

Variation in the apomictic microspecies of *Alchemilla vulgaris* L.

III. Geographical distribution and chromosome number

By GÖTE TURESSON

It is well known that a number of our *Alchemillas* has an extended geographical distribution beyond the limits of the Scandinavian peninsula. Thus *A. Wichurae* reaches Greenland, and *A. glomerulans* and *A. filicaulis* are both native to Greenland as well as to North America (cf. Samuelsson 1943). Other species extend far to the east and some of them, *A. acutiloba*, *A. micans*, *A. pastoralis* and *A. subcrenata*, even reach the Ob in Siberia (cf. Komarov *et al.* 1941). It is also a well known fact that the frequency of the *Alchemillas* in a given area is much influenced by human action. They all seem to profit by the change of vegetation brought about by man, and when "new" soil arises in cultivated areas they are often found to invade such habitats. In Sweden, where the original vegetation is so largely disturbed by man, it is even difficult to separate the true natives from more or less recent immigrants, although some species inhabiting the mountain regions now generally are considered as being native to the country (cf. Samuelsson 1943). The informations given by Hultén (1950) in mapping our northern *Alchemillas* evidence the fact, however, that the majority of these species prefer cultivated ground, meadows and pastures.

The results presented below are based on transplant material from the experimental garden belonging to the Institute of plant systematics and genetics at the Swedish Agricultural College. Most of the material is of Swedish origin, and only a few species are represented also from abroad, *viz.* *A. acutiloba*, *A. pastoralis* and *A. subcrenata* (from Switzerland), *A. glaucescens* and *A. pastoralis* (from Latvia), *A. borealis*, *A. glomerulans*, *A. subcrenata* and *A. Wichurae* (from Norway), and *A. glabra* (from the Faroes). While in some cases — especially in the case of

species with a very limited distribution — only one or a few transplants have been available, some of our most widespread species are represented by transplants from our southernmost province (Scania) and from the extreme North (the Abisko region in Lapland) — a stretch of country about 1500 km in length — as well as from intermediate points.

The material treated includes the following species:

<i>A. acutiloba</i> opiz	<i>A. oxyodonta</i> (Bus.) C. G. West.
<i>A. borealis</i> Sam. (ined.)	<i>A. pastoralis</i> Bus.
<i>A. cymatophylla</i> Juz.	<i>A. plicata</i> Bus.
<i>A. filicaulis</i> Bus.	<i>A. sarmatica</i> Juz.
<i>A. glabra</i> Neyg.	<i>A. subcrenata</i> Bus.
<i>A. glaucescens</i> Wallr.	<i>A. subglobosa</i> C. G. West.
<i>A. glomerulans</i> Bus.	<i>A. vestita</i> Bus.
<i>A. micans</i> Bus.	<i>A. Wichurae</i> (Bus.) Stef.
<i>A. Murbeckiana</i> Bus.	<i>A. xanthochlora</i> Rothm.
<i>A. obtusa</i> Bus.	

The chromosome countings, based on root tips from two clone plants from each transplant series, were carried out from time to time and mainly during the years 1948—1952. The roots were fixed in Karpechenko, cut and stained in gentian or in crystal violet. As a rule it is difficult (even after cooling) to find plates where the numerous chromosomes are sufficiently spaced to allow exact counts. Thus in spite of repeated fixations it has not been possible to fix the chromosome numbers with absolute certainty, and therefore the numbers are given within the margin of counts from the countable plates. Likewise, in the transplants where only one determination is stated, this result, sometimes obtained from fewer plates than in the series with varying numbers, should not be looked upon as the absolutely definitive number.

Before discussing the present results mention should be made of the data on the point published in previous literature. Böcher (1938) gives the chromosome number $2n=c. 64$ for *A. glomerulans*, and Turesson in Löve and Löve (1942) gives the number $2n=c. 90$ for *A. glabra* and *A. subcrenata*. According to Ehrenberg (1945) *A. acutiloba* and *A. glabra* have $2n=\pm 100$, while *A. pastoralis* was found to have the number $2n=\pm 101$, and *A. micans* $2n=\pm 93$. Gentcheff and Gustafsson (1940) presume the basic number to be 7 and conclude that the series $2n=\pm 91—\pm 105—\pm 119$ applies to the whole group of *A. vulgaris* S. lat.¹

¹ The $2n$ number, 91—191, given by Darlington and Wylie (1955), citing Gentcheff and Gustafsson, must be a misprint, since the numbers given by the latter are the above mentioned.

In the present investigation the main bulk of the species has been tabulated in Table 1. On account of the much deviating chromosome numbers in *A. borealis* and in *A. oxyodonta* these species are tabulated separately in Table 2. In order to obtain a view as to where the chromosome numbers within the marginal numbers in Table 1 are found, all the counts are given in Table 3 to show their frequency in the different species. As seen from the table there is a rather distinct accumulation around $2n=105-106$. This is especially marked in *A. glomerulans*, *A. Murbeckiana*, *A. pastoralis*, *A. subcrenata* and in *A. Wichurae*. The counts, for instance, in *A. acutiloba*, *A. filicaulis*, *A. glabra*, *A. glaucescens* and *A. micans* seem, on the other hand, to indicate the presence of more than one chromosome number in these species. It stands to reason that the material is insufficient, although a variation in the chromosome number seems plausible. Considering the apomictic mode of reproduction in the high polyploid *Alchemillas* a slight variation in the chromosome number seems altogether reasonable. The question, however, whether the numbers really vary to the extent stated in earlier reports must be settled by further investigations.

Table 2 deserves special attention, not only because of the fact that the two species here listed show considerably higher chromosome numbers than the bulk of the *Alchemillas* just discussed, but also because of the greatly varying numbers found in *A. borealis*. This species, as also *A. oxyodonta*, belongs to the critical *Acutidens*-group, which is insufficiently known, and which probably contains still undescribed forms. To this group the very little known *A. oleosa* Sam. (ined.) also belongs, and it does not seem unlikely that this or closely allied species are hidden in the heterogeneous *A. borealis*-group. As to *A. oxyodonta* none of our other *Alchemillas* has been found to attain the high chromosome number of this species, viz. $2n=165-168$.

In a previous paper (Turesson 1943) it was pointed out that our apomictic *Alchemilla* species, or microspecies, are to be considered as agamospecies in the terminology of the writer. It was further shown that within our common *Alchemilla* agamospecies a marked physiological variation, ecotypical in character, prevailed. As the term ecotype is restricted for the climatically and edaphically specialized biotype groups in sexual species the term agamotype was proposed for analogous groups in apomictic species. In a subsequent paper (Turesson 1956) some morphological characters were investigated in seed progenies, and the conclusion was made that the differences found

Table 1. Agamospecies, localities (from South to North) and chromosome number

No.	Agamospecies	Locality	2 n
1	<i>A. acutiloba</i>	Zürich, Switzerland	105-106
2	»	Arkelstorp, Scania	108-109
3	»	Gothenburg	106-107
4	»	» Kålltorp	107
5	»	Ärtemark, Dalsland	108
6	»	Dalarö, Sörmland	106
7	»	Simtuna, Uppland	105-107
8	»	Skrikjädra, Uppland	106-109
9	»	Uppsala no 134, Uppland	109
10	»	» no 135, »	108
11	»	Gimo, Uppland	105-106
12	»	Sollefteå, Ångermanl.	106-109
13	<i>A. cymatophylla</i>	Storlien, Jämtland	106-107
14	<i>A. filicaulis</i>	Kungsmarken, Scania	103-105
15	»	Nässjö, Småland	103-108
16	»	Gothenburg	103-106
17	»	» Kålltorp	106-108
18	»	Ärtemark, Dalsland	102-109
19	»	Simtuna no 169, Uppland	103
20	»	» no 171, »	105-107
21	»	Vik, Uppland	105-108
22	»	Öregrund, Uppland	105-106
23	»	Saltoluokta, Lapland	109-110
24	»	Abisko, Lapland	105-109
25	<i>A. glabra</i>	Dalby Norreskog, Scania	106
26	»	Tormestorp, Scania	104-107
27	»	Nässjö, Småland	108-109
28	»	Eksjö, Småland	107-110
29	»	Gothenburg	102-110
30	»	Ärtemark no 161, Dalsland	102-107
31	»	» no 148, »	108-109
32	»	Pungpina, Uppland	108-110
33	»	Storlien, Jämtland	102-106
34	»	Åre, Jämtland	107-110
35	»	Åreskutan, ca 900 m s.m., Jämtland	110
36	»	Geilo, Norway	102-103
37	»	Arjeplog, Lapland	107-108
38	»	Faroe Isles	103-104
39	<i>A. glaucescens</i>	Kungsmarken, Scania	108
40	»	Vickleby, Öland	104-107
41	»	Riga, Latvia	105-108
42	»	Gothenburg	103-105
43	»	Mösseberg, Västergötland	104-108
44	»	Ärtemark, Dalsland	107-109

Table 1 continued.

No.	Agamospecies	Locality	2 n
45	<i>A. glaucescens</i>	Skrikjädra, Uppland	109-110
46	<i>A. glomerulans</i>	Pungpina, Uppland	101
47	»	Simtuna, Uppland	106
48	»	Storlien no 72, Jämtland	103-105
49	»	» no 112, »	105-108
50	»	» no 103, »	104
51	»	Åre, Jämtland	106-107
52	»	Åreskutan ca 950 m s.m., Jämtland	102-106
53	»	Geilo, Norway	102-104
54	»	Vilhelmina, Lapland	105
55	»	Arjeplog, Lapland	109
56	»	Porjus, Lapland	101
57	»	Saltoluokta, Lapland	105-106
58	»	Kerkau ca 900 m s.m., Lapland	107
59	»	Abisko, Lapland	105
60	<i>A. micans</i>	Vickleby, Öland	108-109
61	»	Nässjö, Småland	106
62	»	Eksjö, Småland	109
63	»	Göteborg	106
64	»	Ärtemark, Dalsland	105-110
65	»	Loka, Västmanland	105-107
66	»	Vik, Uppland	106-110
67	»	Ultuna, Uppland	105-108
68	»	Särna, Dalecarlia	109
69	»	Sollefteå, Ångermanland	104-107
70	»	Östersund no 146, Jämtland	109
71	»	» no 147, »	107-110
72	»	Storuman, Lapland	107
73	»	Luleå, Norrbotten	105-107
74	»	Porjus, Lapland	105-109
75	<i>A. Murbeckiana</i>	Vik, Uppland	104-106
76	»	Uppsala Slottsbacken, Uppland	106-107
77	»	Öregrund, Uppland	106-109
78	»	Särna, Dalecarlia	107-109
79	»	Sollefteå, Ångermanland	106
80	»	Storlien, Jämtland	102-109
81	»	Åre, Jämtland	105-106
82	»	Trondheim, Norway	105
83	»	Storuman, Lapland	102-108
84	»	Arjeplog no 1, Lapland	104-108
85	»	» no 16, »	102-106
86	»	Porjus, Lapland	104-108
87	»	Saltoluokta, Lapland	104-107
88	»	Kerkau ca 900 m s.m., Lapland	106

Table 1 continued.

No.	Agamospecies	Locality	2 n
89	<i>A. Murbeckiana</i>	Abisko no 77, Lapland	103—105
90	»	» no 78, »	104
91	»	Vassitjokko, Lapland	105
92	<i>A. obtusa</i>	Brokind, Östergötland	103
93	<i>A. pastoralis</i>	Zürich, Switzerland	109
94	»	Kungsmarken, Scania	103—108
95	»	Riga, Latvia	108
96	»	Gothenburg	109
97	»	Ärtemark, Dalsland	106
98	»	Loka, Västmanland	106—107
99	»	Vik, Uppland	105—107
100	»	Säter, Dalecarlia	104—105
101	»	Särna, Dalecarlia	109
102	»	Sollefteå, Ångermanland	106—107
103	»	Storlien, Jämtland	106
104	»	Åre no 21, Jämtland	104—107
105	»	» no 143, »	105
106	»	Trondheim, Norway	108
107	»	Vojmán, Lapland	106—107
108	»	Storuman no 20, Lapland	105—108
109	»	» no 24, »	104—107
110	»	Luleå, Norrbotten	104—108
111	»	Arjeplog, Lapland	104—106
112	»	Porjus, Lapland	105—107
113	»	Jaurekaska, Lapland	107
114	»	Abisko, Lapland	104—106
115	<i>A. plicata</i>	Nässjö, Småland	105
116	»	Ärtemark, Dalsland	107—108
117	»	Bo, Uppland	104—107
118	»	Simtuna no 150, Uppland	107
119	»	» no 166, »	104—105
120	»	Skrikjädra, Uppland	107—108
121	<i>A. sarmatica</i>	» »	105—106
122	<i>A. subcrenata</i>	Zürich, Switzerland	109—110
123	»	Kungsmarken, Scania	104
124	»	Nässjö, Småland	106
125	»	Eksjö, Småland	104
126	»	Gothenburg	106
127	»	Simtuna, Uppland	106
128	»	Skrikjädra, Uppland	105—107
129	»	Säter, Dalecarlia	105
130	»	Särna, Dalecarlia	107—108
131	»	Sollefteå, Ångermanland	106
132	»	Storlien, Jämtland	106—109

Table 1 continued.

No.	Agamospecies	Locality	2 n
133	<i>A. subcrenata</i>	Åre, Jämtland	106
134	»	Trondheim, Norway	106
135	»	Vilhelmina, Lapland	107—109
136	»	Porjus, Lapland	106—110
137	»	Abisko, Lapland	104—107
138	<i>A. subglobosa</i>	Nässjö, Småland	102—105
139	»	Mösseberg, Västergötland	105—108
140	»	Simtuna, Uppland	102—104
141	»	Vik, Uppland	108
142	»	Uppsala Carolinap., Uppland	105—108
143	»	Västanfors, Västmanland	104
144	<i>A. vestita</i>	Skrikjädra, Uppland	110
145	<i>A. Wichuræ</i>	Norrköping, Östergötland	104—105
146	»	Simtuna, Uppland	105
147	»	Vik, Uppland	103—105
148	»	Uppsala Slottsb., Uppland	104—106
149	»	» Carolinap., Uppland	106
150	»	Särna, Dalecarlia	105—106
151	»	Åre, Jämtland	104—105
152	»	Sollefteå, Ångermanland	105—106
153	»	Geilo, Norway	105—106
154	»	Myrdal, Norway	104—106
155	»	Malgomaj, Lapland	104
156	»	Storuman, Lapland	107
157	»	Porjus, Lapland	104—105
158	<i>A. xanthochlora</i>	Sjöbo, Scania	105

Table 2. The chromosome numbers in *A. borealis* and in *A. oxyodonta*

No.	Agamospecies	Locality	2 n
1	<i>A. borealis</i>	Storlien no 6, Jämtland	150—152
2	»	» no 7, »	130—141
3	»	Åre no 2, Jämtland	130—138
4	»	» no 3, »	134—139
5	»	Trondheim, Norway	138—144
6	»	Porjus no 36, Lapland	134—137
7	»	» no 56, »	131—133
8	»	Abisko no 50, »	130
9	»	» no 76, »	131
10	<i>A. oxyodonta</i>	Åresk. Mörviksh., Jämtland	165—168

Table 3. Frequency of counts of chromosome numbers in the different agamospecies

Agamospecies	101	102	103	104	105	106	107	108	109	110
<i>A. acutidens</i>	—	—	—	—	3	8	4	5	5	—
<i>A. cymatophylla</i>	—	—	—	—	—	1	1	—	—	—
<i>A. filicaulis</i>	—	2	6	1	7	5	1	3	4	2
<i>A. glabra</i>	—	6	4	5	1	4	5	4	2	6
<i>A. glaucescens</i>	—	—	2	4	5	—	3	4	2	1
<i>A. glomerulans</i>	1	3	3	9	8	7	5	2	1	—
<i>A. micans</i>	—	—	—	2	6	10	8	2	8	3
<i>A. Murbeckiana</i>	—	3	4	7	8	14	8	4	5	1
<i>A. obtusa</i>	—	—	2	—	—	—	—	—	—	—
<i>A. pastoralis</i>	—	—	4	6	9	18	14	5	5	—
<i>A. plicata</i>	—	—	—	3	4	1	4	2	—	—
<i>A. sarmatica</i>	—	—	—	—	1	1	—	—	—	—
<i>A. subcrenata</i>	—	—	—	5	4	13	5	1	3	2
<i>A. subglobosa</i>	—	2	—	3	3	1	—	3	—	—
<i>A. vestita</i>	—	—	—	—	—	—	—	—	—	2
<i>A. Wichurae</i>	—	—	1	6	11	9	2	—	—	—
<i>A. xanthochlora</i>	—	—	—	—	2	—	—	—	—	—

between the agamotypes, physiological and morphological, were due to genetic variation and not to modification.

Now, it is of a special interest to study the geographical distribution of the different chromosome numbers in the agamospecies treated in the above. As seen from Table 1 there is a rather uniform distribution of the numbers within the area. The higher numbers are found to be spread with the lower ones with no special trend towards north or south. Thus no marked accumulation of higher numbers are found in the north and, therefore, the Hagerup-Tischler theory, implying an increase in the chromosome number and in the degree of polyploidy with the higher latitude, does not seem to be applicable in the present case. This appears to be true not only of the agamospecies considered by Samuelsson (1943) to be undoubtedly indigenous (as for instance *A. filicaulis*, *A. glabra*, *A. Murbeckiana*, *A. Wichurae*) but also of the more doubtful ones in this respect (for instance *A. glaucescens*, *A. micans*, *A. pastoralis*). As to *A. borealis* and *A. oxyodonta* in Table 2 the former is too heterogeneous, as said before, to allow any conclusions, and the latter is represented from only one locality.

Our *Alchemillas* apparently do not adapt themselves to different habitats by any change in chromosome number but probably by the

process of autosegregation (cf. Gustafsson 1947, Turesson 1956). The differentiation of climatically (and edaphically) specialized biotype groups in our *Alchemillas*, viz. the agamotypes, has its parallel in the sexual plant species, where the differentiation of ecotypes also takes place without changes in chromosome number (Turesson 1938).

As pointed out in the introduction the majority of the northern *Alchemillas* favour cultivated ground, meadows and pastures, and most of them profit by the changes in the plant cover brought about by man. Thus these high polyploids seem to hold their own in localities where competition is less keen, enabling them to start and develop without the severities brought about by a dense and close plant cover. According to my own experience the "seeds" of our *Alchemillas* germinate slowly as a rule, and the development in the earlier stages of the plants is also slow. From numerous artificial and quite a number of natural polyploids we now know, that the rate of growth in general is markedly slower in the polyploids than in the corresponding diploids (cf. Schwanitz 1954). It seems most likely that the cause of the prevalence of our high polyploid *Alchemillas* in disturbed and "man made" habitats is a question of competition, the slow rate of growth being the decisive factor.

Summary

1. The chromosome numbers of 19 agamospecies of the genus *Alchemilla* have been determined, and the results are given in Tables 1—2.

2. There is no marked increase in the chromosome number or in the degree of polyploidy with higher latitude. The differentiation of the agamotypes is probably due to autosegregation.

3. It seems most probable that the cause of the prevalence of the high polyploid *Alchemillas* in disturbed and "man made" habitats is a question of competition, the slow rate of growth being the decisive factor.

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Experimental Studies in *Cardamine amara*

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(Meddelanden från Lunds Botaniska Museum, Nr 118)

In the genus *Cardamine* the species *C. amara* is one of the more common representatives of the section *Eucardamine* growing in Europe. Now and then this Linnean species has been split up, and taxa of different values have been described. The only taxon more commonly regarded as a species parallel to *C. amara* L. is *C. opizii* Presl (Presl et Presl 1819). A great number of minor fractions have been named, the value of some of which will be discussed in a future paper.

C. amara occurs in moist localities, mostly in connection with *Alnus* woods, along small rivulets and brooks. Sometimes it is found growing on sun-exposed slopes where spring-water bubbles up. The species is highly favoured by polluted brooks and ditches.

The reproduction of *C. amara* is sexual as well as vegetative, the latter by means of runners. The vegetative reproduction is most important; whereas the sexual one seems to be of limited value in nature, at least in undisturbed plant communities. The seeds ripen and are spread during the most extensive period of vegetation development and germinate in a few days, if it is moist enough. However the chance for the germ plant to survive is very small. It is obvious that in most localities the plants represent one or a few clones, because of the preference for the vegetative reproduction over the sexual one.

The investigations published below include cultivation experiments, determinations of chromosome numbers, induced polyploidization and crossings. Most of the studies have been carried out parallel to a similar but much more extensive work on the *C. pratensis* complex (Lövkvist 1956).

Most of the material investigated has been collected by the author himself on excursions in Scandinavia and the Alps. The author is in-

debted, however, to a number of botanists who have kindly sent living plants of great importance for these studies.

Chromosome Studies

Earlier investigations. — Lawrence (1931) seems to have given the first report of a chromosome number of *C. amara*. He finds the somatic number $2n=16$. The same number is given by Manton (1932) and others (see Table 1). Mattick (in Tischler 1950) has found the tetraploid number 32 in plants from the Alps. Banach-Pogan (1955) reports the diploid number for *C. amara* from 9 Polish localities and gives the same number for the very closely related *C. opizii* from 11 localities in southern Poland. Her investigations are the most extensive hitherto published.

Present investigations. — The determinations of chromosome numbers of *C. amara* reported in this paper (Table 2) are all made from plants collected in nature and never from material received from botanical gardens. Fixation and staining work have followed the scheme described in an earlier publication (Lövkvis 1956).

The diploid and tetraploid numbers, 16 and 32 respectively, point to the basic number 8. So far this is the only basic number in *C. amara*. The cytological conditions seem to be very simple in this species, thus contrary to the situation in the *C. pratensis* complex where genomes with 7 and 8 chromosomes are connected in numerous combinations (comp. Lövkvis 1956).

The cytological differentiation into one diploid and one tetraploid population is of taxonomical importance and will be discussed in a future paper.

Table 1. Somatic chromosome numbers reported in the literature for *C. amara* s. lat.

Author and locality	Chromosome number	
	2 x	4 x
Lawrence 1931 — England: Merton	16	—
Manton 1932 — England	16	—
Mattick in Tischler 1950 — Austria	—	32
Banach-Pogan 1955 (comp. Skalinska 1950)—South- ern Poland, nine loc. (<i>C. amara</i>)	16	—
— eleven loc. (<i>C. opizii</i>)	16	—
Lövkvis 1956 — Sweden	16	—
— The Alps	—	32

Table 2. List of somatic chromosome numbers of *Cardamine amara*

Locality (altitude in m s.m.)	No. pl.	Chromosome number	
		2 x	4 x
Sweden			
S k å n e			
Baldringe, Fylan, 26	3	16	—
Benestad, Bäckarna, 48	10	16	—
Hjärnarp, Hulebäckseröd, 144	5	16	—
—, Skorstensgård, 78	3	16	—
Osby, Kalhult, 70	18	16	—
Röstånga, Nackarp, 58	1	16	—
Svalöv, Källstorp, 77	30	16	—
S. Sandby, Fågelsång, 35	25	16	—
Torrlösa, Trolleholm, 90	25	16	—
Ö. Broby, Krögerslund, 50	4	16	—
S m å l a n d			
Traryd, Strömnäsbruk, 135	8	16	—
Ö s t e r g ö t l a n d			
Tollstad, Alvastra, 105	5	16	—
V ä s t e r g ö t l a n d			
Alingsås, 59	6	16	—
Hjo, Grenabo, 151	4	16	—
H a l l a n d			
Onsala, Kungsbackaviken, 5	21	16	—
Ö. Karup, Högaskog, 153	5	16	—
V ä r m l a n d			
Munkfors, Gersheden	6	16	—
H ä l s i n g l a n d			
Norråla, Vågbro	19	16	—
J ä m t l a n d			
Åre, Brudslöjan, 470	2	16	—
—, Storlien, 595	9	16	—
—, Vikböle, 378	3	16	—
L a p p l a n d			
Jukkasjärvi, Tornehamn, 340	16	16	—
Denmark			
Grib Skov, Stenholt Hegn	24	16	—
North of Ireland			
Shaw's Bridge (Antrim)	12	16	—
France			
Condé en Brie (Aisne)	3	16	—
Austria			
Koralpe, Glashütte (Styria), 1400	2	—	32
S:t Sigmund (Tirol), 1500	2	—	32
Perlsteinbach (Tirol), 1600	1	—	32
—, 1750	3	—	32

Cultivation Experiments

One aim of the experimental studies of *C. amara* was to obtain an idea of the modificatory capacity of the plant, as the species in nature often shows considerable diversity from one locality to another. Cultivation experiments with individuals from a number of localities brought together in the experimental garden should elucidate the problem. In these investigations diploid plants from 32 localities and tetraploids from 5 were involved. Chromosome numbers had been counted for plants from 25 of the localities with diploids and from 4 with tetraploids. The morphological differences between diploids and tetraploids were sufficient for the determination of the plants in which the chromosome number had not been counted.

The cultivated tetraploids all originated from the Alps. Difficulties arose in keeping them alive, and they seldom flowered simultaneously with other *Cardamine* plants.

The diploids, on the other hand, were easily kept in cultivation and could be studied. The following results refer to the diploids only.

In Sweden glabrous as well as pubescent *C. amara* plants are found. Investigations in the province of Skåne made it likely that a continuous variation occurs. However, pubescent plants grow mostly in sun-exposed localities, while the extremely glabrous plants are found in the shade under very wet conditions. The rough surface of the leaflets should not be mistaken for pubescence.

Some pubescent plants from Benestad and some glabrous ones from Baldringe (very near Benestad) were placed in two groups in a greenhouse, each group consisting of representatives for both localities. The first group was exposed to the sun throughout the day, while the second one was placed in the shade under a table. The light differences were considerable. All plants in the light were transferred into a pubescent form, while all plants in the shade became glabrous. Unfortunately plants of an extremely pubescent clone, perhaps outside the continuous variation, were not included in this experiment.

It seems reasonable to conclude that the plants involved in this observation are highly modificatory regarding the pubescence. The extreme pubescent plants mentioned may represent another biotype which can behave in a different way.

Observations on leaf size and shape showed considerable changes when the pubescent plants placed in the shade produced new leaves. These were much larger than those in nature and those produced

by the plants exposed to the sun. The colour of the leaves of all plants in the shade was dark green, while that of all plants exposed to the sun was greyish green, at least partly depending on epidermal alterations. The shape of the leaves changed in the shade, so that all leaflets increased their breadth comparatively more than their length. The middle cauline leaves of the pubescent plants from Benestad had a leaflet area 8—11 times larger in the shade experiment than the year before when growing in nature.

The height of the pubescent plants when in flower was between 8 and 14 cm, while the same plants when cultivated in the shade the following year grew to 24—37 cm (the plants being more prostrate contrary to the erect habitus at Benestad).

It may be understood that the present author regards some minor fractions of *C. amara* doubtful, e.g., *hirsuta*, *glabra*, *grandifolia*, *macrophylla*, *microphylla*, *minor*. This does not mean that no fixed taxa occur. It is well known that among plants modified in an extreme environment even plants genetically fixed to the same habitus under all conditions exist. Such cases have been experimentally investigated by Turesson (1922) in *Centaurea jacea* L. and *Succisa pratensis* Moench.

Differences in the development were found when plants from different regions grew together in the experimental garden, as they were genetically adapted to the length of the vegetation period of the region in which they had grown. Generally the cultivation experiments showed that *C. amara* plants flowered earlier in the garden the more northerly their place of origin. Two interesting exceptions may be dealt with.

At Tornehamn in the Torneträsk area of Swedish Lapland a clone of *C. amara* is growing. When cultivated this clone flowered at the same time as did plants from the neighbourhood of Gävle (prov. Gästrikland) in the middle part of the Swedish east coast, where the vegetation period is about twice as long as that at Tornehamn. In the author's opinion the clone at Tornehamn is a recent introduction, its late flowering being the best evidence. The distance from here to the nearest locality is considerable.

Another introduction of *C. amara* has been observed at Mt. Blåhammaren (prov. Jämtland). The plants in cultivation from this place were not determined as to their chromosome numbers, but were without any doubt diploids. At the refuse heap of the fjeld station Blåhammarstugan (1085 m s.m.) two clones are growing. The present author has visited the locality three years in the middle of August. The one clone had then

finished its flowering, while the second clone was still in bud. Only one year, 1952, have a few flowers been observed during the very short visits to the station. The cultivation experiments showed that the early flowering clone may be selected under the same circumstances as that from Storlien (15 km N of Blåhammaren) at 595 m s.m., as they flowered at the same time. The late flowering clone was simultaneous with plants from the Uppsala region. In the experimental garden the flowering period of the two clones overlapped for a few days.

Induced Polyploidy

The vegetative reproduction by means of runners, which occurs in *C. amara*, makes this species useful for studying the effect of chromosome doubling. If it were possible to produce tetraploid runners by colchicine treatment and keep other runners at the diploid stage, the same plant could be investigated both at diploid and tetraploid level and with exactly the same balance between their chromosome genes. All morphological differences between the diploid and the artificially produced tetraploid should depend on the differences in chromosome number.

Colchicine treatments were carried out on young runners, which had been cut and placed for a few days in water, until small roots were produced at the nodes. Before treatment the runners were dried for one hour on a blotting-pad in order to remove surplus water. The experiments were performed with the following concentrations of colchicine in water, 0.25, 0.5, 1, and 2 %. The runners were kept for $\frac{1}{2}$, 1, 2, 4, and 24 hours in the solutions. A total of 20 treatments were carried out. The experiments were successful with one plant only, but that specimen produced tetraploid plants as well as one octoploid plant from the treated runners. The successful result was obtained after keeping the runners for half an hour in an 1 % solution, whereafter they were planted in moist sand without rinsing in water.

Three years after the treatment the same plant was studied at diploid, tetraploid and octoploid levels. From natural material it has been very difficult to study extreme autopolyploidy and the effect of polyploidy itself without any inclusions of genetic material from other individuals or species. The results given below may be considered very carefully as they come from one original plant only.

The results compiled in Table 3 show that the artificial tetraploid and octoploid differ in many respects from their diploid clone plant. The



Fig. 1. *Cardamine amara*. The same individual at diploid, tetraploid and octoploid level.

anthocyanin colouring of the lower part of the stem is less pronounced in the tetraploid and octoploid than in the diploid. In *C. pratensis* L. anthocyanin occurs in the diploid and tetraploid populations, while it is not visible in the hexaploid except under very dry conditions. The polyploidization may be responsible for the different behaviour of the anthocyanin in these cases.

The pilosity of the margin of the leaflets is of great interest, as a continuous increase in the frequency of hairs with higher polyploid level is observed.

The number of flowers per inflorescence decreases markedly in the octoploid.

Measurements of a number of details of the flower have been made and they show in some cases striking differences, particularly in calyx and corolla leaves. The contrast between the obvious increasing length-breadth index of the calyx leaves with higher chromosome number and the pronounced decreasing length-breadth index of the corolla leaves is considerable. Particularly the differences between the petals of the plants at the three levels (Fig. 1) are easily observable.

Most crucifers have their stamina in two groups, four tall and two short ones. Generally the filaments of the two groups differ from 1.5 to 3 mm in length. In *C. amara*, however, the difference is very slight,

0.5 mm only. At the tetraploid level the same difference is maintained, while at the octoploid level the two groups have been levelled.

The filaments of the stamina increase considerably in thickness with higher chromosome numbers (Fig. 1).

A change in the appearance of the anthers accompanies the induced polyploidy. The anthers of the diploid are long and narrow, those of the tetraploid are of about the same length but thicker, while the octoploid has nearly barrel-shaped anthers.

Observations of the runners showed that the thickness increases with higher chromosome numbers and the internodes become shorter.

Some of the clone plants were chimeras after the colchicine treatment, but repeated cloning altered this condition, so that roots and sexual apparatus were definitely tetraploid and octoploid. All comparisons are made from such plants. The fact that some plants were chimeras is evident from a study of some crossings carried out with diploid *C. amara* plants as females and the produced octoploid as the male. Pods developed producing 18 seeds in only one cross. Three of the seeds germinated, but one of the plants soon died, while the other obtained full growth having $2n=16$ and 24 respectively. Other crossings using the same plant as male gave no results, and it seems reasonable that one stem was a diploid-tetraploid chimera, while the others were octoploid. When cloned up later, only the thickest runners were used.

The two plants developed after the crossing mentioned above were studied. The triploid began to flower 14 days earlier than the diploid and had more runners developing from the base of the stem than the diploid sister plant. The diploid had a smooth stem, the triploid a grooved, the diploid had 4 and 5 cauline leaves, the triploid 10. Nearly all leaflets of the triploid had petioles and were dentate with undulated margin, while these characters were not so pronounced in the diploid. Only few pollen grains were well developed. The anthocyanin colour of the anthers of the triploid was lighter than that of the diploid.

Crossing experiments were carried out between diploid plants of *C. amara* and a certain octoploid clone plant. No seeds at all were produced, indicating a strong sterility barrier caused by the great difference in chromosome number.

Crossing Experiments

In order to obtain information about the genetic isolation between *C. amara* and some species of the section *Eucardamine*, crossing experi-

Table 3. Observations of some characters of the same *C. amara* individual at diploid, tetraploid and octoploid level

Characters	Diploid	Tetraploid	Octoploid
Anthocyanin colour of stem	traces on lower 1/3	traces just above rosette leaves	traces just above rosetate leaves
Pilosity of leaflet margin	sparse	obvious	pronounced
Flowers per inflorescence	16	15	12
Calyx leaves			
length of, mm	4.0	4.7	5.2
breadth of, mm	1.8	2.0	2.0
length-breadth index	2.10	1.85	1.38
Corolla leaves			
length of, mm	10.5	12.0	11.0
breadth of, mm	5.0	6.5	8.0
length-breadth index	2.10	1.85	1.38
Filament length of			
long stamina	6.5	8.0	7.2
short stamina	6.0	7.5	7.2
Style length	7.0	9.0	9.0

ments were carried out. Unfortunately the material of the natural tetraploid population from the Alps was very small, and because of cultivation difficulties the flowering could very seldom be synchronized with that of other plants. Some of the combinations represent parts of an investigation of the hybridization potentialities of the diploids of the section *Eucardamine*. Crossings in which the artificial polyploids are involved have been described above (p. 430).

For the most part the pollinations were carried out after emasculation made in buds. Afterwards the plants were bagged and left for a few days before being pollinated. When pollination was performed the same bag was used again for the plant. In combinations with plants of species which are normally pollinated already when in bud, the pollinations were mostly carried out in connection with the emasculation.

Together with diploid and tetraploid *C. amara* L. the following species are involved in the crossing experiments: *C. flexuosa* With. $2n=32$, *C. hirsuta* L. $2n=16$, *C. impatiens* L. $2n=16$, *C. rivularis* Schur $2n=16$, *C. pratensis* L. $2n=30$ and 44 , *C. palustris* Peterm. $2n=56$, 60 , 64 , 68 , 72 , and 76 , "the Portuguese diploid" of the *C. pratensis* complex (comp. Lövkvist 1956), and *C. raphanifolia* Pourret $2n=46$ (44).

Crossings within diploid *C. amara*. — The plants of *C. amara* found in nature often represent one or a few clones in a locality. Studies of this phenomenon have shown that the vegetative reproduction is much more

Table 4. Crossings within *Cardamine amara*

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. amara</i> 2n=16 × <i>C. amara</i> 2n=16					
Norråla, Hälsld., Sw. × Grib Skov, Denm.	5	5	29	5.8	13
— × —	7	6	32	5.3	11
— × Norråla	4	2	7	3.5	3
Munkfors, Värml., Sw. × —	9	9	49	5.4	19
— × Alingsås, Vgld., Sw.	8	7	26	3.7	6
Kalhult, Sk., Sw. × —	11	9	67	7.6	26
Total	44	38	210	5.5	78
<i>C. amara</i> 2n=16 × <i>C. amara</i> 2n=32					
Onsala, Hld., Sw. × Mt. Koralpe, Austria	5	0	—	—	—
Munkfors, Värml., Sw. (non-emasculated) × —	2	2	10(3)	5.0	0
<i>C. amara</i> 2n=16 × artific. <i>C. amara</i> 2n=64					
Five combinations, total	39	0	—	—	—
One combination with chimera male (see text)	8	3	18(3)	6.0	2

The figures in parentheses under No. of seeds indicate well-developed seeds, without parentheses all seeds are good.

important than the sexual one, because the runners constitute a very effective system of propagation and colonizing. In nature the seed setting of the partly autogamous *C. amara* is good. In recent years, however, it has very often been disturbed by insects of the same species as those invading the fields of cruciferous oil crops. The average seed setting observed in nature in some districts of southern Sweden was 24 seeds per pod.

In the crossing experiments the seed setting is very low, the mean being 5.5 seeds per pod. Whether the emasculation procedure has something to do with the marked decrease in seed setting is still a problem, but it may be so. The lowest seed setting (see Table 4) was found when two plants from Norråla (prov. Hälsingland, Sweden), probably of the same clone, were crossed. Another plant from Norråla, very likely of the same clone, gave when placed in an isolation box 16 seeds per pod. The highest seed setting was found when a plant from Kalhult (prov. Skåne) was given pollen from a plant from Alingsås (prov. Västergötland). It is evident that the experimental conditions are unfavourable for the seed setting.

Crossings between diploid and tetraploid *C. amara*. — Due to lack of material and cultivation difficulties only one crossing has been carried out

after emasculation. A diploid plant from Onsala (prov. Halland, Sw.) was crossed with a tetraploid from Mt. Koralpe (Austria). Five stigmas were pollinated but no pods developed (Table 4).

Two non-emasculated flowers of a diploid *C. amara* from Munkfors (prov. Värmland, Sw.) were given pollen from an Austrian tetraploid when its flowers were already open. Two pods developed producing 10 seeds, 3 of which were apparently good. None, however, germinated.

All seeds obtained in the crossings between diploid plants of *C. amara* were well developed. In the crossing in which non-emasculated flowers of the diploid were used as the females and the tetraploid as the male, only 3 out of 10 seeds showed good development. It seems reasonable to regard the poorly developed seeds as triploid and the seed setting as due to the fact that pollen tubes of legitimate pollen may have helped the tubes of the illegitimate pollen (from the tetraploid) to reach the embryo sacs. The combination in which emasculated flowers were used for the crossing developed no seeds in spite of 5 stigmas being pollinated.

In the crossings with the induced polyploid plants (Table 4), it is found that seeds developed and gave 2 good plants when the pollen used probably had 8 and 16 chromosomes, thus analogous with the foregoing crossing (comp. p. 430).

Crossings between diploid *C. amara* and tetraploid *C. flexuosa*. — In 8 crossings with emasculated *C. amara* as the female, 57 flowers were pollinated with pollen from *C. flexuosa* plants. No pods at all developed. In 9 crossings with emasculated *C. flexuosa* plants as the females and diploid *C. amara* as the males 28 flowers were pollinated, but no pods developed (Table 5).

Pollinations were also carried out without emasculations and gave some interesting results. Twelve open flowers of a *C. amara* plant were pollinated with *C. flexuosa* pollen. All the styles developed into pods and produced 130 seeds, 76 of which were well developed (58.5%). This is contrary to what has been found in the legitimate *C. amara* combination where all seeds were well developed. It seems reasonable to regard the poor seeds of these crossings (54) as hybrid seeds.

In another crossing 5 *C. amara* flowers were given *C. flexuosa* pollen while in bud. Only 1 pod developed giving rise to 14 seeds all well developed, 11 of which germinated developing into pure *C. amara* plants.

In 4 crossings 18 non-emasculated flowers of *C. flexuosa* were pollinated with *C. amara* pollen and produced 17 pods with a total of

Table 5. Crossings between diploid *C. amara* and tetraploid *C. flexuosa* and diploid *C. hirsuta*

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. amara</i> 2n=16 × <i>C. flexuosa</i> 2n=32					
Eight combinations, emasculated, total	57	0	—	—	—
Tollstad, Alvastra, Ögld., Sw. (non-emasculated) × Svansjön . .	12	12	130(76)	18.3	} see text
Norråla, Hälsld., Sw. (non-emasculated) × —	5	1	14	14.0	
<i>C. flexuosa</i> 2n=32 × <i>C. amara</i> 2n=16					
Nine combinations, emasculated, total	28	0	—	—	—
Four combinations, non-emasculated, total	18	17	339	19.9	see text
<i>C. amara</i> 2n=16 × <i>C. hirsuta</i> 2n=16					
Two combinations, emasculated, total	8	0	—	—	—
<i>C. hirsuta</i> 2n=16 × <i>C. amara</i> 2n=16					
Three combinations, emasculated, total	10	1	0	—	—

339 seeds (19.8 per pod). All seeds were well developed and gave rise to pure *C. flexuosa* plants only.

Crossings between diploid *Cardamine amara* and the diploid *C. hirsuta*. — *C. amara* has been used as the female plant in 2 combinations only. Eight emasculated flowers were pollinated with *C. hirsuta* pollen. No pods were produced.

In the other direction, that is with *C. hirsuta* as the female plant 3 crossings have been made, 10 flowers pollinated with *C. amara* pollen. One pod developed producing 2 very small seeds, which may better be regarded as ovules probably fertilized and only having undergone a few cell divisions.

Crossings between diploid *Cardamine amara* and diploid *C. impatiens*. — Twelve crossings have been carried out with *C. amara* as the female parent and *C. impatiens* as the male one. A total of 92 flowers have been pollinated, but no pods developed (Table 6).

In the opposite direction, thus with *C. impatiens* as the female parent, the result is a little more interesting. Plants of *C. impatiens* from two different localities have been used as the females. When plants from Sunnersta in the neighbourhood of Uppsala, Sweden, were used, no pods developed after pollination of 35 flowers. When plants from Uddeboö, Norrtälje, Sweden, were pollinated with *C. amara* pollen the 2 crossings carried out, 23 flowers gave rise to 4 pods with 25 seeds, 16 of which

Table 6. Crossings between diploid *Cardamine amara* and diploid *C. impatiens*

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. impatiens</i> 2n=16 × <i>C. amara</i> 2n=16					
Sunnersta, Uppsala, Sw. × Norrala, Hälsld., Sw.	14	0	—	—	—
— × Källstorp, Skåne, Sw.	10	0	—	—	—
— × Norrala, Hälsld., Sw.	11	0	—	—	—
Uddeboö, Norrtälje, Sw. × —	13	3	17(9)	5.7	—
— × Alingsås, Vstgll., Sw.	10	1	8(7)	8.0	—
Total	58	4	25(16)	6.3	—
<i>C. amara</i> 2n=16 × <i>C. impatiens</i> 2n=16					
Twelve combinations, total	92	0	—	—	—

seemed to be well developed. However none of these germinated. It has to be pointed out that emasculated flowers of *C. impatiens* pollinated with its own pollen give rise to only well-developed seeds. The high frequency (64 %) of well-developed seeds in the two combinations in which *C. impatiens* plants from Uddebö were the females is peculiar. The most probable interpretation should be that some pollen grains may have escaped from the anthers during the emasculation procedure and their tubes can have helped the tubes of the illegitimate pollen grains of *C. amara* to grow down to the embryo sacs, giving rise to the poorly developed seeds. Actually the stigmas were always carefully examined before pollination, so this explanation seems rather improbable.

Crossings between diploid *C. amara* and members of the *C. pratensis* complex.

— A great number of crossings have been performed between *C. amara* and members of the *C. pratensis* complex. Most of them have been carried out in an attempt to demonstrate a hypothesis that *C. amara* is involved in the origin of a population of 76-chromosomic *C. palustris* with broad dentate leaflets of all cauline leaves, named *C. palustris* var. *isophylla*. However, in crossings with importance for this hypothesis, no hybrids were obtained.

Some of the crossings reported in this paper have been published before (Lövkvis 1956), but for a more complete picture of the conditions of *C. amara* the earlier results will be included here with the present findings. The members of the *C. pratensis* complex which are involved in the crossings are given in Table 7. "The Portuguese diploid" mentioned in the table is earlier discussed (comp. Lövkvis 1956, p. 88).

When diploid, emasculated *C. amara* flowers were given pollen from

Table 7. Crossings between diploid *C. amara* and diploids of the *C. pratensis* complex

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. amara</i> 2n=16 × <i>C. rivularis</i> 2n=16					
Grib Skov, Denn. × Koralpe, Austria	13	6	28(0)	4.7	0
Norråla, Hlsld., Sw. × —	6	0	—	—	—
— × —	5	0	—	—	—
— × —	9	0	—	—	—
— × —	9	4	14(0)	3.7	0
— × —	4	1	1(0)	1.0	0
Munkfors, Vrml., Sw. × —	5	2	10(0)	5.0	0
Källstorp, Sk., Sw. × —	7	3	6(0)	2.0	0
Onsala, Hld., Sw. × —	5	1	7(0)	7.0	0
Total	63	17	66(0)	3.9	0
<i>C. rivularis</i> 2n=16 × <i>C. amara</i> 2n=16					
Koralpe, Austria × Alingsås, Vstrgtl., Sw.	5	2	0	0	—
<i>C. rivularis</i> 2n=16 × { <i>C. rivularis</i> 2n=16 <i>C. amara</i> 2n=16	4	4	16(3)	4.0	0
Mt. Koralpe, Austria × { Alvastra, Östgtl., Sw.					
<i>C. amara</i> 2n=16 × "The Portuguese diploid"					
Shaw's Bridge, N. Ireland × Coimbra, Port.	4	0	—	—	—
Alvastra, Östgtl., Sw. × —	3	0	—	—	—
— × —	4	0	—	—	—
— × —	4	0	—	—	—
Total	15	0	—	—	—
"The Portuguese diploid" × <i>C. amara</i> 2n=16					
Coimbra, Port. × Munkfors, Vrml., Sw.	4	4	0	—	—
"The Portuguese diploid" × { <i>C. amara</i> 2n=16 <i>C. pratensis</i> 2n=44					
Coimbra, Port. × { Alvastra, Östgtl., Sw. Grignon, France	8	8	55(0)	6.9	2

The figures in parentheses in No. of seeds indicate well-developed seeds.

diploid *C. rivularis* only 3 crossings out of 9 were sterile. However all seeds produced were poor and did not germinate. Contrary to these crossings are those in which plants of the "Portuguese diploid" were used as males. Here all 4 were completely sterile.

In the combination *C. rivularis* × *C. amara* 5 emasculated flowers produced 2 pods without any seeds. The same phenomenon appeared when the "Portuguese diploid" was given pollen from diploid *C. amara* after emasculation, 4 pods developed but they had no seeds.

Some co-pollinations have been carried out. The idea was that a few pollen grains from a plant of the same taxon as that used as female should be placed on the stigmas together with a large amount of pollen

Table 8. Crossings between diploid *C. amara* and tetraploid *C. pratensis*

Parent combinations	No. poll frs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. amara</i> 2n=16 × <i>C. pratensis</i> 2n=30					
Källstorp, Sk., Sw. × Linnebjerg, Sk., Sw.	19	1	21(0)	24.0	0
Norråla, Hlsld., Sw. × Vessige, Hld, Sw.	4	0	—	—	—
— × —	3	1	5(0)	5.0	0
— × —	9	1	14(0)	4.7	0
— × —	6	0	—	—	—
— × Sibräcka, Bhl, Sw.	5	0	—	—	—
— × —	4	0	—	—	—
— × Angers, France	4	1	9(0)	9.0	0
— × —	5	0	—	—	—
— × —	7	0	—	—	—
Kalhult, Sk., Sw. × —	9	0	—	—	—
Munkfors, Vrmlid., Sw. × Sibräcka, Bhl, Sw.	7	0	—	—	—
Total	82	6	52(0)	8.7	0
<i>C. pratensis</i> 2n=30 × <i>C. amara</i> 2n=16					
Ten combinations, total	52	0	—	—	—

The figures in parentheses in No. of seeds indicate well-developed seeds.

from plants of another taxon. In this way there should be a chance for the tubes of the legitimate pollen to help those of the illegitimate ones grow down to the embryo sacs in order to produce hybrid seeds together with a few normal ones. In one combination 4 stigmas of a diploid *C. rivularis* plant were simultaneously pollinated with a very small amount of pollen from another plant of the same taxon and a large amount of pollen from diploid *C. amara*. Four pods developed giving 16 seeds, 3 of which were apparently good. No seeds at all germinated.

Another co-pollination was made with a plant of the "Portuguese diploid" as the female parent. In this case the 2 male plants both were illegitimate, namely diploid *C. amara* (2n=16) and hexaploid *C. pratensis* (2n=44). Eight pollinated styles developed pods producing 55 seeds, all poor. However 2 of them germinated, giving rise to hybrids with *C. amara*. The chromosome numbers of the hybrids were 2n=14 and 16 respectively. The 14-chromosomic plant was apetalous and died very soon after its first flowering, while the plant with 2n=16 grew very vigorously. It has later been propagated vegetatively. This hybrid is completely sterile. On the male side the development seems to stop immediately before the first meiotic division.

In the combination diploid *C. amara* × tetraploid *C. pratensis* (Table 8) a total of 12 crossings were carried out, 4 of which produced seeds. All seeds were poor and did not germinate. In the opposite direction 10 cross-

Table 9. Crossings between diploid *C. amara* and some different *C. palustris*

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod	No. of plants
<i>C. amara</i> 2n=16 × <i>C. palustris</i> 2n=56					
Källstorp, Sk., Sw. × Fågelsång, Sk., Sw.	25	2	30(0)	15.0	0
Kalhult, Sk., Sw. × Exminster, Engl.	9	0	—	—	—
Norråla, Hlsld., Sw. × —	8	0	—	—	—
— × Kungsmarken, Sk. Sw.	9	0	—	—	—
— × —	6	0	—	—	—
Munkfors, Vrml., Sw. × —	15	0	—	—	—
— × —	19	0	—	—	—
Onsala, Hld., Sw. × —	5	0	—	—	—
Total	96	2	30(0)	15.0	0
<i>C. palustris</i> 2n=56 × <i>C. amara</i> 2n=16					
Five combinations, total	51	0	—	—	—
<i>C. amara</i> 2n=16 × <i>C. palustris</i> 2n=60					
Five combinations, total	49	0	—	—	—
<i>C. palustris</i> 2n=60 × <i>C. amara</i> 2n=16					
Four combinations, total	19	0	—	—	—
<i>C. palustris</i> 2n=64 × <i>C. amara</i> 2n=16					
Högebacke, Sk., Sw. × Fågelsång, Sk., Sw.	6	1	1	1.0	(1)
Gräsö, Upl., Sw. × Norråla, Hlsld., Sw. ...	2	0	—	—	—
Växiö, Sml., Sw. × —	3	0	—	—	—
Kungsängen, Upl. Sw. × Munkfors, Vrml., Sw.	4	0	—	—	—
Total	21	1	1	1.0	(1)
<i>C. amara</i> 2n=16 × <i>C. palustris</i> 2n=68					
Five combinations, total	31	0	—	—	—
<i>C. palustris</i> 2n=68 × <i>C. amara</i> 2n=16					
Three combinations, total	16	0	—	—	—
<i>C. amara</i> 2n=16 × <i>C. palustris</i> 2n=72					
Ten combinations, total	59	0	—	—	—
<i>C. palustris</i> 2n=72 × <i>C. amara</i> 2n=16					
Six combinations, total	34	0	—	—	—
<i>C. amara</i> 2n=16 × <i>C. palustris</i> 2n=76					
Five combinations, total	29	0	—	—	—
<i>C. palustris</i> 2n=76 × <i>C. amara</i> 2n=16					
Three combinations, total	20	0	—	—	—

sings involving 52 emasculated and pollinated flowers did not set seed at all.

A total of 11 combinations have been carried out in these crossing experiments between *C. amara* and representatives of *C. palustris* (Table 9). Seeds developed in only 2 crossings belonging to 2 different combinations.

When 25 emasculated flowers of diploid *C. amara* were pollinated with pollen from a 56-chromosomic *C. palustris*, 2 pods developed, producing 30 seeds, all poor. No seeds germinated.

Table 10. Crossings between *C. amara* $2n=16$ and combinations between *C. palustris* $2n=56$ and *C. pratensis* $2n=30$

Parent combinations	No. poll. flrs.	No. of pods	No. of seeds	Seeds per pod
$(56 \times 30) \times C. amara$ $2n=16$	12	3	0	—
$/30 \times (56 \times 30) / \times C. amara$ $2n=16$	9	9	0	—
— \times —	6	6	0	—
— \times —	11	8	0	—
$[(56 \times 30) \times 56 / \times 30] \times C. amara$ $2n=16$	19	17	0	—
— \times —	10	7	0	—
$[(56 \times 30) \times 30 / \times 30] \times$ —	3	0	—	—

The figures 30 and 56 indicate the chromosome numbers of *C. pratensis* and *C. palustris* respectively.

In a crossing between a 64-chromosomic *C. palustris* as the female and a diploid *C. amara* 1 pod developed out of 6 pollinated styles, producing 1 seed only. This seed was well developed and germinated. The plant, however, showed difficulties in growing and died when the second leaf above the cotyledons was developed.

Crossings between diploid *C. amara* and derivatives from *C. palustris* \times *C. pratensis*. — When studying compatibility problems in the *C. pratensis* complex, a series of crossings and backcrossings was carried out between *C. pratensis* $2n=30$ and *C. palustris* $2n=56$. The hexaploid F_1 hybrid was found to be fertile. One of these hybrids and some backcrossing derivatives were used in crossings with *C. amara* as the male. The crossings are compiled in Table 10. The most interesting fact is that in 7 out of 8 combinations the ovaries developed into pods, but all without any seeds. Such a development sometimes occurs, but very rarely, in other combinations carried out in the genus. Examinations of the pods showed that no ovules seem to have undergone any growth, but nevertheless some sort of stimulus might have operated. The origin of the stimulus is difficult to trace, but it may be from the pollen tubes or from a fertilization of the ovules without embryonic development.

Some of the derivatives from *C. pratensis* \times *C. palustris* had a very complicated origin. It is understood from Table 10 were the figures 30 and 56 indicate *C. pratensis* and *C. palustris*, respectively.

Crossings between diploid *C. amara* and hexaploid *C. raphanifolia*. — Pollinations performed after emasculation of *C. amara* plants include 9 crossings with 56 flowers, none of which produced pods. All the plants of

C. raphanifolia used as males have the same origin (Pic du Midi de Bigorre, French Pyrenees). In the opposite direction 3 combinations with *C. raphanifolia* as the females gave no pods from the 25 flowers pollinated.

In 1 combination 4 non-emasculated flowers of *C. amara* were used for crossing. They gave rise to 4 pods, with a total of 8 seeds, 2 well-developed, but no germinated ones. Here again it is found that if legitimate pollen cooperates with illegitimate seeds develop.

Conclusions from the Crossings

From the crossing experiments it is evident that at least the diploid *C. amara* ($2n=16$) is genetically isolated from other diploids of the section *Eucardamine* used in these studies, e.g., *C. hirsuta* ($2n=16$), *C. impatiens* ($2n=16$), *C. rivularis* ($2n=16$), and the "Portuguese diploid" ($2n=16$). However it is very difficult to estimate the importance of the development of poor seeds. Only in one combination were hybrids obtained, the result of a co-pollination with two illegitimate taxa. Both hybrids were intermediates between *C. amara* and the "Portuguese diploid". The isolation from *C. flexuosa* ($2n=32$) is good. The isolation from tetraploid *C. pratensis* ($2n=30$) is good. The number of seeds per pod is greater in the combination with tetraploid *C. pratensis* as the male than with diploid *C. rivularis*, but the frequency of developed pods is much lower in the former combination, 6 out of 82, than in the latter, 17 out of 63. In a crossing with *C. palustris* only one well-developed seed was found. This seed germinated, but the plant died. Otherwise the isolation from *C. palustris* was found to be good.

The crossing experiments show that the best way to obtain hybrids seems to be co-pollinations.

The fact that in a crossing 2 seeds out of 55 produced plants, in spite of no seeds being well developed, is of importance. Thus there may be possibilities for hybrids to arise, but in nature such plants will have no chance of competing with the surrounding vegetation as they are very delicate and vague.

Summary

Determinations of chromosome numbers, cultivation experiments, induced polyploidy and artificial crossings have been carried out with *C. amara*. — *C. amara* is diploid, $2n=16$, all over its distribution area, at high altitudes in the Alps, however, tetraploids, $2n=32$, occur. — Cultivation experiments show that some characters are easily modified. — By colchicine treatment it was possible to study the same indi-

vidual at diploid, tetraploid and octoploid level. — Crossings experiments were carried out between *C. amara* and a number of other species. One hybrid only developed. However, it was found that in crossings between different species copollination was to be preferred.

Sammanfattning

Kromosomtalsbestämningar, odlingsexperiment, inducerad polyploidi och korsningsförsök har utförts med *Cardamine amara*. — *C. amara* har $2n=16$ inom större delen av sitt utbredningsområde, men i Alperna finns även en tetraploid population med $2n=32$. Det diploida talet redovisas från 25 lokaler, det tetraploida från 4. — Odlingsexperiment visar, att hårlighet, bladstorlek och form samt planthöjd starkt modifieras. Solexponerade plantor är håriga, småbladiga, lågvuxna men upprätta. Skuggigt växande plantor är däremot glatta och storbladiga, med lång, ofta nedliggande stjälk. — Skillnader i utvecklingsrytm beroende på vegetationsperiodens olika längd inom ursprungsområdena kunde iakttagas. Det framgick t.ex. klart av den långsamma utvecklingen att beståndet av *C. amara* vid Tornehamn i Lappland torde härstamma söderifrån. — Colchicinbehandling av utlöpare gav tetraploida och en octoploid planta av en och samma diploida ursprungsindivid. Jämförelser kunde göras mellan diploida, tetraploida och octoploida plantor med samma genbalans (Table 3). — Korsningsförsök utfördes mellan *C. amara* och en rad andra arter (Table 4—10). Endast en hybrid utvecklades, mellan en »Portuguese diploid» som moder och en *C. amara* som fader. Vid artkorsningsförsök visade sig sampollinering överlägsen ur frösättningsynpunkt.

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Beitrag zur Kenntnis der Variabilität der Fichte

II. Die Wirkung von γ -Strahlung auf *Picea abies*

Von HANS W. TRALAU

Vergleichende Untersuchungen physiologischer als auch genetischer Art über das Verhalten pflanzlicher und tierischer Objekte gegenüber experimentell produzierbarer Strahlungen verschiedener Qualität und Quantität sind in einer Reihe von Publikationen bekannt geworden.

Die vorliegende Arbeit soll sich einerseits mit der Frage befassen, ob innerhalb einer Art Rassen zu finden sind, die sich gegenüber dem Verhalten der Norm der Art bei γ -Strahlung durch besondere Strahlungsresistenz auszeichnen und andererseits, ob es möglich ist Kriterien für die Diagnostik von strahlenresistenten Rassen, Populationen oder Individuen zu finden. Diese letzte Frage scheint gerade jetzt bei den intensiven Versuchen mit radioaktivem Material zu militärischen, wissenschaftlichen und wirtschaftlichen Zwecken aktuell und die damit verbundenen bekannten Befürchtungen immer stärker zu werden. Dergleichen soll diskutiert werden in wie weit der physiologische und genetische Wert von Rassen oder Populationen einer Art durch Reaktionen auf Strahlungen beurteilt werden darf.

Material und Methodik. — Das zu den Versuchen ausgewählte Fichtensamenmaterial war aus der Ernte von 1955 und bestand aus vier verschiedenen Provenienzen: 1. eine Provenienz aus dem Harz (Deutschland) bei Clausthal-Zellerfeld, Höhe=600 m u.M., und 52° n.B. mit einem Tausendkorngewicht von 8,9 gr. 2. eine Probe aus Schleswig-Holstein (Deutschland) bei Lübeck, Höhe=20 m ü.M. und 54° n.B. mit einem Tausendkorngewicht von 8,2 gr. 3. von Maltesholms gods in Kristianstads län (Schweden), Höhe=25 m ü.M. bei 55° n.B. sowie 4. aus Jämtland (Schweden) Höhe=400 m ü.M. und 64° n.B. Alle vier Provenienzen stammen aus Gebieten zwischen dem 10. und 14. Längengrad mit mehr oder minder stark atlantischem Klima.

Das Tausendkorngewicht der beiden letzten Provenienzen wurde an das der ersten beiden angeglichen durch Selektionierung der grössten Samen im Schüttelrost und betrug für Provenienz Nr. 3 8,4 gr und für Nr. 4 7,4 gr. Diese Massnahme schien dadurch nötig, dass eine Beurteilung eines möglichst homogenen und physiologisch einheitlichen, normal reagierenden Materials vorgenommen werden sollte. Hierdurch wird natürlich das Bild zu Ungunsten der beiden ersten Provenienzen verschoben, doch dürfte sich diese Massnahme in der Tatsache rechtfertigen, dass das physiologisch minderwertige kleinsamige Material bei ungünstigen Verhältnissen sowieso und in der Natur wohl generell ausfällt und somit auch keineswegs in der Representation einer späteren Generation Anteil haben wird. Ausserdem bedingt die Beurteilung einer rassischen Qualität, was das Ziel dieser Arbeit sein soll, eine möglichst starke Einschränkung der physiologischen Varianz. Zur weiteren Homogenisierung des Materials wurde dieses einer Röntgendiagnose unterworfen und nur Samen mit voll entwickeltem Endosperm und der Embryoklasse vier zugelassen. Das Problem, ob das, was das Röntgenbild zeigt, tatsächlich lebendes Material darstellt oder nicht, muss bisher wegen Mangel an einer geeigneten Methode ausser Acht gelassen werden. Der Feuchtigkeitsgehalt der Samen wird bei allen Provenienzen ein Höchstmass an Gleichmässigkeit gehabt haben, da diese vor der γ -Bestrahlung 10 Tage lang im gleichen Raum und 8 Tage lang im Exsiccator gelegen haben. Eine Differenz des Wassergehalts kann also nicht so gross gewesen sein, dass sie die Versuchsergebnisse wesentlich beeinflussen konnte.

Die Bestrahlung wurde mit dem Co^{60} -Aggregat in Bogesund¹ ohne Filterung der Strahlen und mit unverändertem Abstand von 1,08 m vorgenommen. Als Strahlungsdosen wurden verwendet:

0, 50 r, 100 r, 150 r, 300 r, 600 r, 1200 r.

Die bestrahlten Samen sowie die Kontrolle wurden in drei Wiederholungen zu je 50 Samen in Kästen im Gewächshaus ausgesät und aufgezogen. Jede Pflanze wurde am Tage der Keimung registriert und später gemessen sowie Frisch- und Trockengewicht jeder einzelnen Wiederholung der verschiedenen Bestrahlungsgruppen bestimmt, um das Ausmass einer eventuellen Stimulation, der zu erwartenden Depression und somit sekundär die Resistenz der verschiedenen Provenienzen beurteilen zu können.

¹ Statens Skogsforskningsinstitut, Stockholm. Versuchfeld Bogesund.

Resultat. — Die naheliegendste Möglichkeit sich ein Bild über die Wirkung einer chemischen oder physikalischen Einflussnahme auf die Entwicklung von Pflanzen zu verschaffen ist die Beobachtung des Keimverlaufes. Also jener Erscheinung in der sich die Vitalitätspotenz des Objekts am ersten zeigt.

Wie zu erwarten war, zeigten sich im Keimverlauf der verschiedenen Provenienzen und unter diesen wiederum in den einzelnen Behandlungsgruppen mehr oder weniger starke Differenzen. Die Abbildungen 1—4 zeigen, dass die Keimung der unbestrahlten Kontrollen nur bei der nördlichsten Provenienz beträchtlich langgestreckter — träger ist als die der drei anderen Herkünfte. Diese zeigen einen Keimverlauf der früh einsetzt, intensiv voran geht und entsprechend früh abgeschlossen ist. Aus den Tabellen geht weiterhin hervor, dass eine leichte Stimulation der Keimgeschwindigkeit nach einer Bestrahlung mit 150 und 300 r in allen Provenienzen zu verzeichnen ist. Wobei sich zeigt, dass der Keimverlauf dieser „stimulierten“ Pflanzen analog dem Verhalten der unbestrahlten Kontrolle ist. Der Unterschied besteht nur in einer geringen Verfrühung des Gesamtvorganges. Ob eine Keimgeschwindigkeit-Stimulation dieses recht geringen Ausmasses von Bedeutung sein kann oder aber ob nicht gar schon bei der für eine solche Stimulation notwendige Strahlendosis schädigende Wirkung — wenn auch nur reversibler Art — eintritt soll später erörtert werden. Die Dosen von 50 und 100 r haben auf die Keimung keinen bemerkenswerten Einfluss, wie aus den Tabellen hervorgeht. Hingegen verdienen die Wirkungen der Strahlendosen von 600 und 1200 r ein besonderes Interesse. Hier zeigt sich nämlich, dass man für die einzelnen Provenienzen verschiedene Resistenz gegen Strahlen annehmen darf. Die Abbildungen 1, 2 und 3 lassen erkennen, dass die Keimung der drei südlichen Provenienzen bei der Dosis von 600 r in ihrer Keimgeschwindigkeit nur unwesentlich verzögert sind d.h. unter unserem augenblicklichen Gesichtspunkt, dass diese der unbestrahlten Kontrolle gegenüber nur gering benachteiligt und geschädigt zu sein scheint. Dagegen zeigt die 600-Röntgengruppe der nordschwedischen Provenienz eine bemerkenswerte Depression in der Keimgeschwindigkeit. Deutlicher wird diese Reaktionsdifferenz dann bei der Dosis von 1200 r. Hier zeigen die drei ersten Herkünfte eine Schädigung, die ein wenig stärker ist als die der Jämtlandsamen nach Bestrahlung mit 600 r. Die nördlichste Provenienz aber beginnt nach der 1200 r-Bestrahlung mit der stark verzögerten Keimung erst am 20. Tag nach der Aussaat und hat am 25. Tag 50 % erreicht. Somit dürfte eine rassistisch bedingte Reaktionsverschiedenheit bei Fichte auf

Keimprozente

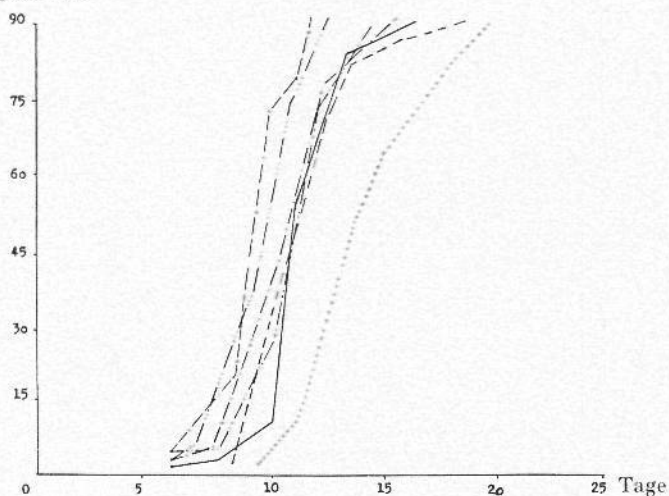


Abb. 1. Keimgeschwindigkeit der Samen der Harzprovenienz ohne und nach γ -Bestrahlung.

— Kontrolle, - - - 50 r, ····· 100 r, - · - · 150 r, - · - · 300 r,
- - - 600 r, ····· 1200 r.

Keimprozente

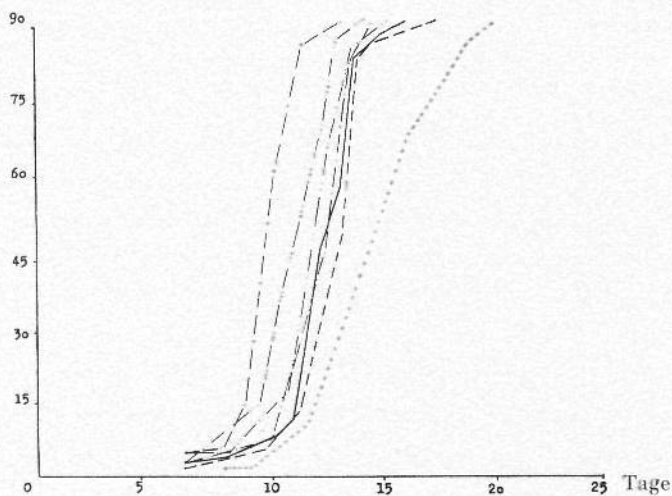


Abb. 2. Keimgeschwindigkeit der Samen der Schleswig-Holsteinprovenienz ohne und nach γ -Bestrahlung.

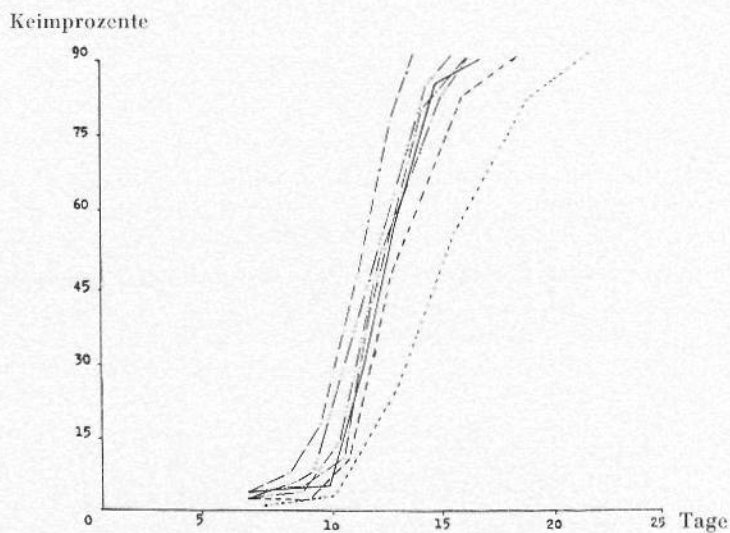


Abb. 3. Keimgeschwindigkeit der Samen der Kristianstads län Provenienz ohne und nach γ -Bestrahlung.

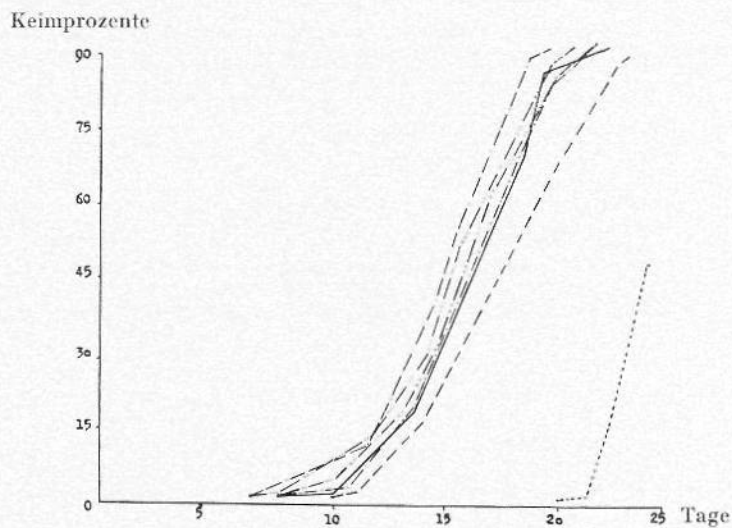


Abb. 4. Keimgeschwindigkeit der Samen der Jämtlandprovenienz ohne und nach γ -Bestrahlung.

Strahlung bezüglich der Keimgeschwindigkeit als gesichert angesehen werden.

Eine weitere Fragestellung galt der Substanzproduktion der einzelnen Provenienzen sowie deren verschiedenen Bestrahlungsgruppen. Wegen der einseitig berichteten Selektion des Saatgutes kann hier auf die erblich bedingten Differenzen für den Trockensubstanzgehalt (Bornebusch 1935) sowie die Wachstumsgeschwindigkeit und Periodizität (Engler 1913 und Burger 1926) der Fichtenprovenienzen im Allgemeinen und der hier untersuchten Herkünfte im Besonderen nicht eingegangen werden.

Da die Substanzproduktion des Frisch- und Trockengewichtes in einer bestimmten Relation zur Wachstumsintensität und somit zum Längenwachstum steht, soll zuerst der Zuwachs der Länge der Pflanzen behandelt werden. Die Keimlinge wurden zu diesen Untersuchungen zehn Tage nachdem 90 % der ausgesäten Samen gekeimt waren vorsichtig dem aus Quarzsand bestehendem Keimbett entnommen und zuerst, um jeder Fehlerquelle, die durch das Welken der Pflanzen entsteht aus dem Wege zu gehen, gewogen und anschliessend gemessen. Die Ergebnisse der Messungen sind graphisch im oberen Teil der Abbildungen 5 bis 8 dargestellt. Aus ihnen geht hervor, dass bei den beiden deutschen Herkünften ein geringer Längenzuwachs nach einer Bestrahlung mit 150 r zu verzeichnen war. Mit steigender Dosis fällt dann aber der Längenzuwachs kontinuierlich. Ebenso lassen die schwedischen Provenienzen ein Absinken im Längenwachstum nach 300 r in Erscheinung treten. Hier zeigt sich jedoch, dass die nördlichste Provenienz aus Jämtland eine statistisch nicht zu sichernde „Stimulation“ des Längenwachstums bei 100 r zeigt.

In folgender Tabelle sollen die Zahlenverhältnisse der Messwerte in Mittelwert und mittlerem Fehler dargestellt werden:

Dosis in r:	0	150	300	1200
	m ± E	m ± E	m ± E	m ± E
P 1	8,3 ± 0,71	8,6 ± 0,92	8,1 ± 0,87	7,2 ± 1,87
P 2	8,2 ± 0,83	8,3 ± 0,85	7,9 ± 0,70	7,2 ± 1,10
P 3	7,6 ± 0,70	7,7 ± 0,62	7,5 ± 0,85	6,5 ± 1,21
P 4	5,8 ± 0,82	5,9 ± 0,72	5,7 ± 0,74	4,4 ± 0,55

P 1 = Harz, P 2 = Schleswig-Holstein, P 3 = Kristianstads län, P 4 = Jämtland.

Deutlicher jedoch werden diese Verhältnisse, wenn man den nach 1200 r -Strahlung gesunkenen Längenzuwachs in Prozenten mit dem

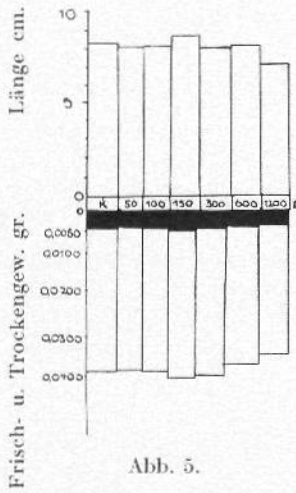


Abb. 5.

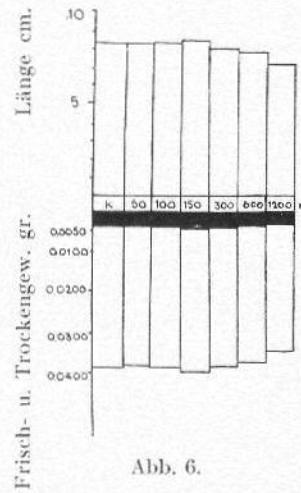


Abb. 6.

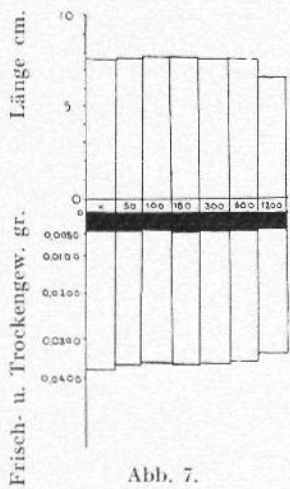


Abb. 7.

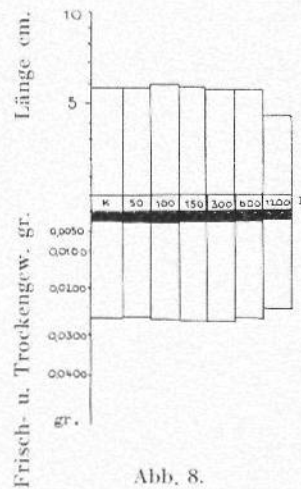


Abb. 8.

Abb. 5. Länge sowie Frisch- und Trockengewicht der Keimlinge der Harz-Provenience in den einzelnen Bestrahlungsgruppen.

Abb. 6. Länge sowie Frisch- und Trockengewicht der Keimlinge der Schleswig-Holstein-Provenience in den einzelnen Bestrahlungsgruppen.

Abb. 7. Länge sowie Frisch- und Trockengewicht der Keimlinge der Kristianstads län-Provenience in den einzelnen Bestrahlungsgruppen.

Abb. 8. Länge sowie Frisch- und Trockengewicht der Keimlinge der Jämtland-Provenience in den einzelnen Bestrahlungsgruppen.

der entsprechenden Kontrollen vergleicht. In Provenienz 1 ist der Zuwachs um 13,3 % gesunken, in 2 um 12,2 %, in 3 um 14,5 % und in Provenienz 4 um 25,9 %.

Ein weiteres sehr charakteristisches Bild ergab sich bei der Aufnahme der verschiedenen Längengruppen der Keimlinge. Hierzu wurden die Längen von je 30 Keimlingen einer jeden Wiederholung für die Schemata der Abbildungen 9 bis 12 verwendet. Hier zeigt sich, dass die grösste Anzahl der Keimlinge der deutschen und südschwedischen Provenienzen in der unbestrahlten Kontrolle eine Länge von 7—9 bzw. 10 cm hat und sich somit durch eine recht beachtenswerte Homogenität bezüglich dieses Merkmals auszeichnet. Die Keimlinge der Jämtlandherkunft lassen diese Homogenität vermissen und zeigen dem entsprechend nach einer Bestrahlung mit 1200 r eine bedeutende Verlagerung der Pflanzenlänge in niedrigere Grössenordnungen. Die Länge des Gros der Keimlinge der drei südlichen Provenienzen liegt nach der 1200 r -Bestrahlung zwischen 5 und 9 cm während die entsprechenden Werte der Jämtlandfichten zwischen 2 und 5 cm liegen. Es wird hiernach postuliert werden dürfen, dass je homogener das Verhalten einer Population unter Normalbedingungen ist, was eine absolut intakte physiologische Konstitution voraussetzt, desto widerstandsfähiger wird sie gegenüber äusseren Einflüssen sein. Das Schädigungsspektrum wird von vorneherein durch die geringe natürliche Varianz des Objekts eingeschränkt.

Die Verhältnisse, die sich bei der Bestimmung des Frisch- und Trockengewichtes ergaben laufen parallel mit den Erscheinungen, die bei der Untersuchung des Längenwachstums zeigten. Auch hier macht sich ein leichtes Ansteigen der Frisch- und Trockensubstanz bei allen Provenienzen nach einer Bestrahlung mit 150 r bemerkbar. Statistisch lässt sich jedoch eine Differenz zwischen Kontrolle und den 150-Röntgengruppen nicht sichern. Die kritische Grenze der Strahlungstoleranz hinter der bei ständig steigender Strahlungsdosis die Substanzproduktion kontinuierlich sinkt scheint bei Fichte unter Inachtnahme der durch das Objekt gegebenen Varianz bei 150 r zu liegen. Die natürliche — als physiologisch-genetisches Charakteristicum — sowie die durch physikalische Einflussnahme bedingte Varianz manifestieren sich als Konstitution der physiologischen Varianten.

Diskussion. — Die erste Frage, die sich aufdrängt, ist ob diese in den Untersuchung gefundene »Stimulation« von ökonomischem Wert sein kann. Die Tatsache der Splitterung in Teilstimulationen — eine Stimulation der Keimgeschwindigkeit nach Bestrahlung mit 300 und des

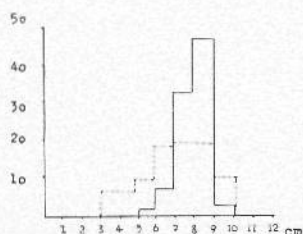


Abb. 9. Harzprovenienz.

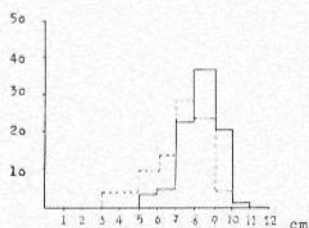


Abb. 10. Schleswig-Holstein-Provenienz

Verhältnis der Keimlingslängen in verschiedenen Längengruppen nach Bestrahlung mit 1200 r und in der Kontrolle. (Kontrolle —, 1200 r - - - -)

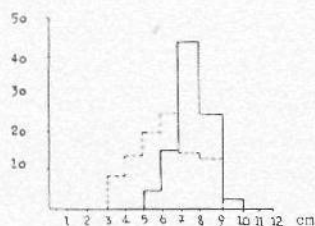


Abb. 11. Kristianstads län-Provenienz.

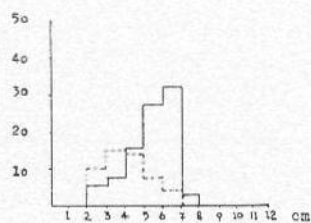


Abb. 12. Jämtlandprovenienz.

Zuwachses nach einer Strahlendosis von 150 bzw. 100 r — stimmt nicht gerade aufmunternd. Von einer echten Stimulation sollte ein Höchstmass der Einschränkung der Varianz, möglichst eine Hebung des Niveaus der Gesamtheit der Objekte in der gewünschten Richtung sowie die Gleichzeitigkeit der Förderung verschiedener Entwicklungskomponenten gefordert werden können. Die erste und letzte Forderung jedoch sind keineswegs erfüllt. Hinzu kommt der Verdacht, dass bei einer Dosis von 300 r, bei der die Keimgeschwindigkeit gefördert wird, eine Schädigung physiologischer Prozesse — vielleicht auch gewisser morphologischer Strukturen — einzutreten scheinen, was sich darin äussert, dass die potentielle Substanzproduktion im Sinken begriffen ist. Es kann aber eine Stimulation der Keimgeschwindigkeit nicht erstrebenswert sein, wenn damit die Gefahr einer Schädigung des Organismus verbunden ist.

Rassen-physiologische Varietäten-Konstitutionen innerhalb einer botanischen Art, die sich im Laufe der Phylogenese unter Einfluss des Klimas, Standortes etc. durch natürliche Selektion der Erbmasse mani-

festiert haben, sind Gegenstand vieler Untersuchungen gewesen (Langlet 1936 u.a.m.). In der vorliegenden Arbeit soll auf die deutliche Reaktionsdifferenz solcher physiologischer Varietäten gegenüber radioaktiven Strahlungen hingewiesen werden. Es würde aller Glaubwürdigkeit entbehren, wollte man diese Differenz lediglich morphologisch bedingt, mit unterschiedlichen Grössenordnungen der Chromosomen begründen.

Nybohm (1956) hat sehr charakteristische Vertreter der Phanerogamen auf die Relation von Chromosomengrösse und Radioresistenz geprüft und hat gefunden: „One can hardly avoid the conclusion that the size of the chromosomes does play a great role for the specific sensitivity, and that the effects of the radiation on the chromosomes is perhaps decisive for the damage leading to induced inhibition, abnormal development and death“. Die Beweisführung ist bestechend, doch scheint es so, dass innerhalb physiologischer Varianten einer Art ein anderes Verhalten herrscht. Die Relation von Chromosomengrösse/Strahlungsresistenz wird noch in einer anderen Arbeit an diesem Objekt untersucht werden, doch scheint es nicht so als liesse sich die Reaktionsdifferenz der Fichtenrassen lediglich auf dieser Basis begründen. Wenn auch Forssberg (1945) bezüglich des Katalasegehaltes nach Röntgenbestrahlung zu dem Ergebniss kommt: „It is for instance noticeable that when dosis are given which produce fairly strong histological disturbances in the cells or even later on cause death, a great many fundamental biochemical reactions appear to be practically unaffected by the irradiation“, so liess sich andererseits jedoch auch zeigen, dass Röntgenstrahlen und somit auch die ihnen physikalisch ähnlichen γ -Strahlen den Zustand des hormonalen Systems — möglicherweise verschiedene gegeneinander wirkende Systeme — der Pflanzen nicht unerheblich zu Gunsten des einen oder anderen zu beeinflussen vermögen (Skoog, 1935). Zu einem Ergebnis, dass in gleiche Richtung geht, kommen Virgin und Ehrenberg (1953) nach der Untersuchung der Plasmaviscosität bei *Helodea* nach radioaktiver Strahlung: „As regards the biological effects of radioactive radiations, the direct breaking of the chromosomes is an important factor, but especially in the case of radiations with low ionization densities, plasmatic effects have to be regarded, too“. Also auch hier ist es ein physiologisches Moment, das in bestimmten Grenzen den entscheidenden Ausschlag gibt.

Sicher ist das hier untersuchte Objekt, die physiologischen Varietäten von Fichte, nicht gerade das idealste. Die Untersuchungen über die Konstanz der gefundenen Faktoren sollten mindestens über zwei bis drei Generationen hindurch geführt werden können. Doch wurde

kürzlich von Lamprecht¹ über eine von ihm aufgefundene strahlenresistente Zuchtlinie von *Pisum* berichtet, deren Resistenz auf dem Vorhandensein eines einzigen Gens beruht, das also zum Mindesten eine physiologische Teilkonstitution steuert, die für die Resistenz gegenüber der radioaktiven Strahlung verantwortlich zu machen ist. Andere Beispiele zeigen überdies auch, dass sensitive Substanzen der Histon- und Protamingruppen, so wie das die Sensibilität herabsetzende NH_4OH chromosomengrößenunabhängig wirken.

Abschliessend soll gesagt werden, dass der Schluss, den Gunckel und Sparrow (1954) nach ihren Untersuchungen ziehen, dass nämlich die meisten oder vielleicht gar alle „Radiomorphosen“ „result from the induced physiological or biochemical disturbances“ die Möglichkeiten der Physiologie sicher überschätzt. Andererseits spielen die genetisch bedingten physiologischen Varietäten innerhalb einer Art bei der Beurteilung der Strahlungsresistenz eine mindestens ebenso bedeutende Rolle wie die morphologische Konstitution des Individuums. Diese allein ist somit ein ungünstiges diagnostisches Objekt.

Sammanfattning

Fysiologiska varieteter av *Picea abies* från fyra provenienser — Harz (Tyskland), Schleswig-Holstein (Tyskland), Kristianstads län och Jämtland — ha undersökts i fråga om sin resistens mot γ -strålar. En stimulans av grobstigheten efter bestrålning med 300 r och ett ringa befrämjande av substansproduktionen efter 100 resp. 150 r kan fastställas. En produktionsökning av ekonomiskt värde anses icke given, då enhetlighet saknas hos de enstaka befrämjningskomponenterna. Dessutom synes cellens fysiologiska tillstånd hotad vid den strålningsdosis, som befrämjar grobstigheten. Den relativa strålningsresistens som visat sig hos de tre sydliga provenienserna i jämförelse med den nordliga Jämtlandsproveniensen anses vara en genetiskt betingad fysiologisk variation.

Zusammenfassung

Physiologische Varietäten von *Picea abies* aus vier Provenienzen — Harz, Schleswig-Holstein, Kristianstads län, und Jämtland — werden auf ihre Resistenz gegenüber γ -Strahlen geprüft. Eine Stimulation der Keimgeschwindigkeit nach Bestrahlung mit 300 r und eine geringe Förderung der Substanzproduktion nach 100 bzw. 150 r konnte festgestellt werden. Eine echte Stimulation von ökonomischem Wert wird als nicht gegeben angesehen, da eine Einheitlichkeit der einzelnen Förderungskomponenten fehlt und darüber hinaus der Anschein besteht, dass bei Strahlungs Dosen, die die Keimgeschwindigkeit fördern, der physiologische Zustand der Zelle bedroht zu

¹ Bekannt gemacht auf dem radiobiologischen und genetischen Kongress im genetischen Institut des Forstforschungsinstituts im Herbst 1956 in Stockholm.

sein scheint. Die relative Strahlungsresistenz, die sich bei den drei südlichen Provenienzen gegenüber der nordischen Jämtlandherkunft gezeigt hat, wird als genetisch bedingte physiologische Varianz gedeutet.

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The Apomictic Development in *Malus Sieboldii*

By H. HJELMQVIST

(Meddelanden från Lunds Botaniska Museum, Nr 119)

In a genetical-cytological investigation of the tetraploid *Malus Sieboldii* (Reg.) Rehd. Oldén (1953) presented some facts which indicate that this form is more or less apomictic. In order to confirm this embryologically and to obtain closer information about the apomictic course of development the present writer made an investigation of the same two trees in the Botanical Garden of Lund that were investigated by Oldén. As noted by Oldén, these trees have been grown from seeds obtained from Japan in 1899; probably the seeds have come from Sapporo (or otherwise from Tokyo, from where seeds of *M. Sieboldii* were obtained in the same year). Flower buds and flowers were collected in May 1956 and May—June 1957, at intervals of a few days, and fixed in the solution of Navashin-Karpechenko, after a previous short treatment in Carnoy's fixative. Staining was made with haematoxylin according to Heidenhain. Supplementary material was obtained from the year 1952 through the courtesy of E. J. Oldén.

The general organization of the ovule is the typical one for *Pomoideae* (cf. Jacobsson-Stiasny, 1914): there are two integuments and a vigorously developed nucellus, which is enlarged by division of the epidermis, as well as of the tapetal cells, into several layers; an obturator also occurs. In the young, undeveloped ovule there is beneath the epidermis a group of cells which cut off tapetal cells outwards; these cells are in *Rosaceae* generally regarded as an archesporium, which thus is pluricellular. The tapetal cells as well as their sister cells, the secondary archesporial cells, divide further; as a rule, however, in *Malus Sieboldii* only one of the last-mentioned cells, a central one, develops into a megaspore mother cell (MMC) and undergoes meiosis. The same is also known to occur in other genera in *Rosaceae*, as in *Sorbus* (Liljefors, 1953). Thus only one cell, as a rule, functions as archesporial cell; the rest of them should perhaps be regarded as potential archesporial cells.

The formation and development of the embryo sac was subjected to separate investigations for the two specimens of *Malus Sieboldii* in Lund, as the genetical investigation had shown a certain difference between them. To begin with the western tree (w), an early stage of the development of the ovule is shown in Fig. 1 *a*. The inner integument has begun to develop around the nucellus and the outer one is just appearing outside of it. The nucellus is still short, almost hemispherical, with a one-layered epidermis. Beneath the epidermis, in the central part of the nucellus, a number of cells (in a longitudinal section about 4—6 such cells may appear beside each other) have by periclinal or oblique walls cut off tapetal cells outwards, which later on begin to divide further. Among the inner daughter cells especially one is conspicuous, in the centre, through its size and especially through its large nucleus; this cell develops into a megaspore mother cell (MMC).

The fully developed MMC is visible in Fig. 1 *b—e*. The nucellus now has increased and is oblong and a little broader upwards, the epidermis is partly two-layered and the tapetal cells form two or more layers. In Fig. 1 *b* a MMC is visible with the nucleus in prophase to the first meiotic division, Fig. 1 *c—d* shows the metaphase of the same division, and Fig. 1 *e* an anaphase. In all cases there may be observed at the base or the side of the MMC vigorous cells, rich in cytoplasm, with big nuclei and nucleoli, the first beginning to secondary, aposporic embryo sacs, which compete with the normal one arising from the MMC. Several such cells are generally present, though sometimes only one is conspicuous in a special section.

Besides the primary MMC, however, there may occur in some cases another, that arises later and at greater depth in the nucellus. Fig. 2 *e* shows such a secondary MMC; in this case the first formed MMC has already passed through meiosis and immediately beneath it a secondary MMC has been formed, the nucleus of which is in prophase to the first meiotic division. Similar secondary MMC:s occur according to several authors (Wanscher, 1939; Hough, 1947; Schneider, 1953) in *Malus communis* beneath the primary one; they apparently appear especially in varieties with triploid or aneuploid chromosome number or else with reduced fertility.

In the further development either a MMC by way of meiosis forms a normal embryo sac, or aposporic unreduced embryo sacs arise. The undisturbed development of the MMC is shown in Fig. 1 *f*, 1 *g* and 1 *h*. In Fig. 1 *f* a dyad is visible that has just arisen; in the upper dyad cell peripheral remnants of the phragmoplast are still conspicuous. In

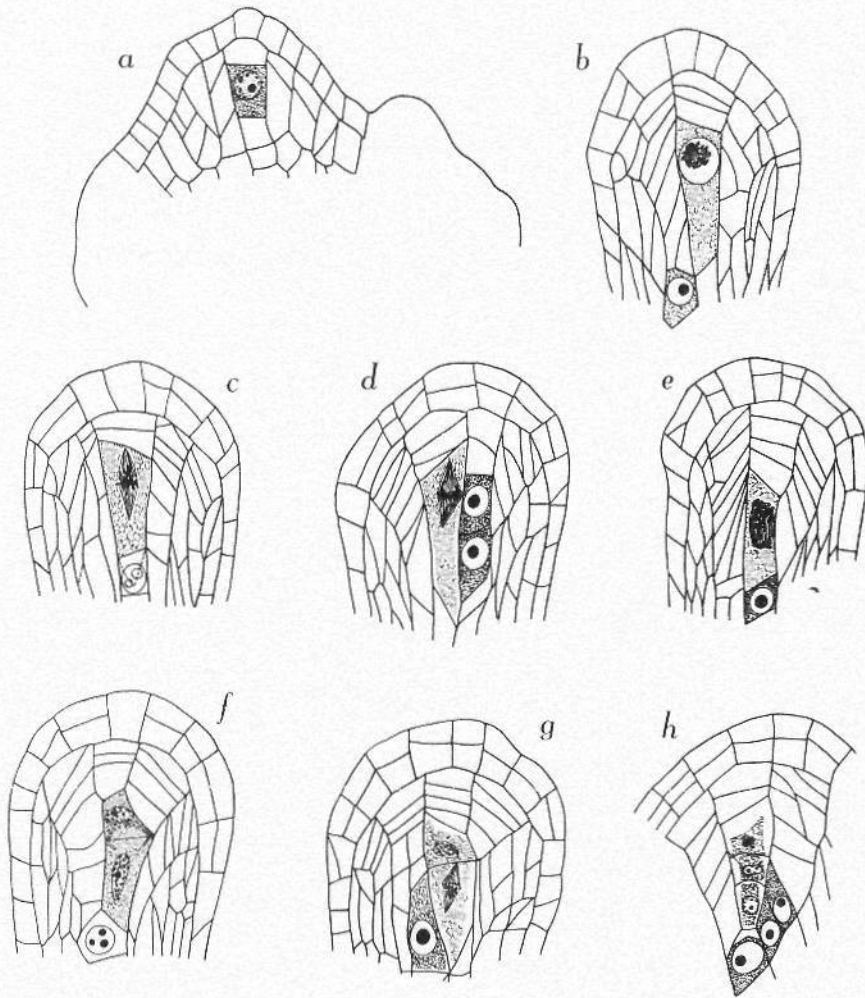


Fig. 1. *Malus Sieboldii* (w), development of megaspores. *a* Young ovule with a secondary archesporial cell in the centre developing into MMC. *b* Later stage, the central MMC in prophase, a secondary embryo sac initial develops below. *c—e* First meiotic division of the MMC, aposporic embryo sacs begin to develop below or at the side of the MMC. *f* A dyad just formed, a developing secondary embryo sac visible below. *g* The second meiotic division, the lower dyad cell with metaphase, the upper one with prophase, a secondary embryo sac developing at the side of the lower cell. *h* Triad with two megaspores and the upper dyad cell still in division, below three aposporic embryo sacs developing, with much bigger nuclei than the megaspores. — Enlargement about $\times 400$.

Fig. 1 *g* is shown how the second meiotic division has just been initiated; the nucleus of the lower dyad cell is in metaphase, in the upper it is in prophase. Fig. 1 *h* finally shows how the megaspore formation has been finished; the tetrad is, however, not complete, as the division of the upper dyad cell has not been completed before the degeneration takes place. In such a way only three cells are formed (though the nucleus of the upper may have divided), a triad arises instead of a tetrad. This condition is earlier known (Jacobsson-Stiasny, l.c., p. 778) for several genera in *Pomoideae*, whereas in the genus *Pyrus* and in *Malus communis* (Tab. III) four megaspores are said to arise; in this respect *Malus Sieboldii* thus differs from *M. communis*. — Also in these stages of development vigorous cells, rich in cytoplasm, and with big nuclei, may be observed near the dyad or triad; these cells are marked off in the figures; often only one is visible in a special section, but then there are more in other sections.

The development from MMC to megaspore just described is, however, often disturbed at varying stages. In Fig. 2 *a—b* illustrations of this are shown. Here the original MMC has been pushed aside; it is more or less compressed, as well as its nucleus. This ousting has taken place at an early stage; the nucleus has apparently been in different stages of prophase. Replacing the MMC some cells in the vicinity develop into aposporic embryo sacs; in Fig. 2 *b* only two such cells are visible, but there is at least one more, in another plane. They are distinguished by a dense cytoplasm, big nuclei and especially nucleoli. An inconsiderably later stage in the development of the aposporic embryo sac is shown in Fig. 2 *c*. It has now increased and vacuolized and may be regarded as a uninucleate embryo sac. Two or three additional aposporic embryo sacs were present, which were not equally far developed. The nucleus of the primary MMC was not visible, but the cell was recognized by its length and the light, reticulate cytoplasm; also in this case the MMC was thus apparently ousted before it had divided.

In other cases, however, the MMC had divided into two or three cells before the supplanting and disintegration. In one case a dyad was thus observed that obviously was just in degeneration, and in several cases megaspores were seen that were very small and weakly developed and undoubtedly were ousted by the secondary, aposporic embryo sacs. An instance of this is seen in Fig. 2 *d*: as usual the upper dyad cell has not divided — the nucleus here is in prophase — and the two lower cells are small and have somewhat irregular nuclei with small nucleoli; probably they both are going to degenerate. Immediately beneath them

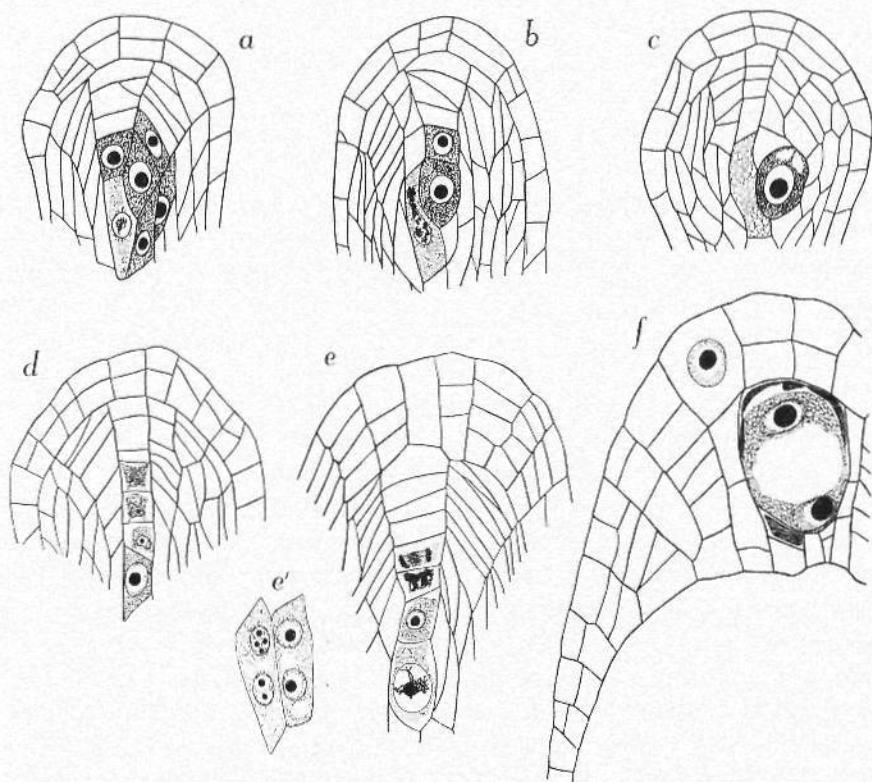


Fig. 2. *Malus Sieboldii* (w), ousting of the MMC and development of aposporic embryo sacs. *a* A group of aposporic embryo sacs develops around a degenerating MMC with the nucleus in prophase. *b* Similar stage, the MMC a little more advanced before the supplanting. *c* An aposporic embryo sac, with vacuolization, is ousting the MMC, the nucleus of which is not visible. *d* A degenerating triad with a developing aposporic embryo sac below. *e* Beneath the primary triad a secondary MMC has developed; both are however ousted by aposporic embryo sacs, now partly in binucleate stage (*e'*). *f* Part of epidermis cap with a binucleate aposporic embryo sac. — Enlargement about $\times 400$.

there is a vigorous cell that in size, cytoplasm-content and above all in the size of nucleus and nucleolus surpasses by far the megaspores; certainly this cell is developing into an aposporic embryo sac. There are possibly one or a few other potential aposporic embryo sacs, though they are not as vigorous as this. In another case with a similar triad (where, however, the nucleus of the upper cell was in metaphase) there were several about equally vigorous potential secondary embryo sacs. A special case of a degenerating triad is visible in Fig. 2 *e*. Here a

secondary MMC has developed beneath the primary triad, as sometimes occurs (cf. above), but at the side of the central cell row, where the primary and secondary MMC have developed, two vigorous aposporic embryo sacs have arisen (Fig. 2 *e*¹) both of which have reached the binucleate stage and undoubtedly will win in the competition, ousting the megaspore already formed as well as the secondary MMC.

In later developmental stages, when the embryo sac has increased vigorously and pushed aside the surrounding cells, it is often not possible to decide whether it is aposporic or not. Those degenerating triad cells that must be present above the normal reduced embryo sacs can now, as a rule, no longer be distinguished, and consequently there is generally no criterion that separates these from the unreduced aposporic embryo sacs. In some cases the two types may, however, be distinguished from the position of the embryo sac or other conditions.

In Fig. 3 *b*, thus, an embryo sac is shown that to all appearances is normally developed, reduced. It is four-nucleate and the nuclei are in division. In one of the division figures the number of chromosomes, though they could not be exactly counted, could be approximately estimated to the diploid number, not the tetraploid one which must be found in unreduced embryo sacs. The developing embryo sac is here also situated above some other, small ones, which undoubtedly are aposporic. In Fig. 3 *a*, however, another case is seen. Here there is a larger, binucleate embryo sac and some smaller, uninucleate ones. Owing to its deep position in relation to the nucellus and to the smaller embryo sacs, the binucleate embryo sac is certainly aposporic. In Fig. 3 *c* two mature embryo sacs are shown beside each other; one of these is a little larger and more advanced, as the secondary nucleus here has been formed, whereas in the other the two polar nuclei are still visible. In the larger embryo sac a pollen tube has intruded and a male gamete has migrated to the secondary nucleus with which it is about to fuse while there is no such gamete at the nucleus of the egg cell. For this reason this embryo sac is probably an aposporic one, where the secondary nucleus alone is fecundated, thus an instance of pseudogamy, which according to the experiments of Oldén (1953, p. 125) must occur in the apomictic *Malus Sieboldii*.

While the aposporic embryo sacs, as a rule, are formed in the inner part of the nucellus, in a few cases it was also observed that they may derive their origin from the epidermis. In Fig. 2 *f* thus an aposporic, binucleate embryo sac is visible, which has developed in the apex of the nucellus, in the here of several cell-layers consisting epidermis tissue.

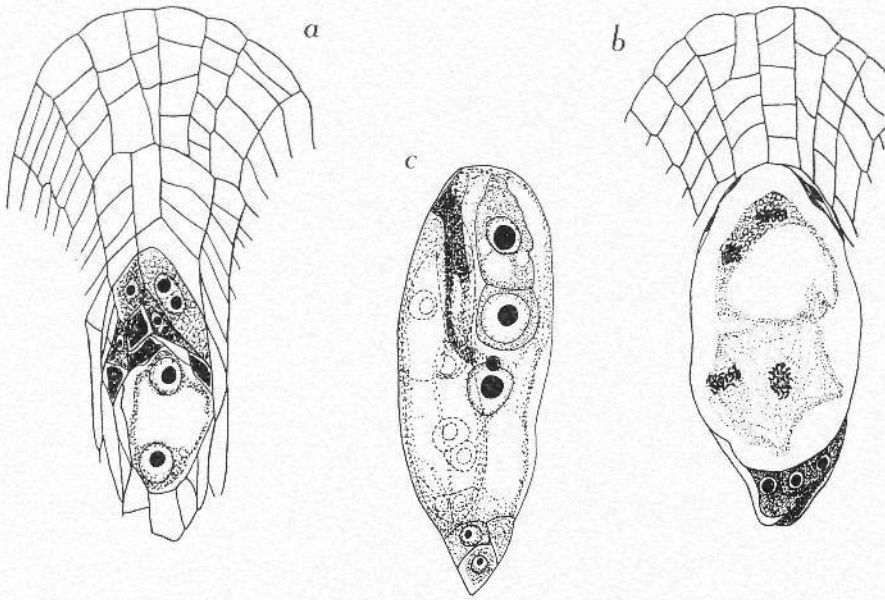


Fig. 3. *Malus Sieboldii* (w), development of embryo sac. *a* A binucleate embryo sac, certainly aposporic, ousting some 1-nucleate above it. *b* Embryo sac, probably reduced, with four dividing nuclei. *c* Two mature embryo sacs, one of them larger and more advanced; in this a pollen tube has intruded and a male gamete fuses with the secondary nucleus. — Enlargement about $\times 400$.

A cell to be left there of, higher up, with a big nucleus is possibly an additional potential secondary embryo sac. Only those cell layers that belong to the epidermis are drawn in the figure; beneath them there was at the usual place a 4-nucleate embryo sac, which, however, had considerably smaller nuclei than the binucleate one, and in addition probably also a small embryo sac beside it. It is not impossible that the embryo sac drawn might be winning in the competition. — Aposporic embryo sacs that have been formed from the epidermis have earlier been described by Rosenberg (1908) for *Hieracium aurantiacum*, where they usually have this origin; otherwise it is apparently an uncommon condition.

It is thus obvious that in the specimen of *Malus Sieboldii* investigated both reduced and unreduced, aposporic, embryo sacs develop. Even though the unreduced embryo sacs according to Oldén (l.c., p. 109—111) sometimes may be fertilized and give rise to seed plants with increased chromosome number, these are exceptional cases and, as a rule, they

must be held to develop apomictically. The apomixis is here, however, facultative.

As regards the proportion between reduced and unreduced embryo sacs, it must be taken into consideration that this, as pointed out by Oldén (l.c., p. 123—124) is possibly influenced by external conditions: the temperature may be of effect and bad pollination conditions may favour a later development of aposporic embryo sacs. In the spring of 1957, however, the aposporic embryo sacs were — at open pollination — obviously more common than the reduced ones. Thus in the material from the described tree (w) 12 triads were observed with a weakly developed basal megaspore which certainly or probably was going to degenerate, and 7 triads where the basal cell probably would develop further. Even if such a development takes place, a supplanting may, of course, occur at a later stage, and in addition a such one may often be found in an early stage, so that no megaspore formation at all occurs. It is thus obvious that the mature aposporic embryo sacs must have completely dominated over the reduced ones, in agreement with the results from Oldén's crossings of 1948, when of 11 seed plants 10 must have arisen from unreduced embryo sacs, only 1 from a reduced one.

The hitherto described conditions refer only to one of the specimens of *Malus Sieboldii* in Lund (w). The secondary, east specimen (e) showed some minor deviations. The general development of MMC and embryo sac was, of course, the same, but the disturbances in the meiosis of the MMC were apparently not so great and the developed triads with megaspores more common. The basal megaspore was also often normally developed and apparently capable of further development (Fig. 4 *a—b*), though it was, of course, exposed to competition from surrounding aposporic embryo sacs. In some cases, on the other hand, there were also here signs of degeneration (Fig. 4 *c*). A calculation of the proportions, in the year 1957, showed that of 45 triads with megaspores, or with a 1-nucleate embryo sac and megaspore remnants, 30 contained an apparently competitive basal megaspore or embryo sac, whereas in the 15 remaining cases the basal megaspore was weakly developed, obviously at the point of degenerating. Of course it is also possible in this case that some of the apparently normally developed megaspores may succumb in the later competition; a degeneration in an earlier stage could also be observed, so that megaspore formation never took place. These conditions, of course, counteract the preponderance of the reduced embryo sacs that seems to appear from

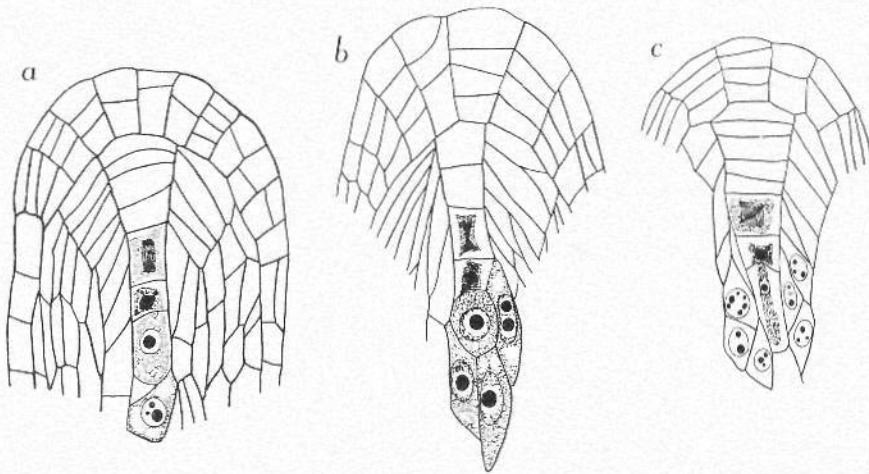


Fig. 4. *Malus Sieboldii* (c). a Triad with a vigorous basal megaspore and below it a 1-nucleate aposporic embryo sac. b A group of four uninucleate embryo sacs, one of them formed from a megaspore, reduced, with two disintegrating triad cells above it, the other 3 aposporic, unreduced. c A triad with the basal megaspore in degeneration; around it aposporic embryo sacs develop.

Enlargement about $\times 400$.

the numbers mentioned, but it is still evident that here these embryo sacs are comparatively more common. The numbers obtained by Oldén (l.c., p. 111) in crossings between this specimen (♀) and *Malus Eleyi* (♂) also indicated that the number of reduced and unreduced embryo sacs on this occasion (in the year 1950) were about equal. In another experiment, when the tree was crossed with the tetraploid variety Mère de Ménage 260/38 (♂) Oldén is of the opinion that the seed plants formed through apomixis were by far preponderant; if this really was the case, it can, as mentioned by Oldén, possibly be due to special conditions, for instance that the male gametes have not been appropriate for fertilization, and that therefore the primary embryo sacs have degenerated and apomictic ones have developed in their place.

The apomixis occurring in the tetraploid *Malus Sieboldii* thus is a facultative apospory, more or less pronounced. In an embryological respect there is a great agreement with the apospory that was described by Dermen (1936) for the triploid *Malus hupehensis*; this author, however, states that even if the apomixis here is not total but fertilization sometimes occurs, apparently all embryo sacs are aposporic and unreduced; the apomictic tendency thus is more pronounced than in the

tetraploid *Malus Sieboldii*. Also with the apomictic *Sorbus* species investigated by Liljefors (1953) there is a great similarity, perhaps especially with the development of the tetraploid *Sorbus hybrida*, where the MMC may either degenerate or pass through meiosis and form a reduced embryo sac, in competition with aposporic embryo sacs arising in the vicinity.

The cause of the apomictic development in the tetraploid *Malus Sieboldii* is probably disturbances in the meiosis. That such disturbances occurred was clear from the frequent spreading of the chromosomes in the division of the MMC, some of them lagging behind, others going ahead the major group, as well as from the fact that some chromosomes or chromosome fragments often were excluded from the daughter nuclei. These irregularities appeared greater in the one tree (w), which also had a more pronounced apomixis. The material was too small, it is true, for a certain comparison, but it appeared as if disturbances in this tree were more common and in some cases also more pronounced than in the other specimen (Fig. 5). In the apomictic development here the primary factor thus apparently is not the activity of the aposporic embryo sacs, but the passivity of the primary MMC or its derivatives.

The cause of the irregularities in the meiosis and therewith probably also of the apomixis is a matter of debate. Judging from recent investigations (see Liljefors, 1955, p. 100) the apomictic development seems at least in some cases (e.g. in *Potentilla* and *Sorbus*) to be due to recessive genes which through hybridization come into dominance, polyploidy also playing a role. For the apomictic triploid species *Malus hupehensis* Dermen (l.c.) assumes that the apomixis should be attributed to hybridogeneity. Is this also the case in *Malus Sieboldii*? As a matter of fact the partly apomictic form treated here shows some differences from the typical species: the leaves are greater, less incised, only on some shoots with a slight indication of lobation, on flowering branchlets often entire, the flowers are also larger (about 3 cm across) and with overlapping petals, the pubescence is weaker. Some of these characters are also found in *M. Sieboldii* var. *arborescens* Rehd., which is distinguished by large, less lobate leaves and weaker pubescence (Rehder, 1940), but it appears as if the deviations of the trees in Lund were greater than in the typical variety. A similarity is also present with *M. zumi* (Mats.) Rehd., which according to Rehder (l.c.) has arisen through hybridization between *M. baccata* var. *mandshurica* Schneid. and *M. Sieboldii*, but by Asami (1927) and Ohwi (1953) is regarded as a variety of *M. Sieboldii*. *Malus zumi* is distinguished by more or less un-

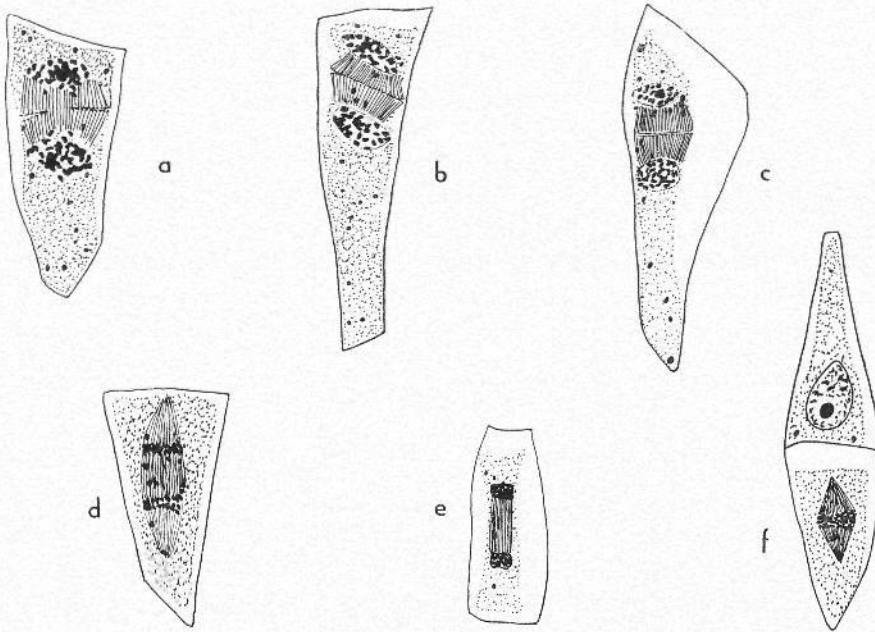


Fig. 5. Meiosis in the MMC in *Malus Sieboldii* (w), a—c, and in *M. Sieboldii* (e), d—f. a—c Dyad formation, with rather great irregularities. d Anaphase of the first meiotic division. e Telophase, the cell certainly degenerating. f Dyad with lower cell in division, here no excluded chromosomes. — Enlargement about $\times 900$.

divided leaves, those of flowering branchlets entire or nearly so, and greater flowers, 2.5—3 cm across (Rehder, l.c.); it differs however also in having larger (about 1.2 cm across) and redder fruits, whereas the investigated trees of *M. Sieboldii* have fruits of the typical appearance for the species (about 6—8 mm broad). Furthermore *M. zumi* (Rybin, 1926) is not tetraploid, but diploid. Another species, with which there apparently is a still greater agreement, is the closely to *M. Sieboldii* related *M. Sargentii* Rehd., which according to Rehder (l.c.) differs from *M. Sieboldii* in having horizontally spreading, often spinescent branches, suborbicular, overlapping petals, rounded at base, large flowers and glabrous calyx; these characters are all found in the two specimens investigated (the calyx is at least nearly glabrous). The chromosome number may in *M. Sargentii* also be tetraploid (Rybin, l.c.; Darlington and Wylie, 1955). *M. Sargentii* has, however, more incised leaves, those of shoots mostly 3-lobed, and a little larger fruits (about 1 cm across), of dark red colour (Rehder, l.c.). Moreover this form according to

Japanese authors is not a good species: Asami (1927, p. 44—45) regards it as a variety and says that it is a very occasional form without sharp delimitation against the main form, and Ohwi (1953, p. 665) includes it without variety name in *M. Sieboldii*. Apparently there is around *M. Sieboldii* a form complex including *M. zumi*, *M. Sargenti* and some varieties, which partly certainly has arisen through hybridization with *M. baccata* var. *mandshurica* — possibly also with participation of *M. prunifolia* (Willd.) Borkh. — and in which more or less apomictic microspecies have developed. The form of *M. Sieboldii* (sens. lat.) treated here apparently is such a microspecies. Other microspecies are presumably also formed or in development; the final elucidation, however, of the systematical conditions in this group and the genesis of the different forms most probably cannot be completed except by studies of the form complex in its Japanese district of origin.

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Observations on the Conjugation in *Netrium digitus*

By ROLF GRÖNBLAD

In a sample from the Sammatti parish in SW Finland, collected September 20th 1936, I found a great number of zygospores and conjugating cells of the desmid *Netrium digitus* Itz. & Rothe. (According to De Bary (1858, p. 49) the Conjugatae are conjugating most frequently in the spring.) The material was kept living for some time and I was able to follow the development of the zygospores from their first beginning to the mature zygospore. The conjugation always took place during the night. In a couple of nights the conjugation was abundantly going on. Then, abruptly, on the third day, there was no further conjugation, and some of the conjugations already begun were never completed.

Observations on these processes are very scarce and since, according to West & Fritsch (1927, p. 226) "in *Netrium* the details are not known", I think it worth while to publish a short account of my observations. I regret to say that these are very incomplete, and it is most regrettable that no part of the interesting material was preserved for subsequent studies. However, also these incomplete observations may, perhaps, serve the purpose of inciting further studies.

The descriptions of the various stages of the process follow in connection with the drawings.

Case Nr 1. — Fig. 1 (22.30 o'clock). The two conjugating cells lie parallel and close to each other, the slenderer and the thicker ends in the same direction. As far as one may judge from the shape of the conjugating cells, they are the product of a cell-division which has taken place immediately before the beginning of the conjugation. (Cf. De Bary, p. 48) Whether or not this assumption really is true, I was not able to establish. The chromatophores were coarsely grained, their shape scarcely changed, the nucleus between the two chromatophores clearly visible. There was no enveloping mucilage to be seen during the whole process.

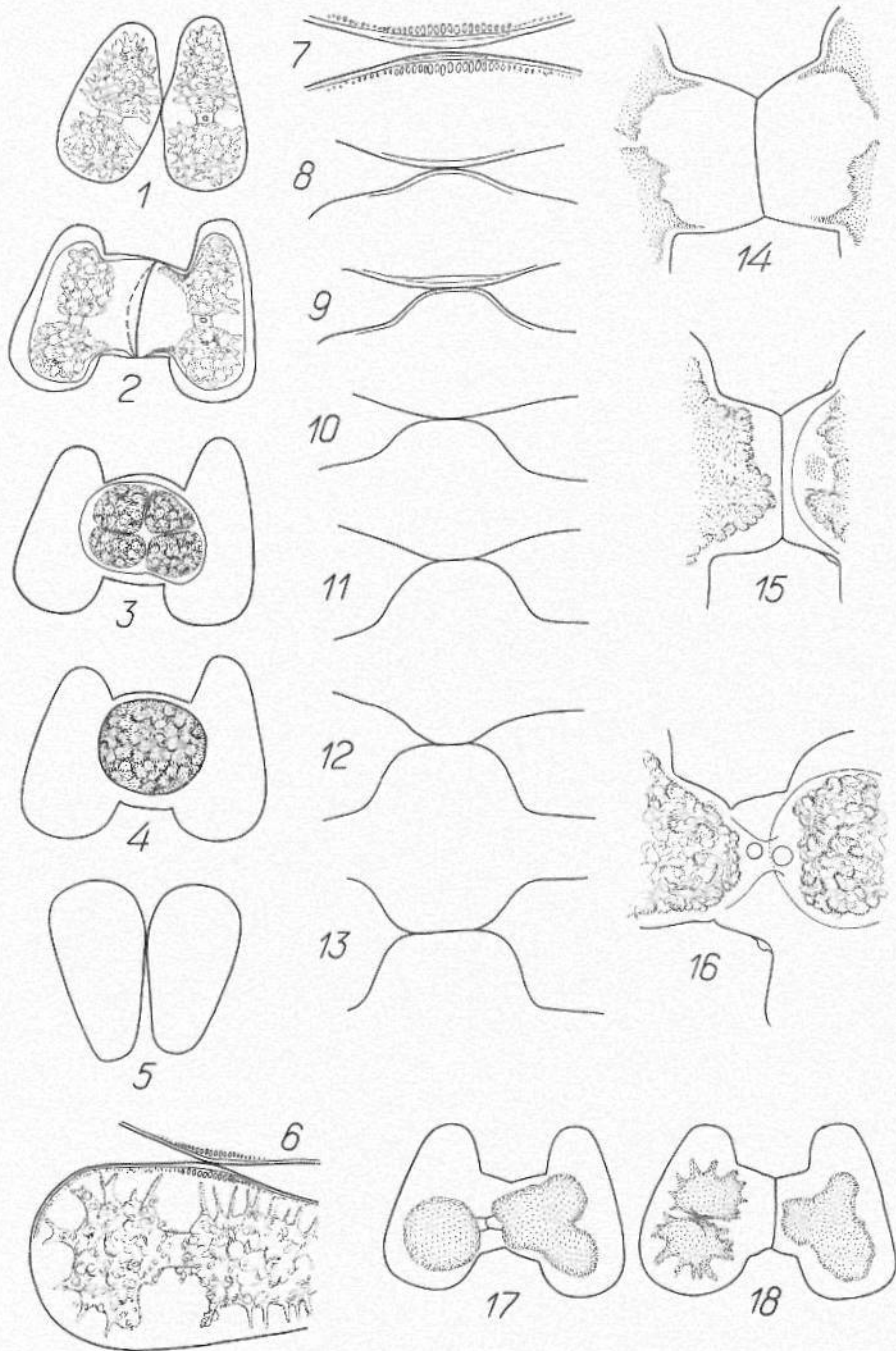


Fig. 2 (23.15). The two conjugating cells have already each of them put out broad protuberances, which have become connected by means of a convex septum. The content of the nuclei is divided into 4 parts. The whole of the plasm is of a yellowish colour. In the conjugating cells the plasm has become contracted and removed from the cell wall. In the conjugating tube there are grained slings of plasm along the walls up to the dividing septum.

Fig. 3 (23.35). A few seconds earlier the conjugation had suddenly taken place. The moment of conjugation in this case I didn't see, because unfortunately I did not look into the microscope for a few seconds when this just happened. (In another case I could see that the conjugation was completed just in a moment.) The whole content of the cells is now contracted into an irregularly spherical lump where the 4 chromatophores are separately visible.

Fig. 4 (23.45). The zygospore is now almost mature and has become exactly spherical. The zygospore wall is not yet of mature thickness. The whole process of conjugation had taken one hour and 15 minutes. (De Bary states 15—20—40 minutes from the first beginning to the spherical shape of the zygospore.)

Case Nr 2. — I took another selection of my material and it was only a short time before I again met two cells in the beginning of conjugation.

Fig. 5 (23.58 o'clock). The cells lie parallel beneath each other as before. The protuberances are scarcely evolved.

Fig. 6 (00.37). The grained structure of the chromatophores is clearly visible. At the point where the cells meet the cell wall is thickened, and inside of this the plasm stream has brought together a conglomeration of colourless oblong grains. (De Bary, p. 49: "linsenförmige Ansammlung".)

Fig. 7 (00.47). A more detailed drawing. The two layers of the cell-wall are visible. (This is a somewhat unexpected sight, because the cell wall of the saccoderm Desmids is supposed to consist of a single layer.) The conjugating cells are separated from each other by a small space of 2.2 μ . (cf. De Bary p. 27) Greatest thickness of the cell wall 2.4 μ . The grains at the meeting point increase in size and become more numerous. The tiny flaps of the chromatophores become more scarce. The plasm of a more strongly yellowish colour.

(01.05) The chromatophores become more and more contracted and grained, the plasm more yellowish, the grains at the contact point more

numerous. The plasm circulation is going on very actively. The distance between the cells is unchanged.

(02.03) Distance between cells 2 μ . Thickening of cell wall 3.4 μ . No plasmolytic contraction visible.

(03.10) The grains at the point of contact become melted to a colourless layer.

(03.38) Nuclei clearly visible.

Fig. 8 (03.42). In the lower cell the protuberance begins now quickly to enlarge. (De Bary, p. 4 also tells of an enlargement that does not take place simultaneously in the two conjugating cells.) The plasm layer on the inside of the contact point has disappeared. In the upper cell the layer is yet visible.

Fig. 9 (03.44).

Fig. 10 (03.47). In the upper cell the content of the nucleus is divided into 4 parts. In the lower cell nucleus not visible.

(03.51) Plasmolytic contractions are beginning at first in the upper cell and almost instantly after that in the lower cell. Chromatophores not markedly changed.

Fig. 11 (03.53).

(03.54) The protuberance in the upper cell begins suddenly to enlarge.

Fig. 12 (03.55).

Fig. 13 (04.00).

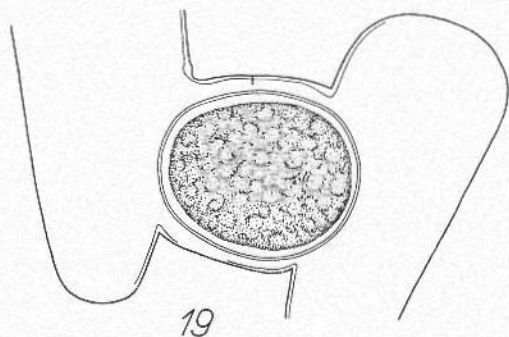
Fig. 14 (04.11). Strips of the plasm push forward into the conjugating tube. The upper cell is to the right, the lower cell to the left.

Fig. 15 (04.17). The whole content of the cell is pressed forward into the conjugating tube. At the right angles of the conjugating tube of the right cell the two layers of the cell wall are clearly visible. The right cell is more developed than the left one.

Fig. 16 (04.37). The nuclei seem to meet within a connecting sheet of plasm. The right nucleus greater, colourless, the left one smaller and more grained.

Fig. 17 (04.42). Curiously enough this conjugation never became completed. On the contrary, on the next day at 15.45 o'clock (fig. 18) the content of the cells had drawn itself back. A separating membrane has appeared between the two cells. We must suppose that some disturbing factor had interrupted the process. (cf. De Bary, p. 4. "am Object-träger wurde die Kopulation in 2 Stunden vollendet, aber niemals zum Zygote entwickelt").

During the following nights I tried attentively to follow this interesting process, but in vain. A great deal of the *Netrium* cells had already



formed zygospores, some of the cells lay close to others as if beginning to conjugate, but no further progress of the conjugation could be seen.

Fig. 19. This is a mature zygospore. In this case the cells are in opposite position to each other, the thicker end of one cell corresponding to the thinner end of the other cell. Both this position and the other one described above were met with. At a later time the wall of the conjugating tube undergoes a gelatination and the zygospore becomes free.

Magnification of fig. 1—5 and 17—18 $\times 67$, fig. 6 and 8—16 and 19 $\times 265$, fig. 7 $\times 445$.

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Smärre uppsatser och meddelanden

Några ord om de svenska förekomsterna av *Physcia elaeina*

Under resor jag förliden sommar företog i olika delar av Sydsverige — i samband med mina studier över collemataccéer — kom jag att besöka båda de hittills kända svenska lokalerna för den sydliga laven *Physcia elaeina* (Sm.) A. L. Sm. [= *Ph. adglutinata* (Flk.) Nyl.], nämligen Botaniska trädgården i Visby, Gotland, och Solberga kyrkogård, Bohuslän. Då ej på länge någon rapport lämnats om dessa förekomster, beslöt jag göra en hastig inventering av bestånden. Studier med vissa tidsintervall rörande dylika sällsyntheter och deras uppträdande synas mig vara av värde.

I Botaniska trädgården i Visby — eller som det officiella namnet lyder: Sällskapet D.B.V:s [= De Badande Vännernas] trädgård (se Ekberg 1955 och där anförd litteratur) — upptäcktes arten av G. E. Du Rietz 26/5 1918, växande tämligen rikligt på den släta barken av en *Abies*-art (se vidare Du Rietz 1923 s. 88; utan lokal angiven såsom ny för Sverige i samma tidskrift 1921 s. 168). Den 23/7 1932 hade jag själv tillfälle se laven — nu sparsam — på samma lokal och substrat (se närmare Degelius 1936 s. 94). Den 30/5 1957 besöktes fyndplatsen på nytt, och jag gjorde då följande iakttagelser. På det tidigare kända substratet, en vacker och tämligen grov spansk ädelgran (*Abies pinsapo* f. *glauca*), kunde laven nu ej anträffas trots ivrigt sökande. Däremot fann jag den lokalt riklig och samhällsbildande (täckande flera dm²) på en stor, c. 17 m från *Abies* växande *Sorbus aria* v. *incisa*, vid stängslet mot vägen (Studentallén). Den uppträdde här på den mot vägen vända sidan av stammen, tillsammans med bl.a. *Physcia orbicularis* och *Xanthoria parietina*. Kanske vi här ha den ursprungliga spridningshärden för arten? Den senare sågs även sparsam på en *Morus alba* f. *multicaulis* i närheten. Efterforskningar på andra träd och buskar i och utanför Botaniska trädgården gävo negativt resultat, men små exemplar av arten kunna lätt undgå uppmärksamheten. — *Physcia*-vegetationen är i Botaniska trädgården — liksom i omgivningen — rik; arter av detta släkte äro, jämte *Xanthoria parietina* (lokalt även *Parmelia physodes* och *P. sulcata*), de viktigaste och mest framträdande bladlavarna här. Följande *Physcia*-arter antecknades f.ö.: *ascendens* (allmän, jämte *orbicularis* den allmännaste), *grisea* (lokalt riklig, på en stor alm t.ex. täckande stora delar av stammen), *nigricans* (flerstädes men tydligen ej allmän), *orbicularis* (allmän, jfr ovan), *pulverulenta* (sparsam men bl.a. sågs ett mycket stort fertilt ex.), *tenella* (inom trädgården sparsammare än den närstående *ascendens* men utanför ibland tämligen riklig); utanför trädgården även *aipolia* och *stellaris*.

På Solberga kyrkogård anträffades *Ph. elaeina* 12/8 1933 av A. H. Magnusson. Enligt Magnusson 1935 (s. 123) växte den här vid basen av en alm på den mot söder vettande sidan invid vägen, som går förbi kyrkogården, och täckte åtminstone ett par dm². Själv hade jag tillfälle att 4/6 1938 iakttaga och samla arten på denna lokal. Den 22/8 och 15/9 1957 besökte jag ånyo lokalen och antecknade följande. Arten förekom på två almar ingående i den rad av olika slags träd, som för c. 100 år sedan planterats utmed vägen innanför muren (i äldsta delen av kyrkogården). På den ena almen var den riklig mot basen av den mot landsvägen vända sidan av stammen (täckande en sammanlagd yta av åtminstone 10 dm²), men enstaka exemplar anträffades även högre upp (till c. 2 m från marken) samt på den inåt vända sidan av stammen; få andra lavar förekommo på dessa ytor (bl.a. *Xanthoria parietina* lokalt riklig, *Lecanora Hageni*, *Physcia ascendens* och *Ph. orbicularis*). På den andra (invid stående) almen sågs *Ph. elaeina* blott ytterst sparsam och nära basen. Almen var det rikast representerade trädslaget i raden runt de äldre delarna av kyrkogården och förekom i olika åldrar. Den bar en rik lavvegetation (liksom ock övriga trädslag: lind, hästkastanj, oxel, vanlig lönn, sykomorlönn, naverlönn). De på alm förekommande arterna antecknades, och listan, som ej gör anspråk på fullständighet, meddelas här som bidrag till en karakterisering av lokalen: *Evernia prunastri*, *Parmelia acetabulum* (ett enda medelstort ex., ster., tydligen tillkommet efter Magnussons besök, då arten saknas i M:s anteckningar från lokalen), *P. fuliginosa*, *P. isidiotyla* (sic!, ett enda medelstort ex., ster.), *P. sulcata*, *Physcia aipolia*, *Ph. ascendens* (allmän), *Ph. dubia*, *Ph. grisea*, *Ph. orbicularis* (allmän), *Ph. pulverulenta* (d:o), *Ph. tenella* (d:o), *Ramalina farinacea*, *R. fastigiata*, *R. fraxinea*, *Xanthoria candelaria*, *X. fallax* (lokalt riklig), *X. parietina* (allmän); av skorplavar bl.a. *Arthopyrenia* sp., *Bacidia luteola*, *Buellia punctata*, *Caloptera chlorina*, *C. phlogina*, *Candelariella vitellina*, *Lecania cyrtella*, *Lecanora Hageni*, *L. subrugosa*, *Lecidea olivacea* (även en *sorediös* typ), *Pertusaria globulifera* v. *Henrici*, *Phlyctis argena*; av alger *Trentepohlia umbrina*. På en vanlig lönn sågs ock *Physcia nigricans* (sparsam). — *Ph. elaeina* söktes även på träd (alm, ask) utanför kyrkogården men förgäves.

Är *Ph. elaeinas* sällsynthet hos oss verklig eller blott skenbar? Olika meningar ha här gjort sig gällande. Även om artens obetydliga storlek gör, att sparsamma förekomster lätt undgå uppmärksamheten, är jag övertygad om det förstnämnda alternativets riktighet. Arten uppträder nämligen på en typ av ståndorter — starkt stoftutsatta träd vid vägar, gårdar o.dyl. —, som varit föremål för ingående undersökningar i lichenologiskt hänseende i Sydsvrige (av Almborn, Magnusson m.fl.).

Denna *Physcia*-art är ej med säkerhet känd från våra grannländer (betr. en gammal uppgift från Danmark se Lyng 1935 b s. 231). Enligt nuvarande kännedom börjar den uppträda först i Mellaneuropa, där den dock i stort sett synes vara sällsynt. De svenska förekomsterna äro tydligen resultat av långspridning och jämförbara med t.ex. uppträdandet av *Parmelia dubia* vid Uppsala (se Hasselrot 1945 s. 238—241). Vad förekomsten i Botaniska trädgården i Visby beträffar kan man tänka sig — lika gärna som en vindspridning — en invandring genom människan, i samband med inplanteringen av träd och buskar på 1800-talet. Enligt vad stiftsjägmästare Nils Ekberg (Göteborg), för-

fattare till den ovan citerade minnesskriften, meddelat mig, får man räkna med att en del av de i trädgården förekommande lignoserna som unga plantor införskaffats från Mellaneuropa. Diasporer av laven kunna ha medföljt dessa. I sådant fall skulle man ha att göra med samma typ av spridning som jag antagit betr. *Xanthoria lobulata* på Island (Degelius 1957 s. 44).

Det är anmärkningsvärt, att här ifrågavarande förekomster i så ringa utsträckning kunnat tjänstgöra som spridningshärdar, även när det gäller närmaste omgivning; vegetativa diasporer (soredier) äro dock rikligt förhända hos arten (apothecier ej anträffade hos oss). Dylika iakttagelser kunna emellertid ofta göras vid arters utbredningsgränser, och företeelsen torde främst stå i samband med ökad konkurrenssvagheter.

Ph. elaeina påminner till utseendet om en liten *Ph. orbicularis*, men loberna äro tunnare och mer tilltryckta (laven mer skorplik). Betr. viktigare skillnader f.ö. (pyknokonidier m.m.) hänvisas till ovan citerade arbeten samt till allmänna floror och monografier (t.ex. Lynge 1935, Nádvořník 1947). Detsamma gäller utbredningen utanför Skandinavien.

Göteborg, Botaniska trädgården, i sept. 1957.

GUNNAR DEGELIUS

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Carex extensa anträffad i Bohuslän

I en samling kärlväxter från Västkusten, som av överlärare Manne Ohlander (Göteborg) hösten 1956 inlämnades till Botaniska trädgården i Göteborg för bestämning, fann jag ovannämnda *Carex*-art, på svenska kallad segstarr eller (sämre namn) östersjöstarr. Exemplaret, som nu tillhör Botaniska trädgårdens herbarium, hade samlats av O. den 3/8 1956 på Fredagsholmen i Skaftö socken i mellersta Bohuslän (holmen ifråga förs ibland felaktigt till Morlanda socken); det är väl utvecklat och bär flera strån (det längsta närmare 3 dm).

Fyndet är mycket intressant. Arten ifråga är nämligen tidigare aldrig sedd på svenska västkusten norr om Skåne (och även i detta landskap är den sällsynt). Den tillhör de havsstrandsväxter, som i Sverige huvudsakligen äro utbredda utmed Östersjöns kust, och den sydliga typen bland dessa (artens nordgräns ligger i nordligaste Uppland, se karta 399 hos Hultén 1950). Den är emellertid mycket utbredd i Danmark, särskilt i de södra delarna ehuru även funnen på några lokaler i norra Jylland (Nordsjökusten och Limfjorden) samt på Läsö (se också Wiinstedt 1943 s. 182—183 och karta fig. 22), och blev nyligen påvisad från en lokal i Norge, nämligen Skåtøy nära Kragerø i Telemark (se Höeg & Lid 1949 s. 87—91). Dessa förekomster i Danmark och Norge göra Bohusläns-fyndet mindre överraskande. I Finland saknas arten med undantag för Åland. — Betr. totalutbredningen se anförda arbeten av Wiinstedt och Höeg & Lid.

I samband med denna arts utbredningstyp kommer man att tänka på några andra *Carex*-arter bundna till havsstränder. *C. glareosa* tillhör också östersjöarterna i Sverige men är en nordlig typ (i stort sett bunden till Bottenviken-Bottenhavet, se karta 345 hos Hultén). Den är ännu ej sedd på vår västkust, trots att två norska lokaler ligger mycket nära Bohusläns-gränsen (arten bör alltså efterspanas på svenska sidan). *C. glareosa* har — till skillnad från *C. extensa* — en vid utbredning i Norge samt i Nordens östra delar (även utmed ishavskusten); i Danmark saknas den. — *C. Mackenziei* har en utbredning mycket likartad *glareosas*, men arten finnes även på svenska västkusten (i dess norra delar) och går utmed kusten av Östersjön längre mot söder (se karta 347 hos Hultén). — *C. distans*, tillsammans med vilken *C. extensa* ibland uppträder, tillhör den sydliga typen och är ganska utbredd även på svenska västkusten (liksom i Danmark och sydligaste Norge; se karta 404 hos Hultén).

Den 15/9 1957 hade jag tillfälle att i sällskap med upptäckaren avlägga ett kort besök på *extensa*-lokalen i Bohuslän. Därvid gjorde jag följande anteckningar om lokalen och artens uppträdande.

Den högklippiga, numera helt obebodda lilla ön Fredagsholmen ligger vid inloppet till Ellösefjorden söder om den större ön Jonsborg, alltså mellan Skaftölandet och Orust. Vid en liten vik på nordväst-sidan av ön, nära den gamla husruinen, är växtplatsen för *C. extensa*. I den 13—15 m breda sänka mellan klipporna, som här går ner till vattnet, kunde en tydlig vegetationszonering iakttagas. Längst ner förekom en m.e.l.m. gles vegetation av bl.a. *Scirpus maritimus* och *Puccinellia maritima*. Därövanför vidtog ett samhälle med dominerande *Juncus Gerardi* (bland övriga arter kunna nämnas *Centaureum pulchellum*, *Potentilla anserina*, *Trifolium fragiferum*; på några stenar rätt obetydligt höjande sig över marken bestod lavvegetationen av framförallt *Candelariella vitellina*, *Rhizocarpon constrictum* och *Xanthoria parietina*). På den något högre liggande (alltså torrare) marken omedelbart intill vidtog ett samhälle med dominerande *Carex distans* (bland övriga arter t.ex. *Centaureum pulchellum*, *Plantago maritima*, *Potentilla anserina*; på här förekommande lägre stenar bl.a. *Candelariella vitellina*, *Lecanora atra*, *Parmelia fuliginosa*, *P. pulla*, *Physcia tenella* v. *marina*, *Rhizocarpon constrictum*, något *Xanthoria parietina*). Det var i detta bälte, alltså bland rikligt uppträdande *C. distans*, som *C. extensa* förekom. Den sistnämnda arten var sparsam på lokalen (ett 20-tal fruktbärande strån iakttogos), men genom sin tydligt grågröna färg

stack den av mot den rent gröna *C. distans*.¹ Den förekommer här alltså något högre upp (torrare) än den annars brukar (dess vanliga plats i zonerings-schemat synes vara något nedanför *C. distans*).

Man frågar sig om denna förekomst av *C. extensa* är gammal eller om det rör sig om en sen invandring av arten. Höeg & Lid (l.c.) äro för den norska lokalens vidkommande osäkra betr. växtens ålder men utesluta ej möjligheten av en sen invandring (med havsströmmar eller fåglar). Wiinstedt (l.c.) räknar med, att arten i Danmark ej ännu avslutat sin vandring mot norr. Vad uppträdandet i Bohuslän beträffar, synes mig en sen invandring mest sannolik. Arten är som nämnts sparsam på lokalen, och denna senare ligger tämligen exponerad.

Uppdykandet i Bohuslän av *C. extensa* kan jämföras med det av en annan havsstrandsväxt, *Atriplex sabulosa*, som jag år 1943 anträffade på Nordkoster i samma landskap såsom ny för Sverige (som vildväxande; se Degelius 1944 s. 122—123). Den har senare blivit funnen på ytterligare två lokaler på Sveriges västkust, båda i Halland (se Segelberg 1954 s. 246—247, Hylmö 1955 s. 417—418). »Sannolikheten är stor för att arten är nyinvandrad till den svenska västkusten på samtliga tre lokaler» skriver Hylmö (l.c.) om denna *Atriplex*-art.

Göteborg, Botaniska trädgården, i sept. 1957.

GUNNAR DEGELIUS

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Globularia cytology — an explanation

In an interesting paper on the chromosome numbers of the genus *Globularia*, the Danish botanist Larsen (1957) makes some remarks on the first correctly determined chromosome number for a species of this genus reported by the present writers in 1944. Since these remarks may cast a certain doubt not only on the identification of the material but also on the correctness of the number itself and even the origin of the plants, a short explanation seems appropriate.

¹ Höeg & Lid 1949 (s. 89): »Levende er planten friskt mørkgrønn . . . ; pressede planter får en mer grågrønn farge.» Denna uppgift om den levande växtens färg stämmer ej överens med min erfarenhet.

The chromosome number $2n=16$ reported by Löve & Löve (1944) for the species *G. vulgaris* was determined on material collected in a field at the Tuna area of Lund by the writers themselves. As always during the twenty years the writers have made cytological studies of wild material, herbarium material was taken from the collection, and the plant was identified as *G. vulgaris* by aid of available floras. We did not know then that most of these floras take the species in its wide sense, including also some taxa which are good species themselves. We did not feel the occurrence of this species at Lund "strange as the species in Sweden is reported to grow wild on the islands of Öland and Gotland only", to quote Mr. Larsen, since we could easily see that our specimens were weeds which could even have originated from the Botanical Garden or some other cultivated area.

Later on, when the writers went through the herbarium material after having learnt about other species of *Globularia*, they could state that the plant from Lund actually is not the species *G. vulgaris* s.str. but rather the species *G. Willkommii* often regarded only as one of its races. This correction was, however, never published, but it was given to Professor G. Tischler prior to the publication of his Chromosomenzahlen in 1950. Therefore, Larsen is mistaken in his statement that Tischler had "wrongly quoted" our number for this latter species. Also, Larsen is wrong in his twice repeated statement that he had been unable to confirm our count, since he has determined the very same number in four collections of the species *G. Willkommii*.

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Heat Tolerances of *Koenigia islandica*

In a detailed paper on the relation between summer temperature and the distribution of alpine plants in the Fennoscandian lowlands, Dahl (1951) pointed out that although several species usually restricted to high altitudes and latitudes can easily be grown in botanical gardens in more temperate climates, many such plants do not survive more than a few years in warmer regions without certain precautions being taken. Plants brought from the north into a southern garden in the late summer easily survive the first winter and commence to grow quite satisfactorily during the early part of the next summer. When the summer heat comes, however, the plants appear to dry out even when being watered excessively, and if they survive, they usually succumb not later than the second summer in the garden. Because of this observation, Dahl (l.c.) suggested that alpine and arctic plants were restricted to their areas

not by competition or other conditions usually thought to be the main restrictive factors, but mainly by their lack of tolerance to a certain maximum summer temperature. This hypothesis was supported by observations made by other scientists, but lack of facilities prevented Dahl from testing it himself by aid of experiments. However, by aid of distribution maps and meteorological data, Dahl showed how isotherms for certain temperature maxima corresponded nicely to the southernmost limits of very many Fennoscandian alpine plants.

Although the hypothesis and reasoning by Dahl (l.c.) were mainly based on observations on perennial plants, his calculations also included the arctic-alpine annual *Koenigia islandica*. This is known to be restricted to the cold regions of the north and some few high mountains in Asia and North America south to about the 40th parallel (cf. Löve and Sarkar, 1957). The species is met with down to sea level in Greenland and Iceland, where the temperature rarely surpasses 15–20°C during the exceptionally hot summer days, but Dahl (l.c.) showed that in Scandinavia it is restricted to the areas north of or above the 24°C isotherm for the warmest summer days. It, therefore, seemed logical to conclude that the species did not have tolerances enabling it to grow farther south than where this temperature maximum occurs, and since *Koenigia* is a very frail annual producing seeds with a short storage life, there seemed reason to suggest that it would not survive in areas where higher temperatures are the rule.

The present writers have had the opportunity to make some experiments with plants grown from seeds of *Koenigia* from its southernmost locality in North America, in the Rocky Mountains of Colorado (Löve and Sarkar, 1957). The first populations were grown at room temperature (ca. 25°C) and in a moderately warm greenhouse (20–27°C) where they grew from seed to seed in four to six weeks. In these conditions the growth was very normal, although additional light was required to prevent the plants from etiolating during the winter months, but the length of day did not seem to affect their flowering. Neutrality to the length of day is, of course, already indicated by the distribution area of the plant including the arctic regions as well as high mountains as far south as the 40th parallel.

Since the first results of our cultivation of *Koenigia* indicated that the plant not only could survive but also thrive perfectly at temperatures reaching above the maximum postulated by Dahl (l.c.), further experiments were planned in order to check the real maximum tolerances of this species, which is one of the very few annual species of the arctic regions. Variation in temperature was induced by aid of a lighted heating chamber where the plants, cultivated in pots with moist sand, could be kept for some time at constant temperature. As long as the heat was kept at the same level as the maximum temperature in the greenhouse (ca. 27°C), no effect was observed on any of the plants, and they grew excellently and produced flowers. During the first day of excessive temperature, the heat was raised to 40°C for 2 1/2 hours without any adverse effect on any of the plants, and the result was the same when this treatment was repeated for seven hours on the two following days. During the fourth day, the temperature was raised to 45°C for six hours. After this treatment, about 1/3 of the plants in all the pots showed signs of withering at the

top, and when this treatment was repeated for seven hours the next (fifth) day, these individuals withered completely, whereas the other specimens showed no detectable effect of the heat. During the sixth day the 45°C temperature was kept for only 2 1/2 hours; another 1/3 of the original plants withered, but no effects were observable on the remaining 1/3. On the seventh day of the experiment the plants were kept at about 25°C under very moist conditions. None of the affected plants recovered, but the other individuals still grew quite normally and appeared to be unaffected. When the temperature was again raised to 45°C for seven hours on the eighth day of the experiment, the remaining plants also dried out completely despite excessive watering. None of these plants recovered when moved back to the greenhouse the following day.

This experimental evidence, though rather preliminary, seems to indicate that although the annual species *Koenigia islandica* prefers to grow in cold regions and never occurs naturally south of the 24° isotherm for the warmest days in Fennoscandia, this restriction of its area of distribution is hardly due to a lack of tolerances to considerably higher temperatures. In fact, our experiments seem to indicate that the plant can flower and set seed at distinctly higher temperature and that although it is among the most frail of annuals it can stand even very high temperatures for several days. The experiment seems to show that other factors must restrict the plant from growing farther south, since it survived temperatures rarely surpassed in regions far from its area of distribution and did not succumb until after several days of maximum temperatures characteristic of regions of the far south. Since this species prefers to grow in solifluction areas where competition from other plants is small, it may seem logical to conclude that while temperature maxima do not restrict its area of distribution as indicated by the present experiments, it will be unable to compete with other plants on more stabile soils. It would be premature, however, to generalize from these results for plants other than this annual. The hypothesis by Dahl (l.c.) may well fit for all the other species he listed, but the results here presented indicate the necessity of experimental confirmation for at least some perennials before it is accepted that the ecologically most important of the factors delimiting the distribution of arctic and alpine perennial species is their inability to survive certain temperature maxima. As a whole, plant distribution is such a complicated phenomenon that it is hardly likely that any one factor can be found to be generally restrictive except in extreme cases (cf. Went, 1957).

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Summary

The hypothesis by Dahl that the main restrictive factors for arctic and alpine plants in the lowlands may be high summer temperatures, has been tested on the annual arctic-alpine species *Koenigia islandica*. Since its tolerances make it possible for this plant to survive maximum temperatures of between 40 and 45°C for several days,

the restrictive factors for this species must be sought elsewhere. It is pointed out, however, that this does not necessarily invalidate the hypothesis for perennial plants although it needs experimental verification before it is definitely accepted.

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Über eine haploide Form von *Populus tremula* aus Uppland

In der Salicaceen-Gattung *Populus* treten recht häufig auch unter natürlichen Verhältnissen meiotische Störungen auf, was eine beträchtliche Varianz der Valenzstufen zur Folge hat.

Die erste Publikation über Chromosomenzahlen einer haploiden *Populus tremula* (und *P. canadensis*) stammt von Graf (1921). Er gab an bei *Populus tremula* haploid 4 Chromosomen gefunden zu haben, was sich später jedoch als unrichtig herausstellte. Weitere Angaben über Chromosomenzahlen von *P. tremula* machen Blackburn and Harrison (1924) und stellen hierbei für diese Art die Zahl diploid $2n=38$ fest. Weitere Chromosomenzählungen am gleichen Objekt wurden von v. Wettstein (1933) anlässlich einiger Kreuzungsversuche in der Gattung *Populus* vorgenommen und ergaben für *P. tremula* ebenfalls das Resultat $2n=38$. Die berühmte Gigas-Pappel, von Nilsson-Ehle (1936) auf Lillö entdeckt, wurde von Müntzing (1936) in zytologischer Untersuchung als triploide Form festgestellt. Hier traten in der Anaphase I und Metaphase II ± 57 Chromosomen in Erscheinung. Die Metaphase I zeigte eine Reihe von Trivalenten neben Bi- und Univalenten. Weitere triploide Formen von *P. tremula* wurden von Blomqvist (1937) in Medelpad und Melander (1938) in Norrbottens län gefunden. Beide Formen wurden von Tometorp (1937) zytologisch untersucht. In nachstehender Tabelle sind die wichtigsten zytologischen Untersuchungen für diese Art zusammengestellt:

<i>Populus tremula</i>		
	n	2n
haploide:	4(?)	
		Graf (1921)
diploide:	19	38
		Blackburn and Harrison (1924)
		v. Wettstein (1933)
	19	38
		Müntzing (1936)
		Johnsson (1940)
triploide:	$\pm 57/2$	± 57
		Müntzing (1936)
		± 57
		Tometorp (1937)
		$\pm 57 \pm 76$
		Johnsson (1940)

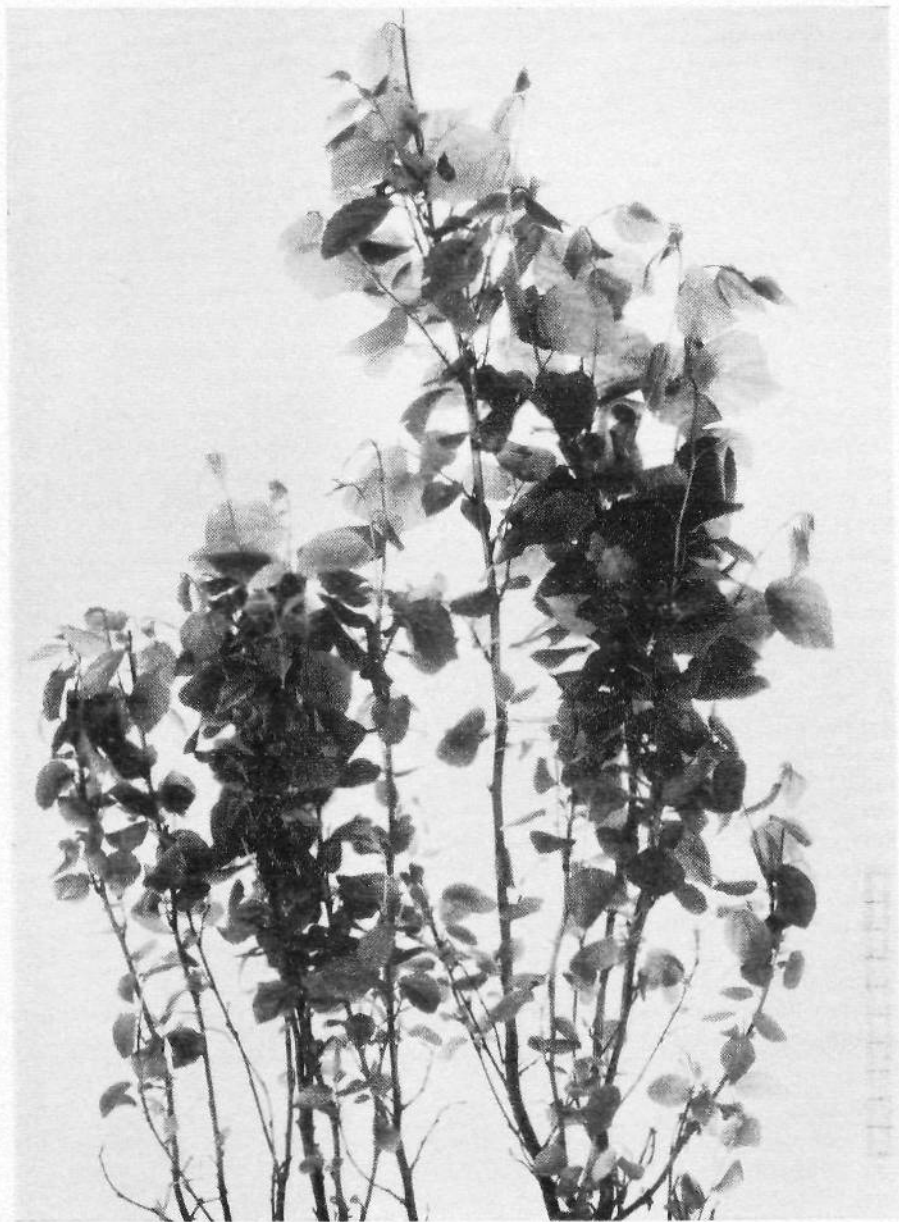


Fig. 1. *Populus tremula*, haploide Form aus Uppland.

Von Interesse scheint die auf der Abbildung gezeigte *Populus tremula* zu sein. Sie trat spontan in freier Absaat in Enebyberg (Uppland) auf und ist besonders augenfällig wegen des geringen Wuchses und der ausserordentlich kleinen Laubblätter. Die in Carnoy fixierten und mit Orcein gefärbten Wurzelspitzen haben Chromosomenzahlen von $2n = \pm 19$. Die Pflanze ist 6 ± 1 Jahre alt, die Blattoberfläche beträgt $3,6 \pm 1,1$ cm² gegenüber $15,5 \pm 2,5$ cm² diploider Individuen und hat eine Höhe von 55 cm. Augenfällig ist der strauchartige Wuchs der Pflanze sowie die zugespitzten Blätter, also eine Form wie sie von Jugendstadien der Aspe bekannt sind. In der Umgebung, *Pinus silvestris* und *Betula verrucosa* und *B. pubescens* sind hier zusammen mit *Populus tremula* waldbildend, konnte trotz intensiven Suchens kein weiteres Exemplar dieser Form gefunden werden. — Herrn Lunell, Enebyberg, danke ich für das Überlassen des Fundes.

Stockholm den 20. juni 1957.

HANS TRALAU

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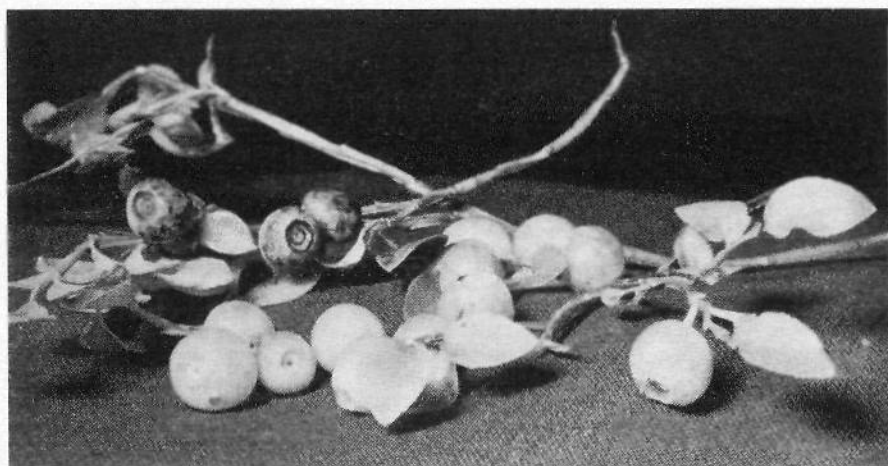


Fig. 1. Vita blåbär från Klockarberget.

Nytt fynd av vita blåbär i Västmanland

Ett nytt fynd av vita blåbär har gjorts i Skinnskatteberg, ett litet samhälle i norra delen av Västmanland. Växtplatsen heter Klockarberget och själva platsen, där blåbärriset växer, är typisk moränmark. Bären växer kring en gammal stubbe, som är helt överväxt av mossa och blåbärris. Skogen runtomkring består av blandskog, barr- och lövträd.

Skinnskatteberg, sept. 1957.

OLLE DANIELSSON

Epipogium aphyllum i Västerdalarna

I Västerdalarna är *Epipogium aphyllum* känd från två lokaler: Transtrand, Millarssäterna och Järna, Vansberget (Almquist 1949, sid. 204). Det förstnämnda fyndet, som gjordes år 1932 på fäbodvallen, har jag tidigare beskrivit i denna tidskrift (Lundberg 1947, sid. 385). Jag skall här redogöra för lokalen vid Vansbergets fäbod och för två nya lokaler 1—2 km söder därom vid Källfallets fäbod.

Hösten 1940 fann fru Lisa Persson *Epipogium aphyllum* ca en km nordväst om Vansbergets fäbod väster om sjön Van i Järna socken. Det var 7 eller 8 blommande exemplar, som växte tätt tillsammans, som de vore planterade i en blomkruka. Följande år blommade *Epipogium* åter på samma ställe, men blommorna stodo då ej så tätt som första året. Detta år tog fru Persson ett exemplar, vilket fotograferades och avbildades i Mora Tidning. Samtidigt publicerades en kort notis om fyndet (Mora Tidning nr 104 sid. 4 1941). Sedan dess har fru Persson återfunnit *Epipogium* varje år utom 1956, då inga blommande exemplar kunde upptäckas. Antalet har varierat mellan 5 och 8, och de ha i allmänhet kommit upp på nya ställen varje år inom ett område

av omkring 100 m². I år besökte jag platsen den 29 juli, men då kunde ingen *Epipogium* iakttagas. Möjligen gjordes besöket en eller två veckor för tidigt.

År 1943 upptäckte Alfred Kristiansson fyra blommande exemplar av *Epipogium* ca en km nordväst om Kilfallets fäbod, vilken ligger omkring 1,5 km söder om Vansbergets fäbod. Två av dem hade fyra blommor och voro över två dm höga. Herr Kristiansson har sedan besökt denna lokal varje år utom år 1956 och varje gång funnit blommande exemplar. Antalet har varierat men ej varit mindre än sex. Ett år räknade han till över 50, av vilka 30 växte i en mycket tät grupp.

Något år senare, troligen år 1945, fann herr Kristiansson *Epipogium* på en ny lokal, belägen väster om Kilfallets fäbod vid Övre Kilfallskällan. Här har *Epipogium* återfunnits nästan varje år (inget besök gjordes 1956). Antalet exemplar har varierat mellan 1 och 6.

Ej heller på dessa båda lokaler ha blommorna kommit upp på samma stäl- len år efter år. Ibland är blommorna knappast synliga över mossan, och ibland kan stängeln mäta två dm eller mera.

Den 17 augusti i år hade jag tillfälle att tillsammans med herr Kristiansson göra ett besök på dessa båda lokaler. På den förstnämnda, som är ca 60 m lång och 5 m bred, funno vi sex exemplar med 1—3 blommor; på den sist- nämnda, som är ungefär hälften så stor som den förra, ett exemplar med tre blommor.

Dessa tre Järna-lokaler för *Epipogium* äro ganska sumpiga. De två först- nämnda ha på de senare åren överväxits och beskuggats av björk och gran, vilket haft till följd, att antalet blommande exemplar minskat. Lokalen vid Övre Kilfallskällan är mera öppen, men även här förekommer björk och gran. Omedelbart nedanför källan är det mycket fuktigt, och fuktigheten minskar åt sidorna och nedåt. *Epipogium* har ej iakttagits på de fuktigaste ställena, utan den brukar växa på mosstuvor eller på andra ej alltför våta platser.

Det är ej vanligt, att *Epipogium* återkommer år efter år under så lång tid på samma lokaler.¹ Jag undersökte därför lokalen vid Kilfallskällan närmare, och vid mitt besök där den 17.8.1957 antecknades förutom björk och gran följande fanerogamer och kärlekryptogamer:

<i>Athyrium filix-femina</i>	<i>Equisetum arvense</i>	<i>Majanthemum bifolium</i>
<i>Carex echinata</i>	— <i>silvaticum</i>	<i>Melampyrum silvaticum</i>
— <i>pauciflora</i>	<i>Geranium silvaticum</i>	<i>Melica nutans</i>
<i>Chrysanthemum leucan-</i>	<i>Geum rivale</i>	<i>Orchis maculata</i>
<i>themum</i>	<i>Hieracium (vulgat.) cala-</i>	<i>Oxalis acetosella</i>
<i>Cirsium palustre</i>	<i>tharium</i> ²	<i>Parnassia palustris</i>
<i>Coralliorrhiza trifida</i>	<i>Lastrea dryopteris</i>	<i>Phleum alpinum</i>
<i>Deschampsia caespitosa</i>	<i>Linnaea borealis</i>	<i>Pinguicula vulgaris</i>
<i>Empetrum nigrum</i>	<i>Listera cordata</i>	<i>Polygonum viviparum</i>
<i>Epilobium palustre</i>	— <i>ovata</i>	<i>Potentilla erecta</i>

¹ Frisendahl anför tre exempel på blomning år efter år: vid Oppmannasjön i Skåne på 1850-talet. Frösåker i Västmanland 1842—1848 och vid Östersund 1880—1910 (Frisendahl 1910 sid. 92, 94, 99).

² (verisim.) det. S. Nordenstam.

<i>Pyrola minor</i>	<i>Salix</i> sp.	<i>Vaccinium vitis idaea</i>
— <i>secunda</i>	<i>Solidago virgaurea</i>	<i>Veronica officinalis</i>
<i>Ranunculus acris</i>	<i>Trientalis europaea</i>	<i>Viola palustris</i>
<i>Rubus saxatilis</i>	<i>Vaccinium myrtillus</i>	

Av dessa äro följande 9 ej förut nämnda i samband med *Epipogium* i Dalarna (jfr Samuelsson 1917, sid. 80, 81, Arwidsson 1926, sid. 163—165, Lundberg 1947, sid. 385):

<i>Carex pauciflora</i>	<i>Empetrum nigrum</i>	<i>Listera ovata</i>
<i>Chrysanthemum leucanthemum</i>	<i>Equisetum arvense</i>	<i>Parnassia palustris</i>
<i>Cirsium palustre</i>	<i>Geum rivale</i>	<i>Pinguicula vulgaris</i>

På den norra lokalen, som beskuggas av uppväxande björk och gran, dominerar *Athyrium filix femina*. Här gjordes ingen fullständig inventering, men artantalet var här ej så stort som vid Kilfallskällan. Som nya antecknades *Lastrea phegopteris* och *Paris quadrifolia*.

Följande mossor insamlades vid Kilfallskällan (levermossorna bestämda av Elsa Nyholm, övriga av Stig Waldheim):

<i>Aulacomnium palustre</i>	<i>Mnium pseudopunctatum</i>	<i>Rhytidiadelphus triquetrus</i>
<i>Barbilophozia lycopodioides</i>	— <i>rugicum</i>	<i>Riccardia pinguis</i>
<i>Brachythecium salebrosum</i>	<i>Paludella squarrosa</i>	<i>Scapania undulata</i>
<i>Bryum pseudotriquetrum</i>	<i>Philonotis fontana</i>	<i>Sphagnum parvifolium</i>
<i>Calliergon stramineum</i>	<i>Pleurozium Schreberi</i>	— <i>plumulosum</i>
<i>Dicranum majus</i>	<i>Polytrichum commune</i>	— <i>Warnstorffii</i>
<i>Hylocomium splendens</i>	<i>Ptilium crista-castrensis</i>	<i>Tomenthypnum nitens</i>
	<i>Rhytidiadelphus squarrosus</i>	

Epipogium är uppgiven för några lokaler i södra delen av Vänjans socken ej långt från Vansberget. Det är Finngruvans, Kättbo och Landbobyns besparingsskogar (Almquist l.c.). Om förekomsten i Kättbo besparingsskog skriver Vesterlund (Vesterlund 1918, sid. 23):

»Aldrig har jag dock sett skogsfrun blomma så rikligt som förliden sommar [1916] på Kättbo besparingsskog¹ i södra delen av Vänjans socken, Dalarna. Inom ett mycket tätt granbestånd av ungefär 2 hektars ytvidd räknade jag därstädes icke mindre än ett femtiotal blommande exemplar. Några stjälkar hade ända till fyra blommor. Två å tre är annars det vanliga. Mindre exemplar hava ofta nog blott en blomma.

I allmänhet uppträda de blommande exemplaren enstaka, men här fann jag på ett ställe en hel buket av åtta stycken.»

Här liksom vid Vansberget och Kilfallets fåbodar har *Epipogium* uppträtt i täta grupper. De fem exemplaren från Millarssättern i Transtrand stodo också tätt (Lundberg l.c.). Ett liknande exempel från Pesisvare i Jukkasjärvi anföres av Sernander (Sernander 1928, sid. 486). Han skriver: »*Epipogium*-beståndet upptog en mycket liten fläck på omkring en kvadratdecimeter av

¹ Väster om Brintheadarna.

14 nära varandra stående stänglar, ovisst om hur många individ de representerade».

Det är troligt, att det i dessa fall rör sig om för första gången blommande individ. Efter groningen tillväxa de underjordiska delarna omkring groningen-platsen, och när den första blomningen äger rum, har rhizomet ej hunnit växa så långt. Stänglarna komma därför att stå tätt. Rhizomet växer sedan perifert och breder ut sig över allt större yta, vilket har till följd, att stänglarna komma upp glesare och glesare för varje år. Så har utvecklingen tydligen varit vid Vansbergets fäbod.

De blommande exemplaren skulle alltså vara delar av ett och samma individ (d.v.s. vara en klon). Detta skulle kunna ge en förklaring till den dåliga frukt-sättningen hos *Epipogium* (högst 1 % enl. Frisendahl 1910, sid. 104).

Kungälv, oktober 1957.

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Starkare förkortningar

- AAS: Acta Agriculturae Scandinavica, Stockholm.
ACGen: Atti IX Congr. Intern. Genet. Bellagio 1953, 2, Caryologia 6, Suppl., 1954, tr. 1956.
ACS: Acta Chemica Scandinavica, Köbenhavn (tr. i Helsinki).
AFB: Arkiv för Botanik, Stockholm.
AFK: Arkiv för Kemi, Stockholm.
Agri Hort. Gen.: Agri Hortique Genetica, Landskrona.
BN: Botaniska Notiser, Lund.
ECR: Experimental Cell Research, New York (tr. i Uppsala).
GP: Grana Palynologica. N.S. Utg. av G. Erdtman, Stockholm.
Her.: Hereditas, Lund.
JGD: Jord-Gröda-Djur. Svensk Jordbruksforskning, Stockholm.
KLA: K. Lantbrukshögskolans Annaler, Uppsala.
KSLT: K. Skogs- och Lantbruksakademiens Tidskrift, Stockholm.
Nat. i Vb. o. Nb.: Natur i Västerbotten och Norrbotten. U. red. av F. Ebeling och K. Curry-Lindahl, Stockholm.
NJ: Nordisk Jordbruksforskning, Stockholm.
NST: Norrlands Skogsvårdsförbunds Tidskrift, Stockholm.
PFÅ: Sveriges Pomologiska Förenings Årsskrift, Stockholm.
PP: Physiologia Plantarum, Köbenhavn (tr. i Lund).
SBT: Svensk Botanisk Tidskrift, Stockholm.
SJ: Statens Jordbruksförsök. Meddelande, Stockholm.
SkN: Skånes Natur, Lund.
SS: Statens Skogsforskningsinstitut, Stockholm.
SST: Svenska Skogsvårdsföreningens Tidskrift, Stockholm.

SUT: Sveriges Utsädesförenings Tidskrift, Svalöv.

SV: Statens Växtskyddsanstalt, Experimentalfältet.

SvN: Sveriges Natur, årsbok och tidskrift, Stockholm.

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3. BONNER, J. T., and EDEN, M.: The form of the frequency distribution curve of cell and nuclear sizes. ECR 11, 265—269.
4. BRODIE, H. J.: The structure and function of the funiculus of the Nidulariaceae. SBT 50, 142—162.
5. DAHLGREN, K. V. O.: Fruktchimärer särskilt hos Äkeröpplen. SBT 50, 287—298, summary 297.
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9. HÅKANSSON, A.: Seed development of *Brassica oleracea* and *B. rapa* after certain reciprocal pollinations. Her. 42, 373—396.
10. — Seed development of *Picea abies* and *Pinus silvestris*. Medd. SS 46: 2, 23 s., sammanfattn. 19—20.
11. IKUSE, M.: Some noteworthy pollen grains from Japan. GP 1: 2, 148—150.
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15. LEYON, H.: The structure of chloroplasts. Sv. kem. tidskr. 68, 70—89. (Äv. diss. Uppsala.)
16. L. (LJUNG), A.: Egendommeligt växtsätt hos en *Bellis*. Hallands Natur 20, 40—41.
17. v. LÜRZER, E.: Megasporenmembranen bei einigen Cupressaceen. GP 1: 2, 70—78.
18. MAURIZIO, A.: Pollengestaltung bei einigen polyploiden Kulturpflanzen. GP 1: 2, 59—69, summary 68.
19. MÜLLER-STOLL, W.: Über das Verhalten der Exine nonaperturater Angiospermen-Pollen bei Quellung und Keimung. GP 1: 2, 38—58, summary 57.
20. PEASE, P.: Some observations upon the development and mode of attachment of the flagella in *Vibrio* and *Spirillum* species. ECR 10, 234—237.
21. PRAGLOWSKI, J.: On the size of the pollen grains in *Helicia*, *Heliciopsis*, and *Hicksbeachia*. GP 1: 2, 150—153.
22. RAJU, M. V. S.: Development of embryo and seed coat in *Turnera ulmifolia* L. var. *angustifolia* Willd. BN 109, 308—312.

23. RAJU, M. V. S., and PATANKAR, J. B. V.: Pollen morphology in three species of *Drosera*. GP 1:2, 153—155.
24. RIBI, E., and SALVIN, S. B.: Antigens from the yeast phase of *Histoplasma capsulatum*. I. Morphology of the cell as revealed by the electron microscope. ECR 10, 394—404.
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26. STÄLFELT, M. G.: Morphologie und Anatomie des Blattes als Transpirationsorgan. Handb. d. Pflanzenphysiologie III, 324—341.
27. SVEDELIUS, N.: Are the haplobiontic Florideae to be considered reduced types? SBT 50, 1—24.
28. TEILING, E.: On the variation of *Micrasterias mahabuleshwariensis* f. *Wallichii*. BN 109, 260—274.
29. TURIAN, G., et KELLENBERGER, E.: Ultrastructure du corps paranucléaire, des mitochondries et de la membrane nucléaire des gamètes d'*Allomyces macrogynus*. ECR 11, 417—422, summary 422.
30. WEIBULL, C.: The nature of the 'ghosts' obtained by lysozyme lysis of *Bacillus megaterium*. ECR 10, 214—221.
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Se även nr 96, 109, 141, 217, 223, 228 a, 252, 271, 399, 401, 559, 563.

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32. AL KHOLY, A. A.: On the assimilation of phosphorus in *Chlorella pyrenoidosa*. PP 9, 137—143.
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34. BERGQVIST, R.: The acid-soluble nucleotides of wheat plants. ACS 10, 1303.
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Genetik. Cytologi

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H. HJELMQVIST.

Litteratur

CARL P. SWANSON: Cytology and cytogenetics. 596 sid. — Prentice-Hall, Inc. Englewood Cliffs, N. J., april 1957. — Pris doll. 13,75.

Detta är en ganska välkommen bok. Vi ha under senare år fått ganska många nya läroböcker i genetik med ett innehåll motsvarande ungefär vad som kan fordras till 2 betyg i fil. ämbetsexamen men ej mera, för mera avancerade studier ha sammanfattande arbeten med undantag av Goldschmidts *Theoretical genetics* knappt annat än rörande specialområden kommit ut. Och med läroböcker i cytologi är det klenst beställt, med undantag av Whites *Animal cytology and evolution*. I ett förord säger författaren »this book brings together in integrated fashion the findings of cellular morphology, behaviour, physiology and biochemistry, which have been grouped under the general term »cytology», and then considers these data in their relation to inheritance and evolution.» Bokens innehåll är med dessa ord angivet.

Som författaren själv upplyser om består boken av tre delar. De fyra första av de 18 kapitlen är av mera översiktlig natur och meddela elementära fakta i genetik och kromosomforskning. Man finner framställningen vara modern, bl.a. återfinnes t.ex. D. von Wettsteins elektronmikrofotografier av kloroplast från normal kornplanta och *xantha*-mutant. Sedan följer bokens huvudinnehåll, som utgöres av nio kapitel, vilka visserligen äro ganska utförliga men därför naturligtvis ej ha handbokskaraktär. Kapitlet om kromosomstruktur har sålunda 43 sidor och som specialtyper av kromosomer behandlas här lampborst- och spottkörtelkromosomer jämte accessoriska, vilka senare kallas supernumerary. De senare få blott två textsidor. De flesta specialkapitlen ha ungefär samma storlek som detta. De äro skrivna på ett lättförståeligt sätt och ge tillsammans en lättläst, rikt illustrerad sammanfattning av den moderna forskningen. Kapitlet om variationen av kromosomernas struktur och antal kompletteras av ett, som behandlar strukturella olikheter och poly- och aneuploid. I kapitlet om kromosomernas rörelser behandlas utom rörelser i kärnspolen även utförligt sådana inom kärnmembranen, kontraktioner, spiralisering och synapsis. »Crossing over and chiasma formation»-kapitlet behandlar även tetradanalys hos *Neurospora* och även motsvarande förhållande (t.ex. transduktion) hos bakterier och virus. Bellings hypotes anses märkvärdigt nog ge den mest sannolika förklaringen till vanlig crossing over; många forskare ha ansett den osannolik eller rent av utsluten. I starkt omstridda frågor refererar förf. olika meningar opartiskt, utan att själv taga bestämd ståndpunkt. Kapitlet kallat »Variations in chromosome behaviour» innehåller mycket av det mest fräppanta i cytologin: endomitosis, diminution och elimina-

tion, preferential segregation (rättare väl pref. non-disjunction, det gäller t.ex. accessoriska kromosomer hos råg) m.m. Kapitlet om spontana och inducerade kromosomaberrationer behandlar även rätt utförligt inverkan av strålning och kemikalier på kromosomerna, ett område där författaren själv varit verksam; det är en välkommen sammanfattning. Kapitlet om kärnans och kromosomernas kemi är däremot kortare. Slutligen behandlas »kromosomer och gener» rätt utförligt, det diskuteras olika moderna uppfattningar av genens natur och storlek, mutationers framkallande, *Ac-DC* effekt i majs. Andra hithörande aspekter behandlas snävare.

De sista kapitlen, som författaren själv erkänner mera kortfattade, ge dock utförliga litteraturanvisningar. Evolution av karyotyper och könsbestämmande mekanismer, kromosomaberrationens och polyploidins roll i evolutionen samt apomixis och partenogenesis ha alltså fått en annorlunda, mera översiktlig behandling än den rena cytogenetiken.

ARTUR HÅKANSSON

PIERRE DANSEREAU: Biogeography. An ecological perspective. — The Ronald Press, New York. 1957. Pris 7.50 dollars.

Amerikanska läroböcker i botanik har visat sig ha ett ganska begränsat intresse för skandinaviska universitet, eftersom de i vanliga fall skrivits för ett stadium, som står någonstans mellan läroverket och ett-betygs-kursen. I andra fall är de för specialiserade, och grundliga översikter för ett högre stadium finns endast för ett fåtal områden, ty ingenstans i den Nya Världen studeras alla botanikens faser så i detalj, som man anser nödvändigt i Sverige innan specialiseringen börjar. Dock har amerikanska biologer skrivit några av de förnämsta läroböcker, som finns tillgängliga för högstadiet, huvudsakligen inom evolutionens och växtgeografiens domäner. En kurs i genetik utan Dobzhanskys och Stebbins översikter vore ofullständig, och en botanik-kurs utan Stebbins och Cains böcker kan knappast anses vara modern.

Den nya bok om biogeografi, som Pierre Dansereau just publicerat, ser ut att tillhöra den grupp av litteratur, som nog kommer att anses oumbärlig i en modern botanik-kurs. Eftersom dess perspektiv är så brett, att det inkluderar alla sidor av den moderna växtgeografien och ekologien, ger den en grundläggande information av det slag som knappast finns annorstädes, på samma gång som den ger detaljerade diskussioner, vilka för läsaren betydligt längre in i ekologiens »djungler» än t.ex. Cains i övrigt utmärkta bok kunde göra, då den publicerades för nära ett och ett halvt årtionde sedan. På mindre än 300 sidor får läsaren hos Dansereau först lära sig alla de många grundläggande teser och termer, som den moderna biogeografien rör sig med, och sedan de flesta av de detaljer, som kännetecknar nutidens studier av växternas distribution och historia, bioklimatologi, synekologi och autekologi, så väl som människans och landskapets samspel. Ett otal exempel ges i klagörande syfte från olika delar av världen, eftersom författaren personligen och mera ingående känner till flera världsdelar än de flesta andra nu levande växtgeografer. Bilder och upplysande diagram pryder nästan varje sida av boken. Tyvärr verkar det som om ganska många av bilderna kopierats från färgfotografier, varför de

har förlorat i skärpa i reproduktionen, men teckningarna tillhör det bästa som tryckts i botaniska läroböcker.

Att ge en detaljerad översikt över denna väl skrivna och koncentrerade lärobok skulle ta allt för mycket plats, och en diskussion av dess mera speciella drag, särskilt författarens kanske ej alltid konventionella åsikter, kunde föra oss allt för långt ifrån de ännu kanske ej fullt vedertagna grunderna för somliga av de olika växtgeografiska och ekologiska hypoteserna. Även om författaren har lyckats förvånansvärt väl att undvika att ta bestämd ställning, då han ger läsaren nödvändiga upplysningar om biogeografiens många faser, har han dock satt sin tydliga prägel speciellt på kapitlet om autekologi och i synnerhet på dess tre slutartiklar om populationens struktur, dess tillfälle till utveckling, och lagarna om ekologisk lämplighet, eftersom han själv bidragit i så hög grad till studierna av just dessa fenomen.

Dansereaus Biogeografi är en bok, som man vill rekommendera till alla intresserade i växtgeografiens olika delar. Den är på en gång en utmärkt inledning för dem, som vill specialisera sig på olika områden av denna vittomfattande vetenskap, och en förstklassig översikt för specialister inom andra fack, vilka anser sig behöva lära mera om växtgeografiens betydelsefulla fält. Specialisterna kommer nog att hitta diskutabla påståenden eller onödiga luckor i litteraturhänvisningarna, och här och där i boken har smärre fel insmugit sig som i alla goda böcker. Det är också sannolikt, att somliga kommer att känna sig frestade till att motbevisa vissa av teserna eller att kontrollera vissa såkallade lagar med hjälp av experiment eller mätningar. Men alla kommer säkert att känna sig stimulerade av boken och ingen kommer att lägga den ifrån sig utan att ha lärt en hel del nytt, både i teori och terminologi. Tillsammans med Cains och Stebbins välkända böcker kommer Dansereaus Biogeografi att fylla ett behov för en fullt modern kurs i systematisk botanik och växtgeografi för högstadiet, var som helst i världen.

ÅSKELL LÖVE

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