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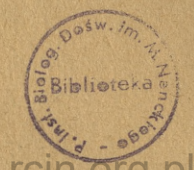
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Analiza zbiorowego gatunku *Betula alba* L. na podstawie pomiarów liści.

*Część I: Cel i metoda pracy na przykładzie *Betula verrucosa* Ehrh.*

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

*Part I: Aim and method of the work on the example of *Betula verrucosa* Ehrh.*

Mémoire

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

présenté le 13 Juin 1949 par M. W. Szafer m. t.

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I. Aim and method of the work

Biometric studies of the collective species *Betula alba* L., aiming at a characterization of the various species at present included therein and a determination of their variability, were begun by the author already before the last World War. She then published two parts of her studies, of a preliminary character, in the »Travaux et Comptes rendus de l'Institut de Recherches des Forêts Domaniales, Pologne«. In the first part, entitled »Polymorphism of the leaves of birches« (1937), the author arrived at the conclusion that every birch-tree, irrespective of its species, has four types of leaves distinctly differing from one another (i. e. leaves on dwarf shoots with catkins, on dwarf shoots not terminating in a female catkin, on long shoots and on sprouts) and that among these leaves the ones on vege-

tative dwarf shoots — i. e. without catkins — are least variable. It was on the latter leaves, therefore, that the author decided to base her further investigations.

In the second part, entitled: »The possibility of hybridisation between species *Betula verrucosa* Ehrh. and *Betula pubescens* Ehrh.« (1938), it was the author's aim to determine whether, and to what degree, the above-mentioned two species, commonly occurring in Europe, are able to cross. It is a fact that for the author the essential question was whether the material collected in the field for the biometric studies — and determined by eye as belonging to one species or the other — might be considered as pure, the more so as in pre-war works on birches frequently encountered is the opinion that the above-mentioned species cross with each other in nature to such degree that hardly any pure forms exist in nature, only hybrids, and furthermore hybrids which have come into existence through repeated crossings. On the basis of birch pollen collected from the atmosphere the author reached the conclusion that in the Polish climate *Betula verrucosa* Ehrh., which blossoms about 10 days sooner, has extremely small chances of being pollinated with strange pollen. Only a small part of *Betula pubescens* Ehrh. could be pollinated with the pollen of *Betula verrucosa*, or eventually of hybrids, if the pollen of the latter is at all fertile, and this might increase the number of forms which we include in the species *pubescens* on the basis of the pubescence of branchlets, or of other characters.

After these preliminary investigations the author took up the actual subject of her work. During the war (1939—1945) she had no opportunity for scientific work. However, by fortunate chance, the material collected prior to the war and the records of measurements were not destroyed. Therefore, towards the end of 1945 the author was able to proceed with her studies, the results of which are herein published.

The delay in the execution of this work was not to its disadvantage, inasmuch as in the course of the last ten years there was a great increase in the interest in birches as cultivated trees. Birches became the subject of exact cytologic and experimental research, particularly in Scandinavia and North America. This led to an elucidation of many problems and, first of all, to dis-

persion of the legend concerning the easy crossing of birch species, especially of *Betula verrucosa* and *Betula pubescens*.

Johnsson's very interesting work (1945) has shown that in cultivation it is difficult to obtain hybrids from these birch species, while in free nature both Johnsson (1944) and Lindquist (1947), and prior to the war Wettstein and Propach (1939), found such hybrids to constitute a very small percentage. This made the author's own work easier, inasmuch as it confirmed her conviction that the material on which her measurements were carried out was a pure one, and that the determined variability is indeed a variability congenital in the given species, and not the result of its hybrid origin. Furthermore since interest in birches has increased and the number of works on this subject is growing, it has become important to begin, at last, a precise elaboration of birches also from the taxonomic side, and this can be done on the basis, above all, of accurate measurements.

The author based her studies primarily on abundant material collected especially for this purpose at various points in Poland and adjacent countries, in addition to which she made use of the material in herbariums.

Material for study of the northern birches was collected for the author before the war by Dr Bronisław Jaroń, a young and promising Polish botanist, who perished during the war in the German concentration camp at Oświęcim. Materials from the Caucasus, collected on the Polish Mountaineering Expedition to the Caucasus in the summer of 1935, were obtained by the author from a member of the expedition, Dr Tadeusz Wiśniewski, who was shot in 1943 in a German prison in Warszawa. For materials from the Alps the author is indebted to Prof. Werner Lüdi of Zürich and Mr. Jerzy Fabijanowski, Engineer, for materials from the Sudety Mountains, to Dr Stefan Macko of Wrocław; and for materials from England, to Mr. Stefan Batko. In collecting materials from Poland the author profited by the assistance of the Forestry Research Institute in Warszawa before and after the war, and by the assistance of numerous forest-district managements, and also of fellow botanists. The author owes profound gratitude to all who were not sparing in the use of their time or in giving trouble to themselves in order to collect the necessary materials, and who thus enabled the author to carry out the present work.

Linnaeus used the name *Betula alba* to designate all arborescent birches occurring in Europe. Regel, who occupied himself with a taxonomic classification of the difficult genus *Betula*,

extended in his monograph the conception, and under the specific name *Betula alba* L. he united a number of arboreal birches of Eurasia and America, dividing them into eight varieties, breaking up the latter into smaller forms (*luzus*). As the knowledge of birches extended, the above-mentioned collective species was divided into a number of species, characterized in a better or worse degree, and the old name *Betula alba* L. was substituted by the name *sectio* or *subsectio albae*. The difference between many of these birch species is up to the present day quite unsettled and the species are insufficiently characterized. It has been accepted that in Europe there are two species, named, after Ehrhart, *Betula verrucosa* and *Betula pubescens*, while other birches are mostly dealt with as their varieties. The most important ones among the latter, on account of a large geographical range, are *Betula tortuosa* Ledeb., which grows in Europe at the northern forest limit, and *Betula carpatica* Waldst. et Kit., known from the upper forest line in numerous European mountains. Furthermore, of special interest in Poland, occurring as they do within its boundaries, are *Betula obscura* Kotula and *Betula oycoviensis* Bess.

As regards *Betula celtiberica*, described by Rothmaler and de Carvalho e Vasconcellos in 1940, and *Betula callosa* Nöto, described in 1945 by Lindquist, the author knows only what has been published by the above-mentioned botanists and does not possess any material for study. The question must be left for local biometric elaboration. Gunnarsson's Scandinavian species cannot be taken into consideration at all until they are elaborated by Swedish botanist in a truly scientific manner and their existence confirmed.

The aim of the author's work was to characterize accurately the six above-mentioned birch species and to assign to them their proper taxonomic position. The starting-point of the author's studies were Poland and terrains lying near its boundaries. That is the central point of the occurrence of the two birch species most widely spread in Europe: *Betula verrucosa* and *Betula pubescens*. Within such territorial bounds the author elaborated the birches accurately, and then she linked up the results obtained here to the wide distributional area of the two tree species. Such an elaboration is essentially a local one; however, owing to the pos-

sibility of good observation of the trees in the terrain, taking into consideration the habitat in which they occur, the author was able to draw conclusions which, presumably, are in a large degree applicable to the whole distributional area of these birches, and which might explain certain phenomena also in other species from outside Europe.

The author based her attempt of characterizing the birch species, above all, on the leaves of dwarf shoots and the eventual pubescence of branchlets. As a matter of fact, having oriented herself in the abundant material collected by her, the author arrived at the conclusion that leaves are more easily measurable than are bracts and fruits which are not only small, but have shapes that are not easily determinable by the biometric method. Furthermore, fruits, and especially bracts, differ distinctly from one another even in one catkin, depending on the fact whether they come from the middle part of a catkin, from its tip, or base. Inasmuch as mature catkins are quickly scattered, it is difficult to obtain material as strictly comparable as is the case, for instance, with leaves taken from vegetative dwarf shoots. The author executed, in a tenfold magnification, several hundred drawings of bracts and fruits of 50 northern birch-trees from materials brought by herself in 1925 from Lapland, i. e. the same birch which was accepted as a basis for his work by Morgenthaler (1915), who based his work only on four specimens and deemed the birch to be a pure *pubescens*. This convinced the author of the herewith presented studies that all shapes of bracts may be found there, from narrow and long ones to short and wide ones, bracts with lateral lobes ranging from ones which are strongly bent down to ones which are elevated and as long as the middle one, as in *Betula nana*. The fruits may range from ones which are almost wingless to ones which are winged with wings wider than the nut. These observations strengthened the author's conviction that she might be led into a blind alley if she began her work from the reproductive organs. In addition, birches in the terrain do not always produce fruit, for instance, on peat-bogs, or at the limits of their distributional area, while in forests they bear fruit on the tree-tops, and this makes collecting difficult. Consequently, the author's starting-point for characterizing the different species and their

variability were, first of all, leaves, while an elaboration of bracts and fruits was postponed till a later date.

As regards the tree-bark, the occurrence of rough bark in the lower part of the trunk is dependent in the Polish climate on the tree's age, above all, and the author has never succeeded in linking up this phenomenon with the shape of leaves as does Lindquist in his work on Scandinavian varieties of the species *verrucosa* (1947).

The material studied by the author was large, inasmuch as it included more than 60 points from where the local samples were taken, not taking into account the samples taken from single trees for the purpose of investigating individual variability. The samples for taking measurements were collected in such manner that endeavours were made to collect in a given terrain mechanically, without choosing, at least 50 branchlets, or simply 50 dwarf shoots, each from a different tree, and only in several cases, when it was difficult to find 50 trees, was the author content with less abundant material. When the material had been dried, the author would measure from each branchlet two leaves proceeding from the same dwarf shoot, taking pains to avoid a subconscious selection of leaves more normally developed or more suitable for measurements. Included in one sample in most cases were 100 leaves from 50 trees. Thus the author measured more than 7000 leaves. The author determined each leaf with regard to 15 characters, in a similar manner as she had done in the first part of her biometric studies (1937). Two characters concerned the petiole, i. e. the petiole length and its ratio to the blade length, this being a criterion whether leaves are short-stalked or long-stalked. The leaf-blade was characterized by the author as to length and width, and also as to its shape, i. e. the ratio of length to width, the angle of the base and the midrib, the angle of the apex and the midrib (measuring approximately to the third tooth), and also the position of the widest part, this position being determined by dividing the length by the distance separating the widest part from the blade base. The bigger the resultant quotient, the nearer to the base lay the widest part of the blade. This character is more precisely expressible as the percentage of blade length; in view of the fact, however, that pre-war measurements were carried out by the author

in the manner described above, she kept to the same system in order that the measurements be comparable. Other properties of the blade were expressed in seven characters. Three of them pertained to the nervation, i. e. the number of pairs of lateral nerves, the mean distance of nerves, and the angle of the second lateral nerve and the midrib. Four characters were to characterize the dentation, i. e. the distance of the first tooth from the blade base, and the same character in relation to the blade length (length divided by the distance of the first tooth from the blade base), and furthermore the distance between the tips of the second and third lateral nerve, and the number of teeth in this intervening space, including in the count both teeth at the nerve tips and the ones between them. Thus, if both nerves were terminated with teeth, and two more teeth were situated between them, the author would register four teeth, and if there were no intermediate teeth, two would be registered, etc. In the materials measured before the war the author designated also the type of dentation, according to a scale drawn up on the basis of variously dentated birch-leaves, but this scale was lost during the author's compulsory wartime translocations, and it has been impossible to reconstruct it from memory, and so, unfortunately, the author could not continue to designate this so important character, and the data recorded before the war became useless. The sixteenth character was the number of leaves on the vegetative dwarf shoot which was being studied. Finally, the author made a note of the presence or absence of hairs in the axils of the nerves, and on the youngest parts of the branchlet from which had been taken the dwarf shoot for the purpose of measurements.

The author admits that having carried out such a large number of measurements she did not know what to do with her numerical material. The usual routine in biometrical work is to list the samples in pairs and to compare in them each pair of characters separately. On the basis of the arithmetic mean and the standard deviation one calculates then the degree of their similarity. In view of such a large number of samples of which was composed the author's material, and of the sixteen characters taken into account, the number of possible combinations was enormous, and in the latter it is possible to lose oneself. In addition, one must frequently conduct investigations on correlation

and regression, which again entail long computations. In such manner one arrives at numerical results which are perhaps accurate, but often not easily legible even to the investigator himself.

As to the author, her aim was to make her work a taxonomic one and one which would be intelligible to every taxonomist, even if he were unfamiliar with biometric methods. Furthermore, experience had taught the author that one ought to be circumspect and critical in applying statistical methods in biometrics, and that life demonstrates how even some fundamental statistical presentations give a wrong picture of actual conditions. The author meditated, therefore, in view of the fact that shape is the manifestation of all the characters contained in a given object, whether it would not be possible to compare a leaf as a whole, i. e. whether one might not discover some coefficient of shape, one which would be an expression of all the characters contained in a leaf. The discovery of such a coefficient, expressible by a number, is a difficult matter. First of all, figures resulting from measurements of various characters are incommensurable. For instance, the mean length of the leaf-blade of *Betula verrucosa* is approximately 42 mm, the mean width approximately 33 mm, while the ratio of length to width, which alone is the essential character of shape, amounts to 1.27 on the average. Some numbers, which are used for taking measurements, would have here an enormous superiority over numbers, which designate shape. It is possible, as a matter of fact, to find a method of revaluing such numbers, but the author feared that such a procedure would be too mechanical and consequently faulty, all the more so as the value of the same characters is different for various species. The author decided, therefore, to follow a different course. As an initial unit of comparison the author adopted the mean values of characters, obtained from measurements of 100 leaves from 50 trees from the whole distributional area of *Betula verrucosa* in Europe. This unit, therefore, represented a theoretical leaf of *Betula verrucosa*, all of whose dimensions would correspond to the mean values calculated from 100 leaves from the whole European distributional area. Next the author took a local sample, which she wished to compare with the sample from the whole

distributional area, and for each character she determined by how much the arithmetic mean is here smaller or larger than the value of the same character in the author's comparative unit.

This will be explained on an example presented in Table I. In the first column there is a list of the characters which were used to designate the size and shape of the measured leaves. These characters are tabulated in such manner that in the upper part, separated by a horizontal line, are the characters which the author terms quantitative characters, or characters of size, i. e. the ones which change in dependence on the size of the leaf. Below the above-mentioned line are the characters which may be termed qualitative, or characters of shape. At the boundary-line between the two groups is character N° 7, i. e. »Number of teeth between tips of second and third nerve«; although this character denotes quantity, and consequently is apparently a quantitative character, it does not, however, increase proportionally to the size of the leaf, being rather connected with its shape. As character N° 16 the author accepted the number of leaves on the dwarf shoot from which two leaves were measured.

In the second column, under the heading M_1 , are the mean values for all characters, obtained from measurements of 100 leaves from 50 trees of *Betula verrucosa* from the whole distributional area in Europe. In the third column are the mean values obtained from measurements of a local sample from the Carpathian foreland, from the locality of Dobra near Limanowa. The fourth column shows the ratio of the arithmetic means of the two samples. Tabulated here are figures derived from each division of M_2 by M_1 . We have expressed in this column, therefore, by how many times the mean values of the studied sample are larger or smaller than the mean values of the author's comparative unit. Thus we have arrived at a series of figures which are not only comparable with one another, but are also expressible graphically in the manner shown on Fig. 1. The author's comparative unit is represented as a straight line, running vertically and designated with the Figure 1. The small figures on the horizontal line at the top designate the decimal parts of this unit, and thus to the right: 1·1, 1·2, etc., and to the left: 0·9, 0·8, etc. Now we mark the points expressing the ratio $M_2:M_1$, i. e. for a petiole length 1·02, for a blade length

0.98, etc., and we connect them with straight lines. Thus we obtained a polygonal line which represents the difference of the mean shape of leaves of the local sample in comparison with the sample from the whole distributional area. In this diagram we see distinctly that in the local sample the leaves had petioles which were slightly longer on the average, and blades which were shor-

TABLE I

	The characters	M_1	M_2	$M_2 : M_1$
1.	Petiole length	15.77	16.16	1.02:1
2.	Blade length	41.30	40.70	0.98:1
3.	Blade width	32.65	33.75	1.03:1
4.	Number of pairs of lateral nerves	6.68	7.02	1.05:1
5.	Distance of first tooth from blade base	12.59	11.27	0.89:1
6.	Distance between tips of second and third nerve	6.63	6.71	1.01:1
7.	Number of teeth between tips of second and third nerve	4.81	4.89	1.02:1
8.	Ratio of blade length to petiole length	2.71	2.53	0.93:1
9.	Ratio of blade length to blade width	1.29	1.21	0.94:1
10.	Mean distance of nerves	6.17	5.84	0.95:1
11.	Ratio of blade length to distance of first tooth	3.39	3.73	1.10:1
12.	Position of widest part of blade	3.19	3.58	1.12:1
13.	Axil of second nerve	38.20	43.10	1.13:1
14.	Base angle	68.50	74.80	1.09:1
15.	Apex angle	19.20	16.95	0.88:1
16.	Number of leaves on dwarf shoot	2.16	2.26	1.05:1

ter, but wider (characters N^o 1—3). There were more lateral nerves than in the comparative unit (4). There was a considerable difference in the distance between the first tooth and the base, which in the local sample was small on the average, meaning that the dentation had its beginning near the blade base (5). The interval between the second and third nerve was slightly larger in spite of the shorter blades (6); the mean number of teeth in the intervening space was also slightly larger (7). Bigger differences existed in the leaf shape

i. e. a smaller ratio of blade length to petiole length (the petioles being longer — 8), and a smaller ratio of blade length to blade width (the leaves being wider — 9). The mean distance between the nerves was also smaller, i. e. the nervation was denser (10). In character N° 11 we observe that the distance of the first tooth from the base was not small (5) on account of the blades being smaller (2), but for the reason that the leaves in the local samples had indeed their dentation near the base on the average, this distance being contained more times in the blade length than it was in the comparative unit. Marked differences existed also as to the position of the widest part or the blade (character N° 12), as to the axil of the second nerve (13), and as to the angle of the base (14). The leaves of the local sample, as a rule, had a wider base, and their widest part was located nearer the blade base, while on the other hand their apexes were narrower (15). The number of leaves on the dwarf shoot in the local sample was larger on the average than it was in the comparative unit (16).

In Fig. 2 we have two leaves, the dimensions of which conform more or less to the arithmetic means of the two above mentioned samples. To the eye the leaves do not differ from one another in a marked manner, appart from the fact that the right leaf has a wider blade base than the left one-

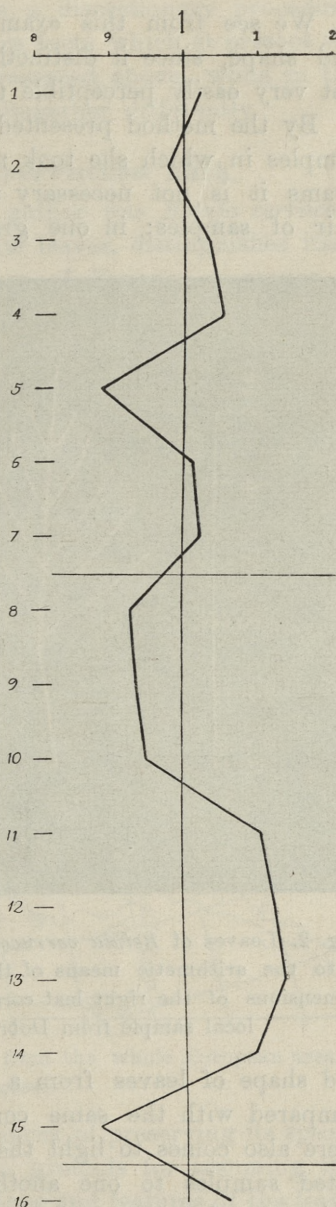


Fig. 1.

We see from this example how sensitive is the line of size and shape, since it distinctly brings to view details which are not very easily perceptible to the eye.

By the method presented above the author compared all the samples in which she took measurements. In preparing the diagrams it is not necessary to trace a separate graph for each pair of samples; in one graph one may show the lines of size

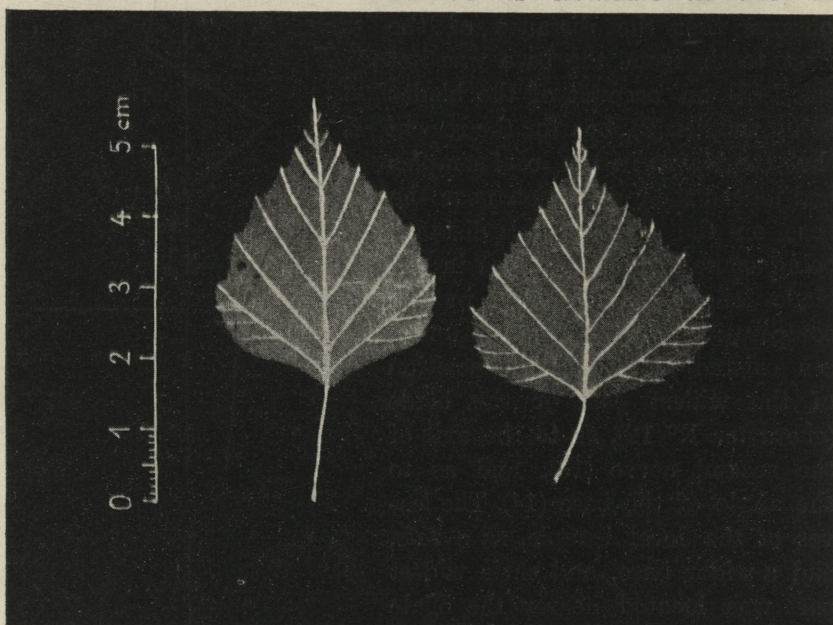


Fig. 2. Leaves of *Betula verrucosa*. Dimensions of the left leaf correspond \pm to the arithmetic means of the sample from the whole European area. Dimensions of the right leaf correspond \pm to the arithmetic means of the local sample from Dobra near Limanova. (see Table I).

and shape of leaves from a whole series of samples if they are compared with the same comparative unit. In the latter case there also comes to light the mutual relationship of the investigated samples to one another. The following chapters will explain what it was possible to make out of the graphs prepared by the author.

At the end of the III part of her work the author give tables with the numerical results of her measurements. The

fact is that interpretation is always a discretionary procedure, while the results of measurements are facts which at present the author interprets in the manner presented above, while in the future someone else may interpret altogether differently.

II. Analysis of *Betula verrucosa* Ehrh.

The first species studied by the author was *Betula verrucosa* Ehrh. This birch, by the shape of its leaves, distinguishes itself well from the other arboreal birches of Europe; moreover, in the Polish climate it blossoms 10—12 days sooner than *Betula*

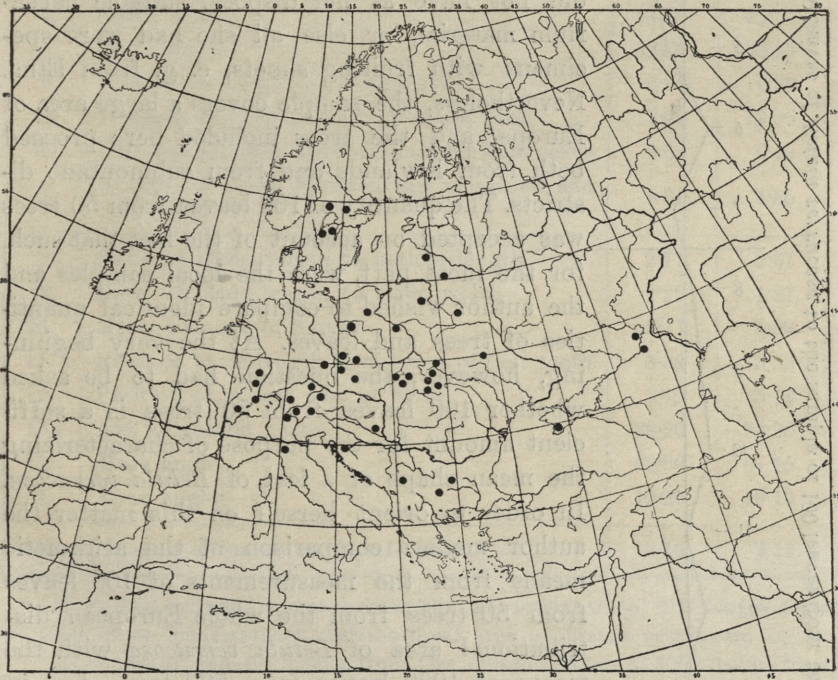
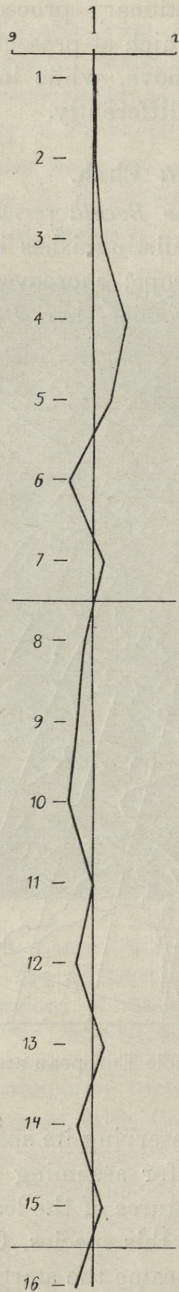


Fig. 3. The stations of trees investigated from the whole European area of *Betula verrucosa*.

pubescens Ehrh., having thus all chances of preserving its species in purity. The author had, therefore, grounds for assuming that what she would determine as the shape and features of the leaves of *Betula verrucosa* are indeed characteristic of this species. Consequently, a careful study of *Betula verrucosa* became the starting-point and foundation of the author's work.

Fig. 4. Ratio of the sample of 1000 leaves of *Betula verrucosa* to the sample of 100 leaves from the whole European area.



The comparative unit adopted by the author, as already stated above, consisted of the arithmetic means of measurements of 100 leaves from 50 trees from the whole distributional area of *Betula verrucosa* in Europe. The stations of these trees are shown in Fig. 3. We see from the map that lacking in the author's sample were several peripheral stations of *Betula verrucosa*, the reason therefore being that at the time of elaborating the sample the author did not have at her disposal suitable herbarium material, or else all she had were specimens with fruiting shoots, e. g. from Etna. Nevertheless, the sample covers a large area of Europe, and the trees included here proceed both from lowlands and from submontane districts. The quantity of 100 leaves from 50 trees was accepted on account of the fact that such, for the most part, were the local samples and the author wished to compare identical quantities of trees and leaves. At the very beginning, however, the question had to be asked whether 100 leaves from 50 trees is a sufficient amount for the purpose of characterizing the mean shape of a leaf of *Betula verrucosa*. In order to orient herself on this matter the author made a comparison of the arithmetic means from the measurements of 100 leaves from 50 trees from the whole European distributional area of *Betula verrucosa* with the means of 1000 leaves from 500 trees, but in the latter case the majority of trees were from Poland and neighbouring countries, inasmuch as the author did not have at her disposal such abundant material from the whole area.

A comparison of these means is shown in Fig. 4, and the pertinent figures in Table II. We perceive that between the mean values

of the two samples there is a very small difference. The largest difference concerns the number of lateral nerves, inasmuch as the mean number of pairs of lateral nerves in the sample with 1000 leaves is 1.04 times bigger than in the test with 100 leaves ($6.96:6.68 = 1.04$). This difference, however, is

TABLE II

	The characters	M_1	M_2
1.	Petiole length	15.77	15.71
2.	Blade length	41.30	41.50
3.	Blade width	32.65	33.15
4.	Number of pairs of lateral nerves	6.68	6.96
5.	Distance of first tooth from blade base	12.59	12.86
6.	Distance between tips of second and third nerve	6.63	6.45
7.	Number of teeth between tips of second and third nerve	4.81	4.85
8.	Ratio of blade length to petiole length	2.71	2.67
9.	Ratio of blade length to blade width	1.29	1.27
10.	Mean distance of nerves	6.17	5.99
11.	Ratio of blade length to distance of first tooth	3.39	3.39
12.	Position of widest part of blade	3.19	3.12
13.	Axil of second nerve	38.20	38.90
14.	Base angle	68.50	67.15
15.	Apex angle	19.20	19.40
16.	Number of leaves on dwarf shoot	2.16	2.11

M_1 = The arithmetic means from the measurements of 100 leaves from 50 trees from the European distributional area of *Betula verrucosa*.

M_2 = the arithmetic means from the measurements of 1000 leaves from 500 trees.

not essential, amounting as it does to 0.28, while its error, calculated according to the formula:

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

amounts to 0.095; the difference, therefore, is slightly smaller than the triple error. In the characters pertaining to shape (8—15) the differences between the mean values are very slight and not

one of them is essential. It is noticeable therefrom that so far as the arithmetic means are concerned they do not change when a larger number of leaves is measured, and that a sample including 100 leaves from 50 trees is altogether sufficient for determining the shape of leaves of *Betula verrucosa*. Such a sample, therefore, taken, from almost the whole European distributional area, became the author's initial unit of comparison.

With the arithmetic means of the sample covering the whole distributional area, i. e. with the comparative unit, the author compared nine local samples of *Betula verrucosa* collected from various localities in Poland and adjacent countries. This comparison is shown in Fig 5. The localities from which material for the samples was collected are marked with black dots on the map in Fig. 6. These samples consist of 86–100 leaves from 43–50 trees. Three of these samples — two from Podolia (Ulaszkowce and Skala) and one from the Carpathian foreland (Dobra near Limanowa) — come from terrains where there are no natural stations of *Betula pubescens*.

If we look at Fig. 5 we see, first of all, that the differences between the local samples and the one covering the whole distributional area are not large, amounting at most to ± 0.24 ; this means that the mean value of a given character is bigger or smaller by $\frac{1}{4}$ from the mean value for the whole distributional area. We next see that markedly small differences exist in the size of the leaves (characters N^o 1–3), but, in spite of this, big differences are revealed in the distance of the first tooth from the blade base (5). On the other hand, in the qualitative characters, i. e. in the characters of shape (8–15), special differences are noticeable in 11–14: in the distance of the first tooth after eliminating the size, in the position of the widest part of the blade, in the axil of the second nerve, and in the angle of the base. The most striking point, however, is the one which caused the author to trace thinly the lines that in these characters are on the right side of the system, and thickly those that are on the left side. The fact is that these lines cross one another between characters N^o 10 and N^o 11, so that all the thin lines pass over to the left side and the thick ones to the right side. In character N^o 8 (ratio of blade length to petiole length) there is no distinct separation of the thin and thick lines,

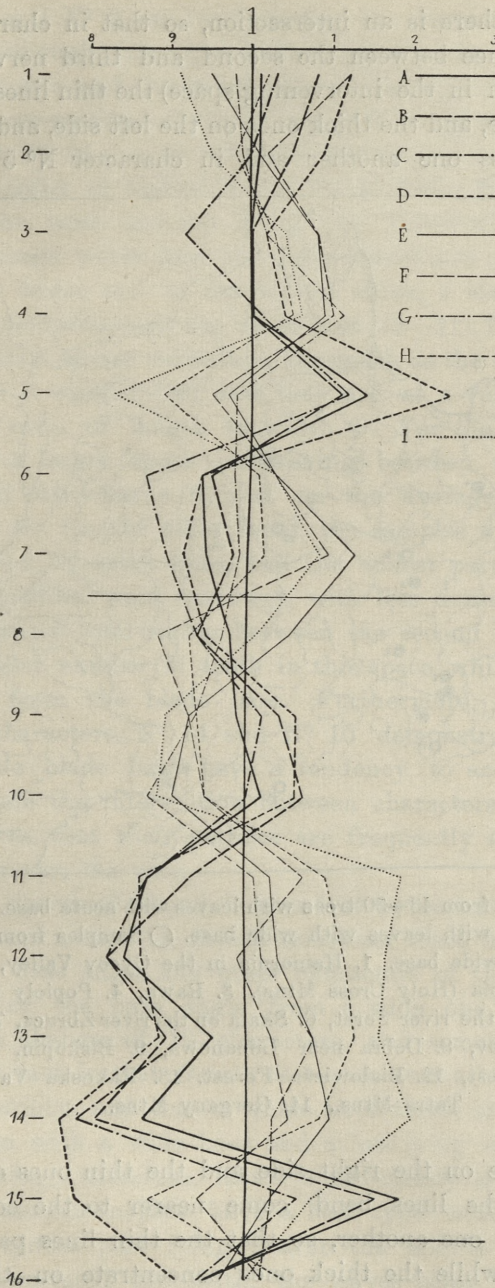


Fig. 5. Ratio of the local samples of *Betula verrucosa* to the sample of the whole European area. A — Hamernia, B — Grzegorzewice, C — Rawa, D — Popioly, E — Ulaszkowce, F — Skala, G — Wola Forest, H — Dobra, I — Biskupin.

but here also there is an intersection, so that in characters N° 6 and N° 7 (distance between the second and third nerve, and the number of teeth in the intervening space) the thin lines are again on the right side, and the thick ones on the left side, and then once more they cross one another and in character N° 5 the thick



Fig. 6. ● Samples from 43—50 trees with leaves with acute base. ⊙ Samples from 44—50 trees with leaves with wide base. ○ Samples from 9—35 trees with leaves with wide base. 1. Hamernia in the Oycov Valley, 2. Grzegorzewice near Słupia (Holy Cross Mtns), 3. Rawa, 4. Popioły near Toruń, 5. Ułaskowce on the river Seret, 6. Skala on the river Zbrucz, 7. The Wola Forest near Cracov, 8. Dobra near Limanowa, 9. Biskupin, 10. Grodno, 11. Kampinos Forest, 12. Białowieża Forest, 13. Rakuska Valley in the Tatra Mtns., 14. Gorgany Mtns.

lines concentrate on the right side and the thin ones on the left. At this point the lines bend, come nearer to the comparative unit, and cross one another, so that the thin lines pass over to the right side, while the thick ones concentrate on the left, although the differences between them are small. Not until charac-

ters N^o 1 and N^o 2 are reached does the separation become less distinct, although the thin lines show a tendency to pass over to the left side and the thick ones to the right. Neither is there a distinct separation of the thick and thin lines in characters N^o 15 and N^o 16, i. e. in the ones pertaining to the apex angle and the number of leaves on the dwarf shoot. This goes to show that all the local samples which had leaves with a base angle on the average wider than the comparative unit (character N^o 14), also had a wider axil of the second nerve, a lower-lying widest part, and dentation near the blade base (13—11); furthermore, they had distinctly denser nervation, inasmuch as the mean distance of the nerves is smaller (10), and they are, as a rule, wider, having a smaller ratio of length to width (9). For the most part they also have a larger space intervening between the tips of the second and third nerve (6) and, on the average, more teeth in this space (7). On the other hand, the samples with a more acute base, marked by thick lines, had the widest part situated nearer the blade middle, were narrower, with less dense nervation, had a smaller space intervening between the second and third nerve, and a smaller number of teeth in this space, while the first tooth began far from the blade base. Furthermore, the intersection between characters N^o 14 and N^o 15 demonstrates that leaves with a wide blade base have a tendency to acquire acuminate apices, while the intersection between characters N^o 1 and N^o 2 demonstrates that their petioles are frequently shorter, this not being, however, the rule.

Fig. 5 discussed above, is proof of two interesting facts. The first of these is that in *Betula verrucosa* there is correlation between the base angle and other characters of the leaf, and that a change of the base angle from a wide one to an acute one involves a change of 10 characters, and sometimes even more. The other fact is that *Betula verrucosa* seems to have a distinct local variability, and that a whole birch forest or copse has either a leaf type with a wide base and a low-lying widest part, such forests having, therefore, leaves approximately triangular, or else whole forests or copses have a leaf type with an acute base, with the widest part lying nearer the middle and with other features associated therewith, the leaves being, therefore, of an outline which is more or less deltoidal. Diagrams of such two

leaves — one drawn on the basis of arithmetic means from Biskupin, the other on the basis of means from Grzegorzewice — are shown in Fig. 7.

Apart from the samples shown in Fig. 5 there were five more local samples, smaller ones, composed of 70—168 leaves, but only from 9—35 trees. The localities from which they came are designated with circles in Fig. 6. The lines of mean size and shape from these tests are shown in Fig. 8. They differ

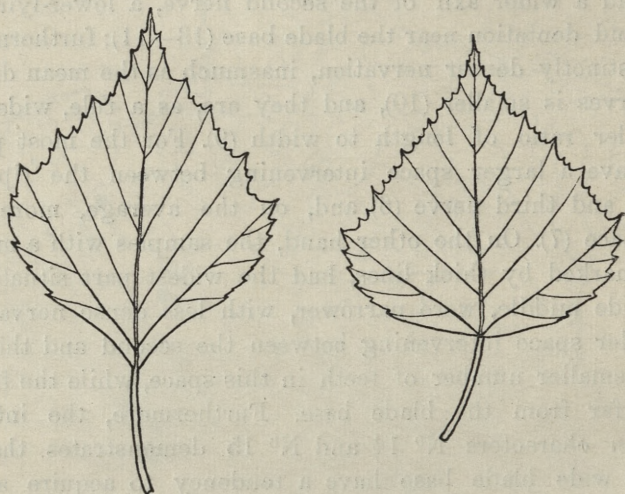


Fig. 7. Two types of leaves of *Betula verrucosa*. The left leaf is drawn on the basis of the arithmetic means of the sample from Grzegorzewice near Słupia (type with a cuneiform base). The right leaf is drawn on the basis of the arithmetic means of the sample from Biskupin (type with a wide base). The dentation is shown schematically.

from one another much more by the leaf size than the samples from a larger number of trees, this being understandable, inasmuch as here individual variability is more strongly marked. For instance, nine trees from the Kampinos Forest had markedly small leaves, a fact which exerts its influence also on characters N^o 5 and N^o 6. The lines of their shape, however, are characteristic of leaves with a wide base and with a low-lying widest part. Fourteen trees from the Gorgany Mountains were the only ones that had a mean angle of the base hardly differing from the comparative unit.

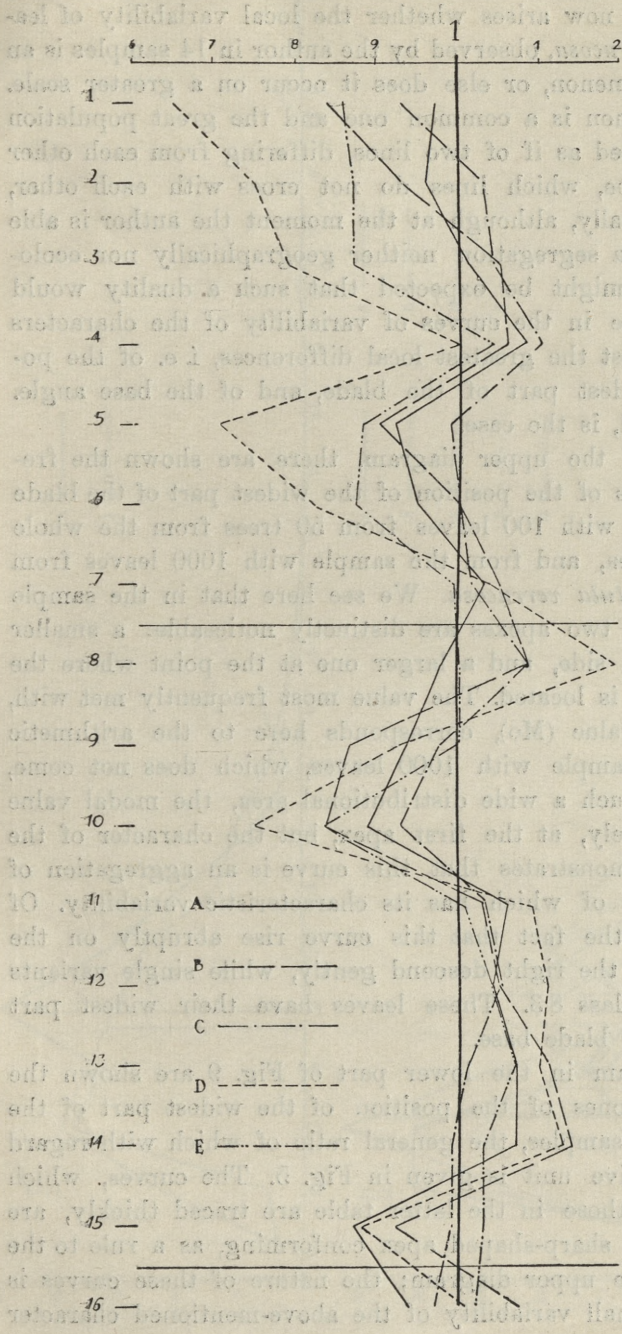


Fig. 8. Ratio of the local samples from 9—35 trees of *Betula verrucosa* to the sample of the whole distributional area of this species. A — Grodno (70 leaves from 35 trees), B — Rakuska Valley (100 leaves from 9 trees), C — Goryany Mtns. (168 leaves from 14 trees), D — Kampinos Forest (100 leaves from 6 trees), E — Białowieża Forest (100 leaves from 25 trees).

The question now arises whether the local variability of leaves of *Betula verrucosa*, observed by the author in 14 samples is an accidental phenomenon, or else does it occur on a greater scale. If the phenomenon is a common one and the great population is indeed composed as if of two lines, differing from each other by the leaf shape, which lines do not cross with each other, but segregate locally, although at the moment the author is able to explain such a segregation neither geographically nor ecologically, then it might be expected that such a duality would become noticeable in the curves of variability of the characters among which exist the greatest local differences, i. e. of the position of the widest part of the blade, and of the base angle. And such, indeed, is the case.

In Fig. 9, in the upper diagram, there are shown the frequency polygons of the position of the widest part of the blade from the sample with 100 leaves from 50 trees from the whole distributional area, and from the sample with 1000 leaves from 500 trees of *Betula verrucosa*. We see here that in the sample with 100 leaves two apexes are distinctly noticeable: a smaller one on the left side, and a larger one at the point where the arithmetic mean is located. The value most frequently met with, i. e. the modal value (Mo), corresponds here to the arithmetic mean. In the sample with 1000 leaves, which does not come, however, from such a wide distributional area, the modal value is located inversely, at the first apex, but the character of the whole curve demonstrates that this curve is an aggregation of two types, each of which has its characteristic variability. Of interest also is the fact that this curve rise abruptly on the left side, and on the right descend gently, while single variants occur even in class 8.3. These leaves have their widest part situated near the blade base.

In the diagram in the lower part of Fig. 9 are shown the frequency polygons of the position of the widest part of the blade in 9 local samples, the general ratio of which with regard to the comparative unit is given in Fig. 5. The curves, which analogically to those in the latter table are traced thickly, are uniapical, with a sharp-shaped apex conforming, as a rule to the first apex of the upper diagram; the nature of these curves is proof of the small variability of the above-mentioned character

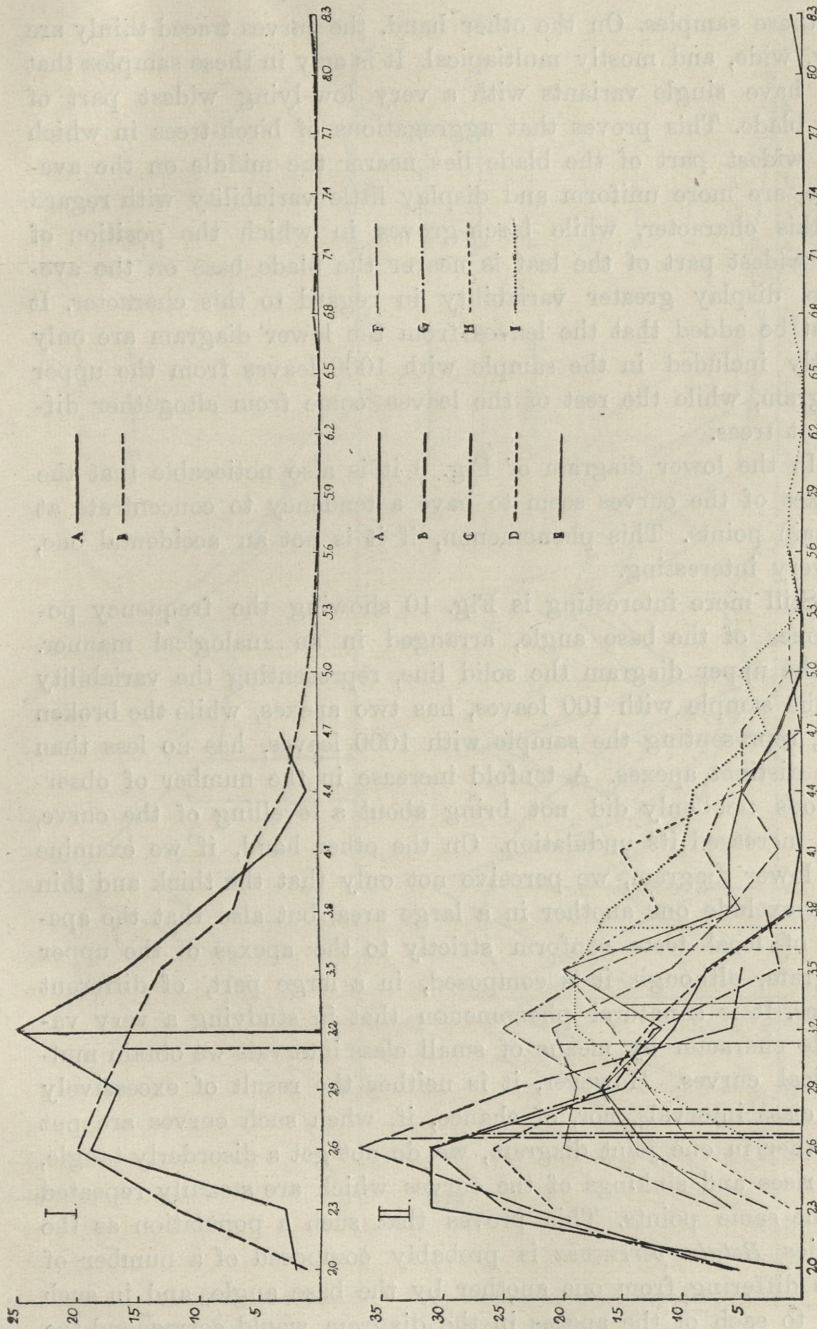


Fig. 9. Frequency polygons of the position of the widest part of leaves of *Betula verrucosa*. I A — Sample from 100 leaves from the whole European area, I B — Sample from 1000 leaves, II. Local samples, A — I as on Figure 5.

in these samples. On the other hand, the curves traced thinly are low, wide, and mostly multiapical. It is only in these samples that we have single variants with a very low-lying widest part of the blade. This proves that aggregations of birch-trees in which the widest part of the blade lies nearer the middle on the average, are more uniform and display little variability with regard to this character, while birch-groves in which the position of the widest part of the leaf is nearer the blade base on the average, display greater variability in regard to this character. It must be added that the leaves from the lower diagram are only partly included in the sample with 1000 leaves from the upper diagram, while the rest of the leaves come from altogether different trees.

In the lower diagram of Fig. 9 it is also noticeable that the apexes of the curves seem to have a tendency to concentrate at certain points. This phenomenon, if it is not an accidental one, is very interesting.

Still more interesting is Fig. 10 showing the frequency polygons of the base angle, arranged in an analogical manner. In the upper diagram the solid line, representing the variability in the sample with 100 leaves, has two apexes, while the broken line, representing the sample with 1000 leaves, has no less than five distinct apexes. A tenfold increase in the number of observations not only did not bring about a levelling of the curve, but increased its undulation. On the other hand, if we examine the lower diagram, we perceive not only that the thick and thin lines exclude one another in a large area, but also that the apexes of local tests conform strictly to the apexes of the upper diagram, although it is composed, in a large part, of different leaves. It is a natural phenomenon that in studying a very variable character by means of small class intervals we obtain multiapical curves. However, it is neither the result of excessively big class intervals, nor, of chance, if, when such curves are put together in one joint diagram, we do not get a disorderly tangle, but rises and sinkings of the curves which are steadily repeated at the same points. This proves that such a population as the species *Betula verrucosa* is probably composed of a number of lines differing from one another by the base angle, and in such case to each of the apexes in the diagram would correspond the

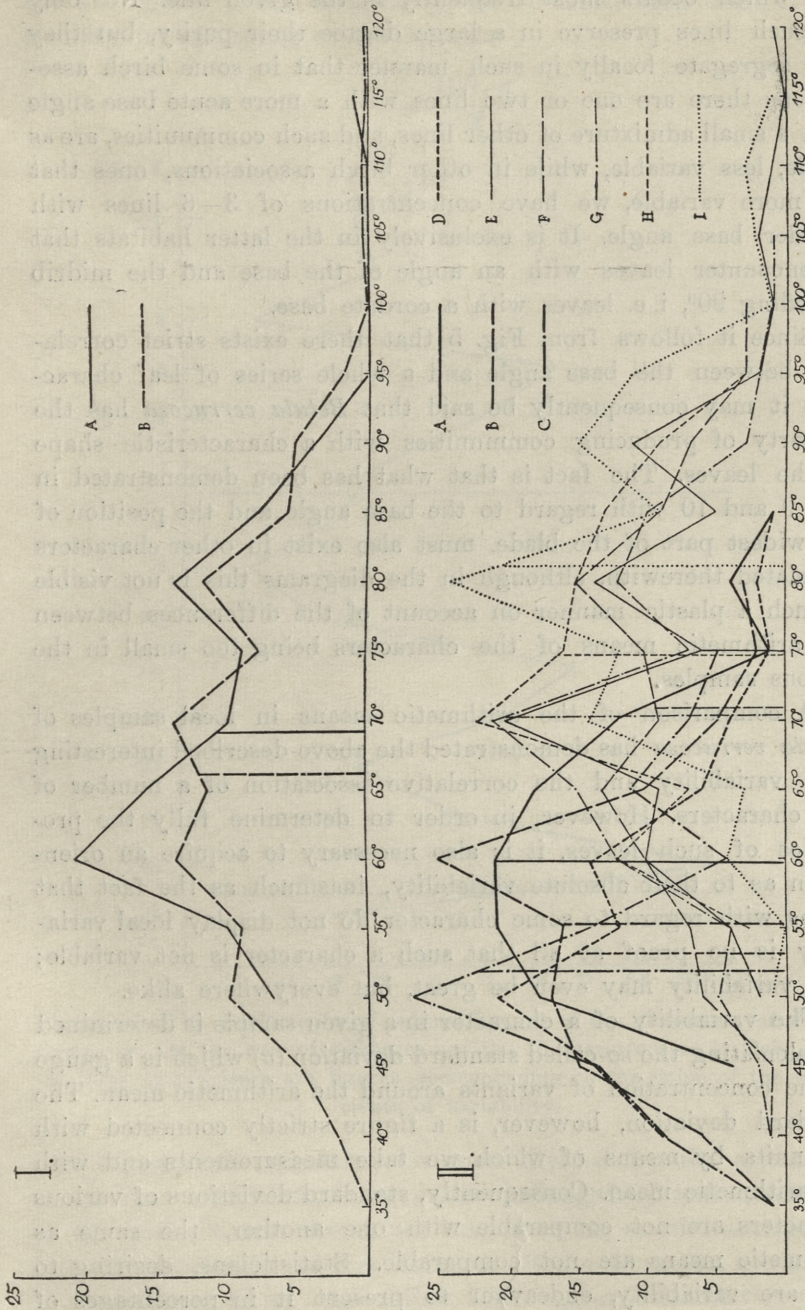


Fig. 10. Frequency polygons of base angle of the leaves of *Betula verrucosa*. I A — Sample from 100 leaves from the whole European area, B — Sample from 1000 leaves. II. Local samples, A — I as on Figure 5.

size which occurs most frequently in the given line. Not only do such lines preserve in a large degree their purity, but they also segregate locally in such manner that in some birch associations there are one or two lines with a more acute base angle with a small admixture of other lines, and such communities, are as a rule, less variable, while in other birch associations, ones that are more variable, we have concentrations of 3—6 lines with a wider base angle. It is exclusively in the latter habitats that we encounter leaves with an angle of the base and the midrib exceeding 90° , i. e. leaves with a cordate base.

Since it follows from Fig. 5 that there exists strict correlation between the base angle and a whole series of leaf characters, it may consequently be said that *Betula verrucosa* has the property of producing communities with a characteristic shape of the leaves. The fact is that what has been demonstrated in Fig. 9 and 10 with regard to the base angle and the position of the widest part of the blade, must also exist in other characters correlated therewith, although in the diagrams this is not visible in such a plastic manner on account of the differences between the arithmetic means of the characters being too small in the various samples.

A comparison of the arithmetic means in local samples of *Betula verrucosa* has demonstrated the above-described interesting local variability and the correlative association of a number of leaf characters. However, in order to determine fully the properties of such leaves, it is also necessary to acquire an orientation as to their absolute variability, inasmuch as the fact that leaves with regard to some character do not display local variability is no proof at all that such a character is not variable; such variability may even be great, but everywhere alike.

The variability of a character in a given sample is determined by calculating the so-called standard deviation (σ) which is a gauge of the concentration of variants around the arithmetic mean. The standard deviation, however, is a figure strictly connected with the units by means of which we take measurements and with the arithmetic mean. Consequently, standard deviations of various characters are not comparable with one another, the same as arithmetic means are not comparable. Statisticians, desiring to compare variability, endeavour to present it in percentages of

the arithmetic mean, computing the so-called coefficient of variability (v) according to the formula:

$$v = \frac{100 \cdot \sigma}{M}$$

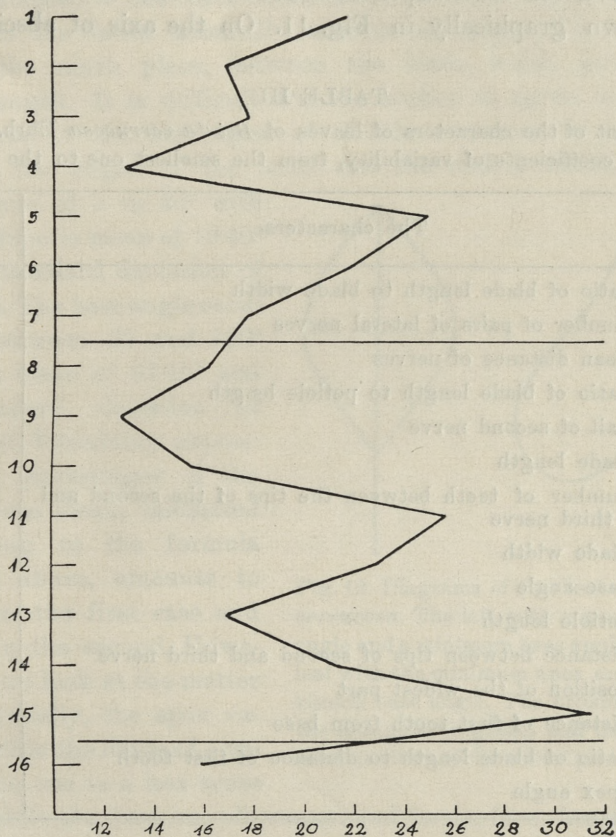


Figure 11. The coefficients of variability (v) of the characters of *Betula verrucosa*. On the axis of ordinates are the 16 characters as in Tab. I. On the axis of abscissas are figures corresponding to the value of the coefficients of variability.

i. e. the centuple standard deviation divided by the arithmetic mean. This coefficient, however, is challenged by some scientists. In the author's case the values calculated for » v « did not picture well the variability of the leaves of *Betula verrucosa*, a variability regarding which the author had a general orientation after

having carried out such a large number of measurements, but could not express this variability in an exact manner. However, in view of the fact that she has no other method of presenting variability, the author calculated » v «, according to the formula given above, for the sample with 1000 leaves of *Betula verrucosa*; it is shown graphically in Fig. 11. On the axis of abscissas in

TABLE III

Arrangement of the characters of leaves of *Betula verrucosa* Ehrh. according to the coefficients of variability, from the smallest one to the biggest.

	The characters	v
1.	Ratio of blade length to blade width	12.60
2.	Number of pairs of lateral nerves	12.82
3.	Mean distance of nerves	15.53
4.	Ratio of blade length to petiole length	16.10
5.	Axil of second nerve	16.76
6.	Blade length	16.82
7.	Number of teeth between the tips of the second and third nerve	17.73
8.	Blade width	17.77
9.	Base angle	21.44
10.	Petiole length	21.58
11.	Distance between tips of second and third nerve	21.71
12.	Position of the widest part	22.76
13.	Distance of first tooth from base	24.81
14.	Ratio of blade length to distance of first tooth	25.66
15.	Apex angle	31.24

The number of leaves on the dwarf shoot has $v = 15.64$, and therefore it would occupy a place between characters No 3 and No 4.

This table figures corresponding to the value of the coefficient of variability, while on the axis of ordinates are the author's 16 characters, arranged in the same order as in Table I. In Table III is a list of characters of the leaves of *Betula verrucosa*, arranged according to the coefficients of variability, from the smallest one to the biggest.

It follows from these tables that the least variable are the ratio of blade length to blade width, the number of pairs of lateral nerves, and the mean distance between the nerves; the most variable are the position of the widest part, the distance of the first tooth and the apex angle; the variability of the latter markedly exceeds all others. The base angle is in the ninth place, between the blade width and the petiole length. It is difficult for the author to agree to this. The acuteness of the leaf apex of *Betula verrucosa* is indeed variable; the angle of the apex and the midrib oscillates within the limits of 5 to 40° with

an arithmetic mean of 19·40° and a standard deviation of $\pm 6\cdot06$. The base angle oscillates between 35 and 120° with a mean of 67·15° and a standard deviation of $\pm 14\cdot40$. Variability expressed in percentages of the arithmetic mean, calculated according to the formula

quoted above, amounts to 31·24 in the first case and 21·44 in the second. However, if we look at the matter geometrically, the apex varies within the limits of a very acute one to a less acute one, while the base has all transitional forms, from heart-shaped to wedgeshaped, and this changes the blade shape in a fundamental manner. We see this plastically in Fig. 12, in which there are diagrams of two leaves. One leaf has a minimum base angle and a maximum apex angle of those encountered in *Betula verrucosa*, while the other leaf has a maximum base angle and a minimum apex angle. The variability of the blade base from cordate to acutely cuneiform must be considered by every naturalist to be greater than the variability of a more or less acute apex, although mathematically the matter appears inversely. In Fig. 12 there is also marked, by means of a broken line, the minimum

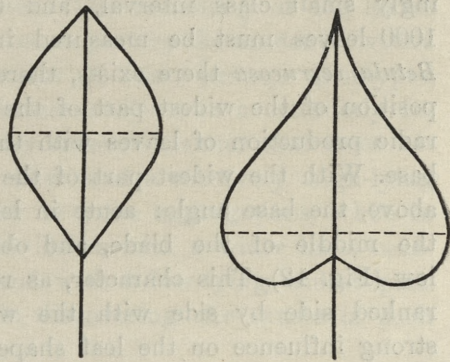


Fig. 12. Diagrams of two leaves of *Betula verrucosa*. The left with a maximum apex angle and a minimum base angle. The right leaf with the minimum apex angle and maximum base angle. The broken lines mark the minimum (highest) and maximum (lowest) position of the widest part of the blade.

and maximum position of the widest part of the blade. This figure serves as an example of how careful one must be when applying statistical methods in biometrics.

On the basis of her observations the author was inclined to consider the position of the widest part of the blade of *Betula verrucosa* as the most variable character on account of the fact that the frequency distribution of the sample with 1000 leaves (as may be seen in Fig. 9), although distinctly concentrated within 14 classes, does extend farther to the right owing to single variants in six classes more. This is not the result of an exceedingly small class interval, and this is proof that more than 1000 leaves must be measured in order to fill up the gap. In *Betula verrucosa* there exists, therefore, great plasticity as to the position of the widest part of the blade, with tendency to a sporadic production of leaves with their widest part lying near the base. With the widest part of the blade correlates, as mentioned above, the base angle: acute in leaves with their widest part in the middle of the blade, and obtuse when the widest part lies low (Fig. 12). This character, as regards its variability, must be ranked side by side with the widest part; both exert a very strong influence on the leaf shape. In correlation with the latter characters are also the distance of the first tooth from the blade base (the wider the base angle, the lower lies this tooth) and the axil of the second nerve.

Characteristic of the leaves of *Betula verrucosa*, therefore, is the plasticity of the entire lower half of the blade. A change of the apex angle exerts a smaller influence on the blade shape, and consequently the variability of this character is of secondary importance.

As regards the arrangement of the variability of other characters in Table III, it is difficult for the author to say anything certain on this point; however, on the basis of what has been already stated above, one must show much reserve concerning the entire table.

Although the author's biometric studies of the leaves of *Betula verrucosa* allowed her to characterize the shapes of these leaves with great accuracy, she was not able to characterize with equal accuracy the variability of these shapes.

III. Discussion

Summarizing the results of leaf measurements of *Betula verrucosa*, it may be stated that the leaves on dwarf shoots without catkins are, on the average, relatively little variable as to size, but more variable as to shape; the factor conducive to this is, above all, the plasticity of the lower part of the blade. However, as a result of the correlation existing between the base angle and the position of the widest part of the blade on the one hand and a whole series of other characters on the other hand, the leaves of *Betula verrucosa* have shapes which are formed with great precision. The variability of the leaves of this birch is caused for the most part by the existence, within the tree's population, of a number of lines, perhaps genotypes, which are not mixed up with one another in a disorderly fashion, but are segregated locally in such manner that trees having leaves with a cuneiform base and a relatively high-lying widest part of the blade occur in some aggregations, while in others there are trees that have leaves with a wider base, occasionally even a cordate one, and with a low-lying widest part. The author did not succeed in discovering the causes of such a segregation.

In literature the author found only one report on the geographical segregations of birches with leaves that have a cuneiform or wide base within the population of *Betula verrucosa*. It is Lindquist's work from 1947, obtained by the author after she had finished her studies. Lindquist distinguishes in Sweden two geographical varieties of the species *Betula verrucosa*: the southern one (*var. saxatilis* Lindq.) reaches as far north as the distributional area of leaf-trees does in that region, and it has smaller leaves with a cuneiform base; the other variety, the northern one (*var. lapponica* Lindq.), grows in central Sweden and in the north as far as extends the distributional area of the pine, and this variety is said to have larger leaves with a wide base. Furthermore, Lindquist finds certain differences to exist between these two varieties in their bark: the northern variety is said to have white bark to the bottom of the trunk, i. e. it does not produce rough bark; its buds have a different shape, the lateral dwarf shoots are occasionally several centimetres long and full of leaf-scars, branches less pendulous, larger bracts and

nuts, verdure more intense, etc. Unfortunately, Lindquist gives only descriptions, without expressing any of these characters numerically. He goes on to compare the varieties distinguished by himself with other birches of the same species from Eurasia, basing his comparison on herbarium specimens or descriptions, and then he divides the whole population of *Betula verrucosa* according to the same plan that he applies to the Swedish birches. He even concludes that the variety having leaves with an acute base is attached to central Europe and that from there, from the south, it has emigrated to Sweden, while the variety having leaves with a wide base is of boreal origin and has come to Sweden from the north.

There is no the proper place to polemize against Lindquist's deductions, inasmuch as the aim of the work presented herein is a different one. Nevertheless, on the basis of material studied by herself, the author is obliged to state as regards leaves that the above mentioned two forms, with a wide base and with an acute one, occur, as already mentioned above, more or less in equal numbers in central Europe in separate aggregations. The leaves of the birches shown by Lindquist in Fig. 3 as *Betula verrucosa* var. *lapponica* Lindq. and in Fig. 7 *Betula verrucosa* var. *platyphylla* (Sukacz.) Lindq. are altogether similar, as regards the dwarf shoot without catkin, to the most frequently encountered leaf type on identical dwarf shoots in the Polish aggregations of birches that have leaves with a wide base. In the aforesaid work of Lindquist, the *Betula verrucosa* var. *saxatilis* Lindq. shown in Fig. 4 has leaves only on fruiting dwarf shoots and on long shoots, which, as the present author stated in her work published in 1937, constitute two separate leaf types and are not comparable with leaves on vegetative dwarf shoots.

As far as the other characters described by Lindquist are concerned the author can only point out that in Poland the birch aggregations with a certain leaf shape are not attended by a greater or smaller ability of producing rough bark. However, the retention of white bark on trees growing at the northern limit of the distributional area might be associated with the slower growth of trees in the northern climate. As regards the length of dwarf shoots, the author must add that in materials

proceeding from *Betula tortuosa* from Finland, collected from some 1000 birch trees between the Arctic Circle and the ocean and described in the next part of the author's work, the length of these shoots is also characteristic of the latter species. Who knows whether this also is not a climatic phenomenon, caused by the fact that in the north trees produce fewer summer shoots, and the dwarf shoots remain for a number of years as dwarf shoots with an extremely small annual growth amounting to several millimetres, while long shoots do not grow out of them in summer as this happens in Polish birches. As regards the intensity of verdure in plants growing in the north, it is associated with the long period of daytime and it is a known fact.

The author has not yet studied the shape of buds in Polish birches and she is not able to state what differences exist between them. However, the bud shape may be associated with the leaf shape.

Neither does the author wish by any means to assert that her two types of birch aggregations, differing as to leaf shape, correspond to the two varieties of *Betula verrucosa* described by Lindquist; she only wishes to point out that Lindquist's division of the whole population of *Betula verrucosa* into a southern and northern variety is, in the author's opinion, premature and insufficiently substantiated.

Finally, the author wishes to add that before the war she obtained, thanks to the kindness of Mrs. H. Popławska-Sukaczewa, material from four trees of *Betula verrucosa* from the Crimea described by the latter in 1928. In the Crimea this species is undoubtedly at the southern limit of its distributional area. From these trees the author measured 48 leaves, i. e. 12 leaves from 6 dwarf shoot from each tree. The leaves of these trees were mostly large, on the average 1.2 times longer than the mean length from the whole distributional area, and in all their characters they were identical with leaves described above by the author, the ones with a base wider than the mean from the whole distributional area (see Fig. 5). The author also measured 48 leaves from 8 trees from the vicinity of Stalingrad; the leaves were also large, but their base was cuneiform, with all other characters correlated therewith. These samples are small ones, but they tend to demonstrate that also in southern Europe

there exists a local division of birches, differing as to the shape of their leaves. This phenomenon is worth studying by accurate biometric methods both in Sweden and elsewhere within the distributional area of this tree. Perhaps then one would succeed in explaining the causes of the interesting local segregation of *Betula verrucosa*.

As regards the numerous leaf forms of the species *Betula verrucosa*, distinguished by botanists, they are all contained in the above-described variability, with the exception of the form *dalecarlica* and similar mutants with deeply incised leaves, the shapes of which ought to be determined biometrically in a different manner. Extremes as to leaf shape often encountered in herbariums and described by botanists, are exceedingly rare in nature, and for this reason the author once more warns taxonomists who are making a study of birches that herbarium materials give a false picture of the shapes and variability of the genus *Betula*, and that studies cannot be based exclusively on such materials.

IV. Comparison of *B. verrucosa* with *B. pubescens*

Having become familiar with the differences in leaf shape of *Betula verrucosa* within its population, there still remains to be characterized the leaf shape of this species in comparison with the leaves of *Betula pubescens* which grows in the same area. For this purpose the author accepted as a comparative unit the means obtained by measuring 100 leaves from 50 trees of *Betula pubescens* from its whole European distributional area. It is a unit which is analogous to the comparative unit of *Betula verrucosa*, described on page 188. The numerical values of the arithmetic means will be published in the second part of this work.

With this new unit, i. e. with the arithmetic means of the sample covering the whole European distributional area of *Betula pubescens*, the author next compared the sample covering the whole distributional area of *Betula verrucosa* and also its local samples. The comparison is shown in Fig. 13.

If we examine in Fig. 13 the thickest, black polygonal line (*J*), representing the ratio of the arithmetic means of the characters of *Betula verrucosa* from the sample covering its whole

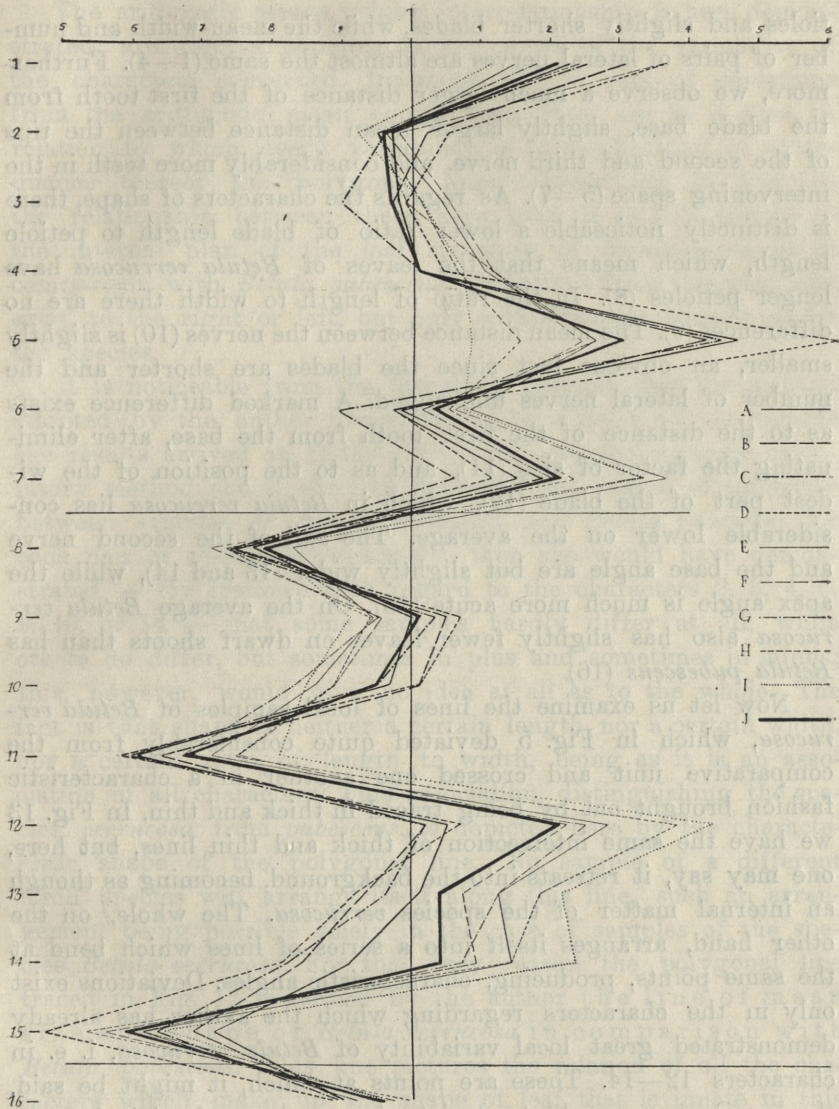


Fig. 13. Ratio of samples of *Betula verrucosa* to the sample *Betula pubescens* from the whole European distribution area. 1 = the sample of the whole area of *Betula pubescens*. A — I as on figure 5. J — Sample of *Betula verrucosa* from the whole distributional area.

distributional area to those of *Betula pubescens*, we perceive that *Betula verrucosa* for the most part has considerably longer pe-

tioles and slightly shorter blades, while the mean width and number of pairs of lateral nerves are almost the same (1—4). Furthermore, we observe a much larger distance of the first tooth from the blade base, slightly larger mean distance between the tips of the second and third nerve, and considerably more teeth in the intervening space (5—7). As regards the characters of shape, there is distinctly noticeable a lower ratio of blade length to petiole length, which means that the leaves of *Betula verrucosa* have longer petioles (8). In the ratio of length to width there are no differences (9). The mean distance between the nerves (10) is slightly smaller, an obvious fact since the blades are shorter and the number of lateral nerves unchanged. A marked difference exists as to the distance of the first tooth from the base, after eliminating the factor of size (11), and as to the position of the widest part of the blade (12), which in *Betula verrucosa* lies considerable lower on the average. The axil of the second nerve and the base angle are but slightly wider (13 and 14), while the apex angle is much more acute (15). On the average *Betula verrucosa* also has slightly fewer leaves on dwarf shoots than has *Betula pubescens* (16).

Now let us examine the lines of local samples of *Betula verrucosa*, which in Fig. 5 deviated quite considerably from the comparative unit and crossed one another in a characteristic fashion brought out by being traced in thick and thin. In Fig. 13 we have the same intersection of thick and thin lines, but here, one may say, it retreats into the background, becoming as though an internal matter of the species *verrucosa*. The whole, on the other hand, arranges itself into a series of lines which bend at the same points, producing, characteristic angles. Deviations exist only in the characters regarding which the author has already demonstrated great local variability of *Betula verrucosa*, i. e. in characters 12—14. These are points at which, it might be said, the species has a right to deviate, inasmuch as plasticity of the lower part of its blade is innate in the species, and consequently characteristic thereof. The other lines run so closely parallel to the lines from the whole distributional area that there is no doubt whatever that what we have here are samples of leaves whose shapes, and therefore the relation of all the characters, are governed by the same rules.

The arithmetic means, whose interrelationship is here demonstrated, are figures standing in the centre of the variability of the characters concerned. Inasmuch as the sum of deviations from the arithmetic mean equals zero, they are as if axes, in relation to which every variability is in equilibrium; in consequence thereof the polygonal lines representing in Fig. 13 the relationship between these axes, give us as if a picture of the internal plan of the leaf structure of *Betula verrucosa* in comparison with *Betula pubescens*. Deviations from this plan may exist, to the right or left, but only within bounds determined for the species.

It is noticeable from the foregoing example that the method adopted by the author turned out to be a good one as regards the results arrived at. If the author had adopted a purely calculatory method and if she had compared the degree of similarity between samples of *Betula verrucosa* and *Betula pubescens* for each pair of characters separately, then she would have demonstrated — for instance with regard to the characters 2, 3, 4, 6, 9, 10, or 14 — that some samples hardly differ at all, while others do differ, but sometimes in plus and sometimes in minus; this, however, would give no idea at all as to the whole. The fact is that shape is neither a certain length, nor a certain width, nor a certain ratio of length to width, being as it is an association of all characters. This association, distinguishing the species *verrucosa* from *pubescens*, is depicted here by the characteristic shape of the polygonal line. No sample of a different birch species will arrange itself along this line, such an arrangement being possible solely in the case of samples of the species *Betula verrucosa*. For that very reason the polygonal line traced in Fig. 13 is termed by the author the line of mean size and shape of *Betula verrucosa* in comparison with *Betula pubescens*. This line pictures the relation of all the characters which make up the shape of leaf that is innate in this species and which have to be in harmony with one another. This harmony may be slightly altered by small changes in the relationship of certain characters, but these changes cannot pass beyond the plan of the structure which is characteristic of the species concerned.

V. Summary

The aim of biometric studies of the collective species *Betula alba* L. is to characterize the species that are at present included therein and to assign to them their proper taxonomic position. The first thing to be studied were the leaves, being the most easily measurable, while study of the bracts, fruits, and other not easily measurable characters has been postponed. The work is based solely on the leaves of vegetative dwarf shoots which are the least variable from among the four separate leaf types existing in each birch, as determined by the author (1937).

The method of the present work consisted in making a comparison of samples, simultaneously with regard to 16 characters. This was carried out by demonstrating graphically the ratio of the arithmetic means of leaf characters from local samples to the arithmetic means of a sample covering the whole distributional area of the species concerned.

The first species to be studied was *Betula verrucosa* Ehrh. The local samples came from Poland and adjacent countries, and the results arrived at are linked up by the author to the whole European distributional area of this species. On the basis of tables prepared in the above-mentioned manner, the following conclusions were drawn:

1. *Betula verrucosa* displays small local variability of its leaves as to size, and slightly larger variability as to shape.
2. Between the base angle and the position of the widest part of the blade on the one hand and a whole series of other leaf characters on the other hand there exists correlation, owing to which the leaves have very characteristic and well-defined shapes.
3. The leaves of *Betula verrucosa* have great innate plasticity of the lower half of their blades, owing to which we encounter in this species all possible transitions from leaves with an acute base and their widest part lying in the middle of the blade, to leaves with a cordate base and their widest part lying near the base.
4. *Betula verrucosa* displays characteristic local variability of leaf shape, owing to which in some birch aggregations we en-

counter trees having leaves with an acute base, and in others leaves with a wide base and all other characters correlated with this property. The author did not succeed in discovering the causes of such local segregation.

Having studied the shapes and the variability of the leaves of *Betula verrucosa* within its population, the author endeavours to characterize the leaf shape of this species in comparison with the leaves of *Betula pubescens*. She compares all the investigated samples of *Betula verrucosa* with the sample of *Betula pubescens* taken from the whole European distributional area of the latter tree. All these samples, shown graphically, arrange themselves along a characteristic polygonal line which consequently depicts the relationship of characters in the leaves of *Betula verrucosa*. In view of the fact that only samples pertaining to the species *Betula verrucosa* arrange themselves parallel to the above-mentioned polygonal line, and samples of no other species do so, this line is termed by the author the line of mean size and shape of the leaves of *Betula verrucosa* in comparison with *Betula pubescens*.

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Badanie ras utajonego wirusa X w świetle pozafioletkowym.
Investigations on the strains of potato virus X in ultra-
violet light.

Mémoire

de M^{lle} **A. KOZŁOWSKA** m. c.

présenté le 5 Décembre 1949.

Plate 9.

The phenomenon of fluorescence in the ultra-violet light of tobacco leaves containing certain kinds of virus diseases was described for the first time by Best (1936)¹⁾, and then by Eicke and Bode (1947). According to these authors, the phenomenon accompanies, in a most characteristic way, some virus diseases as for instance, potato virus X in the strongly virulent strains, nekrosen virus E. N., ring spot virus, but does not appear in the case of the classic virus disease — tobacco mosaic. Besides the tobacco plant, fluorescence in U. V. light caused by virus diseases was found, though in a weaker degree, on *Datura stramonium* and *Petunia*. On other species of the family *Solanaceae*, such as *Capsicum annum* and *Solanum tuberosum*, it was not observed.

Not discussing for the moment the cause of this phenomenon, we shall give its description, estimating critically the significance of this method in the discovery of the masked strains of potato virus X.

Methods

Tobacco leaves were investigated in U. V. light because fluorescence appears most intensively on *Nicotiana tabaccum*. Tobacco seedlings were inoculated with the juice of several hundred sprouts and leaves of selected kinds of potatoes which con-

¹⁾ I quote after Bawden as the original work of Best was not available.

tained a whole range of virus X strains. For inoculation the carborundum method was used. These observations were made in filtered ultra-violet light (quartz-lamp type Hanau with Wood filter). The presence of the masked virus X in the investigated leaves has been confirmed by the serological method of complement fixation. According to Craigie (1939) the complement fixation test is at least 10 times more sensitive than the precipitation test. Thus it is possible to detect virus diseases where the precipitation test fails. Although it is the most sensitive serological method, nevertheless our investigation showed that it does not detect absolutely the presence of virus X in the plant tissue.

TABLE I

Potato stock Nr. 81 Tubers:	Antiserum X Complement fixation of sprouts 24. III.	Antiserum X Complement fixation of haulms 24. V.	Inoculation on tobacco	Antiserum X Compl. fix. of tobacco leaves. 2. VI.
1	—	±	24. V.	+
2	—	±	24. V.	+
3	—	±	24. V.	++
4	—	±	24. V.	++
5	—	±	24. V.	++

All marks of complement fixation refer to antiserum diluted 1:20. Each time control was done in all experiments with normal antiserum. — = complete hemolysis, ± = almost complete hemolysis, + = weaker hemolysis, ++ = almost no hemolysis, +++ = no hemolysis at all.

Tubers of selected healthy potato stock Nr. 81 were brought from Pomerania to Kraków. In spring the complement fixation reaction was carried out with the juice of tuber sprouts, using virus X antiserum. According to Table I the reaction was negative, giving a complete lysis of the red blood corpuscles. In May the complement fixation reaction was carried out for a second time with the juice of the potato foliage derived from the same tubers. An almost complete hemolysis appeared. At the same time young tobacco leaves were inoculated with the juice of the same potato leaves. Eight days after the inoculation the complement fixation reaction was carried out with those tobacco

plants which showed no symptoms of virus diseases. This time there was no hemolysis at all, which indicated the presence of the virus *X* in the leaves. The virus *X* must therefore have been in the leaves, most probably already in the sprouts of the potato tubers, but in such small quantities that it could not be detected by the complement fixation reaction. In the tobacco plant the amount of the virus substance increased and therefore the complement fixation reaction was positive.

The task of this work is to analyse the phenomenon of fluorescence of tobacco leaves infected with the virus *X*, assuming that the complement fixation reaction is a test for the presence of a certain definite amount of virus *X*.

Inoculated tobacco plants

The observations were made on two different kinds of tobacco, *Nicotiana tabacum* var. *White Burley* and var. *Virginia*. The most frequently used was the variety *W. Burley* as the most sensitive to infection with virus *X*.

It was most important to confirm whether the non infected tobacco leaves do not produce in the U. V. light the fluorescence phenomenon. The observations in the U. V. light on healthy tobacco leaves planted in a glasshouse were made in the course of two or three months, from the moment when the young plants had only two small leaves. It was evident that the young tobacco seedlings with small roundish leaves showed no trace of fluorescence in the U. V. light. In the course of their development the haulms shot up and on the lower layer of the elongated leaves the veins showed a weak bluish shine. The complement fixation reaction performed with the juice of those leaves, using the virus *X* antiserum, was negative which indicated a lack of virus *X* in the leaves.

A distinct vein fluorescence appeared, however, when the leaves began to become yellowish and to die. This happened especially when the young tobacco seedlings were in bad conditions, for instance, in a low temperature. We then found on the same plant the green upper leaves without any fluorescence and the lower yellow ones with veins shining strongly in U. V. light. It is interesting that inoculations performed with juice from dead

haulms cause the same light phenomenon. Consequently it was important to use for observations only, the healthy leaves of tobacco seedlings in their very young stage.

The second important factor in our experiments was to raise the tobacco plants in sterilized soil. The tobacco plants raised in the usual hot-bed soil always showed strong fluorescence in U. V. light on those places where the leaves and the stem touched the ground. In sterilised soil this phenomenon appears also but in a very weak degree and only on the stem and on parts of the roots.

Experimental material used for inoculation

First of all it was necessary to confirm if juices from healthy potatoes and other species inoculated on young tobacco seedlings do not cause by themselves the fluorescence phenomenon. To perform such kinds of experiments is rather difficult. It is always doubtful whether we possess in our conditions absolutely virus *X* free potatoes.

The virus *X* free potato variety »President« derived from tubers originally supplied by Dr K. Smith (Cambridge) in 1946, raised only at us in the glass-house, showed, in 1949, the presence of a masked virus *X* in leaves and tubers.

We obtained, in 1949, thanks to the kindness of Dr. Roland (Belgium), the virus free potato tubers variety »Bintia«. We took for inoculation different parts of the tuber: pieces of skin, eyes, the middle part of the conducting tissues etc. Fluorescence did not appear on the tobacco leaves and serological tests were also negative. Inoculation done with infected tuber gave an opposite result. (Table II).

Many inoculations were made also with different plant species, such as: *Potentilla*, *Fragaria*, *Syringia*, *Senecio*, *Cucumis* etc. Fluorescence on tobacco leaves did not appear. Only juice taken from *Galinsoga parviflora* gave a weak fluorescence phenomenon.

Finally it was necessary to investigate whether the bacterial and fungus diseases of potatoes do not produce the same light phenomenon as virus *X*. Tobacco leaves inoculated with tuber — bacteriosis gave no light phenomenon. The experiment performed with potato blight *Phytophthora infestans* gave a different result. The mycelium of *Phytophthora* produced from infected potato tu-

TABLE II

Tuber of virus free potato var. <i>Bintia</i> *				Tuber of potato Nr. 21 Stock infected with virus X			
Comp. fix. anti- serum X	Date of in- oculation	Observations on tobacco in U. V. light 27. X.	Compl. fix. of tobacco	Comp. fix. anti- serum X	Date of in- oculation	Observations on tobacco in U. V. light 27. X.	Compl. fix. of tobacco
Eye 1	17. X.	—	—	+	17. X.	weak veins clearing spots	+
Eye 2	17. X.	—	—	+++	17. X.	inoculated leaves shine strongly	+++
Eye 3	17. X.	—	—	+++	17. X.	vein clearing	+++
Eye 4	17. X.	—	—	++	17. X.	main vein shines	+++
Conducting tissue	17. X.	—	—	+++	17. X.	weak vein clearing	+
Cond. tis. near the eye	17. X.	—	—	++	17. X.	strong vein shining	+++
Skin	17. X.	—	—	++	17. X.	vein clearing	+++
Under Skin	17. X.	—	—	+	17. X.	weak vein clearing, spots	++
Storage parenchyma	17. X.	—	—	—	17. X.	weak vein clearing	±

bers was rubbed against young tobacco leaves. After several days the veins showed a weak but distinct shine. It is evident that for inoculation it is necessary to take potato free from blight.

The potato virus X strains

The different potato virus X strains discovered on potatoes can be divided, according to many scientists, such as Köhler, Salaman (1938), into two definite differentiated groups; strains which produce no visible symptoms on tobacco leaves and strains producing visible symptoms, as, for instance, types of mottle and local necroses. Investigations in U. V. light are evidently of fundamental importance in the latter case. To have an exact picture of this light phenomenon we began our observations with several strong virulent strains which produce distinct symptoms on tobacco leaves. They are defined, according to Salaman.

A. Strong virulent virus X strains

1). Strains which produce on tobacco leaves local necroses (according to Salaman X^s and X^n). On the eighth to tenth day after inoculation systemic symptoms make their appearance. Commencing with a distinct mottle, they subsequently take the form of rings and figures of diverse shape with necrotic centres; often chlorosis and the accompanying necrotic changes occur at the apex of the leaf and gradually extend toward the base. Eicke and Bode (1947) give photos made in U. V. light of several strains belonging to this category. They are isolated by Köhler as strains U_{44} , Cs_{44} , Us/r , Cs/n . According to their observations our tobacco leaves infected with X^s at the beginning of necrotic changes always showed, in U. V. light, a strong shine of larger and smaller veins on their lower layers.

In order to investigate the progress of this phenomenon the seedlings of *W. Burley* inoculated with juice of sprouts of the variety *Robusta*, last year entirely attacked by X^s , were observed in U. V. light every three days. On the third day after inoculation a strong shine of larger and smaller veins appeared on the lower layer. In several cases light spots appeared in interveinal areas. Three days later the fluorescence enlarged and passed from the infected leaf to the next one. On several leaves appeared

light shining rings. On the 12th day after inoculation, when the rings and necrotic centres were well defined on the leaves, shining of the veins and rings reached its optimum. As the plant grew older the fluorescence gradually diminished. In plants 2 months old with defined symptoms the fluorescence does not become visible.

2). Mixture of the virus Y and virus X strains. 2 or 3 weeks after inoculation a distinct vein clearing appeared on the leaves. In all the cases the presence of virus X was serologically confirmed. In U. V. light the leaves showed a strong shine of larger and smaller veins. After 2 and 3 months the symptoms changed. The characteristic vein — clearing observed in normal light disappeared. In the interveinal area a bright yellow clearing was visible and the tissue nearer to the veins became green. In U. V. light fluorescence was not visible.

3). X^L strain (Salaman). 2 or 3 weeks after inoculation a yellow mottle appeared without any trace of necrosis. Such leaves always gave the fluorescence phenomenon in U. V. light, but not to the same degree in every case. Sometimes the shining of the vein was very distinct, sometimes only segments gave some light effect. In several spots the yellow mottle gave a weak bluish shine. In still older plants the fluorescence phenomenon disappeared.

B. Masked virus X strains on tobacco (X^H , X^G Salaman).

The juice of apparently healthy potatoes inoculated on tobacco seedlings often does not produce any symptoms, although the tobacco plant has been infected with virus X. According to Salaman, it is the so called strain H, which does not give any visible symptoms on tobacco plants but appears as a delicate mottle on *Capsicum annum*. The latter is much less sensitive to infection than *W. Burley* seedlings. An inoculation of the strain H on *Capsicum* gave, in our experiments, only a certain percentage of positive results.

The fact that tobacco seedlings have been infected with strain X^H can be confirmed either by serological reactions, most effectively by complement fixation, or by inoculating virulent strains X^S , which did not take. Those methods are complicated

and take much time. It is, therefore, important to confirm whether masked strains of virus *X* on tobacco leaves give visible symptoms in U. V. light.

Two weeks after inoculation with X^H , the leaves showed on their lower layer, contrary to the virulent strains X^L , X^S in the U. V. light, the fluorescence phenomenon, but to a different degree.

In order to prove a relation between even a weak fluorescence and the masked virus *X*, several experiments were made from April to October, some of which I will cite.

Experiment I. Potato stock Nr. 926, selected in Pomerania was bred for 2 years in Kraków, without showing any symptoms of a virus disease. Inoculated on *W. Burley* seedlings it showed no trace of a virus disease. On *Capsicum annum*, however it caused a weak mottle pointing to the presence of virus X^H .

Eight tubers derived from one plant were planted in pots in a green-house in December. At the end of February one plant was cut in segments and serologically examined with the complement fixation method, using virus *X* antiserum. In no case was there any hemolysis of blood corpuscles, pointing to the presence of a masked virus *X* in the whole plant. In April the complement fixation reaction was carried out with the juice of potato leaves. At the same time the *W. Burley* seedlings were inoculated with the juice of the same potato leaves. After 4 days the tobacco leaves were observed in U. V. light. The result is given in Table III.

All the infected tobacco leaves gave almost the same picture in U. V. light. The large veins showed a distinct bluish shine. On the 6th day after inoculation the complement fixation reaction was performed with the same leaves. The result was as follows:

Dilution of antiserum <i>X</i>	$1/10$	$1/20$	Control without serum	
<i>W. Burley</i> not infected	—	—	—	
<i>W. Burley</i> infected	+++	++	—	
Virus <i>X</i> extracted	+++	+++	—	
" " " "	—	—	—	Control serum

Experiment 2. Tubers of selected healthy potato stocks were received from Pomerania. The juice from tuber sprouts, by complement fixation reaction gave complete lysis of the red blood corpuscles. Each tuber was cut into two, one part was planted in Kraków the other in Zakopane in the Tatra mountains. During the whole period of vegetation until October the plants showed no symptoms of disease. At the end of September the leaves were examined with complement fixation reaction

TABLE III

Stock		Compl. fix. of potato leaves	Date of inoculation	Observ. of tobacco leaves in U. V. light. 3. V.
926	Upper leaf.	+++	29. IV.	distinct shining of veins
1	Lower leaf.	+++	29. IV.	main vein shine weakly
926		+++	29. IV.	" " " "
2				
926		+++	29. IV.	distinct shining of veins
3				
926		+++	29. IV.	main vein shine
4				
926	Upper leaf.	++	29. IV.	" " "
5	Lower leaf.	±	29. IV.	" " "
926		+++	29. IV.	" " "
6				
926	Upper leaf.	+++	29. IV.	" " "
7	Lower leaf.	-	29. IV.	" " "
926		+++	29. IV.	" " "
8				

using virus X antiserum. At the same time tobacco seedlings were inoculated with the juice of the same leaves. The tobacco leaves were examined in U. V. light twice, in the first case every 3 days, in the second every 6 days. Table IV. shows the results.

Of 34 examined potato leaves, 14 cases gave a negative result in complement fixation reaction, while in 20 cases the result was positive. The tobacco leaves, on the other hand, showed in all 34 cases the presence of virus X. The fluorescence on tobacco leaves was also confirmed in all cases, but in a very different degree, beginning with a weak shine of the veins up to a strong

TABLE IV

Date:	24. IX	27. IX	30. IX	30. IX
Potato stocks Kraków	Compl. fix. of potato leaves	I Observation in U. V. of tobacco leaves	II Observation in U. V. of tobacco leaves	Compl. fix. of tobacco leaves
81 (1)	+++	weak vein clearing	veins shine	+++
(2)	+	—	main vein shines, spots	+++
346 (1)	—	—	in place of inoculations distinct spots	+++
(2)	—	main vein shines	on 2 leaves veins shining	+
53 (1)	—	main vein shines	all inoculated leaves shine	+++
(2)	++	veins of inoculated leaves shine	distinct shining	++
(3)	+++	main veins of inoculated leaf shine	strong shining of veins	++
(4)	—	distinct shining	all inoculated leaves shine strongly	+++
(5)	+++	weak vein shining	intensive shining in place of inoculation	+++
Date				
Zakopane	6. X	12. X	18. X	
54 (1)	+	shining in place of inoculation	distinct shining of veins	+++
(2)	+	weak vein clearing	weak vein clearing	++

(3)	-	in place of inoculation	veins clearing	++
(4)	-	in place of inoculation	in place of inoculation	++
53	++	in place of inoculation spot	distinct shining of veins	++
(2)	-	-	weak vein clearing	++
(3)	+	weak vein clearing	weak vein clearing	+
(4)	++	main vein shines distinctly	strong shining	++
(5)	+	distinct shining	strong shining	++
926	++	in place of inoculation	shining of veins and spots	++
(2)	-	main vein shines distinctly	strong shining	++
(3)	-	vein shines	veins shine distinctly	++
(4)	-	distinct shining	distinct shining	++
(5)	++	veins clearing	veins clearing	++
326	-	in place of inoculation	veins clearing	++
(2)	++	vein shining	distinct veins shining	++
(3)	-	distinct veins shining	distinct veins shining	+
(4)	+	in place of inoculation	distinct veins shining	+

shining. We must state that in general the second observation showed a more intensive fluorescence in comparison with the first.

Experiment 3. We took this time sprouts of 28 potato tubers belonging to 8 varieties, which had showed in the preceding year a kind of degeneration, pointing to a virus disease.

On the 5th of May the sprouts were cut longitudinally. With the juice of each half was performed the complement fixation reaction with virus X antiserum. We inoculated *W. Burley* seedlings with the juice of the second half. The inoculated tobacco leaves were examined every two days in U. V. light. Every 4 days we pressed out the juice of those leaves and performed the complement fixation reaction. Two weeks after inoculation we observed visible symptoms of a virus disease. Table V shows the results.

Of 28 examined potato sprouts 15 gave no positive serological reaction. Tobacco leaves, on the contrary, already showed, after two days in 23 cases, a weak fluorescence phenomenon, which, in several cases, was especially intensive in the place of inoculation. Two days later the shining was more distinct, and in 3 cases only it was not confirmed. The complement fixation reaction was in 6 cases very weak. In corresponding sprouts it was, according to Table V, negative. Six days after inoculation the shining was in most cases distinct, and the complement fixation reaction was stronger. Finally, 12 days after inoculation fluorescence was also visible on the neighbouring leaves and complement fixation reaction was in most cases complete. The tobacco leaves which remained after our experiments showed in 20 cases no visible virus symptoms, therefore they contained the masked virus X.

In this experiment the fluorescence phenomenon increased within 12 days, and at the same time the serological reaction, which proved that the amount of virus X was augmented. In most sprouts it was present in such small quantities that even the very sensitive complement fixation reaction could not discover it.

Although the increase of those two phenomena were parallel to each other, yet there was no direct dependence between the intensity of the fluorescence and the serological reaction. Fluo-

rescence can already be observed on tobacco leaves two days after inoculation, whereas virus X cannot yet be confirmed with complement fixation reaction. However, there were also cases when with a very weak shine, the serological reaction was strong.

The fact that we could not observe a shining of tobacco leaves with a positive complement fixation reaction was, in our experiment, not an isolated case. In such cases, fluorescence usually appeared later, 2 or 3 weeks after inoculation.

Table VI shows some examples.

TABLE VI

Date	19. IX	23. IX	27. IX	30. IX	30. IX	11. X
Stocks	Date of inoculation	I Observation of tobac. leaves in U.V. light	II Observation of tobac. leaves in U.V. light	III Observation of tobac. leaves in U.V. light	Compl. fix. of tobacco leaves	IV Observation of tobacco leaves
81	19. IX	—	—	—	—	—
1	19. IX	—	—	—	—	—
2	19. IX	—	—	—	++	main vein shines
3	19. IX	—	—	Trace of shining of main vein	+++	veins shine
4	19. IX	—	—	Trace in place of inocul.	+++	veins shine
5	19. IX	—	—	Weak shining	+++	distinct shining of veins
18	19. IX	—	—	—	++	distinct shining of veins
50	19. IX	—	—	—	+	vein clearing

Results of field investigations

In the course of last season we inoculated *W. Burley* tobacco seedlings with the juice of 570 potatoes which belonged to 117 separate stocks, formerly selected in Pomerania. 181 potatoes, that belonged to 38 stocks, had been for 3 years in culture in Kraków and had entirely degenerated. Virus X had been positively confirmed in them serologically. 389 potatoes, belonging to 79 stocks, had been for two years in culture in Kraków. Weak degeneration symptoms were visible, nevertheless the

TABLE V

Date	5. V $\frac{1}{2}$ sprout Compl. fix.	7. V I observ. in U. V. of tobacco leaves	9. V II observ. in U. V. of tobacco leaves	9. V Compl. fix. of tob. leaves	11. V III observ. in U. V. of tobacco leaves	11. V Compl. fix. of tob. leaves	17. V IV observ. in U. V. of tobacco leaves	17. V Compl. fix. of tob. leaves
Potato stocks								
Capella billa 1	-	shining in place of inoculation	veins shine	+			the rest shine weakly	+
2	-	shining in place of inoculation	vein shines	±			the rest shine distinctly	++
Prisa 1	-	-	-	±				
44 1	-	very weak in place of inoculation	vein shines weakly	±				
926 1	-	-	-	-				
2	-	-	very weak in place of inoculation	-				
Flaming 1	-	vein shines weakly	vein shines distinctly		vein shines distinctly	++		
2	-	weak in place of inoculation	shining spot		shining spot	++		
Robusta 1	-	-	very weakly		veins shine weakly	++		
2	+	veins clearing	veins clearing		strong shining	++		
926 3	+	veins clearing	veins clearing		veins clearing	+		
94 1	+	very weak	very weak		very weak	±		

94	2	weak in place of inoculation	vein shines, a spot	+	+
Capella billa	3	veins clearing, a spot	2 leaves shine		++
	4	vein shines	2 leaves shine		++
Prisca	2	veins clearing	veins clearing		++
	3	in place of inocul.	strong shining in place of inocul.		++
Johanna	1	very weak	1 leaf veins clearing		+
	2	in place of inocul.	distinct shining of veins		++
Robusta	3	1 leaf weak shining	1 leaf weak shining		++
	3	1 leaf veins clearing	all leaves shine		++
44	4	1 leaf veins clearing	2 leaves veins shine		++
	2	—	—		++
926	3	weak veins clearing	distinct shining of veins		++
	4	1 leaf very weak	1 leaf shining of veins		++
94	5	1 leaf very weak	2 leaves very weak		+
	3	1 leaf weak	2 leaves veins clearing		++

presence of virus *X* was serologically confirmed. The inoculated tobacco was only once examined in U. V. light. In the first and second case the results were as follows:

	Infected tobacco plants	External symptoms of virus <i>X</i>	No symptoms	Fluoresc.	No fluorescence or weak
Potatoes of 3 rd year culture	181	93	88	51	37
Potatoes of 2 nd year culture	389	234	155	88	67

In both cases there were more tobacco plants with masked symptoms than with visible ones. More than half of the first plants showed distinct fluorescence in U. V. light, which pointed to the presence of virus *X*. The rest either showed a weak shining or, in very few cases, none, although virus *X* was serologically confirmed in them. Here we must add that our observations in U. V. light were made only once. Without doubt, a repetition of our observations would yield a much higher percentage of distinct shining leaves.

It is, of course, quite clear that the method of investigating tobacco leaves with masked virus *X* detects this virus in much higher percentage than observation in normal light, but nevertheless it does not detect it always.

Discussion

The above described experiments yield the following suggestions.

Virulent strains of virus *X* always show on tobacco leaves a characteristic fluorescence in U. V. light. On the other hand, on tobacco leaves infected with masked virus *X*, serologically confirmed, fluorescence appears in U. V. light in a varied intensity, sometimes showing none at all. We distinguish the following characteristics: 1) no fluorescence at all, 2) the leaves showing a hardly visible shine, 3) the shine appearing only on the vein in the place of inoculation, 4) the veins showing a light blue shine, 5) the veins shining quite distinctly in their whole length, or part of it (Fig. 2).

It is also important to state that fluorescence appears in different periods of time. It appears the most often on the second or third day after inoculation, before virus *X* can be serologically detected. It is, therefore, in these cases, the most sensitive test for the presence of virus *X* in tobacco leaves. But there are also cases when fluorescence appears much later, after 6 or even 12 or 14 days after inoculation. Sometimes it does not appear at all. Therefore observations in U. V. light do not confirm absolutely the presence of virus *X*.

Finally, we must discuss the nature of the fluorescence itself. There is no doubt that the shining in U. V. light of tobacco leaves infected with virus *X* is not a direct shining of the virus nucleoproteid. Proof that this phenomenon only accompanies the disease, is provided by the following facts:

1) The virus nucleoproteid extracted from the plant tissue causes no fluorescence phenomenon in U. V. light.

2) The phenomenon appears especially distinctly only on infected tobacco. On other species infected with virus *X*, for instance on potatoes, it is not visible.

3) Fluorescence on tobacco leaves is not directly correlated with the intensity of the disease. It often appears on the leaves even when the virus could not yet have developed there.

4) A distinct fluorescence appears in the first month after infection, disappearing in the later stages, although virus *X* is present there.

As fluorescence of the tobacco leaves in U. V. light may be caused not only by virus *X* but also by other factors — namely, contact with the microflora of the soil, decomposition of organic substances in the yellowing leaves — it seems to be quite probable that compounds exist in tobacco leaves, which, under the influence of virus *X* in the cell, or of another stimulus, undergo a change, unknown to us, effecting that very fluorescence.

According to Eicke and Bode that substance cannot be nicotine. Tobacco leaves infected with virulent strains of virus *X*, shining very brightly in U. V. light do not contain a higher percentage of nicotine than normal leaves. Furthermore, there can be no question that non fluorescing nicotine becomes fluorescing as confirmed with virus *X* infected *Datura* and *Petunia*

leaves which showed the fluorescence phenomenon although they never contained any nicotine.

The character of the shining of the veins proves that this substance is most probably placed in the sieves.

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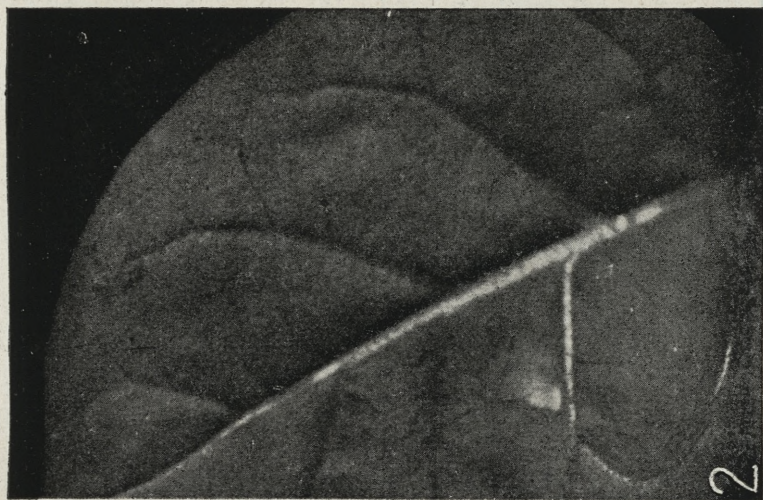
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Explanation of figures

Fig. 1. The tobacco leaf in day light. The white spot marks the place of infection.

Fig. 2. Tobacco leaf with masked virus X in U. V. light. Main vein shining distinctly in their whole length.



B. Kozłowska

Studia genetyczne nad rodzajem Aegilops. IV. Dziedziczenie się niektórych cech w krzyżówkach międzyodmianowych Aegilops ventricosa Tausch., Ae. triuncialis L. i Ae. ovata L. — Genetic studies in the genus Aegilops. IV. The inheritance of some characters in the intervarietal crosses of Aegilops ventricosa Tausch., Ae. triuncialis L. and Ae. ovata L.

Mémoire

de M. K. MICZYŃSKI

présentée le 25 Mars 1949 par M. T. Lityński m. c.

Plate 10

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Introduction

The literature on *Aegilops* hybrids is rather abundant. However the greatest part of the papers published on that subject up to the present is mainly concerned with the cytology and the genome analysis of the interspecific hybrids, the inheritance of the racial differences within the same species has hitherto been investigated to a much smaller extent.

Several *Aegilops* species are characterized by a rather wide range of racial variability and show in that respect an analogy to the species of *Triticum*. On account of the number of easily distinguishable varieties and races as well as the facility of obtaining intervarietal hybrids, the species of *Aegilops* present a suitable material for the factorial analysis.

Some technical difficulties in these experiments are caused by the heterogamy of several species. As a rule the artificial isolation by means of the isolatory bags is indispensable to preserve the purity of the strains used for crossing and to protect the F_1 and F_2 generations from spontaneous pollination. Another difficulty is created by the brittleness of the rachis of nearly all *Aegilops* species which disarticulates very easily at the base of the spike. This feature renders difficult the harvest and storage of the ripe plants and can also cause some errors in the statistical calculations if a number of plants must be discarded on account of the loss of their spikes.

In the communications of 1926 and 1933 we gave account of the results obtained in crossing different varieties of *Aegilops speltoides* Jaub. et Sp. The present paper deals with the intervarietal crosses made within three species: *Aegilops ventricosa* Tausch., *Ae. triuncialis* L. and *Ae. ovata* L. All the researches were carried out in the Plant Breeding Department in Dublany during the years 1927—1942. Some of these results were published in the form of a brief communication in the Proceedings of the Seventh Intern. Genetical Congress (Miczyński (1941)).

A. Crosses within *Aegilops ventricosa* Tausch.

Inheritance of the glume colour

The most common glume colorations of the different *Aegilops* forms are white and black or greyish-black. The brownish-red coloured varieties are comparatively rare which may lead to the supposition that there are no red coloured *Aegilops* forms at all (Lewicki 1929). They have, however, been found by Popova (1923) among the varieties of *Aegilops triuncialis*, *Ae. cylindrica*, *Ae. squarrosa* and *Ae. crassa*. Among the forms of *Ae. ventricosa* var. *vulgaris* Eig. we have found in our collection three types of glume coloration: white, red and black. After

Ducellier (1936), all these three types are common in the fields of Algeria.

Cross I

There were crossed the following varieties of *Aegilops ventricosa*:

♂ N° 5 g. *Ae. ventricosa* var. *vulgaris* subvar. *obscura* Micz. (1929). Glumes black. Obtained from prof. L. Ducellier, Maison Carré, Algeria.

♀ N° 5 d. *Ae. ventricosa* var. *vulgaris* Eig. Glumes brownish-red. Obtained from Mr. Coupin, Tunis.

The four F_1 plants were all black glumed and fully fertile. During the flowering period they were isolated by means of the pergament paper bags. In F_2 320 plants were raised and were found to segregate in black and red in the following ratio (Table I):

TABLE I
Segregation of the glume colour. Cross I

Family N°	Black	Red	Total
12/33	67	13	80
13/33	48	16	64
14/33	37	11	48
15/33	97	31	128
Total	249	71	320
Expected (3:1)	240	80	320

$$\chi^2 = 1.35 \quad P = 0.20 - 0.30$$

Thus the difference between the black and red glume colour is dependent upon one pair of genes.

B. Crosses within *Aegilops triuncialis* L.

Material

The material used in these crosses consisted of the following forms of *Aegilops triuncialis*:

N° 3 b. Ear white. Rhachis very brittle, disarticulating at the base of each spikelet. Empty glumes of the lateral spikelets

terminating in 2 or 3 awns. Awns 37—43 mm long. Unripe plants green coloured, without waxy bloom. Belongs to the ssp. *typica* Zhuk. Derived from Afghanistan, obtained from the Institute of Plant Industry, Leningrad. From this material following true breeding types were isolated:

3 b α . Glumes »glabrous«, covered only with rare and very short (about 0.15 mm) scabrid hairs (var. *muricata* Zhuk).

3 b β . Glumes pubescent, hairs about 0.4 mm long (var. *hirta* Zhuk),

3 b γ . Glumes pubescent, hairs about 0.7 mm long (var. *hirta* Zhuk).

N^o 3 c. Ear white, rhachis comparatively tough, disarticulating only at the base of the spike. Glumes glabrous, as in N^o 3 b α , lateral spikelets awnless. Unripe plants have a bluish tint on account of the waxy covering. Belongs to the var. *persica* (Boiss.) Eig. subvar. *glauca* Micz. (1929). Derived from Transcaspia, obtained from the Institute of Plant Industry, Leningrad.

N^o 3 d. Ear white, rhachis brittle, glumes pubescent, hairs ca. 0.7 mm long. Unripe plants green coloured, without waxy bloom. Derived from Afghanistan, sent by the Institute of Plant Industry, Leningrad.

Among the plants of this form we have established the existence of three different types of awning:

3 d α . Lateral spikelets awnless. The empty glumes terminating in a tooth 3—7 mm long (var. *persica* subvar. *hispida* Micz. 1929).

3 d β . Empty glumes of the lateral spikelets short awned, awns 20—35 mm long.

3 d γ . Empty glumes of the lateral spikelets fully awned. Awns 40—60 mm long (ssp. *typica* var. *hirta* Zhuk.).

N^o 3 g. Ear white, sometimes pigmented with anthocyanin. Rhachis tough, the spike disarticulates as a whole at the base. Empty glumes pubescent, terminating in two or three awns 35—45 mm long. Hair length about 0.4 mm. Belongs to the var. *typica* Eig. Obtained from dr Emcet Jekta Eskishehir, Turkey.

Among the plants belonging to this biotype we have found two different types in regard to the development of the waxy bloom:

3 g α waxless, green,

3 g β waxy, bluish-green.

Waxy bloom and pubescence of the glumes

In a previous paper (1933) we have reported upon the inheritance of the glume pubescence in crosses between the diffe-

rent strains of *Aegilops speltoides* Jaub. et Sp. It has been proved that the pubescent state is dominant to the glabrous state. In F_2 segregation into pubescent and glabrous was observed in a ratio of 3:1.

Among the strains of *Aegilops triuncialis* L. used in these experiments we have established the existence of three true breeding types of glume pubescence. One of them is designated as »glabrous«, and is characterized by very scarce and short scabrid hairs (about 0.0—0.15 mm long). The other two have pubescent glumes, the hair length of the second type measuring about 0.4 mm, that of the third type about 0.7 mm. In the Tables the hair length is given in units of the micrometer scale each unit corresponding to 35 μ .

The inheritance of the bluish waxy covering on ears and stems of cereal varieties has been already investigated by many genetists. In the majority of cases it behaved as a dominant character. Heribert Nilsson (1917) crossed waxy and waxless rye strains and obtained an F_2 generation segregating into bluish (waxy) and green (waxless) individuals according to the monohybrid ratio 3:1. The same character was studied by Mieczyski sen. (1907) and Tschermak (1923) in crosses between wheat varieties of the hexaploid group. Mieczyski sen. found it to be dominant in a cross between *T. compactum* and *T. vulgare*. According to Tschermak several Mendelian factors are concerned in the production of the waxy covering. In a cross between two waxy wheat varieties: Rivet (*T. turgidum*) \times Red Fife (*T. vulgare*) investigated by Biffen and Engledow (1926) a segregation into waxy and waxless was observed in a 15:1 ratio, which proves that the development of the waxy bloom may be conditioned by two factors.

Detailed genetical analysis of *T. turgidum* \times *T. vulgare* crosses is given by Watkins (1930). According to his interpretation the waxy bloom of the parental forms is conditioned by two polymeric genes *W* and *W'*. One of them belongs to the genome of *T. turgidum*, the other is located in the extra chromosomes of *T. vulgare*.

According to Meurmann (1926) the wax formation in oats is dependent upon one partially dominant factor *W*. The crosses between waxy and waxless plants showed segregation in F_2 into

three types: *WW*, *Ww* and *ww* in a 1:2:1 ratio. The dominance of the waxy bloom has been also stated by Nishivana (1929) in the interspecific *Avena* hybrids.

In contrast to the above described cases, the waxy bloom behaved as a recessive character in crosses between *Triticum pyramidale* (waxless) and *T. durum* (waxy) investigated by the author (1930). The F_1 plants were waxless and the F_2 consisted of 3/4 waxless and 1/4 waxy individuals.

Popova (1923) found that the genetic behaviour of the waxy bloom in the interspecific hybrids of *Aegilops* may be different according to the hybrid combination. In a cross between *Aegilops crassa* (waxless) and *Ae. juvenalis* (waxy) the waxy condition was dominant and in an *Ae. triuncialis* (waxy) \times *Ae. crassa* (waxless) cross it behaved as a recessive character.

In our crossing experiments with *Aegilops* the presence or absence of the bluish waxy covering on the ears and stems was determined at an early stage in the nursery, the pubescence of the glume surface and the awning were examined in the laboratory after the harvest.

Cross II

N^o 3 g β (ear waxy, pubescent) \times N^o 3 g α (ear waxless, pubescent).

The difference between the parent strains consisted exclusively in the presence or absence of the waxy bloom. All the 9 F_1 plants were waxless and hairy, the second generation was composed of waxless and waxy individuals in the following ratio (Table II):

TABLE II
The inheritance of the waxy bloom. Cross II

N ^o of the F_2 family	Waxless	Waxy	Total
63/35	155	46	201
64/35	87	40	127
65/35	36	21	57
Total	278	107	385
Expectation (3:1)	288.75	96.25	385

$$\chi^2 = 1.60$$

$$P = 0.20 - 0.30$$

Thus the waxy condition behaved as a recessive character and the segregation was monohybrid. As was expected, all the F_2 plants had pubescent glumes.

Cross III

N^0 3 g α (ear pubescent, waxless) \times N^0 3 c (ear glabrous, waxy).

The length of the glume hairs of the female parent 3 g α was equal to 11–14 units of the micrometer scale, the scarce scabrid hairs of the »glabrous« variety 3 c were 3–4 units long. Six F_1 plants were uniformly green and pubescent, their hair length equaling 8–9 units.

The F_2 generation was tested in respect of the waxy bloom in the nursery and showed the following segregation (Table III):

TABLE III
The inheritance of the waxy bloom. Cross III

	Waxless	Waxy	• Total
Obtained	92	33	125
Expectation (3:1)	93.75	31.25	125

$$\chi^2 = 0.13 \quad P = 0.70 - 0.80$$

The waxy bloom appeared again to be a recessive character. The mode of distribution indicates the existence of one inhibitory factor in the variety 3 g α .

The measurements of the hair length were made after the harvest. The results are presented in Table IV:

In order to get clearer picture of the segregation, the F_2 individuals were grouped into two classes of glume pubescence: »glabrous« (hairs 3–4 units long) and hairy (hairs longer), as shown in Table V.

The observed segregation corresponds very well to the expected dihybrid ratio 9:3:3:1. The difference between »pubes-

TABLE IV
The inheritance of glume pubescence in F_2 . Cross III

	Hair length in units of the micrometer scale													Total
	3	4	5	6	7	8	9	10	11	12	13	14		
Number of plants														
Waxless. . .	2	17	1	1	10	15	6	6	11	5	1	1		76
Waxy		6	1	3	2	1	1	3	4	1	2			24
Total	2	23	2	4	12	16	7	9	15	6	3	1		100

Remark: The total number of individuals in Table IV is smaller than in Table III because some of the plants were damaged during storage and discarded.

TABLE V
The segregation of the glume pubescence and waxy bloom. Cross III

	Pubescent		Glabrous		Total
	waxless	waxy	waxless	waxy	
Obtained	57	18	19	6	100
Expected (9:3:3:1)	56.25	18.75	18.75	6.25	100

$$\chi^2 = 0.05 \quad P = 0.99$$

cent« and »glabrous« depends upon a single gene. Both characters, pubescence and waxy bloom segregated independently.

Cross IV

N^o 3 c (ear glabrous, waxy) × N^o 3 b a (ear glabrous, waxless).

Both parents had »glabrous« glumes, they differed however in the development of the waxy bloom. The F_1 plants were »glabrous« and waxless. The F_2 exhibited the segregation presented in Tables VI and VII:

The F_2 plants were »glabrous«, as expected. The appearance of two individuals with pubescent glumes was probably due to the spontaneous pollination of the F_1 plants with foreign pollen caused by the insufficient isolation.

TABLE VI
Hair length in F_2 . Cross IV

Hair length in units of the micrometer scale	3	4	5	6	7	8	Total
Number of individuals	15	24	4			2	45

TABLE VII
The inheritance of the waxy bloom. Cross IV

	Waxless	Waxy	Total
Obtained	35	11	46
Expected (3:1)	34.5	11.5	46

$$\chi^2 = 0.36 \quad P = 0.80 - 0.90$$

As in the preceding cross, the formation of the waxy bloom is cheked by one inhibitory gene.

Cross V

N^o 3 c (ear glabrous, waxy) \times N^o 3 b β (ear pubescent, waxless).

The F_1 plants had waxless, pubescent ears. The presence or absence of the waxy bloom in F_2 plants was determined in the nursery before harvest. The results of countings are given in Table VIII:

TABLE VIII
Inheritance of the waxy bloom in F_2 . Cross V.

Family N ^o	Waxless	Waxy	Total
10/29	61	3	64
10/31	47	4	51
Total	108	7	115
Expectation (15:1)	107.81	7.19	115

$$\chi^2 = 0.008 \quad P = 0.90 - 0.95$$

The hair length was measured after the harvest on the ripe plants. Some of the F_2 plants, damaged during storage, have not been taken into account (Table IX).

TABLE IX
Inheritance of the glume pubescence. Cross V.

Generation	Hair length in units of the micrometer scale									Total
	3	4	5	6	7	8	9	10	11	
N ^o 3 c	10									10
P_1 N 3 b β						1	1	3	3	8
F_1					3	3				6
F_2 Waxless	8	15	4	14	19	13	6	7	4	90
F_2 Waxy	1	6								7
Total	9	21	4	14	19	13	6	7	4	97

In this cross the ratio waxless to waxy was 15:1 thus indicating that the waxless type is here conditioned by two polymeric inhibitory genes. At the same time it is interesting that all the waxy plants were »glabrous«. Thus the F_2 consisted of only 3 phenotypes: waxless pubescent, waxless glabrous and waxy glabrous in a ratio 67:23:7, very close to 12:3:1. Such a segregation indicates that one of the wax inhibitory genes is linked with the gene for glume pubescence.

Cross VI and VII

N^o 3 c (ear waxy, glabrous) \times N^o d α (ear waxless, pubescent).
N^o 3 d γ (ear waxless, pubescent) \times N^o 3 c (ear waxy, glabrous).

The F_1 obtained from the first cross consisted of 14 plants, that of the second cross of one plant. Both crosses gave similar results and are treated together. The F_1 individuals were waxless and pubescent, their hair length being intermediate (Tab. X). The F_2 exhibited segregation into two at first sight easily distinguishable types: »glabrous« (small scabrid hairs 2–5 units long) and »pubescent« (hairs longer than 7 units of the scale), in a ratio of 1:3. All the pubescent plants were waxless, all the glabrous were covered with waxy bloom (Table XI).

TABLE X
Hair length in the varieties N° 3 c, N° 3 d and in F_1

	Hair length in units of the micrometer scale																	Mean
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
N° 3 c	3	7																3.7
N° 3 d α											1		4	2	1	1	1	15.9
F_1							1	3	5	3								10.8

TABLE XI

Segregation of the waxy bloom and hairiness in F_2 . Crosses VI and VII

Cross	Family N°	Waxless		Waxy		Sum
		pubescent	glabrous	pubescent	glabrous	
3c \times 3d α	12/41	12	—	—	3	15
"	13/41	40	—	—	6	46
"	14/41	26	—	—	12	38
"	15/41	8	—	—	3	11
"	16/41	25	—	—	13	38
"	17/41	21	—	—	6	27
"	18/41	22	—	—	10	32
"	19/41	35	—	—	6	41
"	20/41	61	—	—	12	73
"	21/41	18	—	—	3	21
"	22/41	13	—	—	4	17
"	41/41	97	—	—	41	138
3d γ \times 3c	23/41	35	—	—	13	48
Total		413	—	—	132	545
Expected (3:1)		408.75	—	—	136.25	545

$$\chi^2 = 0.57, \quad P = 0.30 - 0.50$$

Both crosses thus showed a complete linkage of the glume pubescence with the absence of the waxy bloom and vice versa. The distribution of the F_2 individuals between the different hair length classes is given in Table XII. The hair length curve is distinctly trimodal and the frequency distribution is very close to the simple monohybrid ratio 1:2:1 thus indicating that one pair of factors for hairiness is involved.

Iwata (1938) has described a similar hybrid made between two varieties of *Aegilops triuncialis* sent by the author to the

TABLE XII
Hair length in F_2 . Cross VI

Number of F_2 plants	Hair length in units of the micrometer scale											Sum
	2-3	4-5	6-7	8-9	10-11	12-13	14-15	16-17	18-19	20-21	22-23	
	68	10	0	7	96	78	25	49	19	4	3	359

Genetical Department of the College of Science in Kyoto. From the cross: subvar. *hispida* (N^o 3 d a). × subvar. *glauca* (N^o 3 c) an F_2 generation was raised, composed of 51 waxless and 13 waxy individuals. This distribution agrees quite well with the ratio 3:1.

Cross VIII

N^o 3 c (ear waxy, glabrous) × N^o 3 b γ (ear waxless, pubescent). This cross was analogous to the crosses VI and VII and gave similar results. The female parent was waxy and »glabrous« (rare scabrid hairs 2—3 units long), the male parent was waxless and characterised by long (17—21 units) glume hairs. In F_2 two main types appeared: waxless pubescent and waxy glabrous in the 3:1 ratio. Again the linkage between the two characteristics was complete. Apparently the strains 3 b γ and 3 d contain the same gene which inhibits the wax formation. The results of this cross are presented in Tables XIII and XIV.

TABLE XIII

Segregation of waxy bloom and pubescence in F_2 . Cross VIII

	Hair length in units of the micrometer scale										Sum
	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	
Waxless				21	34	9	2	20	6	2	94
Waxy	33	2									35
Total	33	2		21	34	9	2	20	6	2	129

TABLE XIV

	Number of F_2 individuals		Sum
	waxless pubescent	waxy glabrous	
Obtained	94	35	129
Expected (3:1)	96.75	32.25	129

$$\chi^2 = 0.31, \quad P = 0.50-0.70$$

Cross IX

N^o 3 b α (ear waxless, glabrous) \times N^o 3 b γ (ear waxless, pubescent). Both parental strains were investigated previously in other crosses. According to the results of the Cross IV the strain 3 b α contains one factor inhibitory for wax formation which is not linked with the factor for pubescence, the strain 3 b γ , as shown in Cross VIII, contains probably another wax inhibitory gene. It was therefore expected that the F_2 generation of the hybrid between these two waxless strains would segregate in waxless and waxy according to the 15:1 ratio. The results presented in Tables XV and XVI show that our suppositions were right. The F_2 generation consisted of 12/16 waxless pubescent, 3/16 waxless glabrous and 1/16 waxy glabrous individuals. The linkage between the waxy bloom and glabrousness was very distinct.

The hair length in Crosses VIII and IX shows a trimodal frequency curve and corresponds to the simple Mendelian ratio: 1 glabrous: 2 short haired: 1 long haired.

TABLE XV

Segregation of the waxy bloom and glume pubescence in F_2 . Cross IX

	Hair length in units of the micrometer scale										Sum
	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	
Waxless	27	1	1	10	36	22	12	10	19	2	140
Waxy	10										10
Total	37	1	1	10	36	22	12	10	19	2	150

TABLE XVI

	Number of F_2 individuals				Sum
	waxless pubescent	waxless glabrous	waxy pubescent	waxy glabrous	
Obtained	112	28	0	10	150
Expected (12:3:0:1)	112.500	28.125	0.000	9.375	150

$$\chi^2 = 0.04, \quad P > 0.99$$

Discussion

In the investigated crosses between different varieties of *Aegilops triuncialis* the following facts were established in respect of the inheritance of the glume pubescence and wax formation:

The waxy bloom was always inherited as a recessive character. The F_2 segregated according to the 3:1 ratio waxless to waxy in the following crosses:

Cross	II: 3 g β (waxy) \times 3 g α (waxless)
"	III: 3 g α (waxless) \times 3 c (waxy)
"	IV: 3 c (waxy) \times 3 b α (waxless)
"	VI: 3 c (waxy) \times 3 d α (waxless)
"	VII: 3 d γ (waxless) \times 3 c (waxy)
"	VIII: 3 c (waxy) \times 3 b γ (waxless).

In crosses V (3 c — waxy \times 3 b β — waxless) and IX (3 b α — waxless \times 3 b γ — waxless) the F_2 generation segregated in a ratio of 15 waxless to 1 waxy.

The lack of waxy bloom is due to the action of the inhibitory genes. Apparently the strain 3 b β used in the Cross V contains two polymeric inhibitory gene while in the other waxless strains only one such gene is present.

The pubescence of the glumes is dependent upon a single partially dominant factor H . Therefore the crosses between hairy and glabrous segregate in a ratio of 1 HH :2 Hh :1 hh . The crosses between glabrous strains give glabrous F_1 and F_2 generation (Cross IV), the crosses between the pubescent forms give only pubescent offspring (Cross II).

In Cross III (3 g α — pubescent, waxless \times 3 c — glabrous waxy) pubescence and wax segregated independently, which proves that the wax inhibiting factor which may be designated as Z_2 is not linked with the factor H . On the contrary, in Crosses VI, VII and VIII, the pubescence and the lack of the waxy bloom were absolutely linked and vice versa. It is evident that the strains 3 d and 3 b γ contain another wax inhibiting factor- Z_1 , which is linked with the H -factor for hairiness.

In the Cross V (3 c — waxy glabrous \times 3 b β — waxless pubescent) three main phenotypes appeared in F_2 : waxless pubescent, waxless glabrous and waxy glabrous in the 12:3:1 ratio thus indicating that the strain 3 b β contains two factors inhi-

biting the wax formation: Z_1 linked with the H -factor and Z_2 segregating independently. A quite similar segregation i.e. 12 waxless pubescent: 3 waxless glabrous: 1 waxy glabrous was observed in cross IX between the strains $3b\alpha$ and $3b\gamma$. Each parental waxless form contain evidently different wax inhibitory gene.

In the brief communication of 1941 the author admitted the incomplete linkage between the wax inhibitory gene Z_1 and the gene for glume pubescence H , with 4—6 cross over percentage. This supposition made on the basis of the preliminary observations appeared to be incorrect and was caused by an experimental error and the wrong classification of some F_2 plants. The repeated, carefully controlled crossing experiments described above showed absolute linkage of the two named factors and no individuals with recombined characters have been found.

On the basis of the analysis given above, the genic formulae of the investigated strains of *Aegilops triuncialis* may be designated as follows:

- $N^0 3b\alpha$ — $z_1 Z_2 h$ (waxless, glabrous)
- $N^0 3b\beta$ — $Z_1 Z_2 H$ (waxless, pubescent)
- $N^0 3b\gamma$ — $Z_1 z_2 H$ (waxless, pubescent)
- $N^0 3c$ — $z_1 z_2 h$ (waxy, glabrous)
- $N^0 3d$ — $Z_1 z_2 H$ (waxless, pubescent)
- $N^0 3g\alpha$ — $z_1 Z_2 H$ (waxless, pubescent)
- $N^0 3g\beta$ — $z_1 z_2 H$ (waxy, pubescent)

Multiple alleles of glume pubescence

It has been previously stated that among the varieties of *Aegilops triuncialis* three different types of glume surface may be distinguished:

- 1) long haired — hairs about 0.7 mm long, represented by the strains $3b\gamma$ and $3d$,
- 2) short haired — hairs about 0.4 mm long, represented by the strain $3b\beta$,
- 3) the hird type, designated as »glabrous« with only minute scabrid hairs, no longer than 0.15 mm. Here belong the strains $3b\alpha$ and $3c$. These three types are presented in Fig. 1.

It has been proved that all these types of hairiness breed true and remain constant when isolated during several generations.

Three strains: $3b\alpha$, $3b\beta$ and $3b\gamma$, representing all the three types of glume hairiness, were chosen for the crossing experiments

and crossed in the three different combinations: long haired \times glabrous, long haired \times short haired and short haired \times glabrous.

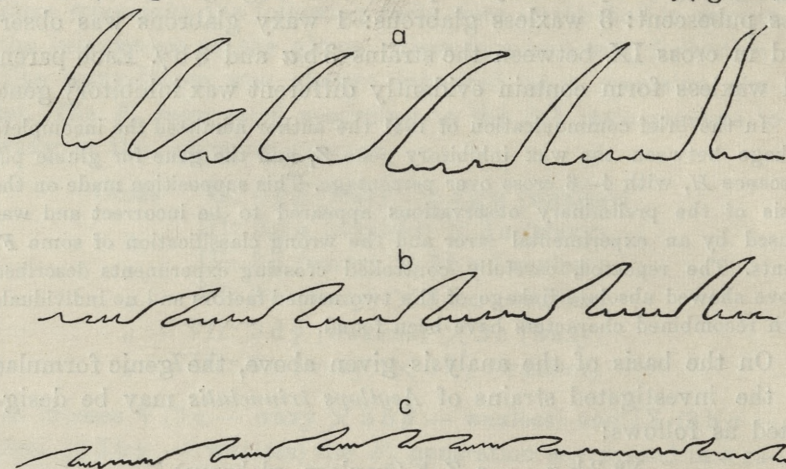


Fig. 1. Types of the glume surface in *Aegilops triuncialis* L.
a) N° 3b γ (long haired) b) N° 3b β (short haired) c) N° 3b α («glabrous».)
Magnification about 35 \times

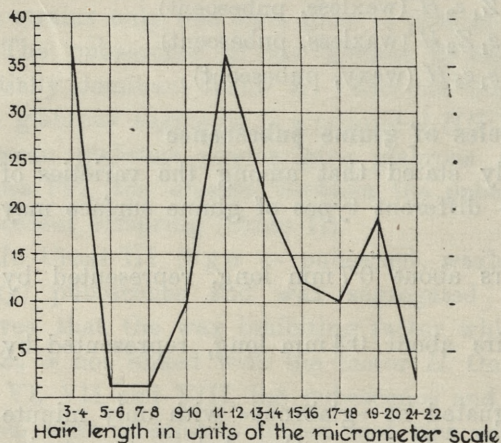


Fig. 2. Segregation of the hair length in F_2 of the Cross IX (glabrous \times long haired).

the Table XV and in Fig. 2. As was already mentioned, the frequency curve is distinctly trimodal, the ratio hairy to glabrous being 3:1. A similar segregation was observed in Crosses VI, VII and VIII (Tables XII and XIII).

Cross IX

N° 3b α (glabrous) \times
 \times N° 3b γ (long haired).

The results of this cross have been already described above. The hair length of the female parent was 3–5 units of the micrometer scale, that of the male parent 17–21 units. The character of the F_1 plants was exactly intermediate (11–12 units), the F_2 generation segregated as shown in

Cross X

N^o 3b β (short haired) \times N^o 3b γ (long haired).

The hairs of the short haired form had a length of 8—11 units of the micrometer scale, the F_1 plants were intermediate (14—16 units). F_2 exhibited again monohybrid segregation, the long haired type being partially dominant. The results are presented in Table XVII, and in Fig. 3.

TABLE XVII
Segregation of the hair length in F_2 . Cross X

Generation	Hair length in units of the micrometer scale													Sum			
	7	8	9	10	11	12	13	14	15	16	17	18	19		20	21	
3b γ												1	2	2	3	1	9
3b β		2	5	2	1												10
F_1							1		2								3
F_2	4	9	15	7	2	10	18	12	23	17	21	13	13	4	1		169
Expected (1:3)			37						132								169
			42.25						126.75								

$$P = 0.30 - 0.50$$

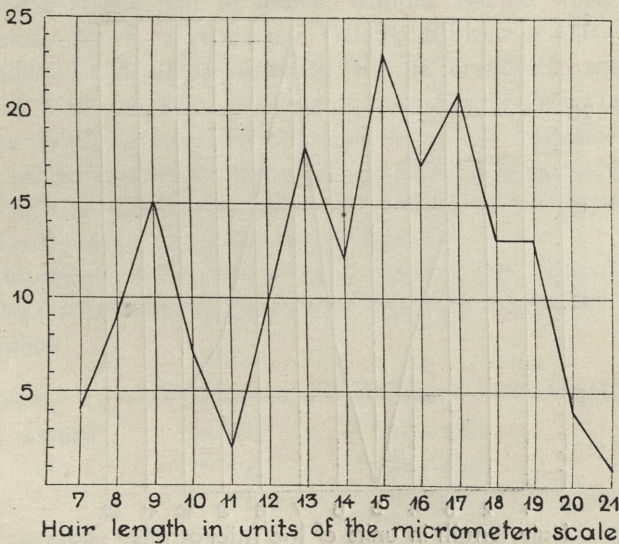


Fig. 3. Segregation of the hair length in F_2 of the Cross X (short haired \times long haired).

Cross XI.

N^o 3 b α (glabrous) \times N^o 3 b β (short haired).

The results of this cross are presented in Table XVIII, and in Fig. 4.

TABLE XVIII
Segregation of the hair length in F_2 , Cross XI

Generation	Hair length in units of the micrometer scale									
	3	4	5	6	7	8	9	10	11	Sum
3 b α	1	7	2							10
3 b β						2	5	2	1	10
F_1					1	1	1			3
F_2	14	8	0	8	24	15	8	5		82
Expected (1:3)	22				60					82
	20.5				61.5					

$$P = 0.70 - 0.80$$

The F_1 were intermediate, but more similar to the pubescent parent (hair length 7—9 units), the F_2 segregated in hairy and glabrous according to the monohybrid ratio (3:1). Similar results were obtained from the Cross V (Table IX).

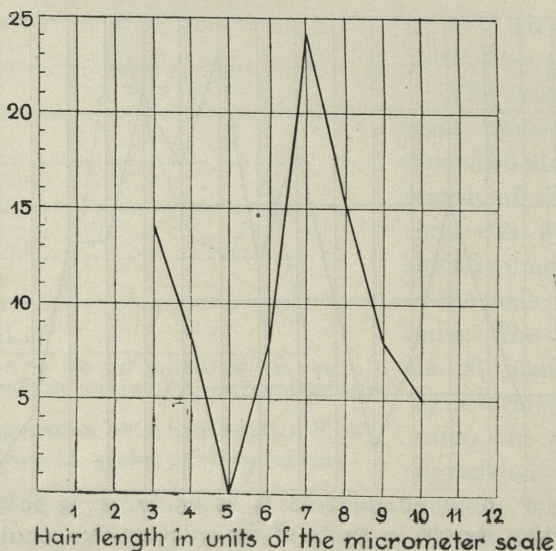


Fig. 4. Segregation of the hair length in F_2 of the Cross XI (glabrous \times short haired).

As demonstrated above, the crosses between the three different types of glume hairiness give all monohybrid segregations. Thus it is evident that the degree of hairiness is controlled by a system of multiple alleles.

The following symbols are proposed for the above indicated alleles: H — long haired, H^s — short haired, h — »glabrous«.

The existence of multiple allelism concerning the factors which are responsible for the development of the hairs on the epidermis has already been established in different plant species, so e. g. in *Matthiola incana* by Saunders (1930), in *Triticum* by Nilson Ehle (1920), in *Galeopsis pubescens* by Müntzing (1939).

Awn length

In the previous papers (1926, 1933) we have presented the results of the investigations concerning the inheritance of the awning in *Aegilops speltoides* Jaub. et Sp. It has been stated that the awned condition of the lateral spikelets peculiar to the var. *ligustica* is completely dominant over the awnless type *aucheri*, the difference between these two varieties being dependent upon a single pair of genes. Similar results were obtained subsequently by Schiemann (1928), Kihara and Lilienfeld (1932). In *Aegilops speltoides* the differences in awning are concerned with the awn development on the flowering glumes, the empty glumes being awnless in all varieties of that species. In *Ae. triuncialis* the main varietal differences in awning are due to the different number and length of the awns or awn-like projections on the empty glumes.

As described above, there were isolated the following types of *Aegilops triuncialis* in respect of the awn length of the lateral spikelets:

Type	Variety	Average awn length in mm
1. Fully awned	N ^o 3 b	37—43
„	N ^o 3 g	35—45
„	N ^o 3 d γ	40—60 (Fig. 7 — a)
2. Short awned	N ^o 3 d β	20—35 (Fig. 7 — b)
3. Awnless	N ^o 3 c	4—5
„	N ^o 3 d α	3—7 (Fig. 7 — c)

For the study of the inheritance of the awn character the following crosses were taken into account:

Cross III: N° 3 g (fully awned) × N° 3 c (awnless)

Cross VII: N° 3 d γ (fully awned) × N° 3 c (awnless)

Cross XII: N° 3 d α (awnless) × N° 3 d γ (fully awned)

Cross XIII: N° 3 d β (short awned) × N° 3 d γ (fully awned).

The measurements of the awn length were made on three well developed spikes per plant and the longest lateral awn was always measured. From these three measurements the mean length for each plant was calculated. The results of the measurements of P_1 , F_1 and F_2 generations are presented in Tables XIX, XX, XXI and XXII. The F_2 segregation of the Crosses III, XII and XIII is also shown in the form of the frequency curves on Figs. 5 and 6.

TABLE XIX

The inheritance of the awn length. Cross III
(fully awned × awnless)

Generation	Awn length in mm										Sum
	0	5	10	15	20	25	30	35	40	45	
P_1 3 g α									6	4	10
P_1 3 c	3										3
F_1			1	2							3
F_2	1	6	12	12	16	20	20	11	2		100

TABLE XX

The inheritance of the awn length. Cross VII
(fully awned × awnless)

Generation	Awn length in mm												Sum
	0	5	10	15	20	25	30	35	40	45	50	55	
P_1 3 d γ										2	4	1	7
P_1 3 c	5												5
F_1			1										1
F_2	4	11	5	8	6	4	2	3	1		2		46

TABLE XXI

The inheritance of the awn length. Cross XII
(awnless \times fully awned)

Generation	Awn length in mm											Sum	
	0	5	10	15	20	25	30	35	40	45	50		55
P_1 3 d α		4	1										5
P_1 3 d γ										2	3		5
F_1				1									1
F_2	16	69	34	28	32	24	22	18	17	17	9	1	287

TABLE XXII

The inheritance of the awn length. Cross XIII
(short awned \times fully awned)

Generation	Awn length in mm									Sum
	20	25	30	35	40	45	50	55	60	
P_1 3 d γ		1	4							5
P_1 3 d β						2	3			5
F_1				1						1
F_2	17	19	39	53	32	27	34	8		229

Two crosses between fully awned and awnless (VII, XII) showed a distinct preponderancy of the shorter awned type, in the two other crosses the inheritance was rather intermediate although in the Cross III the greater part of the F_2 individuals belonged to the longer awned forms.

Vavilov and Jakushkina (1925) and Lepin (1930) have found that in hybrids between the tetraploid wheat species the length of the apical tooth of the empty glume is dependent upon a number of cumulative genes, the short tooth being dominant over the long one. Two of the above

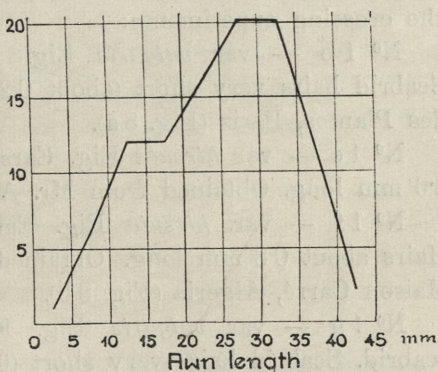


Fig. 5. The segregation of the awn length in F_2 of the Cross III (fully awned \times awnless).

described crosses show a similar partial dominance of the short awn (tooth) in the other two crosses no distinct preponderance of either type was observed.

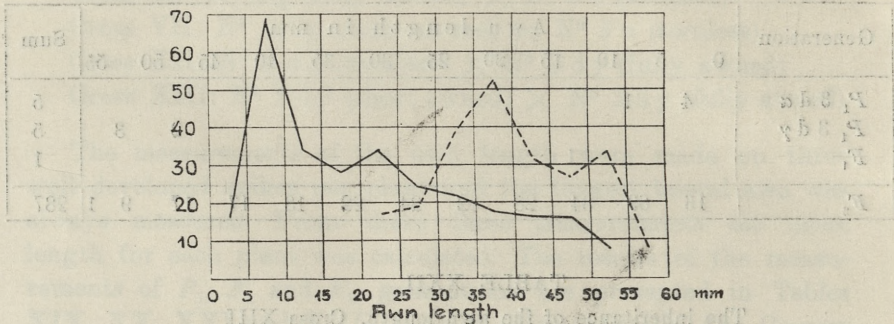


Fig. 6. Segregation of the awn length in F_2 of the Crosses XII and XIII.

— Cross XII (awnless \times fully awned).
 - - - - Cross XIII (short awned \times fully awned).

The detailed factorial analysis could not be done without examination of the F_3 generation and it is not certain whether the different awn dimensions are caused by the combination of the cumulative factors or by a series of multiple alleles.

C. Crosses within *Aegilops ovata* L.

Inheritance of glume colour and pubescence

The following strains of *Aegilops ovata* L. were chosen for the crossing experiments:

N° 1 b — var *vulgaris* Eig. Ears white, slightly scabrid. Scabrid hairs very short (about 0.25 mm). Obtained from Jardin des Plantes, Paris (Fig. 8 a).

N° 1 e — var *hirsuta* Eig. Ears white, pubescent, hairs about 0.6 mm long. Obtained from Mr. A. Coupin, Tunis.

N° 1 f — var *hirsuta* Eig. Ears brownish-black, pubescent. Hairs about 0.8 mm long. Obtained from Prof. L. Ducellier, Maison Carré, Algeria (Fig. 8 b).

N° 1 g — var *vulgaris* Eig. Ears brownish-black, slightly scabrid. Scabrid hairs very short (0.25 mm). Obtained from Prof. L. Ducellier, Maison Carré, Algeria.

Two crosses were made and the inheritance of glume colour and pubescence was studied in F_1 and F_2 .

Cross XIV

N^o 1 b (ear white, scabrid) × N^o 1 f (ear black, pubescent).

The length of the glume hairs of the parent plants was 0.25 mm and 0.8 mm respectively. The F_1 plant had black and pubescent glumes like the male parent (hair length 0.8 mm). Thus the dominance of the black glume colour and hairiness was complete. The F_2 generation exhibited a segregation into four types of individuals, as shown in Table XXIII:

TABLE XXIII
Inheritance of glume colour and pubescence in F_2 . Cross XIV

	Black pubescent	Black scabrid	White pubescent	White scabrid	Total
Obtained	38	15	10	6	69
Expected (9:3:3:1)	38.75	12.95	12.95	4.35	69

$$\chi^2 = 1.29 \quad P = 0.70 - 0.80$$

Cross XV

N^o 1 g (ear black, scabrid) × N^o 1 c (ear white, pubescent).

The F_1 plant showed again a complete dominance of black colour and pubescence of the glumes (hair length 0.6 mm). In F_2 the following segregation was observed (Table XXIV):

TABLE XXIV
Inheritance of the glume colour and pubescence in F_2 . Cross XV

	Black pubescent	Black scabrid	White pubescent	White scabrid	Total
Obtained	16	8	8	3	35
Expected (9:3:3:1)	19.6	6.6	6.6	2.2	35

$$\chi^2 = 1.55 \quad P = 0.50 - 0.70$$

Both crosses gave similar results thus indicating that each of the characteristics studied i. e. the glume colour and the degree of glume pubescence is controlled by a single pair of genetic factors which segregate independently from each other.

Summary

The author gives a genetical analysis of several intervarietal crosses made within three *Aegilops* species: *Ae. ventricosa* Tausch., *Ae. triuncialis* L. and *Ae. ovata* L. The following characteristics were investigated: glume colour, pubescence of the glumes, waxy bloom on the ears and stems and awn length of the lateral spikelets.

Among the varieties of *Ae. ventricosa* two types of glume coloration were crossed: red and black. The F_1 generation had black glumes, the F_2 segregated into black and red according to the 3:1 ratio.

The author isolated several strains of *Ae. triuncialis* L. differing in the degree of the glume pubescence as well as in the development of the waxy bloom. The crosses waxy \times waxless gave always waxless F_1 generation, the waxy condition being recessive. One part of the crosses segregated in F_2 in a ratio of 3 waxless to 1 waxy, in one of these crosses a ratio of 15 waxless to 1 waxy was observed. Similar segregation exhibited one cross between two waxless strains. Thus the waxless condition is dependent upon one or two dominant polymeric genes.

The crosses between the pubescent and »glabrous« types showed the incomplete dominance of the pubescent glume surface. In the F_2 a segregation into pubescent and »glabrous« was observed according to the 3:1 ratio. Five crosses showed an absolute linkage of the waxy bloom with the absence of the glume pubescence while in the other two crosses no linkage was observed.

The results of the crossing experiments may be explained as follows: The pubescence of the glumes is dependent upon a single dominant factor H (the hh individuals are »glabrous«). The formation of the waxy covering is checked by one or two polymeric inhibitory genes Z_1 and Z_2 . One of these genes — Z_1 is linked with the H -gene for pubescence, the other — Z_2 is transferred independently.

Within the species *Aegilops triuncialis* three different true breeding types of glume surface were found: »glabrous«, short haired and long haired. The crossings between these three types made in the three different combinations i. e.: glabrous \times long

haired, glabrous \times short haired and short haired \times long haired showed that the three genes H , H^s and h which control the development of the glume hairs form together a series of multiple alleles. In all crosses the F_1 plants were almost intermediate and the F_2 generation segregated into 2 or 3 distinctly different types giving a bimodal or trimodal frequency curve of the hair length according to the 3:1 or 1:2:1 ratio.

The author isolated several strains of *Aegilops triuncialis* characterized by a different average length of the glume awns on the lateral spikelets. The crosses between the awnless and fully awned forms showed in F_2 in the majority of cases the preponderance of the shorter awned type. In the other crosses the inheritance of the awn length was rather intermediate. A detailed genetical analysis could not be done without examination of the F_3 generation.

The author crossed varieties of *Aegilops ovata* L. differing in glume colour (black or white) and in the degree of hairiness of the glume surface. In two different crosses there has been established a complete dominance of the black colour over the white and of the pubescent over the slightly scabrid glume surface. Each of these two pairs of characters appeared to be dependent upon a single pair of factors. In F_2 both characteristics segregated independently.

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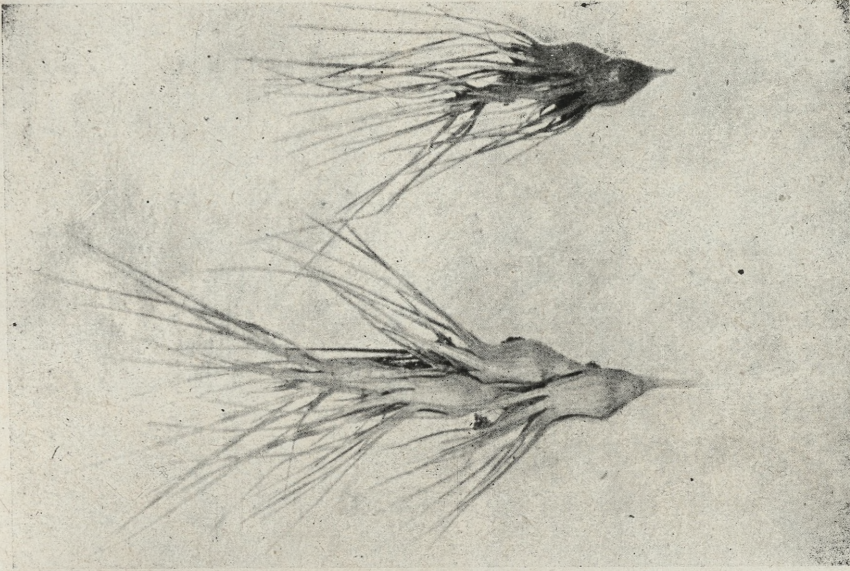
Explanation of plate

Fig. 7. a) *Aegilops triuncialis* L. fully awned (N° 3 d γ).

b) „ „ short awned (N° 3 d β).

c) „ „ awnless (N° 3 d α).

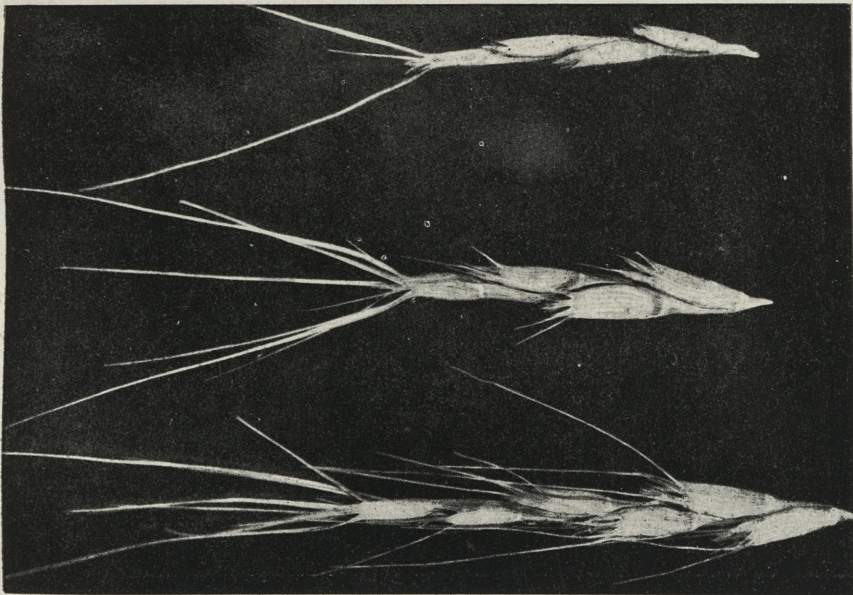
Fig. 8. *Aegilops ovata* L. (a—N° 1 b, b)—N° 1 f.



b

Fig. 8.

a



c

b

Fig. 7.

a

K. Miczyński

*Problem Heterozji. IV. Dziedziczenie bujnych rozmiarów.
The problem of Heterosis. IV. Inheritance of vigorous
growth.*

Mémoire

de M. E. MALINOWSKI m. t.

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1. Introduction

The examination of the F_2 generation of our kidney bean crosses has revealed the fact of transgressive inheritance regarding the size of plants and of their organs. We obtained in F_2 numerous individuals larger than the F_1 plants. In order to find out to what extent these differences are hereditary we isolated

some vigorous F_2 plants and raised their progeny in the following years.

As I have already pointed out in the first paper of this series, the F_1 plants of the cross *Phaseolus vulgaris melleus* × Inexhaustible Bean blossom much longer than the parental forms and the majority of the F_1 seeds ripen in this country only under favourable conditions, i. e. when the growing season is warm and rather dry. In the F_2 generation many individuals start blossoming much later than the F_1 plants, and such individuals either do not produce mature seeds at all or they give only a small number of ripe seeds.

It is difficult under normal conditions to get seeds from the largest F_2 plants because of their late blossoming. To obtain seeds we covered some late blossoming F_2 individuals with wooden boxes, giving them 8 or 10 hours of daylight. But we never know in advance which plant will be the most vigorous, and even the date of unfolding of the first flowers is not always correlated with the size of the plants. Besides it is too late to start covering the plants when they begin to flower. Our inbred strains therefore, which have been grown over a period of several years, cannot be considered as representing the highest vigour possible. In any case, in our own experiments some of the inbred families have proved more vigorous than the F_1 generation grown side by side for comparison. I reported this fact in my paper of 1924 and in a communication published in the Proceedings of the V Int. Gen. Congress in Berlin in 1928. Since 1928 I have carried out more extensive researches on the inheritance of vigorous growth in *Phaseolus vulgaris*.

I present in this paper the results of my investigations conducted both before and after the year 1928. These investigations cover 11 generations of vigorous plants. We have always chosen for our experiments on heterosis as uniform a piece of ground as possible. Some lines were grown in pots.

2. The F_3 generation

In 1926 we grew nine F_3 lines in the field. These lines were descended from the F_2 plants which were more vigorous than the F_1 individuals.

Some individuals of the F_3 generation grown in the field surpassed the largest F_1 plants both in height and in the length of their terminal leaflets. But no one F_3 plant weighed more than 180 g, the F_1 plants attaining 185 g and even 200 g. As has been pointed out we weighed the dry plants without their leaves and seeds.

The largest F_3 lines have been on an average smaller than the F_1 generation grown side by side with them. There were however always relatively numerous plants in the F_3 lines which displayed

TABLE I

Statistics of the height of the F_3 and F_4 lines grown in the field in 1926 and 1927

F_3 lines (1926)					F_4 lines (1927)				
N ^o of line	<i>n</i>	\bar{x}	μt	<i>s</i> ^o / _o	N ^o of line	<i>n</i>	\bar{x}	μt	<i>s</i> ^o / _o
808	21	47.86	7.07	31.69	292	30	61.00	6.53	28.19
843	23	49.78	9.55	43.37	592	28	71.43	6.98	24.74
211	39	43.34	4.74	33.50	134	40	63.75	6.90	33.59
184	53	70.94	7.58	38.52	129	13	64.62	14.52	35.72
160	51	70.20	6.19	31.19	938	51	82.94	6.42	27.36
22	76	54.87	4.81	38.24	901	14	75.00	15.81	35.19
93	117	64.36	4.10	34.66	349	29	46.21	5.51	30.82
232	126	68.73	3.81	31.34	499	24	54.58	4.66	19.77
216	4	71.25	0.60	45.59	<i>Phas. v. melleus</i>	22	35.00	2.65	16.68
					<i>Inexhaustible</i>	18	60.00	3.41	11.11

the same or even a more pronounced vigour as the F_1 individuals. So, for instance, the average length of terminal leaflets of line N^o 232 was 13.57 cm, the average length of F_1 being 17.33 cm (Table II). But in line N^o 232 there were several individuals in which the leaflets were on an average 18 cm long or even more. Eight of the above-described F_3 lines were also grown in pots in 1926. The results obtained under such conditions have been similar to those found in the field. Some individuals of the F_3 lines Nos. 184 and 506 grown in pots in 1926 are shown in the Plates 2 and 3 together with the F_1 plant and two individuals of the parental varieties (Fig. 10). All plants shown in the Plates mentioned were photographed to the same scale.

In 1926 we had 6 F_1 plants grown in the field. One was exceptionally large, the weight of its dry vines being 250 g. The number of the internodes of this plant was 491 and its height 110 cm. Another F_1 plant of that season, weighing 150 g, had only 259 internodes; it was intermediate as to the vigour, its height being 90 cm. Some F_3 plants of the line N° 184 were composed of a larger number of internodes. So, for instance, the plant, the dry vines of which weighed 170 g, had 560 internodes

TABLE II

Statistics of the length of terminal leaflets of F_3 and F_4 grown in the field in 1926 and 1927

F_3 lines (1926)					F_4 lines (1927)				
N° of line	n	\bar{x}	μt	$s\%$	N° of line	n	\bar{x}	μt	$s\%$
808	21	12.67	1.35	22.90	292	30	12.50	0.77	16.23
843	23	12.43	1.47	26.71	592	28	13.21	0.50	9.56
211	52	13.98	0.87	22.25	134	40	15.05	0.93	19.20
184	53	14.87	0.76	18.53	129	13	14.08	1.49	16.83
160	52	14.42	0.83	20.59	938	51	16.00	0.75	16.65
22	76	13.41	0.70	22.71	901	14	15.29	1.82	19.85
93	118	13.50	0.54	21.96	349	28	13.14	0.57	10.90
232	124	13.57	0.61	21.71	499	24	15.00	0.97	15.03
216	4	17.50	5.28	16.41	<i>Phas. v. melleus</i>	22	11.09	0.47	9.38
					Inexhaustible	18	12.17	0.55	8.77

(its height being 139 cm). It is shown in Fig. 1. This was one of the largest of the F_3 plants grown in the field and the other numbers of internodes obtained that year were: 405 for a plant weighing 145 g and 150 cm high (from line N° 184), 448 internodes for a plant weighing 97 g and 75 cm high (from line N° 22) and so on.

Statistics of the height of the F_3 lines grown in the field in 1926 are given in Table I, those of the length of the terminal leaflets and the weight of dry vines are shown in Tables II and III respectively.

As to the plants in pots, they had on the average a smaller number of internodes. In 1926 we grew in pots the same F_3

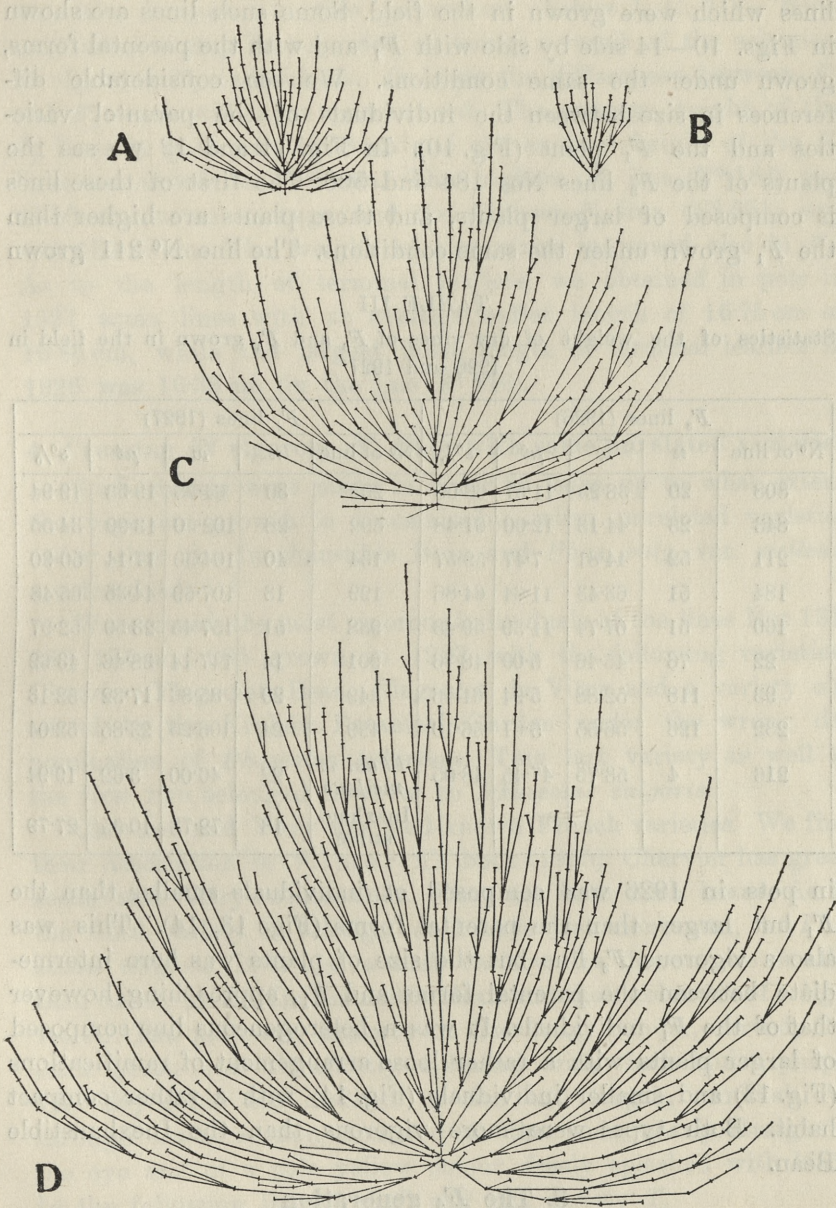


Fig. 1. Diagrams showing all internodes of the following plants grown in the field in 1926: A — Inexhaustible Bean, B — *Phas. vulg. melleus*, C — F_{17} , D — one of the F_3 plants. All diagrams drawn to the same scale.

lines which were grown in the field. Some such lines are shown in Figs. 10—14 side by side with F_1 and with the parental forms, grown under the same conditions. We see considerable differences in size between the individuals of the parental varieties and the F_1 plant (Fig. 10). In Fig. 11 and 12 we see the plants of the F_3 lines Nos 184 and 506. The first of these lines is composed of larger plants, and these plants are higher than the F_1 grown under the same conditions. The line N° 211 grown

TABLE III

Statistics of the weight of dry vines of F_3 and F_4 grown in the field in 1926 and 1927

F_3 lines (1926)					F_4 lines (1927)				
N° of line	n	\bar{x}	μt	$s^0/0$	N° of line	n	\bar{x}	μt	$s^0/0$
808	20	38.25	11.57	63.00	292	30	64.33	19.53	19.94
843	23	44.13	12.00	61.48	592	28	102.50	13.99	34.55
211	52	44.81	7.47	59.57	134	40	104.50	17.14	50.90
184	51	63.43	11.64	64.86	129	13	107.69	44.35	65.48
160	51	67.74	11.39	59.43	938	51	157.45	23.59	52.97
22	76	45.46	5.09	48.76	901	14	147.14	38.46	43.62
93	118	52.88	5.94	61.46	349	29	85.86	17.32	52.13
232	126	56.55	5.61	56.10	499	24	106.25	23.85	52.04
216	4	53.75	47.45	48.05	<i>Phas. v. melleus</i>	22	40.00	3.62	19.94
					Inexhaustible	18	72.78	10.35	27.79

in pots in 1926 was composed of individuals smaller than the F_1 but larger than the parental forms (Figs 13, 14). This was also a vigorous F_3 line but the size of plants was here intermediate between the parental forms and F_1 , approaching however that of the F_1 individuals. It was a heterogeneous line composed of larger plants with a rather loose arrangement of ramifications (Fig. 13) and smaller individuals (Fig. 14) with a rather compact habit. Both types were more vigorous than the Inexhaustible Bean.

3. The F_4 generation

The eight F_4 lines grown in 1927 in the field proved on an average a little higher than the F_3 lines of the previous year. The weight of the plants and the total number of internodes

were also increased in this generation (Tables I, II, III). Such a difference may be regarded as being a result of the selection of vigorous F_3 individuals. In pots the differences between F_4 and F_3 were still more pronounced. The average height of the F_3 lines in pots was 78.58 cm and the average height of the F_4 lines amounted to 99.69 cm. The highest F_3 line (N^o 184) was 99.50 cm on an average and the highest F_4 line (N^o 251) was 154.28 cm. The weight of dry vines increased also in F_4 . As to the length of terminal leaflets, we obtained in pots in 1927 some lines with an average leaflet length of 16.75 cm or 16.86 cm, while the largest mean length of terminal leaflets in 1926 was 16.36 cm (in the line N^o 216).

4. Crossing of vigorous F_4 lines with some unrelated varieties

Such crosses were made in order to learn up to what extent the vigorous growth is transmissible when unrelated varieties (other than the Inexhaustible Bean and *Phas. vulg. var. melleus*) are involved.

We crossed the most vigorous individuals of the lines Nos 131, 132, 174 and 205 grown in 1927 with the following varieties: Chevrier Flageolet Bean, Flageolet de Vitry and a variety obtained by the Kraków Botanical Garden under the wrong denomination of *Phaseolus tuberosus*. This last variety as well as the first two belonged however to *Phaseolus vulgaris*.

Chevrier and Vitry are well-known French varieties. We find their description in Vilmorin's book (1925). Chevrier has green seeds and Vitry white ones. They are both bush beans. As to the third variety it belongs, as I have just mentioned, to *Phaseolus vulgaris*. It is also a bush variety. Its flowers are smaller than those of the Inexhaustible Bean and their colour is of a light violet. The pods are uniform in size, long, slender, curved, flat, dark green and abundantly splashed with dark bluish purple. The dry seeds are medium in size and length, roundish oval through cross section, rounded at the ends, nearly straight at the eye and of a pale yellow colour, freely splashed with black. In the following lines I shall call this variety *T*.

The four characters described in connection with hybrid vigour, namely the size of leaves, the height of plants, the weight of dry vines and the time of flowering were similar in the above

varieties and they did not differ much from the Inexhaustible Bean and *Phas. vulg. melleus*. This is seen from Tables IV and V. The most important difference concerns the length of the terminal leaflets, which are larger in Vitry than in the Inexhaustible Bean and *Phas. vulg. melleus* (Table IV).

The F_1 plants obtained in 1928 from the crossing of particular vigorous F_4 lines with the varieties described above exhibited much similarity with the F_1 generation of hybrids between the Inexhaustible Bean and *Phas. vulg. melleus*. The variability of the particular characters however was much larger in the former case. This indicates that the F_4 lines in question were not homozygous. The F_1 generation of the cross 131 \times Vitry exhibited larger leaves than the F_1 plants of the cross *Phas. vulg. melleus* \times Inexhaustible Bean (Tabl. IV).

In F_2 we have grown only 4 lines being the progeny of the following crosses: 1) 131 \times Vitry, 2) 132 \times variety *T*, 3) 205 \times variety *T* and 4) variety *T* \times 205.

There were differences in the degree of vigour between these lines. The progenies of the first (131 \times Vitry) and of the second (132 \times variety *T*) crosses were on an average more vigorous than that of the fourth cross (variety *T* \times 205). And it is interesting to note that all characters concerning vigour were enlarged proportionally. From the Table V it is seen that the average height of the F_2 plants of the three crosses in question was 114.29 cm, 107.17 cm and 73.09 cm respectively, the average weight of dry vines was 233.33 g, 208.00 g and 124.09 g respectively and the average length of terminal leaflets 21.32 cm, 20.08 cm and 15.82 cm. It would be difficult to attribute to mere chance such an association of the characters in question in all three cases and possibly this phenomenon might be looked upon as a manifestation of factors determining a simultaneous increase of all characters of heterosis.

The results of our experiments carried out in pots in 1928 agree with those just described for the experiments in the field. The height of plants as well as the length of terminal leaflets proved to be larger in F_1 obtained from the crosses between the F_4 lines and the unrelated varieties than in F_1 of the cross *Phas. vulg. melleus* \times Inexhaustible Bean. The average height of F_1 of the cross *Phas. vulg. melleus* \times Inexhaustible Bean was 67.50 cm

TABLE IV
 Statistics of the F_1 generation of the crosses between vigorous F_4 individuals and some unrelated varieties

	Height of plants				Length of leaflets				Weight of vines			
	n	\bar{x}	μt	$s^0/\%$	n	\bar{x}	μt	$s^0/\%$	n	\bar{x}	μt	$s^0/\%$
<i>Phas. vulgaris melleus</i>	38	26.32	1.93	22.09	38	9.55	0.37	11.69	38	20.79	1.92	27.88
Inexhaustible Bean	25	38.80	3.00	18.32	25	11.12	0.40	8.56	25	36.80	3.09	19.92
<i>Phas. vulgaris</i> , variety <i>T</i>	25	29.20	2.36	19.12	26	11.08	0.36	7.89	26	24.62	3.28	32.33
Vitry	20	32.50	2.57	16.50	20	13.75	0.80	12.14	20	32.00	3.59	23.39
F_1 — <i>Phas. vulg. melleus</i> \times Inexh.	5	106.00	6.80	4.62	5	20.20	0.56	1.98	5	100.00	23.23	16.73
F_1 —132 \times Vitry	9	66.67	17.61	32.40	10	20.10	2.27	15.00	9	76.67	25.49	40.79
F_1 —131 \times Vitry	3	116.67	37.95	10.69	3	23.00	6.57	9.39	3	103.33	75.90	24.14
F_1 —132 \times variety <i>T</i>	17	82.94	16.54	37.62	17	18.59	2.13	21.60	16	85.00	22.43	47.97
F_1 —variety <i>T</i> \times 132	2	70.00	127.06	14.29	2	16.00	12.71	6.25	—	—	—	—
F_1 —variety <i>T</i> \times 131	5	74.00	11.00	10.81	5	16.60	3.12	13.52	5	86.00	11.10	9.30
F_1 —variety <i>T</i> \times 174	8	75.00	6.32	9.43	8	17.25	0.97	6.32	8	91.25	5.36	6.57
F_1 —variety <i>T</i> \times 205	2	85.00	127.06	5.88	2	18.50	31.76	13.51	—	—	—	—
F_1 —205 \times variety <i>T</i>	5	84.00	25.74	22.08	5	18.40	2.08	8.13	5	110.00	45.61	29.88

and the cross 205 \times variety *T* exhibited in F_1 an average height of 86.67 cm.

As to the leaf size the length of the terminal leaflets of F_1 of the cross *Phas. vulg. melleus* \times Inexhaustible Bean in pots was 15.50 cm and in the cross 131 \times Vitry it amounted to 17.40 cm on an average.

The range of variation of F_2 was larger than that of F_1 and in this generation (which was grown only in the field in 1929) numerous plants appeared to be much more vigorous than the F_1 individuals of the previous year.

The largest number of internodes obtained in F_2 grown in the field was 552 for the cross 131 \times Vitry and 559 for the cross 132 \times variety *T*. The F_1 plants grown in ground in 1928 possessed the following numbers of internodes: 203 in the cross 131 \times Vitry and 262 in the cross 132 \times variety *T*. The number of internodes of the two varieties used in these crosses were as follows: in Vitry 42 in 1928 and 112 in 1929 and in the variety *T* 64 in 1928 and 85 in 1929. The variability of the number of internodes ranged in F_2 from 93 to 552 in the cross 131 \times Vitry and from 141 to 559 in the cross 132 \times variety *T*. In spite of a relatively small number of F_2 plants (21 individuals in the cross 131 \times Vitry and 60 in the cross 132 \times variety *T*) we obtained in this generation very vigorous individuals exceeding twice the F_1 generation of the preceding year as to the number of internodes and nearing in this respect the most vigorous plants ever met with in our experiments.

Fig. 15 b shows an F_1 plant obtained in 1928 after crossing a vigorous F_4 plant (line 174) with var. Chevrier. This plant (Fig. 15 b) is more vigorous than the plants of the line N° 174 (Fig. 15 c, d, e). In Fig. 15 a the variety Chevrier is shown. Fig. 16 shows the dry vines of 2 F_1 plants (Fig. 16 C, D) of the cross between F_4 and the variety *T*, and also the dry vines of 2 F_1 plants (Figs. 16 G, H) of the cross Vitry \times F_4 . In Fig. 17 we see a row of F_1 plants of the cross variety *T* \times F_4 , grown in the field and also some plants of the variety *T*. In Fig. 18 the dry vines of vigorous plants of the F_2 generation are shown. These F_2 plants (Fig. 18 A, B) were obtained in 1929 from the cross Vitry \times F_4 . We also see a small F_2 plant, an F_2 segregate (Fig. 18 C). Fig. 18 D represents the dry vines of Vitry. In Fig. 19

TABLE V
 Statistics of the F_2 generation of the crosses between vigorous F_4 plants and two unrelated varieties: Vitry and the variety T

Plants grown in the field in 1929	Height of plants				Length of leaflets				Weight of vines			
	n	\bar{x}	μt	$s^0/0$	n	\bar{x}	μt	$s^0/0$	n	\bar{x}	μt	$s^0/0$
Vitry	7	41.43	8.32	20.11	7	16.29	2.49	15.29	7	45.71	13.98	30.62
<i>Phaseolus vulgaris</i> , variety T	15	42.00	5.21	21.65	15	12.47	0.69	9.66	15	35.33	6.58	32.47
F_2 — 131 × Vitry	21	114.29	13.55	25.41	22	21.32	0.98	10.14	21	233.33	59.04	54.25
F_2 — 132 × variety T	60	107.17	7.19	25.84	60	20.08	0.71	13.67	60	208.00	23.29	43.13
F_2 — 205 × variety T	3	73.33	94.06	42.15	3	15.67	15.18	31.84	3	150.00	302.23	66.22
F_2 — variety T × 205	165	73.09	1.97	17.54	184	15.82	0.27	11.79	181	124.09	7.11	38.99

we see the extreme types of F_2 obtained after crossing a vigorous F_4 plant with the variety T . Fig. 19 A, C represents vigorous F_2 plants, Fig. 19 B — the smallest F_2 individual and Fig. 19 D — an individual of the variety T .

5. The F_5 generation

In 1928 the F_5 generation was raised in the field and in pots. That year we grew also 5 F_1 plants in the field and 4 F_1 plants in pots.

The F_5 lines displayed a further increase of vigour in comparison with that of the preceding generations (Tables VI, VII, VIII). The mean of all \bar{x} concerning the height of particular F_5 lines is slightly larger than that of the F_4 lines. It attains namely 66.10 cm. The leaf size increased too in this generation. Some lines proved more vigorous than the F_1 generation. So, for instance, the line N^o 544 which exhibited the greatest vigour, surpassed F_1 in the height of plants and in the weight of dry vines. As regards the length of leaflets it has been on an average a little smaller (19.71 cm) than in the F_1 grown side by side (20.20 cm); but there were in the line N^o 544 individuals with an average leaflet length of 22 cm, viz., larger than in the largest F_1 plant grown in that year and which exhibited the average leaflet length of 21 cm only.

The dry vines of 2 individuals of line N^o 544 are represented in Fig. 24 C, D. We see that these individuals are larger than the F_1 plants shown in Fig. 23 C, D and photographed to the same scale. On the Fig. 24 A, B two individuals of line N^o 533 are shown. This is the F_5 line almost as vigorous as line N^o 544. Fig. 22 shows line 544 and Fig. 21 line N^o 533. Both lines were grown in the garden. We see from the photographs that both lines are comparatively uniform. The average height of the first line amounted to 124 cm and that of the second to 93 cm. The height of the plants was measured after the harvest. The plants were pulled out and hung up by the roots and then measured from the cotyledon scars to the top of the hanging vines. The height obtained in this way was always greater than when measured with a batten set on the soil surface beside the growing plants.

TABLE VI
Statistics of the height of F_5 and F_6 grown in the field

1928						1928						1929					
N° of line	n	\bar{x}	μt	$s^{\circ}/_o$		N° of line	n	\bar{x}	μt	$s^{\circ}/_o$		N° of line	n	\bar{x}	μt	$s^{\circ}/_o$	
165	9	67.78	22.00	39.82		211	33	74.24	5.43	20.45		486	43	98.84	6.56	21.40	
533	9	93.33	15.37	20.20		205	20	68.00	8.67	26.55		461	38	90.53	9.43	31.44	
564	3	86.67	31.71	19.61		132	7	62.86	18.28	29.10		278	5	126.00	55.93	31.98	
197	18	73.89	16.11	42.59		174	33	49.70	3.11	17.50		525	61	99.34	5.33	20.85	
521	6	73.33	32.30	38.30		547	11	57.27	11.28	27.95		293	26	95.77	10.42	26.41	
151	12	60.00	19.91	50.00		117	13	47.69	9.61	32.01		257	14	112.86	13.67	20.21	
544	7	124.29	14.97	12.06		131	15	68.00	11.69	29.99		<i>Phas. v. melleus</i>	14	39.29	4.21	17.91	
216	16	60.00	9.33	28.26		463	16	58.12	9.37	29.31		<i>Inexhaustible</i>	10	59.00	4.06	9.13	

TABLE VII
 Statistics of the weight of vines of F_5 and F_6 grown in the field in 1928 and 1929

F_5 lines, 1928						F_5 lines, 1928						F_6 lines, 1929					
No of line	n	\bar{x}	μt	s^2/σ		No of line	n	\bar{x}	μt	s^2/σ		No of line	n	\bar{x}	μt	s^2/σ	
165	9	63.33	23.06	44.65		211	33	85.45	13.10	42.84		486	43	126.28	19.60	50.08	
533	6	105.00	22.75	18.85		205	20	78.00	11.22	29.96		461	38	159.74	33.26	62.86	
564	3	73.33	79.86	35.81		132	11	52.73	15.35	41.30		278	5	288.00	170.76	42.72	
197	18	83.33	22.31	52.31		174	33	47.27	4.34	25.66		525	61	181.48	21.19	45.38	
521	6	71.67	50.30	61.04		547	11	60.00	22.28	52.11		293	31	161.94	43.20	69.13	
151	12	46.67	14.42	46.56		117	13	40.00	16.18	64.30		257	29	165.17	24.66	38.57	
544	7	150.00	38.14	25.45		131	15	68.67	16.73	42.50		<i>Plus, v. mellicus</i>	14	32.86	5.28	26.80	
216	16	69.38	23.94	62.72		463	16	62.50	15.38	44.72		Inexhaustible	10	53.00	11.21	28.05	

TABLE VIII
 Statistics of the length of terminal leaflets of the F_3 and F_6 lines grown in the field in 1928 and 1929

F_3 lines, 1928						F_5 lines, 1928						F_6 lines, 1929					
N ^o of line	n	\bar{x}	μt	$s^0/\%$	N ^o of line	n	\bar{x}	μt	$s^0/\%$	N ^o of line	n	\bar{x}	μt	$s^0/\%$			
165	9	16.44	2.04	15.20	211	33	17.79	0.92	14.43	486	44	17.43	0.76	14.28			
533	9	18.89	1.98	12.83	205	20	16.95	1.44	17.75	461	38	15.63	0.86	16.63			
564	3	19.33	3.79	6.45	132	11	15.45	2.09	19.19	278	5	19.40	2.86	10.61			
197	19	15.89	1.93	24.57	174	33	13.91	0.43	8.56	525	61	17.97	0.62	13.44			
521	6	15.33	4.82	27.33	547	11	15.00	2.38	22.56	293	27	17.19	1.26	18.20			
151	14	17.07	2.46	24.10	117	13	13.69	1.92	22.26	257	14	19.00	1.20	10.53			
544	7	19.71	1.16	5.89	131	17	15.35	1.35	16.56	<i>Phas. v. mellens</i>	14	12.07	0.53	7.32			
216	17	13.71	1.01	13.88	463	16	15.94	1.96	22.35	Inexhaustible	10	12.60	0.60	6.35			

For the sake of comparison the F_1 generation is shown in Fig. 20. The three photographs (Figs. 20, 21, 22) were made to the same scale. Beside the F_1 line we see in Fig. 20 (to the right of the batten with a scale) some individuals of the Inexhaustible Bean. This variety, as we know, is the larger of the two parental forms (the second being *Phas. v. melleus*). The letters X—X in Fig. 20 mark the beginning and end of the F_1 generation, while the letters 0—0 indicate the beginning and end of the row of the Inexhaustible Bean.

The large number of internodes observed in the particular lines of the F_3 and F_4 generations was maintained in F_5 . We had to deal in this generation with plants showing 644 internodes (within the line N° 533 grown in the field), the number of internodes of the F_1 plants being at most 306. The Inexhaustible Bean had at the same time 160 internodes and *Phaseolus vulg.* var. *melleus* had 58.

Fig. 2 shows diagrammatically all internodes of the parental forms (A and B), of F_1 (C) and of an individual of the F_5 generation belonging to line N° 533 (D). All diagrams are drawn to the same scale.

The F_5 plants grown in pots in 1928 were kept for a certain time in a greenhouse, and were injured to a certain degree by the red spider. At the end of May they were transferred to the garden. But we could not control the red spider in the garden either, and the plants suffered greater damage than usually occurs in plants started out of doors. Therefore all plants grown in pots in 1928 were smaller than in others years. I think however that they may be compared to one another because the red spider spread more or less uniformly over all plants. In order to give an idea as to the relative size of F_5 plants we have reproduced some photographs made to the same scale of typical individuals of the parental varieties (Fig. 25 a, d), the largest F_1 plants (Figs. 25 b, c) and some individuals of three lines of the F_5 generation (Figs. 26, 27, 28). All these F_5 lines are composed of plants larger on an average than the F_1 generation. There are however some differences from line to line. The most vigorous proved to be line N° 521. The leaves are very large, larger than those of F_1 . This line is represented in Fig. 26. Very similar to that just mentioned is line N° 132

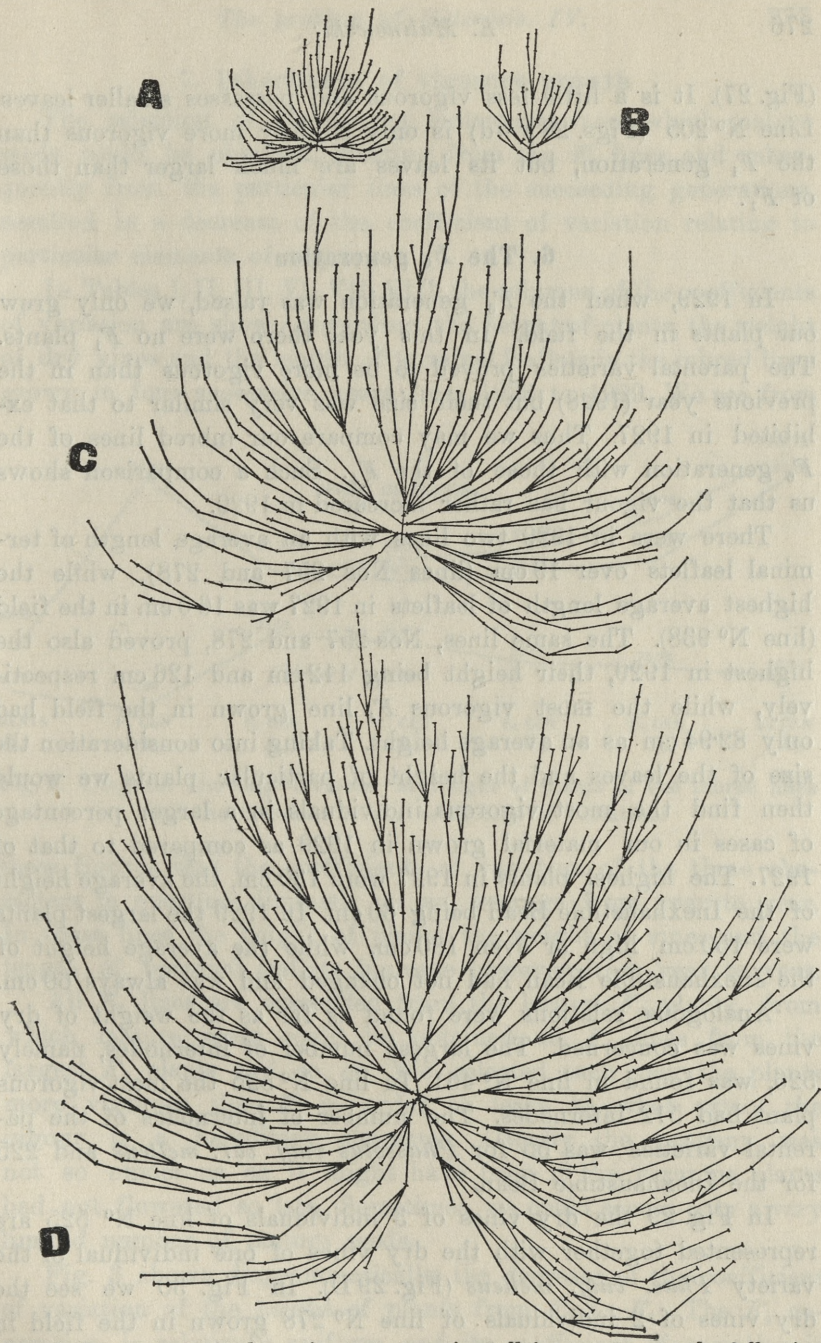


Fig. 2. Diagrammatic drawing representing all internodes of the following plants grown in the field in 1928: A — Inexhaustible Bean, B — *Phas. vulg. melleus*, C — F_1 plant, D — one of the F_2 plants. All diagrams drawn to the same scale.

(Fig. 27). It is a little less vigorous and possesses smaller leaves. Line N° 205 (Figs. 28 a—d) is only slightly more vigorous than the F_1 generation, but its leaves are much larger than those of F_1 .

6. The F_6 generation

In 1929, when the F_6 generation was raised, we only grew our plants in the field. In this year there were no F_1 plants. The parental varieties proved to be more vigorous than in the previous year (1928) but their size was very similar to that exhibited in 1927. Thus we may compare our inbred lines of the F_6 generation with those of the F_4 . Such a comparison shows us that the vigour has rather increased in 1929.

There were in 1929 two lines with an average length of terminal leaflets over 19 cm (lines Nos 257 and 278), while the highest average length of leaflets in 1927 was 16.0 cm in the field (line N° 938). The same lines, Nos 257 and 278, proved also the highest in 1929, their height being 112 cm and 126 cm respectively, while the most vigorous F_4 line grown in the field had only 82.94 cm as an average height. Taking into consideration the size of the leaves and the height of particular plants we would then find the most vigorous individuals in a larger percentage of cases in our material grown in 1929 as compared to that of 1927. The highest plants in 1927 were 130 cm, the average height of the Inexhaustible Bean being 60 cm. In 1929 the largest plants were 150 cm high or even 180 cm, while the average height of the Inexhaustible Bean had not changed and was always 60 cm.

Analogous relations were found as far as the weight of dry vines was concerned. The largest number of internodes, namely 526, was found in line N° 461. In line N° 525 the most vigorous plant had 512 internodes. The number of internodes of the parental varieties was 55 for *Phaseolus vulg. var. melleus* and 225 for the Inexhaustible Bean.

In Fig. 29 the dry vines of 3 individuals of line N° 525 are represented together with the dry vines of one individual of the variety *Phas. vulg. melleus* (Fig. 29 D). In Fig. 30 we see the dry vines of 2 individuals of line N° 278 grown in the field in 1929 and also one individual of the variety Inexhaustible Bean (Fig. 30 C).

7. Inheritance of vigorous growth

The selection of the largest individuals from which mature seeds could be obtained, starting from the F_3 lines and subsequently from the particular lines of the succeeding generations, resulted in a decrease of the coefficient of variation relating to particular elements of vigour.

In Tables I, II, III, VI, VII, VIII, the columns of the coefficients of variation are shown regarding the height of plants, the weight of dry vines and the length of terminal leaflets in the inbred lines grown in four successive years from 1926 to 1929. We see from

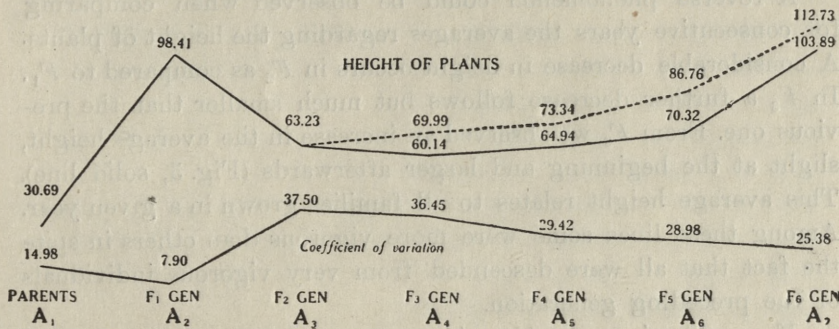


Fig. 3. Diagram showing increase in height of plants of the inbred lines and the decrease in the coefficient of variation.

these figures that the coefficients of variation of the three characters in question diminish on an average from year to year. In those lines the height of plants, the weight of vines and the length of terminal leaflets increase however from year to year.

All F_3 lines are descended from the largest F_2 plants, from which mature seeds could be obtained, all F_4 lines from the largest F_3 plants and so on. We selected each year the plants more vigorous than F_1 in order to learn to what extent the vigour is a hereditary character. Usually the progeny was not so numerous as it might have been if the vigorous plants had not flowered so late. Sometimes we could secure only a very limited number of mature seeds.

Fig. 3 shows diagrammatically the decrease of the coefficient of variation of the height of plants from F_2 to F_6 . The F_1 generation is relatively uniform and its coefficient of variation is low. The ordinate of the point A_1 (Fig. 3) represents the average

of the coefficients of variation of the parental varieties grown in the field in 1926 and 1928. The ordinate of the point A_2 represents the average of the coefficients of variation of two F_1 generations grown in the field in 1926 and 1928. The ordinate of the point A_3 refers to the F_2 generation grown in the field in 1925, and it represents the coefficient of variation of this generation. The ordinates of the remaining points refer to the subsequent generations and each of them represents the average of the coefficients of variation of all families grown in successive years.

A reverse phenomenon could be observed when comparing for consecutive years the averages regarding the height of plants. A considerable decrease in height occurs in F_2 as compared to F_1 . In F_3 a further decrease follows but much smaller than the previous one. From F_3 we observed an increase in the average height, slight at the beginning and larger afterwards (Fig. 3, solid line). This average height relates to all families grown in a given year. Among these lines some were more vigorous than others in spite the fact that all were descended from very vigorous individuals of the preceding generation.

If we take into consideration only three of the most vigorous lines and if we calculate the mean value of all averages for each year separately, we shall get a larger increase in height from year to year than in the previous case (Fig. 3, dotted line). This last case shows an average height of 112 cm in F_6 and such a height exceeds that of F_1 by 14 cm. We may conclude that our selection has brought about positive results and a strain or strains higher than the F_1 generation were obtained.

In 1929 the lines Nos 278, 525 and 257 were the most vigorous. These three lines descended respectively from the lines Nos 131, 544 and 205 grown in 1928, and these last lines in turn came from two F_4 lines grown in 1927, namely Nos 938 and 134 (see Tables IX, XII).

Other elements of vigour like the weight of vines and the length of terminal leaflets behave more or less in the same way, as may be seen from Tables X, XI, XIII, XIV.

The F_6 lines were composed of heavier plants than those of the preceding generations and they also had larger leaves. Some F_6 lines attained an average height, an average number of in-

ternodes and an average weight which had never been reached by any F_1 generation.

We may trace out all our F_5 and F_6 lines from 3 F_2 plants. This is represented diagrammatically in Tables IX—XIV for the progenies of 2 F_2 plants (Nos 216 and 232). In these figures the arithmetic means and the coefficients of variation concerning the height of plants, the weight of vines and the size of leaves

TABLE IX

Statistics of the height of plants of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
		N° 131 \bar{x} = 68·00 s^0_0 = 29·99	N° 278 \bar{x} = 126·00 s^0_0 = 31·98
		N° 132 \bar{x} = 62·86 s^0_0 = 29·10	N° 293 \bar{x} = 95·77 s^0_0 = 26·41
N° 232 \bar{x} = 68·73 s^0_0 = 31·34	N° 938 \bar{x} = 82·94 s^0_0 = 27·36	N° 544 \bar{x} = 124·29 s^0_0 = 12·06	N° 525 \bar{x} = 99·34 s^0_0 = 20·85
		N° 533 \bar{x} = 93·33 s^0_0 = 20·20	N° 461 \bar{x} = 90·53 s^0_0 = 31·44

TABLE X

Statistics of the weight of dry vines of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
		N° 131 \bar{x} = 68·67 s^0_0 = 42·50	N° 278 \bar{x} = 288·00 s^0_0 = 42·72
		N° 132 \bar{x} = 52·73 s^0_0 = 41·30	N° 293 \bar{x} = 161·94 s^0_0 = 69·13
N° 232 \bar{x} = 56·55 s^0_0 = 56·10	N° 938 \bar{x} = 157·45 s^0_0 = 52·97	N° 544 \bar{x} = 150·00 s^0_0 = 25·45	N° 525 \bar{x} = 181·48 s^0_0 = 45·38
		N° 533 \bar{x} = 105·00 s^0_0 = 18·85	N° 461 \bar{x} = 159·74 s^0_0 = 62·86

of particular lines are given and the connections between the lines of different years are shown.

TABLE XI

Statistics of the length of terminal leaflets of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
N° 232 $\bar{x} = 13.57$ $s^0_0 = 21.71$	N° 938 $\bar{x} = 16.00$ $s^0_0 = 16.65$	N° 131 $\bar{x} = 15.35$ $s^0_0 = 16.56$	N° 278 $\bar{x} = 19.40$ $s^0_0 = 10.61$
		N° 132 $\bar{x} = 15.45$ $s^0_0 = 19.19$	N° 293 $\bar{x} = 17.19$ $s^0_0 = 18.20$
		N° 544 $\bar{x} = 19.71$ $s^0_0 = 5.89$	N° 525 $\bar{x} = 17.97$ $s^0_0 = 13.44$
		N° 533 $\bar{x} = 18.89$ $s^0_0 = 12.83$	N° 461 $\bar{x} = 15.63$ $s^0_0 = 16.63$

TABLE XII

Statistics of the height of plants of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
N° 216 $\bar{x} = 71.25$ $s^0_0 = 45.59$	N° 134 $\bar{x} = 63.75$ $s^0_0 = 33.59$	N° 197 $\bar{x} = 73.89$ $s^0_0 = 42.59$	N° 486 $\bar{x} = 98.84$ $s^0_0 = 21.40$
		N° 205 $\bar{x} = 68.00$ $s^0_0 = 26.55$	N° 257 $\bar{x} = 112.86$ $s^0_0 = 20.21$

TABLE XIII

Statistics of the weight of dry vines of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
N° 216 $\bar{x} = 53.75$ $s^0_0 = 48.05$	N° 134 $\bar{x} = 104.50$ $s^0_0 = 50.90$	N° 197 $\bar{x} = 83.33$ $s^0_0 = 52.31$	N° 486 $\bar{x} = 126.28$ $s^0_0 = 50.08$
		N° 205 $\bar{x} = 78.00$ $s^0_0 = 29.96$	N° 257 $\bar{x} = 165.17$ $s^0_0 = 38.57$

The graph (Fig. 4) shows the increase in the average weight of several vigorous lines selected from year to year. In F_6 we arrived at a very high average weight, reaching 211g

against 141 g obtained in the F_1 generation, grown in such a favourable year as was 1926. In 1928, when F_5 was raised, the

TABLE XIV

Statistics of the length of terminal leaflets of particular lines grown in the field

F_3 (1926)	F_4 (1927)	F_5 (1928)	F_6 (1929)
N° 216 \bar{x} = 17.50 $s^0/0$ = 16.41	N° 134 \bar{x} = 15.05 $s^0/0$ = 19.20	N° 197 \bar{x} = 15.89 $s^0/0$ = 24.57 N° 205 \bar{x} = 16.95 $s^0/0$ = 17.75	N° 486 \bar{x} = 17.43 $s^0/0$ = 14.28 N° 257 \bar{x} = 19.00 $s^0/0$ = 10.53

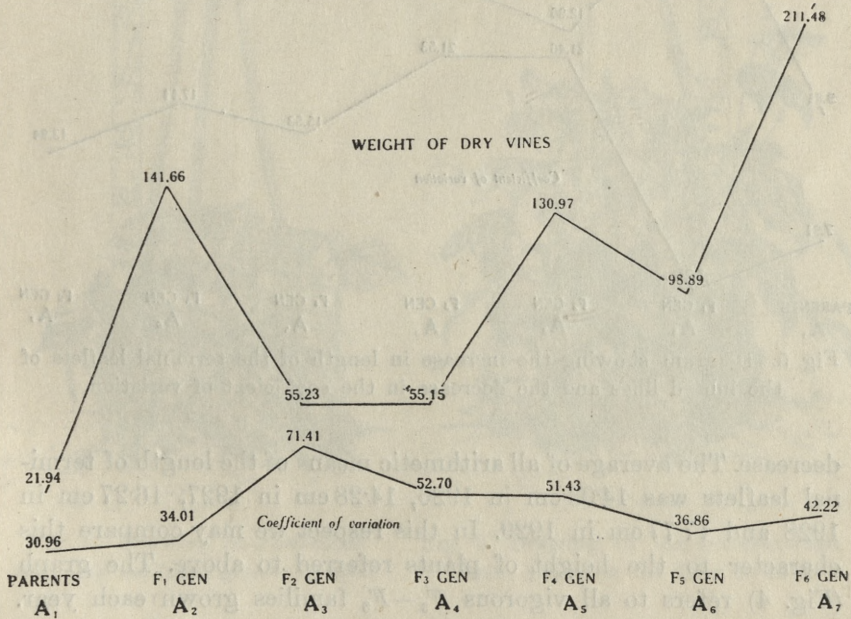


Fig. 4 Diagram showing the increasing in weight of plants of the inbred lines and the decrease in the coefficient of variation.

weather was rather unfavourable, the precipitations being smaller than in 1927 or 1929. This, probably, may account for the decrease in the average weight shown in the above graph. The

number of internodes and what approximately amounts to the same thing, the weight of the dry vines, is easily influenced by the amount of water available. This character changed more than the height when plants were grown in pots.

In other plants so far examined the height is also subject to variation in a lesser degree than such characters as weight of plants or yield of seed (Jones 1918).

As to the terminal leaflets we observed a steady increase in their length (Fig. 5) and in spite of less favourable weather conditions in 1928 this character did not show in that year any

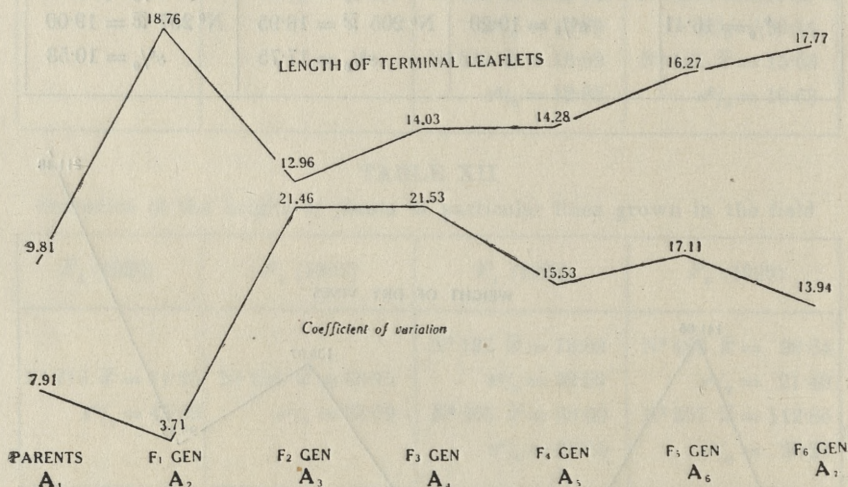


Fig. 5. Diagram showing the increase in length of the terminal leaflets of the inbred lines and the decrease in the coefficient of variation.

decrease. The average of all arithmetic means of the length of terminal leaflets was 14.03 cm in 1926, 14.28 cm in 1927, 16.27 cm in 1928 and 17.77 cm in 1929. In this respect we may compare this character to the height of plants referred to above. The graph (Fig. 4) refers to all vigorous F_3 – F_6 families grown each year.

The above described selection experiments carried out up to the F_6 generation may be summarised as follows:

- 1) Vigorous growth greater than that of the F_1 generation is transmitted from generation to generation.
- 2) As the selection proceeds, the mean value of particular characters (height of plants, weight of dry vines and the length

of terminal leaflets) increases from generation to generation and the coefficient of variation decreases.

8. The F_7 generation

After 1929 I carried on the selection experiments and grew F_7 in 1932, F_8 in 1935, F_9 in 1938, F_{10} in 1941 and F_{11} in 1943.

In 1932 we grew two F_7 lines in the field. They were vigorous, and some plants exceeded in vigour the F_1 individuals

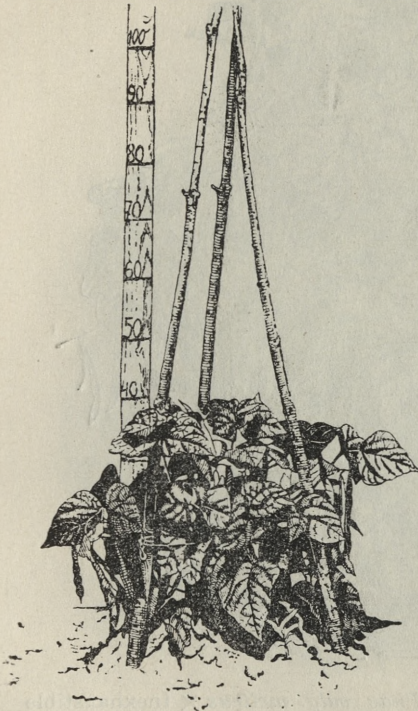


Fig. 6. Drawing of *Phaseolus vulgaris melleus*, grown in 1932.



Fig. 7. Drawing of the Inexhaustible Bean, grown in the field in 1932.

grown side by side with them. The largest individual of the F_1 generation grown in 1932 is represented in Fig. 33 and the vigorous F_7 plants in Figs 34, 35, 36. The photographs were made to the same scale. The parental forms are also shown to the same scale in Figs. 31, 32. The F_7 lines proved to be on an average more vigorous than the F_1 generation grown side by side. One of

the vigorous F_7 plants is shown in Fig. 9. This figure is a copy of a drawing made from the photograph reproduced in Fig. 35. This drawing is made to the same scale as those shown in Figs. 6, 7 and 8, representing the parental forms (Figs 6—7) and the F_1 plant (Fig. 8) grown side by side with them in 1932.



Fig. 8. Drawing of F_1 of the cross *Phas. vulg. melleus* \times Inexhaustible Bean, grown in the field in 1932.

Fig. 8 is reproduced from a photograph of the F_1 plant in the same way as Fig. 9 of the F_7 plant. This F_1 plant seems smaller than the F_1 plant shown in Fig. 33. This is because the vines of the F_1 plant shown in Fig. 33 were stretched out in order to take a picture and propped up with several stakes. This is why on the photograph its size is a little enlarged. The other photographs of 1932 (Figs 34, 35, 36) representing the F_7



Fig. 9. Drawing of a vigorous F_6 plant grown in the field in 1932. The drawings shown in Figs 6—9 are made to the same scale.

individuals were made from plants in their normal position. Fig. 8 and Fig. 33 represent of course different F_1 plants grown in 1932.

9. The time of flowering

I reported in the first paper of this series that the F_1 plants start flowering a little earlier than the Inexhaustible Bean, and the flowering of these plants lasts much longer. In F_2 a large number of individuals appeared which started flowering later than F_1 and some of these individuals unfolded their first flowers even a month later than F_1 . These were usually the most vigorous plants. Our vigorous F_2 individuals taken as mother plants for F_3 lines were also late flowering ones.

TABLE XV

Statistics of the time of flowering of the F_3 and F_6 lines
The time is expressed in the number of days passed since 15th of May

The F_3 lines (1926)					The F_6 lines (1929)				
	<i>n</i>	\bar{x}	μt	<i>s</i> ^o / _o		<i>n</i>	\bar{x}	μt	<i>s</i> ^o / _o
<i>Phas. v. melleus</i>	21	50.48	0.99	4.22	<i>Phas. v. melleus</i>	14	52.50	2.47	7.87
Inexhaustible Bean	18	55.56	1.45	5.10	Inexhaustible Bean	10	67.50	2.53	4.97
N ^o 184	53	84.81	4.27	18.18	N ^o 486	44	84.20	5.20	20.17
„ 216	4	93.75	7.61	4.42	„ 461	38	75.66	4.69	18.70
„ 808	21	64.52	7.65	25.41	„ 278	5	99.00	39.11	28.46
„ 211	50	74.40	5.01	23.54	„ 525	64	81.17	4.52	22.18
„ 160	51	89.02	4.28	17.02	„ 293	27	76.85	7.01	22.62
„ 22	76	68.88	4.33	27.40	„ 257	13	100.38	11.67	18.48
„ 93	118	68.05	2.91	23.41					
„ 232	125	75.68	2.82	20.98					

Observations on the time of flowering were made on all inbred lines grown in 1926, 1928 and 1929. We recorded for these lines the time of unfolding of the first flowers on each plant and the date of this unfolding was taken as the time of flowering for a given plant.

Each year the seeds were sown on May 15th. We shall express the time of flowering by the number of days elapsing from May 15th, the date of sowing, up to the date of flowering. Some inbred lines were on an average later as to their time of flowering than the F_1 generation. We calculated for each line the average time of flowering, that is to say, the arithmetic mean (designated in Table XV by \bar{x}) of its fre-

quency distribution. So, for instance, the F_3 line N° 216 started flowering on an average on the 93rd day from the date of sowing, viz., the difference between the time of flowering of this line and that of the Inexhaustible Bean, which started flowering on the 55th day, was 38 days. Analogous differences were found in F_4 , F_5 and F_6 . In Table XV only the statistics of the time of flowering of F_3 and F_6 are given.

10. The F_{10} generation

The most important data concerning the problem of inheritance of vigorous growth were obtained for the F_{10} generation grown in 1941. We raised that year a more numerous F_1 generation than usual. We grew namely 94 F_1 plants and 137 individuals belonging to three F_{10} lines, namely to the lines Nos 108, 135 and 153.

All three F_{10} lines proved to be more vigorous than the F_1 generation grown in the field beside them in alternate rows. The coefficients of variation of particular characters were relatively low as compared to the coefficients of variation of the preceding generations. We calculated for the year 1941 the coefficients of variation for the same main characters as in the preceding years, namely for the height of plants, the weight of dry vines and the length of terminal leaflets. This is shown in Tables XVI, XVII, XVIII, XIX. We see in these Tables the frequency distributions for the characters just mentioned and the respective statistics x, s and $s\%$. The mean value of each of the characters in question proved to be greater than the mean value of F_1 and the coefficient of variation in all cases turned out to be lower than in the lines of the preceding generations.

The height of the F_{10} plants was about 15 cm greater than that of the F_1 generation and the weight of dry vines exceeded that of F_1 by about 40 g. As to the difference in the length of terminal leaflets we see from Table XVII that the terminal leaflets of line N° 153 were on an average 1 cm longer than in F_1 , those of line N° 135 over 1 cm longer and line N° 108 had on an average rather shorter terminal leaflets than the F_1 generation. The difference was equal to 0.19 cm in favour of F_1 . But

TABLE XVI
 Frequency distributions of height of the parental forms, of F_1 and of three F_{10} lines grown in the field in 1941

	Height of plants in cm																				n	\bar{x}	s	$s^0/\%$								
	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110					115	120	125	130	135	140	145	
<i>Phase. only. melleus</i>																													140	22.89	3.65	15.95
Inexhaustible Bean																													134	38.02	6.25	16.43
F_1							1																						94	83.88	9.35	11.15
F_{10} line N° 108										5	1																		50	99.90	14.05	14.06
F_{10} " " 135												1	1	3	9	8	4	7	8	1	3	3	1						40	97.38	10.50	10.78
F_{10} " " 153													1	1	3	9	6	7	6	4	4	—	1	1	2	1			47	98.56	15.40	15.62

TABLE XVII
Frequency distributions of the length of terminal leaflets of the parental forms, of F_1 and of three F_{10} lines grown in the field in 1941

	Length of leaflets in cm															n	\bar{x}	s	$s^0/\%$						
	5.6	6.1	6.6	7.1	7.6	8.1	8.6	9.1	9.6	10.1	10.6	11.1	11.6	12.1	12.6					13.1	13.6	14.1	14.6	15.1	15.6
	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0					13.5	14.0	14.5	15.0	15.5	16.0
<i>Phaseolus v. melleus</i>	1	—	3	2	3	6	11	34	29	23	2	2	2									116	9.37	0.90	9.61
Inexhaustible Bean			1	2	3	14	20	31	14	14	5	3	3	9	29	27	12	5	3	1		104	9.19	0.80	8.71
F_1											1	1	1	11	14	16	2	4				93	13.05	0.77	5.90
F_{10} line N ^o 108											1						1	10	11	12	4	50	12.87	0.69	5.36
F_{10} " " 135																					2	40	14.42	0.55	3.81
F_{10} " " 153												3	1	4	6	5	8	7	8	4		46	13.61	1.11	8.16

TABLE XVIII
 Frequency distributions of the breadth of terminal leaflets of the parental forms, of F_1 and of three F_{10} lines grown in the field in 1941

	Breadth of leaflets in cm																n	\bar{x}	s	s ² /o						
	4.1	4.6	5.1	5.6	6.1	6.6	7.1	7.6	8.1	8.6	9.1	9.6	10.1	10.6	11.1	11.6					12.1	12.6	13.1	13.6	14.1	14.5
<i>Phaseolus v. melleus</i>	4	1	5	6	6	7	7	8	8	9	10	10	11	11	12	12	13	13	13	14	14	15	116	7.41	0.75	10.12
Inexhaustible Bean				2	4	22	34	20	17	4	1												104	6.91	0.65	9.41
F_1								1	—	1	2	2	8	29	23	15	7	1	2				91	11.08	0.84	7.58
F_{10} line No 108									1	—	1	3	9	15	10	8	1	2					50	10.89	0.81	7.44
F_{10} " " 135												1	—	—	6	13	11	7	1				40	12.52	0.67	5.35
F_{10} " " 153											1	1	3	4	4	7	9	6	6	6	4	1	46	12.08	1.16	9.60

TABLE XIX

Frequency distributions of the weight of dry vines of the parental forms, of F_1 and of three F_{10} lines grown in the field in 1941

	Weight of plants in g																\bar{x}	s	s %																		
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150-159				160-169	170-179	180-189	190-199	200-209	210-219	220-229	230-239	240-249	250-259	260-269	270-279	280-289	290-299	300-309	310-319		
<i>Phas. v. mellensis</i>	6	63	49	1																														119	18.78	5.22	27.80
Inexhaustible	16	38	28	20	10	6	2																										120	34.67	14.14	40.78	
F_1				1	2	2	—	1	—	1	—	5	6	2	7	14	12	13	5	4	9	2	3	—	2	2	—	—	—	—	—	—	93	163.06	41.92	25.71	
F_{10} line N° 108						1	—	—	—	1	—	—	—	1	1	4	1	—	4	5	9	7	3	2	2	4	3	1	—	—	1	—	50	206.60	43.77	21.19	
F_{10} line N° 135												1	2	—	—	—	1	2	1	—	2	2	5	9	6	4	—	1	3	—	1	—	40	227.75	40.85	17.94	
F_{10} line N° 153						1	—	—	—	2	—	—	—	1	2	1	5	1	2	1	7	5	3	5	3	3	3	1	2	—	—	2	47	206.28	50.72	24.59	

of course the leaflets of line N^o 108 were much longer than those of *Phaseolus vulg. melleus*, the difference being 3.48 cm in favour of line N^o 108. The data obtained in 1941 and recorded in Tables XVI—XIX prove that the F_{10} lines are beyond any doubt more vigorous than the F_1 generation grown side by side with them in the garden under the same conditions. I think these data are sufficient to demonstrate that the vigour due to heterosis may be a hereditary character.

Some individuals of the F_{10} lines were photographed together with F_1 and the parental forms. One of such photographs is represented in Figs 37 a—f. We see from left to right: a) individual of *Phaseolus vulg. melleus*, b) Inexhaustible Bean, c) F_1 plant, d) individual of line N^o 153 (its height was 116 cm, weight of dry vines 230 g, and the average length of terminal leaflets 15.17 cm), e) individual of line N^o 108 (its height was 99 cm, weight of dry vines 230 g, and the average length of terminal leaflets 12.70 cm), f) individual of the line N^o 153 (its height was 101 cm, weight of dry vines 200 g, and the average length of terminal leaflets 14.70 cm).

The average length of terminal leaflets was calculated in 1941 for the first time during our kidney bean investigations by dividing the total sum of lengths of all terminal leaflets in a given plant by the number of leaves in this plant. All terminal leaflets in all plants were measured. In preceding years we measured in each plant only 5 terminal leaflets taken at random and we regarded the average length of such leaflets as the leaflet length characteristic of a given plant. Our data therefore calculated in 1941 for the length of terminal leaflets are comparable only to a certain extent with those of the preceding years.

The F_{10} lines are characterized by relatively late flowering. They resemble in this respect the lines of the preceding generations. We determined the time of flowering in the F_{10} lines by recording the dates of unfolding of the first flowers in each plant. As I already pointed out in the first paper of this series, we proceeded in 1941 in the following way: if the first flower on a given plant developed more than 3 days earlier than the second, the date of opening of the latter was taken as the date of the beginning of the flowering of the plant in question. We proceeded in this way because sometimes one solitary flower un-

folded much earlier than the rest and the regular unfolding of flowers in succession started only with the second flower. The frequency distributions for the time of flowering estimated in this way for the parental forms, F_1 , F_2 and the F_{10} lines in question, are shown in Table XX. In this Table, as in the preceding ones, the time of flowering is expressed by the number of days elapsing from May 15th, the date of the sowing of our plants, up to the date of flowering. The range of variation proved to be very large. The first plants of the F_2 generation started flowering on June 30th simultaneously with the first plants of *Phaseolus vulg. melleus* and the last individual developed its first flower only on September 5th. The majority of the F_2 plants started flowering at the same time as the parental forms and the F_1 plants. Out of 574 individuals of the F_2 generation 374 started flowering before July 22nd, i. e. simultaneously with the last F_1 plants, and 200 F_2 plants unfolded their first flowers after that date. Such late flowering plants of the F_2 generation were for the most part very vigorous and their vigour often exceeded that of the largest F_1 plants.

The time of flowering begins much later in F_{10} lines and it lasts much longer than in F_1 . Under favourable weather conditions the F_1 plants kept in daylight of normal length come to maturity at the beginning of September, or at least they give at that time a large percentage of mature seeds. But the F_{10} lines which start flowering about one month later than the F_1 plants do not mature at all because they succumb to early frost. As I have already pointed out, we get seeds from such plants only by growing them under the conditions of a short daylight.

11. The F_{11} generation

In 1943 we raised the F_{11} generation from the seeds of some vigorous F_{10} plants and we again obtained vigorous families. Fig. 37 shows from left to right: g) the largest F_1 individual grown in 1943, h) the Inexhaustible Bean, i) a vigorous plant of line N^o 5 grown in 1943. We see from these figures that the F_{11} individual is more vigorous than the F_1 plant. The whole line N^o 5 was composed of vigorous individuals and its mean value was greater than that of the F_1 plants.

These vigorous F_{11} plants started flowering much later than the F_1 plants and they were still flowering abundantly in September when the first frost arrived. Table XXI shows the course of flowering of 2 F_1 plants in 1943 and Table XXII — the course of flowering of 3 plants belonging to vigorous F_{11} lines. We counted the unfolding flowers each day, but in both the above-mentioned Tables the number of flowers opening is given at intervals of 3 days. The F_1 plants in our case started flowering on July 24th and the last flowers unfolded in the first of

TABLE
Frequency distributions of the time of flowering of the parental

	Days of July															
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31
	Number of days															
	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76
	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77
<i>Phaseolus vulgaris melleus</i>	2	27	64	19	3	1										
Inexhaustible Bean						2	54	32	9	3	2	1				
F_1					4	38	30	12	4	2	1	2				
F_2	8	39	70	68	70	49	30	12	18	6	4	15	15	7	18	17
F_{10} line N° 108																
F_{10} " " 135																
F_{10} " " 153																

these individuals on October 1st and in the second on September 30th. One of the plants of the vigorous F_{11} line started flowering on September 3rd, the second on August 1st, and all the plants were still flowering on October 10th. But the frost came that day and injured our plants. We had to discontinue our observations. As we see from these Tables, the plants of the F_{11} generation flowered more abundantly than the F_1 plants although they developed later in the season and consequently were growing at lower temperatures. A slight decrease in the number of unfolded flowers during the last days before the frost may be accounted for by the drop in the temperature.

I should like to mention here that the vigorous plants in all generations have been very healthy. The parental forms and especially the Inexhaustible Bean often suffered from bacterial and virus diseases. In this respect the F_1 plants and also the vigorous plants of the subsequent generations were marked off from other plants. This healthy appearance is a characteristic feature of our vigorous plants.

As regards the *Petunia*, the second object of my researches regarding heterosis, I did not try to obtain the F_3 generation and I do not know anything about the inheritance of vigorous growth in these plants. But as we know in the F_2 generation of *Petunia* crosses plants larger than the F_1 individuals do not appear.

XX

varieties, F_1 , F_2 and three F_{10} lines grown in the field in 1941

Days of August														Septem.			n	\bar{x}	s	s ^o / _o	
2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	1	3					5
elapsed since 15 th of May																					
78	80	82	84	86	88	90	92	94	96	98	100	102	104	106	108	110	112				
79	81	83	85	87	89	91	93	95	97	99	101	103	105	107	109	111	113				
																		116	50.50	1.50	2.97
																		103	58.29	2.06	3.53
																		93	57.17	2.64	4.62
26	8	16	7	22	10	10	13	7	2	3	2	—	—	1	—	—	1	574	64.10	14.18	22.12
				1	5	2	10	14	6	3	2	1	3	1	1	1		50	96.00	5.26	5.48
		1	—	2	4	2	6	11	11	1	5	1	2					46	93.43	4.34	4.65
	1	1	1	1	2	—	10	8	10	2	2	1	—	—	—	1		40	94.70	5.22	5.51

12. Discussion

It seems to me that the data presented in this paper prove that the vigorous growth characteristic of F_1 showing heterosis or even more vigorous than F_1 , may be transmitted to the following generations and relatively uniform families may be arrived at after several years of selection. Vigour due to heterosis is a hereditary character in *Phaseolus vulgaris*. I called attention to this rather peculiar case in 1924 and I presented some data showing that vigorous growth breeds true in F_3 and F_4 . Later

TABLE XXI

Course of flowering of 2 individuals of *Phaseolus vulgaris* *mellensis*, 2 indiv. of the Inexhaustible Bean and 2 indiv. of F_1 grown in the field in 1943

	Number of flowers unfolding at 3-day intervals																														
	July						August						September						Oct.												
	14	17	20	23	26	29	1	4	7	10	13	16	19	22	25	28	31	3	6	9	12	15	18	21	24	27	30	1	1		
<i>Phaseolus</i> <i>v. mell.</i> Plant 1	1	6	11	15	14	20	38	5																							
" " " 2		3	13	18	14	27	34	14	4																						
Inexhaust. Plant 1					2	11	30	52	29	5	1																				
" " 2				10	9	16	25	38	9	4	3																				
F_1 Plant No 1					1	11	33	49	70	32	20	23	44	60	50	20	21	13	10	15	16	17	36	25	18	6	3	1			
F_1 " " 2					1	8	39	35	53	39	15	28	14	51	50	23	17	28	30	44	25	26	41	11	8	4	2				

TABLE XXII

Course of flowering of 3 F_1 plants belonging respectively to lines Nos 1, 5 and 9 growing in the field in 1943

Line 1, plant No 22	Number of flowers unfolding at 3-day intervals																								
	August						September						October												
	1	4	7	10	13	16	19	22	25	28	31	3	6	9	12	15	18	21	24	27	30	3	6	9	
" 5, "	1	4	7	10	13	16	19	22	25	28	31	3	6	9	12	15	18	21	24	27	30	3	6	9	
" 9, "	1	5	9	4	—	3	2	—	1	6	9	9	26	35	62	63	121	138	87	138	108	81	37	32	32
" 24										1	2	8	7	10	11	55	65	72	94	94	92	57	62	55	

on I repeated the experiments more extensively and more accurately. I used zinc pots of a special type (22 cm in diameter) in order to obtain more uniform conditions for plant growth. And I obtained the same results under such conditions. In 1928 I published a short report stating that some F_3 and F_4 lines grown in pots were composed of individuals larger than the F_1 plants grown under the same conditions. I did not give in this communication any numerical data concerning the size of plants, postponing this to a later paper, which I am in a position to publish now after several years of further researches.

There are in the literature some indications that vigorous size due to heterosis may be transmitted to the following generations. Collins (1921) writes as follows: »An examination of the maize literature indicates that the difficulty of securing uniform strains with the vigour of the first generation has been assumed rather than demonstrated. No case was found where selection following hybridisation had been continued long enough to approximate homozygosity. There are also very few cases where the more vigorous F_2 individuals have been chosen as parents of the F_3 «. Further on Collins writes: »Height is probably the most satisfactory character to use as a measure of heterosis. There are 23 comparisons of F_1 and F_2 populations in the work of Emerson and East. To these six can be added from our own experiments. In these 29 cases the mean of the F_2 was below that of the F_1 in every instance but in ten of the 29 cases the largest of the F_2 plants equalled or exceeded the largest of the F_1 individuals and in every case where a progeny was grown from a plant near the upper limit of the range of the F_2 its mean exceeded that of the F_1 «.

The paper by Emerson and East is an important publication, and as far as I know Jones's theory of the dominance of linked factors was based upon the numerical data of this work.

Veatch (1930) in his paper on soybeans gives some examples in which hybrid vigour appears to be carried beyond the F_1 generation. This author used the yield or weight of seed produced per plant as one of the principal criteria of hybrid vigour.

The soybean is normally a self-fertilized plant. The flowers are completely self-fertile. Veatch writes that in his material there were segregates in all but one of the F_2 populations that yielded at least twice as much as the interpolated F_1 yields and that the actual heights of the F_1 given in Table VI of his paper are below those of the tallest segregates in the F_2 in all cases, except in the Tall Manchu \times A. K. 2 cross.

On the basis of his experimental data Veatch advances an explanation of hybrid vigour and according to this explanation, there is a possibility of securing segregates that are higher as well as those that are lower than the F_1 . The results of the investigations on the soybean indicate, according to Veatch, that both types have been secured but that it remains to be seen whether or not these types are homozygous or can be made so without reducing yield. Veatch's experiments however were not carried on beyond the F_2 generation.

Bredemann and Heuser (1931) found in rye some cases in which F_2 plants were more vigorous than F_1 .

Whaley in his review paper on Heterosis in 1944 quoted the above-mentioned publications by Veatch (1930), by Bredemann and Heuser (1931) and by myself (Malinowski 1928), and he expressed the opinion that it remained for such cases to arise under very carefully controlled conditions before any detailed consideration was necessary. My opinion in 1928 was very similar to that of Whaley expressed in his paper of 1944, and this is why since 1928 I have carried on my investigations in order to get more experimental data. These investigations, conducted for 11 generations and presented in this paper, corroborate satisfactorily my first observations published in 1924 and 1928.

Summary

Vigorous growth due to heterosis proved hereditary in *Phaseolus vulgaris*. Selection of vigorous plants carried on till the F_{11} generation have given positive results and vigorous lines were arrived at exceeding in size the F_1 plants grown side by side with them.

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Explanation of Tables

In the Tables of this paper the following statistics are given: n = number of individuals, \bar{x} = arithmetic mean, nt = limit which can be exceeded by the sampling error of \bar{x} in 5% of cases, s = standard deviation, $s\%$ = coefficient of variation.

Explanation of Plates

Fig. 10. — *Phaseolus vulgaris melleus* (left), F_1 (centre), and Inexhaustible Bean (right), grown in 1926.

Fig. 11. — Plants of the F_3 line N° 184, grown in 1926.

Fig. 12. — Plants of the F_3 line N° 506, grown in 1926.

Fig. 13 and 14. — Plants of the F_3 line N° 211, grown in 1926. This line was composed of two types of plants, i. e. a more vigorous one with rather loose vines (Fig. 13) and a smaller one with a rather compact habit (Fig. 14).

Fig. 15 a — the variety Flageolet Chevrier, b — F_1 between Flageolet Chevrier and a vigorous F_4 plant belonging to the line N° 174 c—e — plants of the line N° 174. All plants were grown in 1928.

Fig. 16 A, B — dry vines of the variety *T* (see text), C, D — F_1 between the variety *T* and a vigorous F_4 plant, E, F — dry vines of 2 individuals of Vitry, G, H — F_1 between the variety Vitry and a vigorous F_4 plant. Plants grown in the field in 1928.

Fig. 17. — F a row of F_1 plants obtained after crossing a vigorous F_4 plant with the variety *T*, T — some plants of the variety *T*. Plants grown in 1928.

Fig. 18 A, B, C — Plants of the F_2 generation obtained after crossing a vigorous F_4 plant with the variety Vitry, D — variety Vitry. Plants grown in 1929.

Fig. 19 A, B, C — Plants of the F_2 generation obtained after crossing a vigorous F_4 plant with the variety *T*. D — Variety *T*. Plants grown in 1929 in the field.

Fig. 20. X — a row of F_1 plants from the cross *Phas. vulg. melleus* × Inexhaustible Bean. O — some plants of the Inexhaustible Bean. Plants grown in 1928.

Fig. 21 — a row of plants belonging to the F_5 line N° 533, grown in 1928.

Fig. 22 — a row of plants of the F_5 line N° 544, grown in 1928.

Fig. 23 A — *Phaseolus vulg. melleus*, B — Inexhaustible Bean, C, D — F_1 plants of the cross *Phaseolus vulg. melleus* × Inexhaustible Bean. Plants grown in 1928 in the field.

Fig. 24 A, B — F_5 plants of line N° 533, C, D — F_5 plants of line N° 544. Plants grown in 1928.

Fig. 25 a — Inexhaustible Bean, b—c — F_1 , d — *Phas. vulg. melleus*. Plants grown in 1928.

Fig. 26. — F_5 plants of line N° 521, grown in 1928.

Fig. 27. — F_5 plants of line N° 132, grown in 1928.

Fig. 28. — F_5 plants of line N° 205, grown in 1928.

Fig. 29 A, B, C — dry vines of vigorous F_6 plants of line N° 525 grown in 1929 in the field, D — *Phas. vulg. melleus*, grown under the same conditions.

Fig. 30 A, B — dry vines of vigorous F_6 plants of line N° 278, grown in the field in 1929, C — Inexhaustible Bean, grown under the same conditions.

Fig. 31. — *Phas. vulg. melleus* in 1932.

Fig. 32. — Inexhaustible Bean in 1932.

Fig. 33. — F_1 plant of the cross *Phas. vulg. melleus* × Inexhaustible Bean, grown in 1932.

Fig 34 and 35. — Vigorous F_7 plants of line N° 161, grown in 1932.

Fig. 36. Vigorous F_7 plant of line N° 108, grown in 1932. This line had very large leaves. All plants shown in Figs 31—36 are photographed to the same scale.

Fig 37 a — *Phas. vulg. melleus*, b — Inexhaustible Bean, c — F_1 of the cross *Phas. vulg. melleus* × Inexhaustible Bean, d — vigorous F_{10} plant of line N° 135, e — F_{10} plant of line N° 108, f — F_{10} plant of the N° 153. The above plants were grown in the field in 1941. g — F_1 plant of the cross *Phas. vulg. melleus* × Inexhaustible Bean grown in 1943, h — Inexhaustible Bean, i — vigorous plant of the F_{11} generation (line N° 5), grown in the field in 1943.

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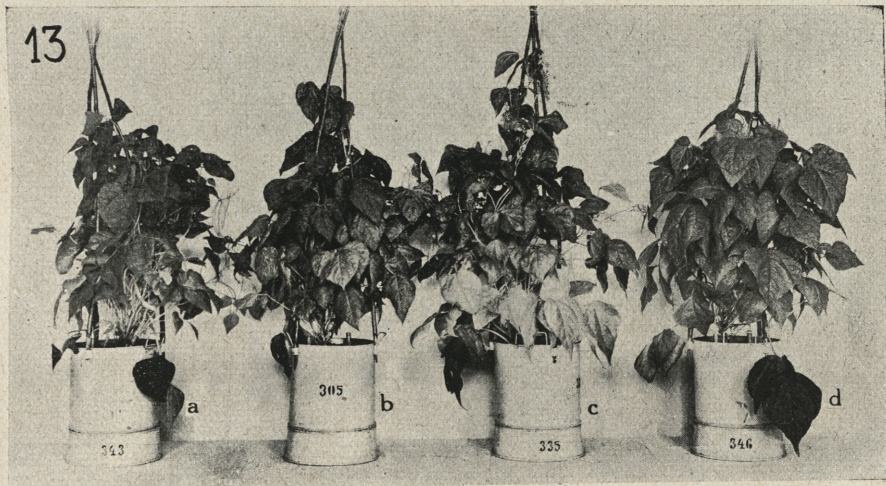
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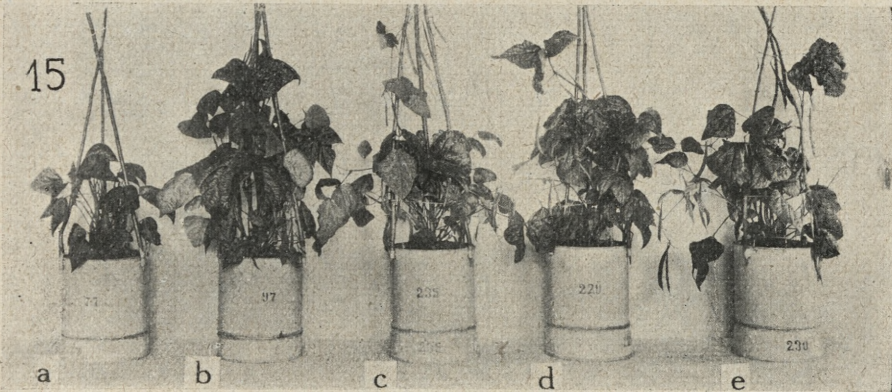
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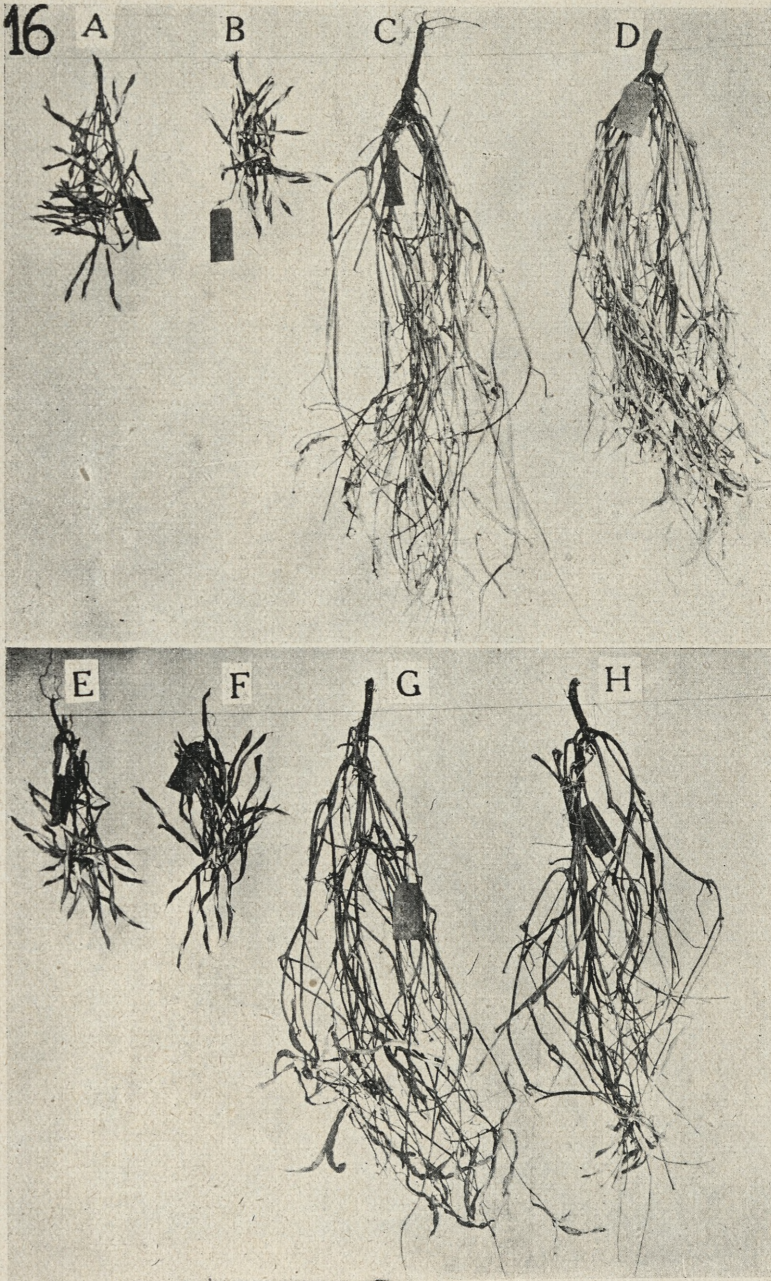


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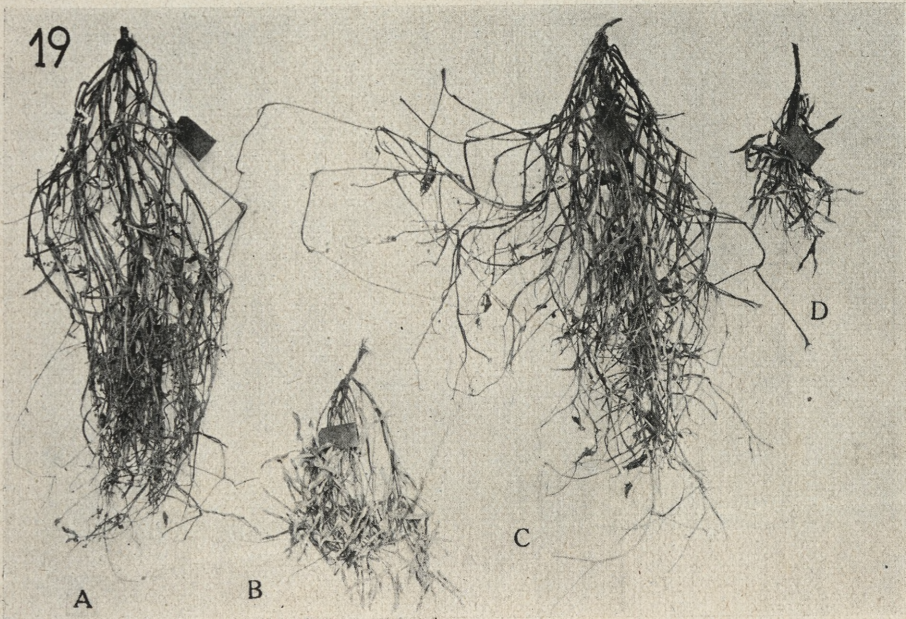
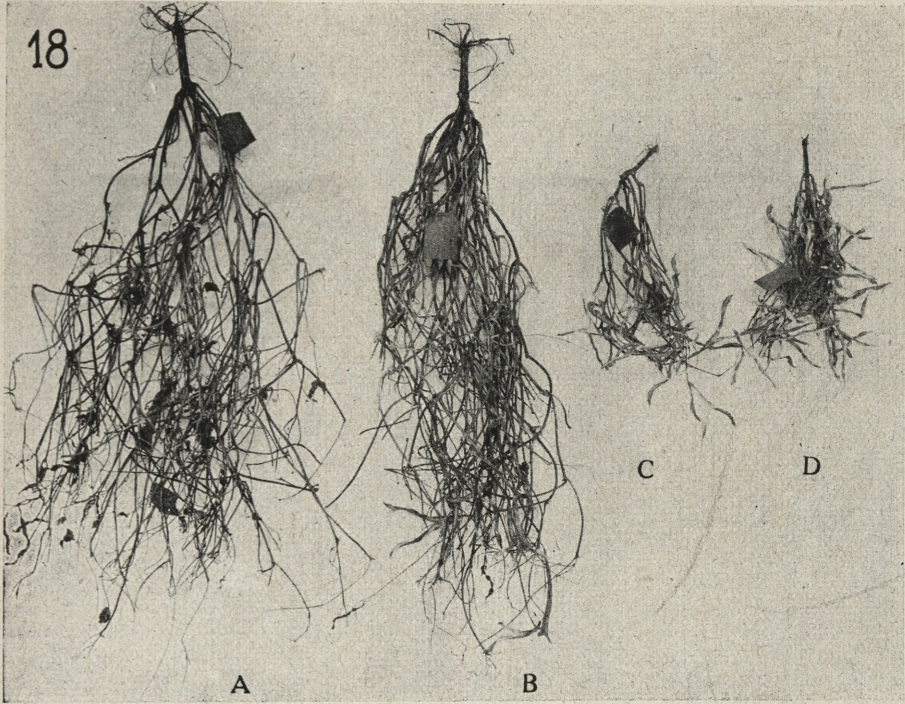
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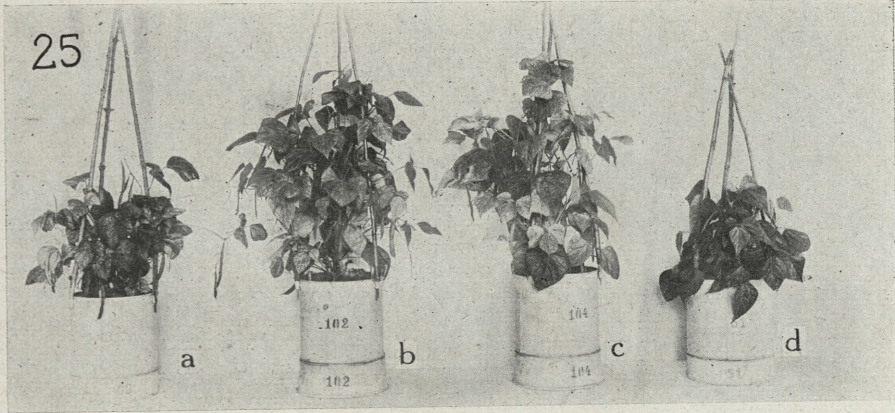
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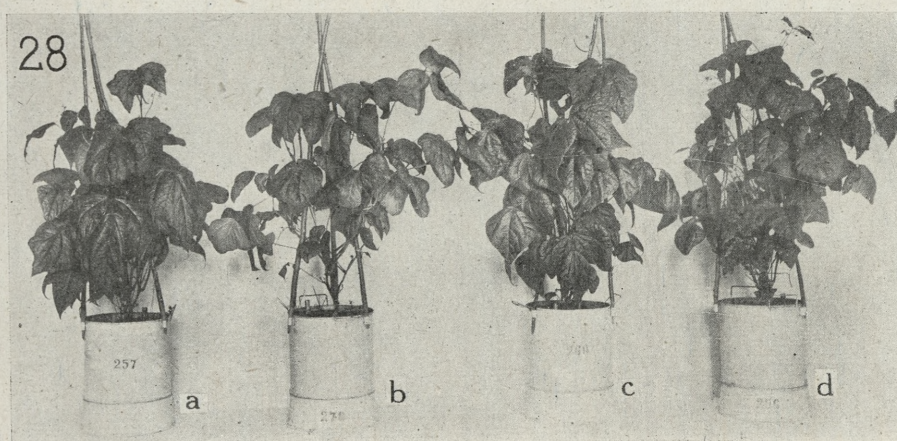
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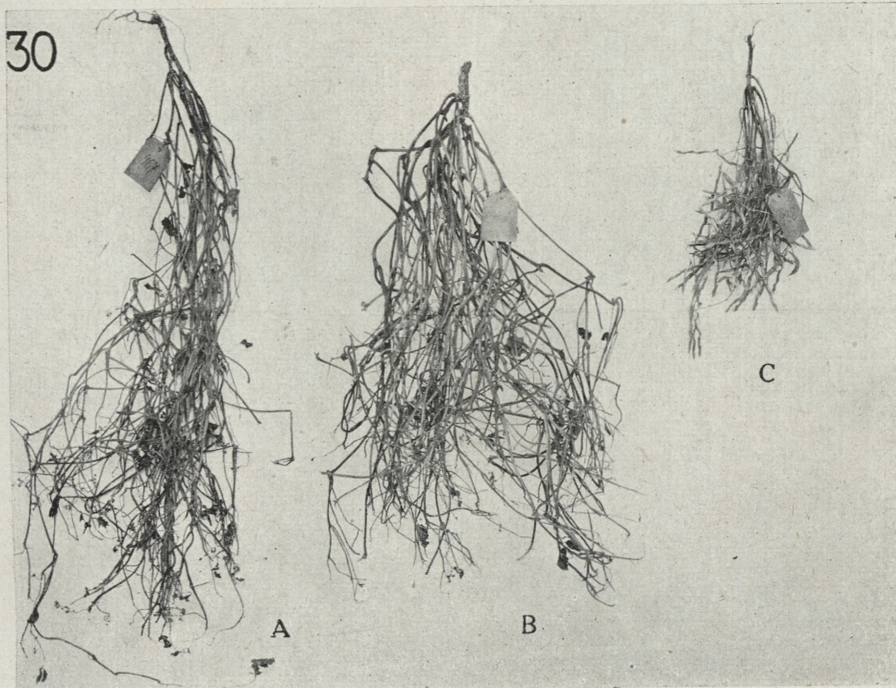


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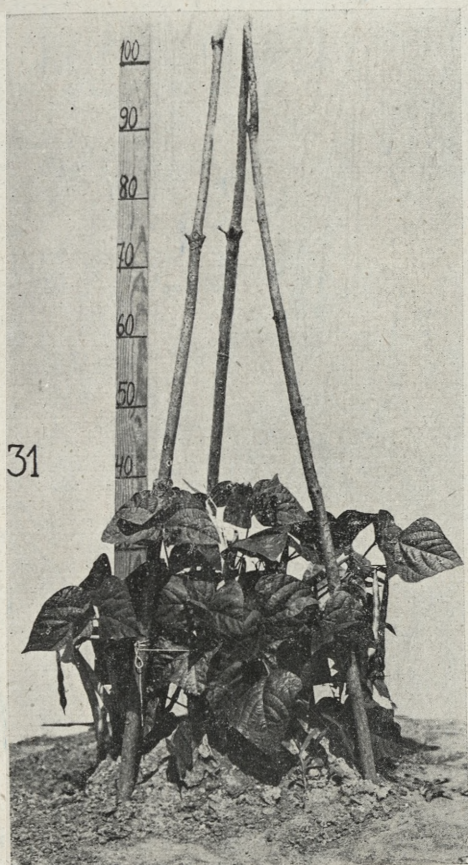


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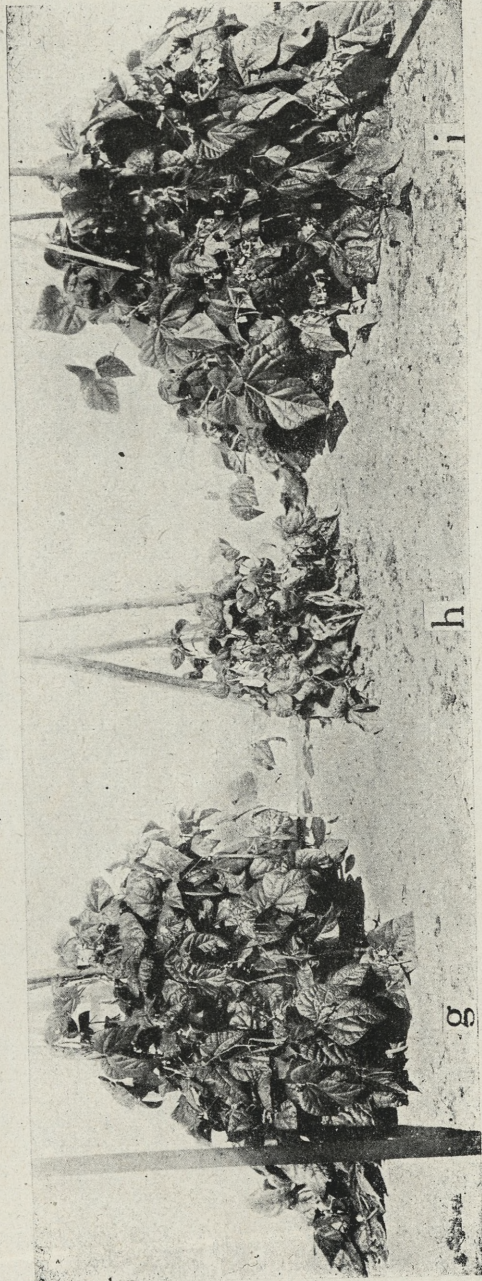
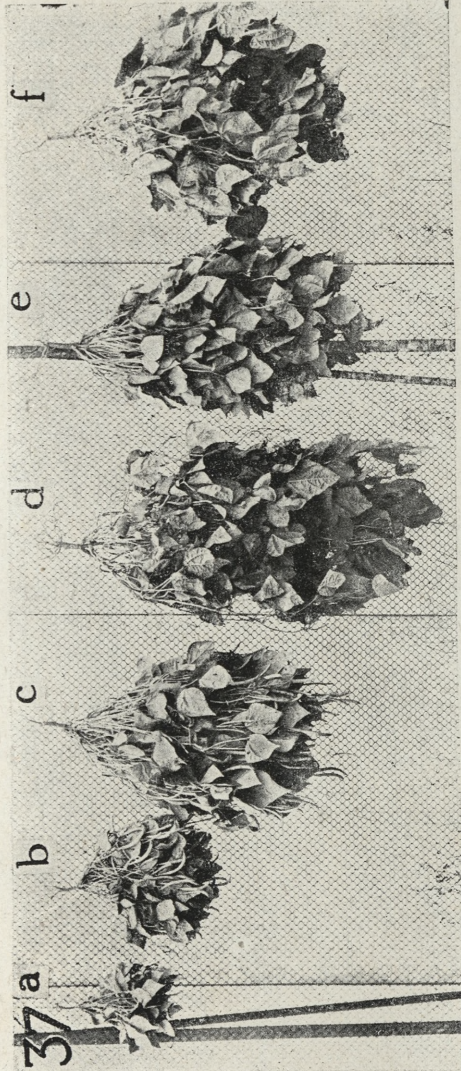
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