Some new results concerning apomixis, sexuality and polymorphism in Potentilla.

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I. Introduction.

Thirteen years ago the occurrence of pseudogamy in different biotypes of *Potentilla Tabernaemontani, collina* and *argentea* was demonstrated (Müntzing 1928). In the same paper the basic chromosome number of the genus was reported to be seven, and it was also found that *P. argentea* L. included biotypes with different chromosome numbers. In a second paper (Müntzing 1931) some further cytological results were reported, comprising the somatic chromosome numbers of 19 biotypes and meiotic observations in diploid and hexaploid *argentea* and in duodecaploid *Tabernaemontani*. The somatic chromosome numbers were found to range from 14 to 84, all being multiples of seven. Not only *P. argentea* but also all the other species studied (*Tabernaemontani, Crantzii* and *collina*) were found to include biotypes with different chromosome multiples.

After this second paper the *Potentilla* work was interrupted for some years, but the material was preserved. In 1937 the junior author took up the *Potentilla* work again, and during the following years new results were obtained which justify a brief report. In the first place this report will deal with the discovery of sexual and partially sexual strains in *P. argentea* and *Tabernaemontani* and with true hybrids raised from crosses with these strains. Further the morphological and cytological polymorphism within *P. argentea* L. has been subject to a special study. For this work a number of new strains were raised from seed samples collected by ourselves or by other persons. For this valuable cooperation we wish to express our sincere gratitude to Prof. O. Rosenberg, Dr. H. Westberg, Messrs. B. Hylmö, S. Kilander, T. Nyholm, G. Östergren and T. Håkansson.

II. The Scandinavian forms of Potentilla argentea *L.*

1. **The material.** In the paper of 1931 (MÜNTZING 1931) *P. argentea* L. was reported to comprise biotypes with 2n=14, 42 and 56. Of the two Scandinavian biotypes studied at that time one was diploid, the other one hexaploid. Both were from Skåne, Sweden (Dalby and Lomma respectively). Since it seemed desirable to determine, whether the Swedish *argentea*-types were generally diploid or hexaploid, and if they also included biotypes with other multiples of seven, a number of new strains were raised. The seeds had in most cases been collected from single individuals growing in the field. In this way the number of Scandinavian *argentea*-strains was increased from 2 to 53. Two of these strains are from Norway, all the others from Sweden. The 53 strains were collected at 37 quite separate localities. Thus, in some cases progenies were raised from more than one plant at the same locality. Twentytwo of the 53 strains were transplanted to the field last summer and have not yet flowered, but the other 31 strains were raised earlier, have flowered and have been subject to close inspection.

2. **Constancy and polymorphism. Chromosome numbers.** Though the number of individuals in each progeny was in most cases limited to about 16 or 20, the *complete uniformity* in each plot has been very striking. Among all these plants not a single true aberrant has been observed. One single progeny comprised a mixture of two different morphological types. However, the plants belonging to the first type were all found to be diploid, those belonging to the second type were all hexaploid. Thus, in this case the seed collector had evidently happened to mix seeds from two different mother individuals. In two of the strains (»*A*—*A*» and »*A*—*B*») the number of individuals observed was as high as about 100, but even in these cases complete constancy was met with.

The constancy within each progeny was found to be accompanied by quite clearcut and often very striking differences between progenies from different localities. The 31 *argentea*-strains which have flowered and, thus, have been fully observed, are *all different from each other.* These differences do not only concern all kinds of morphological details but also physiological characters such as rust resistance, degree of perennial duration, earliness etc.

As expected the progenies studied were found to be characterized

by different chromosome numbers. Thirtysix progenies were *diploid* (2n = 14), eleven were *hexaploid* (2n = 42), three were *tetraploid* (2n = 28), one progeny comprised a mixture of diploid and hexaploid plants and one single progeny was found to be *pentaploid* (2n = 35).

The pentaploid biotype, collected at the west coast of the province of Skåne (Fortuna) is especially interesting. In the first place it represents a new chromosome number within *P. argentea* L., and secondly it combines complete constancy (20 individuals so far observed) with an odd multiple of seven. Thus, since meiosis in this biotype must be irregular (cf. below) the constancy can only be explained by the assumption of a completely apomictic seed formation. By experimental work apomixis has already been demonstrated for 6 other *argentea*-biotypes, including the two Swedish strains *A*—*A* (diploid) and *A*—*B* (hexaploid) (MÜNTZING 1928, 1931). Under such circumstances it is practically certain that the complete uniformity of all the other Scandinavian *argentea*-biotypes is also due to apomixis.

The finding of a few tetraploid *argentea*-biotypes is also quite interesting and fills the previous gap between the chromosome numbers 14 and 42. The tetraploid strains were all raised from seed samples collected at three different localities in the vicinity of Ronneby in the province of Blekinge (South Sweden). These tetraploids have not yet flowered and it has not yet been possible to decide, whether the strains represent the same or different biotypes. At any rate, however, judging from the vegetative characters, they are certainly nembers of *P. argentea* L.

3. **Distribution areas.** In comparison with the diploids and hexaploids the tetraploid biotypes must have a rather limited or localized distribution, which has to be further studied. Comparing the diploid and hexaploid *argentea*-types, it seems rather clear that *the diploids have a more northern distribution area than the hexaploids.* The distribution areas are overlopping, however, and at five different localities in South Sweden (Dalby and Bäckaskog, Skåne; Ronneby, Blekinge; Kristineberg, Bohuslän and Vickleby, Öland) they were found to grow either quite mixed or in more or less close proximity. In the surroundings of Ronneby *P. argentea* L. is evidently represented not only by tetraploid biotypes but also by diploids and hexaploids.

In order to state our present knowledge about the geographical distribution of the *argentea*-biotypes with controlled chromosome

numbers more precisely the following localities may be enumerated (in approximate order from south to north).

Diploid biotypes. In the province of *Skåne*: Skanör, Anklam, Sjöbo, Sjöbo-Veberöd, Veberöd, Dalby, Höör, Axelvold, Bäckaskog, Hovs hallar. In *Blekinge*: Ronneby, Härstorp, Fågelmara. At the isle of *Öland*: Vickleby. In *Småland*: Kalmar, Västervik. In *Halland*: Laxvik, Haverdal, Åsa, Tjolöholm, Gottskär. At the isle of *Gotland*: Sundre. In *Bohuslän*: Stenungsund, Kristineberg. In *Västergötland*: Trollhättan. In *Södermanland*: Stockholm. In *Jämtland*: Frösön. In *Ångermanland*: Offer. In *Norway*: Ringebu (Opland), Hjelle i Breitstad s:n, Nordtröndelag.

Hexaploid biotypes. In *Skåne*: Dalby, Lomma, Kävlinge, Rönneberga backar, Bäckaskog. In *Blekinge*: Ronneby. At the isle of *Öland*: Vickleby. At the isle of *Gotland*: Visby. In *Bohuslän*: Kristineberg.

Tetraploid and pentaploid biotypes. As already mentioned tetraploid *argentea* was obtained from Ronneby (Blekinge) and pentaploid *argentea* from Fortuna (Skåne).

From the lists given above it is evident that the most northern hexaploids so far established were collected at Gotland and at Kristineberg (Bohuslän). Diploid *argentea*-biotypes were observed at seven more northern localities, including Offer' (Ångermanland) and Hjelle (Nordtröndelag, Norway).

Other evidence that the hexaploids have a more southern distribution is represented by the fact that two biotypes collected at Harzgebirge and Müncheberg in Germany were both found to be hexaploid and of the same general appearance as the Swedish hexaploids.

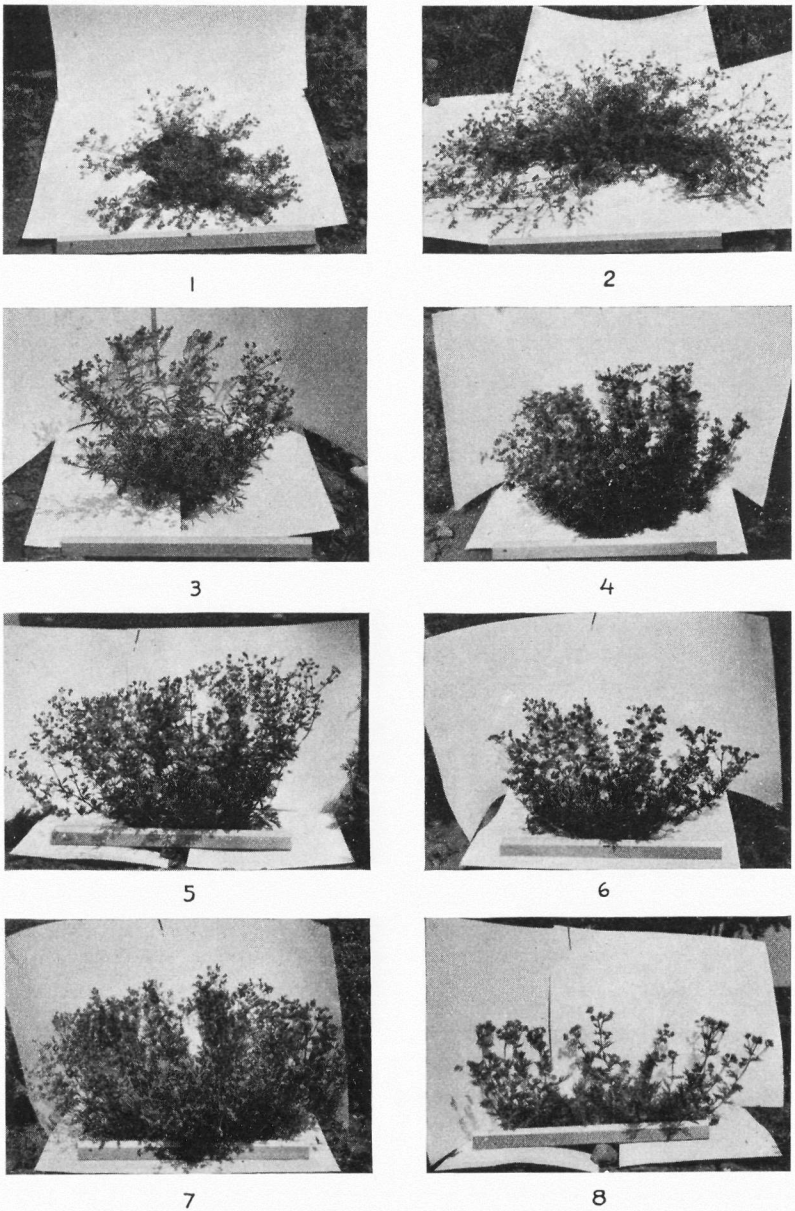
4. **Morphology.** The morphological comparison between *argentea*-biotypes with different chromosome numbers was much stimulated by a paper by MARKLUND (1933). This author finds that the Finnish representatives of the collective species *P. argentea* could easily be divided into two rather well differentiated groups *P. argentea sensu strictu* and *P. impolita* WAHLENB. From herbarium studies MARKLUND also concludes that most other biotypes of the collective species in question can be referred to either one or the other of these two categories. MARKLUND also states, however, that in south Europe there are certainly also other species belonging to the *P. argentea*-group. He also considers it possible that a more close study of the *argentea*-types growing in north and middle Europe may lead to the establishment of some other species-units besides *impolita* and *argentea sensu strictu*. From the brief descriptions of cytologically controlled *argentea*-biotypes by MÜNTZING (1928, 1931) MARKLUND concludes that *P. impolita* is probably hexaploid, *P. argentea* (*s. str.*) diploid. Finally, MARKLUND

points out that *P. impolita* has a more southern distribution than *P. argentea* (*s. str.*). — To avoid misunderstandings it may be convenient in the following to denote the whole collective species as *P. argentea* L. and the two species units described by MARKLUND as *P. impolita* WAHLENB. and *P. argentea*, MARKL.

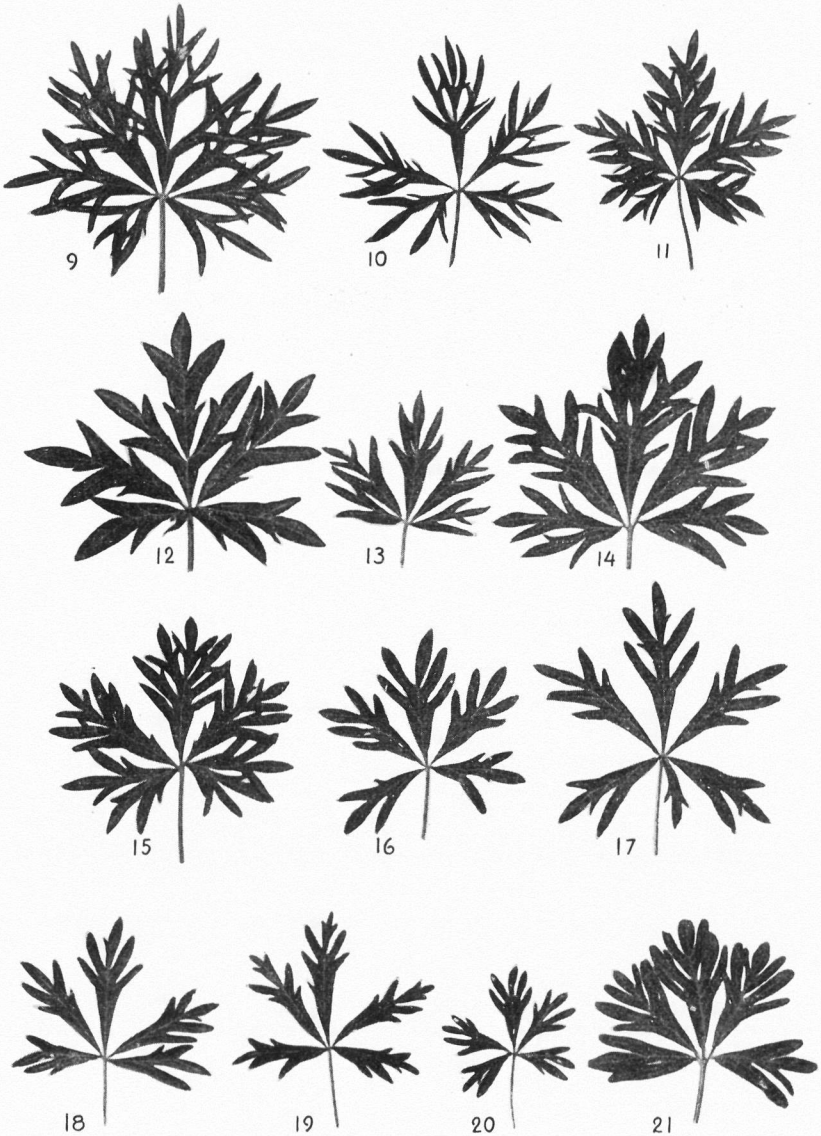
Since about 50 different progenies of *P. argentea* L. with a known origin have been observed in our cultures and have been cytologically examined, we have had a very good opportunity to test, whether our hexaploid strains fit the diagnoses given by MARKLUND for *P. impolita* WAHLENB. and *P. argentea* MARKL.

In the summer of 1940 we had 22 different biotypes of *P. argentea* L. in culture in the same field and under quite comparable conditions. Sixteen of these were diploid, one pentaploid and five hexaploid (cf. Figs. 1—8). These biotypes, which were all different, were examined with a morphological key based on MARKLUND's diagnoses. The following characters were examined in each biotype.

Character nr.	*P. impolita* WAHLENB.	*P. argentea* MARKL.
1.	Shoots high and coarse.	Shoots low and weak.
2.	Shoots erect.	Shoots procumbent.
3.	Leaves more or less densely hairy on the upper side.	Leaves smooth or with sparse hairiness.
4.	Leaflets close to each other with broad base (Figs. 9—15).	Leaflets more separate with narrow base (Figs. 16—20).
5.	4—5 leaf dents at the longest leaflet of the rosette leaves.	Rarely more than 3 leaf dents.
6.	Leaf dents, acute, squarrose.	Leaf dents obtuse.
7.	Stipules on the middle shoot-leaves often bilobate.	Stipules undivided or with one lobe.
8.	The flower stalks start at acute angles.	The flower stalks have a more lateral direction.
9.	Flower stalks long.	Flower stalks short.
10.	Bracts not much developed.	Bracts more developed.
11.	Sepals rather hairy.	Sepals less hairy.
12.	Flower buds with short outer sepals.	Buds with rather long outer sepals.
13.	Sepals acute.	Sepals rather obtuse.
14.	Flowers large, petals broad (Fig. 22).	Flowers smaller, petals narrow (Fig. 22).
15.	Flowers bright yellow, anthers and gynoecium dark yellow.	Flowers, anthers and gynoecium pale yellow
16.	Anthers large and thick, styles thick.	Anthers small, styles thin.
17.	Late flowering.	Early flowering.



Figs. 1—8. Field plants of *Potentilla argentea* L. with different chromosome numbers. — Figs. 1—3, diploid biotypes (2n = 14) from Kalmar (Småland), Veberöd (Skåne) and Hjellum (Norway). Fig. 4 the pentaploid biotype from Fortuna (Skåne). Figs. 5—7, hexaploid biotypes (2n = 42) from Lomma (Skåne), Dalby (Skåne) and Müncheberg, Mark (Germany). Fig. 8, the octoploid type (2n = 56) obtained from the Botanical garden of Iasi. This vigorous type has just started to flower and will later on reach much greater dimensions. — The length of the measure is 50 cm.



Figs. 9—21. Basal leaves of different biotypes of *Potentilla argentea* L. — Fig. 9, the octoploid biotype from the Botan. Garden of Iasi. Figs. 10—14, five hexaploid biotypes (from Dalby, Kävlinge, Harz, Müncheberg and Lomma respectively). Fig. 15, the pentaploid biotype from Fortuna. Figs. 16—20, five diploid, apomictic biotypes (from Frösön, Hjelle, Dalby, Kalmar and Åsa respectively). Fig. 21, a leaf from the diploid, sexual strain *A*—*G*. — × 0,55.

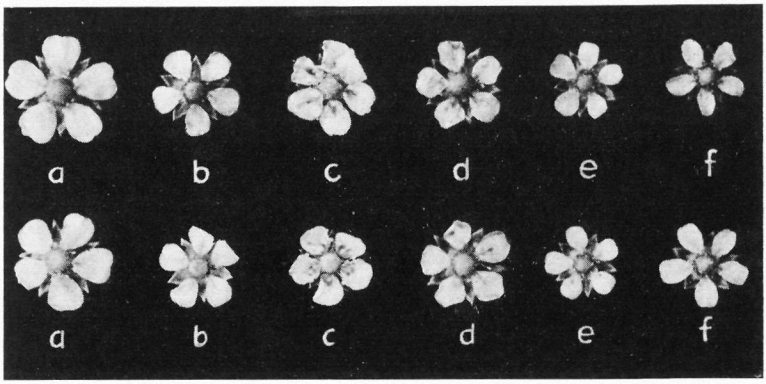


Fig. 22. Flowers of different biotypes of *Potentilla argentes* L. a, octoploid (2n = 56); b and c, hexaploid (2n = 42); d, pentaploid (2n = 35); e and f, diploid (2n = 14). — × 1,0.

For each biotype studied the occurrence of *impolita*-characters was noted with + signs, the occurence of *argentea* MARKL.-characters with — signs. If the character observed was neither typically *impolita* nor *argentea* MARKL. it was noted as 0. The sum of the +, — and 0 signs may evidently be regarded as a rather good measure of the similarity to *impolita* or *argentea* MARKL. According to the key a complete and ideal *impolita* should have the value + 17, an ideal *argentea* MARKL. the value — 17.

However, after the observations had been carried through it was found, that none of the 22 biotypes tested had reached any of these extreme values. Nevertheless, there was a quite clear division into two groups. One group consisted of the five hexaploid and the single pentaploid biotype, the other group comprised the 16 diploid biotypes. In the former group the five hexaploids had the morphological values + 13, + 13, + 12, + 9 and + 7 (M = + 10,8), the corresponding value of the single pentaploid biotype being + 8. Among the diploids the morphological values ranged from — 5 to — 12 with an average of — 8,2.

The above analysis evidently represents a clear verification, firstly of MARKLUND's establishment of two distinct species units within the collective species *P. argentea* L., viz. his *P. impolita* WAHLENB. and *argentea* MARKL. Secondly, his supposition that *P. impolita* is generally hexaploid and *P. argentea* MARKL. diploid has also turned out to be correct. However, the finding of a pentaploid biotype (Fig. 4) with

just as good *impolita*-characters as some hexaploid biotypes shows that *P. impolita* is not quite homogenous with respect to the chromosome number.

During the morphological study of the 22 biotypes it was found that some characters had a much higher diagnostic value than others. This was tested arithmetically in the following way. With respect to character number one the five hexaploid strains had given + signs in two cases and a 0 in the other three. Thus, the average will be + 2 : 5 = + 0,40. If all 5 biotypes had given + signs, the average value would have been + 1,00. In the same way there were nine — and seven 0 among the diploids, the average value thus being — 9 : 16 = — 0,56. If all 16 biotypes had given — signs, the average would have been — 1,00. Thus, in extreme cases, if the character in question has a very good diagnostic significance, the difference between *impolita*- and *argentea*-values may reach a maximum of + 2,00. If the characters are less good, the difference will be smaller, and if the characters are quite useless, the differences will be about ± 0 or have negative values. With respect to the 17 characters tested the following result was obtained:

Character nr.:	1	2	3	4	5	6	7	8
Hexaploids:	+ 0,40	+ 0,40	+ 1,00	+ 0,40	+ 1,00	+ 1,00	— 0,20	+ 0,80
Diploids:	— 0,56	— 0,63	— 1,00	— 0,81	— 0,94	— 1,00	— 0,81	± 0,00
Difference:	+ 0,96	+ 1,03	+ 2,00	+ 1,21	+ 1,94	+ 2,00	+ 0,61	+ 0,80

Character nr.:	9	10	11	12	13	14	15	16	17
Hexaploids:	+ 1,00	+ 0,60	+ 1,00	+ 0,20	+ 0,80	± 0,00	+ 1,00	+ 0,80	+ 0,60
Diploids:	— 0,62	+ 0,25	+ 0,94	+ 0,56	+ 0,19	— 0,94	— 0,88	— 1,00	— 0,94
Difference:	+ 1,62	+ 0,35	+ 0,06	— 0,36	+ 0,61	+ 0,94	+ 1,88	+ 1,80	+ 1,54

Judging from the above figures characters nr. 3 and 6, i. e. the hairiness of the leaves and the shape of the leaf-dents, have an excellent diagnostic value (cf. Figs. 9—20). Characters nr. 5, 15 and 16 (number of leaf dents, flower colour and size of the anthers and styles) are also quite valuable. Of the remaining 12 characters studied 9 are more or less useful, the values of the differences ranging from + 1,62 to + 0,61. Three characters, however, nrs. 10, 11 and 12, were found to be quite or almost quite useless, the differences in these cases having the values + 0,35, + 0,06 and — 0,36 respectively.

5. **Duration of life. Rust resistance.** In addition to the diagnostic characters discussed above it may be mentioned that some other typical differences between the diploid and polyploid groups were observed in our cultures. In the first place it should be mentioned that there is a very marked average difference between the duration of life of the diploid and polyploid types. The hexaploid (as well as the pentaploid) *P. impolita*-types are all strictly perennial, whereas the diploid *P. argentea* MARKL. is scarcely more than biennial. If seeds of biotypes belonging to the latter species group are germinated in the spring,

and the young plants are transplanted to the field in the summer of the same year, they will survive the following winter very well. Next summer they will reach full development and flower abundantly. (They also flower to some extent in the first summer.) After this summer they generally survive the next winter rather poorly or die completely in contrast to the hexaploids, which retain their full vigour during several years. Though there is a quite typical average difference between the two groups *impolita* and *argentea* as regards duration of life, it should be noted that minor but quite clearcut biotype differences were observed within the diploid group. Some biotypes were found to be more perennial than others. Among the hexaploids no such differences have been found, all the types being strictly perennial. Also the single pentaploid biotype behaved in the same way.

It might be suspected that the different degrees of perennial life duration are due to differences in cold resistance. This is not the case, however, firstly because the diploids show a perfect winter hardiness during their first winter, secondly because they were found to have a more northern distribution than the hexaploid *impolita*-types. Thus, there is a true difference in periodicity between the two groups which is quite independent of the winter hardiness as such.

Another observation may be mentioned which also demonstrates a difference between *impolita* and *argentea* MARKL. In the spring and summer of 1940 our *Potentilla* cultures were severely attacked by rust. This attack, however, affected the diploid biotypes much more than the hexaploids (and the pentaploid). The latter suffered very little, indeed, in contrast to several diploid *argentea*-types growing close by. Among the diploids there were also clear differences in rust susceptibility. Some biotypes were quite severely attacked, others much less. There was no correlation between degree of rust susceptibility and lack of winter hardiness during the second winter after germination. Some diploid biotypes which had been severely attacked by rust in the preceding summer survived the winter rather well and *vice versa*. Thus, neither differences in winter hardiness, nor in rust susceptibility influence the duration of life. The periodicity is controlled by other genetic factors.

6. **Seed and pollen size** The hexaploid *impolita*-biotypes were found to have larger seeds and pollen grains than the biotypes of diploid *argentea* MARKL. This difference, which is probably correlated with the quantitative difference in chromosome number, seems to be quite typical.

Seed size was measured in samples from 19 diploid, 3 tetraploid and 9 hexaploid biotypes. The 19 diploids belonged to *P. argentea* MARKL., the hexaploids to *P. impolita*. The morphology of the tetraploids has not yet been studied, the measurements being undertaken at the original seed samples obtained. From each biotype 50 seeds were measured. The 19 average values thus obtained in the diploids were found to range from 18 to 23 units with an average value of 20,45. In the 9 hexaploids the average values ranged from 23 to 26, the mean value of this series being 24,61. Since the two series are almost quite separated from each other, statistical treatment of the difference is superfluous. The significance of the difference is further demonstrated by the fact that the seeds of the tetraploid biotypes were found to be intermediate in size, the total average of the tetraploids being 23,83.

Quite similar results were obtained with respect to pollen size. Data are available for pollen samples of 4 diploid *argentea* MARKL.-biotypes and 4 *impolita*-biotypes. In each sample 50 pollen grains were measured. In the four diploid biotypes the average diameter was found to be 8,26, 8,30, 8,30 and 8,56 respectively. In the four hexaploids the corresponding values were 9,40, 9,40, 9,40 and 9,70 respectively.

Adding the values for all the diploid and hexaploid pollen samples the following two series were obtained:

	Pollen diameter							
	7	8	9	10	11	units	n	M ± m
Diploid biotypes	4	128	62	6			200	8,35 ± 0,04
Hexaploid »	1	14	77	105	3		200	9,48 ± 0,05

The difference between the average values 1,13 ± 0,06 is evidently significant (D/m = 18,8).

Thus, it is rather probable that pollen size in *P. impolita* is generally larger than in *P. argentea* MARKL. This difference, though rather slight, may be of importance for herbarium studies. In doubtful cases this character may help to decide to which species unit a certain specimen should be referred. — If ripe seeds are available it is quite easy to tell, whether the plant is diploid or hexaploid. Predictions of this kind could be made for about 20 seed samples and were afterwards found to be correct almost without exception. In a few cases it could not be decided, whether the seed sample was diploid or hexaploid, and in these cases it was later found that the samples had been tetraploid. In one case the seed measurements gave a bimodal curve, and later it was found that the seed sample had given a mixture of diploid and hexaploid plants.

7. **Pollen fertility.** Pollen fertility was examined in 17 diploid, 5 hexaploid and 1 pentaploid biotype. The percentage of good pollen

was determined in a total of 116 plants. In one of the diploid biotypes only one plant was examined, in the pentaploid 10 plants and in all the other biotypes 5 plants per biotype.

A clear difference between the average pollen fertility of the diploid and polyploid biotypes was revealed by these studies. Among the diploids 77 of the 81 plants examined had between 90 and 100 per cent good pollen, only 4 plants having slightly lower percentage values. Among the hexaploids, on the contrary, only 2 of the 25 plants examined had 90—100 per cent good pollen, the corresponding values of the other plants ranging from 30 to 90. In the first group the percentage of plants with at least 90 per cent good pollen will be $95{,}1 \pm 2{,}4$. In the second group the corresponding value will be $8{,}0 \pm 5{,}4$ per cent. The difference $95{,}1 - 8{,}0 = 87{,}1 \pm 5{,}9$ is evidently significant.

As might be expected the pentaploid biotype had rather bad pollen, the percentage of good pollen in the 10 plants examined ranging from 40 to 70 with an average value of 51 per cent. — The counts in all the biotypes may be summarized in the following way:

	Per cent good pollen									
	30—40	40—50	50—60	60—70	70—80	80—90	90—100		n	M
Hexaploid plants (from 5 biotypes)	1	3	10	4	2	3	2		25	63,00
Pentaploid plants (from 1 biotype)		8	1	1					10	48,0
Diploid plants (from 17 biotypes)					1	3	77		81	94,4

Besides the clear difference between diploids and hexaploids the above values also demonstrate that plants belonging to the pentaploid biotype are less fertile than most hexaploid plants.

8. **Meiosis in the pentaploid biotype.** In a previous paper (MÜNTZING 1931) meiosis in the p. m. c. of one diploid and one hexaploid *argentea*-biotype was described. The meiotic divisions were found to be quite regular in the diploid. In the hexaploid there were minor irregularities, including the occasional occurence of multivalents, composed of 3—6 chromosomes. This indicated a certain degree of autopolyploidy.

These previous observations on meiosis in the *P. argentea*-group may now be supplemented with some data from the single pentaploid biotype (from Fortuna, Skåne). The flower buds were partly fixed in chrome-acetic-formalin, partly in Carnoy. The latter fixative gave the best result. The slides were stained with gentian violet.

At *first metaphase* most of the chromosomes are present as bivalents, these bivalents generally being surrounded by a variable

number of univalents. A more detailed study also revealed the occurrence of trivalents. In a few cases quadrivalents could also be distinguished with more or less certainty.

The number of univalents outside the I—M groups (observed in side view) was observed in two slides with the following result:

	Number of univalents.									
	0	1	2	3	4	5	6	7	n	M
Slide nr. 1:	1	2	10	12	11	8	4	2	50	3,60
» » 2:			2	7	11	13	4	1	38	4,34
Total:	1	2	12	19	22	21	8	3	88	3,92

Thus, the number was found to vary from 0 to 7 with an average of about 4 univalents. The actual number may be somewhat higher owing to the difficulty of distinguishing all univalents in some cells. Nevertheless it may be concluded that the average number of univalents is lower than 7.

The complete I—M configurations could be distinguished with some difficulty in 18 cells (14 polar views + 4 side views). These cells represented 11 different configurations, which occurred in the following frequency:

Configuration nr.	Frequency	Configuration nr.	Frequency
1 : $13_{II} + 9_{I}$	1	7 : $3_{III} + 11_{II} + 4_{I}$	2
2 : $14_{II} + 7_{I}$	1	8 : $1_{IV} + 3_{III} + 9_{II} + 4_{I}$	1
3 : $1_{III} + 12_{II} + 8_{I}$	1	9 : $15_{II} + 5_{I}$	2
4 : $1_{III} + 13_{II} + 6_{I}$	1	10 : $2_{III} + 13_{II} + 3_{I}$	2
5 : $2_{III} + 12_{II} + 5_{I}$	5	11 : $1_{IV} + 13_{II} + 5_{I}$	1
6 : $3_{III} + 10_{II} + 6_{I}$	1		

According to these data one or a few trivalents were present in most cells, the most typical configuration probably being $2_{III} + 12_{II} + 5_{I}$. In thirteen of the cells studied the number of bivalents + trivalents was not higher than 14 (counting the occasional quadrivalents as two bivalents). In five cells, however, (configurations 9—11) the sum was as high as 15. At least some of these latter cells were clear enough to be quite convincing.

The most plausible explanation of the observed mode of pairing is that the pentaploid biotype in question contains several more or less homologous genomes. Four of these genomes generally pair as bivalents or form an occasional quadrivalent. The fifth genome may in rare cases occur as 7 univalents, but more frequently some of these chromosomes form trivalents with homologues in the other genomes. The occasional occurrence of 15 bivalents + trivalents may be due to intragenomatic pairing.

These pairing conditions in the pentaploid are illustrated by Figs.

23—27. In Figs. 23—25 there are three cells in polar view showing the probable configurations $1_{IV}+1_{III}+11_{II}+6_{I}$, $2_{III}+12_{II}+5_{I}$ and $1_{IV}+13_{II}+5_{I}$. The quadrivalent in Fig. 23 is situated at 5 o'clock. The quadrivalent in Fig. 25 may possibly be two independent bivalents but more probably it is a zig-zag chain of four chromosomes. Two complete I—M groups in side view are shown in Figs. 26—27, the configurations probably being $3_{III}+11_{II}+4_{I}$ and $2_{III}+13_{II}+3_{I}$ respectively. The trivalents in Figs. 23—27 are either V-shaped chains (the most frequent type), straight chains or ring-and-rod-trivalents (as in Fig. 27).

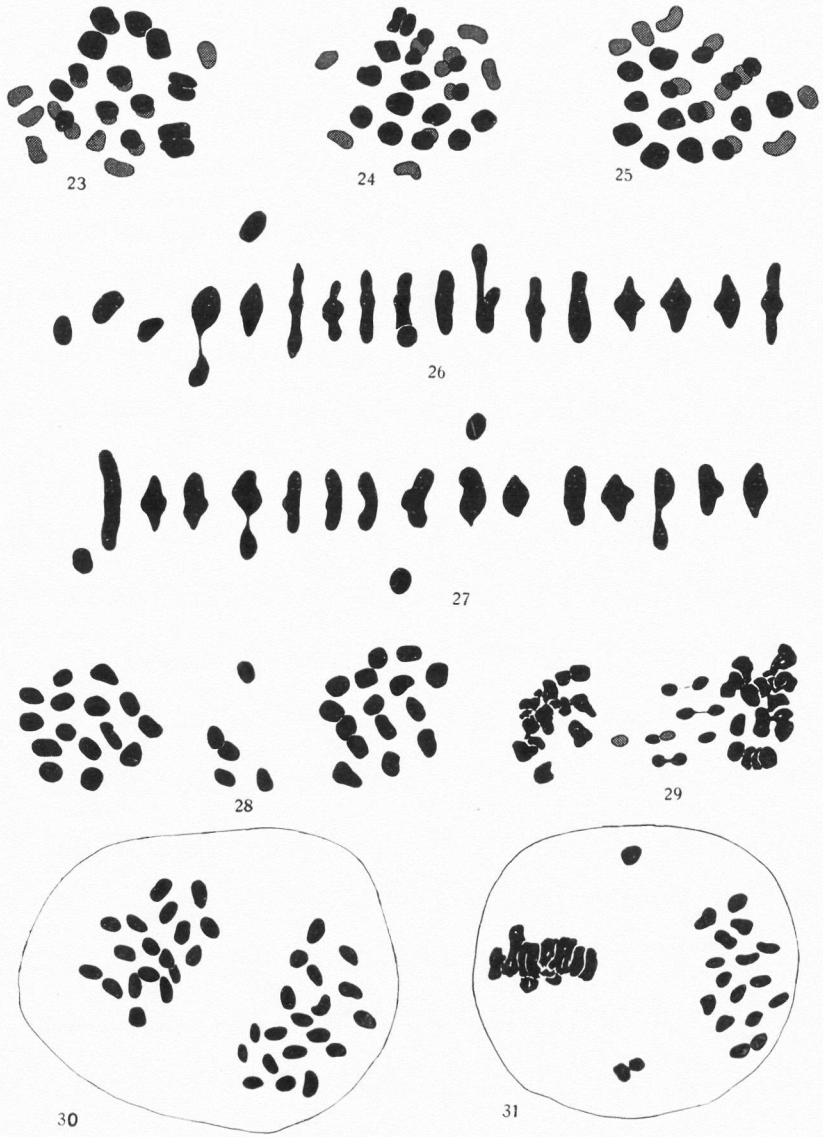
At *first anaphase* lagging and dividing univalents were frequently seen, though several univalents also may pass to the poles without division. An anaphase with division of 5 univalents is represented in Fig. 29. Figs. 28 shows an early first anaphase with undivided univalents between the anaphase-groups. The distribution in this case is 15—5—15. In another cell at exactly the same stage the distribution was 14—6—15. These cells clearly verify that the somatic chromosome number of the biotype in question is really 35.[1]

The number of chromosomes in the second metaphase plates was counted with the following result:

Number of chromosomes	14	15	16	17	18	19	20	n	M
» » plates	3	6	19	13	17	10	2	70	17,0

Since much chromosome elimination occurred at the first division, resulting in a rather high frequency of micronuclei at interphase, the average number of chromosomes at II—M should, from that reason, be much lower than half the somatic number. However, as regards the chromosome number in II—M-plates, the elimination at the first division is partly compensated for by the frequent division of univalents at first anaphase. Thus, in spite of the elimination the average number of chromosomes in the II—M plates was found to be as high as 17,0. At second anaphase, however, there was much chromosome lagging, and therefore the total meiotic result will be gametes which, on an average, have less than half the somatic number. — These conditions are briefly illustrated by Figs. 30—31. In Fig. 30 both II—M plates are possible to count, one having 18 chromosomes, the other one 19. Since the somatic number is 35, this means that 2 univalents have divided at I—A, the halfs being included in the interphase nuclei. Some of the chromosomes in the plates are, indeed, rather small and probably represent the split univalents. — Fig. 31, finally, shows an ordinary cell at II—M with 16 chromosomes in the visible plate and 3 chromosomes outside the plates, which have been eliminated at the first division.

[1] It seems superfluous in the present paper to represent any somatic plates. Quite clear plates with short chromosomes were obtained in *Potentilla* by treatment of the seedlings with low temperature before fixation in diluted chrome-acetic-formalin. (12 hours at ±0—+ 2° C.).



Figs. 23—31. Meiosis in the p. m. c. of pentaploid *P. argentea*. — Figs. 23—25, I—M, polar view. Fig. 23, probably $1_{IV} + 1_{III} + 11_{II} + 6_I$; Fig. 24, $2_{III} + 12_{II} + 5_I$; Fig. 25, probably $1_{IV} + 13_{II} + 5_I$. Figs. 26—27, I—M, side view (separately drawn). Fig. 26, $3_{III} + 11_{II} + 4_I$, Fig. 27, $2_{III} + 13_{II} + 3_I$. Fig. 28, I—A, polar view (separately drawn), distribution 15—5—15. Fig. 29, I—A, division of 5 univalents. Fig. 30, II—M, distribution 18—19 (2 univalents have divided at I—A). Fig. 31, II—M, 3 eliminated chromosomes, 16 chromosomes in the visible plate. — × 4250.

III. Some foreign, deviating argentea-types.

In addition to the Scandinavian members of the *argentea*-group and the hexaploid biotypes from Germany our cultures include some deviating and rather interesting types from other sources.

1. **The octoploid biotype A-E.** The first of these deviating types to be mentioned is an octoploid biotype (»*A*—*E*») obtained from the Botan. Garden of Iasi (middle Europe). This biotype is evidently apomictic just as all other *argentea*-types hitherto described. The original seed sample gave a quite uniform progeny. One of these plants gave a second progeny (after open pollination), consisting of 36 plants, which was also absolutely uniform. Further, the *A*—*E* biotype has given maternal offspring in crosses with two different biotypes of *P. collina* (MÜNTZING 1928, Tab. 5). (Unfortunately there is a misprint in this table. The crosses »*A*—*C* × *C*—*A*» and »*A*—*C* × *C*—*C*» [near the bottom of the table] are in reality *A*—*E* × *C*—*A* and *A*—*E* × *C*—*C*.)

As already mentioned by MÜNTZING 1931, the octoploid *A*—*E* is very vigorous (cf. Fig. 8). This vigour is correlated with a pronounced lateness, the commencement of the flowering being much later than in all the other diploid, pentaploid and hexaploid nembers of the *argentea*-group. *A*—*E* is strictly perennial and in morphological respects a super-*impolita* type. The morphological value (cf. p. 244) was found to be +14. The leaves are rather hairy on the upper surface and with deeply incised narrow and acute leaf dents (Fig. 9). The flowers are rather large (Fig. 22a).

2. **The partially sexual strain A-C.** a. Morphology, constancy and fertility. In previous publications the *argentea*-type *A*—*C*, obtained from the Botan. Garden of Basel, Switzerland, was reported to be diploid ($2n = 14$) and at least partially apomictic (MÜNTZING 1928). There remained some doubt, however, whether it was strictly truebreeding (MÜNTZING 1931, p. 169). Recent results demonstrate, indeed, that this strain is *partially sexual*.

From two typical *A*—*C* plants (4—1 and 4—2) progenies were raised after open pollination. In the first progeny (from 4—1), consisting of 70 individuals, there were two clearly deviating plants and one plant which only sligthly differed from typical *A*—*C*. Typical *A*—*C* (Fig. 32) is characterized by extremely hairy leaves which are greyish or whitish green even on the upper surface (Fig. 34, upper row to the

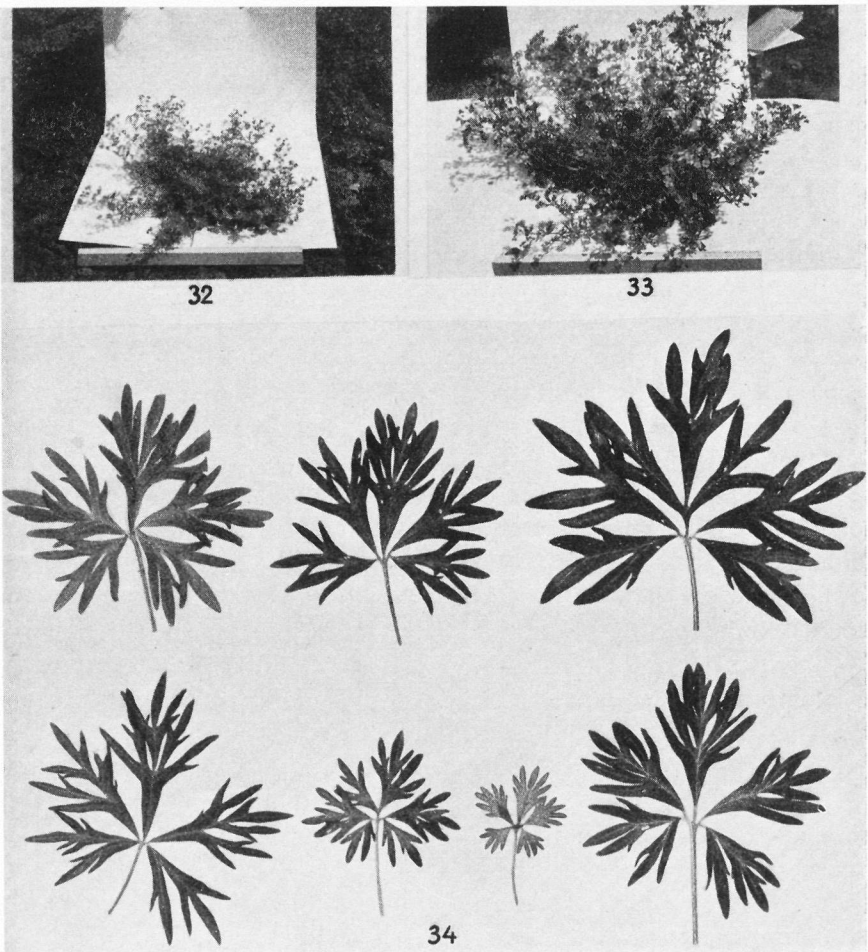


Fig. 32—33. Plants of the partially sexual *argentea*-strain *A—C* (2n = 14). Fig. 32, a typical plant, Fig. 33 an aberrant, vigorous plant. Fig. 34, leaves of different *A—C* plants. Upper row to the left, typical *A—C;* upper row in the middle, a slightly deviating *A—C* type, representing a new, almost constant line, the other five leaves demonstrate the intensive variation in a segregating progeny of an *A—C* aberrant (such as the plant in Fig. 33).

left). The flowers are very large and pale yellow. The plants are strictly perennial. — The three aberrant plants were all found to be diploid like typical *A—C*. Two of them were very vigourous and gave every impression of being spontaneous hybrids with diploid Scandinavian *argentea* MARKL. (cf. Fig. 33). Such biotypes had been growing

near the mother plant. The third aberrant only differed from the type by a more yellowish green leaf colour and some minor vegetative differences. This plant, like typical *A—C* had quite good fertility in contrast to the two supposed F_1-hybrids, which had only 20 and 30 per cent good pollen respectively. All three deviating plants, however, produced much seed, and progenies could be raised. The slightly aberrant and fertile plant gave a progeny of 20 plants after open pollination. This progeny was almost quite constant and identical with the mother but on an average clearly different from a strictly comparable progeny of typical *A—C*. Thus a new, slightly different *A—C* type had arisen (Fig. 34, upper row in the middle), probably by an occasional genetic recombination within the *A—C*-type and not by outcrossing.

The progenies of the other two aberrants, the supposed F_1-hybrids, behaved in a completely different way. They were characterized by a very intensive segregation (cf. Fig. 34), indicating that the mother plants had been purely sexual. A total of 211 plants were studied, 70 obtained after isolation and 141 after open pollination. The progenies of both mother plants behaved in just the same way. Instead of giving long descriptions of the multitude of various forms in this material, it may suffice to state that the plants gave the impression of representing *a typical species cross segregation.* The variation in morphological details was enormous, and as regards vigour there were all transitions between quite abnormal types with poor vigour to extremely well developed plants. Many plants had died at an early stage. Only one of the segregation products was similar enough to the original mother type to be classified as typical *A—C*.

The variation in pollen fertility in the *A—C* strains was studied with the following result.

	Per cent good pollen									
Family nr.	20—30	—40	—50	—60	—70	—80	—90	—100	n	M
149							1	14	15	94,3
150					1	1	1	11	14	90,7
151	1	—	2	—	1	—	—	2	6	61,7
153						1	2	11	14	92,1
154	3	4	11	3	5	3	9		38	57,6

Families nr 151 and 154 (raised after isolation) belong to the segregating material just described. Though highly variable, pollen fertility is better than in the mother plants, the average values being 57,6 and 61,7. As already mentioned the corresponding mother plants had 30 and 20 per cent good pollen respectively.

Family 153 represents the new *A—C* type derived from the slightly aberrant mother plant. Pollen fertility in this family is evidently just as good as in typical *A—C*, the average value being as high as 92,1 per cent. This value may be compared with the first two average values of the table, 94,3 and 90,7 which represent two different progenies of typical *A—C* plants studied in 1940. Family 149 belongs to the offspring of the plant 4—1 mentioned above (p. 252). Family 150 represents the offspring after open pollination of plant 4—2. Also in this progeny there was no absolute constancy, one individual being clearly aberrant (Fig. 33) and of the same type as the probable F_1-hybrids discussed above. Again this aberrant was found to be less fertile than typical *A—C*-plants (fig. 32), the percentage of good pollen being as low as 60 per cent.

Definite proof of the partial sexuality of the *A—C* strain was obtained by a number of crosses between *A—C* as the mother parent and a number of morphologically quite different, diploid Scandinavian types of *P. argentea* MARKL. This material has not yet flowered, but it is already certain that many true hybrids have been produced in addition to the purely maternal plants.

b. Cytological results. In the families 151 and 154, progenies after isolation of the two clearly aberrant *A—C*-plants, root tips were fixed of 4 and 5 plants respectively. The plants fixed were taken completely at random. Of the four plants in family 151, three were found to be diploid ($2n = 14$) and one *triploid* ($2n = 21$). Of the five plants in the other family four were diploid and one triploid. Thus, there is reason to believe that *about 20 per cent of the plants in the segregating families were triploid instead of having the normal diploid number.* Such triploids must have arisen by fertilization of unreduced ovules.

It was not possible with certainty to distinguish other triploids in the field by morphological inspection or by pollen examination. The two controlled triploids had 30 and 40 per cent good pollen resp., but some diploids were even less pollen fertile, the percentage of good pollen in the 7 diploids cytologically examined ranging from 20 to 90. The degree of seed setting seems to be a more valuable indication of the chromosome number, the triploid plants having a much less good seed production in the isolation bags than the plants found to be diploid.

Meiosis in the p. m. c. was studied in the triploids and was found to be quite similar in the two triploid individuals. For comparison meiosis was also observed in diploid *A—C*. In the diploid meiosis was

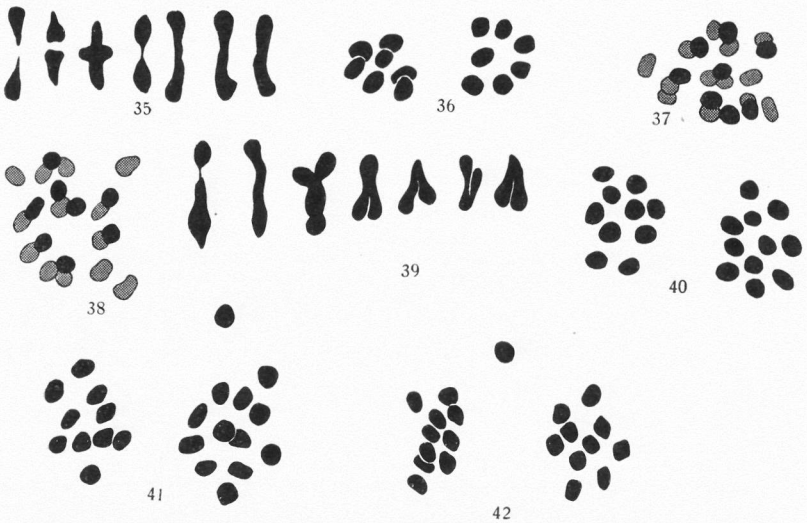


Fig. 35—36. Meiosis in diploid *A—C* (2n = 14). — Fig. 35, I—M (separately drawn), 7_{II}; Fig. 36, II—M, distribution 7—7. — Figs. 37—42. Meiosis in triploid *A—C* (2n = 21). — Figs. 37—38, I—M, polar view; Fig. 37, $4_{III} + 3_{II} + 3_{I}$; Fig. 38, $3_{III} + 4_{II} + 4_{I}$; Fig. 39, I—M, side view (separately drawn), $6_{III} + 1_{II} + 1_{I}$; Figs. 40—42, II—M; Fig. 40, distribution 10—11; Fig. 41, distribution 10—12 (one univalent has divided at I—A); Fig. 42, distribution 10—10, one chromosome eliminated. — × 4250.

perfectly regular. This is evident from Figs. 35—36. Fig. 35 represent a I—M group in side view, 7 bivalents being formed. Fig. 36 is a regular second metaphase with 7 chromosomes in each group. — The triploid plants were characterized by a rather high frequency of trivalents at first metaphase. This is evident from Figs. 37—39. Figs. 37—38 show two I—M groups in polar view with the configurations $4_{III} + 3_{II} + 3_{I}$ and $3_{III} + 4_{II} + 4_{I}$ respectively, and in Fig. 39 there is a side view with $6_{III} + 1_{II} + 1_{I}$. Most of the trivalents are V-shaped chains.

Since the number of univalents at I—M is inversely proportional to the number of trivalents, the frequency of univalents was counted in 80 cells with the following result:

Number of univalents	0	1	2	3	4	5	n	M
» » cells	21	28	21	5	4	1	80	1,33

The average number is 1,33, which would correspond to a trivalent frequency of 5,67. Due to the possibility of overlooking some univalents the average frequency of univalents may in reality be slightly

higher, and, hence, the frequency of trivalents sligtly lower. At any rate, however, trivalents are quite frequent and more frequent than in the pentaploid *argentea*-biotype discussed above.

The presence of univalents at I—M causes some lagging, division and elimination of chromosomes. This is demonstrated by Figs. 41—42, showing cells at second metaphase. In Fig. 41 the two plates contain 10 and 12 chromosomes. One univalent has evidently divided at I—A, the halfs of the univalent being included in the daughter nuclei. In Fig. 42 the chromosome distribution is 10—10, one chromosome being eliminated. Fig. 40, finally, shows the most regular distribution, 10—11. The number of chromosomes was counted in 37 II—M plates. It was found to range from 8 to 13 with an average of 10,41. Due to lagging and elimination at second anaphase the average chromosome number of the gametes will be somewhat lower than 10,41.

3. **A sexual argentea-strain.** a. Diploid plants. In 1937 a new seed generation was raised from a number of *P. argentea*-biotypes in our cultures. The progenies were raised from single openpollinated mother plants. Due to the apomictic seed formation most of these *argentea*-progenies were quite uniform as expected. Two progenies, however, behaved differently. One of them was an *A—C*-family. As was reported in detail in the preceding paragraph this family comprised a few clear aberrants but was otherwise quite or almost quite constant.

Another family, denoted by *A—G*, differed still more strikingly from all the other *Potentilla*-progenies cultivated at that time. It was highly variable, and of the 16 plants in the progeny not two were alike. Thus, this material evidently represented a sexual *argentea*-strain. This was verified by raising a second generation and by successful crosses with other biotypes of *P. argentea* and *opaca*.

The origin of this sexual *P. argentea*-strain is somewhat obscure. In 1925 a great number of seed samples of *P. argentea* were obtained from various botanical gardens. One sample, nr. 1925—39, was from the botanical garden of Edinburgh and gave rise to a family of 16 plants, which were apparently uniform. A cytological examination showed that this biotype was diploid, having $2n = 14$ (MÜNTZING 1931). In 1928 a second generation of this type was raised. This family, nr. 1928—101, consisted of 10 plants, which according to the notes were typical. Seeds were gathered after open pollination from one plant of family 1928—101, and in 1932 this seed sample gave rise to family nr. 1932—9. This family was raised just in order to preserve the biotype in question which, like most other diploid *argentea*-types, was not strictly perennial. Therefore, family nr. 1932—9 was not especially

observed. In 1935 only one plant of 1932—9 was still alive, and this plant (1932—9—1) did not seem to be a quite typical *A*—*G* plant. However, in order to save the diploid *A*—*G*-line, if possible, seeds were collected from this plant after open pollination and were germinated in 1937. These seeds gave the extremely variable and evidently purely sexual progeny just described.

From the above account it is clear that the sexual strain now available is not identical with the original, uniform *A*—*G*-type. Several considerations have led us to the conviction that the sexual material is the result of a spontaneous cross between the original *A*—*G*-line and the partially sexual *argentea*-strain *A*—*C*. This explanation is supported by the following facts.

Firstly, the sexual strain was found to be diploid like the original *A*—*G* and as *A*—*C*. In morphological respects the sexual strain resembles *A*—*C* by its vigour, by a rather marked hairiness (also on the upper surface of the leaves), rather broad leaflets (cf. Figs. 21 and 34), and by the relatively large flowers. Further, the sexual strain is strictly perennial in contrast to the original *A*—*G*.

This is to a still higher degree typical of the *A*—*C* strain in contrast to all other diploid *argentea*-types in our cultures, which seldom live more than two years. Thus, it is highly probable that the single surviving and morphologically deviating plant in the family 1932—9 was an F_1-hybrid between the original and typical *A*—*G* and the *A*—*C*-strain growing close by. This implies that the original *A*—*G*-type was, to some extent, capable of sexual reproduction. Then, after hybridization with *A*—*C*, which is now known to have a rather strong sexual tendency, an F_1-hybrid was produced, in which the genetical system bringing about apomictic seed formation completely collapsed, the result being a highly variable progeny.

According to the above argumentation this progeny represents an F_2-generation of the cross *A*—*G* × *A*—*C*. This is still further supported by the results of pollen examination. In the segregating sexual material all plants were partially pollen sterile, the percentage of good pollen ranging from 10 to 80. In this connection it should be remembered that the spontaneous F_1-hybrids between *A*—*C* and *argentea* MARKL. were found to be rather pollen sterile, the percentage of good pollen in the three plants so far studied amounting to 20, 30 and 60 per cent respectively. In the progeny of these hybrids there was a marked variation and an average increase in pollen fertility (cf. p. 254).

Details about pollen fertility in the sexual *A*—*G* × *A*—*C*-material are given in Table 1. According to this table the average pollen fertility of 10 diploid plants in the first segregating generation (»9—1») was 57,0. The families 158—163 were raised from five of these diploid plants. On an average pollen fertility is evidently considerably higher in this second generation than in the preceding generation. It should be observed that the pollen counts of both generations were undertaken simultaneously. This increase in pollen fertility is accompanied by an obvious decrease in the morphological variation. Some of the families

Table 1. Pollen fertility in a sexual strain of *P. argentea*.

Field number	Per cent good pollen											n	M	Pollen fertility in the mother plant
	0	10	20	30	40	50	60	70	80	90	100			
156						2						2	55,0	1—10
157	12	6	5	6	5	2	2					38	25,0	»
158							1	—	1	1		3	81,7	40
159					1	1	2	—	1			5	63,0	»
160				1	—	—	—	1	1	2		5	77,0	60
161					1	1	—	1	2			5	69,0	40
162								1	2	2		5	87,0	?
163								1	3	1		5	85,0	?
9—1 (diploids)		1	—	—	2	2	3	1	1			10	57,0	—
» (pentaploid)	1											1	5,0	—

in the second generation are rather uniform others are still segregating. This is obviously the same picture as is obtained in F_3 of a species cross between two relatively closely related species. It will be very interesting to test if, and to which extent, the morphological and genetical stabilization will be accompanied by a return to apomictic seed formation.

b. A pentaploid hybrid and its progeny. Among the 16 plants, constituting the segregating progeny of the presumed hybrid between *A*—*G* and *A*—*C*, 15 individuals were found to be diploid, but in addition to these there was also a *pentaploid* plant, having $2n = 35$. Morphologically it did not differ conspicuously from the highly variable diploid sister plants, but it was found to be more sterile than the other plants in the progeny. The percentage of good pollen was something between 0 and 10, and in the isolation bags the seed setting was very poor. However, a fairly large number of seeds was obtained from the openpollinated flowers.

A total of 44 daughter plants were raised from this pentaploid. Two of these came from seeds of isolated flowers, the other 42 were obtained after open pollination. The progeny showed a very strong segregation, probably all the plants being different from each other (cf. Fig. 43). The chromosome numbers of all the plants were determined and found to vary in the following way.

Chromosome number:	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Frequency:	2	3	3	6	11	4	4	5	1	—	1	1	1	—	1	—	—	—	—	—	—	1

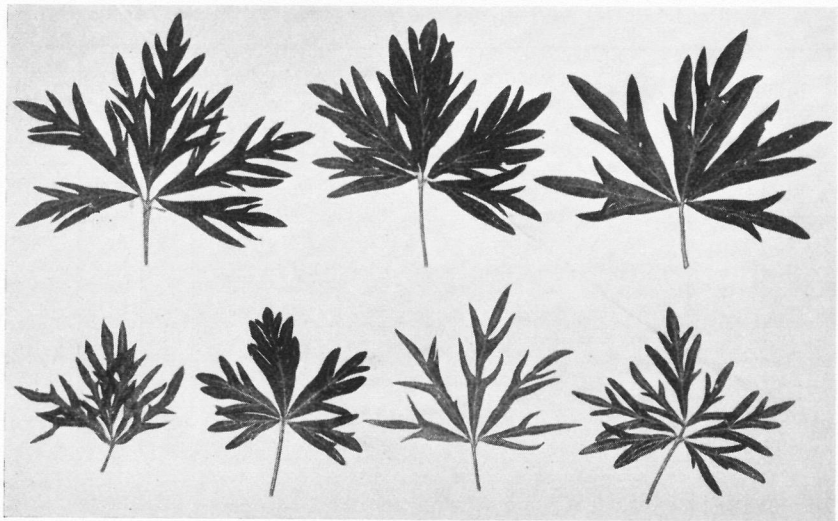


Fig. 43. Leaves of 7 sister plants in the progeny of a sexual pentaploid *argentea*-plant.

The two plants obtained after isolation had $2n = 32$ and 38 respectively.

The strong variation in chromosome number confirms the conclusion to be drawn already from the segregation, *viz.* that the mother plant must have been purely sexual. In the same progeny the variation in pollen fertility was studied. The result is given in Table 1. Family 156 represents the two plants obtained after isolation, family 157 the plants from open pollination. The percentage of good pollen is evidently significantly lower than in the comparable diploid material (Families 158—163). Seed production in the progeny in question was also more or less poor, the most sterile plant being the one with $2n = 49$. Even this plant, however, produced some seeds in openpollinated flowers.

Attempts were made to find a correlation between the different chromosome numbers and different degrees of vigour and fertility. No such correlation could be traced, however.

To explain the occurrence of the exceptional pentaploid individual in the otherwise diploid progeny it is necessary to assume that an exceptional unreduced ovule in the mother was fertilized by pollen from a hexaploid *argentea*-biotype. It should be remembered that the mother plant (1932—9—1, cf. p. 258) was openpollinated, and there-

fore it could easily become pollinated with the pollen of surrounding hexaploid biotypes. As regards the production of unreduced ovules other, and more direct evidence has been obtained as to the occurrence of such gametes in the sexual diploid *argentea*-strain. Thus, in a cross between this strain and another diploid *argentea*-type the chromosome numbers of 9 F_1-plants were determined. One of these was a triploid, all the others being diploid. Triploid individuals, arisen from the occasional functioning of unreduced ovules in the sexual strain, were also observed in the cross sexual *argentea* × *P. opaca* (cf. below).

Finally, it should be mentioned that in crosses with hexaploid *argentea* (= *impolita*) and with hexaploid *Tabernaemontani* the diploid sexual *argentea* did not give any true hybrids with 2n=28 but only a few diploid plants (2n = 14). These individuals are yet to young to decide, whether they are purely maternal or not, but it seems probable, indeed, that they are maternal diploids, and in such a case it is evident that the otherwise sexual strain has also a low proportion of unreduced embryosacs, capable of embryo formation without previous fertilization of the egg cell.

IV. Hybrids between P. argentea and opaca.

1. **Experimental results.** In our cultures we have two strains of *Potentilla opaca* (from Bjerred and Bäckaskog, Skåne). Both strains, which seem to differ from each other in some morphological details, were found to be diploid (2n = 14). The same chromosome number has previously been reported for *opaca* by TISCHLER (1929), who also found a tetraploid race. It has not yet been possible to decide whether our *opaca*-strains are sexual or apomictic. The latter alternative seems most plausible since in progenies after open pollination (74 plants of the Bäckaskog strain, 6 plants of the Bjerred strain) no morphological variation could be detected. When pollinated with *argentea*-pollen, however, *opaca* does not give any seeds. In 1938 plants of *P. opaca* were pollinated with pollen from the sexual diploid *argentea*-strain. The result was quite negative. This is not due to the relatively bad pollen of the sexual *argentea*-plants since exactly the same result was obtained in 1940, using 3 ordinary diploid and 2 hexaploid *argentea*-biotypes as male parents. A total of 73 *opaca*-flowers were pollinated in these crosses, but the result was completely negative. Thus, judging from these results, *P. opaca* seems to be quite incompatible with *P.*

argentea. This is not the case, however. When the sexual, diploid *argentea*-strain was used as female parent, the cross with *opaca* succeeded without the slightest difficulty.

Three different *argentea*-plants were used for the crosses and, hence, three different groups of F_1-plants were obtained, consisting of 122, 39 and 18 plants respectively. This material was partly planted in Svalöf, partly in Lund. The Lund material, which so far has been best observed, consists of 80 plants obtained from the *argentea*-plant 9—1—B as female parent and 18 plants obtained from the *argentea*-plant 9—1—2. With the exception of one single, apparently maternal plant both categories only comprised true F_1-hybrids, but in respect of vigour and general appearance the two groups of F_1-plants are strikingly different. The hybrids from 9—1—B are very vigorous and well developed in contrast to the hybrids from 9—1—2 which are very poorly developed and scarcely viable. The original number of 18 plants in this group has now, after the winter of 1940—41, been reduced to 10. In the other, large group of F_1-plants all individuals survived the winter very well. To a certain extent this strong difference in viability between the two categories of F_1-hybrids is parallelled by a difference in average viability between the non-hybrid offspring of the two *argentea*-plants. The progeny of 9—1—B (after selfing and open pollination) is, no doubt, on an average more vigorous than the progeny of 9—1—2. This difference, however, is quite slight in comparison with the difference between the two groups of species hybrids.

As both the parent strains used for the crosses had $2n = 14$ it was considered superfluous to control the somatic chromosome numbers of the F_1-plants. This was a mistake, however, as meiotic studies revealed the occurrence of a low proportion of triploid F_1-plants in addition to the diploid ones. These triploids are characterized by a very pronounced sterility and are more similar to *P. argentea* than the diploid F_1-hybrids. The triploids certainly result from the union of unreduced *argentea*-gametes with reduced *opaca*-gametes.

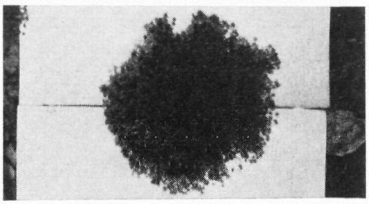
During the meiotic studies two such plants were found. A third plants is certainly also triploid, having a similar morphology and complete pollen sterility just as the controlled triploids. Thus, the minimum frequency of triploid F_1-plants in this material is about 4 per cent. The actual percentage may be slightly higher. Two other F_1-plants are suspected of being triploid on account of a pronounced sterility and certain morphological *argentea*-features.

The appearance of the *argentea* × *opaca*-hybrids and their parents

is shown by Figs. 44—56. — The mode of growth is very different in the parent species. *P. opaca* flowers very early and at this stage it forms a small pillow (under field conditions), covered with flowers. After the flowering the flower stalks with the seeds bend downwards, and in the centre of the plant an erect cluster of rather large leaves is developed. The plant in Fig. 44 has just finished flowering and the central leaf cluster is not yet very well developed.

The other parent species, P. *argentea,* flowers very much later, the chances of natural hybridization between the two species for that reason being very small. The *argentea*-plants used for the cross were rather erect and high (cf. Fig. 46). No rosette-leaves of the *opaca*-type are developed after the flowering.

The F_1-hybrids (Fig. 45) are intermediate in earliness and in general morphology. Already at the period of flowering there is a big bunch of leaves at the centre of the plant, surrounded by a quite closed, prostrate and rather broad and beautiful circle of flowers. Most F_1-plants are quite vigorous and flower abundantly. The flowers were found to be larger in the F_1-plants than in both parent species (Fig. 47).[1] The following average flower diameters were observed: 10,11 ± 0,19 mm (the sexual *argentea*-strain);



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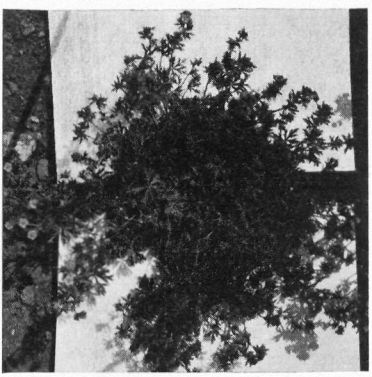

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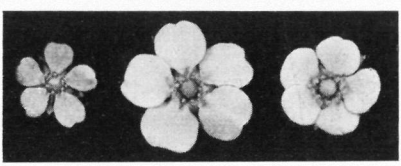
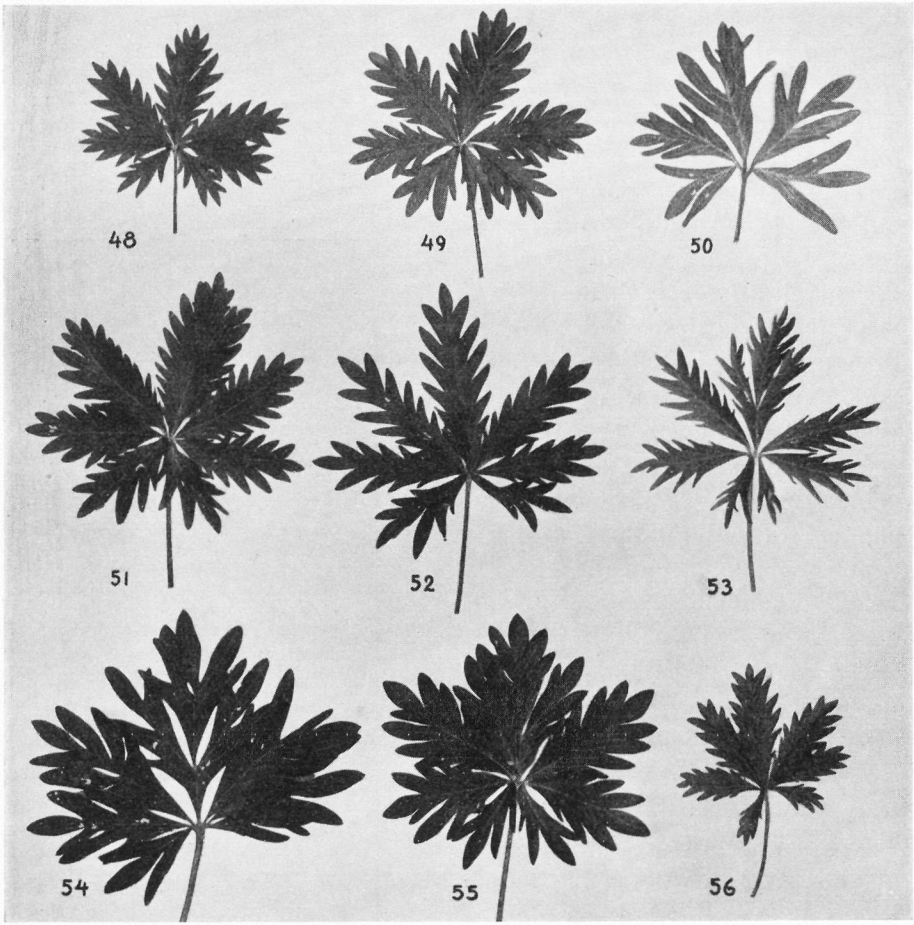


47

Figs. 44—47. The hybrid *P. argentea* × *opaca* and its parents. Field plants of *P. opaca* (Fig. 44), a typical F_1-hybrid (Fig. 45) and *P. argentea* (*A*—*G*) (Fig. 46). Fig. 47, flowers of *opaca* (to the left), *argentea* (to the right) and an F_1-hybrid (in the middle).

[1] The *opaca*-flower reproduced in Fig. 47 was one of the last flowers left on the plant and is therefore somewhat smaller than quite typical *opaca*-flowers.



Figs. 48—56. Basal leaves of *P. opaca* (Fig. 48), *P. argentea* (Fig. 50) and of seven different F_1-hybrids. Figs. 49, 51, 52 and 53, ordinary diploid F_1-hybrids. Fig. 54 and probably also Fig. 55, triploid F_1-hybrids with two *argentea*- and one *opaca*-genome. Fig. 56, a plant belonging to a hybrid family with very poor vigour. — × 0,55.

$11{,}83 \pm 0{,}37$ mm (*P. opaca*) and $16{,}00 \pm 0{,}15$ mm (the F_1-hybrids). The last value is based on measurements in 78 F_1-plants derived from the *argentea*-plant 9—1—B. In the weak F_1-plants derived from the *argentea*-plant 9—1—2 the flowers were smaller. Only 6 of these F_1-plants flowered and gave an average flower diameter of 12,00 mm.

Leaf shape in the parents and F_1 is shown by Figs. 48—56. The leaves from the four diploid F_1-plants (Figs. 49—53) are intermediate between the parents but clearly different *inter se* and were chosen to

demonstrate the genotypical variation among the diploid F_1-plants. This variation, which is also evident in several other respects, is certainly in the first place due to the heterozygosity of the *argentea*-parent. — Figs. 54—55 show leaves from one controlled and one probable triploid F_1-plant. The leaf shape in Fig. 54 conforms to the fact that the plant contains two *argentea*- and one *opaca*-genome. The triploids were also more similar to the *argentea*-parent than the diploid F_1-plants by their erect mode of growth and by the absence of a central bunch of leaves.

The number of leaflets is different in *P. argentea* and *opaca* and was found to be intermediate in F_1. In *argentea* the number of leaflets of the basal leaves is invariably 5, this number being observed without exception in 47 plants of the sexual *argentea*-strain. In *P. opaca* the number of leaflets is always greater than five. In 14 *opaca*-plants available, when the counts were made, the number of leaflets ranged from 7 to 9 with an average of 7,71. In the F_1-hybrids 80 out of 87 plants observed had 7 leaflets, 6 plants had 6 and 1 plant had 5, the average number being 6,91. The vigorous and weak F_1-families were not different in this respect.

As may be expected from species hybrids the F_1-plants were highly sterile with bad pollen and poor seed setting. The *P. opaca*-plants studied have quite good pollen, the average percentage of good pollen in 15 plants examined being 94,6. As pointed out above, the sexual *argentea*-strain available was characterized by a relatively poor but variable pollen fertility. The *argentea*-plants used for the crosses had about 40 per cent good pollen, the corresponding value of their offspring, after isolation or open pollination, being about 70 per cent (cf. Table 1). In the F_1-plants the percentage of good pollen ranged from 0 to 60 with an average of 29,4 per cent.

Seed setting was also poor, but most of the plants were not completely sterile, a low proportion of good seeds being obtained after isolation as well as open pollination. The triploids are evidently still more sterile than the other F_1-hybrids, but from one triploid plant a few seeds were also obtained.

2. **Meiotic observations.** Since the *P. argentea* × *opaca* hybrids were highly sterile, they might be expected to have a rather irregular meiosis. Much to our surprise, however, meiosis in the F_1-plants was found to be almost completely regular. The only difference that could be observed

was a slightly higher frequency of univalents in the hybrid than in the parents. The following frequencies were obtained:

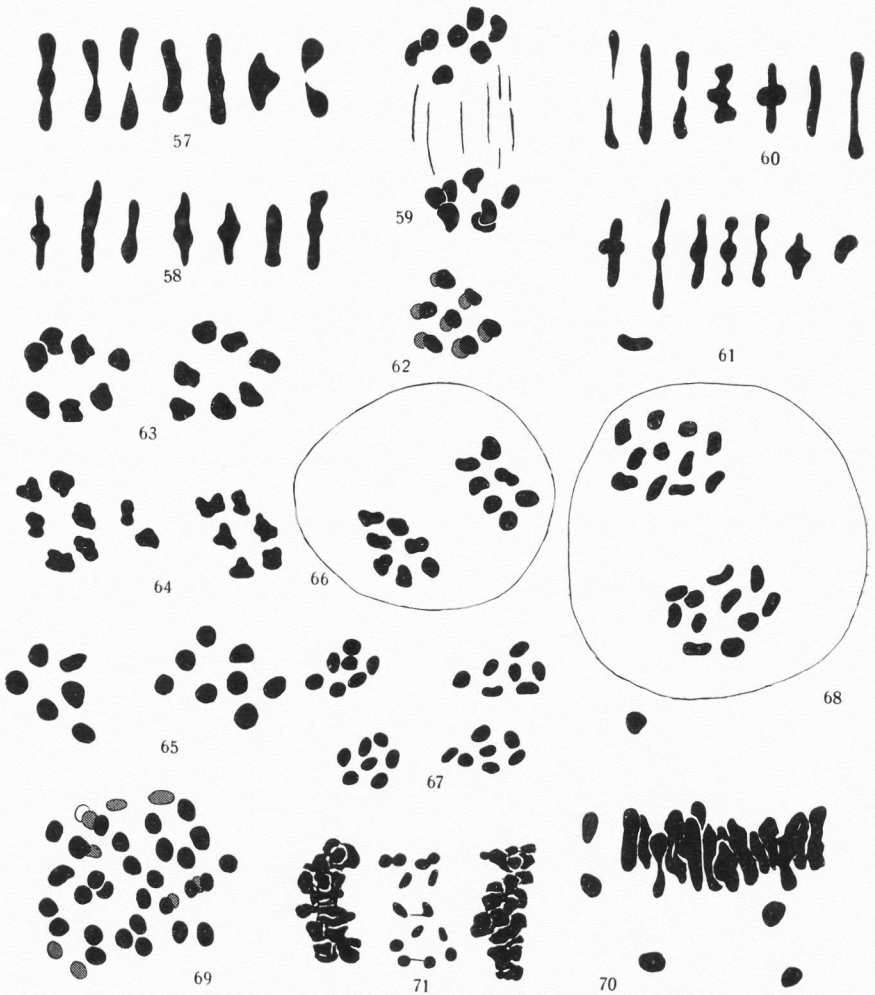
	Number of univalents at first metaphase 0	1	2	3	4	Number of cells	Per cent of cells with univalents
P. argentea, slide nr. 1	107					107	0,0
» » » 2	108					108	0,0
P. opaca	99	—	2			101	2,0
F_1, plant nr. 1	86	—	30	—	2	118	27,1
» » » 2	111	—	3			114	2,7
» » » 3	63	—	11	—	2	76	17,1

The *argentea*-plant studied was the mother plant of the largest F_1-family. The three F_1-plants examined, belonged to this family and were all diploid. Evidently, different F_1-plants or possibly different flowers or anthers may show rather different degrees of non-conjunction. The frequency of univalents in a slide from plant nr. 1 is $27{,}1 \pm 4{,}1$, the corresponding value of plant nr. 2 being as low as $2{,}7 \pm 1{,}5$. The difference is $24{,}4 \pm 4{,}4$ and D/m = 5,5. In spite of this variation among the hybrids it is rather obvious that, on an average, chromosome pairing is less good in the F_1-hybrids than in the parent species.

Some drawings from the meiotic divisions in this material are represented in Figs. 57—68. The perfectly regular first metaphase and anaphase in the parent species is evident from Figs. 57—59. In the F_1-hybrids the typical I—M groups (Figs. 60 and 62) consist of 7 bivalents of quite the same appearance as in the parents. Fig. 61 shows a metaphase with 6 bivalents and 2 univalents. At first anaphase the chromosome distribution is generally 7—7 (Fig. 63) but sometimes 6—2—6 (Fig. 64) or 6—8 (Fig. 65). The regular second division is shown by Figs. 66—67. Fig. 68, finally, shows a second metaphase in a triploid F_1-plant. The two plates contain 11 chromosomes each. One univalent has evidently divided at I—A, the halves of the univalent being included in the interphase nuclei.

V. A non-segregating hybrid between two biotypes of P. Tabernæmontani.

Our *Potentilla* cultures also include two biotypes of *P. Tabernaemontani*, »*T—A*» and »*T—B*», the former being hexaploid (2n = 42), the latter duodecaploid (2n = 84) (MÜNTZING 1928, 1931). Both types



Figs. 57—68. Meiosis in *P. argentea* × *opaca* and its parents. — Fig. 57, I—M in *P. argentea* (*A*—*G*), 7_{II} (separately drawn). Fig. 58, I—M in *P. opaca,* 7_{II} (separately drawn). Fig. 59, *P. opaca,* regular I—A, distribution 7—7. Figs. 60—68, meiosis in *P. argentea* × *opaca,* F_1. Fig. 60, I—M (separately drawn), 7_{II}; Fig. 61, I—M (separately drawn), $6_{II} + 2_I$; Fig. 62, I—M, polar view, 7_{II}; Fig. 63, I—A, distribution 7—7; Fig. 64, I—A, distribution, 6—2—6; Fig. 65, I—A, distribution 6—8; Fig. 66, II—M, distribution 7—7; Fig. 67, II—A, 7 chromosomes in all four groups; Fig. 68 II—M in a triploid F_1-plant, distribution 11—11 (one univalent has divided at I—A). — Figs. 69—70, meiosis in the *Tabernaemontani*-hybrid *T*—*B* × *T*—*A,* F_1 ($2n = 63$). — Fig. 69, I—M, polar view, probably $3_{III} + 25_{II} + 4_I$; Fig. 70, I—M, side view, 6 univalents scattered around the plate; Fig. 71, I—A, division of 7 univalents. — × 4250.

have been quite uniform, a total of more than 50 plants of each biotype being raised after isolation or open pollination. This complete constancy suggests apomictic seed formation. As for the *T—A*-strain this was verified by the exclusive production of maternal plants in crosses with *T—B*, with the hexaploid *argentea*-biotype *A—B* and with two hexaploid biotypes of *P. collina* (*C—A* and *C—C*) (MÜNTZING 1928, Tab. 4 and more recent results). A total of 29 such maternal *T—A* plants have been observed. In crosses with *T—B* as the mother seeds were obtained in several hybrid combinations (MÜNTZING 1928, Tab. 4), but most of these seeds did not germinate. However, the cross *T—B* × *Cr—B* (a biotype of *P. Crantzii*) gave one maternal plant and one plant which, at an early stage was supposed to be deviating. Unfortunately this plant died before its true nature could be revealed. Finally, 6 plants were obtained from the cross *T—B* × *T—A*, three of these being purely maternal, the other three apparantly being intermediate. A cytological examination showed, indeed, that the latter three plants were true hybrids, having $2n = \pm 63$. Thus, the *T—B* biotype, in spite of its constancy, turned out to be partially sexual.

The *T—B*-line is a typical gigas-type in comparison with *T—A*, all parts of the plant being larger. As is evident from Fig. 72, showing leaves and flowers, the F_1-plants are clearly intermediate. The average flower diameter was found to be 21,4 mm. in *T—B*, 16,6 mm. in *T—A* and 19,2 mm. in the hybrids. — Seed production in the F_1-plants was rather good, and progenies from all three hybrids were raised after isolation as well as open pollination. A total of 73 F_2-plants were obtained. These plants are in all morphological respects identical with the F_1-plants and do not show any segregation at all. On the contrary, these progenies from the *T—B* × *T—A* hybrids are just as uniform as the parent biotypes and other apomictic clones. As might be expected the morphological constancy is due to a constant chromosome number. Root tips were examined in all the 73 F_2-plants, and without exception the plants were found to have $2n = \pm 63$. Thus, though the mother plants had arisen in a sexual way they were not themselves capable of sexual reproduction, all their progeny being the result of apomictic seed formation. In other words, *the cross between the duodecaploid and hexaploid biotype has resulted in the sudden creation of a new constant biotype with a new multiple of the basic chromosome number of the genus.*

This biotype gives every impression of being equally viable and capable of survival under natural competition as the parent biotypes.

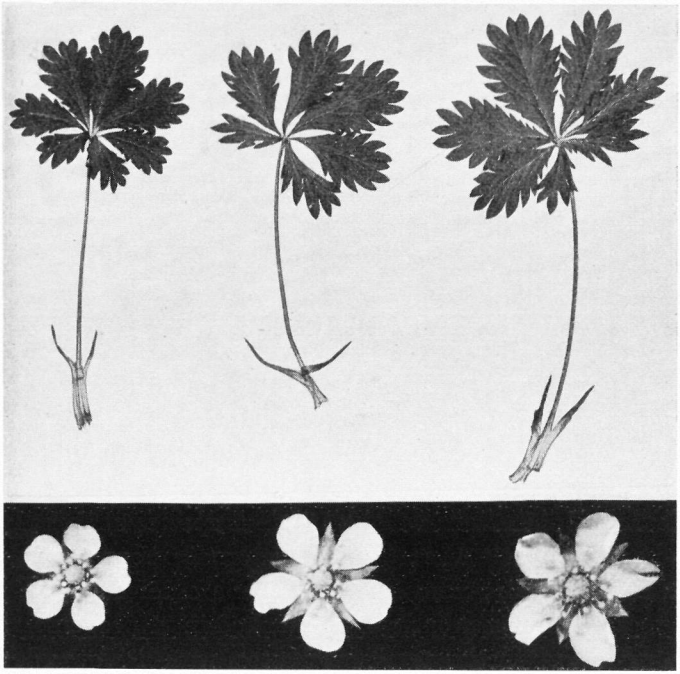


Fig. 72. Leaves and flowers of two *P. Tabernaemontani* biotypes and their F_1-hybrid. To the left, the biotype *T—A* (2n = 42); to the right, the biotype *T—B* (2n = 84) in the middle, the constant hybrid (2n = 63).

In spite of its odd chromosome number it was found to have just as good or even better pollen fertility than the parents. In 10 plants of *T—A* the percentage of good pollen ranged from 20 to 50, the average value being 34,0. In the other parent, *T—B*, the average value of 5 plants examined was 59,0. In the new biotype with 2n = 63 pollen samples from 72 plants were examined, the percentage of good pollen ranging from 40 to 90 with an average of 68,6.

This good pollen fertility is interesting, considering the odd chromosome number of this biotype, which must induce meiotic irregularities. Such irregularities were, indeed, observed. In Fig. 70 there is a first metaphase with six univalents scattered around the plate, and in Fig. 71 seven univalents divide at first anaphase. In the cell shown by Fig. 69, an attempt was made to analyse a I—M group in polar view. The probable configuration was found to be $3_{III} + 25_{II} + 4_{I}$. Of the trivalents one is of the ring-and-rod type, one is V-shaped and the third one a straight chain. Judging from this cell, most chromosomes

form bivalents, the 7 chromosomes in the odd genome partly appearing as univalents, partly forming trivalents with homologues in other genomes. The number of univalents outside the I—M groups was counted in 14 cells and found to vary from 0 to 8 with an average of 3,9.

The observation of this irregular meiosis definitely demonstrates that the constancy in morphology and chromosome number of this hybrid is due to apomixis.

VI. Discussion.

In 1928 pseudogamy was demonstrated for a number of biotypes of *P. argentea, collina, Tabernaemontani* and *Crantzii* (MÜNTZING 1928). Seven years later the occurence of pseudogamy in *Potentilla* was verified by SHIMOTOMAI (1935) and POPOFF (1935). SHIMOTOMAI made 11 cross combinations with 8 different species as female parents. In every cross the result was a purely maternal offspring, not a single hybrid being obtained among the 867 plants studied. POPOFF made 200 species cross combinations, which resulted in 21 progenies. Eighteen of these progenies, including four crosses with *P. argentea* as the female parent, were purely maternal. As SHIMOTOMAI and POPOFF also made control castrations the maternal offspring must be the result of pseudogamy.

In POPOFF's material the occurrence of pseudogamy was further verified by the observation that a certain plant with $2n=63$ gave a uniform progeny, having the same chromosome number as the mother plant. The systematical position of this plant was somewhat uncertain, but it probably belonged to *P. argyrophylla* (cf. POPOFF 1935, GENTSCHEFF 1937).

In POPOFF's experiments, however, 3 of the 21 cross combinations performed resulted in true hybrids. These hybrids were obtained with *P. geioides, rupestris* and *visianii* as the female parents, these species consequently being sexual. A true species hybrid in *Potentilla* (*P. chinensis* × *nipponica*) had also been produced by ARAKI (1932) and another case, *P. nepalensis* × *splendens*, was studied by GENTSCHEFF 1937. GENTSCHEFF also mentions that true hybrids were obtained from the cross combinations *P. argyrophylla* ($2n=56$) × *P. argyrophylla* ($2n=63$) and from *P. norvegica* × *argyrophylla*.

Thus, though apomictic seed formation seems to be quite predominating in the genus, a few species have also been found to be

sexual, and in one case the same species included one sexual and one apomictic type. According to GENTSCHEFF (1937) *P. argyrophylla*, 2n = 56, is sexual in contrast to another biotype within the same species having 2n = 63.

The main result of the present investigation is the demonstration that apomixis in *P. argentea* and *Tabernaemontani* is not absolute, a few strains showing different degrees of *partial sexuality*. This phenomenon has not previously been observed with certainty in *Potentilla*, the occurrence of sexuality being ascribed to entire species or biotypes.

The diploid *argentea*-strain *A—C*, obtained from Switzerland, was observed to give maternal offspring in crosses with one hexaploid *Tabernaemontani*- and two hexaploid *collina*-biotypes (MÜNTZING 1928, Tab. 5). However, expecially on account of a slight morphological variation, this strain had long been suspected of being partially sexual (c. MÜNTZING 1931, p. 169). The observation of a few clearly aberrant individuals in progenies after open pollination verified this view. The degree of sexuality in this strain will be more exactly studied in new progenies obtained after crosses with diploid Scandinavian *argentea*-types. These plants have not flowered yet, but already now it is clear that a rather high proportion of them represent true hybrids. Thus, the *A—C*-strain seems to hybridize rather easily with other *argentea*-biotypes, having the same chromosome number. On the contrary, in crosses with other species, having a different chromosome number, the result is only maternal offspring. These conditions are rather similar to the results obtained by LIDFORSS (1905, 1907, 1912) in *Rubus*. In this genus complete pseudogamy does not seem to occur, and the proportion of true hybrids formed is higher, if the species crossed are relatively closely related.

Also in another respect there is similarity between the *Rubus* hybrids and the spontaneous hybrids between *A—C* and other diploid *argentea*-types. This is the fact that in both cases the hybrids obtained are sexual and give a very marked segregation, producing numerous new types. In the *A—C*-case this is remarkable, since the aberrants in question must be the result of crosses between a partially apomictic strain as female parent and completely apomictic male parents. Under such circumstances the hybrids might be expected to be *more* apomictic than the mother strain. Since, on the contrary, they were evidently typically sexual this probably implies that apomixis also in this genus is brought about by special genetic systems, involving multiple factors. By hybridization this delicately balanced genetic system will be dis-

turbed, and the result is sexual reproduction. Such is the situation in the genus *Poa*, in which a multifactorial basis of apomixis was suggested for *P. alpina* and *P. pratensis* (MÜNTZING 1940, ÅKERBERG 1941). This suggestion is mainly based on the fact that all kinds of genetic alterations, including hybridization and quantitative changes in the chromosome number upset the apomictic propagation more or less completely, the result being sexuality.

In *Potentilla* the *A*—*C*-strain is not the only example of partial sexuality. Another diploid *argentea*-strain was found to be almost completely sexual. All evidence available indicates that this strain was obtained from spontaneous hybridization between the biotype *A*—*G* and the *A*—*C*-strain. Though in the main constant and probably apomictic, the original *A*—*G*-line must have been sexual to some extent. This sexuality resulted in a hybrid with *A*—*C*, and this hybrid, just as the spontaneous hybrids with *A*—*C* as female parent, must have been quite sexual. At any rate, the offspring in the following generations showed a very pronounced segregation. The sexual plants of the F_2-generation were utilized for various crosses and true hybrids were produced in the species cross *argentea* × *opaca*. In this species cross, which succeeded quite easily, both parents had the same chromosome number ($2n = 14$). On the contary, when pollinated with pollen of hexaploid *argentea*- and *Tabernaemontani*-biotypes the otherwise quite sexual *argentea*-strain did not give any true hybrids but only maternal offspring. Thus, just as in *A*—*C*, the result of a cross is not only dependent on the degree of sexuality of the mother type but also on the chromosome number and genetic constitution of the male parent.

The rule that true hybrids in *Potentilla* are sexual is not applicable to the hybrids between the *Tabernaemontani*-biotypes *T*—*B* ($2n = 84$) and *T*—*A* ($2n = 42$). The hybrids, having $2n = 63$, gave a completely uniform progeny, being in all respects just as constant as the parental biotypes. It may be imagined that the lack of sexuality in this F_1-hybrid is due in the first place to a very strong apomictic tendency, in both the parents and, further to the fact that the parents must be genotypically rather closely related. *T*—*B* and *T*—*A* belong to the same species, and the main differences between them are certainly caused by the quantitative difference in chromosome number. *T*—*A* has been found to be completely apomictic, judging from constancy as well as purely maternal offspring in four different cross combinations, and similar though less comprehensive evidence is available for *T*—*B*. However, as this biotype is also capable of forming reduced

and functional ovules, it must be considered to be partially sexual, though the degree of sexuality is probably very low.

The genotypical difference between *T—A* and *T—B* is certainly much smaller than the difference between *A—C* and the diploid Scandinavian *argentea*-types. It was emphasized that the spontaneous F_1-hybrids between these two categories were partially sterile and gave a segregation in next generation of just the same intensity as in a typical species cross. Also in several morphological respects the *A—C*-strain differs conspicuously from the other members of the collective species *P. argentea* L. This marked genotypical difference makes it easier to understand, why the F_1-hybrids are sexual. When two different systems causing apomictic or partially apomictic seed formation are confronted in an F_1-hybrid they cannot cooperate successfully, the balance is disturbed, and sexuality is the result.

Even these hybrids, however, reveal a certain apomictic tendency by the functioning of unreduced ovules. Thus, not only diploid but also triploid individuals were observed in the offspring of the *A—C*-aberrants. Functional unreduced ovules are also formed by the sexual *argentea*-strain derived from the biotype *A—G*. This was evident by the formation of a low proportion of triploid instead of diploid *argentea* × *opaca* hybrids and by the formation of a spontaneous pentaploid hybrid between the diploid sexual strain and hexaploid *argentea*. It should also be mentioned that in an otherwise quite constant and apomictic clone of *P. collina* (*C—A*) a morphologically somewhat deviating individual was observed last summer. Though it has not yet been possible to determine the exact chromosome number of this plant, it is certain that the number is increased, the plant probably being triploid. In such a case this aberrant must have arisen by the exceptional fertilization of an unreduced ovule. At any rate, such processes do occur in *Potentilla* just as in *Poa*. In the latter genus the occasional fertilization of unreduced embryosacs, which otherwise develop apomictically is rather frequent (cf. ÅKERBERG, 1939, 1941 and MÜNTZING 1940). A still higher frequency of fertilization of aposporous embryo-sacs was observed by NOACK (1939) in *Hypericum perforatum*. In this tetraploid and pseudogamous species not less than 28 per cent of the embryos obtained after self-pollination were found to be hexaploid, resulting from fertilization of aposporous eggcells. NOACK also made the important discovery that pseudogamy in *Hypericum perforatum* is combined with fertilization of the central nucleus. One year later GENTSCHEFF and GUSTAFSSON (1940) demonstrated the

occurrence of the same mechanism in some of our *Potentilla*-biotypes (the pentaploid *collina*-biotypes *C—B* and *C—G* and the hexaploid *argentea*-biotype *A—H*). These results emphasize the necessity of further embryological investigations in our *Potentilla*-material.

As pointed out above (p. 238) the apomictic constancy in the material of Scandinavian *P. argentea* is combined with a very marked polymorphism, which is also characteristic of the other *Potentilla* species in our cultures and probably of the apomictic *Potentilla* species in general. The present observations of partial sexuality in certain types of *argentea*, *Tabernaemontani* and *collina* have a bearing on this polymorphism. We have seen that occasional hybrids between different types within the same collective species may entirely loose their apomictic mode of propagation and produce swarms of new biotypes which may become stabilized in later generations. It may also happen that the occasional hybridization of two closely related biotypes gives rise to a single new type, the hybrid being quite apomictic. Finally, self-fertilization within a partially sexual strain (such as *A—C*) or within an otherwise quite apomictic biotype (such as *C—A*) will also lead to new genetical types.

It is true that in spite of their marked polymorphism no trace of sexuality has so far been observed among the Scandinavian *argentea*-biotypes. This does not favour the idea of occasional sexuality as the cause of polymorphism in this group and rather indicates that mutations are responsible for the observed diversity. It is possible, however, that occasional sexuality may occur also in the Scandinavian *argentea*-groups just as in the Swedish *Tabernaemontani*- and *collina*-biotypes (*T—B* and *C—A*), which were previously considered to be completely apomictic.

SHIMOTOMAI (1930 b) and POPOFF (1939) emphasize the importance of species hybridization for the origin of polyploidy in *Potentilla*. We have no reason to deny the correctness of this opinion but, on the other hand, the importance of quantitative autopolyploid changes should not be overlooked. It is now known, for instance, that unreduced ovules may sometimes be fertilized and give rise to triploid offspring. Autopolyploidy is further indicated by the frequent occurrence of intraspecific chromosome races in *Potentilla*. Such races have been observed by us in *P. argentea*, *collina*, *Tabernaemontani* and *Crantzii*, and POPOFF (1939) states that of 13 *Potentilla* species closely studied not less than 11 contain biotypes with different chromosome multiples. In spite of these results POPOFF is uncertain about the rôle

of autopolyploidy in the genus, evidently on account of the absence of multivalents at meiosis. It is now known, however, that absence of multivalents at meiosis is no reliable criterion of allopolyploidy (cf. MÜNTZING and PRAKKEN 1940) and especially in types with high chromosome numbers there may be much more homology between the genomes than is indicated by the formation of multivalents. *Potentilla* seems to behave in much the same way as e. g. *Chrysanthemum*, *Papaver* and *Phleum*, multivalents being rare in the types with even chromosome multiples, but occurring in types with odd multiples such as our pentaploid *P. argentea*. — These problems may be considered in more detail when a larger amount of data on meiosis in *Potentilla* have been gathered.

Finally, a few words may be said about the chromosomal variation and the systematical units in the collective species *P. argentea* L. In addition to the chromosome numbers 14, 42 and 56 previously described (MÜNTZING 1928, 1931) new biotypes with $2n = 28$ and $2n = 35$ have been found. The chromosome number 42 has also been reported by SHIMOTOMAI (1930 a and b) and POPOFF (1935, 1939). So far the biotypes with 28 and 35 chromosomes are only known from one locality each, and the geographical distribution of the octoploid biotype (obtained from the botanical garden of Iasi) is quite unknown. More information, however, is available for the *argentea*-types with $2n = 14$ and 42. The diploid *argentea*-types fall into two categories, one represented by the partially sexual *A*—*C*-strain obtained from the Botanical garden of Basel, the other category by the diploid, strictly apomictic biotypes, having a large distribution area in Scandinavia. As pointed out above the *A*—*C*-strain differs from the other group by a number of morphological characters and is markedly perennial in contrast to the Scandinavian diploids, which seldom live more than 2 or 3 years. As moreover, the hybrids between *A*—*C* and Scandinavian diploids are partially sterile and give a very strong F_2-segregation, the *A*—*C*-strain may be considered to be specifically different from the diploid Scandinavian *argentea*-types.

The hexaploid representatives of the collective species *P. argentea* evidently have a more southern distribution than the diploid Scandinavian *argentea*-types. The hexaploids also grow in middle Europe. The diploid and hexaploid *argentea*-types in Scandinavia differ from each other in a number of morphological characters and were distinguished by MARKLUND (1933) as two different species (*argentea* in the strict sense and *impolita* WAHLENB.). These two agamospecies within the

collective species *P. argentea* L. seem to represent a new verification of the rule discussed by MÜNTZING (1936) that different races or closely related species with different chromosome numbers always have different distribution areas or are ecologically different in other respects. Besides by their different geographical distribution *P. impolita* and *argentea* MARKL. differ from each other by their periodicity, the diploid species being more short-lived and having a more rapid development each year than the hexaploid species. The octoploid *argentea*-type is still slower than the hexaploids. These facts are interesting in relation to the previous observation that perennial species in a number of other genera have a higher average chromosome number than their diploid relatives (MÜNTZING 1936).

P. impolita and *argentea* MARKL. were also found to differ in pollen fertility, the hexaploid species on an average being much less fertile than the diploid. Whether this difference is due to meiotic irregularities in the hexaploids or possibly to premeiotic somatic disturbances is not known with certainty but may perhaps be elucidated by further work with this interesting genus.

VII. Summary.

1) Chromosome counts were undertaken in 53 strains of *P. argentea* L. from 37 different localities in Sweden and Norway. 37 of these strains were diploid ($2n = 14$), 12 hexaploid ($2n = 42$), 3 tetraploid ($2n = 28$) and 1 pentaploid ($2n = 35$).

2) All strains so far observed were completely uniform but always differed from each other in various morphological and physiological respects. The constancy is due to apomixis.

3) A morphological analysis demonstrated that the diploids correspond to *P. argentea* MARKL. and the hexaploids to *P. impolita* WAHLENB. The diploids have a more northern distribution area than the hexaploids. The two groups also differ in periodicity, rust resistance, seed and pollen size and in average pollen fertility.

4) Meiosis in the pentaploid *argentea*-biotype was studied. At first metaphase the most typical configuration was found to be $2_{III} + 12_{II} + 5_{I}$.

5) Some foreign, deviating *argentea*-types are discussed. The first type is an octoploid apomictic biotype, characterized by great vigour, lateness and strictly perennial duration of life. The second type, *A—C*, is a diploid and partially sexual strain. Hybrids between *A—C* and other diploid *argentea*-types are partially sterile and give in F_2 a typical species cross segregation. Thus, *A—C* and the Scandinavian diploids must be regarded to be specifically different. Some F_2-plants were triploid and showed a high frequency of trivalents at meiosis.

6) An almost completely sexual strain of diploid *argentea* was obtained, probably as the result of a spontaneous cross between the *argentea*-biotype *A—G* and the partially sexual strain *A—C*. This new sexual strain could be utilized for

the production of various hybrids. One pentaploid hybrid was purely sexual and gave a highly variable progeny. In the crosses with the sexual strain as female parent unreduced ovules were sometimes fertilized. When pollinated with hexaploid *argentea* and *Tabernaemontani* the otherwise sexual strain gave only maternal offspring. This and other similar evidence indicates that the result of a cross in our *Potentilla*-material is not only determined by the degree of sexuality of the mother strain but also by the chromosome number and the genetical constitution of the male parent.

7) Hybrids between *P. argentea* and *opaca* are described. Most hybrids were diploid, have an almost quite regular meiosis but poor fertility. Some of the F_1-hybrids were triploid, having two *argentea*-genomes and one *opaca*-genome. Most hybrids were very vigorous, but a certain *argentea*-plant, though itself normally developed, gave hybrids with a very poor vigour.

8) A few true hybrids between the *Tabernaemontani*-biotypes *T—B* ($2n = 84$) and *T—A* ($2n = 42$) were obtained. The hybrids ($2n = 63$) gave only apomictic progeny, and, thus, the cross resulted in the sudden creation of a new constant biotype with a new multiple of the basic chromosome number of the genus.

9) The genotypical basis of apomixis and the causes of polymorphism in *Potentilla* are discussed.

Literature cited.

ARAKI, S. 1932. Karyologische Untersuchungen über einen Artbastard zwischen *Potentilla chinensis* (haploid 1 n) und *P. nipponica* (hapl. 2 n). — Journ. Science of the Hiroshima Univ., Series B, Div. 2, Vol. 1, pp. 103—115.

GENTSCHEFF, G. 1938 Über die pseudogame Fortpflanzung bei *Potentilla*. — Genetica XX, H. 3/4, pp. 398—408.

GENTSCHEFF, G. and GUSTAFSSON, Å. 1940. Parthenogenesis and pseudogamy in *Potentilla*. — Bot. Not., pp. 109—132.

LIDFORSS, B. 1905. Studier över artbildningen inom släktet *Rubus* I. — Arkiv för Botanik, Bd. 4, No. 6.

— 1907. Studier över artbildningen inom släktet *Rubus* II. — Ibid. Bd. 6.

— 1914. Resumé seiner Arbeiten über *Rubus*. — Zeitschr. f. ind. Abst.- u. Vererb.-lehre. B. 12.

MARKLUND, G. 1933. Über *Potentilla argentea* L. und *P. impolita* WAHLENB. — Memoranda Societas pro Fauna et Flora Fennica 9, pp. 2—13.

MÜNTZING, A. 1928. Pseudogamie in der Gattung *Potentilla*. — Hereditas XI, pp. 267—283.

— 1931. Note on the cytology of some apomictic *Potentilla* species. Hereditas XV, pp. 166—178.

— 1936. The evolutionary significance of autopolyploidy. — Hereditas XXI, pp. 263—378.

— 1940. Further studies on apomixis and sexuality in Poa. — Hereditas XXVI, pp. 115—190.

MÜNTZING, A. and PRAKKEN, R. 1940. The mode of chromosome pairing in *Phleum* twins with 63 chromosomes and its cytogenetic consequences. — Hereditas XXVI, pp. 463—501.

NOACK, K. 1939. Über *Hypericum*-Kreuzungen VI. Fortpflanzungsverhältnisse und Bastarde von *Hypericum perforatum* L. — Zeitschr. f. ind. Abst.- u. Vererb.-lehre B. 76, pp. 569—601.

POPOFF, A. 1935. Über die Fortpflanzungsverhältnisse der Gattung *Potentilla*. — Planta, Bd. 24, H. 3, pp. 510—522.

— 1939. Karyologische Studien über die Entwicklungsvorgänge in der Gattung *Potentilla*. — Zeitschr. d. landwirtschaftl. Versuchsstation in Bulgarien, Bd. IX, H. 3, pp. 1—58.

SHIMOTOMAI, N. 1930 a. Über die Chromosomenzahlen und die Phylogenie bei der Gattung *Potentilla*. — Bot. Magazine, Vol. XLIV, No. 525, pp. 490—498.

— 1930 b. Chromosomenzahlen und Phylogenie bei der Gattung *Potentilla*. — Journ. Science of the Hiroshima univ., Series B. Div. 2, Vol. 1, pp. 1—11.

— 1935. Zur Kenntnis der Pseudogamie bei *Potentilla*. — Proc. Imp. Acad. Tokyo. Vol. XI, pp. 338—339.

TISCHLER, G. 1929. Revisionen früherer Chromosomen-zählungen und anschliessende Untersuchungen. — Planta, Bd. 8, H. 5, pp. 685—697.

ÅKERBERG, E. 1939. Apomictic and sexual seed formation in *Poa pratensis*. — Hereditas XXV, pp. 359—370.

— 1941. Cytogenetic studies in *Poa pratensis* and its hybrid with *Poa alpina*. — Hereditas XXVIII, pp. 1—126.

Sagina caespitosa (J. Vahl) Lge funnen i Lule Lappmark.

Jämte en sammanställning av artens skandinaviska fyndorter.

Av J. A. Nannfeldt.

Sommaren 1936 vistades jag med understöd av ett Vetenskapsakademiens Krok-stipendium en längre tid i Lule Lappmark och företog härunder en exkursion från Kvikkjokk genom Tarradalen till Virihaur, varvid jag även besökte Unna Tuke (=Unna Toki=Lill-Tokin), vilket berg såsom originalfyndorten för *Arenaria humifusa* Wg just hade fått stor aktualitet genom Nordhagens arbete (1935) över sagda art. Såtillvida blev mig denna exkursion en besvikelse, som jag trots åtskilliga timmars genomsökande av det ganska lilla fjället ej kunde återfinna vare sig denna art eller *A. ciliata* L. **norvegica* (Gunn.) Fr.[1] Mitt besök på Unna Tuke blev dock ej alldeles resultatlöst, då jag lyckades berika fjällets redan tidigare väl kända flora genom fyndet av en annan sällsynt caryophyllacé, nämligen *Sagina caespitosa* (J. Vahl) Lge. Denna förekom sparsamt på uppfrysningsmark på bergets svagt undulerade platå. Växtplatsen var för arten ovanligt torr, och exemplaren voro till följd därav små och förkrympta, men i övrigt fullt typiska.

Denna sällsynta bicentriska fjällväxt, vars totalutbredning hänför den till det »västarktiska» elementet i vår flora, var tidigare i Sverige känd endast från Torne Lappmark, där den dock anträffats på talrika lokaler. I Nordnorge var den känd endast från Troms fylke, tills Nordhagen 1933 upptäckte den på Tausafjell i Nordland. Efter detta sista fynd var det därför ingalunda oväntat, att dess svenska sydgräns skulle förskjutas till Lule Lappmark.

Föranledd av mitt Lule Lappmarks fynd har jag gjort en sammanställning av artens skandinaviska utbredning. Genom tillmötes-

[1] Sistlidna sommar var lyckan fil. lic. Nils Dahlbeck gunstigare, i det denne då återfann *A. humifusa* vid Unna Tuke (se Dahlbeck 1940).

gående från resp. museer har jag beretts tillfälle granska materialet i följande samlingar: Botaniska trädgården, Göteborg (i fyndortsförteckningen förkortat till G), Botaniska museet, Lund (L), Riksmuseums Botaniska Avdelning, Stockholm (S), Botaniska museet, Uppsala (U), Bergens museum (B) och Tromsø museum (Ts), varjämte konservator J. LID välvilligt sänt mig en lista på de skandinaviska exemplaren i Oslo Botaniska Museum (O) och fil. kand. G. SANDBERG, Uppsala, låtit mig taga del av materialet i sitt herbarium. Författaren STEN SELANDER har välvilligt lämnat mig en del upplysningar om sina fynd av arten. Enligt meddelande från kustos emer. dr. H. LINDBERG, Helsingfors, har den icke anträffats inom Finlands gränser. Till alla dem, som på ena eller andra sättet varit mig behjälpliga vid utarbetandet av denna uppsats, uttalar jag mitt varmaste tack.

Nedanstående fyndortsförteckning är grundad på det sålunda sammanbragta materialet och på några trovärdiga litteraturuppgifter:

Norge.

Hedmark. F o l d a l h:d: Fundberget, nära toppen, 12. VII. 1889, A. BLYTT (O). — Langhø, 13. VII. 1889, A. BLYTT (O).

Opland. L o m h:d: Gjuvflyane nära Gjuvvatnet, 3. VIII. 1914, O. DAHL (O); på platån vid Gjuvvashytten, 3. VIII. 1914, H. JOHNSEN (B!). — Eilevstjern (ovanför Smådalsseter), 1932, R. NORDHAGEN (in litt.); 11. VIII. 1934, J. A. NANNFELDT (U!). — Smådalen, nära Smørliseter, VIII. 1884, J. THOMLE (O). — V å g å h:d: Grønhø (på gränsen till Lom), 23. VII. 1935, KAREN & G. HYGEN (O). — L e s j e h:d: under Kvitingshø, 19. VII. 1893, O. DAHL (O). — Under Hyrjonkampen (på sydsidan av Lesjeskogsvatnet), 25. VII. 1893, O. DAHL (O). — Gråhø (nära Håkenstadseter, på gränsen till Vågå och Dovre), 21. VII. 1893, O. DAHL (O).

Sør-Trøndelag. O p d a l h:d: »Dovre», 1828, W. BOECK (O) m. fl. data och samlare. — Knutshø, 17. VIII. 1865, A. FALCK (L!); 1881, 1882, VIII. 1887; 10. VIII. 1888, 17. VII. 1889, 20. VIII. 1893, A. BLYTT (O) m. fl. data och samlare; 1500 m ö. h., 14. VIII. 1890, C. STØRMER (O); S. Knutshø, sydvästsluttningen, c. 1500 m ö. h., 23. VII. 1934, J. A. NANNFELDT (U!); Mellersta Knutshø, VII. 1883, VII. 1894, O. W. REDELIUS (G!, S!); 31. VII.?, C. BAENITZ (Herb. Eur. n. 6441, L!); vid Sprenbekken, 27. VIII. 1928, J. HOLMBOE & J. LID (O); N. Knutshø, VII. 1896, G. HJ. BROBERG (G!); sydostsluttningen, nära toppen, c. 1650 m ö. h., 4. VIII. 1934, J. A. NANNFELDT (U!). — Kaldvellfjellet, Kvernbekkhø, nordsluttningen, 1400—1450 m ö. h., 2. VIII. 1934, J. A. NANNFELDT (B!, O!, S!, U!). — Finnshø, toppen, 1854, C. & R. HARTMAN (U!); högsta toppen, 12. VIII. 1865, S. BERGGREN (L!, S!). — Nystuhø, 2. VIII. 1866, C. ELGENSTIERNA (G!); VIII. 1905, GULDBERG (O). — Armotshø (vid Goveliseter), 7. VII. 1914, HANNA RESVOLL-HOLMSEN (O).

Nordland. Saltdal h:d: Tausafjell (i Junkerdalen vid Skaiti), 6. VIII. 1933, R. NORDHAGEN (B!, O, U!, jfr NORDHAGEN 1935 p. 55).

Troms. Bardu h:d: Rubben, 27. VII. 1891, B. STRØM (O, Ts!). — Øverbygd hd: Nausti (vid Dividalen), reg. alp. på flytjordsvalken. 11. VIII. 1914, TH. C. E. FRIES (O.). — Nordreisa h:d: Javreoiavve, 26. VII. 1905, S. SELANDER (S!).[1]

Sverige.

Lule Lappmark. Jokkmokk s:n: Unna Tuke (= Unna Toki = Lill-Tokin), 29. VII. 1936, J. A. NANNFELDT (S!, U!).

Torne Lappmark. Jukkasjärvi s:n Tjålmetjåkko, nordsluttningen, H. SMITH (1924 p. 449 s. n. *S. nivalis*); mot Kamajaure, 18. VII. 1920, H. SMITH (U!). — Påtsovare, höjdplatån, ej sällsynt, 900 m ö. h., 15. VIII. 1908, T. LAGERBERG (1909 p. (20) s. n. *S. nivalis*). — Abiskojaure, sydändan, på den öppna sandstranden, i spridda individ tillsammans med *S. intermedia*, 16. VIII. 1908, T. LAGERBERG (l. c. p. (21)). — Tsasinnjaskatjåkko, »ej sällsynt», E. STERNER (1916 p. 94 s. n. *S. nivalis*); TH. C. E. FRIES (1919 p. 28); VIII. 1916, G. ERDTMAN (S!). — Nuolja (=Njulja=»Nuljalaki»), 1880, K. P. HÄGERSTRÖM (U!) m. fl. data och samlare; vinderoderad flytjord, c. 1000 m ö. h., 13. VIII. 1916, G. SAMUELSSON (U!); västsidan, 14. VII. 1914, THE SVEDBERG (U!); västsidan, snölega, c. 900 m ö. h., 17. VII. 1938, T. LAGERBERG (1940 p. 143, fig. 129); östsidan, högt uppe på flytjord, 18. VII. 1906, M. SONDÉN (S!); nära toppen, VIII. 1933, G. SANDBERG(!); »de högre delarna ej sällsynt (även på själva toppen)», TH. C. E. FRIES (1919 p. 28); ovan Nuoljatunneln, c. 700 m ö. h., G. SAMUELSSON (FRIES l. c.); materialvägen mellan Abisko och Björkliden, 12. VIII. 1936, R. SANTESSON (S!). — Pallemtjåkko, 24. VII. 1919, TH. C. E. FRIES (S!, U!); ovanför tältlägret, på vinderoderad, tjälskjutande mark, 12. VIII. 1933, G. SANDBERG(!). — Nissontjåkko, H. SMITH (1924 p. 449) m. fl. samlare; c. 1100 m ö. h., 18. VIII. 1924, C. G. ALM (U!); nordostsidan, c. 1300 m ö. h., 30. VII. 1927, H SMITH (G!); mot Tjuonavagge (=»Lapporten»), c. 1100 m ö. h., 30. VII. 1920, C. G. ALM (L!, S!); östra åsen, c. 1400 m ö. h., 14. VIII. 1936, R. SANTESSON (S!); vid Lapporten, 11. VIII. 1920, G. BJÖRKMAN (U!); Tjuonavagge, H. SMITH (l. c.); Nissonreppe, flytjord, c. 1600 m ö. h., 13. VIII. 1935, A. NYGREN (U!). — Nissonreppejokk, grusstrand, c. 800 m ö. h., 5. VIII. 1925, G. SAMUELSSON (S!). — Tjuonatjåkko, snöläge, c. 1000 m ö. h., 6. VIII. 1916, G. SAMUELSSON (L!, S!); östsidan, 25. VII. 1920, H. SMITH (U!); åt Lapporten, 4. VIII. 1920, G. BJÖRKMAN (U!). — Vaimaåive, sydsidan, 8. VIII. 1917, E. ASPLUND (S!, U!). — Vuoskovaara, 28. VIII. 1919, TH. C. E. FRIES (U!). — Suoraåive, c. 1215 m ö. h., 9. VII. 1905, S. SELANDER (S!); på en platå mot Tjuonatjåkko, på platser, där stora snömassor legat under vintern, sparsam, c. 1100 m ö. h., 5. VII. 1906, S. SELANDER (S!). — Kuobletjåkko, H. SMITH (l. c.). — Kuolkotjåkko,

[1] Detta synes vara enda fyndet av denna art från Skandinaviens botaniskt sett kanske rikaste berg. Den saknas också i MEJLAND's nyligen utkomna floralista (1939) härifrån.

H. SMITH (l. c.); 24. VII. 1920, H. SMITH (G!, L!, S!, U!). Pesisvare (=Laireåive), nordostsidan, c. 1050 m ö. h., 11. VII. 1926, H. SMITH (U!). — Tuoptertjåkko (=Stuor Altas), översta ryggen, *Dryas*-hed, c. 1100 m ö. h., 16. VII. 1934, A. NYGREN (U!); inre delen av dalen åt sydväst, 16. VII. 1934, G. SANDBERG(!); utlöparen åt väster, 16. VII. 1934, G. SANDBERG(!). — Ripainen (=»Ripanes»), 15. VII. 1852, R. F. FRISTEDT & FR. BJÖRNSTRÖM (L!, S!, U!) m. fl. data och samlare; »på slättmarker nedanför Ripanes», 17. VII. 1852, R. F. FRISTEDT & FR. BJÖRNSTRÖM (G!, L!, U!). — Karesuando s:n: Moskana, sydöstra delen, c. 1100 m ö. h., 26. VII. 1933, H. SMITH (S!, U!). — Peltsa, södra toppen mot norra foten, c. 1300 m ö. h., 24. VII. 1933, H. SMITH (U!); nordsidan mot Nirijaure, 14. VIII. 1934, R. NORDHAGEN (B!, U!; jfr NORDHAGEN 1939 p. 698).

Vidstående karta visar, att utbredningstypen är ovanligt vackert bicentrisk, och talar i övrigt för sig själv. Påpekas må blott, att arten uppenbarligen har en starkt kontinental dragning i jämförelse med flertalet andra bicentriska arter. Förklaringen härtill torde snarare ligga i ekologiska än i invandringshistoriska förhållanden. En diskussion härav nyttar emellertid föga, sålänge artens ekologi ej är bättre känd än för närvarande är fallet.

Uppsala Botaniska Museum den 10. april 1941.

Litteratur.

DAHLBECK, N., 1940, *Arenaria humifusa* Wg och skyddet av sällsynta växter. — Acta Phytogeogr. Suec. 13.

FRIES, TH. C. E., 1919, Floran inom Abisko Nationalpark. — Ark. f. Bot. 16: 4 (= K. Sv. Vet.-Akad. Skr. i Naturskyddsärenden 2).

LAGERBERG, T., 1909, Några anmärkningsvärdare växtformer från Torne Lappmark. — Sv. Bot. Tidskr. 3.

— 1940, Svenska fjällblommor. Andra tillökade upplagan. — STF:s handböcker om det svenska fjället 1.

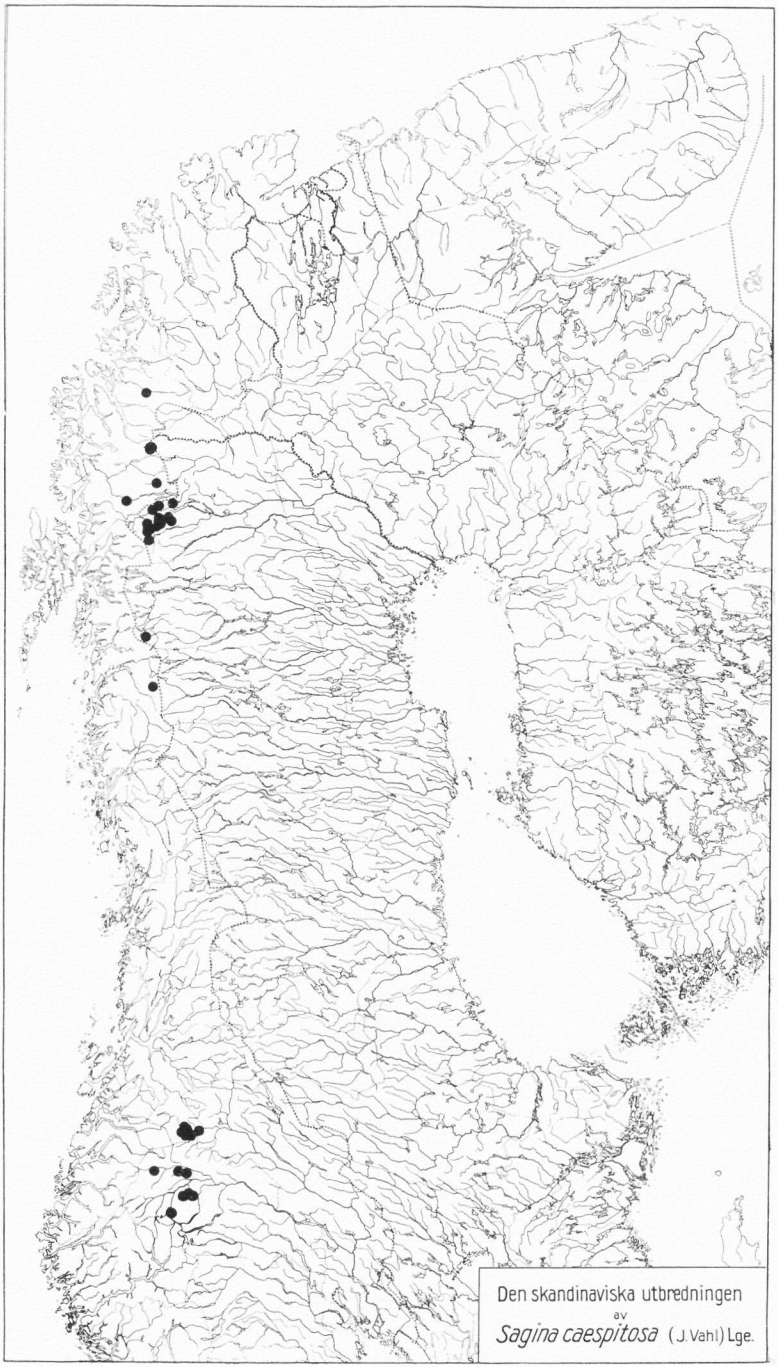
MEJLAND, Y., 1939, Om floraen på Javreoaivve i Nordreisa. — Nyt Mag. f. Naturvidensk. 79.

NORDHAGEN, R., 1935, Om *Arenaria humifusa* Wg. og dens betydning for utforskningen av Skandinavias eldste floraelement. — Bergens Mus. Årb. 1935, Naturvidensk. rekke 1.

— 1939, Bidrag til fjellet Pältsas flora. Et nytt funn av *Stellaria longipes*. — Bot. Not.

SMITH, H., 1924, Bidrag till Torne Lappmarks flora. — Sv. Bot. Tidskr. 18.

STERNER, E., 1916, Floristiska anteckningar från trakten kring Torne träsk och ett par platser i Norges Nordland. — ibid. 10.


Den skandinaviska utbredningen
av
Sagina caespitosa (J. Vahl) Lge.

Summary.

Sagina caespitosa (J. Vahl) Lge found in Lule Lappmark. With a list of its Scandinavian localities.

The author found in 1936 this rare »West-Arctic» species on Mt. Unna Tuke, as new to the Swedish province of Lule Lappmark. Because of this find the author has compiled the above list of its Scandinavian localities and mapped them (fig. 1). The distribution is very distinctly bicentric. It is noteworthy that the species has a strong preference for the easternmost parts of the area occupied by most other bicentric species. Probably, the reasons are rather ecological than migratory.

Über die Sexualität einiger Hydnaceen.

Von Nils Fries.

Die einzigen Angaben, die über die Sexualitätsverhältnisse bei Hydnaceen vorliegen, bestehen soweit ich finden konnte aus Browns (1935) Beobachtungen über Homothallie und Heterothallie bei *Odontia*. Hier werden von Brown 2 Arten als heterothallisch bezeichnet ohne nähere Angabe über die Art der Heterothallie (Bipolarität oder Tetrapolarität), während nicht weniger als 6 Arten den bei Hymenomyceten im allgemeinen seltneren homothallischen Typ vertreten.

Da ich während der letzten Jahre Anlass hatte, eine Reihe Vertreter der — sehr heterogenen — Familie *Hydnaceae* reinzuzüchten, versuchte ich wo es möglich war auch die Sexualität bei den fraglichen Arten zu analysieren. In der vorliegenden Arbeit werden die Ergebnisse der Sexualitätsanalysen von sechs Arten veröffentlicht, nämlich *Hydnum auriscalpium, H. coralloides, H. corrugatum, H. strigosum, Irpex pendulus* und *Radulum Radula* (=*R. orbiculare*), ferner eine Reihe Beobachtungen über Sporenkeimung, Fruchtkörperbildung, Aussehen des Myzels in Kultur usw.

Wie bei den Hymenomyceten gewöhnlich der Fall ist, sind die auf Holz wachsenden Arten bedeutend leichter in Kultur zu bringen als die reinen Bodenpilze. Alle die ebenerwähnten, hier zur Behandlung stehenden Arten kommen in der Natur auf Holz von toten oder lebenden Bäumen vor, und zwar ausser *Hydnum auriscalpium,* das auf im Boden verborgenen Kiefernzapfen wächst, und sämtliche Arten können leicht in Reinkultur gebracht werden mit Sporen als Ausgangsmaterial. Dagegen waren alle Versuche fruchtlos, Sporenkeimung bei humusbewohnenden Hydnaceen zu erreichen, wie *Hydnum repandum, H. imbricatum, H. cyathiforme* und *H. violascens*.

Falls nicht anders angegeben, fand die Züchtung auf Malzagar statt, welcher 1,5 % Agar-Agar und 2,5 % Malzextrakt enthielt. Die Methodik, die bei den Sexualitätsanalysen angewandt wurde, stimmt völlig mit der bei derartigen Untersuchungen gebräuchlichen überein.

Hydnum auriscalpium L. ex Fr.

	1	2	7	5	6	8	9	3	10	4
1	—	—	—	+	+	+	+	—	—	—
2	—	—	—	+	+	+	+	—	—	—
7	—	—	—	+	+	+	+	—	—	—
5	+	+	+	—	—	—	—	—	—	—
6	+	+	+	—	—	—	—	—	—	—
8	+	+	+	—	—	—	—	—	—	—
9	+	+	+	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—	—	+
10	—	—	—	—	—	—	—	—	—	+
4	—	—	—	—	—	—	—	+	+	—

Fig. 1. Schema über das Ergebnis von Kreuzungen zwischen 10 Einspormyzelien von *Hydnum auriscalpium*. + bezeichnet das Vorhandensein, — das Fehlen von Schnallen.

Die Sporenkeimung bei *Hydnum auriscalpium* wurde zum erstenmal bereits 1859 von HOFFMANN beschrieben und abgebildet. Ich habe nur die Richtigkeit seiner Beobachtungen bekräftigen können, sowohl bezüglich der Anschwellung, die die Sporen bei der Keimung erfahren, als ihrer Neigung, eine Keimhyphe von jedem Schmalende auszuschicken. Mitunter schwillt die Spore zu einer kleinen Blase an, von der mehrere Hyphen auswachsen können. Die Keimung tritt im allgemeinen erst nach 3 bis 4 Tagen ein, schwankt jedoch stark für verschiedene Sporen, so dass gewisse Keimungen erst nach mehreren Wochen eintreten. Die Geschwindigkeit, mit der die einzelnen Einspormyzelien auswachsen, schwankt gleichfalls in hohem Grad von Fall zu Fall. Noch nach einer viermonatigen Verwahrung in Dunkelheit und bei $+25^{\circ}$ ist die Keimfähigkeit nicht nennenswert herabgesetzt, nach einem Jahr ist sie jedoch vollständig verloren gegangen.

Der erste Versuch, die Sexualität bei *Hydnum auriscalpium* zu analysieren, wurde im Herbst 1936 durchgeführt. Hierbei wurde Sporenmaterial von einem Fruchtkörper (Nr. I) verwandt, der im »Stadtwald» südlich von Uppsala am 18 Okt. gefunden wurde. 10 Einspormyzelien wurden isoliert und dann paarweise in allen erdenklichen Kombinationen zusammengeführt. Nach ein paar Wochen begann ich die Kombinationskulturen zu untersuchen. Von der im allgemeinen deutlich sichtbaren Grenzlinie zwischen den beiden Myzelien in jeder Kombinationskultur wurden Probestücke genommen, die hinsichtlich

des Vorkommens von Schnallen untersucht wurden. Trotz des eingehendsten Studiums war ich nicht in der Lage, auch nur in einem einzigen Fall Schnallen nachzuweisen.

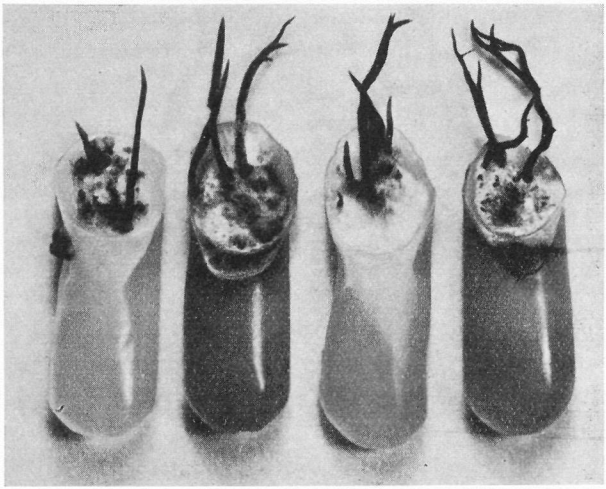


Fig. 2. In Kulturröhrchen gebildete Fruchtkörperanlagen von *Hydnum auriscalpium*. Die Kulturen sind ungefähr drei Monate alt.

Dass *Hydnum auriscalpium* ein im Diploidstadium schnallentragender Pilz ist, davon hatte ich mich schon früher durch die Untersuchung einer Gewebekultur aus einem Fruchtkörper überzeugt. Es bestand indessen die Möglichkeit, dass hier haploide Fruchtkörper in der Natur auftraten und dass ich gerade auf einen solchen als Quelle meines Sporenmaterials und damit meiner Einspormyzelien geraten war. Ich stellte Gewebekulturen aus weiteren 5 Fruchtkörpern her, die am gleichen Standort wie der obenerwähnte eingesammelt wurden, und nahm auch Sporen von zwei von ihnen (Nr. II und III). Sämtliche Gewebekulturen waren reich schnallentragend. Aus der Sporensaat von Fruchtkörper II wurden 5 Einspormyzelien isoliert, mit denen neue Kombinationen hergestellt wurden. Auch diesmal waren keine Schnallen anzutreffen.

Bei diesem letzteren Versuch wurde auch die Dichtsaatkultur untersucht, die auf einer der Malzagarplatten entstanden war, welche bei der Isolierung der Einspormyzelien gegossen worden waren. Es zeigte sich überraschend genug, dass Schnallen hier zahlreich vorkamen.

Blieb die Kopulation in Kulturröhrchen aus oder war die Bildung von schnallentragenden Hyphen dort unmöglich? Der folgende Versuch zeigte, dass auch derartige Erklärungen der durchweg negativen Ergebnisse ausgeschlossen waren. Zwei Einspormyzelien von Fruchtkörper I, zwei von Fruchtkörper II und zwei von Fruchtkörper III wurden paarweise auf übliche Weise in Röhrchen in allen denkbaren Kombinationen zusammengebracht. In allen 12 Kombinationen zwischen

Myzel von verschiedenen Fruchtkörpern konnte das reichliche Vorkommen von Schnallen festgestellt werden. Dies zeigte, dass bei *Hydnum auriscalpium* wie bei allen bisher untersuchten heterothallischen Hymenomyceten interfertile »geographische Rassen» auftreten. Das Problem bezüglich der Natur der Heterothallie bei diesem Pilz blieb indessen bis auf weiteres ungelöst.

Erst im Herbst 1939 wurde die Frage von neuem aufgegriffen. Von einem Fruchtkörper (Nr. IV) vom gleichen Standort wie die oben besprochenen liessen sich Sporen erhalten, die das Ausgangsmaterial für die Reinzüchtung von Einspormyzel bildeten. Bei der Isolierung wurde teils Kartoffel-Dextrose-Agar verwandt (nach ZELLER, SCHMITZ und DUGGAR 1919), teils Malzagar. Es wurden 54 Einspormyzelien isoliert, davon 33 (Nr. 1—33) von dem ersteren und 21 (Nr. 34—54) von dem letzteren Substrat. Bei der danach durchgeführten Sexualitätsanalyse wurden in einer Reihe Kombinationen Schnallen gefunden, und es erwies sich, dass die Einspormyzelien sich nach einem tetrapolaren Schema gruppierten. Die 18 untersuchten Myzelien verteilten sich auf folgende Weise:

$$\begin{cases} \begin{cases} a_1b_1\text{: } 1,\ 8,\ 17;\ 34,\ 37,\ 38. \\ a_2b_2\text{: } 4,\ 6,\ 7,\ 9,\ 12,\ 15;\ 41. \end{cases} \\ \begin{cases} a_1b_2\text{: } 2;\ 35,\ 36,\ 43. \\ a_2b_1\text{: } 42. \end{cases} \end{cases}$$

Bei dieser grossen Sexualitätsanalyse wurden nicht alle möglichen Kombinationen durchgeführt. Ein Jahr später wurde indessen eine neue Untersuchung der gleichen Art angestellt. Der hierbei verwandte Fruchtkörper (Nr. V) war auf derselben Stelle wie die früher benutzten geholt worden. Es wurden 10 Einspormyzelien isoliert, sämtlich von Malzagar. Der Kombinationsversuch hatte auch diesmal ein tetrapolares Schema (Fig. 1) als Ergebnis.

Während dieser letzteren geglückten Versuche traten keine Umstände auf, die eine Erklärung für den negativen Ausfall der ersten Versuche, die Sexualität bei *Hydnum auriscalpium* zu analysieren, zu geben vermochten. Man kann natürlich die Ursache in einem unglücklichen Zufall bei der Auswahl der Einspormyzelien für die Kombinationen suchen, wodurch zufälligerweise nur Myzel der einen und selben Haplontengruppe oder zweier miteinander nicht kopulierender Haplontengruppen ausgewählt wurde. Die Wahrscheinlichkeit hierfür ist jedoch begreiflicherweise sehr gering.

Es ist möglich, dass hier ein Parallelfall zu dem vorliegt, den VAN-

DENDRIES (1933) bei seiner Untersuchung der Sexualität von *Trametes suaveolens* fand. Fruchtkörper Nr. I von *Hydnum auriscalpium* wäre in diesem Fall »latent» tetrapolar, was indessen nicht durch eine spätere Untersuchung gezeigt werden kann, da der Fruchtkörper bei diesem Pilz viel ephemärer als der bei *Trametes suaveolens* und das rein vegetative Bodenmyzel praktisch genommen unerreichbar ist.

Schliesslich liesse sich denken, dass eine Allele des einen der Faktoren, die die Tetrapolarität bedingen, an einen Letalfaktor, einen stark wachstumshemmenden Faktor o. dgl. gekoppelt ist, wodurch also nur Vertreter für zwei Haplontengruppen bei den Isolierungen zu erhalten wären. Da indessen diese beiden Gruppen notwendigerweise intersteril sind, geben alle Kombinationen zwischen den erhaltenen Einspormyzelien negatives Resultat. Dass in der Natur Fälle vorkommen, wo beinahe alle der von einem tetrapolaren Fruchtkörper isolierbaren Einspormyzelien zwei intersterilen Haplontengruppen angehören, wurde vom Verfasser früher erwiesen (FRIES 1940: *Cyathus striatus* Nr. IX).

Bezüglich des Aussehens des Myzels in Reinkultur sei zunächst erwähnt, dass irgendwelche makroskopisch sichtbare Verschiedenheit zwischen haploiden und diploiden Myzelien nicht beobachtet werden konnte. Die individuellen Variationen sind jedoch ziemlich gross hinsichtlich Farbe, Wachstumsweise und Zuwachsgeschwindigkeit. Die Myzelien sind im allgemeinen hellgrau oder graubraun mit keinen oder schwach entwickelten Lufthyphen. Sie entwickeln sich am kräftigsten an und unmittelbar unter der Substratoberfläche. Oft kommen dunklere braune Flecken an älteren Myzelpartien vor. Die wachsende Kante ist bald scharf markiert, bald diffus. Das Myzel ist sehr dicht zusammengewoben und kann oft nur unter Schwierigkeit mit der Impfnadel forciert werden. Drinnen im Substrat wachsen die Hyphen dünner, dringen jedoch in den Kulturröhrchen bis 1 cm tief im Agar hinab. Das Myzel wächst ziemlich langsam, im Durchschnitt ungefähr $^1/_2$ cm in der Woche.

Nach mehrwöchentlichem Wachstum in den Kulturröhrchen beginnen sowohl Haploid- als Diploidmyzel Fruchtkörperanlagen auszubilden. Diese haben in den meisten Fällen die Form von kleinen graubraunen Knöpfchen, die einzeln oder in Gruppen vereinigt meist bei oder auf dem Impfstück selbst liegen, d. h. dem ältesten Teil des Myzels. In gewissen Fällen geht die Entwicklung weiter, und es bilden sich dunkelbraune und sammethaarige Auswüchse von hornförmiger Gestalt, die dem Aussehen nach oft vollständig mit den Fruchtkörperanlagen in der Natur übereinstimmen. In den Kulturröhrchen gelangt

diese Entwicklung jedoch niemals soweit, dass Hüte ausgebildet werden, sondern die erwähnten Auswüchse gehen statt dessen gewöhnlich dazu über, sich mehr oder weniger reich zu verzweigen, so dass in einer Reihe von Fällen schliesslich korallartige Bildungen entstehen (Fig. 2). Als Beispiel sei genannt, dass von 54 am 7. XI. 1939 isolierten Einsporemyzelien am 26. I. 1940, d. h. nach 80 Tagen, sämtliche Fruchtkörperanlagen gebildet hatten, und diese waren von der folgenden Art: in 37 Fällen Knöpfchenbildungen, in 8 Fällen unverzweigte und in 9 Fällen korallartig verzweigte Auswüchse.

Diese Neigung bei den Röhrchenkulturen zur Bildung von Fruchtkörperanlagen veranlasste mich zur Anordnung eines besonderen Versuches zwecks Hervorrufung normaler Fruchtkörperbildung von haploiden oder diploiden Myzelien in Reinkultur. Von den verschiedenen probierten Versuchsanordnungen erwies sich die folgende als beste.

In jeden einer Anzahl 300-ccm Erlenmeyer-Kolben aus Jenaer Glas wurden 3 oder 4 Kiefernzapfen und 10 ccm Malzagar hineingebracht. Die Kiefernzapfen waren auf Nadelwaldboden ausserhalb Uppsalas eingesammelt worden. Nach der Autoklavierung der Kolben wurde ausserdem jedem 20 ccm steriles dest. Wasser zugesetzt. Die Impfung mit *Hydnum auriscalpium* geschah von Röhrchenkulturen, und die Impfstücke wurden auf einem der Zapfen nahe der Oberfläche der Flüssigkeit placiert. Beim Versuch wurden sowohl haploide als diploide Myzelien verwandt. Die Kulturen wurden teils in Dunkelheit bei einer Temperatur von $+25^{\circ}$, teils in einem Gewächshaus mit Tageslicht und einer Temperatur von ca. $+18^{\circ}$ aufgestellt.

Fruchtkörperanlagen von gewöhnlichem Typ bildeten sich in mehreren Fällen bereits innerhalb eines Monats. Nur in einem einzigen Kolben von den 16 des Versuches entwickelte sich ein Fruchtkörper von voll normalem Aussehen. Dieser im Gewächshaus aufgestellte Kolben war mit dem Einspormyzel I : 1 geimpft, und der gebildete Fruchtkörper war also haploid.

Es schien so, als sei die Ursache, dass die im allgemeinen reich entwickelten Fruchtkörperanlagen mit der erwähnten Ausnahme nicht normale hymeniumtragende Hüte bildeten, in der allzu hohen Luftfeuchtigkeit bei den Kulturen zu suchen. Es dürfte auf keine grösseren Schwierigkeiten stossen, den Versuch so anzuordnen, dass die Fruchtkörperanlagen sich durchweg weiter zu Fruchtkörpern von normalem Aussehen entwickeln. Die für einen Hymenomyceten ungewöhnliche Neigung zur Bildung von Fruchtkörpern in Kultur, welche

Hydnum auriscalpium auszeichnet, macht diesen Pilz zu einem anwendbaren Objekt für genetische Untersuchungen.

Hydnum coralloides Scop. ex Fr.

Am 27. IX. 1936 sammelte ich einige schöne Fruchtkörper von *Hydnum coralloides* auf einem toten Espenstamm bei Lurbo im Kirchspiel Bondkyrka der Provinz Uppland. Sporen fanden sich in grosser Zahl und zeigten nach der Überführung auf Malzagar eine hochprozentige Keimung nach 2 bis 3 Tagen. Die Sporen wurden dann in Dunkelheit bei einer Temperatur von $+3^\circ$ oder $+25^\circ$ verwahrt, und die angestellten Proben wiesen, dass die Keimfähigkeit noch nach 6 Monaten nicht nennenswert herabgesetzt war. Nach einer einjährigen Verwahrung bei $+25^\circ$ war sie indessen vollkommen verloren gegangen.

Es wurden 18 Einspormyzelien isoliert und für die Sexualitätsanalyse kombiniert. Wie aus Fig. 3 hervorgeht, wurde ein deutliches tetrapolares Schema erhalten. Die 18 Einspormyzelien verteilen sich ziemlich gleichmässig auf die vier Haplontengruppen:

$$\left\{\begin{array}{l}\left\{\begin{array}{l}a_1b_1\text{: 1, 3, 4, 6, 16.}\\ a_2b_2\text{: 5, 8, 15, 18.}\end{array}\right.\\ \left\{\begin{array}{l}a_1b_2\text{: 2, 9, 10, 11, 13, 17.}\\ a_2b_1\text{: 7, 12, 14.}\end{array}\right.\end{array}\right.$$

Im nächsten Jahr, am 22. VIII. 1937, fand ich Fruchtkörper von *Hydnum coralloides* an einem andern Standort, nämlich auf einem umgestürzten, sehr mächtigen und stark verfaulten Espenstamm im Urwald Fiby im Kirchspiel Vänge und Läby, Uppland. Dieser Fundort liegt 16 km von dem ersten entfernt.

Aus Sporen des neuen Fruchtkörpers wurden 4 Einspormyzelien isoliert. Diese wurden mit den Testmyzelien Nr. 1, 2, 5 und 7 des im Jahre zuvor gefundenen Fruchtkörpers zusammengeführt. In sämtlichen 16 Fällen fand Kopulation statt. Hier liegen also zwei verschiedene »geographische Rassen» vor.

Die Haploid- und Diploidmyzelien sehen für das blosse Auge vollkommen gleich aus, wenn sie auf Malzagar wachsen. Das Luftmyzel ist weiss und bildet einen höchstens millimeterdicken Rasen, dessen Dichte etwas schwankt, weshalb er mitunter ein »flockiges» Aussehen erhält. Im älteren Stadium nimmt er einen mehr graubraunen Farbton an. Das Substratmyzel dringt ungefähr $^1/_2$ cm unter die Oberfläche hinab. Bei allen Kulturen färbt der Pilz allmählich den Malzagar

	1	3	4	6	5	8	2	7
1	—	—	—	—	+	+	—	—
3	—	—	—	—	+	+	—	—
4	—	—	—	—	+	+	—	—
6	—	—	—	—	+	+	—	—
5	+	+	+	+	—	—	—	—
8	+	+	+	+	—	—	—	—
2	—	—	—	—	—	—	—	+
7	—	—	—	—	—	—	+	—

	9	10	11	12	13	14	15	16	17	18
1	—	—	—	—	—	—	+	—	—	+
5	—	—	—	—	—	—	—	+	—	—
2	—	—	—	+	—	+	—	—	—	—
7	+	+	+	—	+	—	—	—	+	—

Fig. 3. *Hydnum coralloides.* Ergebnis der Kreuzungen zwischen 8 Einspormyzelien in allen Kombinationen und zwischen vier Testmyzelien (Nr. 1, 5, 2 und 7) und weiteren 10 Einspormyzelien.

dunkler, so dass er schliesslich eine schöne Bernsteinfarbe erhält.

Die Diploidmyzelien besitzen eine ausgeprägte Tendenz, auch in Röhrchenkulturen Fruchtkörper zu bilden. Diese können von so gut wie normalem Aussehen sein, sind jedoch meistens unregelmässiger gebaut als in der Natur. Dass *Hydnum coralloides* leicht in Kultur Fruchtkörper bildet, wurde früher von BROOKS (1913) beobachtet, der Dichtsaatkulturen auf Eschenholz züchtete und sowohl normale als abnorm gebaute Fruchtkörper erhielt. In einigen Fällen habe ich auch in Kulturen von Haploidmyzel Ansätze zur Bildung von Fruchtkörpern beobachtet, die in diesen Fällen jedoch keine normale Entwicklung erfuhren. Es ist indessen wahrscheinlich, dass man bei geeigneter Kulturtechnik normale haploide Fruchtkörper auch von *Hydnum coralloides* erhalten kann.

Hydnum corrugatum Fr.

Das Untersuchungsmaterial von *Hydnum corrugatum* bestand aus zwei Fruchtkörpern, von denen der eine (Nr. I) am 25. VII. 1937 von einem Birkenstumpf bei Lurbo im Ksp. Bondkyrka, Uppland, aufgelesen wurde und der andre (Nr. II) 3 Tage später von einem toten Espenstamm nur ein paar hundert Meter von dem ersten Standort entfernt. Ausserdem wurden Keimungsversuche mit Sporen von einigen

weiteren Fruchtkörpern von ungefähr der gleichen Einsammelstelle als der obengenannten durchgeführt.

Die Sporen dieser Art keimen sehr unregelmässig. Gewisse Fruchtkörper liefern Sporen, die zum mindesten auf gewöhnlichem Malzagar ausserstande zur Keimung sind. Andre Fruchtkörper dagegen geben Sporenmaterial, das keimfähig ist, indessen sind die Keimungsprozente gewöhnlich sehr niedrig. Die ersten Sporen keimen bereits nach ein paar Tagen, und dann finden neue Keimungen nach und nach während mehrerer Wochen statt. Noch nach einer sechsmonatigen Verwahrung in Dunkelheit bei $+3^{\circ}$ in Exsikkator scheint die Keimfähigkeit unvermindert zu sein.

	3	4	5	8	6	7
3	—	—	—	—	—	—
4	—	—	—	—	—	—
5	—	—	—	—	—	—
8	—	—	—	—	—	—
6	—	—	—	—	—	+
7	—	—	—	—	+	—

	9	10	11	12	13	14	16	18	19	20
5	—	—	+	—	—	+	—	+	—	—
6	+	—	—	—	—	—	—	—	—	+
7	—	—	—	—	+	—	+	—	—	—

Fig. 4. *Hydnum corrugatum.* Ergebnis der Kreuzungen zwischen 6 Einspormyzelien in allen Kombinationen und zwischen drei Testmyzelien (Nr. 5, 6 und 7) und weiteren 10 Einspormyzelien.

Die Untersuchung der Sexualität, die mit Einspormyzel von Fruchtkörper I begonnen wurde, musste leider abgebrochen werden, bevor ein Kombinationsschema von gewünschtem Umfang hergestellt werden konnte. Die ausgeführten und untersuchten Kombinationen dürften indessen einen ausreichend klaren Beleg für die tetrapolare Natur des Pilzes liefern (Fig. 4). Die Einspormyzelien verteilen sich in folgender Weise auf die vier Haplontengruppen:

$$\left\{\begin{array}{l}\left\{\begin{array}{l}a_1b_1\text{: 3, 4, 5, 8, 10, 12, 19.}\\ a_2b_2\text{: 11, 14, 18.}\end{array}\right.\\ \left\{\begin{array}{l}a_1b_2\text{: 6, 13, 16.}\\ a_2b_1\text{: 7, 9, 20.}\end{array}\right.\end{array}\right.$$

Durch die Kombination von Myzel verschiedener Fruchtkörper konnte auch hier das Vorkommen von »geographischen Rassen» nachgewiesen werden.

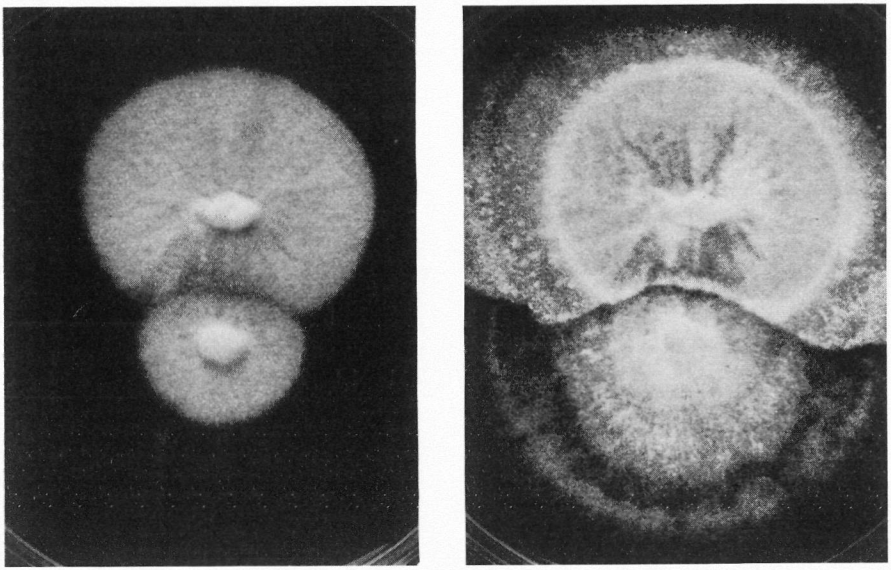


Fig. 5. *Hydnum corrugatum*. Eine Kombinationskultur von zwei nicht miteinander kopulierenden Einspormyzelien, die ein Alter von einem Monat (links) bzw. zwei Monaten (rechts) aufweist.

Haploide und diploide Myzelien von *Hydnum corrugatum* weichen dem Aussehen nach stark voneinander ab. Die Haploidmyzelien wachsen sehr langsam mit einer regelmässigen Kante und bilden einen dichten Hyphenrasen auf der Substratoberfläche. Die Lufthyphen bilden ein kaum mehr als 1 mm hohes, schneeweisses Luftmyzel, und die Substrathyphen dringen bis 1 cm in den Agar hinab. Die diploiden Myzelien bekommen immer einen sehr unregelmässigen Randkreis und kennzeichnen sich vor allem durch die zahlreichen, unregelmässig verstreuten Fruchtkörperanlagen. Diese bedecken oft den grösseren Teil der Myzeloberfläche in der Form von unregelmässigen Knöpfchen oder ± korallartig verzweigten Auswüchsen von weisser oder hellbrauner Farbe. In den Kulturröhrchen können diese Fruchtkörperanlagen oft den grösseren Teil des Luftraumes unmittelbar oberhalb der Agarschrägfläche ausfüllen und sich mitunter zu kleinen, aber normal gebauten Fruchtkörpern entwickeln.

Auf Grund dieses charakteristischen Habitus des Diploidmyzels kann man in der Regel ohne Schwierigkeit in den Kombinationskulturen direkt makroskopisch entscheiden, in welchen Fällen Kopulation stattfand. Insbesondre auf Kulturen in Petrischalen kann man der

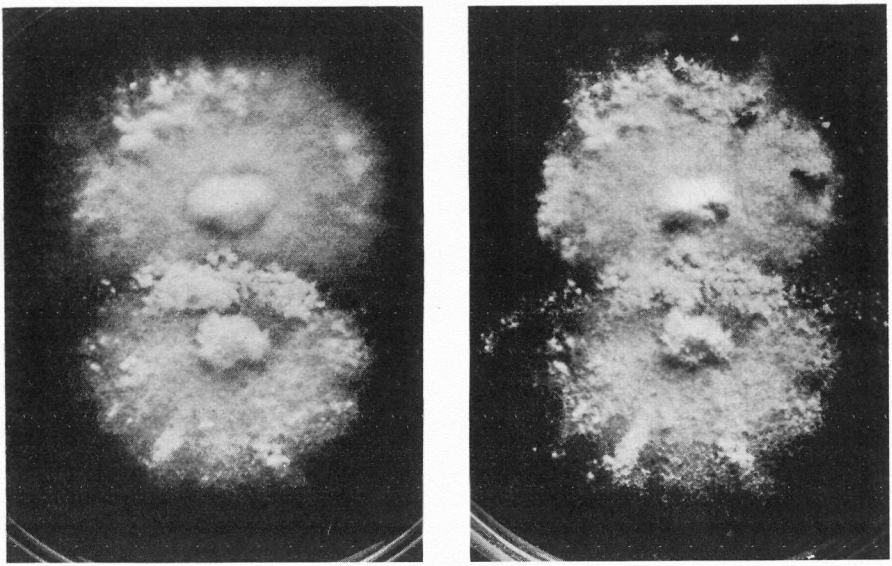


Fig. 6. *Hydnum corrugatum.* Eine Kombinationskultur von zwei miteinander kopulierenden Einspormyzelien, die ein Alter von einem Monat (links) bzw. zwei Monaten (rechts) aufweist.

Diploidisierung von zwei miteinander kopulierenden Myzelien recht schön folgen (Fig. 5 und 6). Wenn die beiden Myzelien zusammentreffen, bildet sich zunächst ein kräftiger Rasen von dicht zusammengewobenen Hyphen, auf dem bald knöpfchenförmige Fruchtkörperanlagen auftreten. Darauf zeigen sich derartige Fruchtkörperanlagen in immer längerem Abstand von der Grenzzone, bis schliesslich — auf alle Fälle nach einigen Wochen — beide Einspormyzelien diploidisiert sind. Irgendwelche genaueren Bestimmungen der Schnelligkeit des Diploidisierungsprozesses wurden nicht angestellt, indessen geht im Hinblick auf das sehr langsame Wachstum des Myzels die Diploidisierung offenbar ziemlich rasch vor sich.

Hydnum strigosum Sw. ex Fr.

Von diesem seltenen Stachelpilz sammelte ich am 11. X. 1936 frische Fruchtkörper in einem hohlen Kirschbaum bei Linnés Hammarby im Ksp. Danmark, Uppland. Die Sporen keimten erst nach einigen Tagen, und am 23. X. 1936 konnten eine Anzahl Einspormyzelien isoliert werden.

	1	2	4	3	5	6
1	—	—	—	+	—	—
2	—	—	—	+	—	—
4	—	—	—	+	—	—
3	+	+	+	—	—	—
5	—	—	—	—	—	+
6	—	—	—	—	+	—

	7	8	9	10	11	12	13	14	15
4	—	—	—	—	—	—	—	—	—
3	—	+	—	+	—	—	—	+	+
5	+	—	+	—	+	—	+	—	—
6	—	—	—	—	—	+	—	—	—

Fig. 7. *Hydnum strigosum.* Ergebnis der Kreuzungen zwischen 6 Einspormyzelien in allen Kombinationen und zwischen vier Testmyzelien (Nr. 4, 3, 5 und 6) und weiteren 9 Einspormyzelien.

Die Sexualitätsanalyse von 15 Einspormyzelien zeigte, dass *Hydnum strigosum* in Übereinstimmung mit den übrigen drei *Hydnum*-Arten tetrapolar ist (Fig. 7). Die Einspormyzelien sind nicht gleichförmig über die vier Haplontengruppen verteilt, sondern es scheint, als ob die zwei Gruppen mit dem Faktor a_2 zu schwach vertreten seien, was indessen auf einer Zufälligkeit beruhen kann:

$$\left\{\begin{array}{l}\left\{\begin{array}{l}a_1b_1\text{: 1, 2, 4, 8, 10, 14, 15.}\\ a_2b_2\text{: 3.}\end{array}\right.\\ \left\{\begin{array}{l}a_1b_2\text{: 6, 7, 9, 11, 13.}\\ a_2b_1\text{: 5, 12.}\end{array}\right.\end{array}\right.$$

Eine habituelle Verschiedenheit zwischen Haploid- und Diploidmyzel wurde nicht beobachtet. Die Myzelien hatten eine graubräunliche Farbe, wuchsen ziemlich dicht und bildeten nur in unbedeutendem Masse Lufthyphen. Ein Ansatz zur Fruchtkörperbildung fand sich nicht.

Irpex pendulus (A. et S.) Fr.

Fruchtkörper dieses ziemlich seltenen Pilzes habe ich nur an einem Standort eingesammelt, nämlich am 6. X. 1940 auf einer blossliegenden dicken Kiefernwurzel, die an einem Fluss-Steilhang bei Kvarnbo im Ksp. Bondkyrka, Uppland, wuchs. Von einem der dünnen, leicht trocknenden Fruchtkörper erhielt ich zahlreiche Sporen. Diese keimten auf Malzagar bereits nach 24 Stunden, und Einspormyzelien konnten ohne Schwierigkeit isoliert werden. Die schnell wachsenden Einspormyzelien sind immer ohne Schnallen und bilden allmählich sehr

kräftige Lufthyphen aus, die bei der Züchtung des Myzels in Kulturröhrchen schliesslich vollkommen die Mittelpartie desselben ausfüllen können. Das Luftmyzel ist locker und üppig, anfangs schneeweiss, doch schliesslich mehr oder weniger braungelb oder braunfleckig. Auch ein kräftiges Substratmyzel bildet sich, das mindestens 1 cm unter die Agaroberfläche hinabdringt.

	1	3	9	6	11	2	4	5
1	—	—	—	+	+	—	—	—
3	—	—	—	+	+	—	—	—
9	—	—	—	+	+	—	—	—
6	+	+	+	—	—	—	—	—
11	+	+	+	—	—	—	—	—
2	—	—	—	—	—	—	+	+
4	—	—	—	—	—	+	—	—
5	—	—	—	—	—	+	—	—

Fig. 8. *Irpex pendulus*. Ergebnis von Kreuzungen zwischen 8 Einspormyzelien.

Auf Malzagar gezüchtete Myzelien von *Irpex pendulus* verlieren ungewöhnlich schnell ihre ursprüngliche Vitalität, und wartet man mit der Umimpfung einer Kultur mehr als 1—1 $^1/_2$ Monat, pflegt das Tochtermyzel deutliche Spuren von Selbstvergiftung aufzuweisen: der Zuwachs hört auf, bevor die ganze Agaroberfläche überwachsen ist, das Luftmyzel bleibt klein und das Substrat wird gewöhnlich stark dunkelbraun oder beinahe schwarz.

Wie aus dem folgenden hervorgeht, ist der Pilz heterothallisch. Das Diploidmyzel ist habituell dem eben beschriebenen Haploidmyzel ziemlich gleich, doch wachsen die Hyphen dichter und feinwolliger, und das diploide Myzel erhält dadurch auch eine weissere Farbe.

Zum Unterschied von den Einspormyzelien sind die Gewebe- und Dichtsaatmyzelien reich schnallentragend. Eine Sexualitätsanalyse von 8 Einspormyzelien in sämtlichen Kombinationen (Fig. 8) zeigte, dass auch dieser Pilz tetrapolar ist.

$$\begin{cases} \begin{cases} a_1b_1\text{: } 1,\ 3,\ 9. \\ a_2b_2\text{: } 6,\ 11. \end{cases} \\ \begin{cases} a_1b_2\text{: } 2. \\ a_2b_1\text{: } 4,\ 5. \end{cases} \end{cases}$$

Wenn die »positiven» Kombinationskulturen sich in einem gewissen Stadium befinden, kann man sie ziemlich leicht rein makroskopisch von den »negativen» unterscheiden. In den ersteren bildet sich nämlich auf der Grenzlinie zwischen den beiden Myzelien ein Band von dichterem und weisserem Diploidmyzel, und in den letzteren kann mitunter eine schwache Aversionszone auftreten. Gewöhnlich wach-

sen jedoch die Myzelien bis zum Zusammentreffen, ohne dass eine besonders markierte Grenzzone vorkommt.

Eine Andeutung zur Bildung von Fruchtkörpern wurde in der Kultur nicht beobachtet.

Radulum Radula (Fr.) Nannf. (= Radulum orbiculare Grev. ex Fr.).

Von *Radulum Radula* wurden zwei verschiedene Isolierungen hergestellt, die erste von einem Fruchtkörper (Nr. I), der am 6. X. 1940 von einem toten Birkenstamm bei Lurbo im Ksp. Bondkyrka, Uppland, geholt wurde, und die zweite von einem Fruchtkörper (Nr. II), der am 28. XII. 1940 von einem toten Birkenzweig im Wald nördlich der Stadt Uddevalla, Provinz Bohuslän, abgenommen wurde. Die frischen Fruchtkörper lieferten eine grosse Menge Sporen, die auf Malzagar sehr schnell keimten, die meisten bereits innerhalb von 24 Stunden. Bei der Aufbewahrung in Dunkelheit behalten die Sporen lange ihre Keimfähigkeit. Zum mindesten ein Teil der Sporen ist noch nach 8 Monaten voll keimfähig.

Ein Kombinationsversuch mit 10 Haploidmyzelien vom ersten Fruchtkörper zeigte, dass *Radulum Radula* zum Unterschied von den andern an dieser Stelle untersuchten Hydnaceen bipolar ist (Fig. 9):

$$\begin{cases} a_1\text{: } 1,\ 2,\ 5,\ 6,\ 8,\ 10. \\ a_2\text{: } 3,\ 4,\ 7,\ 9. \end{cases}$$

Die vier Myzelien I : 1, 2, 3, 4 liessen sich sämtlich mit vier auf's Geratewohl ausgewählten Einspormyzelien von Fruchtkörper II kopulieren, welches bedeutet, dass die beiden Fruchtkörper verschiedene »geographische Rassen» vertreten.

Die Untersuchung der Kombinationskulturen ist sehr leicht, da Schnallen — sobald sie vorkommen — immer in grosser Zahl auftreten. Die Haploid- und Diploidmyzelien unterscheiden sich übrigens unter dem Mikroskop voneinander durch einen etwas verschiedenen Habitus, der doch schwer zu charakterisieren ist. Die Hyphen der Einspormyzelien sind niemals so dick wie die der Diploidmyzelien, und bei den letzteren sind die Zellen oft unregelmässiger und gleichsam angeschwollen. Die schon von BREFELD (1889) beobachteten perlbandartigen Auswüchse von den Hyphen kommen sowohl bei Haploid- als Diploidmyzel vor, im letzteren Fall oft in direkter Konnektion mit einer Schnalle.

In Bezug auf den makroskopischen Habitus des Myzels stimmt

dieser ziemlich stark mit dem oben unter *Irpex pendulus* beschriebenen überein. Sowohl Luft- als Substratmyzel sind indessen hier weniger kräftig entwickelt. Das erstere wächst ferner etwas feiner und dichter als bei *Irpex*, mitunter mit einem gelblichen Ton, und vermag niemals vollkommen den Luftraum im Kulturröhrchen auszufüllen.

	1	2	5	6	8	10	3	4	7	9
1	—	—	—	—	—	—	+	+	+	+
2	—	—	—	—	—	—	+	+	+	+
5	—	—	—	—	—	—	+	+	+	+
6	—	—	—	—	—	—	+	+	+	+
8	—	—	—	—	—	—	+	+	+	+
10	—	—	—	—	—	—	+	+	+	+
3	+	+	+	+	+	+	—	—	—	—
4	+	+	+	+	+	+	—	—	—	—
7	+	+	+	+	+	+	—	—	—	—
9	+	+	+	+	+	+	—	—	—	—

Fig. 9. *Radulum orbiculare*. Ergebnis von Kreuzungen zwischen 10 Einspormyzelien.

Die Diploidmyzelien sind makroskopisch vollkommen den Haploidmyzelien gleich, zeichnen sich indessen durch eine etwas grössere Wachstumsgeschwindigkeit aus. Um einen ziffernmässigen Ausdruck für diese Verschiedenheit zu gewinnen, wurde die Wachstumsgeschwindigkeit von 12 frischisolierten Einspormyzelien von Fruchtkörper I gemessen, ferner bei 12 von Fruchtkörper II sowie 12 Diploidmyzelien, die durch Kombination von Einspormyzel der Fruchtkörper I und II erhalten wurden. Bei der Züchtung auf gewöhnlichem Malzagar wurden folgende Durchschnittswerte des täglichen Wachstums in Millimetern erhalten: (I:) $1{,}73 \pm 0{,}09$, (II:) $1{,}53 \pm 0{,}09$ und (I×II:) $2{,}32 \pm 0{,}06$. Auf Malzgelatine (12 % Gelatine und 2,5 % Malzextrakt enthaltend) wuchsen die Myzelien etwas langsamer: (I:) $1{,}52 \pm 0{,}10$, (II:) $1{,}47 \pm 0{,}07$ und (I×II) $2{,}24 \pm 0{,}11$. Aus den Ziffern ergibt sich, dass die diploiden Myzelien auf den zwei probierten Substraten mit ungefähr 40 bezw. 50 % grösserer Geschwindigkeit wachsen als die haploiden.

Zusammenfassung.

1. *Hydnum auriscalpium, H. coralloides, H. corrugatum, H. strigosum* und *Irpex pendulus* besitzen tetrapolare und *Radulum Radula* (= *R. orbiculare*) bipolare Geschlechtsverteilung. Bei *H. auriscalpium* fielen die ersten Sexualitätsanalysen völlig negativ aus, und die möglichen Ursachen dieses Verhaltens werden diskutiert.

2. »Geographische Rassen» konnten nachgewiesen werden bei *Hydnum auriscalpium, H. coralloides, H. corrugatum* und *Radulum Radula*.

3. Diploide Myzelien von *Hydnum coralloides* und *H. corrugatum* sowie haploide Myzelien von *H. auriscalpium* und *H. coralloides* bilden Fruchtkörper in Reinkultur aus.

4. Bei *Hydnum corrugatum* unterscheiden sich die Diploidmyzelien von den Haploidmyzelien durch stärkere Tendenz zur Fruchtkörperbildung, bei *Radulum Radula* durch ihre grössere Wachstumsgeschwindigkeit.

5. Das Aussehen der gezüchteten Hydnaceen in Reinkultur wird beschrieben.

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Literaturverzeichnis.

BREFELD, O. 1889. Untersuchungen aus dem Gesammtgebiete der Mykologie. VIII. Heft: Basidiomyceten III. Leipzig.

BROOKS, F. T. 1913. Observations on pure cultures of some Ascomycetes and Basidiomycetes. — Trans. Brit. Mycol. Soc., 4.

BROWN, C. A. 1935. Morphology and biology of some species of *Odontia*. — Bot. Gaz., 96.

FRIES, N. 1940. Researches into the multipolar sexuality of *Cyathus striatus* Pers. — Symb. Bot. Ups., IV: 1.

HOFFMANN, H. 1859. Ueber Pilzkeimungen. — Bot. Zeitung, 17.

VANDENDRIES, R. 1933. Nouvelles investigations dans le domaine sexuel des Hyménomycètes. — Bull. Soc. myc. France, 49.

ZELLER, S. M., SCHMITZ, H. et DUGGAR, B. M. 1919. Studies in the physiology of the fungi. VII. Growth of wood-destroying fungi in liquid media. — Ann. Miss. Bot. Garden, 6.

Växtgeografiska bidrag. 6. Ångermanland.

Av Erik Almquist.

Ehuru väl Ångermanland långt ifrån är »en vit fläck på Sveriges botaniska karta» — såsom Dahlbeck (i Bygd och Natur 1939) med hänsyn till bristen på en modern floristisk sammanfattning kallade det —, kan uttrycket i fråga alltjämt tillämpas på vissa delar av landskapet, från vilka nära nog inga botaniska uppgifter föreligga.

Örnsköldsviks skärgård är, om Ulvöarna frånses, ett sådant område. Knappast ens i H. Skottes uppgifter (Haglund 1923), de rikhaltigaste bland dem som hittills berört Örnsköldsvikstrakten, finner man något från havsbandet. I besittning av en del redan ganska gamla anteckningar därifrån, vill jag härmed meddela ett utdrag ur dessa tillika med ett komplement, som assistenten Th. Arwidsson haft den stora älskvärdheten ställa till mitt förfogande.

Det var i augusti 1922, som tillfälle bjöds mig att under en veckas vistelse på Nötbolandet utanför Örnsköldsvik även besöka några fisklägen på närliggande öar (Malmön, Grisslan, Trysunda) och samtidigt ett par obebodda öar (Råskärsön och Skrubban). Förutom smärre strövtåg omkring Nötbolandet gjordes också en exkursion på halvön Skaglandet sydligast i Grundsunda s:n. De flesta utflykterna missgynnades av mindre gott väder, och den begränsade tid, som under dessa stod till buds, gjorde också det botaniska utbytet för mitt vidkommande rätt ofullständigt.

Arwidsson överfor samma skärgård tillsammans med dr G. Hasselberg i juli 1931. Utom nyssnämnda öar besökte de även Ellö, Vågö och några närliggande skär. Tack vare detta värdefulla tillskott torde nedanstående sammanställning någorlunda fullständigt återge, vad som kan vara av intresse inom det besökta området.

Ifrågavarande kuststräcka gör i huvudsak ett botaniskt kargt intryck. Innanför strandklippor, grus- eller klapperfält (delvis av imponerande utsträckning!) möter i regel den triviala barrskogen med insprängda myrar (även på öarna), medan ängs- och lundvegetation är

mycket sparsam. Förstnämnda ståndorter sakna ingalunda intresse, men mera fordrande arter äro väsentligen inskränkta till klyftor och skrevor, en och annan bäckdäld eller bergrot. Högre brantberg — för att tala med GRAPENGIESSER (1934) — finnas icke förrän längre in. Den floristiskt intressantaste ön är antagligen Skrubban, eljest bekant för sitt »fågelberg» och partiellt fridlyst för fågellivets skull. Denna ö vore troligen värd en mera ingående undersökning än som under våra flyktiga besök hanns med.

I artlistan medtagas även en del vanligare växter, då lokaluppgifterna dels kunna erbjuda kartläggningsmaterial, dels vittna om eventuell frånvaro på öarna. Ett urval blir ju något subjektivt, och det kunde möjligen ha varit av intresse att meddela lokaler även för vissa andra (t. ex. *Arctostaphylos, Cornus, Fragaria, Myrica, Scutellaria, Selaginella, Tussilago, Valeriana*), som förekomma m. el. m. allmänt i hela området. — Några sannolika defekter i floran påpekas i slutet.

Förteckningen kompletteras med några anteckningar av mig från ett besök i staden och efterföljande godstågsfärd Örnsköldsvik—Sollefteå (1922) samt med sporadiska iakttagelser under Sollefteå-besök och genomresor olika år.

För ytterligare en del spridda bidrag har jag att tacka professor E. B. ALMQUIST (Aqt), lektor O. B. SANTESSON (Sant.) och docent G. DEGELIUS (Deg.)[1]; den sistnämndes uppgifter äro från 1930, de övriga äldre. — Helt få uppgifter förskriva sig från inlandet ovan stambanan och endast ett par från den västerbottniska länsdelen (Norrfors stn).

Icke signerade fynd äro mina egna, för tydlighetens skull utmärkta med ! i vissa fall, då uppgifter av ARWIDSSON (Arw.) anföras från samma socken. Med * markeras uppgifter, som föreligga både i mina och hans anteckningar.

Lokaler i Örnsköldsvikstrakten (utom Mo s:n) stå i förekommande fall först; övriga föregås av ett tankstreck. — För de förstnämnda betecknas socknarna så: *A.* = Arnäs; *G.* = Grundsunda; *N.* = Nätra; *Sj.* = Själevad. Ett par lokalbeteckningar (i *Sj.*) må förklaras: Guldvik = Guldvikfjärdens nordända; Vikbotten = Vågefjärdens inre ända; Våge tjärn avser den lilla sjön därintill (huruvida detta i mina anteckningar förekommande namn var gängse i orten, minns jag nu icke).

Beläggexemplar av en del arter finnas i Riksmuseet. För ett par

[1] Denne har själv i lichenologiskt sammanhang publicerat en del fanerogamfynd, bl. a. från Gällstaberget i Vibyggerå. Se: G. DEGELIUS, Zur Flechtenflora von Ångermanland. Ark. f. bot. 24 A: 3 (1931), sid. 10 (etc.).

av mina fynd, som redan publicerats, följer här närmare lokalprecisering; i övrigt har jag sökt utgallra i litteraturen förefintliga lokaluppgifter.

Nomenklaturen följer för kärlkryptogamer HOLMBERGS flora, eljest LINDMANS (2:a uppl.).

Achillea ptarmica. — Längs järnv. vid Uvsjön, Anundsjö stn, Mellansel etc.
Actaea spicata. *N.* Skrubban (klyfta vid Måsberget).
Agropyron caninum. *N.* Skrubban rikl.; *A.* Malmöklubb; *G.* Skagen.
Agrostis clavata. Örnsköldsviks bangård (rud.), om härstammande från någon naturlig förekomst i grannskapet eller ditförd med järnvägen, är svårt att säga.
Alchemilla glomerulans. Örnsköldsvik (park).
A. micans. *N.* Trysunda; *Sj.* Vågeänget.
A. Murbeckiana. Örnsköldsvik (park); *A.* Nötbolandet, Råskärsön; *N.* Trysunda. — Sollefteå allm. kring staden; Långsele stn.
A. subcrenata. *A.* Råskärsön.
A. subglobosa. — Sollefteå: Djupöns lastageplats.
A. Wichurae. — Sollefteå fl. vid staden; Långsele stn.
Alisma plantago-aquatica. — Resele: Selsjön; Skorped: Stugusjön.
Alnus glutinosa. *N.* Skrubban (enst. i kärr); *Sj.* Guldvik (skogsbryn vid havet).
Anemone hepatica. *N.* Skrubbans nordsida (få ex., Arw.). [*A.* enl. uppg. vid Nötbolandet o. Alne sågverk.] — Trehörningsjö: Herrbergsliden vid Önskasjön (Sant.).
Apera spica venti. Örnsköldsviks hamn (rud.).
Arabis petraea. I havsbandet allm. inom det besökta området i *N.*, *Sj.* och *A.* åtm. upp till Hörnskaten och Malmöklubb; ej sedd av mig i *G.* (men enl. GRAPENGIESSER 1937 även funnen där).
A. suecica. *N.* N:a Ulvön vid Sörbyn (Deg.).
Aracium paludosum. *Sj.* nära Guldvik och Norrvåge; *A.* Nötbolandet.
Arenaria serpyllifolia. — Sollefteå: Djupökajen (1922).
Arrhenatherum elatius. — Gudmundrå: Strömnäs på banvall (1936).
[*Artemisia absinthium.* *A.* Nötbolandet odlad jämte *Levisticum.*]
Asperugo procumbens. — Sollefteå prästgård (1922).
Asplenium septentrionale. *N.* Skrubban* (spars.), Trysunda (2 lok., Arw.). — Vibyggerå: Fäberget (Deg.).
A. trichomanes. *N.* N:a Ulvön (Deg.), Skrubban fl.*, Trysunda fl.* (i mängd).
Atriplex patulum. Örnsköldsvik vid Framnäs.
Bidens tripartitus. Örnsköldsvik vid Framnäs (SAMUELSSON 1937), rikl. 1922, även i »dike vid hamnen».
Botrychium boreale. *Sj.* Ellö (c. 15 ex. i *Antennaria*-matta, G. Hasselberg enl. Arw.), Vågö (1 ex., Arw.).
B. lunaria. *N.* Skrubban*, Trysunda!
B. multifidum. *A.* Nötbolandet, Skommarhamn (klippspr.), Malmön; *G.* Mattjäl (strandäng), Tennviken — överallt i enstaka ex.

Bromus arvensis. — Härnösand vid elverket (1922); Graninge stn (enst. 1922).
B. secalinus. Örnsköldsviks hamn (rud.). — Torsåker: Aspby (åker, 1936); Sollefteå: Hågesta (veteåker, 1922).
Calamagrostis arundinacea. *N.* Trysunda (vid foten av Bockviksberget); *A.* Råskärsön (Arw.).
C. epigejos. *N.* Skrubban (i myr); *Sj.* Norrvåge, Vågeänget; *A.* Nötbolandet. — Mo: Mo, Söderå, Gottne etc.; Björna: Leding (Sant.).
C. lapponica. *A.* Nötbolandet. — Anundsjö o. Mo fl. utmed järnv.; Ramsele allm. (Aqt).
Calla palustris. *G.* Jordavan på Skaglandet. — Mo: Österalnö.
Callitriche autumnalis. *G.* Tennviken (i havet).
Campanula rapunculoides. [*A.* Hornön, odlad.] — Torsåker: Hjärtnäs (åker, 1931); Sollefteå: Djupövägen (i täppa, steril, 1931).
Carex capillaris. *N.* Trysunda på Kapellsberget (Arw.).
C. chordorrhiza. *Sj.* Vågö (Arw.). På fastlandet förbisedd?
C. diandra. *Sj.* Våge tjärn.
C. digitata. *N.* Skrubban*, Trysunda*; *Sj.* Guldvik etc.!, Vågö (Arw.); *A.* Skommarhamn!, Råskärsön (Arw.).
C. elongata. *Sj.* Vågö (västsidan, Arw.).
C. flava. *N.* Skrubban; *Sj.* Vågeänget; *A.* Hörnskaten.
C. flava×*Oederi.* *A.* Hörnskaten. [*C. Oederi* vanlig i trakten.]
C. glareosa. *N.* Skrubban (Arw.), Trysunda!; *Sj.* Klösan, Vågö holme, Norrklubben (Arw.); *G.* Mattjäl, Skagen fl.
C. Halleri. — Ramsele »i kärr» (Aqt).
C. livida. *Sj.* Skommarhamnstrakten fl.; *G.* Skeppsmaln.
C. loliacea. *A.* Nötbolandet. — Björna stn (Deg.); Trehörningsjö norr om stn samt Hemliden (Deg.).
C. norvegica. *Sj.* Vikbotten, Vågeänget; *G.* Mattjäl, Skeppsmaln.
C. pallescens. Havsbandet t. allm. — Björna: Leding (Sant.).
C. pilulifera. *Sj.* Guldvik fl.; *A.* Skommarhamn.
C. tenella. *Sj.* Guldvik (vid skogsbäck)!, Vågö (västsidan, Arw.). — Trehörningsjö norr om stn (Deg.).
Chaenorrhinum minus. — Helgum stn 1931; Sollefteå stn (SAMUELSSON 1927) 1931, 1936.
Cicuta virosa. *A.* Nötbolandet (bäckmynning); *Sj.* Själevadsfjärden.
Circaea alpina. *A.* Nötbolandet (bäckdal).
Convallaria majalis. *N.* Skrubban fl.*; *Sj.* Ellö (rikl., Arw.). [Enl. uppgift: *A.* L. Buröholmen; *G.* Killingsnäs.]
Corallorrhiza trifida. *N.* Ulvöhamn (Deg.); *Sj.* Klösan o. Vågö (Arw.). — Vibyggerå: Fäberget (Deg.).
Cystopteris fragilis. *N.* Skrubban*, Trysunda*; *Sj.* Ellö, Grisslaön (Arw.); *A.* Råskärsön, Malmöklubb.
[*Daphne mezereum.* *A.* Hornön, odlad.]
Deschampsia bottnica. *Sj.* Vågeänget!, Vågö holme (Arw.); *A.* Skommarhamn!, Råskärsön*, Malmön!; *G.* Mattjäl, Tennviken.
Dianthus deltoides. *Sj.* Norrvåge; *A.* Hornön.
Draba nemorosa. *N.* Trysunda fiskläge (Arw.); *Sj.* Grisslaön (Arw.).

Dryopteris filix mas. *N.* Skrubban* (rikl.); *Sj.* Ellö (Arw.); *A.* Råskärsön (Arw.), Malmöklubb (enst.)!
D. spinulosa. *Sj.* Vågeänget; *A.* Nötbolandet. [*D. austriaca* allm.]
Elatine hydropiper och *E. triandra.* *Sj.* Själevadsfjärden vid Hampnäs.
Elymus arenarius. — Banvallen mell. Ådalsliden o. Åkvisslan fl., rätt rika bestånd (Deg.).
Epilobium collinum. *N.* Trysunda (Arw.); *G.* Stubbsand, Skagen — allt på strandklippor.
E. montanum. *N.* Skrubban!, Trysunda*; *A.* Nötbolandet. — Skorped stn; Anundsjö: Sörböle.
Equisetum pratense. *Sj.* Vågeänget etc.; *A.* Nötbolandet, Råskärsön (rikl.). — Inåt landet väl snarast allm. i älvdalarna.
E. variegatum. *Sj.* Guldvik (bäckstr.), Vågeänget; *A.* Nötbolandet; *G.* Skagen vid Guldbredviken (allt på havsstr.).
Erysimum hieraciifolium. Örnsköldsviks hamn (1931 Arw.). — Resele: Mångmanån vid älven (vintern 1924). — Sannolikt denna art på banvall vid Strömnäs (1936).
Eupteris aquilina. *Sj.* nära Guldvik.
Festuca duriuscula. — Långsele stn (1922), järnvägslinjen Långsele—Österås fl. (1931); på besådda slänter.
F. pratensis. — Utom städerna noterad vid Forse bruk (1922) och några jvstationer: Långsele, Selsjön, Skorped, Mellansel (allt 1922), Trehörningsjö (1931).
Filago montana. — Sollefteå: Djupökajen (1922).
Galeopsis tetrahit. — Selsjön stn (rud., 1922).
Galium aparine. Örnsköldsviks bangård (enst.).
G. mollugo. *Sj.* Själevad stn. — Gudmundrå och Ytter-Lännäs fl. (1931).
G. trifidum. *G.* Jordavan på Skaglandet.
G. triflorum. *N.* Trysunda (vid Kapellsberget* o. Bockviksberget!); *A.* Råskärsön (Arw.).
G. verum. *G.* Skeppsmalns fiskläge. — Långsele gård (nära stationen); Sollefteå vid jvstationen; Resele: Hamptjärnsbäcken (banvall).
Gentiana nivalis. — Graninge: Ledinge vid jämtlandsvägen (1870, Aqt).
Glaux maritima. *Sj.* Vågö holme (Arw.); *G.* Mattjäl, Tennviken.
Glechoma hederacea. *G.* Skeppsmalns fiskläge. — Sollefteå vid kyrkan.
Glyceria maxima. *Sj.* Hampnäs vid Själevadsfjärden (spars.).
Goodyera repens. *N.* Skrubban, Trysunda; *Sj.* nära Guldvik.
Hierochloë odorata. — Resele: Selsjön (Sant.).
Hippuris vulgaris. *Sj.* Våge tjärn!, Vågö (Arw.); *G.* Jordavan på Skaglandet.
Honckenya peploides. *Sj.* Guldvik!, Klösan, Vågö holme (Arw.); *A.* Hörnskaten! (spars.), Råskärsön* (ymn.); *G.* Stubbsand (spars.).
Isoëtes echinosporum. *G.* Långsjön på Skaglandet.
Juncus balticus. *N.* Skrubban fl.!, Trysunda (Arw.); *Sj.* Ellö, Klösan, Vågö holme, Norrklubben (Arw.); *A.* Skommarhamn!, Råskärsön*; *G.* Mattjäl, Skagen.
J. compressus. *A.* Malmöklubb; *G.* Skeppsmaln (båda st. på strandklippor).
J. Gerardi. *N.* Trysunda (Arw.); *G.* Mattjäl (ängsbildande).
Knautia arvensis. — Längs järnv. i Helgum (Gransjö), Ed (fl.) o. Mo (Söderå).

Lamium album. — Härnösand vid elverket (spars. 1922).
L. amplexicaule. *N.* Trysunda. — Sollefteå prästgård; Aspeå stn.
L. intermedium. *N.* Trysunda. — Prästmon (1931).
L. purpureum. Samma ställen som *L. amplex.*, o. eljest fl. (allm.?).
Lapsana communis. — Sollefteå vid Djupövägen (1922).
Lathyrus maritimus. *N.* Ulvöhamn (Deg.); *Sj.* Guldvik!, Klösan o. Vågö holme (Arw.); *A.* Råskärsön* (rikl.).
L. palustris. *G.* Mattjäl (strandäng).
L. pratensis. *N.* Trysunda (Kapellsberget)*. — Aspeå stn (kulturspridd).
Ledum palustre. *Sj.* Guldviksmossen o. berget ovan Vågeänget. — Tåsjö: Bosundet (Sant.).
Lemna trisulca. *Sj.* Vikbotten (mängdvis).
Lepidium densiflorum. — Norrfors stn (enst. 1931).
Lilium bulbiferum. — Säbrå: Gryttjom förv. på banvall (blom. 1936).
Limosella aquatica. *A.* Malmön (havsstr.); *Sj.* Hampnäs vid Själevadsfjärden.
Linaria vulgaris. *Sj.* Vågeänget (spars.), Själevad stn. — Sollefteå vid kyrkan o. Djupökajen; Helgum stn; Moälven (banvall söderut); Trehörningsjö stn, etc.
Listera cordata. *N.* Trysunda; *Sj.* Vågö (Arw.).
L. ovata. — Ramsele på en nipa (1895 Aqt).
Luzula sudetica. *Sj.* Vågeänget; *A.* Nötbolandet (söderut).
Lycopodium inundatum. *G.* Skeppsmaln (översilade klippor, spars.).
Lythrum salicaria. *Sj.* Ellö (Arw.); *A.* Malmöklubb; *G.* Skagen fl. — allt på strandklippor.
Malaxis paludosa. *N.* Skrubban; *A.* Nötbolandet mot Vågeänget — båda lok. på översilade klipphällar(!); på Skrubban även i liten myr.
Matricaria inodora »ssp. *maritima*». *N.* Skrubban (Måsberget).
M. suaveolens. *N.* Trysunda*; *A.* Nötbolandet (spars.), Hornön; *G.* Tennviken, Skeppsmaln. — F. ö. vid alla jvstationer Örnsköldsvik—Sollefteå (ej Aspeå?) 1922, d:o Härnösand—Sollefteå 1931, etc.
Moehringia trinervia. *N.* Trysunda*; *Sj.* Klösan (på strandgrus, Arw.); *A.* Skommarhamn!, Råskärsön (Arw.).
Montia lamprosperma. *N.* Trysunda (Arw.); *Sj.* Guldvik!, Vikbotten!, Vågeänget!, Grisslan!, Vågö o. Norrklubben (Arw.), Hampnäs vid Själevadsfjärden!; *A.* Nötbolandet fl.!, Skommarhamn!, Malmön*; *G.* Mattjäl, Tennviken, Skeppsmaln.
Myriophyllum alterniflorum. — Forse i Faxälven.
M. spicatum. *A.* Nötbolandet (havet); *G.* Långsjön på Skaglandet.
Orchis maculatus. *N.* Skrubban (Arw.); *Sj.* Vågeänget (söderut)!, Klösan (Arw.); *A.* Hörnskaten; *G.* Skagen vid Guldbredviken.
Paris quadrifolia. *N.* Skrubban*, Trysunda!; *Sj.* Vikbotten!, Vågeänget!, Ellö, Klösan, Vågö (Arw.); *A.* Nötbolandet!, Råskärsön*.
Pastinaca sativa. Örnsköldsviks bangård (ett par ex.).
Peucedanum palustre. *N.* Skrubban (rikl.); *G.* Mattjäl, Skagen fl.
Plantago lanceolata. — Mellansel stn (gräsplan, 1922).
P. maritima. *Sj.* Vågö holme (Arw.); *G.* Skagens sydöstra sida.
Platanthera bifolia. *N.* Skrubban* (mjölonhed etc.); *Sj.* Ellö (fl. i klippskrevor) o. Klösan (kråkris-ljunghed, Arw.).

Poa alpina. — Sollefteå: Djupökajen (1931).
P. compressa. *A.* Nötbolandet (villatomt). — Moälven [nuv. Moliden] stn — i båda fallen enstaka ex. (1922).
P. palustris. Örnsköldsviks bangård (rud.).
P. remota. *Sj.* Norrvåge vid Vikbotten (bäckdäld). — Ramsele fl. (Aqt).
Polygonatum officinale. *N.* Skrubban fl.*, Trysunda* (båda bergen). *Sj.* Ellö (Arw.); *A.* Råskärsön (Arw.). — Den för Skrubban uppgivna *P. multiflorum* (KROK 1889) såg ingen av oss.
Potamogeton alpinus. *G.* Långsjön på Skaglandet.
P. filiformis. *Sj.* Vågö holme (Arw.); *A.* Råskärsön (Arw.), Malmön*; *G.* Mattjäl, Tennviken.
P. pectinatus. *Sj.* Vikbotten; *A.* Nötbolandet!, Malmön (Arw.); *G.* Tennviken.
P. vaginatus. *N.* Trysunda fiskhamn; *A.* Nötbolandet.
Potentilla norvegica. Örnsköldsviks bangård; *N.* N:a Ulvön vid Nordbyn (Deg.); *A.* Nötbolandet; *G.* Skeppsmaln. — Moliden stn; Ådalsliden: Näsåker (Deg.); Fjällsjö: Backe (Deg.); Skog: Herrskog (Deg.).
Puccinellia distans. Örnsköldsviks hamn. — Härnösands hamn (1922); Sollefteå: Djupökajen (1931).
P. retroflexa. *N.* Skrubban!, Trysunda*; *Sj.* Klösan, Grisslan, Vågö holme, Norrklubben (Arw.); *A.* Rödflasorna (Arw.), Råskärsön!, Malmöklubb!; *G.* Mattjäl — allt på strandklippor.
Pyrola media. *N.* Trysunda (Kapellsberget); *A.* Nötbolandet (söderut).
Ranunculus Baudotii ssp. *marinus.* *N.* Trysunda; *G.* Tennviken.
R. lapponicus. — Trehörningsjö norr om stn, rikl. (Deg.).
R. peltatus. *G.* Långsjöns avlopp. — Skorped: Stugusjön, Holmsjön.
R. reptans. *N.* Trysunda (kärrgrop); *G.* Långsjön på Skaglandet.
R. sceleratus. *G.* Mattjäl (enst. på havsstranden).
Raphanus raphanistrum. — Ramvik o. Skadom 1931; Sollefteå prästgård 1922; Uvsjön 1922; Anundsjö stn 1922, Mellansel stn 1915.
Rhamnus frangula. *N.* Skrubban (i klyftor).
Rhinanthus major. — Skorped: Lännäs (1922).
Rhynchospora alba. *G.* Skagen fl. i hällkar o. småmyrar.
Ribes alpinum. *N.* Skrubban* (rikl. i klyftorna).
R. Schlechtendalii. *N.* Skrubban (klyfta vid Måsberget).
Rosa cinnamomea. [*A.* Råskärsön enl. uppg.] — Hamre vid Faxälven.
R. virens. *N.* Skrubban (ett par lok.).
Rumex aquaticus. — Långsele vid stationen och Örbäck.
R. crispus. *N.* Skrubban (Måsbergets klippor o. klyftor).
Sagina nodosa. *N.* Trysunda*; *Sj.* Guldvik (sandfält)!, Vågö holme (Arw.); *A.* Malmön; *G.* Tennviken, Skagen.
Sagittaria natans. *Sj.* Själevadsfjärden (ymn.).
Salix livida. — Skadom; Lökom stn.
Sambucus racemosa. — Ed: Österås vid järnv. (1922).
Satureja acinos. — Norrfors stn, gräsmatta (1931 Deg.).
Saxifraga groenlandica. *N.* Skrubbans nordsida (i 2:ne skrevor, Arw.), Trysunda (Kapellsbergets nordv. brant*). Uppgiften från Skrubban hos GRAPENGIESSER (1934, sid. 328) är alltså icke min.
Scheuchzeria palustris. *Sj.* Våge tjärn.

Scirpus acicularis. *A.* Nötbolandet (havet), Malmön (d:o); *Sj.* Själevadsfjärden; *G.* Långsjön på Skaglandet.
Sc. mamillatus. *N.* Skrubban; *G.* Skagen (båda st. i hällkar).
Sc. pauciflorus. *Sj.* Vågeänget; *A.* Skommarhamn; *G.* Mattjäl (allt på havsstr.), Tennviken (fukt. stig), Långsjön.
Sc. Tabernaemontani. *Sj.* Vikbotten i Vågefjärden.
Sedum telephium. *N.* Skrubban fl.*, Trysunda*; *Sj.* Ellö o. Norrklubben (Arw.), Grisslan!; *A.* Skommarhamn!, Råskärsön (Arw.), Malmöklubb!; *G.* Skagen fl. — *S. acre* på bl. a. samma lokaler (ej Ellö?, Råskärsön?).
Senecio silvaticus. *N.* Skrubban fl. (men fåtalig). Svensk nordgräns?
S. viscosus. — Långsele bangård (enst. 1922).
Silene maritima. *Sj.* Vågö holme (Arw.); *A.* Råskärsön (Arw.).
S. noctiflora. — Sollefteå prästgård (talr. i täppa 1916; tillf.?).
S. rupestris. — Björna: Innerlidberget o. Vibyggerå: Fäberget (Deg.).
Sisymbrium altissimum. Örnsköldsviks bangård (några ex.).
S. orientale. Örnsköldsviks bangård (några ex.).
S. sophia. I alla städer — f. ö. vid jvstationer: Mellansel 1922, Väja hpl. 1931.
Sonchus arvensis. *Sj.* Vikbottens strand — sannolikt f. *maritimus,* som uppgivits fr. grannskapet (HAGLUND 1923).
Sparganium affine. *N.* Skrubban!, Trysunda (Arw.); *A.* Malmöklubb; *G.* Skeppsmaln (allt i hällkar).
S. Friesii. *G.* Långsjön på Skaglandet (ej nådd, men tycktes säker).
S. hyperboreum. *N.* Trysunda; *Sj.* Våge tjärn; *A.* Skommarhamn; *G.* Skeppsmaln. — *S. minimum* sågs ej!
Spergularia rubra. *N.* Skrubban (Måsbergets klippor, fullt naturlig ståndort!), Trysunda; *Sj.* Grisslan*; *A.* Malmön; *G.* Stubbsand (strandklippa), Tennviken, Skeppsmaln. — Karakteristisk för fisklägena.
Stellaria longifolia. *N.* Trysunda (Kapellsberget)*; *A.* Nötbolandet fl.
S. nemorum. *Sj.* Norrvåge vid Vikbotten; *A.* Nötbolandet (bäckdälder).
Struthiopteris filicastrum. *Sj.* Norrvåge vid Vikbotten, Västerhus.
Subularia aquatica. *Sj.* Själevadsfjärden; *G.* Långsjön på Skaglandet.
Symphytum officinale. — Härnösand vid elverket (jordhög, 1922).
Tanacetum vulgare. *A.* Nötbolandet vid en gård (spars.).
Thlaspi alpestre. *A.* Degersön (»Dekarsön») även i naturlig ängsmark (Arw.). — Locke by vid och nära landsv. (Deg.); Gryttjom o. Ramvik på banslänter (rikl., 1936).
Thymus serpyllum. *N.* Trysunda*; *Sj.* Guldviksfjärden (allm.)!, Ellö, Klösan, Vågö (Arw.), Grisslan!; *A.* Hörnskaten!, Råskärsön*, Malmön!; *G.* Stubbsand, Tennviken.
Tillaea aquatica. *Sj.* Hampnäs vid Själevadsfjärden.
Trifolium spadiceum. — Björna stn (Deg.).
Turritis glabra. — Frånö (gårdstomt vid banan, 1936).
Urtica urens. *N.* Trysunda*. — Sollefteå prästgård.
Utricularia intermedia. *Sj.* Vågeänget; *G.* Skeppsmaln.
U. minor och *U. vulgaris.* *G.* Jordavan på Skaglandet.
Viburnum opulus *N.* Skrubban (klyfta på västsidan).
Vicia sepium. *N.* Trysunda (Kapellsberget).
V. villosa. — Sollefteå: Hågesta (veteåker, rikl. 1922).

Viola Riviniana. *N.* Skrubban*, Trysunda!; *A.* Nötbolandet, Råskärsön; *G.* Tennviken.

V. tricolor. *Sj.* Vågö (Arw.); *A.* Råskärsön (Arw.), Hornön!

Viscaria alpina. *N.* Skrubban* (allm.), Trysunda*; *Sj.* Ellö, Vågö (Arw.); *A.* Skommarhamn—Hörnskaten fl.; Råskärsön*, Malmöklubb; *G.* Stubbsand, Skagen (allm.).

Woodsia ilvensis. *N.* Skrubban* o. Trysunda* (rikl.); *Sj.* Ellö, Klösan, Vågö, Vågö holme (Arw.), Grisslan*; *A.* Malmöklubb (spars.)!, Råskärsön (Arw.).

Zannichellia palustris. *Sj.* Vågeänget; *A.* Skommarhamn, Malmön; *G.* Mattjäl, Tennviken, Skeppsmaln (rikl.). På sistnämnda plats även var. *pedicellata* (i fiskhamnen).

Anm. Kulturmark, sparsamt förekommande och efter höskörden utan intresse, berördes föga i havsbandet. I mina anteckningar därifrån saknas också en lång rad kulturspridda arter (t. ex. *Carduus, Dactylis, Heracleum, Sinapis).* Men även i fråga om traktens inhemska flora blev det många vakanser (t. ex. *Ajuga, Alopecurus aequalis, Calamagrostis lanceolata, Carex gracilis, leporina, panicea, vesicaria, Pimpinella, Pinguicula, Scrophularia, Typhoides, Viola epipsila*). Kanske föreligger i vissa fall någon kustskygghet. Bland arter, som ej sågos på öarna, må även — utöver vad som framgår av artlistan — nämnas *Carex aquatilis, Equisetum palustre, Lycopodium clavatum.*

Ovan ha citerats: GRAPENGIESSER (Sv. Bot. Tidskr. 1934 o. 1937), HAGLUND (Bot. Not. 1923), KROK, Hartmans flora 12:e uppl. (1889), SAMUELSSON (Sv. Bot. Tidskr. 1927 o. 1937).

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On Formative Effects of Carbohydrates on Root Growth.

By Hans Burström.

Introduction.

Methods of growing isolated roots on synthetic media have opened up a new field for studies on the metabolism of roots under strictly controlled conditions. In several works of this kind attention has also been paid to the carbohydrate requirement (Malyshev 1932, Bonner & Addicott 1937, Robbins & Schmidt 1938, White 1940 a, b). In general, it has been stated that sucrose or glucose at concentrations of 1—2 % are convenient sources af carbon for the roots, and that other sugars or related compounds are inferior in this respect. The growth is then measured relative to the increase in length or weight of the roots. Little interest has been paid, however, to the quantitative influence of the sugars on the root development and to the formative effect of the carbohydrates on the root growth.

Research on phytohormones has given evidence that cell division and cell elongation are distinctly separable phases of growth. Further, it has been shown that the roots are heterotrophous with respect to thiamin and nicotinic acid, the first of which, according to Addicott (1939), specifically promotes cell division. On the other hand, they seem to be autotrophous in respect to hormones of the auxin group (Segelitz 1938, van Overbeek 1939), and external supply of these hormones is, anyhow, not necessary for infinite growth in vitro. Nothing is known, however, of the influence of carbohydrates on the rates of cell division and cell elongation. We must assume that they are indispensable to all phases of both energy and building metabolism, although the quantitative requirements of division and elongation might be so different that an excess or a deficiency of carbohydrates results in distinct — cytological or histological — changes within the roots. This assumption has also been verified by the following results.

The anatomical investigation has been carried out on the epidermis of wheat roots, grown isolated on nutrient solutions to which glucose was added. The dimensions of mature epidermis cells were determined through direct measuring under the microscope. From these values and the dimensions of the roots the number of epidermis cells in longitudinal and tangential direction was calculated. The rate of cell elongation could be computed from the cell number, and dimensions in the meristem and zone of elongation.

SINNOTT & BLOCH (1939 a, b) have made interesting observations concerning the development of the root hairs of different grass species. The validity of their results for wheat roots has been established, and the arrangement and dimensions of root hair cells and root hair-free cells have proved to be a useful indicator for the mode of differentiation of the epidermis at different supply of carbohydrates.

Methods and Material.

C u l t u r e m e t h o d s. Isolated roots of »Diamant» spring wheat were grown on solutions containing mineral salts, glucose, thiamine and in some cases yeast extract of the commercial product Cenovis. The duration of experiment was limited to 10—15 days, and for so short a time additions of growth hormones are not necessary for maximum growth rate. The standard mineral solution used had the following composition: KNO_3 0.2 mmols, KH_2PO_4 0.3, $Ca(NO_3)_2$ 0.4, $CaSO_4$ 0.1, $MgSO_4$ 0.2 mmols per liter, and Fe-citrate or sulfate 1 mg, $MnSO_4$ 1, $CuSO_4$, $ZnSO_4$, KJ, H_3BO_3 and Am-molybdate each 0.02 mg per liter. All the chemicals were Merck or Kahlbaum »zur Analyse». A »low nitrate» solution was obtained by substituting $Ca(NO_3)_2$ with $CaSO_4$, by which the nitrate concentration was reduced from 1 to 0.2 mmols per liter. Glucose was added in varying amounts from $^1/_{1000}$ to $^1/_{10}$ mol per liter. The experiments were performed at 20° C in 100 ml Erlenmeyer flasks with 20 ml solution, each inoculated with four 6—8 mm long root tips from seedlings germinated under sterile conditions in Petri dishes. Each experiment was repeated in at least five duplicates; the figures given in the Tables for fresh or dry weights refer to 20 roots. — Exceptions from this plan of experiment are especially noted in the Tables. — The solutions were autoclaved 20 min. at 110° C.

The roots made very good and uniform growth in these solutions.

Under optimal conditions the main tips grew at a constant rate of 5 to 6 mm per day, after four to five days there appeared regularly extremely narrow lateral branches, the growth of which did not by far reach the figures for the main tips. The standard deviation of the increase in root length amounted to ±15 to 20 %, i. e. the mean error for 20 roots to approximately ±4 %.

The measuring of cell dimensions. By means of direct microscopical investigation the length and breadth of the epidermis cells of the roots were determined. For this purpose the roots were fixed in Navashin's fluid, after one day rinsed with water and treated for 15 min. with 3 % NaClO. The measurings were performed with an ocular micrometer at 250 times enlargement.

On an extensive material which will not be reported in detail, the individual variations in cell size within roots and between roots were determined. The following method of measuring proved satisfactory for the obtaining of reliable values of the cell dimensions. On each root determinations were made at 5 to 7 points at about 10 mm distances. At each point 20 cells were measured. This was repeated on 10 roots of each treatment and the average calculated from the 1000 to 1400 determinations. The length of the cells usually averaged 150 to 200 μ, the mean errors were approximately constant, amounting to 1—1.5 %, i. e. ±2—3 μ. A difference in cell length of 5—10 μ should accordingly be statistically significant. As will be shown later, the length of the cells is far from constant but highly dependent upon nutritional and other environmental conditions; average values were thus obtained ranging from a minimum of 85 to a maximum of 350 μ. Differences of this magnitude were thus determined with a very high degree of significance. The mean errors, which were always computed are only given as examples in the first Tables below. The breadth of the cells, on the contrary, was rather constant 15—17 μ. Significant differences were never found and the values have not been reported in the Tables.

The determination of the rate of cell division. For computing the number of cells within one longitudinal cell row the following quantities must be determined:

total root length (l_r), length of meristem (l_m), average length of mature cells (C) and average length of meristem cells (C_m).

All values given in microns, the number of cells along the root axis (n_l) will become:

$$n_l = \frac{l_r - l_m}{C} + \frac{l_m}{C_m}.$$

The value of C_m was constant irrespective of the treatment of the roots, the cells were calculated to have an average length of 13 μ.

In this formula no allowance is made for the decreasing cell length within the zone of elongation. This is very short, only amounting to 10—20 cells, and the error caused by omitting it is negligible. Only in some cases of very poor growth was a graphical correction made. The length of the meristem (zone of division) must be taken into consideration, since it varies considerably.

The increase in cell number is computed as the difference between n_l and the cell-number of the inoculum. If the directly determined corresponding quantities in the last case are denoted n_l', l_r' and C' the number of cells along the root axis formed during the time of experiment (N_l) was calculated according to the formula:

$$N_l = n_l - n_l' = \frac{l_r - l_m}{C} - \frac{l_r' - l_m'}{C'} + \frac{l_m - l_m'}{C_m} \qquad (1)$$

C' for roots grown on filtering paper averaged 300 μ. Only in cases of very rapid growth could (1) be substituted with the more simple formula:

$$N_l = \frac{l_r - l_r'}{C}, \qquad (2)$$

in most cases, the accurate formula (1) was used.

The thickness of the root was measured at regular intervals and from the diameter (d_r) the number of longitudinal cell rows (N_t) was computed:

$N_t = \frac{d_r \pi}{15}$, where 15 denotes the average cell breadth in microns (cf. above).

The value of N_t is not constant within one root but increases or decreases from the base to the root tip depending upon the rate of cell division in tangential direction. The computation of an average value for each treatment is thus necessary to obtain a value of the rate of total cell divisions per day (R_d):

$$R_d = \frac{N_l N_t}{t}. \qquad (3)$$

t denotes the time of experiment in days.

It must be remarked that this formula only shows the number of cells formed from the growing point per unit time and that no atten-

tion is paid to the number of dividing dermatogen cells. R_d is thus no value of the rate of mitoses within one dividing cell.

The dimorphism of the epidermis cells. When determining the cell lengths due attention was paid to the dimorphism of the cells, already studied by SINNOTT & BLOCH (1939 a, b). In some cases cells with and without root hairs were treated separately; also the percentage of root hair cells were determined and the position of the root hair cells in relation to those free of root hair. In some selected cases also the inseration of the root hairs was studied. These investigations were, of course, carried out on smaller material than normally, usually on about 200 cells of each experiment.

In the tables the following indications have been used:

»+cells» for cells with root hairs, and

»−cells» for cells without root hairs, and accordingly C+ and C− for the lengths of each kind of cells.

In comparison with the observations on isolated roots some determinations were also made of the epidermis structure of roots of intact plants grown under artificial conditions. Three examples are given.

I. 3-week-old intact plants grown on complete nutrient solutions of pH 6; artificial light 22000 Lux.

Cell lengths:	C+	126 ± 3 µ
	C−	171 ± 4 µ
Difference		45 ± 5 µ
Quotient $\frac{C-}{C+}$		1.36

II. Roots of 3 day old seedlings germinated on filtering paper.

Cell lengths:	C+	243 ± 8 µ
	C−	326 ± 14 µ
Difference		83 ± 17 µ
Q $\frac{C-}{C+}$		1.34

It must be noted that in spite of the very large difference in absolute cell lengths in the two cases the quotient $\frac{C-}{C+}$ is approximately constant. This fact will be further exemplified and discussed below.

III. Intact plants one week old grown on distilled water. — In this series also the relative number of + and − cells was determined in addition to their arrangement.

49 % +cells length 202 μ
51 % −cells length 264 μ

$$Q \frac{C-}{C+} \quad 1.30.$$

The arrangement of + and −cells may be illustrated by the number of −cells between consecutive +cells:

number of −cells	% cases
0	17
1	66
2	12
3	5

The 17 % cases with no −cells consisted of 5 % cases in which 3 +cells followed on each other, in the Table reported as 10 % »0» cases, and 7 % cases with 2 +cells together. More than 3 cells of the same kind were not observed together. This means that with slight irregularities epidermis consists of longitudinal rows of alternating + and −cells, in full accordance with the observations, made by SINNOTT & BLOCH (1939) on *Phleum* and *Poa*.

The formation of root hairs. The cell dimorphism is apparent already from the start of the elongation process. Fig. 1 exemplifies the cell lengths of one cell row from the meristem to the mature stage. From the start of the elongation the cells are grouped in pairs, one cell being smaller and less vacuolized than the other. Yet the difference in size is very slight until the formation of root hairs sets in. This happens when the cells have reached about half the final length and proceeds as follows (cfr. Fig. 2). Initially the nuclei of all cells are placed in the middle of the cells. In the small cells richer in plasm, root hairs are initiated as curvatures of the wall immediately distally of the nuclei. The cell as a whole continues to elongate but during the first formation of the hair the distal half of the cell does not elongate at all. Only when the proximal part has doubled its length is the elongation of the distal part set going, and from that point the whole cell grows uniformly. Thus the root hair becomes inserated for a distance of about one third of the cell length from the distal end. When it has reached a length of 40—50 μ the nucleus wanders into it and places itself near the apex. — Another example is given in Table 1.

It is important to note that the proximal half of the +cell elongates as much as the corresponding part of the −cell, in which the

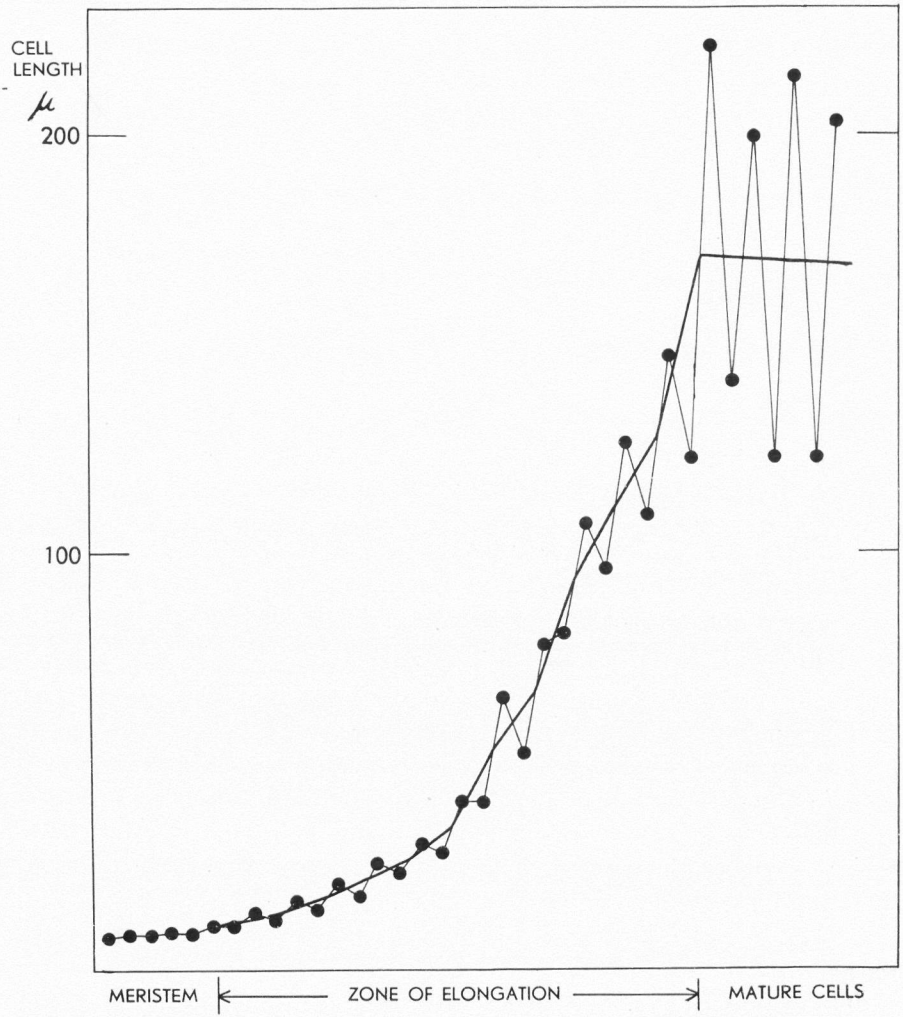

Fig. 1. The cell dimorphism during the elongation. — Each point represents one cell from the meristem to the mature stage. — Average curve heavily drawn.

nucleus is always placed in the middle of the cell. This is also illustrated by Fig. 3, which shows the final cell dimensions, positions of root hairs and nuclei in one experiment with two glucose and two nitrate levels combined.

From the given data it is evident that the point of inseration of the root hair on the mature cell is independent of the final length of both root hair and cell, and the quotient $\frac{C-}{C+}$ thus obtains its constant

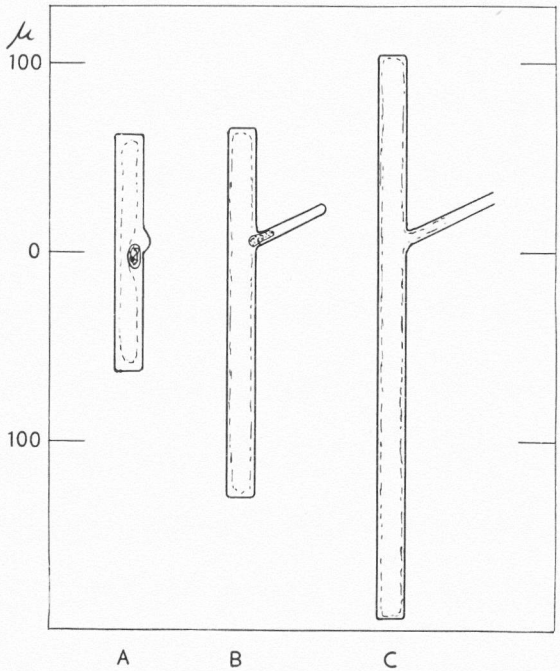

Fig. 2. Three phases in the development of a root hair. A: Initiation of the root hair distally of the nucleus. B: Nucleus passing into the root hair, proximal part of the cell growing rapidly, distal not so. C: All parts of the cell elongating uniformly, nucleus placed near the apex of the root hair.

Table 1. The different growth of distal and proximal half of the root hair cells.

Phase of development	Length μ of		Increase in length μ of	
	distal part	proximal part	distal part	proximal part
A. First signs of root hairs	58	74		
B. Nucleus wandering into the hair	64	128	6	54
C. Mature cells	91	184	27	56

value of 1.3—1.4. The reduced length of the +cells cannot be explained simply by a consumption of material in the root hair formation. It mainly depends upon the fact that the elongation of the distal half of the cell is retarded during the initiation of the root hair. This mode of uneven cell elongation does not necessarily involve some kind of gliding growth during the development of the epidermis.

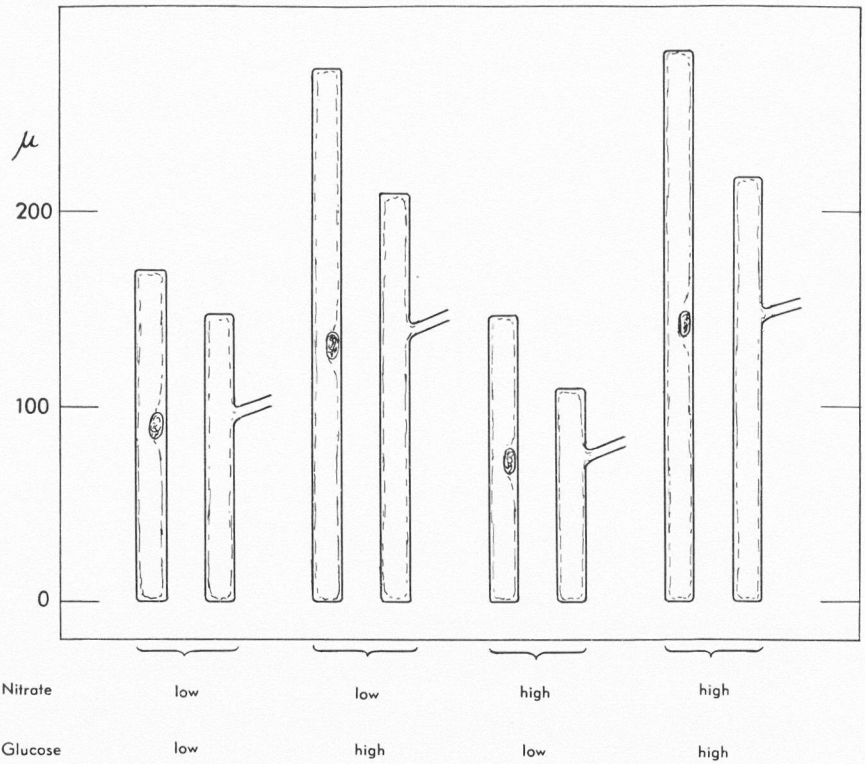

Fig. 3. The dimensions of mature cells with and without root hairs. — Cfr. the positions of the nuclei in the — cells and the attachment of the root hairs. In the + cells the nuclei are placed near the apex of the root hairs. — Four treatments: nitrate $^1/_{5000}$ and $^1/_{1000}$ mol combined with glucose $^1/_{200}$ and $^1/_{20}$ mol.

SINNOTT & BLOCH (1939 a) have shown that the dimorphism is induced in the last division of the meristem cells, the apical daughter cell being smaller than the basal one, and is later increased during the elongation. Our observations verify their results; for Triticum, however, the dimorphism is chiefly due to the unequal elongation.

The determination of the rate of cell elongation. The final length of the mature cells does not illustrate the *rate* of cell elongation. This can be calculated, however, from the number of cells forming the zone of elongation (n_e), C, N_l and t.

The zone of elongation is very sharply set off from the mature cells but passes slowly into the meristem. n_e was thus determined graphically. On 5 roots ten cell rows were chosen and the lengths

of the cells were measured individually from the meristem to the mature part. The average of the series was taken and plotted graphically as is exemplified in Fig. 1. n_e is then easily calculated from the curve. In the average curve two and two adjacent cells have been joined together in order to eliminate the dimorphism, which is apparent already from the start of the cell elongation.

Assuming that cell division and elongation are proceeding continually the time of cell elongation in hours (t_e) will become: $t_e = \frac{n_e 24\,t}{N_1}$. During this time each cell increases in length from 13 to C μ, and hence the rate of elongation in microns per hour (R_e) is found:

$$R_e = \frac{(C - 13)\,N_1}{n_e 24\,t}. \qquad (4)$$

As is apparent from Figures 1 and 2 R_e is not constant during the elongation process. The elongation starts slowly and the rate increases until, in the last phase, it reaches an almost constant value. The found value of R_e thus denotes the average rate which is always less than the maximum rate which is kept during the second half of the elongation process when the root hair development has started (cf. above).

Temperature and root growth. The effect of temperature on root growth has been studied in order to find out, whether isolated and intact roots react equally to some environmental factor, or if the separation of the roots from the aerial parts markedly affects the growth process of the roots. — Two examples are given.

I. Intact plants in darkness. Complete nutrient solution with glucose $^1/_{50}$ mol. Duration of experiment 6 days. 3 parallel cultures each with 4 plants (=36 roots). The results are reported in Table 2.

Irrespective as to whether the root growth is measured as an increase in length or weight the optimum is found at rather high tem-

Table 2. Roots of intact plants at different temperatures. 6 days in darkness.

Growth	Temperature °C.				
	7	15	20	26	33
Increase in					
length mm	11.8	23.1	23.7	32.3	1.0
freshweight mg	81	120	121	140	— 1.9
Cell length μ C	207	215	121	113	x
Cell number N_1	57	88	173	257	x

perature, 26° C or slightly higher; 33° on the contrary is definitely lethal. WHITE reports that wheat (1932) and tomato roots (1937) have a growth optimum approaching 30° C, whereas GALLIGAR (1938) found such a high optimum only for cotton and much lower values for e. g. pea and sunflower.

The increase in length is due partly to an increase in cell number and partly to a change in the cell lengths. The latter decreases with increasing temperature, and at 26° it only amounts to about one half of the length at 7°. Thus the increase in root length solely depends upon the increasing rate of cell division, which rises rapidly with increasing temperature and is approximately linear between 15° and 26° C. The same inverse relation between elongation and division appears also with isolated roots.

II. Isolated roots at varied temperature. Glucose $^1/_{20}$ mol. Duration 14 days. — Table 3.

Table 3. Isolated roots at different temperatures. Glucose $^1/_{20}$-mol. 14 days.

Growth	Temperature °C.				
	8	15	20	25	30
Increase in					
length mm	22.0	56.5	71.3	81.1	45.6
freshweight mg	63	150	193	229	233
Cell length C μ	206	177	157	147	147
Cell number N_1	152	312	413	513	321

The maximum root length is found about 25°, and 30° is supraoptimal. The fresh weight optimum lies somewhat higher, a fact which will be considered later.

The increase in cell number in linear from 8° to 25°. If the curve is computed as a straight line according to the least square method, we obtain an increase in cell number with 21.1 ± 0.2 cells for 1° increase in temperature; the small mean error demonstrates the good agreement with the straight line. This fact which appeared in all temperature series is worth noting since it forms a probable rare exception from the usual type of biological temperature effects. The optimum is sharply marked, and at supraoptimal temperature the cellnumber in a longitudinal direction decreases rapidly.

That the root length-temperature curve has a usual rounded-off optimum depends upon the interaction of the straight N_1-curve with the decreasing values of C as was also the case with the intact roots.

Summarily the growth behaviour is very much the same for intact and isolated roots with respect to the temperature effects. — These experiments also illustrate the independence of the rate of cell division and the final cell length.

The glucose optimum for root growth.

The rate of intake of glucose by wheat roots is approximately proportional to the glucose concentration of the nutrient solution. This is shown by Table 4. The absorption in percent of the amount supplied is not exactly constant, but decreases slightly with increasing concentration. The glucose absorption proceeds further very slowly, thus the optimum must be sought at comparatively high concentrations, about $^1/_{10}$ mol.

Table 4. The absorption of glucose by intact plants. 4 parallels with each 3 plants in 50 cc solution. Time of experiment 6 days.

Glucose in the solution mol	$^1/_{300}$	$^1/_{100}$	$^1/_{30}$	$^1/_{10}$
absorbed mg	15.5	31.6	102.4	283.2
» %	12.9	8.8	8.6	7.9

In the first place, this is true for the increase in fresh or dry weights of the roots; for the logitudinal growth another picture is found. Several series of experiments were performed to investigate this problem, all agreeing perfectly. Two only will be given in detail, one with high nitrate (Table 5) one with low nitrate concentration (Table 6). As shown already in the temperature series the growth determined as an increase in length of the root is of little interest, it must be interpreted in terms of cell numbers and dimensions.

Table 5. Isolated roots at different glucose concentrations. 9 days.

Growth	Glucose mol.				
	$^1/_{1000}$	$^1/_{300}$	$^1/_{100}$	$^1/_{30}$	$^1/_{10}$
Increase in					
length mm	13.4	23.5	40.8	56.0	52.6
freshweight mg	42	77	133	202	231
Cell length C µ	87 ± 1	125 ± 1	152 ± 2	229 ± 3	248 ± 3
Cell numbers N_1	141	162	241	223	214
N_t	82	79	77	89	94
Time of elongation hours	18	13	6	10	11
Rate of					
cell division	1290	1420	2060	2200	2300
elongation µ/h	3.8	8.8	22.8	22.1	21.4

Table 6. Isolated roots at different glucose concentrations. Low nitrate. 9 days.

Growth	Glucose mol.				
	1/1000	1/300	1/100	1/30	1/10
Increase in					
length mm	20.1	33.8	43.1	43.9	34.4
fresh weight mg	41	65	106	156	140
Cell length C μ	143 ± 2	153 ± 1	183 ± 2	213 ± 2	230 ± 2
Cell numbers N_l	116	200	215	196	167
N_t	84	80	80	95	107
Rate of cell division	1080	1780	1910	2060	1980

Concerning the cell lengths the results are very simple, the length of the mature cells steadily increases with increasing glucose concentration. A further analysis of the mode of cell elongation shows, however, that this effect is of a complex nature (Table 5). From the lowest glucose concentration up to 1/100 mol the rate of cell elongation increases very rapidly and in spite of the simultaneously decreasing time of elongation this results in an increasing length of the mature cells. At glucose 1/100 mol however, the rate of elongation has reached its apparent upper limit and the increasing cell length at still higher concentrations is due to an extended time of elongation.

Also with regard to the rate of cell division different conditions prevail above and below 1/100 mol glucose. Up to this approximate limit the rate of cell division increases, especially in logitudinal direction. The divisions tangentially decrease in number, however, the roots thus becoming more slender at 1/100 mol than at lower concentrations. At further increasing concentration another change in the structure of the roots sets in. The total number of divisions is certainly approximately constant, but the rate of division longitudinally decreases and it increases tangentially correspondingly. Morphologically this means that the roots continually increase their diameter, which is particularly evident from the values of the section areas of the roots at different points in Table 7. This experiment was selected because it shows an extreme case of »swelling» of the roots at high glucose concentration, usually the increase in diameter was less prominent, but still obvious, as in Table 6.

The most interesting fact is that this apparent »swelling» of the roots takes place without any significant change in the total number of cell divisions in the meristem. That is to say that a certain number of divisions in the dermatogen change from a

Table 7. Isolated roots at two different glucose levels. 7 days.

Growth	Glucose mol.	
	$^1/_{300}$	$^1/_{50}$
Increase in length mm	23.0	21.8
Cell lengths μ C —	137	200
C + ...	104	141
Q $\frac{C-}{C+}$.....	1.31	1.42
$^0/_0$ + cells	52	49
Cell numbers N_l	192	135
N_t	82	115
Rate of cell division	2260	2230
Section area of the root mm^2		
at the apex	0.107	0.264
middle	0.132	0.215
base	0.150	0.150

transversal to a longitudinal plane of division under the influence of abundant supply of glucose. A computation of the approximate rate of this reversal of the mode of division might be worked out as follows for $^1/_{10}$ mol glucose from Table 5. The initial root tips numbered 87 longitudinal cell rows, during the experiment this number increased to 101. On each initial cell row there thus comes 0.16 longitudinal divisions against 214 transversal; a reversal of only 0.7 $^0/_{00}$ of the divisions is thus sufficient to produce this most apparent morphological change of the root.

It is evident that glucose affects the root growth in two different ways.

The first way, which we may call the primary effect, manifests itself if the glucose concentration increases from zero to about $^1/_{100}$ mol. Without any addition of carbohydrates there are no signs of growth at all, that is to say, no divisions occur in the meristem and no elongation of already present meristematic cells. The primary effect thus might be identified with the »nutritive» effect, the glucose promotes growth acting as a source of carbon in synthetic processes and energy metabolism. The two fundamental phases of growth, rate of division and rate of elongation, both reach their maximum values already at the comparatively low concentration $^1/_{100}$ mol glucose. Only up to this concentration — under the given conditions — does the carbohydrate supply limit all phases of growth.

The secondary effect, on the contrary, does not change either the rate of division or elongation but involves (1) an extension of the time of elongation, which also might be expressed as a delayed passing of

the cells into the mature state, 2) disturbances in the planes of cell division, and (3) a more extensive formation of root hairs, as will be shown below.

It is not certain, however, that these three manifestations of high glucose supply are causally related to each other, and above all they must not necessarily depend upon the increasing utilization of glucose within the roots. It must be borne in mind that glucose $^1/_{10}$ mol has an osmotic value of approximately 2.2 atm., and osmotic forces might be involved in the effect of high sugar concentrations on the root growth.

This question could apparently be easily settled by comparing glucose $^1/_{10}$ mol with some isosmotic solution which does not act as a source of carbon, or some solution of this kind combined with a lower glucose concentration, i. e. some non-assimilable sugar + glucose. There is, however, no carbohydrate except glucose and maltose without injurious effects on the roots at high concentrations. The behaviour of the roots in maltose solutions was therefore studied in comparision with isosmotic glucose solutions.

The influence of maltose on the root growth.

ROBBINS & SCHMIDT (1938) have made a careful comparision of the value of different sugars as sources of carbon for tomato roots, and also noted the morphological appearance of the roots.

They have observed, that the presence of toxic contaminations is an important factor in root growth on sugars of different origin. This fact, especially with regard to the difference between glucose and sucrose, is considered controversial by WHITE (1940 a, b), and has not yet been settled. Concerning maltose, ROBBINS & SCHMIDT tested samples of different purity, some being superior to sucrose for tomato roots, other more impure very inferior or not permitting any growth at all. Nevertheless, they were able to state that »in each instance where growth occurred in the maltose solutions the roots had the same general appearance, irrespective of the sample of maltose used» and »that the type of growth in the maltose cultures was different from that in either the dextrose or sucrose solutions. The branches were long, slender, and very white.»

MALYSHEV (1932) states that for different roots the maltose was inferior to other sugars tested, he found the series: sucrose > glucose >

fructose>maltose. SCHNEIDER (1938) has obtained about the same result.

In our experiments the wheat roots made very good growth in maltose cultures. The preparation was Merck No 937871. It gave a slight yellow colour in water solution and was decolourized with carbon in 1-mol solution.

Table 8. Comparison of glucose and maltose. 5 days.

Growth	Glucose mol.		Maltose mol.	
	1/200	1/20	1/200	1/20
Increase in length mm	18.5	30.0	15.0	26.9
Cell length C μ	131	298	104	199
Section area of the root at the apex mm^2	0.091	0.204	0.102	0.108
Cellnumbers N_l	144	118	142	155
N_t	78	90	82	80
Rate of celldivision R_n	2240	2120	2330	2480

In the experiment reported in Table 8 glucose and maltose were compared in isosmotic solutions. With maltose the roots had the characteristic slender form noticed by ROBBINS & SCHMIDT and also by WHITE (1940 b). This is clearly visible from the figures in the Table. On the whole maltose of any concentration seems to have about the same effect on the roots as a much lower concentration of glucose, with the exception, that maltose only promotes cell elongation and does not cause swelling of the roots. A cell length of 200 μ in glucose cultures was always accompanied by signs of swelling, but not so with maltose (Table 8). — In Table 9 low concentrations of the two sugars have been compared, the effect of maltose 1/100 is almost identical with that of glucose 1/300 mol.

Table 9. Comparison of glucose and maltose at low concentrations. 13 days.

Growth	Glucose mol.		Maltose mol.
	1/300	1/50	1/100
Increase in			
length mm	40.2	51.5	39.7
freshweight mg	95	187	100
0/0 + cells	50	59	41
Cell length μ C +	124	185	139
C −	164	241	179
$Q \frac{C-}{C+}$	1.32	1.30	1.29
Cellnumber N_l	279	247	244

It must therefore be concluded that the swelling of the roots in solutions of high glucose concentrations is not connected with the osmotic properties of the solutions.

The change in diameter of the roots.

The swelling of the roots does not proceed for more than five to ten days after the transfer of the roots to the test solutions. After that approximate time the roots continue to grow with — as far as could be observed — constant diameter. The same is true also of the reducing of the diameter which takes place in solutions of very low glucose content. Thus it seems as if the roots morphologically »adapted» themselves to different nutritional conditions.

WHITE (1936) has also observed the same or a similar phenomenon. He states that the roots always gradually obtain the same thickness irrespective of the initial diameter of the inoculum.

The reversal of the planes of cell division without changing the rate of divisions, which is shown to be involved in this adaption, can be followed more in detail by studying the structure of the epidermis, especially the formation of root hairs.

In general, roots receiving glucose abundantly are characterized by richly developed root hairs. Not only are these longer in high glucose concentrations, up to 2 mm against some tenths of millimeters in dilute solutions, but sometimes they also increase in number. This is especially the case during the adaption period. It is clear that this must necessarily be connected with disturbances in the normal arrangement of + and −cells. Thus the structure of the epidermis during the first ten days in high glucose concentrations shows certain irregularities, two of which are of special interest.

(1) In instances when the swelling — or adaption to high glucose concentrations — proceeds rapidly, as is exemplified in Tab. 7, a complete irregular arrangement of + and −cells might result. Nevertheless, the number of +cells may amount to the normal value of 50 % and the quotient $\frac{C-}{C+}$ to 1.3 to 1.4. One experiment of this type has been treated statistically; the computation has been carried out as in expt. III, p. 315 but for both types of cells and the figures have been added together.

number of cells of one kind between two of the opposite kind	% cases glucose 1/200	1/20 mol
0	20	49
1	68	26
2	7	11
3	3	8
4	1	3
5	1	2
6	—	1

At low glucose we find the normal alternating arrangement of + and −cells with only unimportant exceptions, but at $^1/_{20}$ mol it approaches a distribution at random of the two cell types. Such a highly irregular arrangement, of course, represents an extreme case, but it verifies the conclusion that the effect of abundant glucose supply mainly involves disturbances in the planes of cell division.

(2) In other cases, the percentage of +cells raised above 50, up to 90. Nevertheless, epidermis might consist of rows of alternating large and small cells, most of which had root hairs. One example is given in Table 10. The relation between the lengths of the two size classes of cells was 1.3, which corresponds exactly to the normal difference between + and −cells, but also 38 % — in this case — of the large type had formed root hairs.

Table 10. Glucose 1/20-mol. Cell lengths and number of root hair cells.

Kind of cells	Cell length µ	Number %
Apical cells of each pair C+	253	50
Basal cells C+	343	38
Basal cells C−	328	12

During the adaption to high glucose concentration the roots usually showed a behaviour between those described under (1) and (2) above. That is to say, they showed both deviations from the normal arrangement of large and small cells and an increased number of root hairs. It then became almost impossible to treat the material statistically, but the analysis of the two extreme cases gives a clear idea of the formative changes involved in the »adaption» to high glucose supply.

With regard to the normally strictly regular arrangement of the cells *Triticum* corresponds to the *Poa* type of SINNOTT & BLOCH (1939 a), but the difference in cell size equals that of *Chloris,* with a weaker

apical tendency. Under the influence of high glucose supply, however, it rather resembles *Sporobolus,* with an irregular formation of root hairs. It thus seems as if the polarity was not causally related to the root hair formation, they are only parallel to each other, and there is only a gradual difference in potency of root hair formation of the two kinds of cells.

Discussion.

The most striking result of the investigation is the constancy of the rate of cell multiplication within the dermatogen. That the cell number reaches a maximum value at a much lower glucose supply than the cell elongation need not, however, give rise to speculations as to the demand of carbohydrates or energy of the two processes. It only shows that higher amounts of carbohydrates can not be utilized in the cell divisions.

This may be due to some other factor — hormonal or nutritional — which limits the rate of division, or that the mitotical activity for purely mechanical reasons cannot be accelerated limitlessly. For the second possibility obviously shows that the only hormone known to promote divisions specifically — thiamine — was abundantly present, and that the amounts of nutrient available did not by far limit the growth as a whole — that is to say the formation of new cell material. It is also interesting to compare the studies of HOUGHTALING (1940) on the stem development of three pure lines of *Lycopersicum* and their hybrids. He concludes »that cell number may be genetically controlled, without any influence upon cell size.» That this could be demonstrated apparently without any precautions being taken, in order to keep the nutritional conditions constant, indicates that the rate of cell multiplication is rather independent of external conditions. — Only by drastic operative encroachments did HAVIS (1940) succeed in reducing the rate of cell division of *Brassica* hypocotyls. — On the other hand SINNOTT (1939 a) reports that fruits may obtain a constant volume, with cell number and dimensions varying inversely, and that »large cells indicate either fewer divisions, more expansion, or both» (1939 b).

The rate of multiplication is further independent of the plane of cell divisions. This is true not only under the influence of high glucose supply, but also at supraoptimal temperature. In Table 3 was

shown that the root length and cell number longitudinally reach a maximum at 25°, but that the root weight did not decrease at a still higher temperature. This is partly due to a more abundant initiation of lateral branches, and partly to increased root width. As is evident from Table 11, however, the total cell number is constant; the reduced number longitudinally is compensated by an increase tangentially.

Table 11. Reversal of the plane of cell division at supra optimal temperature.

Growth	Temperature °C	
	25	30
Cell numbers N_l	513	321
N_t	51	81
Rate of cell division	1870	1860

Why an abundance of glucose changes the polarity within the dermatogen cannot be decided at present. However, it is relevant to mention some results of DIEHL & al. (1939). By different applications of heteroauxin to *Helianthus* hypocotyls the growth in length and width could be varied inversely, at constant volume of the organ. Yet it is possible that the similarity is only superficial. In our case we have not studied the cortex and stelar elements and do not know if they behave similarly to epidermis. It is not even necessary to assume a direct action of the glucose concentration on the epidermis itself in this respect. It is possible that cortex only reacts directly to the influence of high glucose supply with increased growth radially, and that the change of the plane of divisions in the epidermis is only a passive adjustement to the increasing width of the cell mantle. In roots, on the other hand, where divisions occur only sparsely in the mature epidermis, the dividing meristem cells ought to be rather equal, especially as in *Triticum* epidermis and cortex differentiate from common periblem-dermatogen initials (HAYWARD 1938).

In any case, the change in shape of the roots must be of a certain physiological importance. The ultimate cause of the disturbances certainly is the increased glucose concentration of the cells, and it can be assumed that the glucose absorption is a function of the root area, but the consumption a function of the root volume or increase in volume. Thus a thick root must get some power to keep the internal concentration low. The swelling of the roots therefore seems to involve a regulation of the internal glucose concentration.

A comparison might also be made with the conditions of the shoot

apex, where according to SCHÜEPP (1914), the rate of cell division is the same in outer and inner cell layers, though in the tunica all divisions are anticlinal and in the corpus are laid in all planes. It ought to be worth studying, if in this case also the carbohydrate supply influences the directions of the divisions, and thus the formation of leaf primordia.

The second phase of growth is the cell elongation. According to current opinion the hormones of the auxin group play the same rôle in shoot and root, with the only exception that in the root they are normally present in supraoptimal quantities (cfr. HEYN 1940). Thus we cannot expect that the hormone supply should limit the cell elongation, if only carbohydrates for synthetical purpose are available in moderate quantities. Above $^1/_{100}$ mol glucose the rate of elongation is also constant, but the time of elongation increases with further increased glucose supply. As will be shown below this undoubtedly depends upon the osmotic condititions of the cells. It is generally assumed that the turgor pressure is the driving force of the elongation; following that the plasticity or elasticity of the cell walls has been regulated by the hormones. But for how long a cell is able to elongate or what sets a limit to the elongation has usually not been considered. The osmotic conditions are instructive in the present case.

Table 12. Osmotic properties of epidermis cells immediately after finished elongation.

Osmotic quantities	Glucose $^1/_{200}$ mol		Glucose $^1/_{20}$	
	normally	plasmolyzed	normally	plasmolyzed
Volume $\mu^3 . 10^2$	423	242	1225	768
Elastic extension %	36	0	35	0
Osmotic value mol glucose ...	0.19	0.33	0.25	0.40
Turgor pressure mol glucose	0.18	0	0.20	0

Table 12 shows some measurings of the osmotic properties of epidermis cells from solutions of $^1/_{200}$ and $^1/_{20}$ mol glucose. Parts of the mature epidermis, immediately behind the zone of elongation, were carefully cut out from most of the underlying cortes to allow the cells to contract freely, and plasmolyzed in glucose solutions. The »normal» values of the Table indicate the properties of the cells in contact with their respective culture solutions, viz. glucose $^1/_{200}$ and $^1/_{20}$ mol. The difference in size of cells from high and low glucose corresponds to values reported earlier, a noticeable fact is, however, that the turgor

pressure is equal in both cases. The cells from high glucose contain 3.7 times the amount of osmotically acting substances as those from low glucose. This whole amount is, indeed, not present from the start of the elongation, but the difference in osmotic value is apparent already here. Exact osmotic values could not be obtained on the not vacuolized meristem cells, but the plasm showed early contraction at 0.35 and 1.0 mol glucose respectively in the two cases. The rest of the osmotic substances must migrate into, or be formed in the cells during the course of elongation. When this has finished all the cells show a turgor pressure of about 0.2 mol. It is not mere chance that the same value was obtained in both cases; other experiments gave the same result independent of cell size and external glucose concentration. The same was also found with roots from intact seedlings germinated on filtering paper. In one case the »normal» cell length amounted to 289 μ, the length of the cells in water to 284 μ and thus the cells in moist air were saturated. The osmotic value and turgor corresponded to 0.19 mol glucose, and the elastic extension — also under normal conditions — to 36 %. The remarkable size of the cells no doubt depends upon the ample supply of carbohydrate from the grain. Though the nutrients migrate into the roots in another way as in experiments with high glucose added, the result becomes the same: increased elongation of the cells and, nevertheless, a final turgor pressure of about 0.2 mol.

It has been emphasized earlier that the difference in cell size between high and low glucose roots only depends upon the time of elongation. The rate is probably determined by hormonal influence, or rate of water intake, or both, but the time of elongation directly depends upon the amount of osmotic substances present in the cell. If this is increased the elongation will go on until the same final state has been reached, and only a difference in cell size will result. It is also significant that the expansion of the time of elongation only begins when glucose is added in concentrations which may be of osmotic importance.

The osmotic value of the cells from $^1/_{20}$ mol glucose exceeds that of $^1/_{200}$ mol with an amount approximately equalling the difference in external concentration. Since it must be assumed that the increase in osmotic value depends upon the accumulation in the vacuole of glucose not consumed in the metabolism, this seems to accumulate at approximately diffusion equilibrium with the external solution.

However, the increased growth at high glucose not only involves an osmotic uptake of water, but also a production of cell material corresponding to the increase in volume. This is obvious from the relation between fresh and dry weight of the roots. In one typical case the percentage of dry matter of roots from glucose $^1/_{200}$ and $^1/_{20}$ mol amounted to 8.5 and 11.3 respectively. From the last value must be drawn a weigt corresponding to the amount of accumulated and not assimilated glucose, which from Table 12 can be estimated to 1.8 %; the rest will become 9.5 %. Further, it must be remarked that more lateral branches are initiated at high glucose with meristems rich in plasm. In any case, the percentage of dry weight is not appreciably lower at high than at low glucose. — Another important fact in this connection is that the elastic extensibility is exactly the same for epidermis cells from moist air, $^1/_{200}$ and $^1/_{20}$ mol glucose. At a turgor pressure of 0.2 mol the cells expand 35—36 % in length. This indicates that the structure of the cell wall is the same, in spite of the threefold elongation at high glucose supply. Of course, this is possible only if sufficient nutrients are available for the building up of new plasm and wall material. Otherwise, the roots will probably behave as under the influence of high concentrations of the slowly utilized maltose: rapid elongation but insufficient assimilation of carbohydrate will make the roots extremely slender. — For the growth of coleoptiles the interaction of hormones and carbohydrates has been illustrated by SCHNEIDER (1938). — The rate of assimilation of the different sugars will be considered in another paper.

It has been shown that during the formation of root hairs, the apical end of the cell does not elongate for a short interval, whereas the growth of the basal part proceeds. In terms of the current theory, this must depend upon temporarily lower plasticity of the apical end of the wall, since the turgor pressure must act uniformely towards both ends of the cell. It is an open question if this mode of differential growth involves some kind of gliding growth, or if the cells are in a fixed position to each other. SINNOTT & BLOCH (1939 b) who have thoroughly studied the same problem, deny any kind of gliding growth. But then it follows that a local change in plasticity of the wall in one cell must cause a corresponding local change of the neighbour wall, or there must arise rather heavy tensions between the cells. This seems to offer an interesting problem as to the interaction of cells in growth.

Summary.

The cell division and cell elongation in epidermis of isolated wheat roots, grown on solutions of different glucose concentration, have been studied.

Epidermis consists of alternating cells without root hairs and shorter cells with hairs, the relation between the length of the two types being constant 1.3—1.4, independent of their absolute length. The root hair is inserted at a distance of one third of the cell length from the apex. This depends upon the fact that, at the initiation of the hair, the elongation of the apical part of the cell is retarded; this is also the main cause of the difference in length of cells with and without root hairs.

Cell division and elongation are highly independent of each other, the former being more constant than the latter. The final length of mature cells varied between 85 and 350 μ (average values under different treatments).

With increasing temperature the rate of division increase linearly to 25° C and then remains constant, the elongation decreases from + 7° to 30°.

Without addition of glucose neither division nor elongation occur.

If glucose is added in increasing amounts up to $^1/_{100}$ mol/liter the rate of both cell division and elongation increases. This might be the nutritive effect of the sugar.

At additions above $^1/_{100}$ up to $^1/_{10}$ mol the cell number remains constant but the roots increase in width, while a number of divisions of the dermatogen are laid longitudinally instead of transversally. Thus the rate of division is independent of the direction of the plane of division. This effect is not connected with osmotic actions of the solutions, but depends upon the abundance of glucose itself. The same phenomenon will appear at temperatures above 25° C.

In the same concentrations of glucose the formation of root hairs is promoted; such are formed also from cells initially not determined as root hair cells.

By additions from $^1/_{100}$ to $^1/_{10}$ mol glucose also the rate of elongation remains constant, but the time of elongation is extended, thus the final length of the cells will steadily increase with increasing glucose supply. The increase in time of elongation is connected with the amount of osmotic substances available in the cells, and the mature cells obtain a constant turgor pressure corresponding to about 0.2 mol glucose (~ 4.2 at.), irrespective of final cell size and external glucose concentration. Nor do these influence the elasticity of the cell wall. The cells of intact roots grown in moist air behave similarly.

References.

ADDICOTT, F. 1939. Vitamin B_1 in relation to meristematic activity of isolated pea roots. — Bot. Gaz. 100.

BONNER, J. & ADDICOTT, F. 1937. Cultivation in vitro of excised pea roots. — Bot. Gaz. 99.

DIEHL, J. M., GORTER, C. J., VAN ITERSON, G. JR. & KLEINHOONTE, A. 1939. The influence of growth hormone on hypocotyls of Helianthus and the structure of their cell walls. — Rec. Trav. Bot. Néerl. 36.

GALLIGAR, G. C. 1938. Temperature effects upon the growth of excised root tips. — Plant Phys. 13.

HAVIS, A. L. 1940. Developmental studies with Brassica seedlings. — Am. J. Bot. 27.

HAYWARD, H. E. 1938. The structure of economic plants. — New York.

HEYN, A. N. J. 1940. The physiology of cell elongation. — The Bot. Rev. 6.

HOUGHTALING, H. B. 1940. Stem morphogenesis in Lycopersicum: a quantitative study of cell size and number in the tomato. — Bull. Torr. Bot. Club 67.

MALYSCHEV, N. 1932. Das Wachstum des isolierten Wurzelmeristems auf sterilen Nährboden. — Biol. Z. Bl. 52.

VAN OVERBEEK, J. 1939. Evidence for auxin production in isolated roots growing in vitro. — Bot. Gaz. 101.

ROBBINS, W. J. & SCHMIDT, M. B. 1938. Growth of excised roots of the tomato. — Bot. Gaz. 99.

SCHNEIDER, C. L. 1938. The interdependence of auxin and sugar for growth. — Am. J. Bot. 25.

SCHÜEPP, O. 1914. Wachstum und Formwechsel des Sprossvegetationspunktes der Angiospermen. — Ber. D. Bot. Ges. 32.

SEGELITZ, G. 1938. Der Einfluss von Licht und Dunkelheit auf Wurzelbildung und Wurzelwachstum. — Planta 28.

SINNOTT, E. W. 1939 a. The cell and the problem of organization. — Science 89.

— 1939 b. A developmental analysis of the relations between cell size and fruit size in cucurbits. — Am. J. Bot. 26.

— and BLOCH, R. 1939 a. Cell polarity and the differentiation of root hairs. — Proc. Nat. Acad. Sc. 25.

— — 1939 b. Changes in intercellular relationships during the growth and differentiation of living plant tissue. — Am. J. Bot. 26.

WHITE, P. R. 1932. Influence of some environmental conditions on the growth of excised root tips of wheat seedlings in liquid media. — Plant. Phys. 7.

— 1936. Plant tissue culture. — Bot. Rev. 2.

— 1937. Survival of isolated tomato roots at suboptimal and supraoptimal temperatures. — Plant Phys. 12.

— 1940 a. Does »C. P. Grade» sucrose contain impurities significant for the nutrition of excised tomato roots? — Plant Phys. 15.

— 1940 b. Sucrose vs. dextrose as carbohydrate source for excised tomato roots. — Plant. Phys. 15.

Institute of Plant Physiology Ultuna, Uppsala May 1941.

Smärre uppsatser och meddelanden.

Lavfloran på toppen av Romeleklint (Skåne).

Sommaren 1939 vistades jag en tid i Skåne för lichenologiska studier. Speciellt ägnades därvid uppmärksamhet åt de gamla slottsparkernas ganska rika och intressanta lavflora. Jag önskade emellertid också få tillfälle att bl. a. studera lavfloran på något av de ganska fåtaliga nakna klippartierna i inre delen av södra Skåne för jämförelse med liknande lokaler å andra håll. Romeleklint i Gödelöv socken blev den plats, jag kom att utvälja. Mitt besök där kom till stånd den 7 juli och skedde i sällskap med med. kand. Gustaf Haglund och fil. mag. Ove Almborn.

Romeleklint utgör med sina 175 m ö. h. ett av de högsta partierna å Romeleåsen. Den är liksom större delen av åsen ifråga täckt av lösa jordlager och skogklädd, dock med undantag av den bl. a. till ytvidden obetydliga topplatån. Den senare, som blev föremål för undersökning, är nämligen skoglös, och naket berg går där ställvis i dagen. De nakna klipporna äro tämligen låga men delvis branta samt sammanlagt av rätt obetydligt omfång. Till största delen äro de mer eller mindre solexponerade, ställvis dock beskuggade av den omedelbart nedanför vidtagande odlade granskogen. Denna senare hindrar en starkare vindexponering. Med hänsyn till lutningsförhållandena förekomma klippytor av alla slag: horisontalytor, vertikalytor, överlutor osv. (överlutorna dock föga betydande). Sipperytor spela ställvis en viss roll. Fågelpåverkan är obetydlig eller ingen, kulturpåverkan större genom närvaron av ett utsiktstorn. Berggrunden består till största delen av grönstenar, dels en äldre amfibolit, dels yngre gångar av hyperitdiabas (se närmare Hjelmqvists diss.-avh. 1934 p. 23, fig. 4).

Under uppehållet här, som varade ett par timmar, blev denna lilla platå föremål för en noggrann inventering med hänsyn till förekommande lavarter. Som jag tidigare flera gånger framhållit äro dylika undersökningar av smärre områden av stort värde ur växtgeografisk synpunkt, därigenom att de — samlade — lämna en långt tillförlitligare bild (även med hänsyn till negativa drag) av de olika arternas utbredning än den som åstadkommes genom mer tillfälligt gjorda insamlingar. De kunna också tjäna ett annat ändamål, nämligen att vara utgångspunkter för studier över lavvegetationens och lavflorans lokala förändringar under årens lopp med hänsyn till ökad eller minskad kulturpåverkan osv.

59 olika arter konstaterades på den nämnda lokalen, vilket är rätt mycket på en så liten yta, även om det ej tål jämförelse med vad liknande lokaler t. ex. i Bohuslän kunna erbjuda. Den uppgjorda artlistan ser i sin helhet ut på följande sätt (nomenklaturen i huvudsak i enlighet med: Förteckning över Skandinaviens växter, utg. av Lunds Bot. För., 4. Lavar, 1936):

Porina chlorotica, Crocynia neglecta, Diploschistes scruposus, Peltigera canina, P. polydactyla, P. rufescens, Lecidea furvella, L. fuscoatra, L. intumescens (på *Lecanora rupicola*), *L. lapicida, L. orosthea, L. scabra, L. sorediza, L. sulphurea, L. tenebrosa, L. uliginosa* (s. str.), *Rhizocarpon badioatrum, Rh. distinctum, Rh. geographicum, Rh. lecanorinum, Rh. obscuratum, Cladonia coccifera, Cl. fimbriata* (v. *minor*), *Cl. Flörkeana* (v. *intermedia*), *Cl. ochrochlora, Cl. pyxidata* (v. *chlorophaea*), *Cl. rangiformis, Cl. scabriuscula, Cl. squamosa, Umbilicaria deusta, U. polyphylla, U. pustulata, Acarospora fuscata* (även f. *Steinii*, det. MAGNUSSON), *Pertusaria leucosora, Lecanora atra, L. badia, L.* (*Asp.*) *caesiocinerea* NYL., *L.* (*Asp.*) *cinerea, L. intricata* (rikligast var v. *soralifera*), *L.* (*Plac.*) *macrocyclos, L.* (*Plac.*) *muralis, L. polytropa, L. rupicola, L.* (*Asp.*) *simoënsis* (blott v. *isidiata*, det. MAGNUSSON), *L. subcarnea, Candelariella coralliza, C. vitellina, Parmelia conspersa, P. furfuracea, P. isidiotyla, P. physodes, P. pulla, P. saxatilis, P. sulcata, Caloplaca ferruginea* (v. *festiva*, syn. *C. festiva*), *Buellia punctiformis, Physcia caesia, Ph. teretiuscula, Ph. Wainioi.*

Av nämnda arter voro följande rikliga: *Lecidea furvella, L. fuscoatra* (vilken uppträdde i flera former, även med mycket ljus bål), *Rhizocarpon lecanorinum, Umbilicaria pustulata, Acarospora fuscata, Lecanora caesiocinerea, L. intricata* v. *soralifera, L. rupicola, L. macrocyclos, Candelariella coralliza, Parmelia pulla, P. saxatilis.* Särskilt sparsamma voro: *Diploschistes scruposus* (ett enda men stort ex.), *Peltigera rufescens, Lecidea sulphurea, Parmelia furfuracea* (ett enda mycket ungt ex.), *P. physodes, Caloplaca ferruginea* v. *festiva, Physcia caesia, Ph. Wainioi. Lecanora muralis, Candelariella vitellina* och *Parmelia sulcata* voro betydligt sparsammare än resp. *Lecan. macrocyclos, Cand. coralliza* och *Parm. saxatilis.* Samtliga *Cladonia*-arter voro mer eller mindre sparsamma, och ingen av dem sågs med apothecier. Bland bladlavarna antecknades blott *Parmelia conspersa, P. pulla* och *P. saxatilis* med apothecier.

Lavfloran kan sägas vara ganska överensstämmande med den på liknande lokaler annorstädes innanför kusten i södra Sverige. Växtgeografiskt sett är ingen av de ingående arterna mer anmärkningsvärd. Dock är den övervägande nordliga *Rhizocarpon badioatrum* rätt sällsynt i sydligaste delen av vårt land. Vidare bör observeras den rikliga förekomsten av *Lecanora intricata* v. *soralifera*, förövrigt ganska sällsynt, samt uppträdandet av *Lecanora simoënsis* v. *isidiata*, om vilken sistnämnda man ej vet så mycket beträffande utbredningen utöver att den är tämligen vanlig i Bohuslän. Ett intressant, lokalens natur belysande negativt drag är saknaden av *Lecidea deustata*; för denna arts uppträdande är platsen ej tillräckligt vindexponerad.

Distinkta lavsamhällen med en eller några få dominerande arter täckande större sammanhängande ytor voro knappast utbildade. En del av de ovan nämnda rikligt förekommande arterna (t. ex. *Umbilicaria pustulata* och *Lecanora caesiocinerea*) kunde dock ställvis sammansluta sig till samhällen av mindre omfång. I allmänhet var vegetationen sammansatt av ett flertal olika arter med mer eller mindre likartad täckningsgrad.

Uppsala, Växtbiologiska Institutionen, i maj 1941.

GUNNAR DEGELIUS.

Atrichum angustatum (Brid.) Br. & Sch. (Catharinaea angustata Brid.) i Skåne.

Vid revision av en samling mossor tagna av f. d. 1:e provinsialläkare G. A. SJÖDAHL, Stockholm, fäste jag mig särskilt vid ett exemplar av ovanstående art. Exemplaret, korrekt namngivet av insamlaren, hade av S. d. 9 Juli 1940 insamlats på en sandig stenmur alldeles intill ett kafé beläget i närheten av den berömda fyndorten för oceaniska växter Klöva Hallar i Sönnarslövs s:n av Skåne. Exemplaret saknade frukt men hade väl utvecklade hanblommor (anteridier just mogna men ej öppnade). De flesta hade nog gått förbi den föga uppseendeväckande mossan, vilken i samlingarna så gott som uteslutande är representerad av fruktexemplar.

Först 1892 upptäcktes *Atrichum angustatum* i Sverige. ARNELL samlade den då vid Rörvik på Orust i Bohuslän (♀-blommor). Samma år tog A. den i Ljungarum s:n i Småland. Då HJ. MÖLLER 1919 behandlade släktet kände han utom dessa lokaler endast en andra lokal för Småland, Madesjö s:n, där den 1912 samlats av S. MEDELIUS. C. JENSENS nya flora kan härtill lägga endast en lokal: Jämshög s:n i Blekinge (MEDELIUS). Vid efterforskning i Riksmuseets samlingar fann jag emellertid tvenne skånska exemplar av arten, bägge tagna av den outtröttlige och skicklige J. PERSSON. Exemplaren, bägge i frukt, voro från Broby s:n, Nöbbelöf å igenväxt åker $^{12}/_{11}$ 1920 och Glimåkra s:n, nära Brötakulla vid vägen till Dalshult $^{7}/_{10}$ 1920. Fru E. NYHOLM vid museet i Lund har haft vänligheten meddela mig att där dessutom förvaras ett tredje skånskt exemplar taget av J. PERSSON nämligen från Emitslöv s:n, Västraby d. $^{6}/_{11}$ 1920 (å etiketten står Broby s:n men enligt fru N. ligger lokalen i grannsocknen Emitslöv).

Atrichum angustatum föreligger alltså från ej mindre än 4 skånska lokaler. Även om denna art säkerligen hör till de mera sällsynta är den sannolikt åtskilligt förbisedd. Till skillnad från den allmänna, med paroik blomställning utrustade *A. undulatum* (Hedw.) PB. är den dioik. Med stor sannolikhet kan man därför räkna med att den relativt sällan sätter frukt. Utan sådan blir den utan tvekan mycket lätt förbisedd.

Atrichum angustatum är överallt i Europa sällsynt. Den går ej alls så långt mot N som *A. undulatum*. Varken från Finland eller Norge känner man densamma. I Danmark finnes den sällsynt här och där. I Osteuropa saknas den över stora områden. I det mediterrana området synes den vara en sällsynthet. Mest samlad är den dels i Storbritannien, dels i de lägre delarna av Mellaneuropas bergskedjor samt i Pyrenéerna. Utom Europa är den känd från Kaukasus, Azorerna, Japan och Nordamerika. Den torde lämpligen böra uppfattas som ett suboceaniskt element, en uppfattning, som jag ej sett framförd förut. Att den i Nordamerika ej uppträder å Stilla Havskusten talar ej mot detta antagande, i själva verket dela en stor del av de oceaniska mosselementen i Europa i Nordamerika upp sig på Atlant- och Stilla Havskusten, ett förhållande av stort intresse. Arten, som har en vid utbredning på Atlantkusten och långt in i landet, är f. ö. i Nordamerika betydligt vanligare än i Europa. Dylika omkastningar ifråga om frekvensen, i ena eller andra riktningen, äro, då det gäller dessa båda kontinenter, ej sällsynta.

Vad växtplatsen angår så väljer *A. angustatum* liknande lokaler som

A. undulatum. Påfallande synes dock vara att den föredrager torrare och mera sandiga lokaler. Även detta talar ej mot uppfattningen av densamma såsom varande i viss mån oceanisk. Man föreställer sig väl gärna att de oceaniska elementen skulle föredraga skuggiga och fuktiga lokaler. I själva verket uppvisa de, vad mossorna beträffar, en stor variabilitet visavi växtplatsen. Alla övergångar finnas mellan helt eller så gott som helt i vatten nedsänkta arter såsom *Fontinalis squamosa* Hedw. och xerofilt betonade arter såsom *Pterogonium gracile* (Hedw.) Br. eur., vilken senare helst uppträder på sydvända, solexponerade klippor.

HERMAN PERSSON.

Litteratur.

Nordhagen, Rolf: Norsk Flora, med kort omtale av innførte treslag, pryd- og nytteplanter. Tekstbind. Pris 22 kr. — H. Aschehoug og Co. Oslo. 1940.

Varje ny flora över Skandinaviens växter bör hälsas med den största tillfredsställelse. Så mycket nytt har framkommit under senare år, och så mycket har vår kunskap om de olika arternas utbredning ökats, att de i litteraturen spridda uppgifterna snart bli oöverskådliga. Den sista norska floran: Blytt-Dahls »Haandbog i Norges Flora» utkom år 1906.

Utbredningsuppgifterna i Nordhagens flora hade nog kunnat göras litet mera lätthanterliga. Om man inte är hemvan i den norska geografien, är det ej så lätt att få en klar bild av utbredningen.

Som förf. i sitt företal framhåller, är floran i första hand avsedd som ett hjälpmedel för lärare och studerande vid läroverken. För att göra arbetet nyttigt även för forstmän och dem, som äro sysselsatta med lantbruk, har ett stort antal gagn- och prydnadsväxter medtagits liksom även ogräs och adventiver.

Mest frapperande, åtminstone för en svensk, är, att förf. tagit upp eller i många fall nyskapat norska namn, vilka föredragits framför de latinska i familje- och släktnycklar. I texten äro dessutom de norska namnen tryckta med fet stil, medan de latinska satts inom parentes och med mindre stil. Detta har motiverats med att »navnforvirringens tid er over oss». Enligt rec:s mening är detta dock en onödig kapitulation inför det från vissa håll framkomna, häftiga kravet på inhemska namn på alla högre växter. De inhemska namnen sägas vara så mycket lättare att lära sig i skolan. Men inte är det mycket vunnet, om man i stället för det distinkta och internationella *Veronica chamaedrys* skall använda »Tveskjegg-veronika» eller för *Senecio integrifolius* »Finnmarks-svineblom». För den, som är aldrig så litet skolad i botanik, säga de latinska namnen betydligt mera om den inbördes samhörigheten mellan arterna än aldrig så vällyckade namn på modernt språk.

Många intressanta uppgifter, i synnerhet beträffande pollinations- och spridningsbiologi, lämnas under de olika arterna, likaså om deras användning inom medicinen. För kritiska eller växtgeografiskt viktiga arter äro ofta uppgifter om kromosomtalen medtagna.

Den nya norska floran är tryckt i litet format, ungefär som Krok och Almquists svenska flora. Genom de långa beskrivningarna och de talrika uppgifterna har sidoantalet stigit till 766. Boken har tryckts på ett mycket tjockt papper och med mycket smala innermarginaler, varigenom den tyvärr har blivit en smula ohanterlig. Detta är dock småsaker. Det är ett verkligt kraftprov att i dessa bekymmersamma tider kunna åstadkomma ett sådant arbete.

Ett supplementband med illustrationer utlovas komma inom de närmaste åren.

H. WEIMARCK.

MEVIUS, WALTER: Miehes Taschenbuch der Botanik. Erster Teil. Morphologie, Anatomie, Fortpflanzung, Entwicklungsgeschichte, Physiologie. 11. verbesserte Aufl. Pris RM. 5,85 — 25 % rabatt. 207 sid. — GEORG THIEME, Verlag. Leipzig. 1940.

Boken är synnerligen koncentrerat skriven. I vissa fall går den ned till rena schemat. Den är, enligt vad förf. framhåller i företalet, avsedd som en stomme, vilken kan vidare utbyggas genom föreläsningar och kurser. Den studerande kan här direkt i boken införa kompletteringar, ty texten är tryckt i smal spalt, lämnande en mycket bred marginal med plats för anteckningar. Genom de talrika illustrationerna, till största delen originalritningar, har en viss njutbarhet trots den knappa texten kunnat vinnas.

H. WEIMARCK.

HARTMANN, MAX, Geschlecht und Geschlechtsbestimmung in Tier- und Pflanzenreich. 110 sidor, 62 bilder. — Sammlung Göschen nr. 1127, Berlin 1939.

Könets och könsbestämningens mysterium, detta problem, som har beröring med nästan alla områden av det mänskliga och biologiska livet, hör till de företeelser, som naturvetarna ha sysselsatt sig med sedan vetenskapens början. — Mysteriet är ännu inte helt löst, men sedan befruktningens mekanism blev klarlagd på 1870-talet och den cytogenetiska könsbestämningen upptäcktes i början av detta sekel, har naturvetenskapen gjort många stora framsteg på detta viktiga område.

Alla biologer känna nu till den cytogenetiska könsbestämningen, könskromosomer och genetisk heterogameti. Men endast få torde känna något ingående till de senare årens undersökningar över könsbestämningens fysiologi hos lägre växter och djur, eller de många teorier och hypoteser, som olika forskare ha framställt för att försöka förklara de nya mysterier, som ha dykt upp, när de gamla fått sin lösning. Och minst kända äro de sista fem årens eleganta resultat av försök med könshormoner och de vida synfält dessa försök ha öppnat för den experimentella biologien.

Allt detta får sin förklaring i professor HARTMANNS lilla bok, som ger en klar översikt över de aktuella undersökningarna på könsbestämningens område. MAX HARTHANN är ett av de stora namnen på detta studiefält, känd bland annat för klarläggandet av protisternas könsbestämning samt för sin teori om könsbestämningen i dess helhet. Naturligtvis dominerar denna omdiskuterade teori hans framställning, dock utan att helt skymma bort de andra uppfattningarna på området.

I denna bok får läsaren först en kort översikt över könsbestämningens grunder men sjunker sedan direkt ner i könsbestämningens halvlösta gåta hos de lägre varelserna. Man får läsa hur utvecklingen går från isogameter över fysiologisk anisogami till morfologisk anisogami och oogami. En lång tid håller författaren läsaren hänförd över denna utveckling inom ett och samma släkte, grönalgen *Chlamydomonas,* visar honom den relativa sexuali-

tetens gåta, där samma individ kan fungera som hanlig varelse gentemot en och honlig gentemot en annan grupp av individer. MOEWUS's i Heidelberg undersökningar av karotinoidernas inverkan på gameterna hos *Chlamydomonas* får sin genetisk-fysiologiska sammanfattning och förklaring. Hos *Chlamydomonas eugametos* f. *simplex* har MOEWUS funnit två slags mycket nära besläktade karotinoida könsämnen, som finns hos båda könen, men i olika proportioner. Dessa ämnen äro Cis-crocetinmethylester (V) och Trans-crocetinmethylester (Ko). Hos de honliga (+) individen finns könsämnena i förhållandet 3 V : 1 Ko, hos de hanliga (—) 1 V : 3 Ko, och för att gruppbildning och kopulation skall kunna äga rum, måste dessa ämnen finnas i dessa bestämda proportioner. Utan kännedomen om dessa ämnen, som först blevo analyserade året 1938, samt om en del andra liknande ämnen, som senare ha upptäckts, fanns ingen förklaring på vissa könsproblem hos alger och protister. HARTMANN har i ett senare arbete föreslagit namnet gamoner för dessa ämnen.

Längre fram i boken ger författaren en kort översikt över de klassiska undersökningarna på könsbestämningens område: CORRENS' *Bryonia*-försök, BRIGDES *Drosophila*-försök och GOLDSCHMIDTS *Lymantria*-undersökningar. Och kommer direkt från dem in på de mycket omdiskuterade teorierna om den fenotypiska könsbestämningen, som de allra nyaste undersökningarna hålla på att skära ner till ett minimum och föra in under den genotypiska.

Könshormonernas utvecklingshistoriska verkan på de sekundära — och till och med primära — könskaraktärerna hos de högre och lägre djuren har de sista åren med god framgång studerats av den landsflyktiga ryskan VÉRA DANTCHAKOFF, som arbetar i Paris. Hennes oerhört intressanta försök med könsförändring hos djur av olika slag ägnar HARTMANN en kort översikt i sitt näst sista kapitel, en översikt som de flesta biologer utan tvivel ha både intresse och nytta av att läsa.

HARTMANNS lilla bok är som sagt en god översikt över de viktiga undersökningar vetenskapsmännen nu göra i sina laboratorier för att klarlägga könsbestämningens mekanism tillfullo. Den är mångformig och klar, men naturligtvis inte oklanderlig på alla områden, det kan en så liten bok om ett så omfattande ämne knappast vara. Men framställningen är så lättfattlig på de flesta områdena, att jämväl den inte initierade har full nytta av att studera denna billiga, väl illustrerade lärobok. Den är utan tvivel den bästa och mest moderna av sitt slag.

ÅSKELL LÖVE.

Upprop.

Undertecknade äro sysselsatta med att göra en översikt över kromosomtalen hos skandinaviska växter. För att listan skall kunna bli så fullständig som möjligt, vore det av största intresse, om de forskare i *de fyra skandinaviska länderna,* som gjort kromosomtalsbestämningar på inhemskt material, snarast ville meddela oss dels nya, ej förut publicerade tal, dels hänvisningar till av dem tidigare publicerade tal, för att säkra deras medtagande i tabellen.

Åskell och Doris Löve (Fil. Kandd.)
Genetiska Institutionen
Lund (Sverige).

Undertecknad är sysselsatt med att utarbeta en karta över utbredningen av Blechnum Spicant i Skåne. Då det är av vikt, att kartan blir så fullständig som möjligt, vore jag tacksam för meddelanden om fynd av arten. Noggranna uppgifter om lokalens läge och beskaffenhet äro önskvärda. De böra vara undertecknad tillhanda senast den 15 november.

H. Weimarck
Botaniska Museet
Lund.

BOTANISKA SEKTIONEN i Uppsala utbjuder till den högstbjudande följande arbeten:

Acta Horti Bergiani, komplett i originalband;
Botaniska Notiser, absolut komplett, bundet exemplar (de två sista årgångarna i häften);
Hegi: Illustrierte Flora von Mitteleuropa, 1. uppl., i originalband;
Linné: Species plantarum, 1. uppl., 1753, vackert exemplar i skinnband.

Intresserade torde före den 1 oktober 1941 hänvända sig till Botaniska Sektionens sekreterare, adr. Botaniska Institutionen, Uppsala.