-mentioned samples are shown in Table I, while the corresponding diagram is given in Fig. 2. We see therefrom that between the arithmetic means of

the samples with 100 and 1000 leaves respectively, there are differences, above all, in the quantitative characters (1—7), and smaller ones in the characters concerning the shape (8—15). The greatest differences exist in the petiole length (character 1), the

TABLE I

	Characters	M_1	M_2	$M_2:M_1$
1.	Petiole length	12·98	13·85	1·07
2.	Blade length	42·90	45·15	1·05
3.	Blade width	33·55	34·65	1·03
4.	Number of pairs of lateral nerves	6·63	7·17	1·08
5.	Distance of first tooth from blade base.	9·71	10·05	1·03
6.	Distance between tips of second and third lateral nerve	6·41	6·68	1·04
7.	Number of teeth between tips of second and third nerve	3·98	4·23	1·06
8.	Ratio of blade length to petiole length.	3·44	3·38	0·98
9.	Ratio of blade length to blade width	1·28	1·31	1·02
10.	Mean distance of nerves	6·51	6·30	0·97
11.	Ratio of blade length to distance of first tooth	4·96	4·79	0·97
12.	Position of widest part of blade	2·60	2·63	1·01
13.	Axil of second nerve and midrib	36·65	36·90	1·01
14.	Angle of base and midrib	65·75	66·20	1·01
15.	Angle of apex and midrib	32·30	30·75	0·95
16.	Number of leaves on dwarf shoot	2·28	2·51	1·10

M_1 = arithmetic means of measurements of 100 leaves from 50 trees from the European distributional area of *B. pubescens*.

M_2 = arithmetic means of measurements of 1000 leaves from 500 trees of *B. pubescens*.

number of pairs of lateral nerves (4), the number of teeth between the second and third nerve (7), the apex angle (15), and the number of leaves on dwarf shoots (16). In Table II are shown the differences between the arithmetic means of these characters, and also the errors of these differences, calculated by means of the formula:

$$m_{\text{diff.}} = \pm\sqrt{m_1^2 + m_2^2}$$

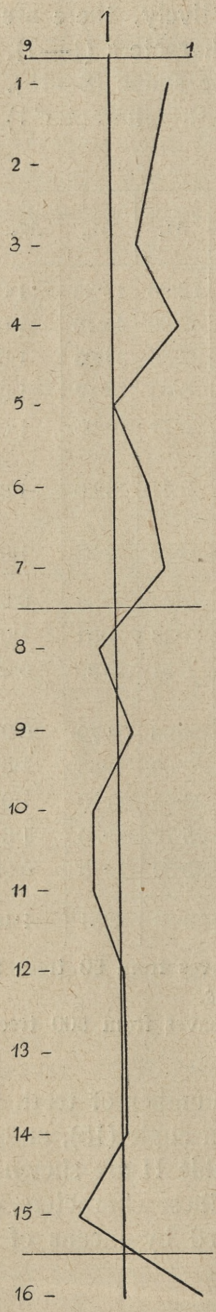

Fig. 2. Graphical comparison of the sample of 1000 leaves with the sample of 100 leaves of *B. pubescens*. Characters 1—16 as on Table I.

The underlined differences exceed their error three times and, consequently, they are essential. In the quantitative characters essential is the difference in the number of pairs of lateral nerves (4) and in the number of teeth between the second and third nerve. However, in view of the fact that there is no essential difference in the mean distance of nerves (10), the difference in character 4 has no great importance. Neither is the difference in the apex angle (15) essential, being such only in the number of leaves on dwarf shoots (16). However, since — as stated by the author in Part I — it is possible to characterize well the leaf shape on the basis of arithmetic means, the author assumes that she will commit no error by adopting the sample comprising 100 leaves from 50 trees of *B. pubescens* from its European distributional area as a comparative unit; with the latter the author will compare the local samples. Anyhow, the aim of the comparative unit is not to represent a typical

TABLE II

Character N⁰	M_1	M_2	Diff. ± m diff.
1.	12·98	13·85	0·87 ± 0·387
4.	6·63	7·17	0·54 ± 0·095
7.	3·98	4·23	0·25 ± 0·033
10.	6·51	6·30	0·21 ± 0·140
15.	32·30	30·75	1·55 ± 0·790
16.	2·28	2·51	0·23 ± 0·065

M_1 = arithmetic means from 100 leaves from the European distributional area of *B. pubescens*.
M_2 = arithmetic means from 1000 leaves of *B. pubescens*.

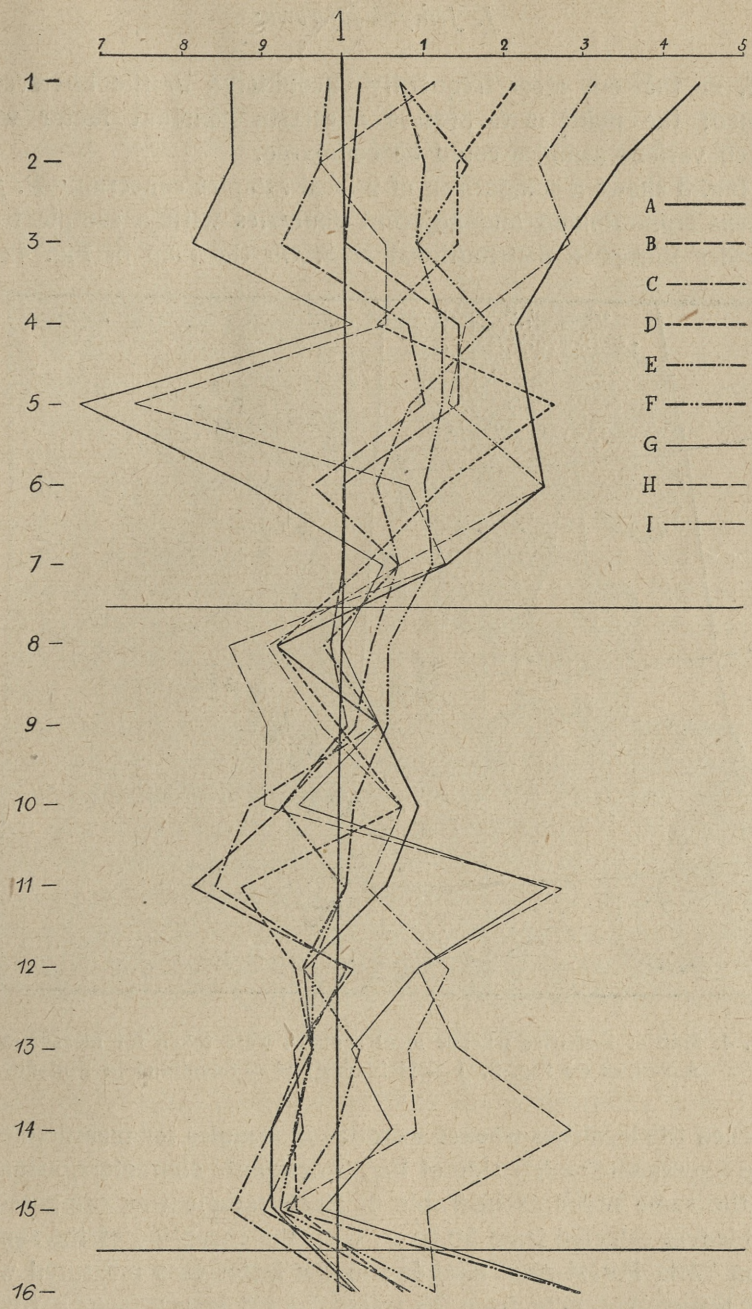

Fig. 3. Comparison of 9 local samples of *B. pubescens* with the sample from the European distributional area of this species. A — Kampinos Forest (reservation); B — Kampinos Forest (Sieraków); C — Kamionka Strumiłowa; D — Orło on the river Bug; E — Białowieża Forest; E — The Wola Forest near Kraków; G — The peat-bog «Na Czerwonym» near Nowy Targ; H — Łeba; I — Mikuszyńce.

leaf, or the one most frequently encountered in the birch concerned; the point is to possess a certain constant factor with which various samples could be compared.

Fig. 3 shows a comparison of 9 local samples concerning *B. pubescens* from Poland and adjacent countries with a sample from a wider European distributional area. On the map in Fig. 4a re

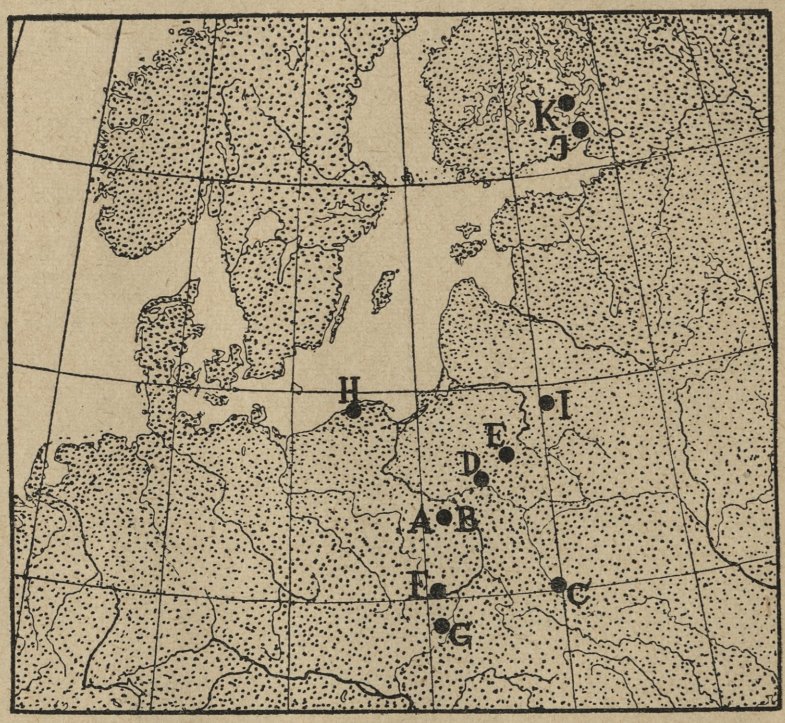

Fig. 4. Map of localities whence local samples were taken for measurements A — I as on Fig. 3. J — Heinavesi; K — Savolinua in Finland.

marked the localities whence were taken samples for measurements. The figures on the left side of Fig. 3 designate characters, arranged in the same order as in Table I. Each sample was composed of 100 leaves colected from 50 trees, with the exception of the sample from Wola Forest near Kraków; in the latter case measured were. 108 leaves, but only from 36 trees, i. e., 3 leaves from a tree.

Particularly striking in Fig. 3 is the fact that among the local samples there is a greater difference in the characters concerning

size than ih those concerning shape. This is to a certain degree unexpected. The fact is that *B. pubescens* is known to possess great variability in its leaves, and one would expect, indeed, to encounter among the local samples big differences in the shape of leaves. However, the characters concerning shape deviate little from the comparative unit, even less than did similar samples of *B. verrucosa* (cf. Part I — Fig. 5). In one sample only we have birches with wide-based leaves; it came from the vicinity of Łeba on the Baltic coast. Other samples however, in spite of coming from localities which were far-distant from one another and which had a different habitat (peat-bog or forest), are on the average very similar to one another.

Next, attention is attracted by the fact that the lines which are drawn thinly as in Fig. 5 of Part I of the author's work and which in characters 11—14 have higher arithmetic means than the comparative unit, do not cross in such a regular fashion the thick lines as was the case with *B. verrucosa*; this had been proof of local variability, as well as of correlation between a considerable number of leaf characters in *B. verrucosa*.

Furthermore, attention is drawn by Fig. 3 to the fact that the author had more samples with leaves larger than the comparative unit, and few samples with smaller leaves. By no means does this prove that *B. pubescens*, in the area investigated by the author, has leaves which are generally larger than the average ones from the whole distributional area. As a matter of fact, in the presence of such great local differences in leaf size and only nine samples studied, it may be but a coincidence, and only the investigation of a larger number of local samples can give some idea of the whole. However, it does explain why in Fig. 2 the sample with 1000 leaves — in great measure composed of leaves from the above-mentioned local sample — has leaves larger than the comparative unit.

It will now be interesting to ascertain — analogically as done by the author with *B. verrucosa* — what is the variability of the base angle and of the position of the widest part of the blade in *B. pubescens*.

In Fig. 5 are shown the frequency polygons of the base angle. In the upper diagram we have the polygons of samples with 100 leaves from the European distributional area, and with 1000 leaves of *B. pubescens*. Both display the existence of three or perhaps

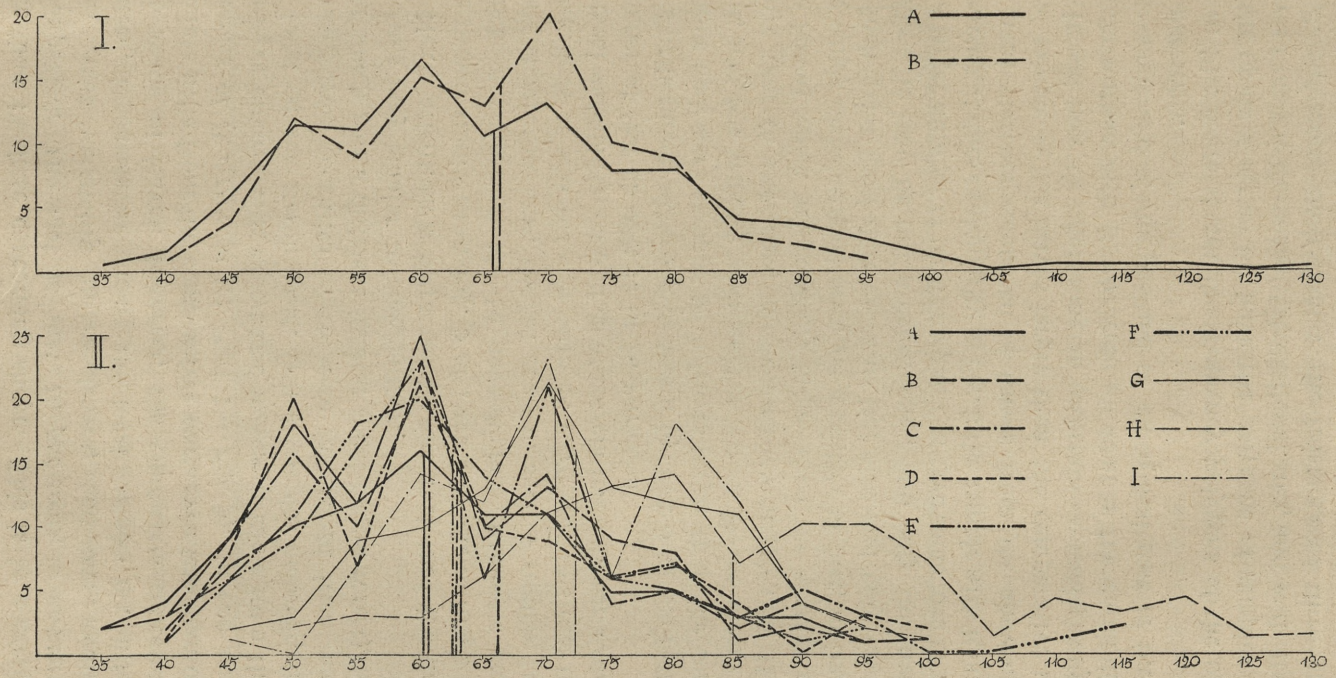

Fig. 5. Frequency polygons of the angle of the leaf base of *B. pubescens* I. A — Sample of 100 leaves from the European distributional area; B — Sample of 1000 leaves. II. A — I as on Fig. 3.

even four apexes. In the lower diagram we have the polygons of local samples; they are also multapical. Their apexes conform to the apexes of the upper diagram, in a similar manner as in Fig. 10 of Part I. This indicates that *B. pubescens*, the same as *B. verrucosa*, is composed of a number of lines possessing a characteristic base angle. However in *B. verrucosa* the geographical distribution of these lines had been such that all the trees growing in certain aggregations had a more acute base, from 35° to 85°, while in other aggregations they had a wide one, from 40° to 120°. Here, on the other hand, in samples with a more acute mean base angle (thick lines), we have all transitions from 35° to 100°, and even 115°, i. e., from acutely cuneiform leaves to cordate ones. It is true that in the samples concerning leaves with a wide mean base (thin lines) there are no variants in the classes 35 and 40, but, on the other hand, only in one sample were there leaves with a strongly cordate base (120° to 130°). In all samples, therefore, there was generally a similar variability of the base angle.

In Fig. 6 are shown the frequency polygons of the position of the widest part. In contradistinction to the great variability of this character for *B. verrucosa*, striking here is the small variability of the position of the widest part of the blade. It is true that the local samples designated with thin lines have their arithmetic means as well as their modal values slightly shifted to the right, i. e., a mean increase of the base angle entails a certain lowering of the position of the widest part of the blade; nevertheless, the thickly and thinly drawn frequency polygons almost conform to one another. In *B. pubescens*, therefore, there exists a large variability of the base angle, but a small variability of the position of the widest part of the blade, this being a further character by which this species differs from *B. verrucosa*.

Summing up what was noticeable on the basis of comparing the arithmetic means of the local samples in Fig. 3 and the frequency polygons in Figs. 5 and 6, it may be stated that the local samples of *B. pubescens* differ strongly from one another by the mean size of their blades, which signifies that entire aggregations of *B. pubescens* in a certain area are either small-leafed or large-leafed. Differences in the mean shape of their leaves are here considerably smaller. Neither did the author observe any definite local differentiation of birch aggregations with regard to leaf shape or cor-

relative association of characters, which is so characteristic of *B. verrucosa*. This suggested that in the absence of correlation may lie the greater diversity in the leaf structure of *B. pubescens*, inasmuch as this gives a larger number of combinations in the mutual relation of characters.

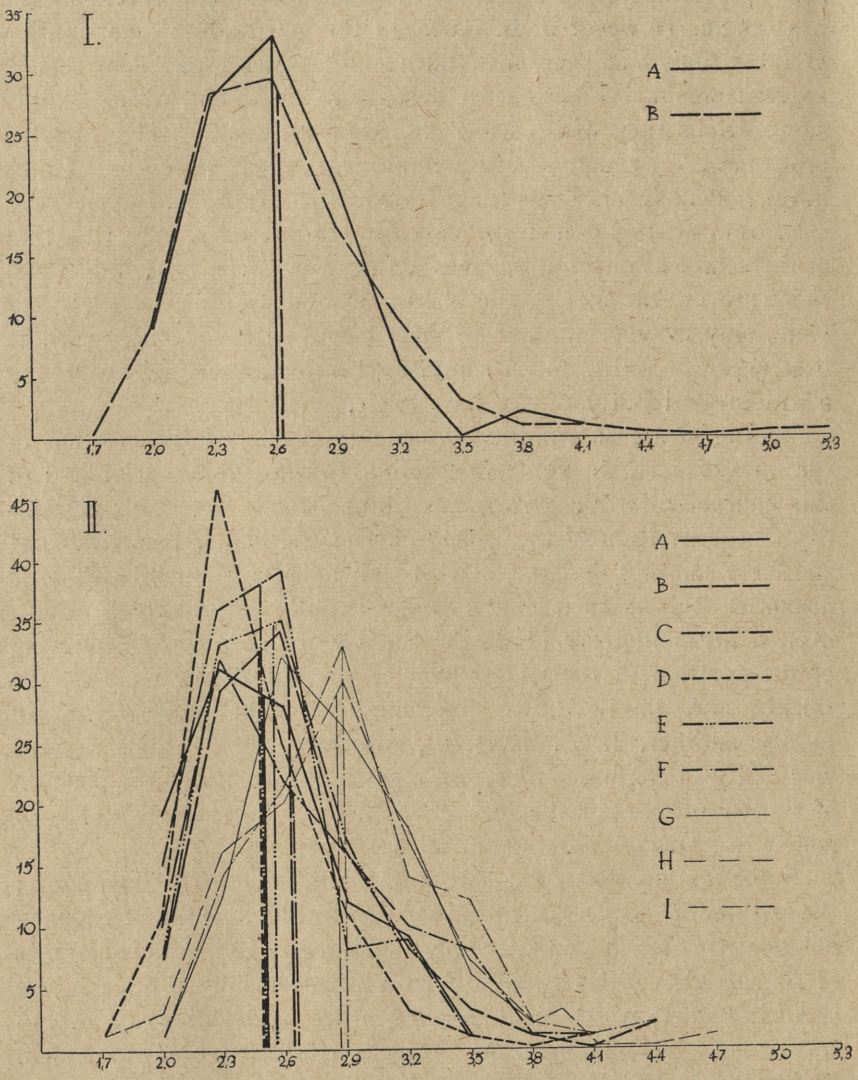

Fig. 6. Frequency polygons of the position of the widest part of leaves of *B. pubescens*. I. A — Sample of 100 leaves; B — Sample of 1000 leaves. II. A — I as on Fig. 3.

The author carried out a further characteristic of the leaves of *B. pubescens* by comparing them with the leaves of *B. verrucosa*. This comparison is shown in Fig. 7. Here the comparative unit

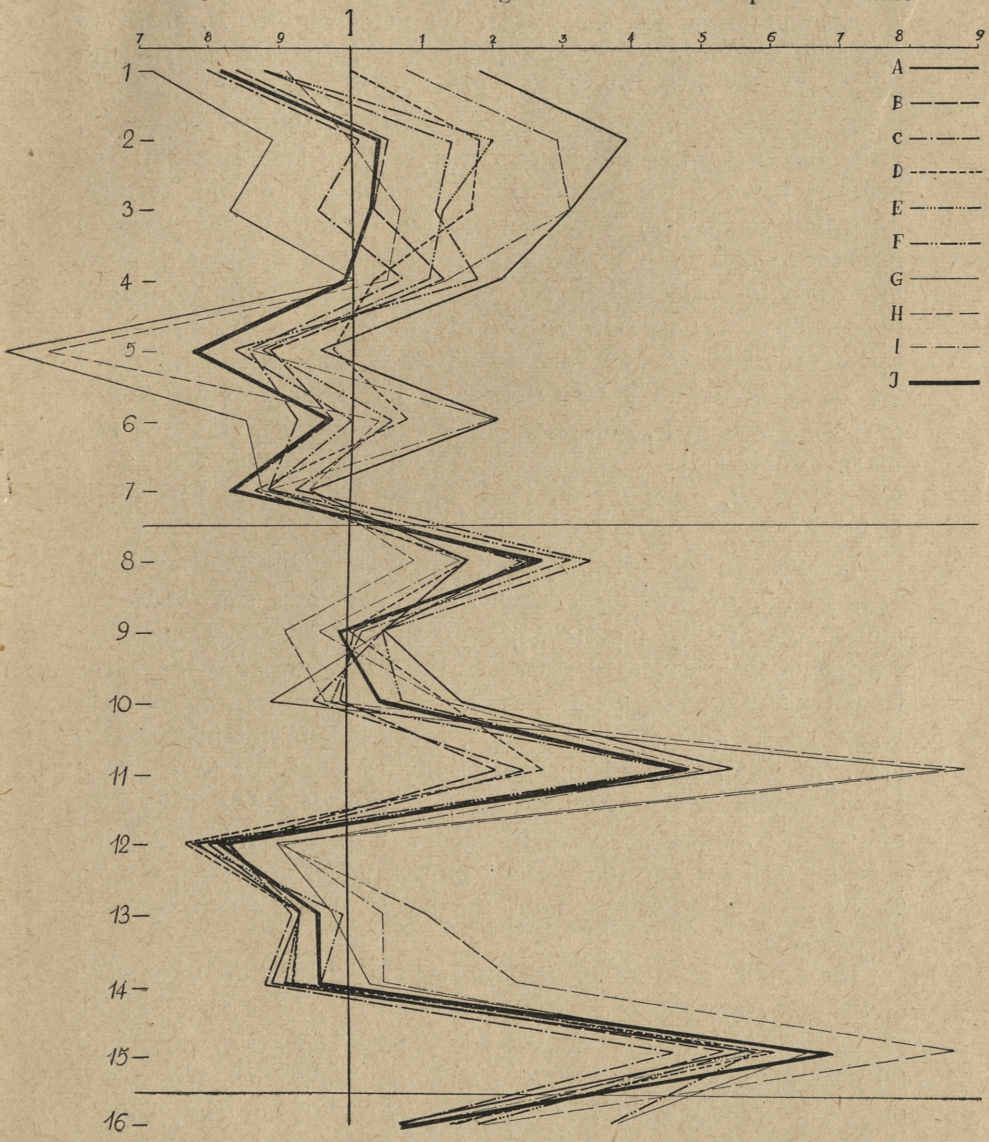

Fig. 7. Comparison of 10 samples of *B. pubescens* with the sample of *B. verrucosa* from the European distributional area. A — I as on Fig. 3; J — The sample of *B. pubescens* from the European distributional area.

is a sample composed of 100 leaves from 50 trees from the European distributional area of *B. verrucosa*. The very thick polygonal line represents a sample composed of 100 leaves from 50 trees of *B. pubescens* from the same area. We perceive that *B. pubescens* generally has shorter petioles (character 1) in connection with longer (2) and wider blades (3). Between the number of pairs of lateral nerves there is no difference in the arithmetic means (4), while the first tooth lies much closer to the blade base (5). The distance between the second and third nerve is, on the average, somewhat smaller (6), while the number of teeth in this space is markedly smaller (7). With regard to characters of shape, a great difference is noticeable in the ratio of blade length to petiole length (8) — because the petioles are, on the average, shorter — and in the distance of the first tooth from the base after eliminating the factor of size (11); furthermore, in the position of the widest part — which in *B. pubescens* lies, on the average, closer to the blade middle (12) — and in the apex angle which is generally wider (15). *B. pubescens* also has, on the average, slightly more leaves on dwarf shoots (16).

Included in the same diagram, by means of the same symbols as in Fig. 3, are nine local samples of *B. pubescens*, studied by the author. As already mentioned, they differ from one another by the size of their leaves; nevertheless, the lines of shape of the leaves from these samples arrange themselves in a parallel manner with regard to the line of shape from a wider European distributional area. We obtain, therefore, analogically to what has been stated by the author on page 211 of Part I, a line of mean size and shape of *B. pubescens* in comparison with *B. verrucosa*. Along this line will arrange itself every sample of *B. pubescens*, but no sample of any other species if the latter differs distinctly from *B. pubescens*.

There still remains to be discussed the absolute variability of the leaf character of *B. pubescens*. In view of the fact, already stated in Part I, that a calculation of the coefficients of variability (v) does not give a good picture of actual conditions, the author did not prepare a table of such coefficients, but she endeavoured to show the differences of character variability in leaves of *B. verrucosa* and *B. pubescens* by comparing their standard deviations, just as she had previously compared the arithmetic means.

If we will take a glance at the results of the authors measurements, given at the end of the III part of this work, we will perceive, that the differences between the standart deviations (σ) of the samples with 100 leaves and the samples with 1000 leaves are considerable, although the differences between the means are very slight (cf. Tab. I). The author will not go here into details of the causes therefor, the fact being sufficient, that samples composed of 100 leaves are adequately large for comparing arithmetic means, but a greater number of observations is necessery for comparing variability. The author does not know whether a sample with 1000 leaves is sufficiently for the purpose of determining the leaf variability of a given birch species, but in any case such a sample is nearer to the truth than one with 100 leaves. Consequently, when comparing variability, the author took into account only the large samples.

In Fig. 8 is shown a comparison of the standard deviations (σ) of leaf characters of the two birch species described above. Adopted as a comparative unit are the standard deviations of all characters in a sample of 1000 leaves from 500 trees of *B. verrucosa* from its European distributional area, with a preponderance of trees from Poland and adjacent countries. The broken polygonal line illustrates the variability of a sample with 1000 leaves from 500 trees of *B. pubescens* from the same area. The solid polygonal line in the same figure illustrated the relation of the arithmetic means from the sample with 1000 leaves of *B. pubescens* to the sample with 1000 leaves of *B. verrucosa* (cf. Fig. 7). We have here as if two diagrams; one compares the arthmetic means, i. e., the shape, while the other compares the standard deviations, i. e., the variability, shifted in such manner that the comparative units have covered one upon the other. In consequence we have a picture of the shape and variability of *B. pubescens* in comparison with the shape and variability of *B. verrucosa*.

Only such a comparison is fully expressive. The fact is that when the variability is alike, the standard deviation increases proportionally to the increase of the arithmetic mean. For instance, when we have two samples of leaves, in one sample the leaves being 2 to 4 cm long with a mean of 3 cm, and in the other from 20 to 40 cm long with a mean of 30 cm, then the standard deviation of the latter leaves is also ten times greater, while the varia-

bility of both samples is the same. Therefore, if we compare two samples as to a number of characters, and we see that parallel to the increase of the arithmetic means increase the standard deviations and vice versa, so the variability of these two samples is equal. On the other hand, when we see — as, e. g., in Fig. 7 —

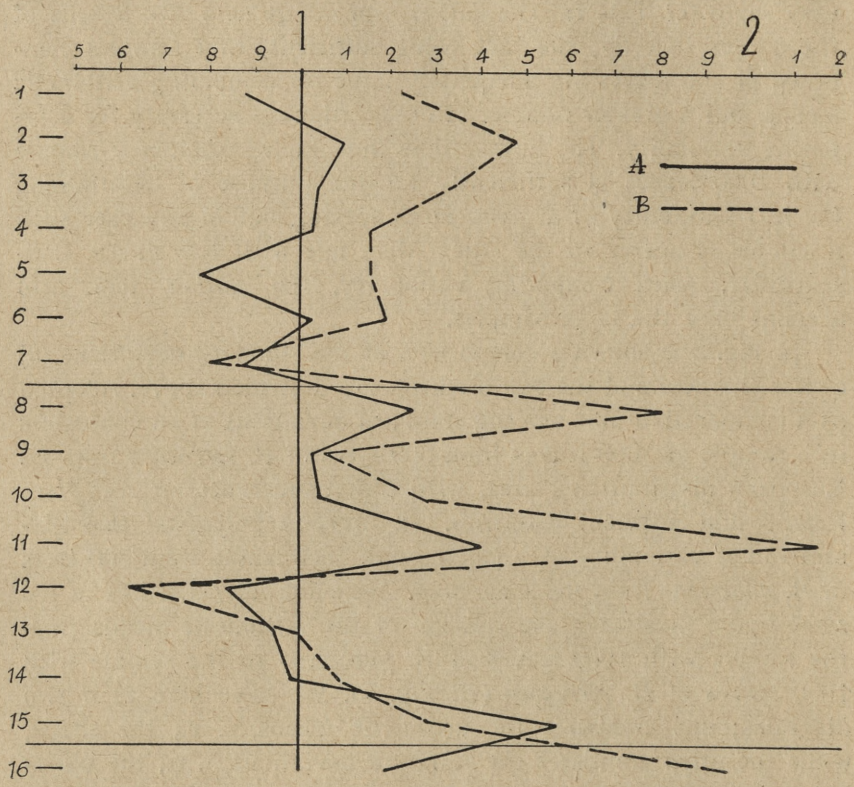

Fig. 8. Comparison between the means (A) and the standard deviations (B) of leaf characters of *B. pubescens* and the means and standard deviations of *B. verrucosa* (straight line).

that the mean petiole length is smaller in *B. pubescens* than it is in *B. verrucosa*, and the standard deviation larger (character 1), or else the blade length only slightly longer, and the standard deviation considerably bigger (2), then in both these characters the leaf variability of *B. pubescens* is greater than the leaf variability of *B. verrucosa*.

Inspection of Fig. 8 shows that the leaves of *B. pubescens* are more variable than those of *B. verrucosa* in all characters with the exception of the number of teeth between the second and third nerve (character 7), the position of the widest part of the blade (12), and the apex angle (15). For the purpose of characterizing both species, character 12 is of particular importance. In *B. verrucosa* it is, as a matter of fact, very plastic, and leaf variability with regard to the position of the widest part is a characteristic feature of this species. In *B. pubescens* this character is stabilized, and the position of the widest part of the blade, with slight oscillations, is close to the blade middle. More variable in this species, on the other hand, are characters 8 and 11, i. e., the ratio of blade length to petiole length, and the absolute distance of the first tooth from the blade base. From the line of shape (solid polygonal line) we know that *B. pubescens* generally has shorter petioles than *B. verrucosa*. The line of variability (broken polygonal line) informs us, however, that we here have great diversity. As the blade increases, the petiole length may also increase, but apart from this we encounter long blades on short petioles, and short blades on long petioles; this imparts a characteristic feature to *B. pubescens*. As regards dentation, it begins, on the average, nearer to the blade base. In individual leaves, however, this character is also very variable.

Let us now consider whether there is any character by which it would be possible to distinguish in an absolute manner the leaves of *B. verrucosa* from those of *B. pubescens*.

If we inspect the diagrams in Figs. 9 and 10, we perceive that in several characters barely are we able to discover extreme variants appertaining to only one of the two species studied. In free nature, however, such variants are relatively rare. In most of the characters the scale of variability of both species almost conforms. The only leaf character of *B. pubescens* not occurring in *B. verrucosa*, is the presence of hairs in the nerve axils on the under side of the leaves. However, within a typical *B. pubescens* we can also find leaves which are completely smooth, and frequently on one dwarf shoot one leaf has the above-mentioned hairs, while another one has not. Furthermore, hairy midveins occur in other birch species as well, not only in *B. pubescens*. The corresponding statistics are listed in Table III (page 34).

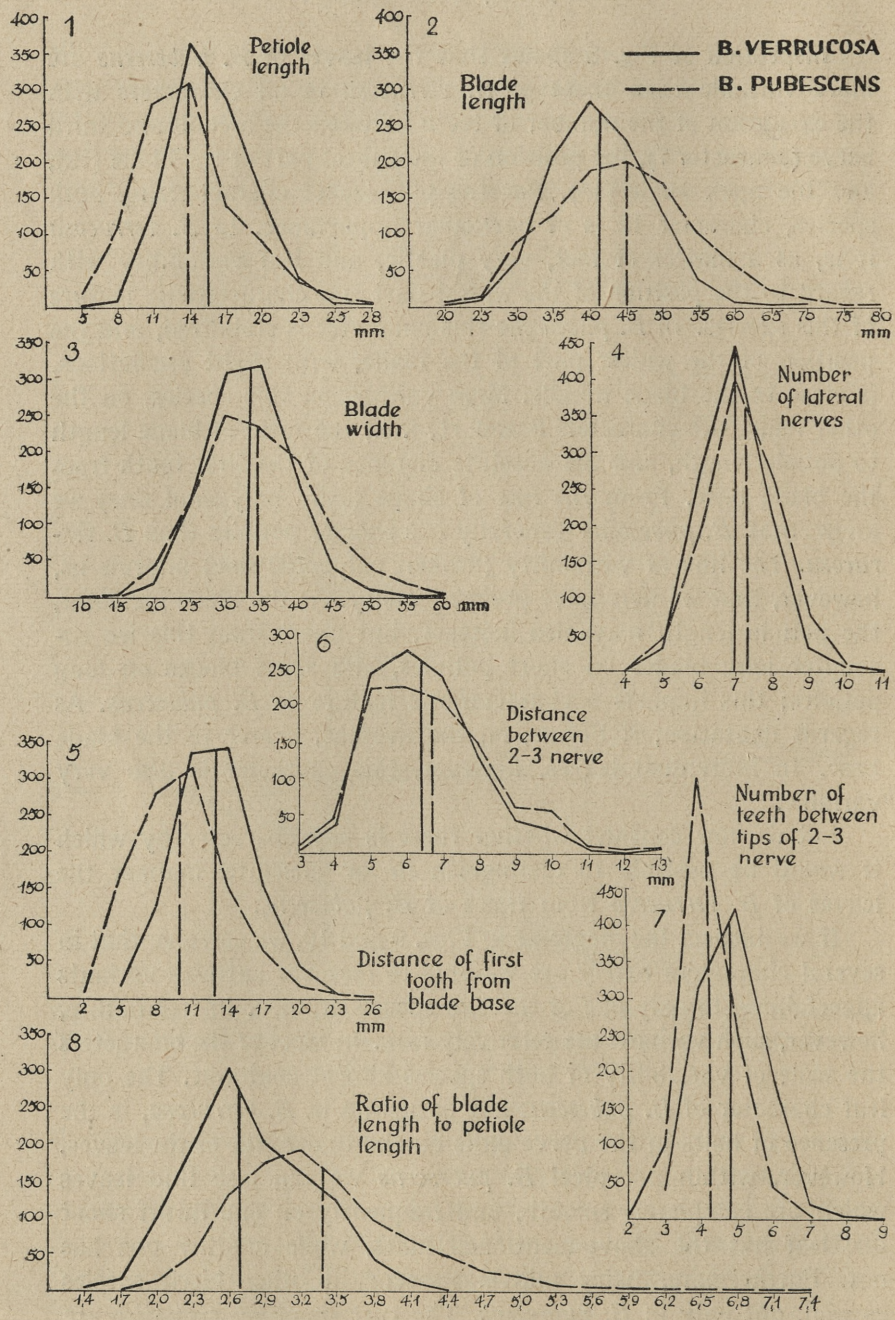

Fig. 9.

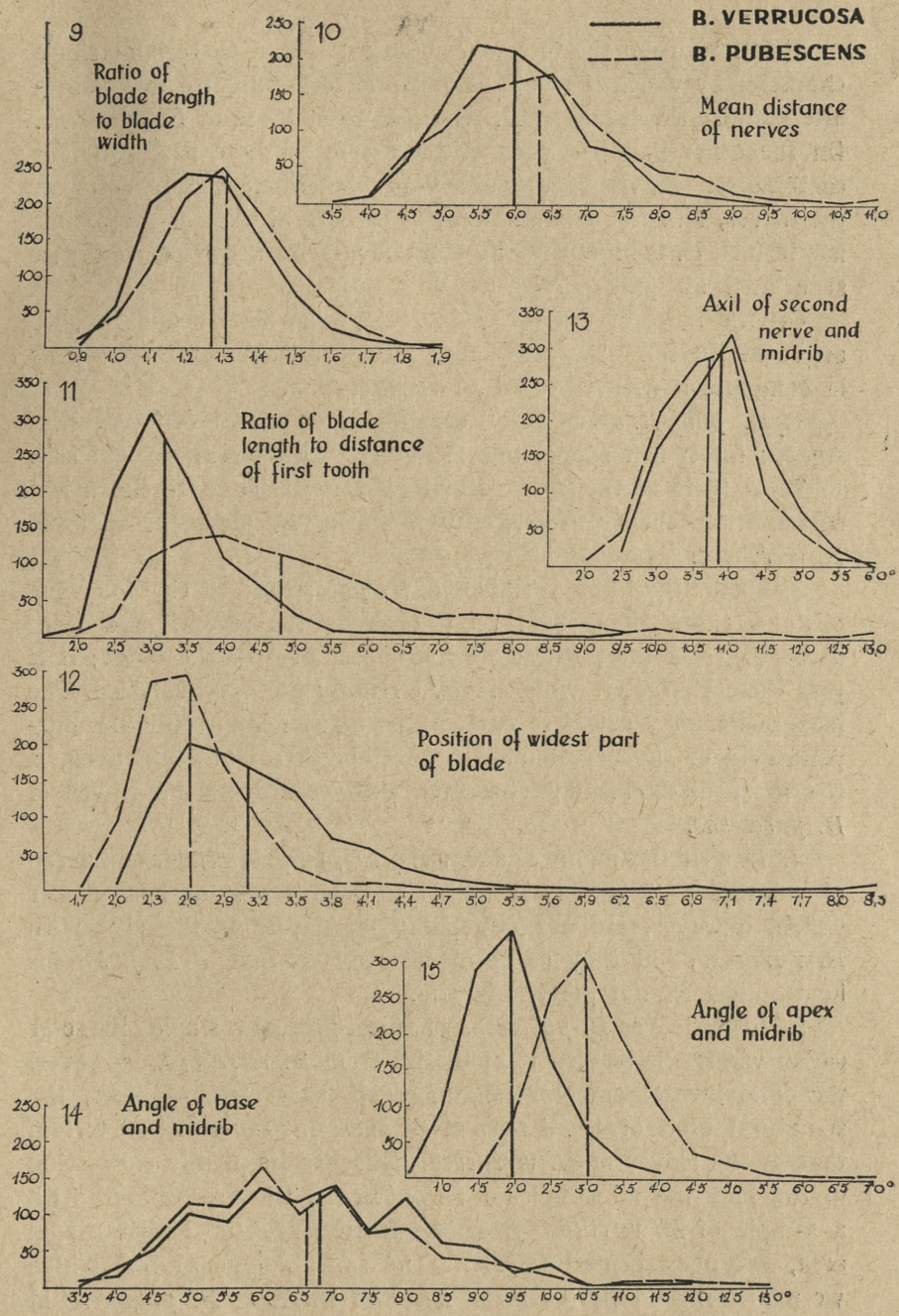

Fig. 10.

It follows from the foregoing description that there is no single character by which it would be possible to distinguish in an absolute manner the leaves of *B. verrucosa* from those of *B. pubescens.* On the other hand, in each of these species there is a different combination in which the above-mentioned characters occur in the leaves, and this combination, or structural plan as the author has termed it, is illustrated by the above-described line of mean size and shape (Fig. 7.).

On the basis of the tables and diagrams described above, we arrive at the following characteristic of the leaves of *B. pubescens* in comparison with those of *B. verrucosa*:

1. *B. pubescens* does not manifest great local differences as regards mean leaf shape, but it does so with regard to leaf size.

2. In spite of the absence of local differences as to mean leaf shape, these shapes are more variable in *B. pubescens* than in *B. verrucosa.*

3. Distinctly little variable in *B. pubescens* are the following characters: the number of teeth between the second and third nerve (6), and the position of the widest part of the blade; it is just these characters which in *B. verrucosa* are very variable. The localization of the widest part of the blade near its middle independently of the base angle, in addition to a less acute apex, is the most distinguishing character with regard to the leaves of *B. pubescens.*

4. In a similar manner as *B. verrucosa*, *B. pubescens* is composed of a number of pure lines (genotypes) with various base angles which, however, are not segregated locally, as is the case with *B. verrucosa*, but they occur in each aggregation of *B. pubescens* in a almost similar percental ratio.

5. In its leaves *B. pubescens* does not possess a single character which would distinguish it distinctly from *B. verrucosa.* However, the fundamental combination of such characters — i. e., the structural plan of the leaves of *B. pubescens* — is different from that of the leaves of *B. verrucosa.* This has its plastic expression in the fact that all samples of *B. pubescens*, when compared with a sample of *B. verrucosa* from the entire European distributional area, arrange themselves along the same polygonal line which we may term the line of mean shape of leaves of *B. pubescens* in comparison with *B. verrucosa.*

II. Betula tortuosa Ledeb. and B. carpatica Waldst. et Kit.

1. Historical outline

In Part I of her work and in the preceding chapter, the author was concerned with a characterization of two birch species which in Europe have the greatest distributional areas and which are common there almost throughout. There now remains to be decided the problem of species which have smaller distributional areas, and their relation to the two species discussed above. The most important of these species are *B. tortuosa* Ledeb., a tree which in Europe grows farthest north and forms the northern forest limit, and its corresponding species in the mountains of Central Europe, *B. carpatica* Waldst. et Kit., which grows there in many places at the upper forest limit. On account of the fact that the problem of *B. carpatica* cannot be decided without being familiar with *B. tortuosa*, which is morphologically and ecologically similar to it, the author will, first of all, deal with *B. tortuosa*.

The name *B. tortuosa* was introduced into taxonomy by Ledebour in Flora Rossica (1846—1851); he so named a birch collected in the subalpine region of the Altai Mountains, along the rivers Uba, Sentalak and Inja. Regel who includes *B. verrucosa* and *B. pubescens* in one species: *B. alba* L., considers *B. tortuosa* Ledeb. as a separate species, differing from *B. alba* L. by the narrow wings of its fruits. In Regel's conception, this species has three forms: 1) *genuina*, which grows in the Sudety Mountains, in the Karkonosze Range, and in the Altai Mountains; it has leaves with a cuneiform or slightly rounded base, and smooth branches; 2) *Kusmischeffi*, which grows along the White Sea; its young branches only are slightly pubescent, while the leaves have a base which ranges from cordate to cuneiform, and the dentation is very coarse and irregular; 3) *pubescens*, with strongly pubescent branchlets; non-fruiting specimens were found by Regel in De Candolle's herbarium, from Vallée de Joux, i. e., from the Alps, on the Franco-Swiss frontier.

In Regel's conception one's attention is arrested by the fact that he was the first to take notice of the similarity of herbarium specimens of mountains birches from the Altai Mountains, the Alps and the Sudety Mountains on the one hand, and of birches

from the far north on the other, and that he included them in one species.

The name *B. carpatica* Waldst. et Kit. is older. It was introduced into taxonomy in 1805 by Willdenow in Species Plantarum; he stated that the authors of this species were Waldstein and Kitaibel, and that it occurs in the Carpathians. This birch was probably collected by Kitaibel on the southern slopes of the Tatra Mountains, because specimens originating from there were found by Javorka (1926) in Kitaibel's herbarium. This birch is not associated by Regel with *B. tortuosa*; he considers it as one of the forms of *B. alba* L.

In his monograph on birches, Winkler — after Ehrhart — divides the European birches belonging to the collective species *B. alba* L. into *B. verrucosa* Ehrh. and *B. pubescens* Ehrh. He divides the latter into a number of varieties, viz.: 1) varietas *typica*; 2) varietas *carpatica* (Waldst. et Kit.) Koch, characterizing it according to the leaf shape only, without quoting its geographical area; 3) varietas *songarica* Regel, from Turkestan, from an altitude of 4000 to 5000 feet; he states that it is very similar to the preceding one; 4) varietas *tortuosa* (Ledeb.) Koehne, in the same conception as the species *tortuosa* f. *genuina* Regel; 5) varietas *Murithii*, from Switzerland; 6) varietas *Kusmischeffi*, from the coast of the White Sea.

At the same time he writes that the last three varieties are very similar to one another; in his opinion this is explainable not by relationship, but by convergence.

Such a confusion of mountain birches with those from the far north, and the fact that they were included by such good taxonomists as Regel and Winkler in one species and then in another, is very characteristic. Both these investigators considered these species purely morphologically, not taking into account their geographical distribution or history. The above-quoted segregation into varieties was based mainly on the pubescence or non-pubescence of branchlets and leaves of the available (not numerous, of course) herbarium specimens, on their dentation and the shape of the blade base; these characters, as it will become evident in the following chapters, are indeed the most variable ones in *B. tortuosa* and *B. carpatica*.

Taking up the problem of the birch species described above, the author based her investigations on abundant, especially collected materials, sized purely geographically. On the one hand, the author took a number of samples collected between the Arctic Circle and the polar forest limit in Finland, Sweden and Norway. In contemporary Scandinavian floras these birches have the name: *B. tortuosa* Ledeb. On the other hand, the author took samples collected at the upper forest limit of various European mountains, from birches which have the name: *B. carpatica* Waldst. et Kit. The author compared these samples with *B. verrucosa*, *B. pubescens*, and with one another. The following chapters contain the results of these studies.

2. Biometric analysis of *B. tortuosa* Ledeb.

For elaborating the birch from the northern limits of Europe — which will be designated herein as *B. tortuosa* — the author began to collect materials already in 1925, during her sojourn in Scandinavia. For the principal part of her materials the author is indebted to Dr B. Jaroń[1], who had participated in a Polish scientific excursion to Finland and northern Sweden and Norway in 1938; from these countries he brought very valuable materials, having collected local samples of birches from eight localities, ranging from southern Finland as far as its northern boundary, and also from Abisco in Sweden and Narvik in Norway. Thanks to the samples collected by Dr Jaroń, the author was able to trace the termination of the occurrence of *B. verrucosa* and *B. pubescens*, and the beginning of *B. tortuosa*. In the lowland terrain of Finland this came out better than it did in Scandinavia where *B. tortuosa* grows not only in the north, but also in the central part of the country, in the mountains at the upper forest limit. The localities whence were collected the samples are designated with circles on the map in Fig. 11. The samples were collected in the following manner: from each of the various localities Dr Jaroń collected about one hundred and fifty dwarf shoots without catkins from the same number of trees, passing from one tree to another and

[1] Dr B. Jaroń a young and promising Polish botanist was arrested by the Germans during the war and sent to the concentration camp at Oświęcim. There, after a year's imprisonment, he was shot; this was a great loss to science.

collecting altogether mechanically, without paying attention to the species.

The first two samples came from the lake country in Finland both from a wet pine-birch forest mixed with alder *Alnus incana*, lying on the shores of a lake (Fig. 4. J. K.). One of the samples was collectedon July 10, 1938, at Savolinua (61°50′ N. and 29° E.), and

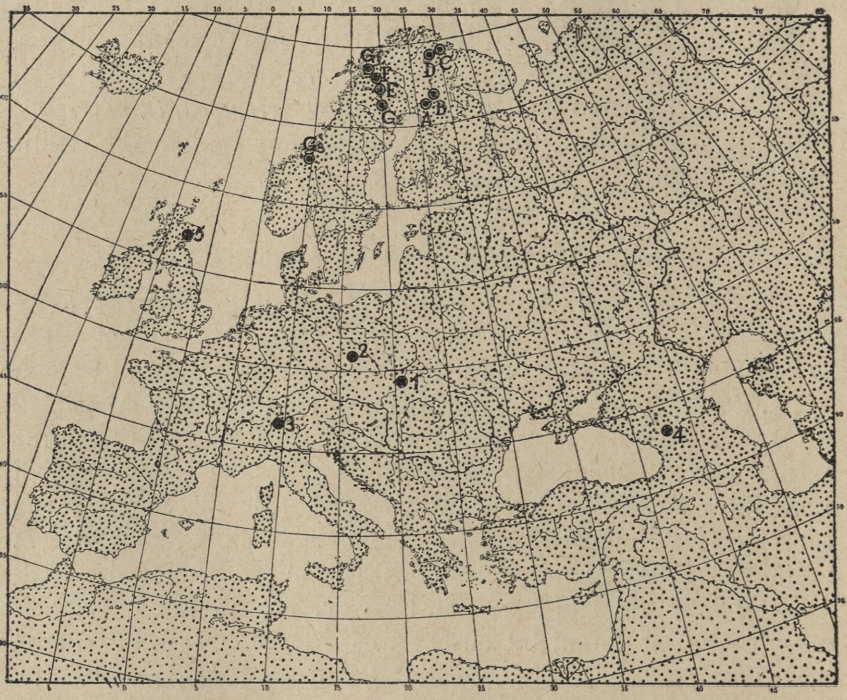

Fig. 11. Map of localities whence the samples of leaves were taken for study. ⊙ *B. tortuosa*; A — Rovaniemi; B — Peuranieni; C — between Petsamo and Ivaho; D — Salmijärvi; E — Abisco; F — Narvik; G_1 — Andenes, G_2 — Kiruna; G_3 — Kongsvoll. ● *B. carpatica*: 1 — The Tatra Mtns.; 2 — The Sudety Mtns.; 3 — The Alps (Engadine); 4 — The Caucasus (the group of Elbruz); 5 — Scotland.

it was composed of 151 dwarf shoots. each from a different tree. Of these, 15 shoots (i. e , 10%) belonged undoubtedly to *B. verrucosa*; the remaining ones, i. e., 136 dwarf shoots (c. 90%), were considered by the author to be *B. pubescens*. Dr Jaroń added to this sample the following note: «Few fruiting specimens, many vegetative ones. Age of the trees: 30 to 40 years». The other sample, with

the same date, was from Heinavesi (62°20′ N. and 28°40′ E.), and among 130 trees there was some 6% of *B. verrucosa* and 94% of a birch determined by the author as *B. pubescens*. The author will discuss these samples later.

The third sample was from a peat-bog with birch and alder *Alnus incana* at Rovaniemi, lying near the Arctic Circle (66°33′ N. and 25 50′ E.), i. e., some 500 kilometres farther north. In this sample, consisting of 150 trees, the author found the birch to be completely similar to the one with which she was familiar from northern Scandinavia and designated there by botanists as *B. tortuosa* Ledeb. In this lowland area, therefore, between 62 and 66 degres north latitude. *B. verrucosa* comes to an end, then *B. pubescens* does the same, and we enter the kingdom of *B. tortuosa* which extends as far as the limit of the tundra. In Dr Jaroń's notes there is no mention of the fruiting vigour of this birch. From her own Scandinavian observations the author knows that in the vicinity of Kiruna, lying some 1·5° farther north, this species bears fruit abundantly and, therefore, it is obviously under conditions which are suitable for its existence.

Consequently, the distributional area of *B. verrucosa* and *B. pubescens* probably does not pass far beyond the Arctic Circle, while the small number of fruiting specimens in the first two samples proves that it is the limit of their occurrence. It is true that Lindquist (1947) writes of *B. verrucosa* in Lapland. However, it occurs there probably only sporadically and rather in its southern part. The author's birch herbarium collected in 1925 in Lapland in the vicinity of Kiruna and around the lake Torne, and then arround Narvik and on the Lofoten Islands, does not contain a single specimen of *B. verrucosa*; neither is there any mention in the author's notes of her having encountered it anywhere in those regions.

Let us now analyze the samples collected by Dr Jaroń in Finland and Scandinavia, supplemented with materials brought by the author from Scandinavia. The author has taken here into account six samples collected by Dr Jaroń (circles A—F in Fig. 11). The seventh sample (G_1, G_2, G_3 in Fig. 11) is from the author's herbarium and it is designated in the diagrams with the name: Scandinavia; this sample is not typical, being composed of material from three localities: from the island of Andenes, from Kiruna,

and from the upper forest limit in the mountains of central Norway (near Kongsvoll). Each of these samples consisted of 100 leaves from 50 trees.

Let us begin by comparing these samples with *B. verrucosa*. In Fig. 12 the vertical line represents the sample of *B. verrucosa* from all of its European distributional area, adopted here as a comparative unit. The heavy polygonal line is the line of mean size and shape of *B. pubescens* in comparison with *B. verrucosa* (cf. Fig. 7). The remaining lines represent the seven above-mentioned samples of *B. tortuosa*. We perceive that the leaves of *B. tortuosa* in comparison with *B. verrucosa* are very similar in their shape to the leaves of *B. pubescens*. However, a closer inspection shows that in character 4 (i. e., the number of pairs of lateral nerves) *B. pubescens* and *B. verrucosa* have the same mean values, while all the samples of *B. tortuosa* have — irrespective of the leaf size — a plainly lower mean number of pairs of lateral nerves. Differences are also in character 13 (axil of the second nerve) and in character 15 (apex angle), where *B. tortuosa* again has higher values. Therefore, there is something which makes all the author's samples distinctly different from those of *B. pubescens*, although they are so very similar as regards leaf shape. Consequently, it is now necessary to compare these two species with each other, and discover whether this difference is essential, i. e., whether in comparison with *B. pubescens* the leaves of *B. tortuosa* have their own distinct line of shape.

In Fig. 13 is shown a comparison of the above-mentioned seven samples of *B. tortuosa* with the sample of *B. pubescens* from the latter's wider European distributional area; the latter serves here as a comparative unit. We see in this diagram that the samples of *B. tortuosa* differ from one another by the mean leaf size, while in the characters of shape, particularly from character 9 to 15, they are surprisingly uniform in comparison with *B. pubescens*, although they come from a number of localities extending from the southern to the northern limit of this species. The same mean shape have the leaves from the non-typical sample from Scandinavia, although this sample, as already mentioned, consists of birches from three localities, far-distant from one another. The most characteristic feature common to all these samples is the sharp deflection of the line of shape in character 13 (axil of the

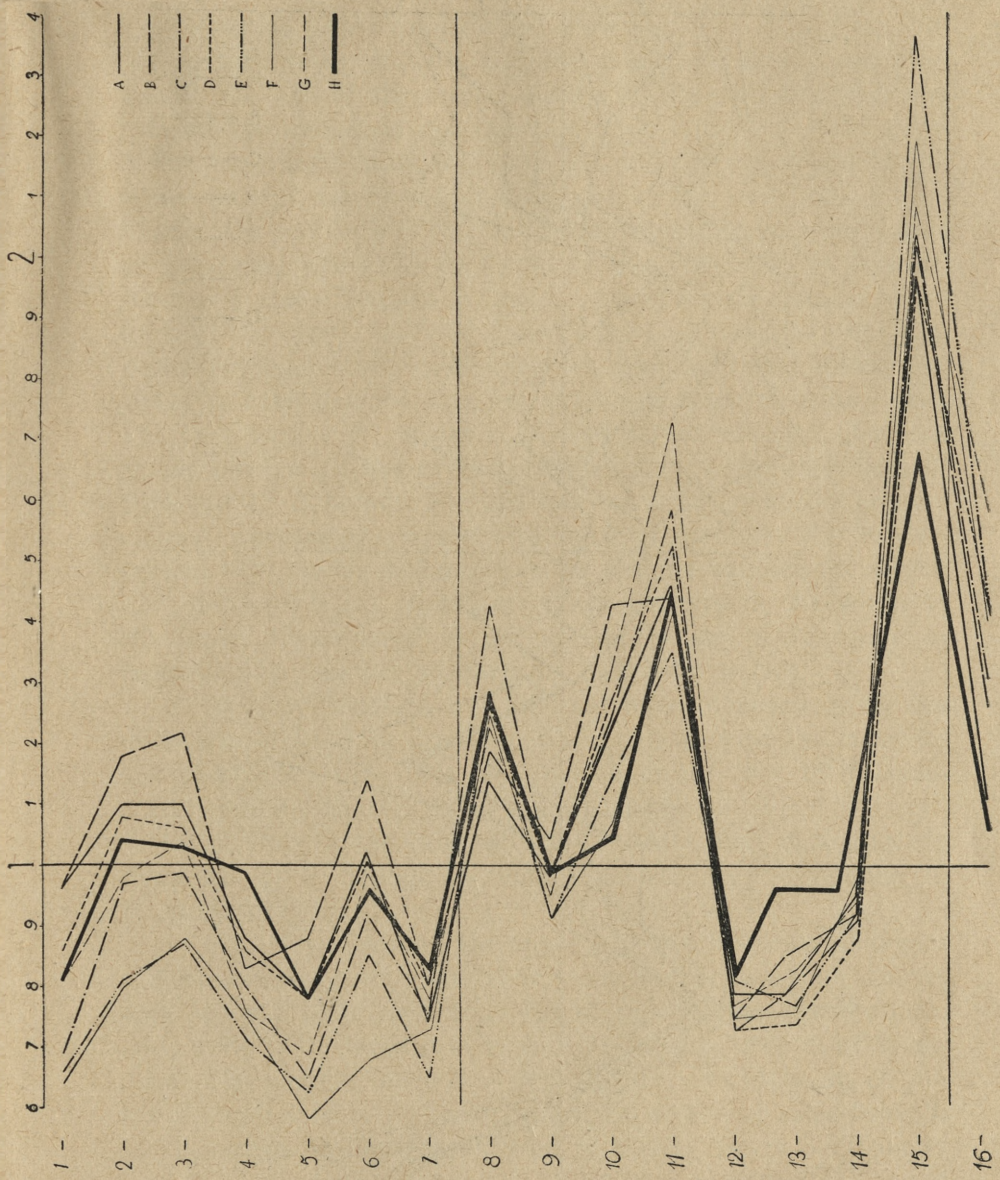

Fig. 12. Comparison of 7 local samples of *B. tortuosa* with *B. verrucosa*. A — Rovaniemi; B — Peuraniemi; C — between Petsamo and Ivaho; D — Salmijärvi; E — «Scandinavia»; F — Abisco; G — Narvik; H — line of mean size and mean shape of *B. pubescens* in comparison with *B. verrucosa*.

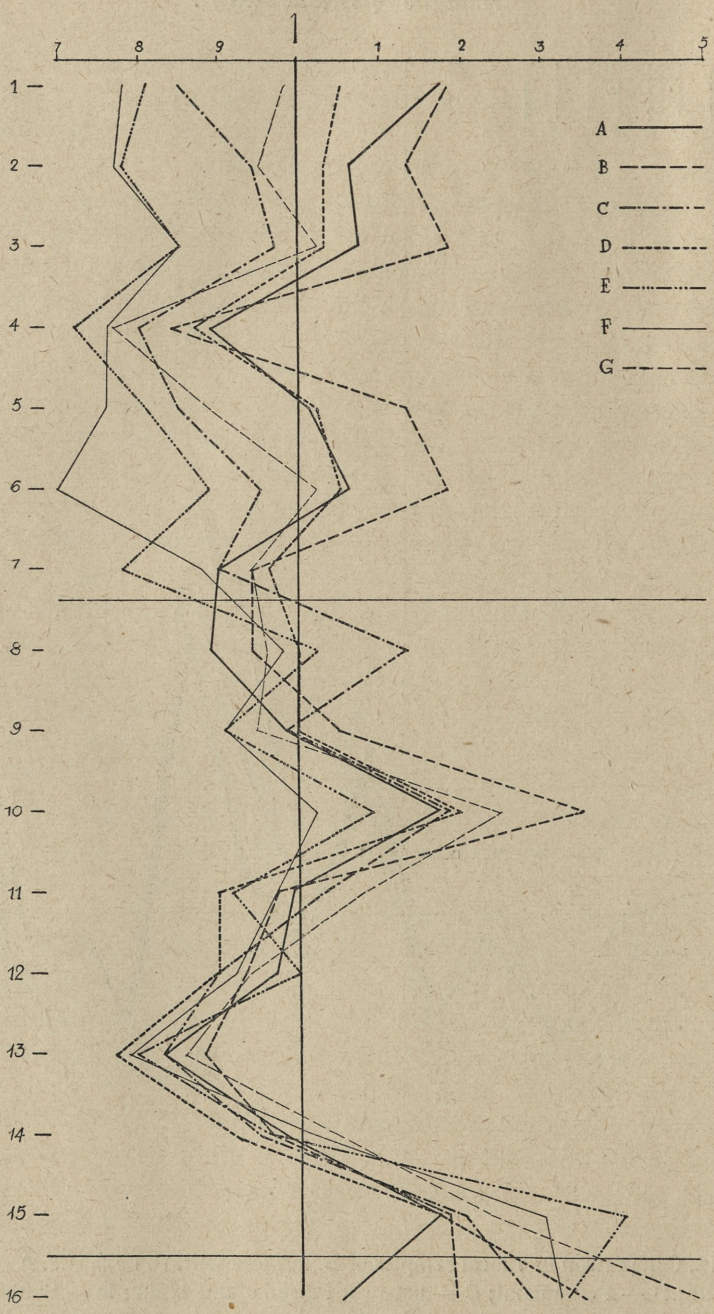

Fig. 13. Comparison of 7 local samples of *B. tortuosa* with the sample of *B. pubescens* from the European distributional area. A—G as on Fig. 12.

second nerve). If we compare this with Fig. 5 or 13 in Part I of the author's work, or with Fig. 3 in this part, we perceive that usually the axil of the second nerve (13) deviated less from the comparative unit than did the base angle (14). The mean value of the base angle being the same and the mean position of the widest part of the blade (12) being almost the same as in *B. pubescens*, the acuteness of the axil of the second nerve appears here as something new and very distinctly associated with *B. tortuosa*. Another equally distinct feature is the markedly greater mean angle of the apex, i. e., more obtuse apexes. A third feature is one which had been observable also in the previous table: irrespective of the fact whether the samples had leaves larger or smaller than the mean ones of *B. pubescens*, all of them had less pairs of lateral nerves (4), i. e., a less dense nervation; this is also observable in character 10. *B. tortuosa* also has, on the average, a smaller number of teeth between the second and third lateral nerve (7); in connection with the big differences in the distance between the second and third nerve (6), this gives great diversity in the width of the teeth. Encountered in *B. tortuosa* is also a tendency to increasing the number of leaves on dwarf shoots (16).

B. tortuosa, therefore, not differing from *B. pubescens* by the mean size of its leaves, possess in comparison with the latter its own distinct line of shape, which means that their leaves differ from one another in an essential manner.

What, then, is the variability of the three most distinguishing characters of *B. tortuosa* in comparison with their variability in *B. pubescens*?

In Fig. 14 we have in the upper part the frequency polygons of the number of pairs of lateral nerves in *B. pubescens* from samples with 100 and 1000 leaves from the whole European distributional area, while in the lower part we have seven local samples of *B. tortuosa*. The number of pairs of lateral nerves oscillates in *B. pubescens* from 4 to 11, the most frequently occurring value being 7. In *B. tortuosa* the number of pairs of lateral nerves is distinctly smaller in all samples, from 3 to 8, and the quality of the curves indicates that there exists the possibility of encountering sporadically also leaves with two pairs of lateral nerves. The number most frequently encountered here is five pairs in samples with smaller leaves, and six pairs in samples with larger leaves. The number

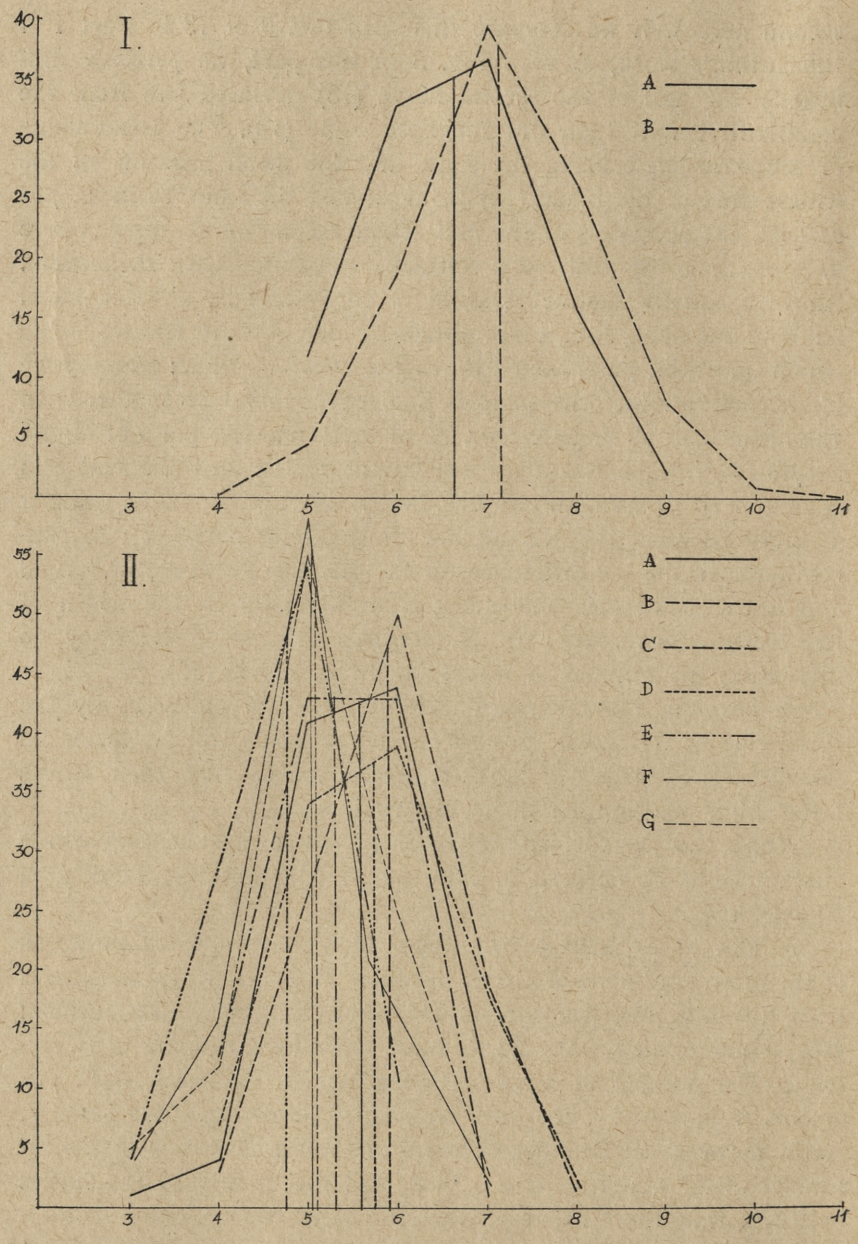

Fig. 14. Frequency polygons of the number of lateral nerves: I B. *pubescens*: A — Sample of 100 leaves from the European distributional area; B — sample of 1000 leaves; II. The local samples of *B. tortuosa*. A—G as on Fig. 12.

of pairs of lateral nerves most frequently encountered in *B. pubescens* — i. e., seven — is represented here only in a small percentage of cases.

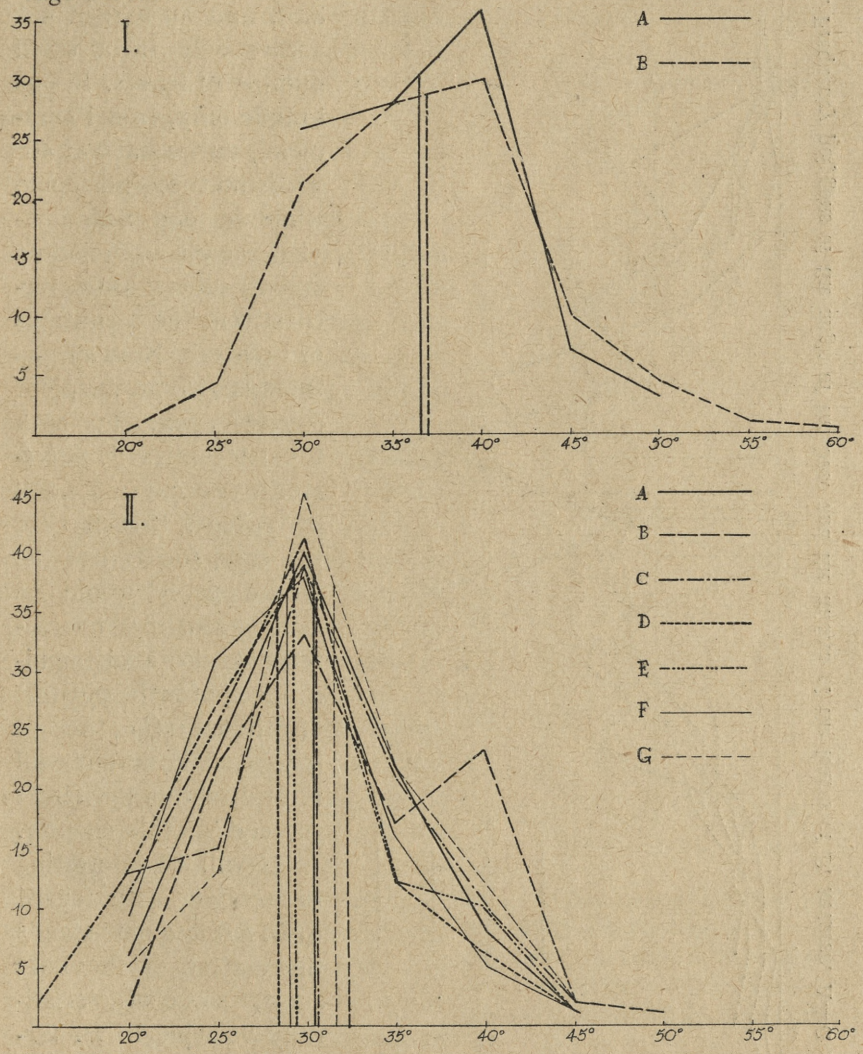

Fig. 15. Frequency polygons of the axil of the second nerve. I and II as on Fig. 14.

In Fig. 15, shown in the same manner are the frequency polygons of the axil of the second nerve. We see here that the value most frequently encountered in *B. pubescens* is an axil of 40° (pre-

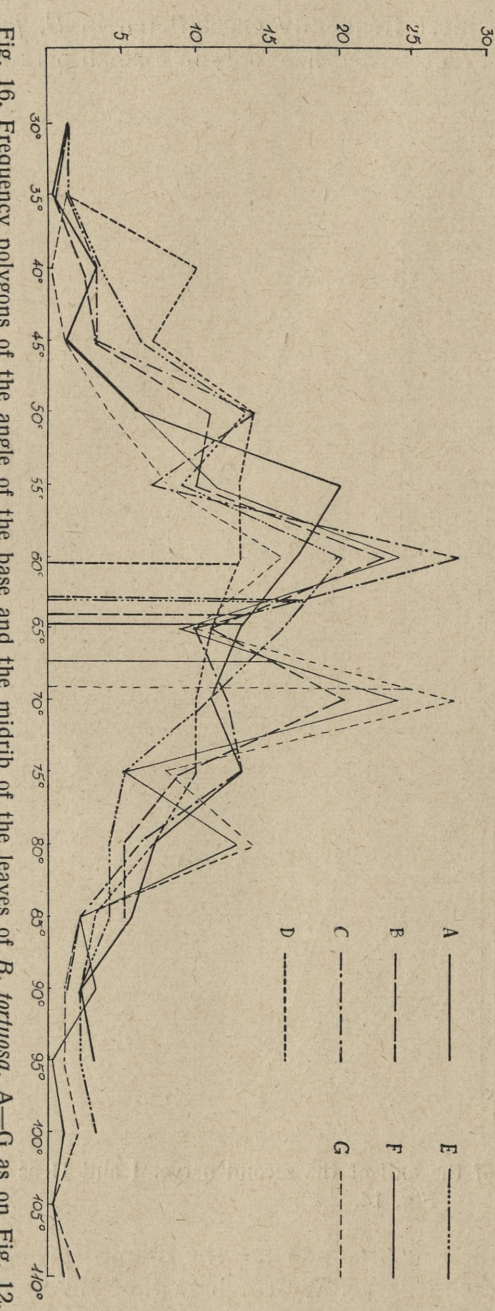

Fig. 16. Frequency polygons of the angle of the base and the midrib of the leaves of *B. tortuosa*. A—G as on Fig. 12.

cisely: from 37° to 42°), while in *B. tortuosa* the axil has 30° (i. e., 27° to 32°), and an axil of 40° occurs only in a small number of leaves. In one sample only, from Peuraniemi, do we have at 40° a distinct second apex, while in one Scandinavien sample — including among others some birches from the mountains of central Norway — there is as if an incipient second apex. In both these localities *B. pubescens* may occur in a smali percentage. If such were the case, the axil of the second neive would be a very sensitive character and also a distinguishing one for the purpose of differentiating the two species. The author will return to this matter at the end of this chapter.

It will be interesting to ascertain with regard to *B. tortuosa* how stands the matter of the base angle, so characteristically variable in *B. verrucosa* and *B. pubescens*. The proper frequency polygons are shown in Fig. 16. We see here again the same phe nomenon as in

Fig. 10 of Part I of this work, and in Fig. 5 of Part II. The presence of a number of pure lines with a base angle of c. 50°, 60°, 70° and 80°, and further ones, is, therefore, characteristic of this birch species, too. Distinguishable in *B. tortuosa* is also a line with a base angle of 40°, which had not been very noticeable in the previous birches. On the other hand, in *B. tortuosa* there is no local differentiation of these lines. They occur in each aggregation approximately in the same percental ratio. Consequently, in each sample of *B. tortuosa* the leaves range from sharply cuneiform to cordate ones.

There still remains to be discussed the absolute variability of the leaves of *B. tortuosa* in comparison with *B. pubescens*. This is illustrated by the diagram in Fig. 17, composed in the same manner as Fig. 8 (cf. the description on p. 31). It is a comparison of the sample comprising 700 leaves of *B. tortuosa* — created by adding the seven local samples — with the sample comprising 1000 leaves of *B. pubescens*. In this figure we are struck by the divergency of the lines of shape and variability of *B. tortuosa* in characters 6 and 7, i. e., in the distance between the tips of the second and third nerve, and in the number of teeth in the intervening space. The arithmetic means are smaller here than in *B. pubescens*, while variability is greater. In *B. pubescens* the most frequently encountered number of teeth in the above-mentioned intervening space is 4. In *B. tortuosa* the number of leaves with 3 teeth and the number with 4 teeth are approximately equal; when combined with the great variability of the distance between

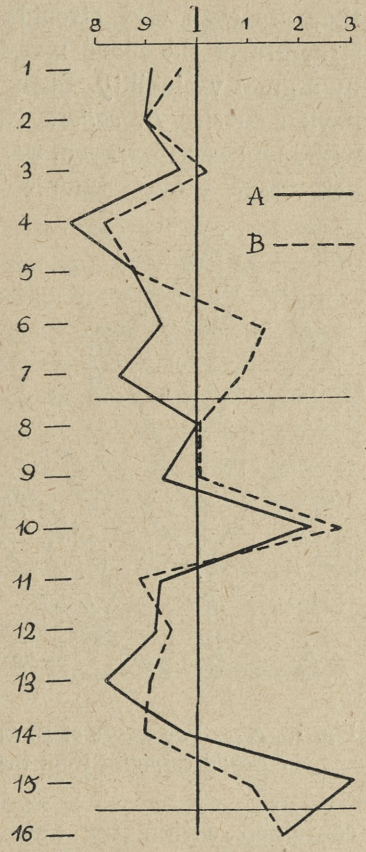

Fig. 17. Comparison between the means (A) and standard deviations (B) of leaf characters of *B. tortuosa* and the means and standard deviations of *B. pubescens* (straight line).

the second and third nerve, this causes that the teeth in the intervening space may be in one case thick, and in another thin. We must add what has not been expressed in measurements, i. e., that the depth of these teeth is very irregular and that occasionally they are even very strongly incised; all together this causes the structure of the blade margin of this species to be characterized by a great variability. Such a leaf type as the one in the Scandinavian species *B. callosa* Notö described by Lindquist (1945), with margins as if frayed, were encountered by the author in a small percentage in every sample of *B. tortuosa* (see Fig. 18). It is easily

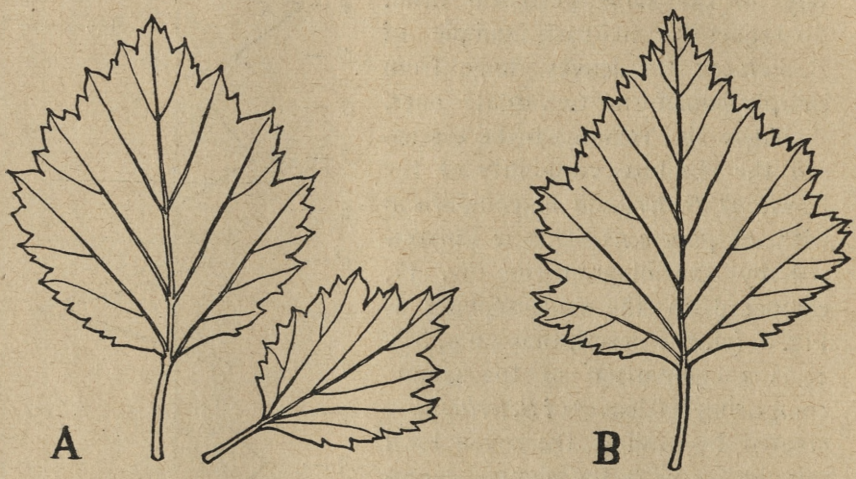

Fig. 18. A — Two leaves of *B. tortuosa* from Peuraniemi (Finland); B — Leaf of *Betula carpatica* from the Niewcyrka Valley in the Tatra Mnts.

contained within the natural variability of this species as an extreme.

There still remains to be discussed the pubescence or non-pubescence of young twigs, and the presence or absence of hairs in the nerve axils on the under side of the leaf. This character, as already mentioned, differentiates quite well from each other the species *verrucosa* and *pubescens*. However, *B. verrucosa* has absolutely smooth young twigs and an absence of hairs in the nerve axils, while in *B. pubescens* — with regard to these characters — there is a certain variability. Indeed, the young twigs are always pubescent, but frequently already in spring such pubescence be-

comes hardly perceptible, and in summer it disappears altogether. As to the hairs in the nerve axils, it must be stated that in *B. pubescens* even a study of the variability within one tree discovers almost always a certain number of leaves without such hairs. In *B. tortuosa*, on the other hand, there exists a distinct variability with regard to both of the above-mentioned characters; in the past this had caused trouble to taxonomists in localizing this species.

In Table III are shown the corresponding numerical data. In samples collected from single trees of *B. pubescens* (N° 1—4), the author paid attention only to the leaves, making but a general note that the twigs of the tree were pubescent. The author regrets that she had not investigated this matter in greater detail, because among the 50 or 100 twigs from a single tree she would have certainly discovered some without any distinctly visible pubescence. In samples collected from a larger number of trees (N° 5—19), determined by the author as *B. pubescens*, the numerical values were variable; e. g., in sample N° 6 all the leaves had hairs, while 25% of the twigs were smooth; in sample N° 17 all the twigs were pubescent, while 2% of the leaves were smooth. All told, among 1823 leaves examined, there were 53 leaves without hairs in the nerve axils, i. e., c. 3%; among 365 twigs examined, 36 were smooth, i. e., c. 10%. The author wishes to point out that frequently on one and the same dwarf shoot there occurred a leaf without hairs together with leaves possessing hairs.

In *B. tortuosa*, with regard to the above-mentioned characters, the author examined the leaves, and only in two samples the branchlets. Among 700 leaves examined, 620 were without hairs in the nerve axils, i. e., nearly 90%, while among 100 shoots examined, 36 were smooth, i. e., c. 36%. The author wishes to note that hairless leaves often occurred on the same dwarf shoots as did leaves with hairs.

Discussing the materials of *B. tortuosa* brought by Dr Jaroń, the author omitted his first two samples, collected in the lake country of Finland. These samples were determined by the author as being composed of *B. pubescens* with a small admixture of *B. verrucosa*. The trees of *B. verrucosa* were too few there to form a basis for characterizing this species at the limit of its occurrence. The author can only state that 14 trees from Savolinua had long

and relatively wide leaf-blades with an averagely wide base angle (*Mo* = 68—72°) and sparse nervation (6 to 8 pairs of lateral nerves). On the other hand, from each of these samples the author was able

TABLE III
Betula pubescens Ehrh.

Sample	Leaves			Twigs		
	with hairs in nerve axils	without hairs in nerve axils	total	pubescent	smooth	total
1 tree, Oblaszki	96	4	100	—	—	—
1 ,, ,,	117	3	120	—	—	—
1 ,, Gawłówka	100	0	100	—	—	—
1 ,, Oblaszki	112	0	112	—	—	—
50 trees, Kampinos Forest	100	0	100	40	10	50
36 ,, Las Wolski	108	0	108	27	9	36
50 ,, Kamionka Strumiłowa	96	4	100	48	2	50
50 ,, Orło on the Bug River	97	3	100	42	8	50
50 ,, Białowieża Forest	99	1	100	49	1	50
50 ,, Kampinos Forest (reservation)	99	1	100	—	—	—
50 ,, peat-bog Na Czerwonem	98	2	100	—	—	—
50 ,, Łeba	95	5	100	—	—	—
50 ,, Mikuszyńce	93	7	100	—	—	—
15 ,, Biskupin	81	9	90	14	1	15
24 ,, all Poland	47	1	48	—	—	—
14 ,, Czechoslovakia	98	0	98	13	1	14
50 ,, all Europe	98	2	100	50	0	50
50 ,, Savolinua (Finland)	94	6	100	—	—	—
50 ,, Heinavesi (Finland	95	5	100	—	—	—
Total	1823	53	1876	329	36	365

to measure 100 leaves from 50 trees of the species which she determined as being *B. pubescens*. The lines of their shape are shown in the diagram in Fig. 19. We perceive here that the birch-trees growing at the two above-mentioned localities had a similar leaf shape. Furthermore, our attention is attracted by a very interesting fact: the axil of the second nerve (character 13) is acute in relation to the base angle and the position of the widest part of the blade. This had never occurred in the author's samples with *B. pubescens* from Central Europe (Fig. 3). The occurrence of such

TABLE IV

Betula tortuosa Ledeb.

Sample	Leaves			Twigs		
	with hairs in nerve axils	without hairs in nerve axils	total	pubescent	smooth	total
50 trees, Rovaniemi	28	72	100	—	—	—
50 ,, Peuraniemi.....	19	81	100	31	19	50
50 ,, between Petsamo and Ivano	0	100	100	—	—	—
50 ,, Solmijärvi	0	100	100	—	—	—
50 ,, Abisco	5	95	100	33	17	50
50 ,, Narvik	21	79	100	—	—	—
50 ,, Scandinavia	7	93	100	—	—	—
Total	80	620	700	64	36	100

a feature of the line of leaf shape at a locality where *B. pubescens* and *B. tortuosa* border upon each other, is proof that these samples are not a pure. In this region there may be hybrids, but it is also possible that what we have here is a mixture, i. e., apart from *B. verrucosa* and *B. pubescens* there may grow in this area also *B. tortuosa*. The fact is that at the limits of their distributional areas these species must have a zone in which they grow mingled together. The author cannot say whether these species cross there, but this is possible in view of the fact that they are related to one another and that they have — as Dr. Helge Johnsson has kindly informed the author — the same number of chromosomes.

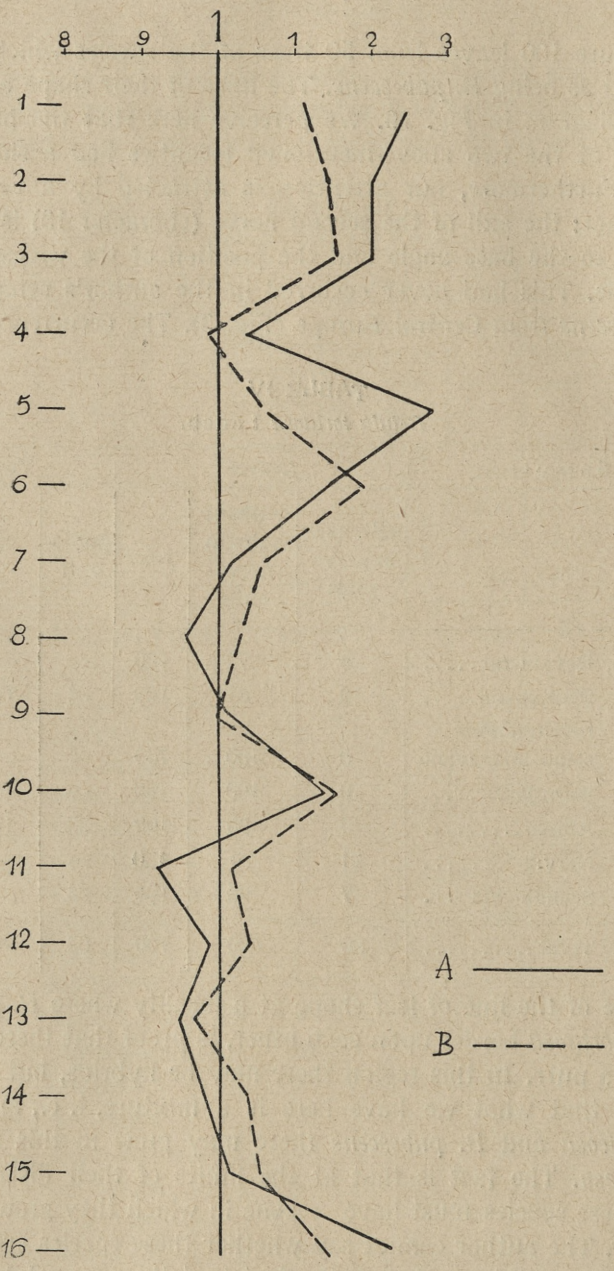

Fig. 19. Two samples of *B. pubescens* from Finland compared with the sample from the European distributional area of this species; A — Savolinua; B — Heinavesi (see the map on Fig. 4).

The frequency polygons of the axil of the second nerve, of the samples described above (Fig. 20), demonstrate an almost equal number of leaves with an axil of 30°, 35° and 40°; this seems to prove the existence of a mixture of two elements with the most frequently encountered values of 30° and 40°. Apart from the fact that what we have here may be hybrids or a mixture, we must not forget that there exists a phenomenon called convergence, i. e., the development of certain similar features in two species growing in similar conditions. The cause of this phenomenon has not been explained; nevertheless, it is known to exist.

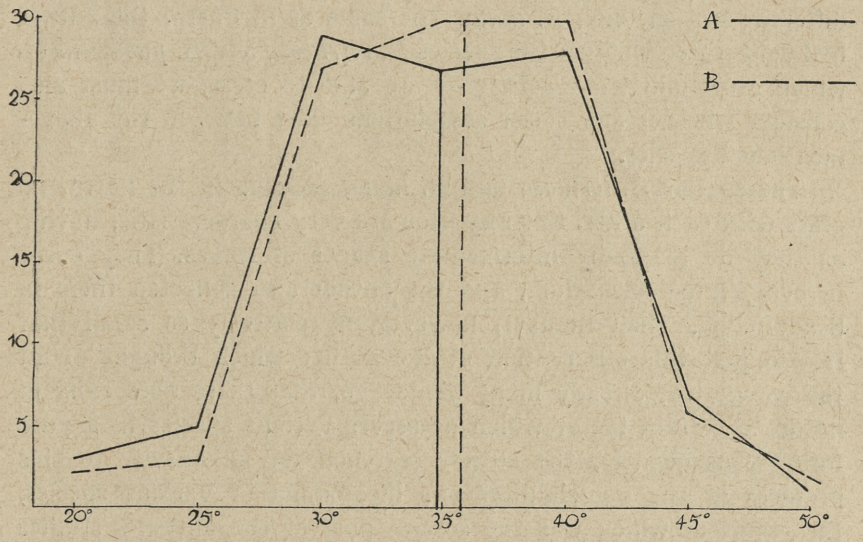

Fig. 20. Frequency polygons of the axil of the second nerve of *B. pubescens* in Finland. A — Savolinua; B — Heinavesi.

Speaking of impure samples — i. e., composed of more than one species — the author wishes to remind that discussing Fig. 15 she drew attention to the fact that in two samples (one from the vicinity of the Arctic Circle in Finland and the other partly from the mountains of central Norway), apart, from the main apex of the frequency polygon of the axil of the second nerve, there was noticeable another smaller apex at 40°: this suggested to the author that the above-mentioned samples may be composed of *B. tortuosa* with a certain small percentage of *B. pubescens*. This would be, at the southern limit of the distributional area of *B. tortuosa*,

a corresponding phenomenon to the one discussed above by the author with regard to the northern limit of the distributional area of *B. pubescens*. The problem concerning the passing of *B. pubescens* into *B. tortuosa* is worthy of a more detailed elaboration, and the author hopes that Finnish botanists will take it up.

In view of the fact that the contact zone of the species *B. pubescens* and *B. tortuosa* is so distinctly noticeable, we cannot disregard the circumstance that in the region of the northern limits of Europe, occupied at present by *B. tortuosa*, grows commonly and thrives just as well a small shrub belonging to an altogether different section, viz., *B. nana*. The same as in Part I the author had deliberated whether the species *B. verrucosa* and *B. pubescens* — which grow mingled together — are able to cross, we must also consider whether any closer associations exist between the above-mentioned species.

The species *B. tortuosa* and *B. nana*, growing in the north, do cross with each other. Such hybrids are very characteristic, having as they do markedly intermediate shapes of leaves. They occur in every large harbarium, and the author also collected them in Scandinavia. Their number, however, is relatively so small that it was just this observation of the author which brought about the conviction, already many years ago, that there does exist in nature a certain factor which preserves various species in a pure form. Consequently, the author searched for an answer to this problem in the non-simultaneous blossoming of various species, the result of which was the second part of the author's studies concerning the collective species *B. alba* L. (1938). At present, owing to the work of Helge Johnsson (1945), we know that it is difficult to cross birches belonging to different sections, and that the hybrids thus obtained are almost sterile. Therefore, the crossing of such hybrids with their parents and hence a disturbance of their specific purity, practically does not exist in nature. However, if we consider the species *pubescens*, *tortuosa* and *nana*, we are struck by a certain fact. The characters, which in such a distinguishing manner differentiate from each other the leaves of species *tortuosa* and *pubescens*, are encountered — but in an unequally greater degree — in *B. nana*. The latter birch, indeed, has leaves with an obtuse apex and with a nervation which is acute with regard to the midrib; it has the widest part of the blade near

the middle, few pairs of lateral nerves, and many leaves on dwarf shoots.

In Fig. 21 we have the lines of leaf shape from a sample of *B. nana* L. (100 leaves from 50 trees from all of its distributional area) and *B. tortuosa* Ledeb. (700 leaves from 350 trees from its European distributional area) in comparison with *B. pubescens* (100 leaves from 50 trees from its European distributional area).

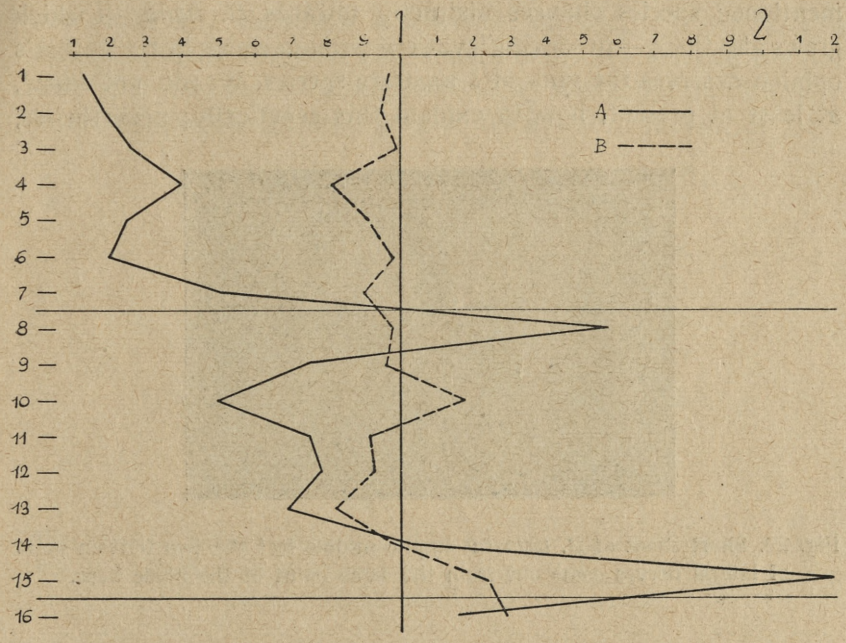

Fig. 21. Comparison of mean size and shape of leaves of *B. nana* (A) and of *B. tortuosa* (B) with *B. pubescens* (straight line).

We perceive in the above-mentioned figure that apart from the characters typical of *B. nana* (such as small leaves, very short petioles in relation to blade length, etc.), in characters 11—16 *B. tortuosa* distinctly deviates from *B. pubescens* towards *B. nana.* Such an intermediateness of characters is by no means explainable by *B. tortuosa* being a hybrid between *nana* and *pubescens* (number of somatic chromosomes of *nana* = 28; of *pubescens* = 56; of *tortuosa*, according to written information from Helge Johnsson, also = 56), nor by assuming that the author's material of *B. tor-*

tuosa, used for the measurements, was not pure, i. e., that it contained hybrids: *tortuosa* × *nana*, inasmuch as they are so typical that a mistake is out of the question. It is but a statement of fact that if we seize the species *pubescens* as broadly as did Winkler, i. e., if we include in the latter all European birches with pubescent branchlets and leaves of a similar shape, then at the northern limit of its distributional area (i. e., beyond the Arctic Circle) the above-mentioned species changes distinctly towards *B. nana* — which grows also there — producing a variety *tortuosa* which in the author's opinion deserves the rank of a separate species. We do not know, at least at present, how to explain this genetically; nevertheless,

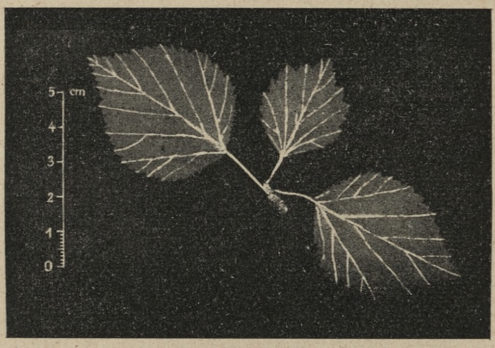

Fig. 22. Short shoot of *B. tortuosa* In the middle leaf the two bottom pairs of lateral nerves come out from the same point of the blade base.

it is a fact which cannot be disregarded. Here, also, comes to mind the word: convergence, although it is but a term that does not explain the cause.

It must be noted yet, that in *B. tortuosa* sporadically encountered are leaves in which the two bottom pairs of lateral nerves come out from the same point at the blade base. Such a leaf is shown in Fig. 22. Such a nerve arrangement does not exist in any other species belonging to the collective species *B. alba* L., but it does occur in the species *B. nana* L.

Finaly I must discuss the problem of the strongly elongated short shoots, which occur commonly in *B. tortuosa*, as the author has mentioned it allready in the Part I of her work. The same is in the species *B. carpatica* (see Fig. 23). The author supposes,

that it is not a feature innate to these species, but that it is connected with the rough climate, in which the trees develop very few long shoots in summer. The short shoots remain then year after year as short shoots with minimal annual increase. This is confirmed by the two graphs on Fig. 24. On Graph. I we have the frequency polygons of the length of short shoots of *B. pubescens* from the Wola forest near Kraków, from Mikuszyce and from Savolinua and Heinavesi in Finland. On Graph II we have the length of short shoots in six samples of *B. tortuosa* (see the maps on Fig. 4 and 11). On these graphs we see distinctly, that the nearer the northern limit of the area of the species, the longer are its

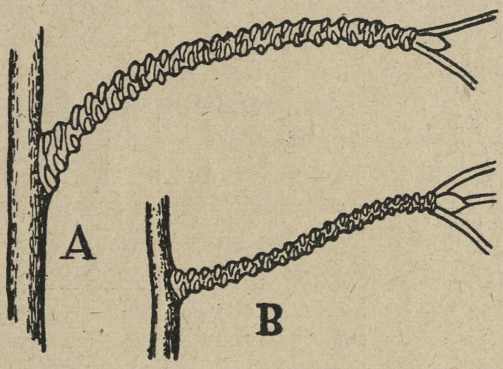

Fig. 23. A — Short shoot of *B. tortuosa* from the upper forest limit near Narvik. B — Short shoot of *B. carpatica* from the Niewcyrka Valley in the Tatra Mnts. Both are more than 20 years old.

short shoots. *B. tortuosa* in Rovaniemi has short shoots similar to *B. pubescens* in Poland. The graph on Fig. 24 give us a proof, that *B. pubescens* do not change gradually into *B. tortuosa*, but that they form two distinct species adapted to quite different climatic conditions. In Rovanieni *B. tortuosa* has good conditions and develops summer long shoots abundantly, while *B. pubescens* probably cannot exist there at all.

Summing up the results of the author's investigations of *B. tortuosa*, it may be stated:

1. In comparison with *B. verrucosa*, *B. tortuosa* and *B. pubescens* have a similar type of leaf.

2. *B. tortuosa* and *B. pubescens*, compared with each other, manifest decided differences in their leaf structure. The leaves

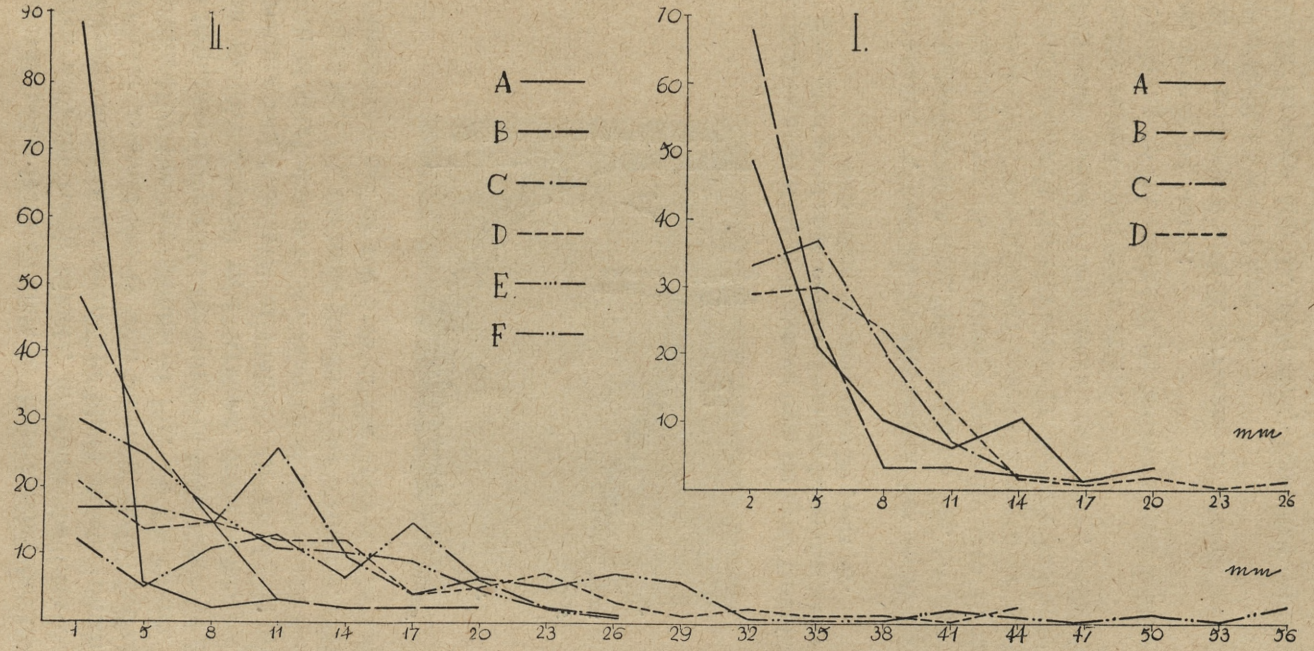

Fig. 24. Two graphs of the length of the short shoots. I. *B. pubescens*: A — The Wola Forest near Kraków; B — Mikuszyńce; C — Savolinua; D — Heinavesi (see Fig. 4); II. *B. tortuosa*: A — Rovaniemi; B — Peuraniemi; C — between Petsamo and Ivaho; D — Salmijärvi; E — Abisco; F — Narvik (see Fig. 11).

of *B. tortuosa*, in comparisson with *B. pubescens*, have their own distinctive, characteristic line of mean shape. Along this line arrange themselves all samples of the leaves of *B. tortuosa*, when compared with *B. pubescens*.

3. The most typical characters of the leaves of *B. tortuosa*, distinguishing them from *B. pubescens*, are the following: sparser nervation, acute angle between the second lateral nerve and the midrib, and a more obtuse apex.

4. The leaves of *B. tortuosa* have a similar congenital variability as do the leaves of *B. pubescens* with the exception of the distance between the tips of the second and third nerve, and the number of teeth in this intervening space; in *B. tortuosa* these characters are much more variable. In combination with great variability of the depth of the incisions, the latter characters produce irregularity of the dentation, typical of this species.

5. *B. tortuosa* displays no local variability with regard to leaf shape. The arithmetic means of all samples are very similar to one another. Local variability exists only as to leaf size, which means that entire birch aggregations are small-leafed or large-leafed.

6. The population of *B. tortuosa* is composed, the same as the populations of the species described above, of a number of pure lines with various base angles. They occur in each aggregation of this species in a similar percental proportion, which signifies that in every sample of *B. tortuosa* we can find leaves ranging from cuneiform ones to cordate.

7. The leaves of *B. tortuosa* are very variable as to the presence of hairs in the nerve axils on the under side of the blade.

8. *B. tortuosa*, with regard to its typical characters of leaf shape, occupies an intermediate position between *B. pubescens* and *B. nana*.

3. Biometric analysis of *B. carpatica*

The author's studies of *B. carpatica* were based on material from three European localities where this species was indisputably stated to exist, viz., the Tatra Mountains, the Sudety Mountains, and the Alps. To these samples added later were other materials as well. These samples, each composed of 100 leaves from 50 trees, were compared with a sample of *B. pubescens* from its European distributional area, in a similar manner as the author had done

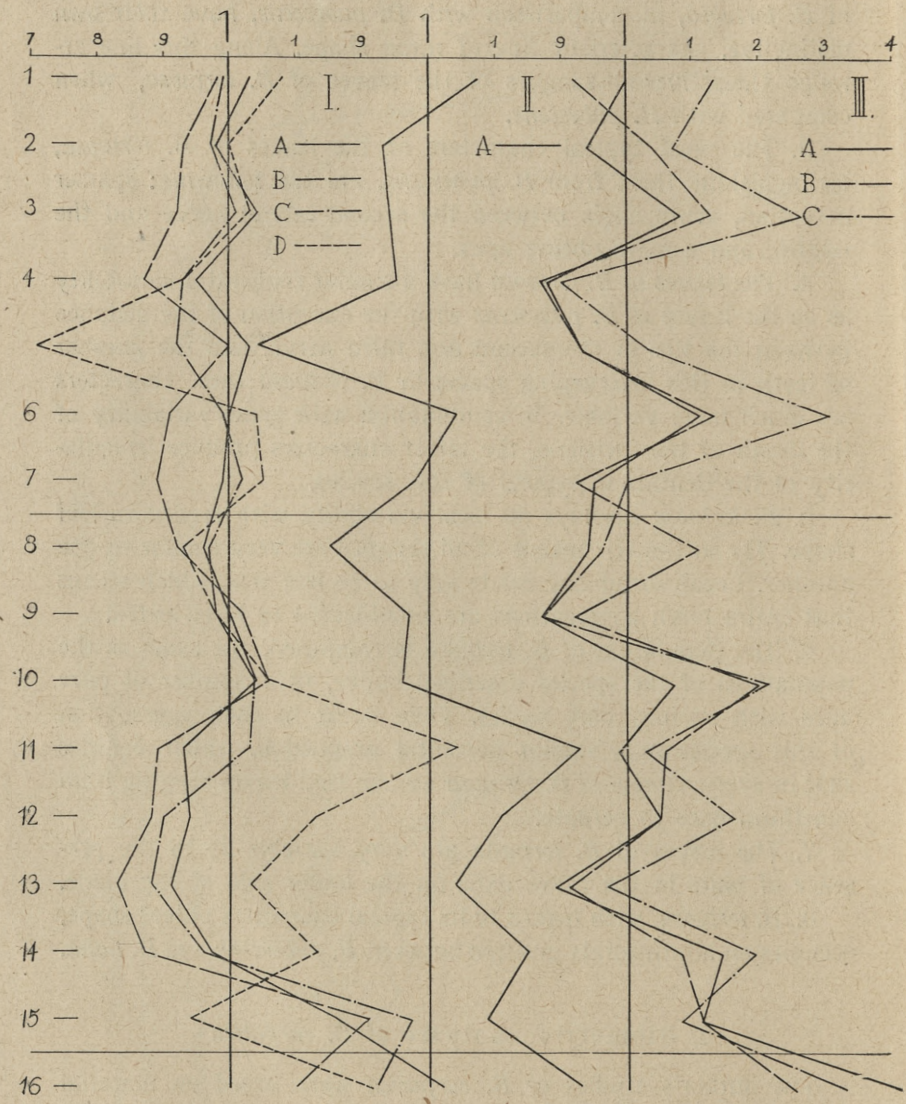

Fig. 25. Comparison of the local samples of *B. carpatica* with the sample of *B. pubescens* from the European distributional area. I. Four samples from the Tatra Mnts: A — The whole area of the Tatra Mnts., B — Opalony Wierch; C — Niewcyrka Valley; D — Roztoka Valley. II. A — The slopes of Mała Kopa near Śnieżka in the Sudety Mnts. III. Three samples from the Alps: A — between Hurter and Spöltal; B — Val Roseg; C — Val Chamuera (National Park in the Engadine).

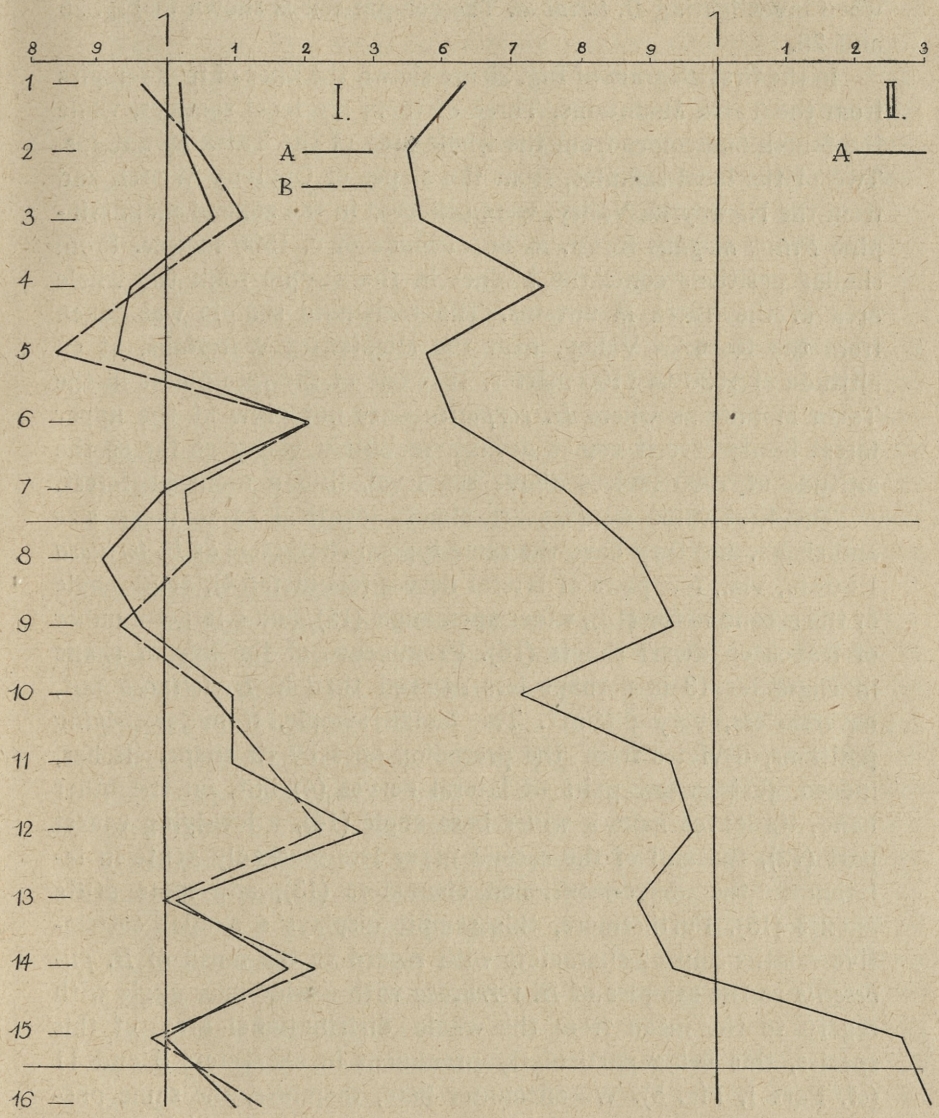

Fig. 26. Comparison of the local samples of *B. carpatica* with the sample of *B. pubescens* from the European distributional area. I. The Caucasus: A — The valley of the river Baksan; B — The valley of the river Bezenga. II. A — Scottish Highland (Aberdeenshire).

when investigating *B. tortuosa*. The comparison is shown in Fig. 25 and 26.

In the first diagram of Fig. 25 are shown the lines of four samples from the Tatra Mountains. Three of them are local samples, while the fourth one comes from the whole area of the Tatra Mountains. Two of the local samples, from the slopes of Opalony Wierch and from the Niewcyrka Valley, were collected in the zone of mountain-pine *Pinus mughus* Scop. at an altidude of c. 1500 metres. From similar positions come the birches in the sample from the whole area of the Tatra Mountains. The remaining sample was taken from the Roztoka Valley, near the Mickiewicz Waterfalls, at an altitude of 1030 to 1100 metres. It is one of the rare places in the Tatra Mountains where *B. carpatica* does not grow at the upper forest limit; here it comes down a mountain valley as far as the altitude of 1000 metres above sea level, into a montane forest.

The first three samples are almost identical as to mean size and shape, and they have the same typical characters as *B. tortuosa* Ledeb., viz., few pairs of lateral nerves (character 4), acute angle of the second nerve (13), wider apex angle (15), and a larger number of leaves on dwarf shoots (16). Prominence of the line of shape in character 13 is perhaps less marked than in *B. tortuosa* but, nevertheless, very distinct. The fourth sample, from lower-lying positions, deviates from the preceding ones by its shape. It has, indeed, just as few pairs of lateral nerves (4) but, on the other hand, its leaves have a wider base angle (14), a low-lying widest part (12), the axil of the second nerve less markedly acute in relation to the above-mentioned characters (13), and more acute apexes (15). Furthermore, this sample displays a similar correlative relationship of characters with regard to the mean of *B. pubescens* as the samples of *B. verrucosa* with a wide base angle with regard to the mean from the whole distributional area of this species, this being particularly prominent in characters 5 and 11 (cf. Part I, Fig. 5). We encounter here, therefore, the same phenomenon which is so typical of *B. verrucosa*, and which we had not observed in *B. tortuosa* or *B. pubescens*, viz., a local segregation of birches with a wider base and a more regular leaf structure in consequence of the correlative linking of characters.

The following diagram shows a sample from the Sudety Mountains, collected on the slopes of Mała Kopa, close to the highest

peak of the Karkonosze Range, Śnieżka, at an altitude of 1000—1300 metres. The birch forms there clusters of shrubs which put out numerous branches close to the ground, creeping like those of the mountain-pine; it adopts, therefore, the same morphological form as in the Tatra Mountains at the upper forest limit. Its bark, also in both mountain chains, is mostly darker than in other birches. The latter sample by the shape of its leaves bears a striking resemblance to the sample from Roztoka in the Tatra Mountains; only the apex angle is here wider on the average. In the two above-mentioned samples the wide base angle is accompanied by a lowering of the position of the widest part and a small distance of the first tooth from the base. What the two samples have also in common is that the birch agregations from which they come descend along the valley of a stream to a low level, as far as an altitude of 1000 metres above the sea. Such a similarity of the two samples of birches growing on the mountains, but in lower situations, is very astonishing. Later on the author will endeavour to explain the cause thereof.

The next diagram shows three local samples from the Alps, also collected above the upper forest limit, in an altitude of 1700 to 2000 metres. All three samples come from the National Park in the Engadine, but each from the slopes of a different valley. These samples are again exceedingly similar to one another by their shape, with the difference that in one sample the leaves had very short petioles. All have a wide mean base angle, and the acuteness of the axil of the second nerve is extremely characteristic. They also have a smaller number of pairs of lateral nerves than *B. pubescens*, in spite of frequently longer blades, a more obtuse apex, and more leaves on dwarf shoots, all these characters being typical of *B. tortuosa*. However, here the wide base angle is accompanied by a lowering of the position of the widest part of the blade, although there is no such strong correlative linking of characters as had existed in the above-described sample from Roztoka; this is noticeable, above all, by the absence of correlation between the base and the distance of the first tooth (5, 11, 14).

The first diagram on Fig. 26 shows samples from an altogether different terrain, viz., from the central part of the Caucasus, from the valleys of the rivers Baksan and Bezenga, in the group of the highest Caucasian peak, Elbruz. The herbarium material of birches

was brought from there by the Polish Scientific and Mountaineering Expedition in 1935. The author obtained the material for investigation from Prof. Marian Sokołowski and Dr Tadeusz Wiśniewski, both of whom took part in the Expedition as botanists; neither is living today. These birches were designated by Soviet botanists with the name *B. Raddeana*, this being in accordance with the distributional area of the latter species as described in the birch monograph of Ponomarew (1933). These samples come from an altitude of 2000—2300 metres, from birch-groves lying above the upper forest limit which is formed here by the pine (Sokołowski 1936, Wiśniewski 1936). In the terrain described above, on the northern slopes above the pine there exists a zone of birch; the latter bushes out in the same manner as the Polish *B. carpatica* or mountain-pine, and it invades partly the highest regions of the pine-forest. Above this birch there is a zone of rhododendron *Rhododendron caucasicum* or subalpine meadows.

As we perceive in Fig. 25, both samples from the Caucasus are almost identical with the samples of *B. carpatica* from the Alps, only their apexes are somewhat more acute, while the dentation in one of the samples began close to the base, although not so close as in the samples from Roztoka or the Sudety Mountains. There is no doubt whatever that the Caucasian birches have leaves of the same structure as the ones of *B. carpatica*, growing under the same climatic and ecologic conditions in the Alps. A detailed investigation of this material will be shortly published separately by the author.

The second diagram in Fig. 26 shows a sample from Scottish Highland from the upper forest limit, from the hill Carn nan Sgliat near Braemar (Aberdeenshire). The sample was collected by Dr St. Batko at an altitude of $\pm$ 750 metres. The polygonal line illustrating this sample differs very much, to the eye, from the previous ones. A detailed inspection shows that the difference lies only in the leaf size. These birches are markedly small-leafed. Their leaflets are, on the average, one-half shorter than the leaves of *B. pubescens* and they also have, therefore, other characters, linked up with leaf size, of corresponding smallness. The number of pairs of lateral nerves (4) — a quite constant character in the species belonging to *B. alba* — decreases here, but not in the same proportion as blade length, and, consequently, the mean distance of the nerves

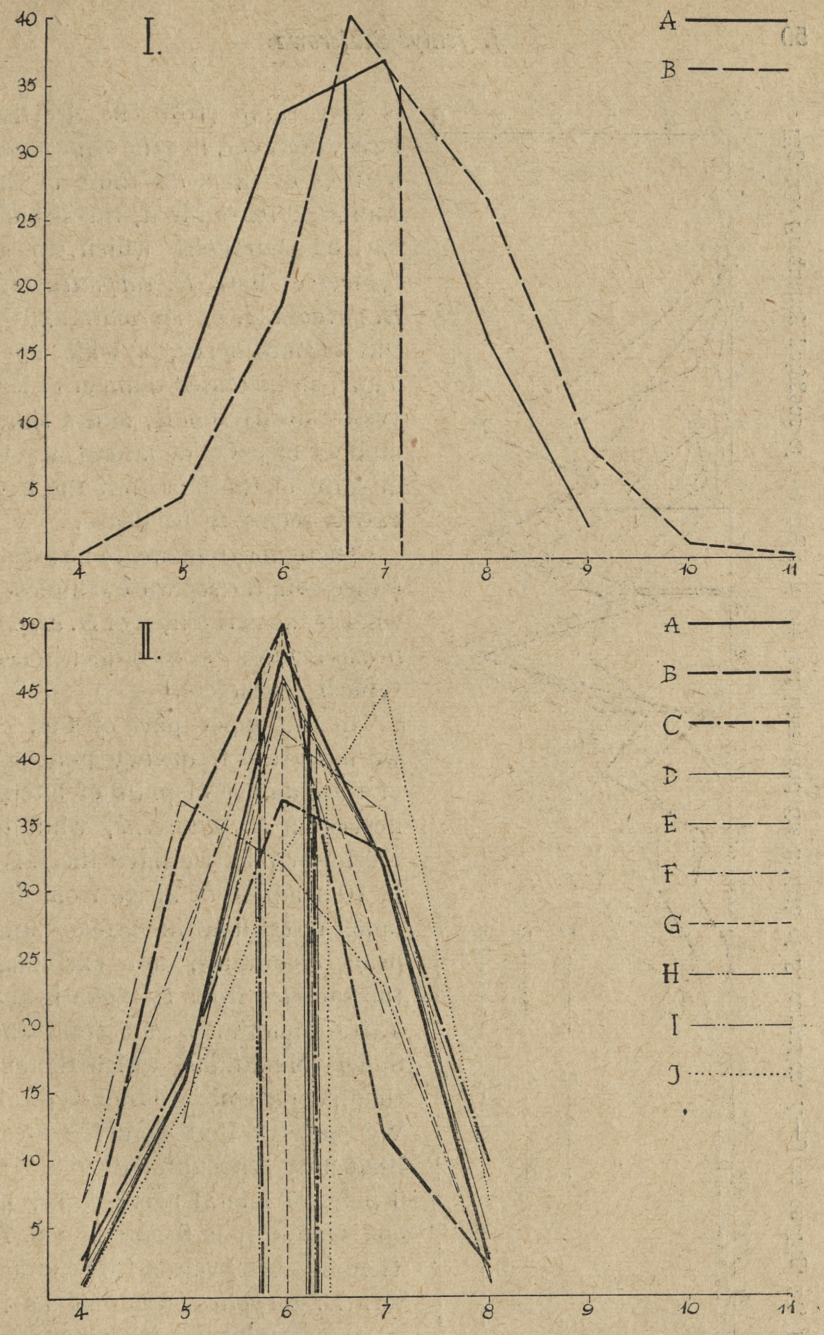

Fig. 27. Frequency polygons of the number of pairs of lateral nerves. I. *Betula pubescens*: A — Sample of 100 leaves from the European distributional area; B — Sample of 1000 leaves. II. *Betula carpatica*: A — Niewcyrka, B — Opalone; C — The whole area of the Tatra Mnts., D — Roztoka Valley; E — The Sudety Mnts., F — Between Hurten and Spöltal; G. — Val Roseg; H — Val Chamuera; I — The valley of the river Baksan; J — The valley of the river Bezenga.

Fig. 28. Frequency polygons of the angle of the leaf base and the midrib of *B. carpatica*. A—J as on Fig. 27, II.

is very small (10). The Scottish birch, however, has the same peculiarities of shape as those of the Alpine or Tatra birch; this is born out by characters which are so typical of both *B. carpatica* and *B. tortuosa*, i. e., an acute axil of the second nerve, a wide apex angle, an increased number of leaves on dwarf shoots, and a small number of pairs of lateral nerves in spite of the fact that the nervation seems to be dense.

There now remains to be ascertained—in the separate samples—what is the variability of *B. carpatica* as regards its above-mentioned typical characters.

In the upper part of Fig. 27 we have the frequency polygons of the number of pairs of lateral nerves in *B. pubescens*, while in the lower part we have the same in 10 samples of birch from the upper forest limit in various European mountains, not excluding the samples from Roztoka in the Tatra Mountains and from the Sudety Mountains, which the author had recognized as non-typical. We perceive that here the most frequently encountered value is 6 pairs of lateral nerves; only in one sample it is 5 and in one 7. Therefore, as regards this character, *B. carpatica* occupies as if an intermediate position between *B. tortuosa* and *B. pubescens*.

Fig. 28 shows the frequency polygons of the base angle. Here again we have the characteristic phenomenon which had occurred in Figs. 5 and 16: superimposition of the apexes. Furthermore, in spite of a local segregation of these birches into ones with ave-

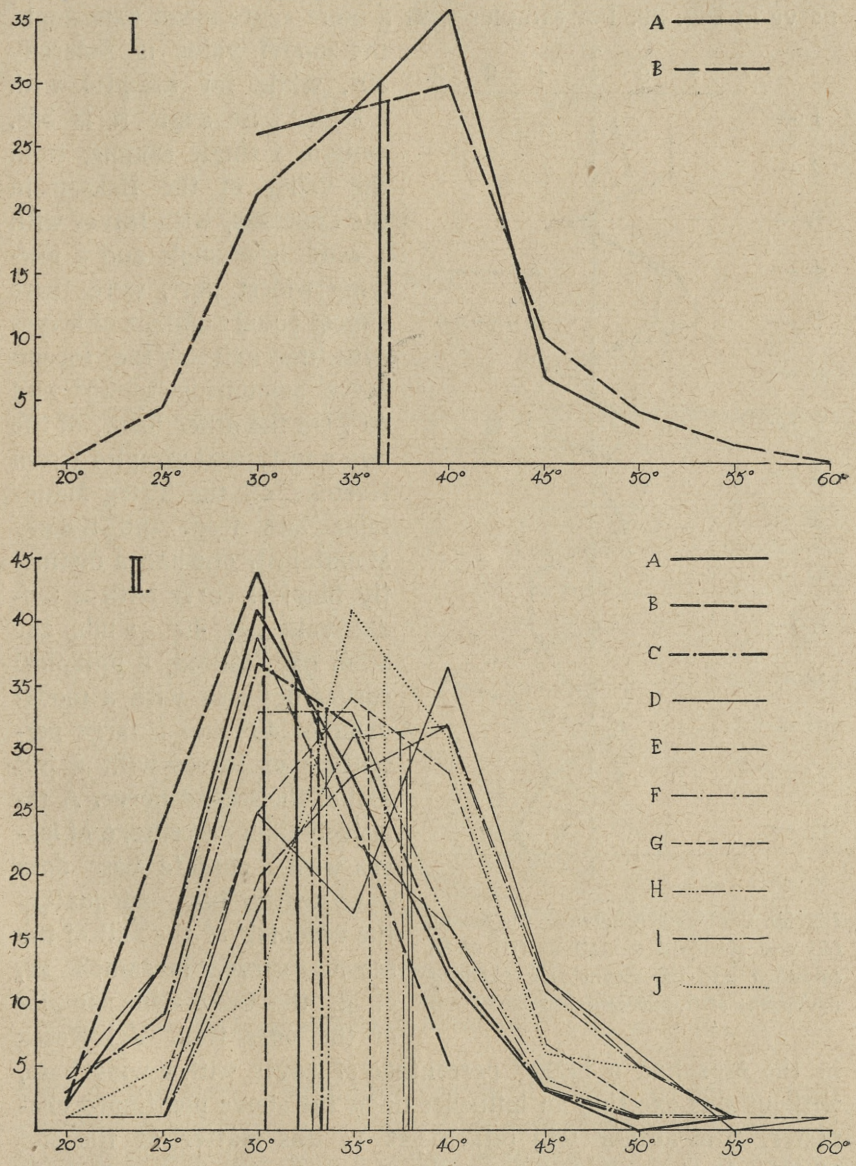

Fig. 29. Frequency polygons of the axil of the second nerve. I—II as on Fig. 27.

ragely acute or wide bases, we perceive that the variability is similar to that in *B. tortuosa* and *B. pubescens*, i. e., in almost every sample we encounter leaves ranging from cuneiform ones to cordate.

Interesting are the frequency polygons of the axil of the second nerve in Fig. 29. For samples with a more acute mean base angle, the modal value is generally 30°, while for samples with a wider base angle it is 35°. Only in a single sample, from the valley of the Baksan in the Caucasus, with leaves with a wide base angle and a low-lying widest part, were there almost equal numbers of leaves with the axil of the second nerve amounting to 35° and 40°. On the other hand, of the two non-typical samples (from Roztoka on the Tatra Mountains and from the Sudety Mountains), one had a distinctly biapical curve with a modal value of 40°, while the other had, indeed, a uniapical curve, but also with a modal value of 40° and a large percentage of leaves with a 30° axil of the second nerve. A relatively high percentage of leaves with a cordate base does not justify here adequately the widening of the axil of the second nerve, inasmuch as, e. g., the Caucasian samples or the ones from Val Roseg in the Alps had a higher percentage of leaves with a wide base, without this exerting an influence upon the above mentioned character. The author will return yet to this matter at the end of this chapter.

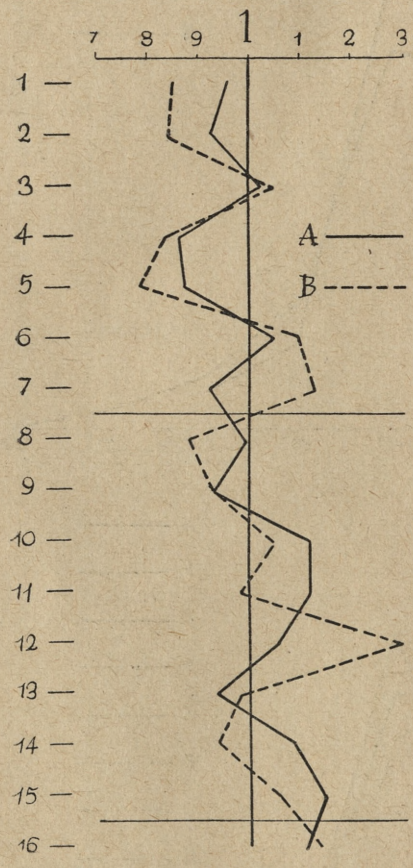

Fig. 30. Comparison between the means (A) and standard deviations (B) of *B. carpatica* and the means and standard deviations of *B. pubescens* (straight line).

The absolute variability innate in *B. carpatica* is shown in Fig. 30. The latter is prepared analogically to Fig. 17, and it shows the lines of shape and variability of *B. carpatica* in comparison

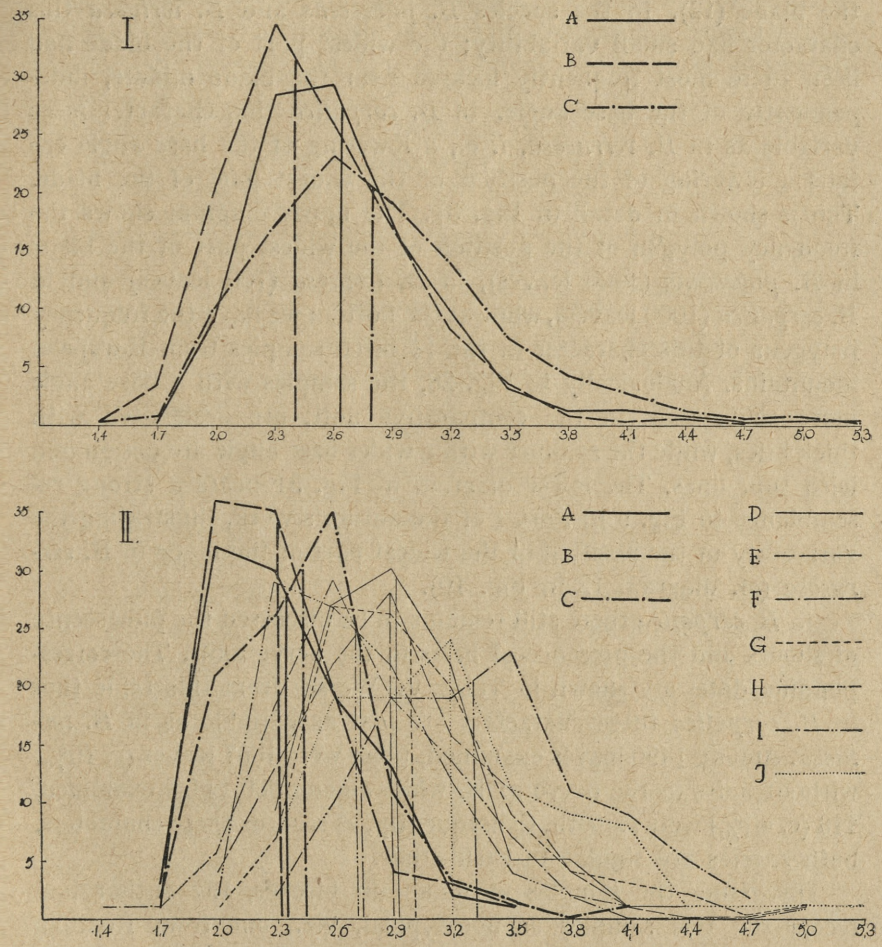

Fig. 31. Frequency polygons of the position of the widest part of the blade. I. A — *B. pubescens* (1000 leaves), B — *B. tortuosa* (100 leaves), C — *B. carpatica* (1000) leaves; II. Local samples of *B. carpatica*. A—J as on Fig. 27, II.

with *B. pubescens*. The author compared here a sample of 1000 leaves of *B. carpatica* — obtained by summing up 10 local tests (without Scotland) — with a sample of 1000 leaves of *B. pubescens*. We perceive that *B. carpatica*, as regards both its shape and varia-

bility, deviates less from *B. pubescens* than does *B. tortuosa* (cf. Fig. 17). As a typical character associated with *B. carpatica*, there emerges here the variability of the position of the widest part of the blade (12). In the species *B. pubescens* and *B. tortuosa* this character had small variability; the widest part of the blade had been there most frequently located near the blade middle, independently of the base angle. In *B. carpatica* this character is as variable as in *B. verrucosa*, i. e., a lowering of the base angle entails a lowering of the position of the widest part of the blade. This is shown in detail in Fig. 31. The upper diagram shows the frequency polygon of the position of the widest part of the blade in *B. pubescens* (1000 leaves), in *B. tortuosa* (700 leaves) and in *B. carpatica* (1000 leaves), while at the bottom we have the frequency polygons of this character in the 11 birch samples from European mountains. Analogically to Fig. 28, the samples with a base angle more acute than in the comparative unit, are designated with thick lines, while the samples with a wider base angle are designated with thin lines. The lower diagram in Fig. 31 bears a strong resemblance to Fig. 9 in Part I of the author's work, illustrating the variability of the position of the widest part of the blade in *B. verrucosa* (cf. diagram 12 in Fig. 10).

In *B. carpatica* there still remains to be discussed the pubescence of shoots and the presence of hairs in the nerve axils. The corresponding data are shown in Table V. We see from this table that in *B. carpatica* these characters are just as variable as in *B. tortuosa*. Among 1490 leaves examined, there were 1067 leaves (c. 70%) without hairs in the nerve axils, while among 300 twigs examined, 118 (c. 40%) were smooth. Consequently, as regards these characters, both species are similar to each other.

Discussing the samples of mountain birches, the author had recognized two samples as non-typical, viz., one from Roztoka in the Tatra Mountains and one from the Sudety Mountains. A common feature of the habitats from which these samples came was that the birches in these stations descended mountain-valleys as far down as the altitude of 1000 metres above sea level, where — at the limit of their distributional area — they come into contact with specimens of *B. verrucosa*, sporadically reaching those places. In all the samples of birches from the upper forest limit in European mountains there is noticeable a great variability of the po-

sition of the widest part of the blade. Furthermore, in the two above-mentioned samples there is the same correlative association of still other characters with the base angle as the one encountered in *B. verrucosa*. Moreover, in the frequency polygon of the variability of the axil of the second nerve, the sample from Roztoka displays the presence of two elements with the most frequently

TABLE V

Betula carpatica Waldst. et Kit.

Sample	Leaves			Twigs		
	with hairs in nerve axils	without hairs in nerve axils	total	pubescent	smooth	total
1 tree, Opalone	—	142	142	—	—	—
1 ,, ,, ...	32	90	122	—	—	—
1 ,, Roztoka	101	25	126	—	—	—
50 trees, Opalone.....	5	95	100	26	24	50
50 ,, Niewcyrka	9	91	100	20	30	50
50 ,, Whole Tatra ...	37	63	100	20	30	50
50 ,, Roztoka	65	35	100	—	—	—
50 ,, Śnieżka	43	57	100	—	—	—
50 ,, Spöltal.....	17	83	100	—	—	—
50 ,, V. Chamuera ...	31	69	100	—	—	—
50 ,, V. Roseg	36	64	100	—	—	—
50 ,, Baksan	2	98	100	46	4	50
50 ,, Bezenga	12	88	100	35	15	50
50 ,, Scotland	33	67	100	35	15	50
Total	423	1067	1490	182	118	300

encountered value of 30° and 40° (Fig. 29). This vividly calls to mind the two samples of *B. pubescens* from the lake country of Finland (p. 33). In the latter case the same phenomenon existed at the contact line of *B. pubescens* and *B. tortuosa*. There it could either be a mixture of species, or else sexual hybrids of these two birch species which taxonomically stand so close to each other. Here a mixture is out of the question. The leaves of *B. verrucosa*

and *B. carpatica* are too characteristic to suppose that the author could have not distinguished them from each other in a sample. On the other hand, after the studies of Helge Johnsson we cannot speak of hybrids between these species until we discover that they are able to cross. If indeed we cannot accept for the time being the existence of hybrids, the more so it cannot be said that the hybrids *verrucosa* × *carpatica* cross further with *carpatica*, disturbing the purity of the latter species and imparting to it certain features characteristic of *verrucosa*. Therefore, the author is not able at present to explain what are the birches from which were taken the two above-mentioned samples that display — speaking in human terms — an «admixture of *verrucosa* blood». The author supposes, however, that this problem will some day be solved.

Prof. M. Skalińska, who is engaged especially in a cytological study of species growing wild in nature, was kind enough — at the author's request — to concern herself in 1935 with the species *B. carpatica*. Two trees, growing above the upper forest limit on the slopes of Opalony Wierch above the lake Morskie Oko in the Tatra Mountains, were examined by her and shown to possess 42 somatic chromosomes (unpublished studies). This means, therefore, that they are triploid, according to older terminology, or hexaploid, as they ought to be correctly termed at present. The fact is that the basic number of chromosomes in birches is 7, and the chromosome number in various species is its multiple, and not the multiple of 14, which is the smallest chromosome number in the gametes of birches existing at present. For instance, in *B. papyrifera* Marsh $n=35$, and $2n=70$; therefore, it is decaploid, and not pentaploid, as originally stated by Woodworth (1929). Birches possessing 42 chromosomes and known from nature as well as cultivation, were hybrids of *verrucosa* × *pubescens*, *lenta* × *pumilis*, or so-called autotriploids of *verrucosa* (Helms and Joergensen 1925, Jack 1895, Johnsson 1945, 1949), and they were characterized by sterility. *B. carpatica* in the Tatra Mountains blossoms and bears abundant fruit, and is rejuvenated naturally in its stations; consequently, it is certainly fertile. A study of two trees is no basis for maintaining that all specimens of *B. carpatica* have 42 chromosomes. However, the fact that the smallest somatic chromosome number occurring at present in birches is 28, does by no means exlude the existence at one time of a birch with a somatic chro-

mosome number $2n=14$. The latter would be the conjectural proto-from of some of the species existing today. In the case of such a birch crossing with a birch having 28 chromosomes and of doubling the chromosome number in the hybrid, produced would be a form with 42 chromosomes; its meiosis might be normal and its seeds would be fertile, the same as is normal the meiosis and fertility of *B. papyrifera* Marsh which has 35 pairs of chromosomes. All this is a hypothesis, but one which is based on probability.

It follows from this chapter that alhough on the one hand the biometric studies of the leaves of *B. verrucosa*, *B. pubescens* and *B. tortuosa* has shed much light on these species, on the other hand the investigation of the 11 samples of birches from the upper forest limit creates a number of problems requiring explanation. There is no doubt that the samples examined here are, as regards the most important characters of the shape of their leaves, very similar to the birch from the northern forest limit. The fact is that they all have a relatively small number of pairs of lateral nerves, and a less dense nervation; all have, on the average, an acute axil of the second nerve, in relation to the base angle, more obtuse apexes than in *B. pubescens*, and a larger number of leaves on dwarf shoots. Some samples differ only from the other by a character which is very variable in all the birch species described above, viz., the mean base angle.

It is a variability to which the locally isolated species are, so to say, entitled. *B. tortuosa* during and after the Glacial Epoch occupied probably great areas of Central Europe, shut in on the north by the front of the ice-sheet, and from the south by glaciers descending from the mountains. There is nothing more simple to suppose, in fact, than that out of the above-mentioned population there became isolated in distant mountain stations lines with narrower or wider base angles, and that they continue to grow there up to the present day as relicts from the Glacial Epoch. Complete isolation, changes of the habitat and of external conditions, and the neighbourhood of new birch species — all this together could have caused these plants, although preserving the original characters of their parent species, to undergo certain changes. These changes consist, above all, in the fact that *B. carpatica* — for climatic, ecologic or internal reasons — stands closer to *B. pu-*

bescens than *B. tortuosa*, and also acquires certain characters typical of *B. verrucosa*, with which it comes into contact in some places at the limits of its distributional area. This character is, first of all, the plasticity of the position of the widest part of the blade.

If it is as the author supposes, if mountain birches are indeed relicts of the Glacial Epoch and descend from the same family tree as *B. tortuosa*, and if their present respective aggregations are genotypes isolated out of a great original population — then in order to gain an idea as to the variability and shape of what we today term *B. carpatica*, it is necessary to examine a much greater number of sample than eleven. This requires, first of all, a good local investigation, particularly in the Alps, then in the Caucasus and in Scotland, and in the Pyrenees as well, where this species has also been quoted to occur. Only this can give an idea as to the actual variability and answer the question whether *B. carpatica* is but a variety of *B. tortuosa*, or does it deserve the rank of a separate species.

At the end of this chapter the author must add that in 1948 Prof. W. Lüdi was kind enough to collect for the author, in Switzerland, a sample of birches growing at an altitude of c. 1900 metres on the slopes of the valley of the Aletsch Glacier in the Bernina Alps. It is a young terrain, recently abandoned by the glacier which is now retreating (Lüdi, 1945). Therefore, these birches are not from the upper forest limit, which passes here higher; nevertheless, even in relation to the great mountain mass of the Alps, it is a very high station. It turned out, to the author's surprise, that all the birches collected for the measurements, belonged to the species *B. verrucosa*. These birches grow in the company of larches and spruce-trees, and are, together with the latter, the first forest pioneers in the young terrain emerging from underneath the glacier. Already Prof. Lüdi, collecting the material, noticed the great variability of their leaves. As he was kind enough to write to the author, it had been such an interesting observation that it recompensed him for the two days' trouble of collecting the sample in a very unpleasant morainic terrain.

Measurements of 100 leaves from 50 trees confirmed that the sample belonged to the species *B. verrucosa*. In Fig. 32 we have in the first diagram the line of size and shape of *B. verrucosa* (100 leaves from 50 trees from its European distributional area),

and the line of size and shape of the Swiss sample compared with *B. pubescens*. These lines run almost parallel. There is no doubt that the Swiss sample is a sample of *B. verrucosa* with small relatively short and wide leaves (characters 2, 3 and 9). In the second diagram of Fig. 32 we have the line of shape and variability (σ) of this sample in comparison with *B. verrucosa* (100 leaves from

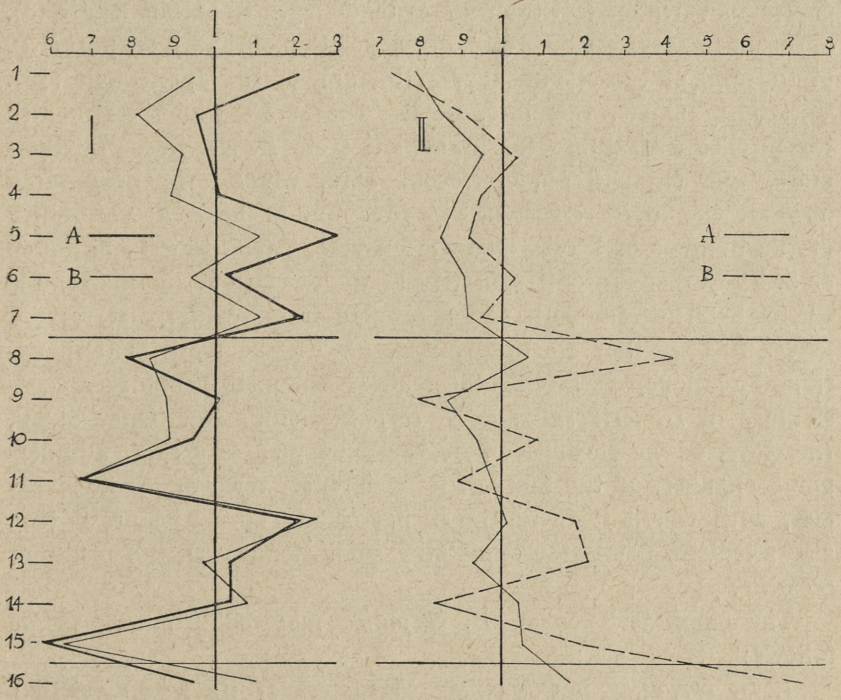

Fig. 32. I. Comparison of the sample of *B. verrucosa* from the European distributional area (A) and the sample of *B. verrucosa* from the Alps (B) with *B. pubescens*; II. Comparison of the means (A) and the standard deviations (B) of *B. verrucosa* from the Alps with the means and standard deviations of *B. verrucosa* from the European distributional area (straight line).

50 trees from its European distributional area), arranged analogically as in Figs. 8, 17 and 30. In the line of shape (solid polygonal line) absent is the correlation of characters — described by the author in Part I of her work — so typical of samples with a wider base angle. Next, striking is the fact that the axil of the second nerve (13) is very acute in comparison with the base angle (14) and

the position of the widest part (12); this reminds us of *B. tortuosa* and *B. carpatica*. The line of variability (broken polygonal line) sheds, indeed, much light on the character of this sample. These birches are less variable as regards the base angle than the sample from the whole distributional area (character 14); this is a feature of every local sample. They are distinguished, however, by an enormous variability of the ratio of blade legth to petiole length (8), of the mean nerve distance (10), of the position of the widest part (12), of the axil of the second nerve (13), and of the apex angle (15). Variability exists, therefore, in the characters which distinguish the birches with pubescent branchlets from *B. verrucosa*. Furthermore, two characters more occur here, which are encountered nowhere else in *B. verrucosa*. The first one is the great variability of the number of leaves on dwarf shoots, amounting to as much as 5. The other is the irregularity of the dentation. In this sample we have all intermediate forms ranging from regularly serrulated leaves to ones that are deeply incised with the teeth bent in various directions, resembling the restless leaf margin one sees occasionally in *B. tortuosa* and *B. carpatica* (Fig. 18). Once again, therefore, do we encounter here the phenomen of a species undergoing changes, at the limit of its occurence, towards another species, with which it there comes into contact — without having any scientific bassis for explaining such changes as the result of crossing.

The characteristics of *B. carpatica* may be summed up as follows:

1. *B. carpatica* has peculiar characters of its leaves, similar to those of *B. tortuosa*.

2. *B. carpatica* deviates less by its shape and variability from *B. pubescens* than *B. tortuosa*.

3. *B. carpatica* displays local variability as regards base angle.

4. *B. carpatica*, in contradistinction to *B. pubescens* and *B. tortuosa*, has great variability as regards the position of the widest part of the blade; this approximates it to *B. verrucosa*.

5. The peculiarities of the leaves of 11 tests of *B. carpatica*, examined by the author, suggest that it originated probably from a great diluvial population of *B. tortuosa* and that it is a relict from the Glacial Epoch, preserved in slightly differing forms in isolated mountain stations.

III. Summary

In present paper the author is concerned with species possessing pubescent branchlets, i. e., *Betula pubescens* Ehrh., *Betula tortuosa* Ledeb. and *Betula carpatica* Waldst. et Kit.

A peculiar feature of the leaves of *B. pubescens*, although they do not differ from *B. verrucosa* by even a single character of shape in an essential manner, is that the structural plan of these leaves — i. e., the relation of their characters — is nevertheless different. This is expressed plastically by the fact that the size and shape of the leaves from all samples of *B. pubescens*, when compared with *B. verrucosa*, arrange themselves along a specific polygonal line which the author terms the line of size and shape of the leaves of *Betula pubescens*.

One of the most distinguishing characters of these leaves are petioles which are on the average shorter than on *B. verrucosa*, together with great variability of the ratio of leaf-blade length to petiole length, in consequence of which encountered are long leaves on short petioles, and short leaves on long petioles. Another distinguishing character is the small variability of the position of the widest part of the leaf-blade, so plastic in *B. verrucosa*. In *B. pubescens* the widest part, even in cordate leaves, keeps close to the middle of the blade. Furthermore, *B. pubescens* manifests great local variability as to leaf size, which means that entire local birch aggregations are large-leafed or small-leafed. It does not manifest, however, local variability with regard to blade shape, so that in each aggregation one may encounter leaves which at their bases are from cuneiform to cordate. Neither is there in this species any distinct correlation between blade base and a whole number of other characters, as previously demonstrated by the author for the species *B. verrucosa*.

B. tortuosa and *B. carpatica*, considered by some authors as varieties of the species *B. pubescens*, were dealt with in the author's studies geographically. Samples of *B. tortuosa* were collected between the Arctic Circle and the Artic Ocean in Finland and Scandinavia; those of *B. carpatica*, at the upper forest limit of various European mountains.

B. tortuosa was discovered to possess leaves of a similar mean shape and similar variability in all samples examined. They differ

from *B. pubescens* by having a smaller number of pairs of lateral nerves in the presence of an almost identical blade length, the widest part situated on the average still nearer to the blade middle than in *B. pubescens*, an acute angle of the second nerve, and a more obtuse apex. With regard to these characters, *B. tortuosa* deviates from *B. pubescens* towards the leaves of *B. nana* which grows in the same areas; this is not explainable by sexual cross-breeding of the above-mentioned species.

B. carpatica has leaves of a shape very similar to that of the leaves of *B. tortuosa*, but it has certain specific characters. The most important of the latter is the plasticity of the position of the widest part of the blade; this position becomes lower as the base angle becomes larger. This character occurred in the species *B. verrucosa*, but not in *B. pubescens* and *B. tortuosa*. Furthermore, *B. carpatica* in isolated mountain areas manifests local variability. In some places encountered are birches with leaves possessing, on the average, a wide base and a low-lying widest part of the blade, while in other places the base is more cuneiform and the widest part lies high.

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Badanie utajonego wirusa X ziemniaków metodą wiązania dopełniacza. — Investigation of masked virus X in potatoes by complement fixation test.

Mémoire

de M^lle^ **A. KOZŁOWSKA** m. c.

présenté le 30 Mars 1950

Introduction

There exist three most important virus diseases which decide the so called degeneration of potatoes, namely virus *Y*, virus *E* and, finally, the masked virus *X*. Both virus *Y* and virus *E* show in all their strains such characteristic symptoms that in a field selection they are quite obvious. Quite different is the case of the masked virus *X*. Some of its strains are often invisible on potatoes and are therefore not detected in a normal field selection. Nevertheless, virus *X* is a factor which sometimes causes a complete degeneration of the potato particularly when it appears together with other virus diseases. The virulence and intensivity of the various strains of virus X is often so changeable that sometimes tubers from an apparently healthy plant produce in the following year strongly degenerated individuals. Therefore a method of the greatest possible exactness that could state the presence of a small amount of virus *X* in tubers and sprouts of apparently healthy potatoes is a most important matter. It would enable us to understand the development of the virus disease in plants and the factors that influence it.

There exist two principal categories of methods which make it possible to state in doubtful cases the presence of virus *X* in plants, namely the serological methods and the biological one. In the present work we used in our serological investigations not precipitation but the complement fixation reaction usually applied in animal virus diseases.

It is the task of this paper to present after experiments of 3 years the diagnostic values of the complement fixation test employed

in the detection of the masked strains of virus *X* in potatoes. For comparison we also applied in our experiments precipitation and inoculation of potato sap on test plants of White Burley tobacco.

Serological methods

Precipitation

The precipitation method is at present generally applied for the detection of masked strains of virus *X* both in laboratories and in field investigations (Jermoliew & Hruska 1947, Markham, Matthews & Smith 1948, Roland 1945).

The principal question in detecting strains of virus *X* with the aid of the serological method is the problem of whether the particular strains differ from each other in their qualities or not. Many experiments carried out to that effect gave no consistant results until today (Bawden 1935, Bawden & Sheffield 1944, Chester 1936, Larson 1946, Roland 1945). We can draw the following conclusions:

1. The particular strains of virus *X* are closely related to each other with regard to their serological qualities, but are not identical. Besides common antigen qualities they have also separate ones.

2. The characteristic symptoms of virus *X* on potatoes and tobacco plants do not always comply with separate serological strains.

3. Potatoes and tobacco with strong virulent strains of virus *X* showing distinct symptoms such as mosaic, ringspots, necrosis, contain not one but usually several strains simultaneously. In practice, antiserum obtained from the sap of those plants gives the phenomenon of precipitation with many strains of virus *X*.

The intensity of precipitation depends on the titre of the antiserum and of the concentration of the virus in the investigated plants. Strong virulent strains of virus *X*, which show on tobacco the phenomenon of necrosis, produce an antiserum of a higher titre than the weakly virulent strains which produce on tobacco the phenomenon of a weak mosaic. Bawden, Kassanis, Roberts (1948), using antiserum *X* in a solution of 1:200, determined in the leaves of the potato variety Majestic, that was infected with different strains of virus *X*, the titre of precipitation. It is the highest dilution of sap with which a visible precipitate can be

obtained. Optimal precipitation titres were 1/1280 with a strain producing on the potato a bright yellow mottle. The strain which produced a mild mosaic gave a precipitation titre of only 1/160. The same correlation is to be found in tobacco; plants showing pronounced leaf symptoms give the highest precipitation titre.

The most essential problem is to discover to what a degree the method of precipitation finds out weak virulent strains of virus *X*, which produce no symptoms on the potato. These strains can be divided into two categories; into those which give a very mild mosaic when inoculated on tobacco and into those strains which show no symptoms at all on tobacco leaves.

According to Matthews (1948) the X^H strains of Salaman, isolated from symptom-free tobacco leaves, do not differ much in their antigen properties from the strains X^L Salaman which show a visible mottle on tobacco. Antiserum X^L gives precipitation with an extract of tobacco containing X^H. Nevertheless, according to the field experiments of Roland (1945), the fresh sap of apparently healthy potato leaves precipitated with antiserum virus *X* on microscopic slides only in those cases when the same sap inoculated on tobacco caused a visible mottle. Markham, Mathews and Smith (1948) are of the opinion that the precipitation method is more sensitive than the inoculation on tobacco, but all the same this method does not detect virus *X* with absolute certainty. Our experiments, carried out with the method of the above mentioned authors, gave a similar result. The sap of tobaccos with a mild mosaic precipitated always, on the other hand, quite symptom-free tobacco leaves, in a way similar to the potatoes with the sap of which the tobacco was inoculated mostly did not precipitate. The presence of virus *X* could always be stated in them by means of the biological method; strong virulent strains (X^S, X^N) inoculated on them did not cause any infection. Complement fixation applied to these tobacco plants at the same time always showed in them the presence of virus *X*.

Complement fixation

The complement fixation test, applied generally in the diseases of men and animals, shows in comparison to precipitation an at least 10 times greater sensitivity. It is therefore quite obvious

that in certain cases complement fixation gives positive results in the absence of visible precipitation. This phenomenon concerns the amount of virus substance in the antigen as well as, though in a higher degree, the titre of the antiserum. According to Merill (1936), by visible precipitation, the relation between the antigen and its antibodies is 1:100. Investigations carried out with electron microscope on tobacco mosaic (Doer 1947, Sigurgeirsson & Stanley 1947) showed that precipitation appeared only in those cases when the amount of antibodies in the antiserum was large enough. On the contrary complement fixation tests give positive results when the antibodies are in considerable dilution and amount to a few γ.

Although the complement fixation test shows so great a sensitivity yet it awaken certain doubts since this test cannot be a specific one. The basis for this serological test is the characteristic feature of complement (fresh normal serum from guinea pigs) bound by the aggregate formed through the interaction of antigens and antibodies. After a certain time of incubation «sensitised» red cells are added as an indicator for the presence of the complement. If an immunological reaction takes place in the first stage, the complement is fixed and removed from the solution and hemolysis is prevented completely or in part. Yet when the complement is not bound complete lysis of red cells appears. In this test, therefore there always exists the possibility that the antigen introduced by us without being bound with corresponding antibodies, contains besides virus substance also chemical compounds which do not specifically absorb the complement. Applying this method with the aid of a great many controls with normal, healthy sera, we must prove that in fact not secondary factors but aggregates of antigen — antibodies cause complement fixation and a prevention of hemolysis.

Investigation of masked virus X in potatoes by the complement fixation test

Preparation of antisera

Whereas a great number of antibodies of antiserum take part in the precipitation, so, as already mentioned above, the prevention of hemolysis in the complement fixation test takes place

when the number of antibodies is very small. In consequence there exists in that test, as being a more sensitive one, a greater danger of finding in the serum even traces of antibodies against albumen contained in the sap of the investigated potato.

In our investigations we obtained specific antisera in three different ways:

1. The sap of tobacco var. *White Burley* and *Datura Stramonium* infected with the sap of contaminated potatoes was expressed. We chose plants with strong disease symptoms, strains X^L or X^S Salaman. We heated the sap to 55°, centrifugated it, then we precipitated normal species albumen with the antiserum of a rabbit inoculated with the healthy albumen of potatoes (variety Bintie imported from Belgium)[1] or tobacco. We made it a rule to add 1 part of antiserum to 4 parts of sap. After 24 hours the sediment was centrifugated. With this antigen we inoculated a rabbit 6 to 8 times every 3 or 4 days. 10 days after the last injection the animal was bled. In the complement fixation test this antiserum gave no reaction with healthy normal albumen of tobacco or potato. On the other hand antiserum produced from the extract of a healthy tobacco plant always gave a positive result both with the sap of healthy and with that of infected tobacco plants. The best result was attained when a rabbit was inoculated with the fresh but not creared sap of infected tobacco plants, which had been previously only precipitated with an antiserum against healthy normal potato or tobacco albumen. When the sap had been cleaned with $(NH_4)_2SO_4$ the produced antiserum had a lower titre.

2. In order to avoid a reaction with antiserum of the albumen of the investigated species, virus *X* was inoculated on species which belong to a family systematically not related to the family of the *Solanaceae*. One year we were able to infect *Cucumis sativus* and *Cucurbita pepo* with the visible strain of virus *X*. In the sap of those plants we centrifugated the chlorophil and we precipitated the albumen several times with $(NH_4)_2SO_4$ afterwards using that solution in our injection. The complement fixation test executed with that antiserum showed no trace of a reaction with the sap of a healthy tobacco or potato plant.

[1]) I take the opportunity of thanking Dr Roland for sending me the tubers of healthy »Bintie« potatoes.

3. The antigen used for inoculation came from the sap of plants which were watered in their young stages of development with a solution of ammonium molybdate. To this end we used the cucumber plant or phlox. Under the influence of molybden an albumen compound is produced in the plant tissue which produces in the rabbit antibodies that react serologically in complement fixation test with the virus *X*. (Kozłowska 1947).

TABLE I

Stocks of potato sprouts		Immune serum for virus X			Immune serum for protein obtained with *Mo*			Normal rabbit serum
		Antiserum dilution		Control without antiserum	Antiserum dilution		Control without antiserum	
		1/10	1/20		1/10	1/20		
47	1	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—
	3	—	—	—	—	—	—	—
	4	—	—	—	—	—	—	—
51	1	—	—	—	—	—	—	—
	2	++	+	—	+	+	—	—
	3	—	—	—	—	—	—	—
	4	—	—	—	—	—	—	—
	5	—	—	—	—	—	—	—
96	1	—	—	—	—	—	—	—
	2	+++	+++	—	+++	+++	—	—
	3	—	—	—	—	—	—	—
	4	—	—	—	—	—	—	—
	5	—	—	—	—	—	—	—
44	1	+++	++	—	+++	+	—	—
	2	+++	++	—	+++	++	—	—
	3	+++	+	—	+++	—	—	—
Germs:								
Johanna		—	—	—	—	—	—	—
915		—	—	—	—	—	—	—
195		++	+	—	+++	+++	—	—
771		—	—	—	—	—	—	—
855		—	—	—	—	—	—	—

Positive complement fixation reaction is indicated by the sign + negative reaction by —

+++ completely prevention of hemolysis
++ part hemolysis
+ incomplete hemolysis

As a control we carried out simultaneously with the above described antisera a series of complement fixation tests using the same antigen. Table I shows that the sera gave the same results.

In order to state finally the values of the antisera produced by us we compared their properties with the serum which I obtained, thanks to Mr. Kleczkowski from Rothamsted. This same serum is used in the English experimental stations in their investigations concerning virus *X* in potatoes. When this serum came to us it

TABLE II

Stocks of potatoes (sprouts)	Immune serum for virus X (Rothamsted)			Immune serum for protein obtained with *Mo*			Normal rabbit serum
	Antiserum dilution		Control without antiserum	Antiserum dilution		Control	
	1/10	1/20		1/10	1/20		
Ostbote 1	+++	+	—	+++	+++	—	—
2	+	—	—	++	+	—	—
3	—	—	—	—	—	—	—
4	—	—	—	+	+	—	—
5	+++	+	—	+++	+++	—	—
326 1	—	—	—	+	—	—	—
2	—	—	—	—	—	—	—
3	+++	+	—	+++	+++	—	—
4	—	—	—	—	—	—	—
5	+++	+	—	+++	+	—	—
Virus X of Nicotiana	+++	++	—	+++	+++	—	—
Sap of healthy Nicot.	—	—	—	—	—	—	—

had already lost its capacity of precipitation, but had retained the capacity to prevent hemolysis in the complement fixation test. A comparison with our antiserum produced from the albumen of plants watered with ammonium molybdate gave the same results (Table II).

The titre of those antisera was in the complement fixation tests 1:160, when the fresh sap of tobacco plants infected with strains X^S, X^N at a solution of 1:30 was used as antigen. The precipitation titre with the same antigen was as a rule lower, namely 1:36, 1:120. Antisera obtained from plants watered with ammonium

molybdate in complement fixation test gave mostly the same titre, namely 1:160, but showed no precipitation at all. Antisera obtained from infected *Datura* and tobacco lost their capacity of precipitation after 2 to 3 months but they retained for some time — even months — the capacity to prevent hemolysis in complement fixation test.

As control we used besides the normal rabbit serum, sera obtained by the inoculation of the sap of healthy tobacco or the serum of the potato variety Bintie which contained no virus *X* disease.

Preparations of antigens

Potato and tobacco leaves, tuber germs, finally single parts of tubers alone were investigated with the complement fixation test.

1. Potato and tobacco leaves. 0·3 g of a fresh green leaf were brayed in a mortar with 10 cm^3 of physiological salt solution (0·85% NaCl). This extract was heated for 7 minutes to 55° C and immediately centrifugated. The opalescing, yellowish, sometimes greenish supernatant fluid was used in the complement fixation test. Thanks to the fact that the plant material was weighed for each antigen preparation the process of the reaction itself was simplified. It was found that when using always the same solutions the titration of the complement gave almost always the same result. It was sufficient to titrate 10 tests of complement out of 50 tests, which facilitated the work. When we prepared extracts of leaves and germs in various concentration, we had to determine in each single case the solution of the complement by titration.

Besides we used another method, we let CO_2 through the extract for 1 to 5 minutes. After centrifugation we received supernatant fluid analogically to the first method. Several tests showed that a 30 times dissolved fresh sap was the most favorable for the complement fixation test. When the concentration was stronger, we had to apply too strong a complement and then the reaction could not prove to be a specific one. Cleaning the leaf sap albumen with $(NH_4)_2SO_4$ was purposeless. The complement fixation test gave the same results with fresh sap as with the several times cleaned and the dissolved albumen sediment.

2. Tuber germs. Our investigations were carried out from the moment when the tubers began to germinate, namely, from the 1-st of February until the end of April. The material was partly exposed to light in order to get light germs and partly kept in darkness in a temperature of 15° to 20°, in order to get longer sprouts of a greater weight. Each sprout was divided in its length. One half was taken for complement fixation, while with sap of the other half we inoculated the test plant, or we carried out precipitation. In order to get strictly the same solutions each half of the sprout was weighed and then ground in a china mortar with a 30 times greater volume of a 0·85% salt solution. After grinding the insoluble parts were centrifugated at 3.000 revolutions. The light brown supernatant fluid always gave a positive Millon reaction which pointed to the presence of albumen. An extract prepared in such a way was, without any further cleaning, most convenient for carrying out the complement fixation test. Titration gave a complement solution of 1:12; this solution usually gave a complete hemolysis. When the germs were weighed the titration results were so similar that it was sufficient, as in the case of the haulms, to titrate only 1/5 of the entire amount of the investigated material.

3. Non-germinated tubers. When investigating parts of tubers, eyes and starch meristem with the help of complement fixation test we meet with serious difficulties. An extract of starch meristem obtained by the above mentioned method, applied by us to leaves and germs, always prevents hemolysis in a not specific way. Antiserum obtained from such an extract caused in our experiments a positive complement fixation test with various antigens: with cleaned tobacco mosaic, virus *X*, an albumen extract of a healthy Cucumber, Phlox etc. Extract of starch meristem, cleaned several times with $(NH_4)_2SO_4$, and then with Cl_3COOH, that always gives a distinct biuret test, and shows no traces of starch, gave in the complement fixation test the same not specific reaction. Only when a fresh tuber extract was twice passed through the Seitz G III filter, or was centrifugated for 5 or 10 minutes at 10.000 revolutions, we obtained an extract which, when used as an antigen, showed specific serological qualities.

Complement fixation test

The first stage of the complement fixation test is the determination of the complement titre, that is to say its solution which caused a hemolysis of the red corpuscles in the presence of antigen and control serum. To this end we pour into 7 tubes 0·25 cm of investigated antigen. 0·25 control serum in a solution of 1 to 10 and complement in different solution from 1:11 to 1:49. We place them in a water-bath at a temperature of + 37° for 30 minutes. Then we add sensitive 3% blood corpuscles and put it into a waterbath for 15 minutes, then we read off in which tube hemolysis appeared. Using haulm antigen it appeared at 1:16, using sprout antigen at 1:19. After the determination of the complement titre we begin the proper complement fixation test. In order to simplify the test we take only two antiserum solutions 1:10 and 1:20. In the antiserum solution of 1:5 hemolysis is often prevented in a non specific way. The third tube is a control without serum. We place in the two first tubes 0·25 cm^3 of antiserum specific for virus *X* in a solution of 1:10 and 1:20, into the third one we pour 0·25 cm^3 of physiological salt solution. We then add to all three tubes 0·25 cm^3 antigen and 0·25 cm^3 of a suitably dissolved complement. We place then in a waterbath at a temperature of 37° for 30 minutes, then we add 0·5 cm^3 blood corpuscles and put them again into the waterbath for 15 minutes. Finally we read off the prevention or appearance of hemolysis. At the same time is set up a control with normal control serum. The test result is quite certain only in the case when both in the third tube without antiserum and in the control complement fixation test with normal serum complete hemolysis followed. The degree of hemolysis prevention can have a different intensity. At a solution of 1:10 in most cases a greater revention of hemolysis follows than in the second tube with an antiserum solution of 1:20. The strongest degree of prevention we mark +++, in the case of a part hemolysis ++, in an incomplete +.

According to our description of the complement fixation test, we took for each investigation 0·25 cm^3, that is, 2·5 drops of 30 times dissolved sap. That is to say the same as 0·008 cm^3 of fresh sap. It is necessary to confirm whether that amount is sufficient to determine the presence of virus *X* in a living plant tissue. We car-

ried out the complement fixation test several times with the same sample of sap, of potato and tobacco plants, that was 30 times dissolved. The results were in all cases entirely similar. This conformity concerned not only those cases where an entire prevention of hemolysis took place (+++), but also in those cases where hemolysis was only partially prevented (+).

The next important methodical problem was to find the limit of a possible solution of antigen in which the complement fixation test still gave positive results. In order to determine the titre of antigen we chose the sap of tobacco seedlings which had been inoculated with a variety of potato Nr 926. This number was entirely infected with a strain of virus *X*, masked both on the potato and on the tobacco plant. The sap of leaves and haulms of Nr 926 as well as of the tobacco plant infected with that sap prevented hemolysis in complement fixation but gave no precipitation. To draw a parallel we took simultaneously the sap of potato sprouts Nr 1619, infected with a strongly virulent strain of virus *X* which produced on the tobacco plant symptoms of mosaic and gave a distinct precipitation with the antiserum of virus *X*. In the first case the solution of antigen of 1:160 when the serum was dissolved 1:10, gave a weak prevention of hemolysis (Table III). In the second case a twice as great solution namely 1:240 gave a positive complement fixation reaction (Table IV). Considering the fact that we take for complement reaction 0·25 cm³ of investigated liquid, the solution of 1:240 corresponds to 0·001 mm³ of 30 times dissolved fresh sap. The titre of precipitation which we obtained in the second case with the same serum amounted in our experi-

TABLE III

Stock of potato.	Immune serum for virus X		
	Antiserum dilution		Control without antiserum
	1/10	1/20	
Nr 926 inoculated on Nicotiana var Virginia.			
1:10	+++	+++	++
1:20	+++	+++	—
1:30	+++	+	—
1:40	++	+	—
1:50	+++	+	—
1:60	+++	—	—
1:80	++	—	—
1:100	++	—	—
1:120	+++	—	—
1:140	++	—	—
1:160	+	—	—
sap of healthy Nicotian.	—	—	—
Virus X of Nicotiana	+++	—	—

TABLE IV

Stock of potato (sprouts)	Immune serum for virus X (Rothamsted)			Immune serum for protein obtained with *Mo*			
	Antiserum dilution		Control without antiserum	Antiserum dilution		Control without antiserum	Normal rabbit serum
	1/10	1/20		1/10	1/20		
1619 (1:30)	+++	++	—	+++	+	—	—
1619 (1:60)	+++	++	—	+++	++	—	—
1619 (1:80)	+++	+	—	+++	+++	—	—
1619 (1:100)	+++	—	—	+++	+++	—	—
1619 (1:120)	++	±	—	+++	++	—	—
1619 (1:140)	++	+	—	+++	—	—	—
1619 (1:200)	++	++	—	++	—	—	—
1619 (1:240)	±	—	—	++	—	—	—
sap of healthy Nicotian.	—	—	—	—	—	—	—
Virus X of Nicotiana v. Virginia	+++	+++	—	+++	+++	—	—

ments to 1:40. As the quantity of the investigated sap amounts at precipitation on slide to 0·1 cm^3, the solution of 1:40 corresponds to 0·025 mm^3 of fresh sap. In comparison with the precipitation the sensitiveness of the complement fixation test was n the described experiment 80 times greater.

Estimation of the presence of masked virus X in potato tubers with the help of the complement fixation test

It is most essential to determ ne the presence of virus *X* in potato tubers both for potato culture and in the connection with the problem of the development of the disease from generation to generation. Applied colorimetric tests (different colouring under the influence of copper compounds) gave no positive results. The method of serological agglutination is the most frequently used. The masked virus *X* is usually denoted by that method not in the tubers themselves but in the sprouts. When investigating sprouts we have but small quantities at our disposal which makes it impossible to obtain greater quantities of sap. It is impossible to carry out precipitation in Wasserman tubes with the undissolved sap of sprouts because we need just for one determination

a minimum of 0·5 cm^3. Because of this the drop-agglutination method has been worked out. This method has been used on a large scale in France, Holland and Czechoslovakia (Jermoliew & Hruska 1947, Roland 1945). It is carried out in the following way. We put upon a slide a drop of sap expressed from a sprout and a drop of antiserum *X*. When virus *X* is present in the sprout we see, even with the naked eye, agglutination on the slide. When the sprout is healthy no agglutination takes place. According to Roland and Jermoliew undissolved serum is used in the drop-method, and the drop of the sap expressed from the sprout is undissolved too. A control is indispensable: either we repeat the same experiment with normal serum, or we use antivirus *X* serum and an extract of a healthy potato or tobacco plant. Agglutination experiments carried out in our laboratory during the last two years gave the following results.

Certain results attained by that method depend on two factors, namely the serum must possess a high enough titre and, moreover, agglutination must be examined on the slide almost immediately after the sap has been expressed. Drops of fresh undissolved sap show on the solide already after 10 minutes the phenomenon of spontaneous coagulation. It is an aggregation of colloidal particles, which striking resembles agglutination. A drop of control serum magnifies this not specific aggregation phenomenon[1]).

The quantity of the plant material needed for the complement fixation test is, as we mentioned before, minimal (0·8 mm^3 of fresh sap). The just germinating sprout of 1/2 cm length and 0·1 g weight ground in 3 cm^3 of water, is sufficient for the complement fixation test, whereas it is impossible to carry out precipitation in Wasserman tubes with such a small amount. The sap expressed from tubers always gives a non specific agglutination. On the other hand, the eye and parts of a tuber ground in physiological solution give, after centrifugation at 10.000 revolutions, a positive and specific complement fixation test. The same extract does not change its antigenal qualities over the course of several days. The control carried out at each experiment excluded an erroneous result. Sera which had already lost for several months the capa-

[1]) The value of Stapps' »Blättchenmethode« is unknown to me, as his publications were not available.

city of agglutination still gave a positive result in the complement fixation test. In consequence the complement fixation test gives at the tuber investigation more certain results than the drop agglutination method.

The sensitivity of the complement fixation test in comparison with the precipitation and biological method when using test plants

Examining the health of our potatoes during three vegetation periods with the complement fixation test we used for comparison in our experiments the variety «Bintie» from Belgium which was free from virus *X*. The variety «President» imported in 1946 from England and cultivated in Poland in greenhouses, showed in our investigations the presence of virus *X*.

We divided two tubers belonging to both varieties into fragments. With the dissolved extract of these fragments we carried out the complement fixation test, inoculating simultaneously with the same undissolved sap tobacco seedlings variety W. Burley. We carried out the complement fixation test two weeks after inoculation with the sap of those tobaccos which did not show any exterior symptoms. The results of this experiment are given in Table V.

Tubers, variety «Bintie» gave a negative result in all their fragments in the complement fixation test. The tobacco seedlings inoculated with the same sap gave the same picture. The same happened in the investigation of haulms and leaves during the whole vegetation period.

A different result was obtained with the tuber variety «President». In several fragments of this tuber we could not confirm virus *X* with the help of the complement test, whereas the tobacco plant gave a positive reaction in all cases, except in the case of the skin.

A similar phenomenon appared in the investigation of haulms. In all investigated cases the sap of tobacco leaves which gave a positive complement fixation test gave no trace of precipitation.

In the above-mentioned way we investigated many selected apparently healthy stocks of potatoes. The tubers, imported direct from Pomerania were investigated in Kraków. The eyes and single fragments investigated with the complement fixation test gave in the greater number of cases a negative result. On the other hand,

tobacco leaves inoculated with the same sap gave, after two or three weeks very little complement fixations reaction without any precipitation. The same concerned the sprouts but to a much higher degree. The investigated sprouts were cut lengthways. With one half we carried out the complement fixation test and with the sap of the second half we inoculated the tobacco seedlings. As a rule the sprouts gave only in a certain percentage a positive complement fixation test, whereas symptom-free tobacco leaves inoculated with the sap of those sprouts showed, almost all of them, the presence of virus *X* without any precipitation (Table VI).

The same was true of the haulms of apparently healthy potatoes. The complement fixation test carried out with the sap of those haulms gave only in a certain percentage a positive result (Table VII). Whilst the corresponding tobacco seedlings gave a positive complement fixation reaction in 100 percent of cases. Nevertheless the sap of symptom-free tobacco never gave any precipitation. Precipitation took place as a rule only when exterior symptoms of the virus disease vere visible on the tobacco plant.

These experiments show without any doubt the quantitative increase of virus *X* in tobacco in comparison with the investigated plant, namely the potato. At the same time

TABLE V

	Eye 1	Eye 2	Eye 3	Eye 4	Eye 5	Eye 6	Eye 7	Skin	Under skin	Conduc. tissue 1	Conduc. tissue 2	Conduc. tissue 3	Stark meristem.	Compl. fixation test
Tuber »Bintje«	−	−	−	−	−	−	−	−	−	−	−	−	−	
Nicotiana tab. White Burley	−	−	±	−	−	−	−	−	−	−	−	−	−	”
Tuber »President«	+++	++	+	++	−	−	−	−	−	+++	+++	+++	+	”
Nicotiana tab. White Burley	+++	+++	+++	+++	+++	+++	+++	−	+	++	+++	+++	+++	”

these comparative experiments show the scale of sensitivity of the applied methods. The complement fixation test gives positive results where precipitation fails but not infallibly. In half the sprouts and fragments of tubers which gave negative results in the complement fixation test virus *X* was present, since we confirmed it afterwards with the same serological method in tobacco, which was inolculated with the sap of the same sprouts.

TABLE VI

Date		5 V	5 V	20 V	20 V
Stock of pot.		$^1/_2$ sprout Complem. fix.		Nicotiana tabaccum symptom free	
				Complem. fix.	Precipit.
Capella billa					
	1	—		+++	—
	2	—		+++	—
	3	+		+++	—
	4	±		+++	—
	5	—		+++	—
926	1	—		+++	—
	2	—		+++	—
	3	+		+++	—
	4	+		+++	—
	5	—		+	—
509	1	—		+++	—
	2	—		+++	—
	3	—		+++	—
	4	—		±	—
	5	—		±	—
313	1	+		+++	—
	2	—		++	—
	3	—		+++	—
	4	—		—	—
	5	—		+	—

$^1/_2$ sprout inoculated on Nicotiana tabaccum var. White Burley

The complement fixation method shows various intensivity of prevented hemolysis. In connection with the investigations of the test plants with the same method it can be an excellent indicator of the degree of intensivity of the disease.

The following experiment illustrates this phenomenon. Stock 81, selected in Pomerania, was cultivated and investigated over a period of three years. We carried out our experiments constantly

with the same plants which invariably showed an increase of the intensivity of that disease (Table VIII). The complement fixation test carried out with haulms in the first year showed traces of prevented hemolysis ±, with the sap of the corresponding tobacco they showed ++, in the second year the sap of the sprouts gave ++, with sprouts inoculated tobacco +++. In the third year sprouts and haulms gave +++, showing a strong increase of the virus disease manifesting itself in the degeneration of the plant.

TABLE VII

Stocks of potatoes		Compl. fix. 6. X. haulms	6. X.	Nicotiana tobaccum	
				Compl. fix. 20. X.	Precipit. 20. X.
54	1	+	Haulms inoculated on tobacco Nicotiana tabaccum var. White Burley	+++	—
	2	—		++	—
53	1	+		+++	—
	2	+		+++	+ mosaic
81	1	—		+++	—
	2	++		+++	—
	3	—		++	—
926	1	—		+++	—
	2	++		+++	—
326	1	—		+++	—
	2	+++		+++	—
18	1	+		+++	+ mosaic
	2	—		+++	—
	3	—		+++	—
50	1	+++		+++	—
	2	—		+++	—

All experiments described above concerned the detection of masked strains of the virus *X* on potato and tobacco plants. Finally the question arises as to what a degree the complement fixation test detects strong virulent strains of virus *X* which produce on tobacco leaves the phenomenon of mosaic or necrotic ring spots. Potatoes contain some times virulent strains of virus in such a low concentration that they do not always give a positive precipitation or complement fixation test. But their sap always gives visible symptoms on tobacco. In the cases of virulent strains as X^L, X^S, X^N the biological method is more sensitive than any

other serological method. A quantity of a strong virulent virus substance can lie in the potato tissue beyond detection even when the complement test is applied but it is sufficient to infect the test plants. In such cases parallel infected tobacco leaves sometimes do not give the same results.

TABLE VIII

Stock 81

I year				II year				III year			
	Compl. fix. 21. IV.	Com. fix. 24. V.	24. V.		27. IV.				Com. fix. 27. IV.	Com. fix. 11. VII
	Germs	Sprouts	Haulms inoculated on tobacco		Sprouts	Sprouts inoculated on tobacco			Sprouts	Haulms
			Com. fix. 10. VI. Nicotiana tabaccum			Com. fix. 17. V. Nicotiana tabaccum				
1	—	±	+	1	—	—	1	1	+++	+++
2	—	±	+	2	++	+++	2	2	+++	+++
3	—	±	++	3	++	+++	3	3	++++	++++
4	—	±	++	4	+	+++	4	4	++++	++++
5	—	±	++	5	—	+++	5	5	++++	++++

Increasing degrees of prevention of hemolysis are expressed by the symbols: — negative reaction, ± trace of prevented hemolysis, + incomplet hemolysis, ++ part hemolysis, +++ completely prevention of hemolysis.

Summary

1. The complement fixation test shows in the investigation of masked virus *X* strains in potato haulms and sprouts an 80 times greater sensitivity in comparison with precipitation.

2. Quite certain results are obtained when the applied antisera are specific, that is when they contain no other antibodies but the antivirus *X*.

3. The virus *X* antisera which have lost after 2 months their capacity of precipitation, retain their capacity to prevent hemolysis in the complement fixation test for a longer time, even for several months.

4. In the examination of the presence of virus in the sprouts of potato tubers the complement fixation test gives more certain results than the precipitation method. With this method we can state the presence of virus *X* even in starch meristem using at the production of antigen a centrifuga at 10.000 revolutions.

5. Strains of virus *X* masked on potatoes and tobacco leaves can be discovered by

the complement fixation test when neither precipitation or test tobacco give any, results. In cases when potato sap with virus *X* antiserum gives in the complement fixation test negative results, tobacco leaves, on the other hand, inoculated with the sap of those potatoes can show in the complement fixation test the presence of virus *X*. This phenomenon is connected with the fact that the quantity of virus substance in tobacco leaves increases in comparison with that of the potato.

6. The known serological and biological methods by which the presence of virus *X* in potatoes is detected can be ranged as to their sensitivity as follows:

a) The precipitation method detects, as a rule, the presence of virus *X*, in haulms and potato sprouts only in those cases when the sap of those potatoes inoculated on tobacco leaves shows on them external symptoms.

b) The complement fixation test which always gives a positive result in cases of precipitation detects moreover virus *X* where, on account of a too small quantity of virus substance, precipitation fails.

c) Finally, the most sensitive indicator of the presence of virus *X* is the investigation by the complement fixation test not only of potatoes but also of tobacco leaves inoculated with the sap of those potatoes.

7. For strongly virulent strains of virus *X* inoculation on test plants remains the most sensitive indicator.

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Badania nad glebami naskalnych zespołów roślinnych Jury Krakowskiej. — Recherches sur les sols des associations végétales rocheuses du Jura de Cracovie.

Mémoire

de M^lle^ **A. KŁAPUT**

présenté le 30 Mars 1950 par M. B. Pawłowski m. c.

Dans les recherches entreprises par un groupe de botanistes sur l'écologie des associations rocheuses des environs de Cracovie, je me suis occupée de certaines caractèristiques du sol des ces associations. L'étude de Kornaś (1949) sur les associations rocheuses servit de point de depart de mes recherches. Parmi les associations qu'il a distinguées, j'ai étudié de façon plus detaillée l'association *Festucetum pallentis* avec ses deux sous-associations. Par contre les recherches sur le sol du groupement à *Geranium sanguineum* ont un caractère moins complet. Quant aux deux autres associations, j'ai renoncé à étudier leur sol, à cause de trop grandes difficultés techniques rencontrées au cours du prélèvement des échantillons. Les échantillons destinés à l'étude du sol ont été recueillis aux endroits mêmes des relevés sociologiques. Je donne ci-dessous la liste des échantillons avec leur numéros d'ordre et l'endroit du relevé correspondant. Dans la suite, je ne me servirai que des numéros des échantillons.

I. *Festucetum pallentis sempervivetosum.*

1. Ojców, vallée de Sąspów, un rocher vis-à-vis du ravin Jamki.
2. Vallée de Bętkowice, une petite vallée située audessous de «Iglica A. Z. S.».
3. Vallée de Mników, au nord du village Mników. Un rocher sur le versant gauche, audessous de la chapelle.
4. Ojców, rochers au nord de l'entrée de «Grota Ciemna».
5. Mników, v. relevé N^o^ 3, un individu un peu audessous.

6. Vallée de Bętkowice, même rocher que N⁰ 2.
7. Bolechowice, rochers pres de l'entrée du ravin, au nord du village. Individu situé sur le versant droit.
8. Vallée de Mników, entre Sanka et Mników. Les rochers sur le versant gauche.
9. Bolechowice, v. relevé N⁰ 7, mais rochers à gauche.
10. Rochers à Przegorzały.
11. Ojców, rochers au dessous de l'entrée de «Grota Ciemna».
12. Przegorzały, v. relevé N⁰ 10, mais 30 m à l'ouest.

II. *Festucetum pallentis neckeretosum.*

1. Vallée de Bętkowice, un individu audessus de «Iglica A. Z. S.».
2. Ojców, rochers près de «Igła Deotymy».
3. Vallée de Bętkowice, un rocher tout près du sentier.
4. Audessus du relevé precedent, un rocher solitaire, ombragé par une saule.
5. V. relevé N⁰ 4, mais 15 m audessus du sentier.
6. Ojców, vallée de Korytania, un rocher à droite, près de l'entrée du ravin.

III. Groupement à *Geranium sanguineum.*

1. Vallée de Popówka, au sud du village Brzoskwinia.
2. V. relevé N⁰ 1, individu en peu loin.
3. Un individu parmi les champs cultivés, au nord du village Zelków, situé entre la vallée de Kluczwoda et le ravin de Bolechowice.
4. V. relevé N⁰ 4, mais 1/2 km à l'ouest.
5. V. relevé N⁰ 4, mais un peu loin.
6. V. des relevés N⁰ 4 et 5, individu au sommet de la colline.

Pour caractériser les différents sols, j'ai analysé leurs propriétés suivantes: I. Physiques — 1) Composition mécanique, 2) Teneur et capacité en air et en eau; II. Chimiques — 1) Teneur en carbonate de calcium, 2) Acidité, 3) Teneur en matière organique.

Propriétés physiques

1. Composition mécanique du sol

J'ai examiné la composition mécanique du sol des deux sous-associations du *Festucetum pallentis*, ainsi que du groupement à *Geranium sanguineum.* Les échantillons ont été prélevés sur une profondeur de 5 à 15 cm; la terre recueillie a été d'abord tamisée avec un crible à trous de 2 mm de diamètre. Les particules squelettiques séparées de cette manière représentaient dans les sols du *Festucetum pallentis* et du groupement à *Geranium sanguineum*

environs 50% du volume de l'échantillon analysé. Le sol étudié doit donc être classé dans le type des sols pierreux (Fabry, 1940).

La sélection des particules terreuses a été effectuée par la méthode de versement, au moyen de l'appareil verseur de Kopecky (Kopecky, 1917; Gessner, 1936). Par cette méthode, nous obte-

TABLEAU I

Composition mécanique du sol

N° de l'échantillon	Répartition des differentes fractions %			
	I	II	III	IV
I. *Festucetum pallentis sempervivetosum*				
1.	24·67	45·00	20·00	10·33
2.	27·00	24·00	36·00	13·00
3.	14·00	24·67	53·17	8·16
4.	32·93	30·71	28·33	8·03
5.	36·50	10·31	24·72	28·47
6.	19·30	31·37	45·60	2·73
7.	18·79	30·03	42·50	8·68
8.	39·90	26·70	14·06	9·34
9.	36·06	14·60	32·37	16·97
10.	10·67	20·67	51·33	17·33
11.	23·57	22·33	38·50	15·60
12.	18·17	22·00	44·83	15·00
II. *Festucetum pallentis neckeretosum*				
1.	21·67	39·17	25·33	13·83
2.	27·97	28·67	39·88	3·48
3.	28·25	29·50	28·00	14·25
4.	19·67	23·33	43·67	13·33
5.	20·23	25·00	45·67	9·10
III. *Groupement* à *Geranium sanguineum*				
1.	38·50	16·83	26·83	17·84
2.	8·33	13·47	47·05	31·15
3.	14·56	9·90	40·79	34·75
4.	4·89	9·80	49·21	36·10
5.	11·64	14·70	45·64	28·02
6.	29·40	15·20	27·50	27·90

nons un classement des particules d'après leur dimension comme suit: I. Particules de 2·0 mm à 0·1 mm, II. Particules de 0·1 mm à 0·05 mm, III. Particules de 0·05 mm à 0·01 mm, IV. Particules de dimension inférieure à 0·01 mm.

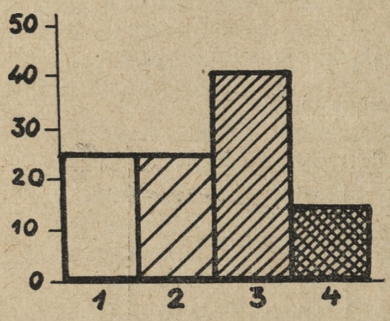

Fig. 1. Composition mécanique du sol du *Festucetum pallentis sempervivetosum*. En abscisse, fractions de grosseur des particules; en ordonnée, pourcentage des particules du sol.

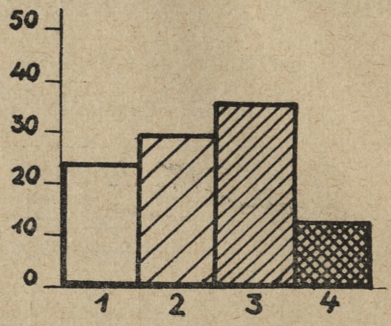

Fig. 2. Composition mécanique du sol du *Festucetum pallentis neckeretosum*. Voir légende de la Fig. 1.

Les résultats de l'analyse sont réunis dans le Tableau I et les Figures 1, 2, 3, qui représentent les moyennes obtenues pour les trois sols étudiés.

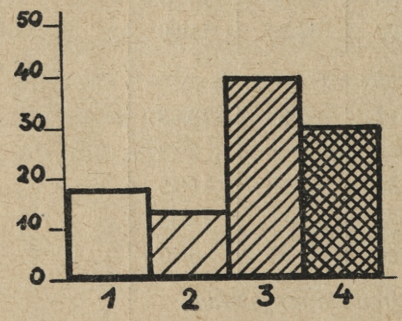

Fig. 3. Composition mécanique du sol du groupement à *Geranium sanguineum*. Voir légende de la Fig. 1.

Dans la sous-association *Festucetum pallentis sempervivetosum*, la composition moyenne des différentes fractions est: I — 25·13, II —25·20, III — 35·95, IV — 12·80%; dans la sous-association *Festucetum pallentis neckeretosum*: I — 25·56, II — 29·13, III — 36·51 IV — 10·80%; enfin dans le groupement à *Geranium sanguineum*: I — 21·46, II — 15·98, III — 47·40, IV — 35·15%. Il résulte de la comparison des valeurs ci-dessus que la composition mécanique du sol des deux sous-associationsde *Festucetum pallentis* est la même: leur trait caractéristique consiste dans un pourcentage élevé des particules relativement volumineuses

(fractions I et II) et dans une quantité négligeable des particules flottantes (inférieures de 0·01 mm). Le haut pourcentage des particules volumineuses semblerait indiquer que sol en question est encore relativement peu développé, étant donné que le procès de formation du sol à partir du substrat provoque au fur et à mesure de son développement l'apparition de particules de plus en plus subtiles. Ce proces n'a visiblement pas été poussé bien loin dans le cas présent, puisqu'il s'est formé si peu de particules flottantes. La composition mécanique de ce type de sol est très favorable au dévelopement des plantes, car la résistance aux racines par les particules du sol est en fonction inverse de leurs dimensions. Or l'effet nuisible de la résistance éprouvée par la racine affecte surtout la partie aérienne de la plante (Bassalik, 1930).

La composition mécanique du sol du groupement à *Geranium sanguineum* est nettement différente de celle de l'association *Festucetum pallentis*. Cette différence se manifeste surtout par le haut pourcentage des particules flottantes, tandis que le nombre des particules de 2·00 jusqu'à 0·05 mm est dans ce sol notablement moindre. La comparaison des résultats de mes analyses avec ceux des analyses publiées par Miklaszewski (1912) et la couleur de jaune de son sol démontrent que ce groupement pousse sur un sol de type loessique. Nous avons vraisemblablement affaire à un loess qui n'est pas développé typiquement en raison de sa profondeur réduite (moins de 45 cm), de l'absence de profil différencié et du grand nombre de particules squelettiques.

2. Teneur et capacité du sol en eau et en air

Pour étudier la teneur et la capacité du sol en eau et en air je me suis servie de la méthode de Siegrist (1931), modifiée par Lüdi et Luzzato (1935). Cette modification consiste à adapter une pompe à l'eau pour l'imprégnation du sol, au lieu d'une pompe aspirante à main. La capacité des cylindres utilisés s'élèvait seulement à 100 cm^3 au lieu de 250, le prélèvement d'échantillons à l'aide d'un cylindre plus grand étant impossible en raison du caractère pierreux et peu profond du sol. D'ailleurs, même en utilisant des cylindres de capacité reduite, le prélèvement des échantillons était difficile et demandait beaucoup de temps.

J'ai recueilli les échantillons au cours d'une seule période de végétation, dans une serie des individus des sous-associations *Festucetum pallentis sempervivetosum* et *neckeretosum*. Le Tableau II et les Figures 4 et 5 résument les résultats des mesures. Ce n'est que dans les relevés N° 10 *(Festucetum pallentis sempervivetosum)*, et N° 4 *(Festucetum pallentis neckeretosum)* que j'ai pris des échantillons trois fois au cours de l'année, au printemps, en été et en

TABLEAU II

Teneur et capacité du sol en eau et en air

N° du relevé	Date de prélèvement de l'échantillon	Teneur		Capacité	
		en eau	en air	en eau	en air
	I. *Festucetum pallentis sempervivetosum*				
10.	26. XI. 46	14·59	44·30	—	—
3.	11. IV. 47	26·84	25·25	36·04	16·05
5.	11. IV. 47	22·40	21·60	30·10	13·90
8.	11. IV. 47	35·05	24·40	57·65	1·80
10.	17. IV. 47	20·17	39·80	46·02	13·95
4.	3. V. 47	34·63	37·70	66·63	5·70
6.	27. V. 47	22·14	41·53	46·32	17·35
10.	29. VI. 47	16·94	41·15	44·71	13·38
3.	10. IX. 47	13·59	31·90	27·09	18·40
1.	1. X. 47	12·12	36·80	42·52	6·40
	II. *Festucetum pallentis neckeretosum*				
6.	3. V. 47	41·22	32·80	53·57	4·70
4.	27. V. 47	29·74	21·98	46·68	4·73
4.	3. VIII. 47	37·27	18·60	54·80	1·07
4.	29. XI. 47	36·15	19·70	46·85	9·00

automne. L'exploitation de mêmes individus pour une observation mensuelle aurait entraîné, en raison de la petite superficie des individus (environs 20 m²) et des difficultés de prélèvement des échantillons non seulement un bouleversement de l'équilibre biologique de l'association, mais encore son extinction totale.

Il résulte des observations faites sur le terrain que le maximum de développement de la végétation dans la sous-association *Festu-*

cetum pallentis sempervivetosum, exposée au sud, a lieu au printemps; pendant l'été et au début de l'automne la végétation des plantes annuelles meurt. Il ne survit qu'un petit nombre de plantes

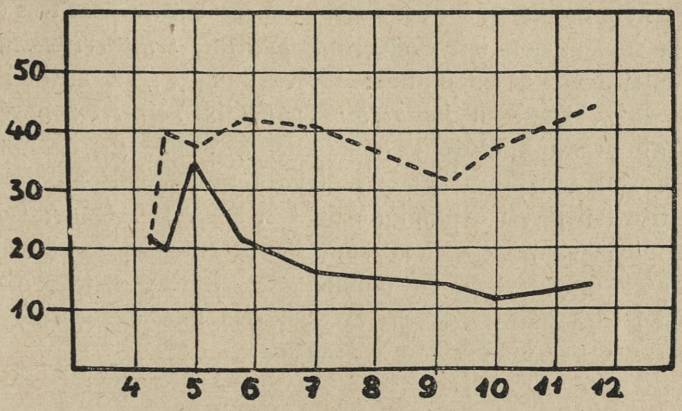

Fig. 4. Teneur du sol en eau —— et en air ---- dans le *Festucetum pallentis sempervivetosum*. En abscisse, les mois.

xérophytes, comme *Festuca pallens*, *Scabiosa ochroleuca* etc. Toute l'association fait à cette époque l'impression d'être «brûlée» par le soleil. Les mesures d'humidité du sol ont confirmé ces observations.

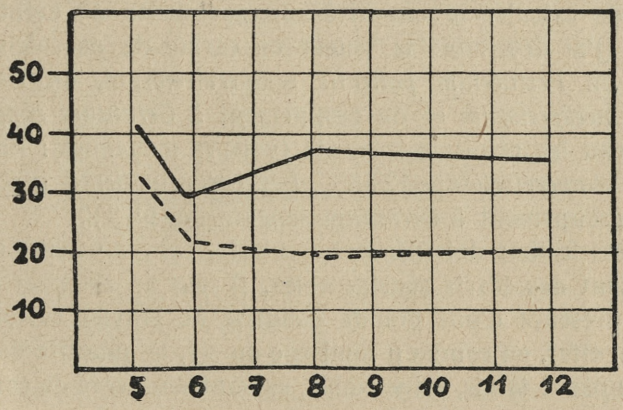

Fig. 5. Teneur du sol en eau —— et en air ---- dans le *Festucetum pallentis neckeretosum*. En abscisse, lesmois.

L'humidité du sol, après avoir atteint son maximum au printemps, diminue ensuite à un tel point qu'en automne la teneur en eau du sol se maintient aux environs de 12%. L'humidité du sol du *Festu-*

cetum pallentis neckeretosum protégé par son exposition septentrionale contre une insolation trop forte, se maintient pendant toute la période de végétation à un niveau à peu pres fixe (30—40%).

La teneur en air du sol des deux sous-associations est très élevée. Dans la sous-association *Festucetum pallentis sempervivetosum* elle est comprise entre les limites: 21·60—39·80%; en automne elle atteint 45%. Dans le *Festucetum pallentis neckeretosum* elle se maintient pendant toute l'année aux environs de la moyenne 23·27%. Des valeurs tellement élevées pouvent s'expliquer par la constitution physico-chimique du sol. Pour la même raison, les valeurs de la capacité en eau sont importantes et la capacité en air montre, que, même au moment de sécheresse maximale, la respiration des plantes supérieures et des microorganismes n'est pas entravée par un manque d'oxygène.

Propriétés chimiques

1. Teneur du sol en carbonate de calcium

Pour doser le carbonate de calcium, j'ai appliqué la méthode de Scheibler, basée sur la decomposition du carbonate de calcium par l'acide chlorhydrique. Le volume de gaz carbonique dégagé permet de calculer la quantité correspondante de carbonate de calcium. J'ai determiné la teneur en carbonate de calcium dans les sols du *Festucetum pallentis sempervivetosum*, du *Festucetum pallentis neckeretosum* et du groupement à *Geranium sanguineum*. J'ai obtenu les résultats suivants (valeurs moyennes): *Festucetum pallentis sempervivetosum* 12·53%, *Festucetum pallentis neckeretosum* 4·86%, groupement à *Geranium sanguineum* 0·72%.

J'omets la liste détaillée des résultats, car les valeurs obtenues présentaient des écarts considerables. Il faut en chercher la cause dans la présence d'une grande quantité de gravier calcaire dans le sol. En effet, en cours du tamisage du sol, la quantite de gravier qui passe par le tamis, est variable, suivant son degré de concassage dans l'échantillon donné. Les valeurs obtenues montrent que les sols étudiés renferment de quantités notables de carbonate de calcium. Il est regrettable que la méthode employée n'indique la quantité totale de carbonate de calcium dans le sol et ne permet pas de déterminer le degré d'absorption du calcium par le complexe d'absorption du sol. Il faut cependant supposer que la grande

quantité de carbonate dans le sol et la proximité du substrat calcaire facilite l'imprégnation du complexe d'absorption du sol par le calcium en assez grande quantité.

2. Acidité du sol

Les sols du *Festucetum pallentis* et du groupement à *Geranium sanguineum* recouvrent partout un substratum calcaire. Leur profondeur réduite est la cause de la grande influence qu'exerce ce

TABLEAU III

Acidité du sol

N° du relevé	pH	N° du relevé	pH
I. *Festucetum pallentis sempervivetosum*		III. *Groupement à Geranium sanguineum*	
2.	7·13	1.	6·64
3.	6·85	2.	7·55
4.	7·31	3.	
5.	7·03	0—15 cm	
6.	6·98	20—30 „	
7.	7·25		
8.	7·15		
9.	7·38		
10.	7·05	4.	
12.	7·23	0—15 cm	6·99
II. *Festucetum pallentis neckeretosum*		30—40 „	7·29
		5.	
1.	7·10	0—15 cm	6·94
2.	7·29	20—30 „	6·82
4.	7·13		

substratum sur leurs proprietés, notamment sur leur acidité. Grâce à la présence du calcium l'acidification du sol est insignificante ainsi qu'il resulte de l'identité ou quasi-identité entre les valeurs du pH des échantillons, mesurées dans la suspension du sol aqueux et dans la suspension de chlorure de potassium. C'est la raison pour laquelle j'ai effectué la mésure du pH dans une solution normale de chlorure de potassium au moyen d'un pH-mètre «Kalk-

dienst» employant une électrode quinhydronique. Les résultats des recherches sont résumés dans le Tableau III. Les réactions des sols étudiés ne présentent pas de différences fondamentales. Elles sont toujours alcalines ou neutres: dans le *Festucetum pal-*

TABLEAU IV

Ligne du pH

N° de l'échantillon	Valeurs du pH		
	printempts	été	automne
I. *Festucetum pallentis sempervivetosum*			
1.	7·58	7·08	6·98
2.	7·17	7·20	6·91
3.	7·19	6·72	6·65
4.	7·21	7·10	6·88
5.	7·26	6·92	6·80
6.	7·32	6·36	6·81
7.	7·50	7·05	7·02
8.	7·33	6·98	7·00
9.	7·59	—	7·04
10.	—	—	6·87
II. *Festucetum pallentis neckeretosum*			
1.	6·80	6·84	6·90
2.	7·12	7·00	6·83
3.	7·03	6·87	7·11
4.	7·08	7·09	7·20
5.	7·20	6·83	7·01
6.	7·17	7·18	7·05
7.	7·12	7·06	7·21
8.	7·06	6·60	7·08
9.	6·78	6·96	7·31
10.	6·84	—	—

lentis pH = 6·85—7·38, dans le groupement à *Geranium sanguineum* pH = 6·64—7·55. Dans ce dernier groupement on note une faible tendance à une différentation du profil: les valeurs du pH des couches supérieures sont un peu plus basses que celles des couches plus profondes.

C'est pour mieux caractériser l'acidité du sol que Jenny (1925) a introduit l'usage de la «ligne du pH». Elle est basée sur la détermination du pH de plusieurs (10) échantillons pris à l'intérieur d'un même individu de l'association donnée. Ces échantillons sont habituellement recueillis sur une ligne droite à une distance fixe, pour autant que les dimensions de l'individu le permettent. On porte les résultats sur les diagrammes, dont les abscisses représentent les numéros des échantillons et les ordonnées les valeurs

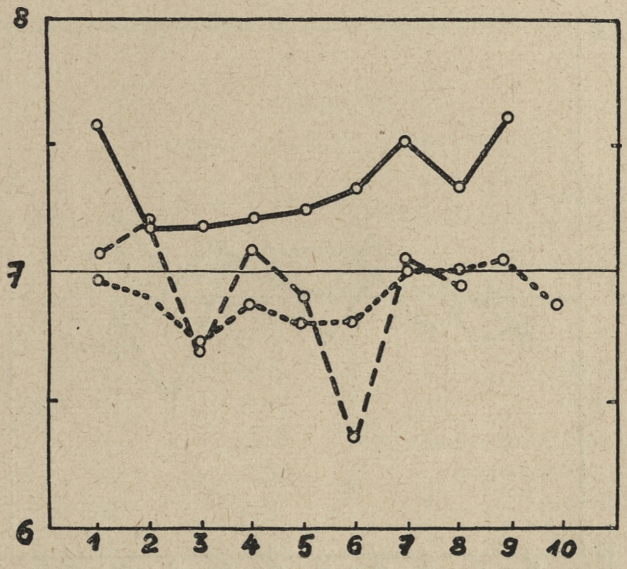

Fig. 6. Ligne du pH dans le sol du *Festucetum pallentis sempervivetosum*. Abscisses: numéros des échantillons, ordonnées: valeurs du pH. — mesure de printemps, ---- mesure d'été, ... mesure d'automne.

du pH. En déterminant les propriétés des sols alpins, Braun-Blanquet et Jenny (1926) ont constaté qu'une ligne de pH à peu près stable (c'est à dire paralléle à l'axe des abscisses) est caractéristique des associations se trouvant en équilibre biologico-floristique, tandis que des valeurs de pH inégales indiquent une association à caractère transitoire.

Les mésures du pH des deux sous-associations du *Festucetum pallentis* ont été éffectuées au printemps, en été et en automne. A cet effet un individu de chacune de ces deux sous-associations a été choisi: le N° 4 pour le *Festucetum pallentis neckeretosum* et le

N° 10 pour le *Festucetum pallentis sempervivetosum*. Les résultats obtenus sont représentés dans le Fig. 6 et 7. Il en résulte avant tout que les valeurs du pH d'une même ligne présentent des écarts plus ou moins grands. Ces écarts sont cependant encore négligeables de sorte qu'en s'appuyant sur les obsérvations de Braun-Blanquet et Jenny on peut admettre que le *Festucetum pallentis* est une association stabilisée et biologiquement équilibrée. Les variations saisonnières de la ligne du pH sont négligeables dans la

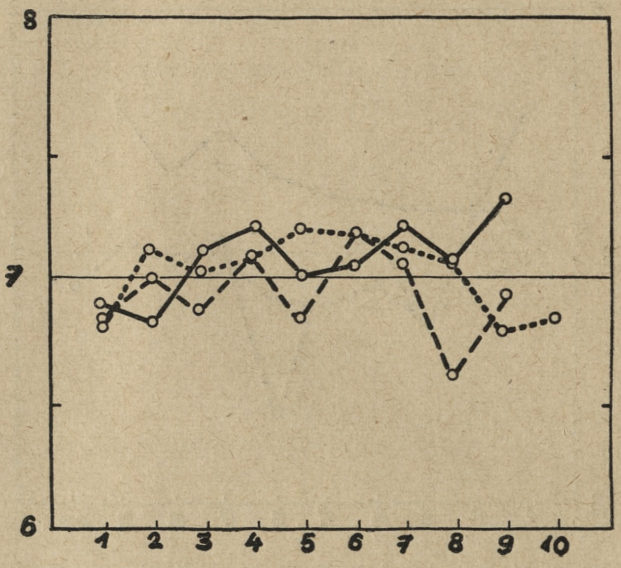

Fig. 7. Ligne du pH dans le sol du *Festucetum pallentis neckeretosum*. Voir légende de la Fig. 6.

sous-association *Festucetum pallentis neckeretosum*, tandis qu'elles sont nettes dans la sous-association *Festucetum pallentis sempervivetosum*. Les valeurs maxima de la ligne du pH baissent au printemps. A cette époque, le sol est très humide, et en même temps fortement ensoleillé, l'association étant exposée au sud. L'évaporation intense du sol pendant cette période provoque l'exsudation des sels dissous dans l'eau du sol (principalement des sels de calcium) et par la même élève un peu les valeurs du pH. Comme l'humidité de la sous-association *Festucetum pallentis neckeretosum* se maintient pendant toute la période de végétation à un niveau fixe et que les

individus sont éxposés au nord, l'évaporation du sol doit être moins intense, et par consequent avec ce fait les variations de la ligne du pH sont négligeables.

3. Teneur du sol en matière organique

J'ai déterminé la quantité d'humus par combustion (Quantin, 1935). Les résultats obtenus sont réunis dans le Tableau V.

Le sol de l'association *Festucetum pallentis* est caractérisé par une grande quantité d'humus. Pour le *Festucetum pallentis sempervi-*

TABLEAU V

Contenu du sol en matière organique

N° de relevé	% de la matière organique	N° de relevé	% de la matière organique
I. *Festucetum pallentis sempervivetosum*		II. *Festucetum pallentis neckeretosum*	
3.	35·11	1.	72·64
4.	43·32	2.	28·37
5.	38·02	4.	60·96
6.	23·63	III. *Groupement à Geranium sanguineum*	
7.	48·63	1.	25·35
9.	39·67	2.	31·59
10.	28·45	3.	17·28
11.	18·67	4.	9·24
12.	37·77	5.	14·01
13.	47·78	6.	13·77

vetosum elle atteint en moyenne 36·11%, pour le *Festucetum pallentis neckeretosum* 53·66%. Parmi les sols polonais etudiés, seuls les sols de haute montagne des associations *Firmetum* et *Versicoloretum tatricum* possèdent un pourcentage aussi élevé de matière organique (Włodek et Mościcki, 1928; Włodek, 1928). Dans le groupement à *Geranium sanguineum* la quantité de matière organique contenue dans la couche d'humus à peine développée est également importante, mais moindre que dans l'association *Festucetum pallentis*. Sa valeur moyenne atteint 18·54%.

Conclusion

Les associations rocheuses des environs de Cracovie, décrites par Kornaś (1949) se développent sur les rochers calcaires du Jura Blanc (Zaręczny, 1894), résistants à l'erosion. Le sol qui se forme sur ce substratum appartient au type des sols squelettiques, qui se distinguent par l'absence de différentiation de leur profil. Ces sols sont habituellement occupés par les associations pionnières: c'est par exemple le cas des sols de haute montagne (Włodek, 1928). Le caractère physico-chimique du sol etudié est très étroitement lié avec le substratum sur lequel il se forme. L'influence du substratum calcaire se manifeste aussi bien dans l'association *Festucetum pallentis* que dans le groupement à *Geranium sanguineum*. Pourtant ces sols se distinguent l'un de l'autre d'une manière sensible, par certaines particularités, surtout par la couleur, la composition mécanique et la teneur en matière organique.

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