

Det Kongelige Danske Videnskabernes Selskab

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EXPERIMENTAL  
AND CYTOLOGICAL STUDIES ON PLANT  
SPECIES

II. TRIFOLIUM ARVENSE AND SOME OTHER  
PAUCIENNIAL HERBS

BY

TYGE W. BÖCHER, KAI LARSEN AND KNUD RAHN



København 1955

i kommission hos Ejnar Munksgaard

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## I. Introduction.

In a previous paper (BÖCHER, LARSEN & RAHN 1953) the genotypical variation of the duration of life, growth and development in annuals was touched on at the demonstration of some cases of inhibition of flowering in certain cultures of *Kohlrauschia*. In *Trifolium arvense*, which is the main subject in the present paper, a similar inhibition occurs very frequently, thus inviting further study.

On the whole the variation in this species is very interesting, and cytologically the species is remarkable by its content of so far one tetraploid among very many diploid populations scattered over large parts of Europe. The other species mentioned in what follows may in different ways contribute to the knowledge of the geographical distribution of certain hereditary and fundamental biological properties in annual or pauciennial herbs.

As in the case of the material mentioned in our previous paper, the present material is to a great extent based on seed samples collected during a journey to SW-Europe in 1949 which was supported by the Carlsberg Foundation. In this journey Director HOLGER S. DAHL together with the two first authors took part. The material was cultivated in the experimental areas of the Botanical Gardens of the University of Copenhagen.

## II. *Trifolium arvense* L.

**Cytology.** The chromosome number  $2n = 14$  was already found by BLEIER (1925) and is further mentioned by KARPECHENKO (1925), although his drawing only shows 13 chromosomes.  $2n = 14$  was later established by ARUTIUNOVA (1940) and LÖVE & LÖVE (1944). As compared with other species of clover *T. arvense* according to ARUTIUNOVA is distinguished by having a normal two-armed chromosome, which is satellited.

Our material was fixed in MÜNTZING'S modification of NAVASHIN-KARPECHENKO'S fixative. The number  $2n = 14$  occurred in 30 cultures; only in one, no. 3093 from Wroclaw in Silesia the tetraploid number  $2n = 28$  was found. The diploids had always two and the tetraploid four large satellites and frequently the connecting link between the satellite and the rest of the chromosome was very long and invisible

(fig. 1 b, c, e). In such cases, however, it was possible to see the connection when using phase-contrast microscopy (fig. 1 d). As described in *Taraxacum* by SØRENSEN & GUDJONSSON (1946, figs. 16—18), the satellites in *Trifolium arvense* are often bent in such a way that they project more or less vertically from the metaphase plane. They were larger than those pictured by ARUTIUNOVA, a fact which may be due to a different fixation technique.

Altogether 37 diploids and one tetraploid is known in *T. arvense*. This confirms the idea that the chance of finding diploid and tetraploid races within the same species

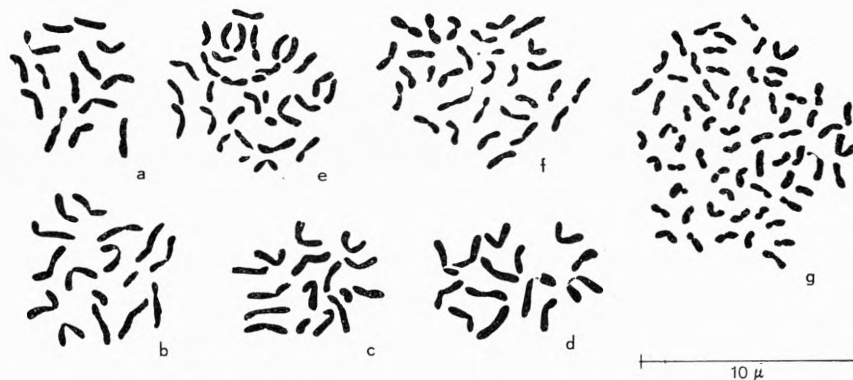


Fig. 1. Mitoses from root tips. a—d diploid, e tetraploid *Trifolium arvense* (a no. 2874, b—c no. 2929, d no. 2923, e no. 3093). f *Kohlruschia velutina* no. 3303. g *Galium aparine* no. 1639. The connections to the satellites are invisible in figs. b, c (two satellites), and e (four satellites). In fig. a they were visible owing to particularly successful staining, in fig. d only when observed in a phase-contrast microscope. In fig. f two minute satellites and two very short chromosomes are seen. In fig. g the two large chromosomes which may have arisen by fusion of four short chromosomes are seen on the right (at 1 and 3 o'clock).

is fairly great provided that the investigations are extended to cover many strains from a large area (cp. BÖCHER & LARSEN 1955).

The tetraploid strain was cultivated in 1952 (Table 3). It was very early, without any inhibition of flowering. It resembled very much some of the southern races among the diploids. Unfortunately no plants from this experiment were dried and, therefore, it was impossible to make a closer study of the size of the seeds, the pollen, and the stomata which might have distinguished the tetraploid from the diploids.

**Experimental cultivations.** Five experiments were made in 1950, 1951, 1952, 1953, and 1954.

1950 (Table 1): 14 cultures (6 from southern, 4 from central, and 4 from northern Europe) were grown in a sandy experimental field at Tokkekøb Hegn, Zealand. In Table 1 the material is arranged according to earliness of flowering. All southern strains were very early and flowered between June 15th and July 30th after being sown early in April. Maximum speed of development was achieved by no. 1671 from the highlands in the eastern part of the Pyrenees. It required 50 days only from germination to flowering. As compared with the other southern cultures

Table 1. *Trifolium arvense*. Cultivations 1950 (sandy soil).  
Each culture consisted of 7-16 individuals.

Cult. no.	Origin. Seeds collected by us in nature or from wild sources through Bot. Gardens (*)	2 n	Ap-proxim. no. of days from germination to flowering	Height (H) in cm Mean and range <sup>1</sup>	Breadth (B) in cm Mean and range <sup>1</sup>	Size index $\frac{B \times H}{100}$	Length of heads in cm Mean and range <sup>1</sup>	Habit of plants in the autumn
1671	S. France, Formiguères, alt. 15-1600 m . . . . .	14	50	20 { 11 25	24 { 19 30	4.8	2.9 { 2.5 3.5	No basal leaves. Stem erect, much branched, with long internodes (open structure). Fruits ripe or already shed.
2394	France, Rouen* . . . . .	14	75	22 { 16 27	24 { 20 34	5.3	2.9 { 2.0 3.5	
2441	Portugal, Coimbra* . . . . .	14	75	27 { 16 40	34 { 22 44	9.2	3.0 { 2.0 3.5	
2393	France, Dijon* . . . . .	14	75	29 { 24 35	39 { 27 48	11.3	3.7 { 3.0 4.5	
1732	S. France, Béziers, Roque Haute . . . . .	14	85	17 { 12 28	24 { 15 40	4.1	1.9 { 1.5 3.0	
1631	S. France, Luchon, bottom of valley . . . . .	14	85	23 { 17 28	55 { 48 78	12.7	2.3 { 2.0 3.5	
1706	S. France, Bouleternère (maquis) . . . . .	14	85	33 { 24 38	70 { 47 35	23.1	2.6 { 2.0 3.5	
1304	S. France, Contis de Bains. Dunes . . . . .	14	100	20 { 14 25	49 { 30 68	9.8	2.6 { 2.0 3.5	Basal leaves retained, ± plagiotropic growth.
2333	Denmark, Amager (the Sound) . . . . .	14	100	about 8	about 32	about 2.6	about 2.1	
2247	Denmark, Boserup . . . . .	14	130	—	—	—	—	Basal leaves retained. Only 2/3 of plants with late flowering.
2442	Hungary, Budapest* . . . . .	14	140-?	—	—	—	—	
2395	Germany, Frankfurt a.M.*	14	140-?	—	—	—	—	Basal leaves retained. A few plants with very late flowering.
2207	Denmark, Gadevang . . . . .	14	(?)	—	—	—	—	
2293	Denmark, Kregme . . . . .	14	(?)	—	—	—	—	Only basal leaves, no flowering stems.

<sup>1</sup> The ranges indicated in braces.

Table 2. *Trifolium arvense*,  
The batches consisted of 7–11 individuals

Cult. no.	Origin (cf. Table 1)	2 n	Approx. no. of days from germination to flowering	Cultures in pots in		
				Height (H) in cm Mean <sup>1</sup>	Breadth (B) in cm Mean <sup>1</sup>	Size index $\frac{B \times H}{100}$
1671	S. France, Formiguères, alt. 15—1600 m .....	14	60—70	16 $\left\{ \begin{array}{l} 11 \\ 26 \end{array} \right.$	45 $\left\{ \begin{array}{l} 35 \\ 57 \end{array} \right.$	7.2
2804	Portugal, Sacavem* .....	14	60—70	34 $\left\{ \begin{array}{l} 27 \\ 38 \end{array} \right.$	48 $\left\{ \begin{array}{l} 43 \\ 59 \end{array} \right.$	16.3
2441	Portugal, Coimbra* .....	14	60—70	31 $\left\{ \begin{array}{l} 24 \\ 38 \end{array} \right.$	55 $\left\{ \begin{array}{l} 50 \\ 61 \end{array} \right.$	17.1
2759	Portugal, Lisbon* .....	14	60—70	38 $\left\{ \begin{array}{l} 35 \\ 44 \end{array} \right.$	43 $\left\{ \begin{array}{l} 38 \\ 50 \end{array} \right.$	16.3
1732	S. France, Roque Haute .....	14	80—90	20 $\left\{ \begin{array}{l} 10 \\ 24 \end{array} \right.$	49 $\left\{ \begin{array}{l} 42 \\ 60 \end{array} \right.$	9.8
1706	S. France, Bouleternère .....	14	80—90	24 $\left\{ \begin{array}{l} 17 \\ 34 \end{array} \right.$	55 $\left\{ \begin{array}{l} 42 \\ 64 \end{array} \right.$	13.2
1631	S. France, Luchon .....	14	80—90	26 $\left\{ \begin{array}{l} 13 \\ 38 \end{array} \right.$	85 $\left\{ \begin{array}{l} 79 \\ 97 \end{array} \right.$	22.1
2758	Yugoslavia, Ljubljana* .....	14	100—110	..	..	..
2779	Austria, Graz* .....	14	100—110	..	..	..
2696	Denmark, Ræbild Bakker .....	14	100—110	40 $\left\{ \begin{array}{l} 37 \\ 45 \end{array} \right.$	61 $\left\{ \begin{array}{l} 50 \\ 70 \end{array} \right.$	24.4
2654	Denmark, Nøddebo Huse .....	14	130—150	..	..	..
2677	Denmark, Muldbjergene .....	—	130—150	..	..	..
2665	Denmark, Bulbjerg Huse .....	14	130—150	..	..	..
2690	Denmark, Lild Strand .....	—	160—170	..	..	..

<sup>1</sup> Mean values and the ranges indicated in braces.



## Cultivations 1951.

(in cult. 2654, 2665 and 2577 : 2-6).

Bot. Gardens		Cultures in the experimental field (clay)					Habits of plants in the autumn
Approx. dry weight pr. plant in g	Length of heads in cm Mean <sup>1</sup>	Height (H) in cm Mean <sup>1</sup>	Breadth (B) in cm Mean <sup>1</sup>	Size index $\frac{B \times H}{100}$	Approx. dry weight pr. plant in g	Length of heads in cm Mean <sup>1</sup>	
3	3.1 $\left\{ \begin{array}{l} 2.0 \\ 4.0 \end{array} \right.$	..	..	..	..	..	No basal leaves, fruits ripe or already shed about September 1st.
4	3.2 $\left\{ \begin{array}{l} 2.4 \\ 4.1 \end{array} \right.$	17 $\left\{ \begin{array}{l} 10 \\ 21 \end{array} \right.$	30 $\left\{ \begin{array}{l} 22 \\ 40 \end{array} \right.$	5.1	3	2.6 $\left\{ \begin{array}{l} 2.1 \\ 4.0 \end{array} \right.$	
6	3.0 $\left\{ \begin{array}{l} 2.3 \\ 3.6 \end{array} \right.$	16 $\left\{ \begin{array}{l} 10 \\ 24 \end{array} \right.$	28 $\left\{ \begin{array}{l} 13 \\ 40 \end{array} \right.$	4.5	4	2.1 $\left\{ \begin{array}{l} 1.2 \\ 3.0 \end{array} \right.$	
8	3.2 $\left\{ \begin{array}{l} 2.2 \\ 3.5 \end{array} \right.$	21 $\left\{ \begin{array}{l} 15 \\ 30 \end{array} \right.$	42 $\left\{ \begin{array}{l} 37 \\ 45 \end{array} \right.$	8.8	8	2.7 $\left\{ \begin{array}{l} 2.4 \\ 3.1 \end{array} \right.$	
6	2.7 $\left\{ \begin{array}{l} 1.8 \\ 3.8 \end{array} \right.$	14 $\left\{ \begin{array}{l} 12 \\ 15 \end{array} \right.$	26 $\left\{ \begin{array}{l} 20 \\ 31 \end{array} \right.$	3.6	2	2.4 $\left\{ \begin{array}{l} 1.8 \\ 2.8 \end{array} \right.$	
7	2.3 $\left\{ \begin{array}{l} 1.0 \\ 3.0 \end{array} \right.$	..	..	..	..	..	
9	2.3 $\left\{ \begin{array}{l} 2.0 \\ 2.8 \end{array} \right.$	18 $\left\{ \begin{array}{l} 11 \\ 23 \end{array} \right.$	47 $\left\{ \begin{array}{l} 37 \\ 61 \end{array} \right.$	8.5	8	1.8 $\left\{ \begin{array}{l} 1.4 \\ 2.1 \end{array} \right.$	
..	..	46 $\left\{ \begin{array}{l} 41 \\ 56 \end{array} \right.$	89 $\left\{ \begin{array}{l} 75 \\ 97 \end{array} \right.$	40.9	12	2.2 $\left\{ \begin{array}{l} 1.8 \\ 2.8 \end{array} \right.$	No basal leaves, fruits ripe or shed about October 8th.
..	..	26 $\left\{ \begin{array}{l} 14 \\ 39 \end{array} \right.$	69 $\left\{ \begin{array}{l} 39 \\ 94 \end{array} \right.$	17.9	6	1.5 $\left\{ \begin{array}{l} 1.2 \\ 1.8 \end{array} \right.$	
8	2.1 $\left\{ \begin{array}{l} 1.5 \\ 2.8 \end{array} \right.$	31 $\left\{ \begin{array}{l} 20 \\ 43 \end{array} \right.$	50 $\left\{ \begin{array}{l} 26 \\ 68 \end{array} \right.$	15.5	6	2.2 $\left\{ \begin{array}{l} 1.5 \\ 3.5 \end{array} \right.$	
..	..	10 $\left\{ \begin{array}{l} 6 \\ 14 \end{array} \right.$	38 $\left\{ \begin{array}{l} 24 \\ 43 \end{array} \right.$	3.8	5	1.7 $\left\{ \begin{array}{l} 1.1 \\ 2.2 \end{array} \right.$	Basal leaves frequently retained, fruits ripe or almost ripe about October 8th.
..	..	about 13	about 47	about 6	6	about 2	
..	..	about 15	about 35	about 5	6	about 2	
..	..	..	..	..	..	..	Basal leaves retained. Flowering commenced on October 8th.

no. 1671 was a rather gracile type and had a low production of matter. Its contrast was no doubt the tall growing no. 1706 from Mediterranean maquis in the eastern Pyrenees (fig. 2). All southern plants very soon lose their basal leaves and get an open shoot structure. Only no. 1305 from the dunes on the Bay of Biscay resembles northern races in keeping the basal leaves. It behaved almost like the Danish no. 2333 from a sandy field on the Sound. In all other cultures the basal

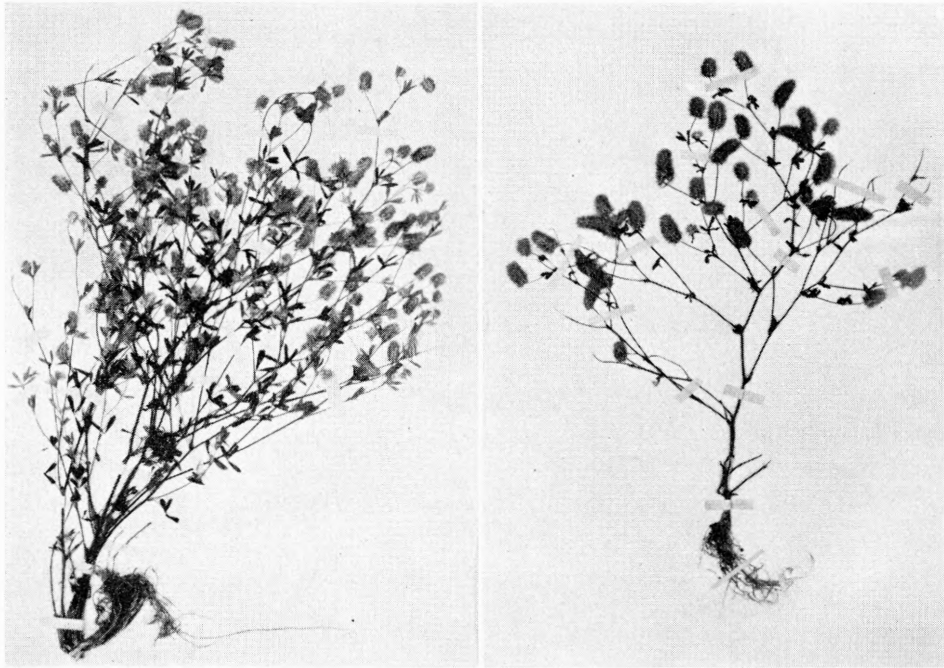


Fig. 2. Two very different Mediterranean races of *Trifolium arvense* in the experiment 1950 (collected Sept. 6th). Left, no. 1706 from a subtropical vegetation in the lowlands; right, no. 1671 from a montane vegetation in the Pyrenees. No. 1671 is very early and has a much lower production of matter. This was very great in no. 1706 (the figure shows only one fourth of a vigorous specimen).  $\times \frac{1}{4}$ .

leaves were retained. They either formed short flowering shoots or did not succeed in flowering at all. Sometimes, however, the stems began to stretch without any floral initiation. Some individuals of these cultures, which were kept in pots in the garden and behaved in a similar manner, were unable to winter.

1951 (Table 2): 14 cultures (including 5 of the strains cultivated in 1950) were grown in pots in the Bot. Gardens or on a loamy experimental field at Albertslund, Zealand. The field soil was rather unfavourable to most of the strains. Plants cultivated in the field were always smaller than those cultivated in pots or cultivated in 1950 on sandy soil.

The flowering and development of the plants correspond to the results from the 1950-experiment. All southern plants were early and without inhibition of flower-

ing, while in a number of northern strains the floral initiation was checked more or less.

Among the cult. nos. from Denmark no. 2696 deviated from the others by developing quite normally although it was late. Its behaviour and size was almost

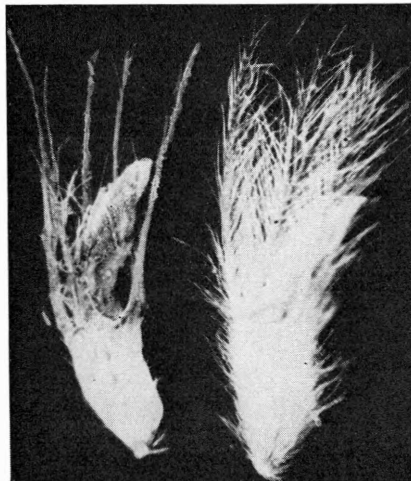


Fig. 3. Above on the left no. 3256 (*Trifolium gracile*) and, on the right, no. 3646 (*T. arvense*) from the 1954 experiment (Table 5). Note the horizontal growth of all secondary stems in *T. gracile*. Below flower of *T. gracile* (no. 3256, on the left) compared with a flower of *T. arvense* (no. 1706).

like the two continental, tall growing samples from Graz and Ljubljana. Of the plants which retained their basal leaves none was able to winter. On the other hand some few plants of southern origin were able to stand the winter and flowered again in 1952.

1952 (Table 3): 19 cultures chiefly from Northern Europe. Seeds of 5 of the cult. nos. were sown partly in September 1951 (denoted as A) partly in April 1952. The two batches differed very much. All plants which germinated in the autumn

Table 3. *Trifolium arvense*, Cultivations 1952.

All cultures diploid ( $2n = 14$ ) with the exception of no. 3093, which was tetraploid ( $2n = 28$ ). A: Seeds of cult. numbers denoted as A were sown partly in April 1952, partly early in September 1951. The latter plants (A or autumn batch), which were exposed to low temperatures and short days during the winter, had all a normal development and flowering.

- 
- I. Cultures liable to inhibition of stem elongation and flowering.
- a. Inhibition complete.
- A. 2871. Denmark, Kramnitze, Lolland (A batch  $\pm$  erect, 20—25 cm high).  
 A. 2874. — Rosenvold, E. Jutland (A batch  $\pm$  erect, about 30 cm high).
- b. Inhibition strong, but not complete, 5—20 per cent. of the plants flowering.
- A. 2882. Denmark, Østerild, NW. Jutland (A batch  $\pm$  erect, 10—20 cm high).  
 2929. — Bulbjerg, —  
 2928. — Haderup, C. Jutland.  
 2907. — Nakkehoved, N. Zealand.
- A. 2872. Sweden, Öland, Greby Alvar (A batch  $\pm$  erect, 12—15 cm high).  
 3098. Poland, Puszczykówko.
- c. Inhibition distinct, but about 50 per cent. of the plants flowering.
- A. 2873. Denmark, Randbøl, C. Jutland (A batch with spreading stems, 10—20 cm high).
- II. Cultures producing numerous elongated flowering stems.
- d. Most plants produce elongated flowering stems; in many plants these, however, wither at an early stage.
2954. Denmark, Kaas, NW. Jutland. Plants more or less prostrate.  
 2926. — Hvide Sande, W. Jutland. Plants with spreading stems.  
 2923. Sweden, Gotland, Gammelgarn. Plants with spreading stems, about 10 cm high.  
 2906. Finland. Åbo region. Irjala<sup>1</sup>. Plants 10—17 cm high with spreading stems.  
 3097. Hungary. Budapest (\*). Plants with spreading or almost horizontal stems.
- e. Almost all plants with normal development and flowering.
2955. Sweden, Fårö, Ajkesvik<sup>2</sup>. Plants 20—25 cm high, with up to 40 cm long ascending shoots.  
 3096. Poland, Osawa Gora. Plants vigorous almost as in 1953 (Table 4).  
 3093. — Wraclaw (\*). Plants  $\pm$  erect, 10—25 cm high, very early.  
 3094. Madeira ((\*) seeds from Lisbon). Plants erect or very ascending, 23—27 cm high, very early.
- 

<sup>1</sup> Seeds collected by Dr. J. JALAS (dry rock vegetation).

<sup>2</sup> Seeds collected by Dr. B. PETTERSSON (*Festuca polesica* among *Ammophila* near the beach).

flowered about July 9th and had ripe fruits in August—September. The plants from the spring could be divided into five groups (a—e Table 3) according to the degree of inhibition of flowering. Southern and some continental strains have a normal development, but most Danish plants are more or less prevented from flowering when sown in April. The three samples mentioned first in Group d from dunes resembled nos. 1304 and 2333 (Table 1), which came from similar habitats.

1953 (Table 4): 6 cult. nos., some of which were repeated from the 1952-experiment, were sown early and germinated about April 1st. After transplantation

Table 4. *Trifolium arvense*, *Cultivations 1953*.  
The batches consisted of 8-14 individuals.

Cult. no.	Origin (cf. Table 1)	2 n	Group in Table 3	Length of photoperiod unaltered					Length of photoperiod 9 1/2 hours					
				Per cent. flowering plants (Sept.)	Height (H) in cm Mean <sup>1</sup>	Breadth (B) in cm Mean <sup>1</sup>	Size index $\frac{B \times H}{100}$	Length of heads in cm Mean <sup>1</sup>	Per cent. flowering plants (Sept.)	Height (H) in cm Mean <sup>1</sup>	Breadth (B) in cm Mean <sup>1</sup>	Size index $\frac{B \times H}{100}$	Length of heads in cm Mean <sup>1</sup>	
3094	Madeira (*), from Lisbon.....	14	e	100	25 { 21 31 }	41 { 35 49 }	10.3	2.5 { 2.0 3.0 }	100 <sup>4</sup>	19 { 12 26 }	47 { 33 58 }	8.9	2.1 { 1.5 3.0 }	
3096	Poland, Osawa Gora.....	14	e	100	42 { 35 48 }	71 { 58 84 }	29.8	3.1 { 2.5 4.0 }	100 <sup>5</sup>	21 { 17 25 }	60 { 47 77 }	12.6	2.0 { 1.0 2.5 }	
2923	Sweden, Gotland (Gammalgarn) <sup>2</sup> .....	14	d	100	30 { 19 39 }	56 { 44 66 }	16.8	3.8 { 2.0 6.0 }	33	Flowering plants not fully developed in Sept.				
3261	Jersey (Ch. Isl.), Bouley Bay (dry slope).	..	..	100	31 { 24 40 }	61 { 41 92 }	18.9	3.0 { 2.5 3.5 }	22	about 16-19	about 38-40	about 7	about 2	
2872	Sweden, Öland, Greby Alvar <sup>3</sup> .....	14	b	100	19 { 17 21 }	37 { 32 45 }	7.0	2.4 { 1.5 3.0 }	0	..	..	..	..	
2871	Denmark, Kramnitz (sandy field on the sea) .....	14	a	100	19 { 12 27 }	45 { 22 86 }	8.6	2.0 { 1.5 2.5 }	0	..	..	..	..	

<sup>1</sup> Mean values and the ranges indicated in braces.  
<sup>2</sup> Seeds collected by Dr. B. PERTESSON (sandy beach).  
<sup>3</sup> Seeds collected by Dr. R. STENNER (dry grassland).  
<sup>4</sup> Habit of plants almost identical in the two batches.  
<sup>5</sup> Habit of plants different from those in the other batch. They had far more leaves and were not reddish as a result of a high content of anthocyanine.

Table 5. *Trifolium arvense* and *T. gracile*, Cultivations 1954.  
The batches consisted of 8–14 individuals.

Cult. no.	Species	Origin	2 n	Group in table 3	Height (H)	Breadth (B)	Size index	Length of heads	Per cent flowering plants (Sept.)
					in cm Mean <sup>1</sup>	in cm Mean <sup>1</sup>	$\frac{B \times H}{100}$	in cm Mean <sup>1</sup>	
3256	<i>T. gracile</i>	Denmark, Vittrup	14	e	20 $\left\{ \begin{array}{l} 13 \\ 24 \end{array} \right.$	50 $\left\{ \begin{array}{l} 32 \\ 64 \end{array} \right.$	10.0	2.4 $\left\{ \begin{array}{l} 2.1 \\ 3.0 \end{array} \right.$	100
3646	<i>T. arvense</i>	Poland, Lodz*	14	e <sup>2</sup>	21 $\left\{ \begin{array}{l} 12 \\ 37 \end{array} \right.$	52 $\left\{ \begin{array}{l} 30 \\ 71 \end{array} \right.$	10.9	1.8 $\left\{ \begin{array}{l} 1.4 \\ 2.7 \end{array} \right.$	100
				b <sup>3</sup>	$\left\{ \begin{array}{l} 13 \\ 15 \end{array} \right.$	$\left\{ \begin{array}{l} 56 \\ 62 \end{array} \right.$	8.3	Not fully developed	22
3530	<i>T. arvense</i>	Austria, Graz*	14	e	28 $\left\{ \begin{array}{l} 21 \\ 41 \end{array} \right.$	68 $\left\{ \begin{array}{l} 51 \\ 85 \end{array} \right.$	19.0	1.8 $\left\{ \begin{array}{l} 1.5 \\ 2.0 \end{array} \right.$	100
3525	<i>T. arvense</i> ssp. <i>longisetum</i>	Turkey Princes Isl. <sup>4</sup>		e	15 $\left\{ \begin{array}{l} 11 \\ 17 \end{array} \right.$	20 $\left\{ \begin{array}{l} 17 \\ 25 \end{array} \right.$	3.0	2.3 $\left\{ \begin{array}{l} 1.7 \\ 3.0 \end{array} \right.$	100

<sup>1</sup> Mean values and the ranges indicated in braces.

<sup>2</sup> Seeds germinated 1st of April.

<sup>3</sup> Seeds germinated 27th of April. Only two plants had elongated flowering stems which could be measured.

<sup>4</sup> Seeds collected by Dr. MORTEN LANGE.

of the seedlings severally in pots they were divided into two batches and placed in frames, one batch in a frame with unaltered day length and one batch in a frame where the length of the photoperiod was reduced to 9 $\frac{1}{2}$  hours. The first type of treatment induced in all cases a normal development and flowering whereas the effect of short days caused such strains as in earlier experiments had a reduced flowering to behave in quite a similar manner, thus two of them, nos. 2871 and 2872, which belonged to Groups a and b in Table 3, remained completely vegetative.

Some few plants distributed in the two types of environment and originating from Vittrup in Central Jutland and Poznan in Poland behaved like nos. 2871 and 3096, respectively.

1954 (Table 5). In this experiment two strains of typical *T. arvense* were compared with *T. arvense* ssp. *longisetum* Boiss. and what has been called ssp. *gracile* Ser. (cp. ASCHERSSON & GRÄBNER 1906—10, pp. 530—534). The culture of the Mediterranean ssp. *longisetum* deviated by its small size (size index only 3) and extremely rapid development. It flowered 60 days after germination and was nearly withered and with ripe seeds in August about 120 days after germination. Already in the first days of September new seedlings had germinated in the pots. Whereas the material of ssp. *longisetum* by no means is clearly separated from some of our Mediterranean strains of typical *T. arvense*, this cannot be said about the culture of ssp. *gracile*, which in our opinion would better be treated as a species (*T. gracile* Thuill. in Flor. Par. ed. 2 (1799), p. 383).

The culture in question (no. 3256) originated from plants found outside a poultry yard where they probably had been introduced with the forage. The plants grew very slowly and were very late, thus still in full flower in the first days of October. Their appearance deviated strongly from all other strains cultivated by us. The stems were dark reddish and the anthocyanine content of the whole plant sometimes very high. The pubescence was very feeble. The leaflets were sublinear to cuneiform and the calyx was almost glabrous even if the lobes sometimes terminated in a few hairs. Some few short and stiff hairs bristling from the dorsal side of the base of the flower may like the narrow calyx lobes facilitate dispersal by animals, fig. 3 (left). The late flowering was without connection with any inhibition effect and the plant lost its basal leaves very soon. Its chromosome number was also  $2n = 14$ .

**Summary of the cultivations with *Trifolium arvense*.** Varied environment experiments (Tables 2 and 4) have revealed that, as regards quantitative characters (size, length of heads, dry matter production), *T. arvense* is subject to much modification, the phenotypical variation being frequently very great. On the other hand, the same characters are evidently determined by a genetical variation of a similar magnitude. The material does not allow any calculation of standard errors. The differences between several of the smallest and the tallest of the cultures, however, are so large that even the ranges do not overlap.

The anthocyanine content in stems and leaves varies much and is modified by changes in environment. It appeared, however, that the tendency towards red colouration was particularly strong in the strains from Mediterranean habitats. In this respect no. 1726 from a maquis at Argèles (cultivated in a few specimens in 1950) was rather extreme although it could not compare with *T. gracile* from Vittrup in Central Jutland (see above).

Numerous investigations have elucidated the interplay between photoperiodic and temperature stimulation of flowering, see e. g. MURNEEK & WHYTE (1948) and WHYTE (1946) and, as regards hereditary differences in reaction to photoperiodism and temperature, CLAUSEN, KECK, & HIESEY (1948), and BÖCHER (1945). While the mutual relations of the components of this intricate temperature-day length complex must be left to the physiologists, the whole complex may by genecologists be treated as a unity and denoted as a TDL complex. It frequently manifests itself as a winter effect (the interplay of low temperatures and short days), which in nature involves winter-annuality.

In the case of *Trifolium arvense* the experiments in 1952 and 1953 make it very probable that the delay or inhibition of flowering in a number of the cultures must be the result of a dependence on the TDL complex. The early germination in 1953 involved that the seedlings were exposed to rather low temperatures and short days. The subsequent treatment of the plants, however, showed that a normal further development depends on the presence of long-day conditions. The conclusion must be that the majority of races of *Trifolium arvense* occurring in Denmark depend on the TDL complex or a winter effect, which in nature usually will manifest itself in

a winter-annual development, more rarely in a summer-annual one, if the germination takes place very early. All southern and a number of eastern races, on the other hand, appear to be completely independent of any winter effect.

### III. *Kohlruschia prolifera* (L.) Kunth and *K. velutina* (Guss.) Reichb.

**Cytology.** To our earlier chromosome countings (fig. 1 in BÖCHER, LARSEN, & RAHN 1953) a few additions may be made. It has been possible to some extent to fill in the gap in the range of the western tetraploid crypto-species with the finding of two tetraploid populations on the Channel Island Jersey. The area of the diploids has further been extended to Northern Spain (no. 3323 from the Barcelona region) and the Sabini Mts. near Rome (no. 3297).

Of special interest is some material from Portugal (no. 3303) of *K. velutina*, which had a pair of very short chromosomes (fig. 1 f), as was the case with the material described in our earlier paper (no. 913, cf. Table 8).

**Experimental cultivations.** Four experiments were undertaken (1950, 1951, 1952, and 1953) comprising in all 42 cult. nos. of *K. prolifera* and 2 of *K. velutina*.

Table 6 is a survey showing the difference between diploids and tetraploids in the four experiments. The two most important expressions of the size of the plants, the height and the breadth of the head, appear in all four experiments to be greatest in the tetraploids if regard is paid to the mean of the average values.

On the other hand it is evident that the ranges of the average values overlap to a great extent, and, therefore, we have no hopes of being able to use the differences in size for a distinction between diploids and tetraploids, this being further rendered impossible because the quantitative characters are greatly liable to be modified by

Table 6. *Kohlruschia prolifera*.

	Diploids			Tetraploids		
	No. of strains	Height in cm Mean <sup>1</sup>	Breadth of heads in cm Mean <sup>1</sup>	No. of strains	Height in cm Mean <sup>1</sup>	Breadth of heads in cm Mean <sup>1</sup>
1950	7	40 { 23 51	1.3 { 0.7 2.9	5	58 { 53 63	1.6 { 1.1 2.2
1951	7	42 { 28 57	1.2 { 0.7 1.8	7	45 { 37 49	1.6 { 1.1 2.3
1952	5	34 { 22 44	1.1 { 1.0 1.3	3	42 { 39 46	2.0 { 1.7 2.5
1953	4	58 { 41 78	1.7 { 1.3 2.0	3	66 { 63 68	2.0 { 1.8 2.1

<sup>1</sup> Mean and range of average values indicated in braces.



changes in environment. The behaviour of *Kohlruschia prolifera* clearly resembles that of British forms of *Valeriana officinalis* (SKALINSKA 1947).

Among diploids two from montane stations in the Pyrenees (no. 1696 fig. 3b in the previous paper) and the Sabini Mts. (no. 3297) were very low and with ascending stems from the base. The latter was cultivated separately in the experimental field in 1953. It deviated strongly from all preceding cultures in the same field and only reached a mean height of 24 cm (range 15—34 cm). The breadth was about 80 cm and the breadth of the heads 1.7 cm (1.2—2.6 cm). Another comparatively low-growing diploid (no. 2880) is from Hammershus on Bornholm in the Baltic. It clearly

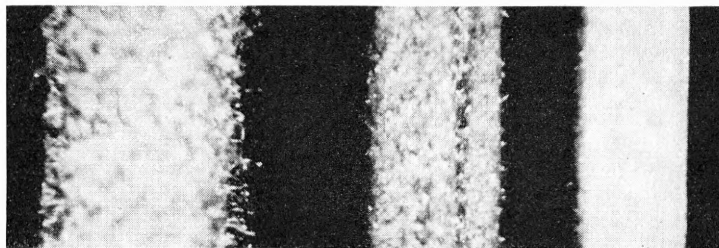


Fig. 4. Stems of *Kohlruschia* showing types of pubescence. The glabrous stem on the right is diploid *K. prolifera* (no. 1627), the scabrous stem in the middle tetraploid *K. prolifera* (no. 3249), and the glandular hairy stem on the left is *K. velutina* (no. 913).

differed from the taller populations nos. 2879 and 2850 from the south coast of the same island (Exp. 1952).

The differences mentioned in our earlier paper as to inhibition or delay of stem formation and flowering were studied again in 1953 using the same day length differences as for *Trifolium arvense* (cf. Table 4). While the experiences from 1953 are summarized in Table 8, Table 7 contains a survey of the three previous experiments. It appears that most populations with complete or partial inhibition of flowering are diploid originating from northern or central Europe. Only one of the southern tetraploids did not flower when cultivated in Denmark. This behaviour may be due to late germination or to long-day influence.

Seeds of three cult. nos. in the Exp. 1952 were also sown in the autumn of 1951 (denoted as A in front of the no. in Table 7) and had in all cases quite a normal development and flowering whereas inhibitory effects were demonstrated in two of these cultures when the seeds were sown in the first days of April. The two Arnager populations (nos. 2879 and 2850) differed in degree of inhibition. On the natural habitat (a south-facing slope) a large number of plants were investigated in the spring. They appeared all to have germinated in the autumn.

Comparatively short days in a certain period, perhaps combined with low temperatures, may apparently be a requirement of many strains of *Kohlruschia*. Short days, however, will later have a similar inhibitory effect as was found in *Trifolium arvense*. This appears from the varied environment experiment 1953 (Table 8),

Table 7. *Kohlruschia prolifera*.

Cultivations 1950 (I), 1951 (II), 1952 (III). Date of germination indicated.

A: Seeds of cult. nos. denoted as A were sown partly in the spring of 1952, partly early in Sept. 1951. The latter plants (A or autumn batch) had all a normal development and flowering.

## I. Cultures liable to inhibition of stem elongation and flowering.

## a. Inhibition complete.

2801. France, Strasbourg * (II, germ. 10.5.)	}	.....	2n = 30
A. 2879. Denmark, Arnager 1, Bornholm (III, germ. 16.4.)			
3114. Poland, Osawa Gora (III, germ. 16.4.)			
2539. Portugal, Lisbon * (I, germ. 10.5.)		.....	2n = 60

## b. Inhibition rather strong, 5—60 % of the plants flowering.

2389. Germany, Marburg * (I, germ. 21.4.)	}	.....	2n = 30
3388. — Frankfurt a. M. * (I, germ. 21.4.)			
2390. France, Dijon * (II, germ. 21.4.)			
1191. Denmark, Samsø (I, germ. 16.4.)			

## c. Inhibition rather weak, up to 95 % of the plants flowering, stem formation, however, delayed and poor.

2233. France, St. Cecilia, Rhone valley (I, germ. 17.4.)	}	.....	2n = 30
2234. — Orange, Rhone valley (I, germ. 17.4.)			
2496. — Strasbourg * (I, germ. 16.4.)			
A. 2880. Denmark, Hammershus, Bornholm (III, germ. 16.4.)			
2850. — Arnager 2, Bornholm (III, germ. 16.4.)			
3113. Hungary, Budapest 2 * (III, germ. 16.4.)			

## II. Cultures producing numerous elongated stems terminating in flowering heads. Almost all plants with normal development and flowering.

1510. France, Gêtre in the Pyrenees (I, germ. 16.4., II, 24.4.)	}	.....	2n = 30
1627. — Luchon in the Pyrenees (I, germ. 16.4., II, 27.4.)			
1696. — Mt. Louis in the Pyrenees (I, germ. 16.4.)			
1700. — Bouleternère maquis (I, germ. 16.4., II, 27.4., III, 8.4.)			
2762. — Caen * (II, germ. 27.4.)			
2497. Austria, Graz * (I, germ. 16.4., II, 24.4.)			
2785. Hungary, Budapest 1 (II, germ. 24.4.)			
2282. Denmark, Kregme, N. Zealand (I, germ. 14.4.)			
2700. — Jernhatten, peninsula Djursland (II, germ. 27.4.)			
2963. Sweden, Karums alvar, Öland <sup>1</sup> (III, germ. 16.4.)			
A. 2878. — Tingslådeåsen, Gotland <sup>2</sup> (III, germ. 16.4.)	}	.....	2n = 60
1430. Spain, Villa Nueva, Old Castile (I, germ. 16.4., II, 24.4.)			
1472. — Soria (I, germ. 14.4., II, 24.4.)			
2763. Portugal, Lisbon * (II, germ. 24.4.)			
2806. — Sacavem * (II, germ. 10.5.)			
2483. — Coimbra * (I, germ. 16.4., II, 24.4., III, 16.4.)			
1715. France, Port Vendres (I, germ. 16.4., II, 24.4.)			
1733. — Béziers, (I, germ. 16.4., II, 24.4., III, 16.4.)			
3111. Madeira * (III, germ. 16.4.)			

<sup>1</sup> Seeds collected by Dr. R. STERNER.<sup>2</sup> Seeds collected by Dr. B. PETTERSSON.

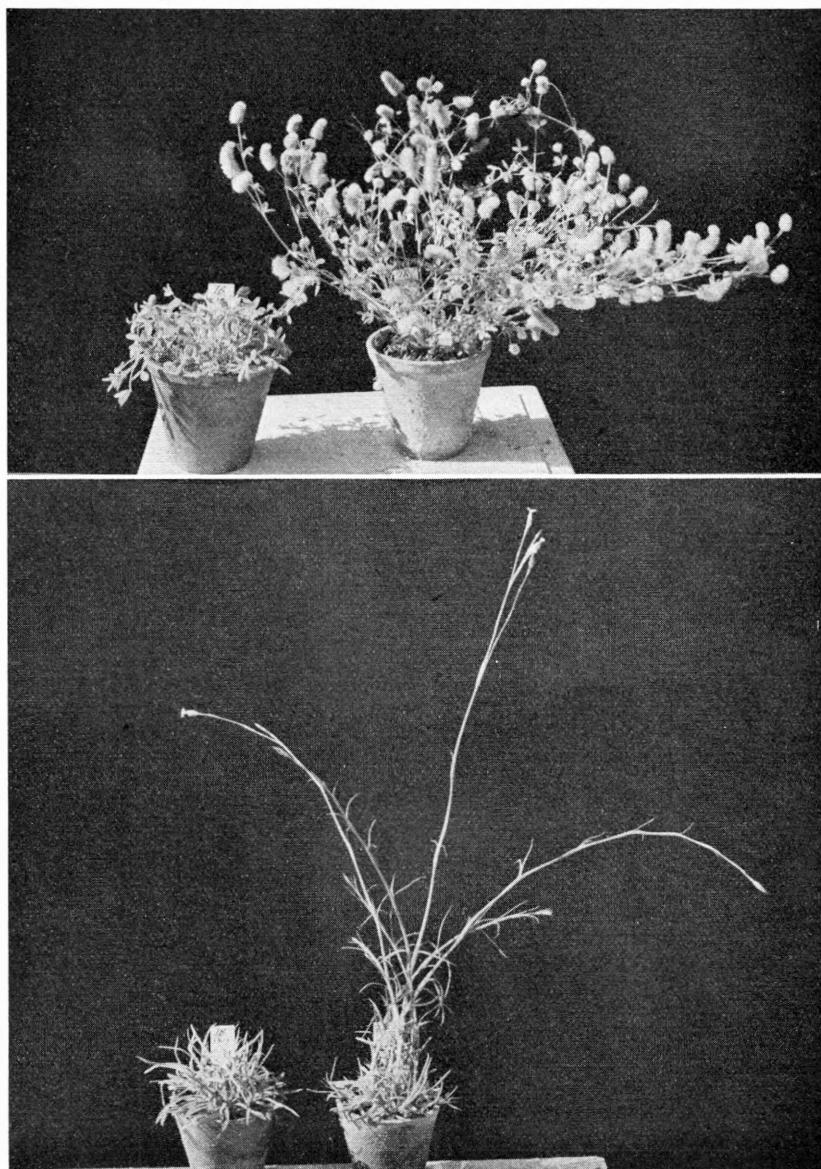


Fig. 5. Varied environment experiment 1953: *Trifolium arvense* (no. 2923 from Gotland) and *Kohlrauschia velutina* (no. 3303 from Portugal). Cultivated in short (left) and long days (right), photographed August 11th. In both cases the inhibition of flowering in the short-day plants was not complete as the plants started flowering in September.

Table 8. *Kohlrauschia*.  
Nos. 913 and 3303 *K. velutina*, the other nos. *K. prolifera*. Mean  
plants were available only the

Cult. no.	Origin	2 n	Length of photo-				
			Sandy soil				
			Height cm	Breadth of head, cm	No. of main shoots	Breadth of stem leaves mm	Diameter of flower mm
913	Belgium, Antwerp (Bot. Gardens) .....	30	33 $\left\{ \begin{array}{l} 28 \\ 37 \end{array} \right.$	1.7 $\left\{ \begin{array}{l} 1.5 \\ 2.0 \end{array} \right.$	1— very few	2.4	4—6
3303	Portugal, Sacavem* .....	30	72 $\left\{ \begin{array}{l} 60 \\ 79 \end{array} \right.$	1.8 $\left\{ \begin{array}{l} 0.8 \\ 2.5 \end{array} \right.$	6	2.8	8
1696	S. France, Mt. Louis (montane station) .....	30	..	not investigated			
3324	Poland, Tomice .....	30	..	not investigated			
3365	Poland, Poznan .....	30	$\left\{ \begin{array}{l} 66 \\ 70 \end{array} \right.$	$\left\{ \begin{array}{l} 0.8 \\ 1.1 \end{array} \right.$	$\left\{ \begin{array}{l} 6 \\ 6 \end{array} \right.$	$\left\{ \begin{array}{l} 2 \\ 3 \end{array} \right.$	$\left\{ \begin{array}{l} 9 \\ 9 \end{array} \right.$
3323	Spain, Tossa near Lloret de Mar, Barcelona <sup>2</sup> .....	30	..	not investigated			
3325	Hungary, Budapest 3* .....	30	70 $\left\{ \begin{array}{l} 54 \\ 78 \end{array} \right.$	1.7 $\left\{ \begin{array}{l} 0.9 \\ 2.7 \end{array} \right.$	many	3.0	10
1700	S. France, Bouleternère .....	30	38 $\left\{ \begin{array}{l} 33 \\ 40 \end{array} \right.$	1.9 $\left\{ \begin{array}{l} 1.7 \\ 2.2 \end{array} \right.$	very few	2.1	11
1715	S. France, Port Vendres .....	60	56 $\left\{ \begin{array}{l} 48 \\ 60 \end{array} \right.$	1.9 $\left\{ \begin{array}{l} 1.5 \\ 2.5 \end{array} \right.$	8	2.0	11
3248	Jersey, Ch. Isl., Ouens Bay .....	60	62 $\left\{ \begin{array}{l} 45 \\ 71 \end{array} \right.$	1.8 $\left\{ \begin{array}{l} 1.3 \\ 2.2 \end{array} \right.$	8	2.5	10
3249	Jersey, Ch. Isl., The Quennevais .....	60	62 $\left\{ \begin{array}{l} 59 \\ 67 \end{array} \right.$	1.9 $\left\{ \begin{array}{l} 1.7 \\ 2.1 \end{array} \right.$	7	2.6	11
3321	Spain, Soria .....	60	$\left\{ \begin{array}{l} 73 \\ 81 \end{array} \right.$	$\left\{ \begin{array}{l} 1.9 \\ 2.0 \end{array} \right.$	$\left\{ \begin{array}{l} 7 \\ 8 \end{array} \right.$	$\left\{ \begin{array}{l} 4.5 \\ 5.0 \end{array} \right.$	$\left\{ \begin{array}{l} 11 \\ 11 \end{array} \right.$

<sup>1</sup> Very early, showing no signs of checking of the flowering and soon without basal leaves.

<sup>2</sup> Seeds from Prof. T. TUTIN.

<sup>3</sup> See fig. 5.

*Cultivations 1953.*

values calculated for batches of 9—15 specimens. When very few ranges are given (in braces).

period unaltered					Length of photoperiod 9 <sup>1</sup> / <sub>2</sub> hours					
Garden soil					Garden soil					
Height cm	Breadth of head cm	No. of main shoots	Breadth of stem leaves mm	Diameter of flower mm	Height cm	Breadth of head cm	No. of main shoots	Breadth of stem leaves mm	Diameter of flower mm	Inhibition effect
34 { 24 46	2.0 { 1.4 2.4	1— very few	2.0	4—6	not investigated					none <sup>1</sup>
85 { 77 93	1.8 { 1.2 2.5	9	3.4	8	48 { 40 56	0.7 { 0.4 1.1	1.4	3.3	—	rather strong <sup>3</sup>
{ 50 56	{ 0.8 1.7	many	{ 2.5 3.0	{ 10 11	Only basal leaves					total
78 { 69 87	1.3 { 1.1 1.5	many	4.1	11	Only basal leaves					total
{ 71 75	{ 1.0 1.1	{ 6 7	{ 3 3	{ 7 8	Only basal leaves					total
43 { 38 51	1.9 { 1.6 2.2	4	2.2	10	45 { 37 51	1.0 { 0.7 1.3	1—2	2.1	8	very weak or none
71 { 65 78	1.6 { 1.0 2.1	many	2.9	11	43 { 40 47	0.8 { 0.5 1.0	many	3.3	10	very weak or none
41 { 38 44	2.0 { 1.5 2.5	very few	2.3	10	42 { 37 50	1.1 { 0.9 1.4	very few	2.2	9	none
63 { 56 68	2.1 { 1.7 2.5	9	2.2	11	43 { 32 55	0.7 { 0.4 1.0	0—5	3.5	10	43 % total 57 % weak
67 { 62 72	1.8 { 1.5 2.0	8	2.7	10	37 { 29 41	0.6 { 0.5 1.0	0—1	4.0	10	7 % total 93 % rather strong
68 { 57 87	2.1 { 1.7 2.8	8	2.4	11	36 { 22 43	0.9 { 0.6 1.2	2	3.4	10	rather strong
{ 86 89	{ 1.5 2.0	{ 7 13	{ 4 5	{ 11 12	{ 57 60	{ 0.5 0.6	{ 1 2	{ 5 6	{ 10 10	weak or none

in which the effect of short days varied from being very limited (e. g. narrow heads) to almost total inhibition of flowering. The inhibition was most pronounced in the diploids, but was absent in plants which were not subjected to short days in summer and which owing to early sowing were exposed to winter conditions during germination.

Very slight differences were found between plants cultivated in sandy soil and in ordinary well-manured garden soil. The difference between the two types of soil, however, was not very great as the sandy soil was not pure. The phenotypical variation of *Kohlruschia prolifera* is on the whole great. For no. 1700 seven measurements from different environments and years of cultivation are at hand. The mean heights vary between 51 and 28 and the mean diameter of the heads between 2.9 and 1.1 cm.

The two strains of *Kohlruschia velutina* (nos. 913, and 3303) cultivated in 1953 (Table 8) are very different but identical as to taxonomic important characters, both having bracts and pubescence of the *velutina*-type (fig. 4) and prickly seeds, which are only 0.9—1.3 mm in length. No. 3303 is a tall race which is rather late and keeps its basal leaves until late. No. 913, on the other hand, is low, with small flowers, very early and without basal leaves. It flowers two months after germinating, whereas no. 3303 takes three months to get into flower. It was also cultivated in two earlier experiments (1947 and 1952) and attained mean heights between 20 and 34 cm and mean breadths of the heads between 1.7 and 2.3 cm. No. 3313, which kept its basal leaves, was influenced by the day length (fig. 5 and Table 8). The flower and stem formation was clearly checked but in September almost all plants of the short-day batch had 1—2 flowering shoots.

**Summary of the cultivations with *Kohlruschia*.** The tetraploid material exhibits rather a limited variation. It consists of generally coarse races with rigid stems and rather broad heads. As a rule the basal leaves are not retained and the plants are independent of the winter-effect. The material from Jersey (nos. 3248—3249) deviated by its scabrous stems (fig. 4) and the leaves which were ciliated along the margins in their basal part.

The diploid material can be divided into two groups corresponding to the two species *K. prolifera* and *K. velutina*, which both show very great variation. In the former we have found races with coarse, rigid, erect stems and races with slender ascendent stems, races which retain their basal leaves and races which only temporarily have basal leaves. Those keeping their basal leaves most frequently depend on the winter effect, and are furthermore of northerly or continental origin. The Mediterranean races are widely different. In all cases they are independent of the winter effect, but they may have a very open erect shoot structure without basal leaves (lowland races, e. g. no. 1700 fig. 3c in the previous paper) and they may retain a basal rosette and from this have a large number of ascendent or even partly procumbent stems (montane races or ecotypes).

#### IV. *Galium aparine* L.

**Cytology.** FAGERLIND (1934, 1937) and HOMEYER (1935) have tried to count the chromosomes in *Galium aparine* without reaching a definite number. The species seems to comprehend tetraploid, hexaploid as well as octoploid races ( $2n$  about 44, 66 and 88). We have examined root tips of 11 strains originating from different parts of Europe and only found one number, viz.  $2n = 64$ . As appears from fig. 1g, two of the chromosomes are particularly large and may have arisen by fusion of two short chromosomes. This would be in agreement with the basic number of the genus which no doubt is 11.

**Experimental cultivations** were undertaken in 1950 and 1951 and are considered in Table 9. Later some few additional samples were cultivated. At least five ecotypes or races may be distinguished, which either may be discrete or more probably ranges of a large clinal variation.

(1) Mediterranean, summer-annual and very early race. The plants develop very fast and wither already in August. The seedlings are coarse and erectly growing. It is hardly ever winter annual; in both winters no seedlings were observed beneath the spruce twigs on which the plants were climbing. No. 2482 (Table 8) and no. 3080 from Madeira which was cultivated in 1952.

(2) Mediterranean, probably not strictly annual race, for the plants when cultivated in Denmark sometimes winter and flower two subsequent summers. The seedlings coarse and erectly growing and the plants very rich in anthocyanine. No. 1471 (Table 9).

(3) Southern, indifferent race which can be summer annual as well as winter annual. During the winter numerous seedlings were observed beneath the old withered plants. The seedlings were upright or ascendent and the plants had a very great production of dry matter. Nos. 1207, 1253, and 1639, Table 9.

(4) Northern, rather late-flowering race without inhibition of flowering. Seedlings adpressed, plants green till late in the autumn; otherwise as the preceding race, although not with so great a production of dry matter. Nos. 2082 and 2265 (Table 9) and among later cultivations no. 3117 from Strasbourg, no. 2440 from Poznan, and no. 3254 from Jutland (Palsgaard wood). No. 2299 from the beach at Sletten (the Sound) may also belong here although no wintering plants or seedlings were observed.

(5) Northern, very late race with a tendency towards inhibition of flowering and, therefore, presumably mostly winter annual in nature. Seedlings small and adpressed. Stems creeping, not climbing. Flowering very late or more or less checked if germination takes place in April. Two morphologically different strains: no. 2691 from a wood in Jutland with narrow leaves, and no. 2614 from a pebble beach on Gotland in the Baltic with short and broad leaves.

Table 9. *Galium aparine*. Cultivations 1950—1951.  
Each culture consisted of 10—12 individuals.

Cult. no.	Origin	2n <sup>2</sup>	Approx. no. of days from germin. to flowering	Habit of seedlings	Length of stems in cm 40 days after germin.	Habit and behaviour of plants in September	Wintering of plants cultivated during the preceding summer	Length of leaves (L) mm Mean <sup>1</sup>	Breadth of leaves (B) mm Mean <sup>1</sup>	Leaf index L:B
2482	Portugal, Coimbra*	64	50 <sup>3</sup>	Erect	16	Completely withered	None	Leaves rather short, not measurable in September		
1471	Spain, Pamplona	64	80	Erect	15 <sup>4</sup>	Green and flowering. Rather large	Some plants able to winter	27 { 22 37	4.5 { 4 6	6.0
1207	France, Noyon . . .	64	60	Intermediate	10	Fruiting. Very large	None	28 { 17 33	4.4 { 3 5	6.4
1639	France, Luchon . .	64	70	Adpressed	8	Green and flowering. Very large plants	Very few able to winter	30 { 25 36	4.0 { 3 6	7.5
1253	France, Celle St. Avant . . . . .	64	75	Adpressed	8		None	32 { 23 37	4.0 { 3 5	8.0
2265	Denmark, Roskilde		90	Adpressed	10	Green ± flowering and fruiting. Rather large	Very few able to winter	33 { 28 40	4.4 { 3 5	7.5
2082	Denmark, Ermelunden . . . . .	64	100	Adpressed	—	Green and flowering	A few plants able to winter	—	—	—
2299	Denmark, Sletten	64	100	Adpressed	—	Green, flowering, fruiting	None	—	—	—
2691	Denmark, Buderupholm . . . . .	64	120—130	Adpressed	8	Creeping, not climbing. Flowering just commenced	None	23 { 19 25	3.3 { 2 5	7.3
2614	Sweden, Gotland	64	130 or more	Adpressed	8	Creeping, not climbing. No or very few flowers	None	22 { 17 26	5.0 { 4 6	4.4

<sup>1</sup> Mean values and ranges (in braces).

<sup>2</sup> 2n = 64 was further counted in a strain from Palsgaard, Denmark (no. 3254) and from Poznan, Poland (no. 2440).

<sup>3</sup> Germination of seeds 3 days before the other strains.

<sup>4</sup> Stems and leaves with high contents of anthocyanine.



In *Galium aparine* the genotypical variation mainly concerns the behaviour of the seedlings and the reaction to the annual climatic changes. The species contains winter annuals, summer annuals, and indifferent races, and Race 2 approaches the two-year flowering biennial type, which is an important and not casually occurring type in *Calamintha*.

### V. *Calamintha acinos* (L.) Clairv.

**Cytology.** The chromosome number  $2n = 18$  was in 1940 found by SCHEERER and later corroborated by LÖVE & LÖVE (1944). Our material had also 18 chromosomes in somatic cells (9 different strains mentioned in Table 10 and three strains cultivated 1953–54 from Edenderry in Eire, Termignon in France (alt. 1300 m), and Frederikssund in Denmark). The strain no. 1539 from Cirque de Gavarnie in the Pyrenees seems to be intermediate between *C. acinos* and *C. alpina*. The latter species according to REESE (1953) has also the chromosome number  $2n = 18$ .

**Experimental cultivations** were undertaken in 1950–1952 and the results are considered in Table 10. The variation is fairly moderate but very interesting. 7 different types may be distinguished. These types may represent ranges within an almost continuous variation, as even a very deviating race, such as no. 1539, which is closely related to *C. alpina*, may be connected with typical *C. acinos* through intermediate types. Herbarium studies reveal that *C. acinos* and *C. alpina* where they meet in the European mountains are not sharply separated. Typical *C. alpina* is perennial with 1.5–2 cm long flowers and the nerves on its leaves are not prominent, whereas *C. acinos* is annual or pauciennial with more prominent nerves and flowers, which are shorter than 1 cm. In *C. alpina* the flowers are frequently placed in a few more or less aggregate whorls, whereas *C. acinos* has many separate whorls. Our material from Gavarnie (about 1300 m above the sea) is intermediate as to size of the flowers and has many separate whorls and prostrate growth. It is further distinctly perennial. It is important to note that hardly any segregation appeared in the material, which was collected as seeds in a natural population. Another culture (no. 1454), which was raised from seeds collected in a xerophilous grassland vegetation in the Sierra Cebollera in N. Spain (12–1300 m above the sea) was also prostrate and showed a clear tendency towards perenniality and had rather large flowers. The Sierra Cebollera material and the Gavarnie material may probably be the results of introgressive hybridization (cf. ANDERSON 1949, BAKER 1951) and represent two different end-results which both owing to back-crossing and outscreening by the habitat of a vast number of segregants have become stabilized and do not vary more than any population of the parental species. It is also possible, however, that such well-differentiated intermediate populations with a very restricted potential variability are to be understood as isolated remnants of a former continuous variation covering both *C. acinos* and *C. alpina* as its two extremes. During the last glaciation this cline may have been

Table 10. *Calamintha acinos*,  
Each culture consisted

Cult. no.	Origin	2n	Duration of life (years)	Approx. no. of days from germination to flowering	Habit
1676	S. France, Formiguères, altitude 15—1600 m . . . . .	18	1	50	Erect
2508	France, Bas Dauphiné (Isère) . . . . .	18	1	70	Erect
2509	S. France, Montpellier* . . . . .	18	1 (2)	60	Erect
1644	S. France, Nebias at Quillan . . . . .	18	1—2	60	Erect
2380	Germany, Frankfurt a. M.* . . . . .	18	(1) 2 (3)	60	Erect
2702	Denmark, Jernhatten, Djursland . . . . .	18	(1) 2	70	Erect
2727	Denmark, Kongerslev, Himmerland . . . . .	..	(1) 2	80	Erect-prostrate
2286	Denmark, Kregme, N. Zealand . . . . .	18	2	70	Prostrate-ascendent
2659	Denmark, Løgstør, Himmerland . . . . .	..	(1) 2	70	Prostrate-ascendent
1454	Spain, Poveda, altitude 12—1300 m . . . . .	18	2—3	50	Prostrate
1539	S. France, Gavarnie, altitude 1300 m . . . . .	18	2	70	Prostrate

<sup>1</sup> Mean values and the ranges indicated in braces.

disrupted. Some populations were isolated in pockets in the mountains, and if they were small and exposed to a severe climate the opportunity for a differentiation of a discrete race may have been great.

The seven different types may be described as follows.

- (A) Perennial alpine type clearly related to *C. alpina*, no. 1539. Perennial and large-flowered. First leaves circular, whereas in *C. acinos* they are more or less ovate. Stems prostrate with many separate whorls.
- (B) Subperennial montane type probably related to *C. alpina*, no. 1454. Prostrate early-flowering and in many respects reminding of the preceding type,

Cultivations 1950—1952.  
of 10—20 individuals.

Mean height <sup>1</sup> , cm			Mean length <sup>1</sup> of longest shoot, cm			Types see p. 24—26
Sept. 1951		Sept. 1952	Sept. 1951		Sept. 1952	
Germin. April 1950	Germin. April 1951	Germin. April 1951	Germin. April 1950	Germin. April 1951	Germin. April 1951	
..	12.4 $\left\{ \begin{array}{l} 6 \\ 17 \end{array} \right.$	..	..	28 $\left\{ \begin{array}{l} 17 \\ 36 \end{array} \right.$	..	Ca
..	24.6 $\left\{ \begin{array}{l} 17 \\ 31 \end{array} \right.$	..	..	32 $\left\{ \begin{array}{l} 15 \\ 47 \end{array} \right.$	..	Cb
..	16.8 $\left\{ \begin{array}{l} 11 \\ 25 \end{array} \right.$	..	..	33 $\left\{ \begin{array}{l} 12 \\ 46 \end{array} \right.$	..	Cb
14.0 $\left\{ \begin{array}{l} 12 \\ 25 \end{array} \right.$	13.6 $\left\{ \begin{array}{l} 6 \\ 23 \end{array} \right.$	..	23 $\left\{ \begin{array}{l} 15 \\ 40 \end{array} \right.$	22 $\left\{ \begin{array}{l} 16 \\ 43 \end{array} \right.$	..	Cc
24.0 $\left\{ \begin{array}{l} 16 \\ 32 \end{array} \right.$	22.3 $\left\{ \begin{array}{l} 11 \\ 31 \end{array} \right.$	28.6 $\left\{ \begin{array}{l} 17 \\ 42 \end{array} \right.$	36 $\left\{ \begin{array}{l} 22 \\ 56 \end{array} \right.$	42 $\left\{ \begin{array}{l} 25 \\ 55 \end{array} \right.$	38 $\left\{ \begin{array}{l} 27 \\ 47 \end{array} \right.$	Cd
..	20.9 $\left\{ \begin{array}{l} 14 \\ 30 \end{array} \right.$	35.2 $\left\{ \begin{array}{l} 14 \\ 49 \end{array} \right.$	..	36 $\left\{ \begin{array}{l} 30 \\ 41 \end{array} \right.$	33 $\left\{ \begin{array}{l} 16 \\ 58 \end{array} \right.$	Cd
..	16.7 $\left\{ \begin{array}{l} 4 \\ 31 \end{array} \right.$	30.5 $\left\{ \begin{array}{l} 20 \\ 43 \end{array} \right.$	..	38 $\left\{ \begin{array}{l} 16 \\ 45 \end{array} \right.$	42 $\left\{ \begin{array}{l} 27 \\ 53 \end{array} \right.$	Cd
15.0 $\left\{ \begin{array}{l} 11 \\ 18 \end{array} \right.$	10.8 $\left\{ \begin{array}{l} 5 \\ 16 \end{array} \right.$	23.0 $\left\{ \begin{array}{l} 13 \\ 35 \end{array} \right.$	22 $\left\{ \begin{array}{l} 16 \\ 24 \end{array} \right.$	36 $\left\{ \begin{array}{l} 27 \\ 43 \end{array} \right.$	27 $\left\{ \begin{array}{l} 17 \\ 39 \end{array} \right.$	Ce
..	9.9 $\left\{ \begin{array}{l} 7 \\ 13 \end{array} \right.$	16.2 $\left\{ \begin{array}{l} 12 \\ 32 \end{array} \right.$	..	29 $\left\{ \begin{array}{l} 26 \\ 36 \end{array} \right.$	24 $\left\{ \begin{array}{l} 17 \\ 38 \end{array} \right.$	Ce
Not measurable in Sept. 1951 (had withered and ceased flowering already in July)						B
8.4 $\left\{ \begin{array}{l} 3 \\ 17 \end{array} \right.$	4.0 $\left\{ \begin{array}{l} 3 \\ 7 \end{array} \right.$	about 3—4	23 $\left\{ \begin{array}{l} 19 \\ 34 \end{array} \right.$	41 $\left\{ \begin{array}{l} 23 \\ 58 \end{array} \right.$	about 40	A

but not perennial when grown in Denmark. Deviated from all other strains by its early fruiting and withering in the second summer. Nevertheless some plants were able to winter in the second winter and might probably have survived still further.

(C) Pauciennial types, all belonging to *C. acinos*.

- (a) montane, annual, very early race with low, erect, and tender shoots no. 1676.
- (b) annual lowland race, rather late, coarse, and erect with many stems from the base, no. 2508 and 2509, the latter with thick stems. The plants sown 1950 had in October of the same year up to 50 and 30 cm long stems, respectively.

- (c) annual or two-year flowering "biennial" race with erect growth and low tender stems and rather large flowers, no. 1644.
- (d) two-year flowering "biennial" (occasionally three-year flowering) race with erect growth (nos. 2390, 2702, and 2727, the latter population segregating in erect, more or less ascendent or even almost prostrate individuals). Presumably a very widely distributed race in central and northern Europe.
- (e) prostrate-ascendent race which otherwise resembles (d). Nos. 2286 and 2659, both strains from slopes facing west, unprotected and exposed to heavy wind from the sea (fjord).

## VI. Discussion and Conclusions.

(1) **Clinal variation and race discrimination.** As pointed out recently by BAKER (1953) there may be a tendency towards clinal variation in outbreeding species and towards race or ecotype discrimination in inbreeding species. This view seems to contribute to a resolution of the difference of opinion between those workers who formulate their conclusions in terms of clines and those who believe in a discontinuous nature of variation and describe this as a series of discrete races or ecotypes. On the other hand BAKER'S view does not exclude that clinal and discontinuous variation are more or less connected with the absence or presence of sharp climatic boundaries (cp. BÖCHER 1949). BAKER mentions *Veronica officinalis* as an instance of an outbreeding species with clinal variation. In this species, the continuity in variation is most striking when continental material is considered, whereas clear-cut ecotypes seem to occur in the Faeroes (cp. fig. 6 in BÖCHER 1944). Here, however, the species according to HAGERUP (1951) is self-pollinating, a fact which supports BAKER'S hypothesis.

In *Trifolium arvense* and *Kohlrauschia prolifera* a sufficient number of cultures is at hand for a discussion of the nature of their variation. Both species seem to be outbreeders although self-pollination may be rather frequent in the case of *T. arvense*. If self-pollination by preference occurs in certain parts of their geographical ranges this can be supposed to involve a localized discontinuity. In this connection it is remarkable that diploid *Kohlrauschia* may be at the point of producing an ecotype in the mountains of southern Europe. Among our cultures it appears to be a discrete race, but its discrimination can only be established through studies of many cultures from different altitudes.

In the case of *Trifolium arvense* we have only found approaches to a clear-cut morphological race differentiation in material from Mediterranean and montane stations in the south as well as from dunes and similar habitats in the west. We do not, however, think that the strains in question can be regarded as more than extremes in a clinal variation. Nor do the data presented in Tables 1—4 give any evidence for concluding that the physiological variation is discontinuous in this species. Its

variation in reaction to the TDL complex resembles the cline found by OLMSTED (1944) in side-oats grama grass. The clinal variation, however, only applies to typical *T. arvense*. From this species to the closely related *T. gracile* there is a great distance, the nature of which ought to be studied by experimental crossings.

The limited number of cultures of *Galium aparine* and *Calamintha acinos* indicate a great range of variation which may be clinal or not. In *Calamintha* two cultures from wind-exposed slopes and two from more sheltered slopes in Denmark indicate an enrichment of prostrate biotypes in the windy habitats. Two other cultures from Southwest European mountains indicate introgressive hybridization (see p. 23).

(2) **Geographical distribution of important hereditary characters.** The geographical distribution of certain genes or gene-complexes can be discussed without considering the degree of continuity in the variation and may from a gene-ecological standpoint be of particular interest. First of all we may try to overlook the physiological variation as to earliness and reaction to the TDL complex. In Tables 1, 2, and 9 the cultures are arranged according to the beginning of flowering. But whereas the differences in earliness of 50 to 85 days in the first-mentioned cultures of *Trifolium arvense* in the 1950 experiment (Tab. 1) must be assumed to be independent of the complex, the other strains in that experiment which have a very delayed flowering, are late as a result of not having been exposed to low temperatures or short days during germination. Also in *Kohlrauschia* and *Galium* the beginning of flowering is independent of or dependent on the TDL complex. If we try only to consider earliness differences between strains which are independent and therefore develop normally as summer annuals, we find a clear tendency towards early flowering in a southerly direction in Europe, in *Trifolium* and *Calamintha* culminating with the montane races from Formiguères (nos. 1671 and 1676), in diploid *Kohlrauschia* with the peculiar type from Bouleternère (no. 1700, cf. Table 4 in the previous paper). With the exception of *Calamintha acinos* all species exhibit a clear geographical distribution of the dependence on the TDL complex. In most cases northern races show different degrees of such a dependence, whereas southern (and some of the northern or continental) races are independent.

It is not quite intelligible why such characters as involve winter annuality are selected in the north. All southern strains which in their natural habitats may be summer annuals are able to carry through quite a normal development also when cultivated as summer annuals in Denmark. Of course winter annuality will advance the time of stem stretching and flowering and this early development may be necessary in climates where the natural vegetation is dominated by perennials which later in the period of growth will cover the ground and compete with or kill the smaller annuals. Very many annuals certainly occur in open spots on dry slopes or in "white dunes" in Denmark, where the competition even in summer is not very strong, but here the surface of the soil will soon be too dry. This indicates that the greater moisture in the soil during the spring connected to some extent with the reduced competition may be decisive. In Mediterranean Europe, however, the winter is wet and there-

fore we ought also there to find races which show adaptations to the complex of winter conditions. In fact such races seem to occur in Portugal and Spain, e. g. *Kohlruschia velutina* from Sacavem (Table 8, fig. 2) the tetraploid *K. prolifera* from Lisbon (Table 4 in our previous paper, on p. 299 by mistake called diploid; Table 7 in the present paper), and perhaps *Galium aparine* from Pamplona in Spain (Table 9, no. 1471).

Size and production of dry matter. It is obvious that the size and dry-matter production is very much influenced by environmental changes, and from the experimental data presented in Tables 4 and 8 it appears that changes in the length of the photoperiod in many strains produce very great size differences. This implies that size differences even between cultures in the same experiment cannot be compared unless the cultures can be considered indifferent as to the TDL complex or show the same reaction to this complex of factors. The matter is further made difficult because no sharp limits can be drawn between the different physiological behaviours (see e. g. the almost continuous variation from very great to almost no difference in size between the two batches in Table 4).

If we only consider the first-mentioned cultures in Tables 1 and 2, the size of which seem to be independent of the TDL complex, we may conclude that in the south of Europe *Trifolium arvense* embraces two different small-sized types, viz. a lowland type (no. 1732) and a highland type (no. 1671). Large-sized types occur in Mediterranean lowlands as well as in continental areas (e. g. 1706 in Table 1, 2758 in Table 2), but may also occur in the north (e. g. no. 2696). It is not possible to ascertain whether all northern strains which show different degrees of inhibition or delay of flowering are low-growing. The experiment in Table 4 discloses the two last-mentioned cultures as small and low-growing and experiment 3 (A-cultures) that nos. 2882, 2872, and 2873 are small, whereas no. 2871 is medium-sized and no. 2874 rather large.

The size differences in *Kohlruschia* in the experiment in Table 8 (photoperiod unaltered) are independent of the TDL complex, and therefore we can without hesitation regard so great differences as e. g. between no. 913 and 3303 and between nos. 1700 and 3325 as significant. In the experiment in 1950 (cf. Table 7) there are four southern and two northern diploids without delay of the stem formation and flowering. The mean heights of the southern strains were 51, 44, and 39 cm (lowland) and 23 cm (no. 1696 from the highlands); the two northern strains reached 31 and 39 cm in mean heights. It is clearly the montane race which deviates significantly from the rest, whereas no difference can be recorded between northern and southern strains.

Duration of life. Within clearly annual species such as *Trifolium arvense* and the two species of *Kohlruschia* the variation in duration of life is greatly governed by the reaction to the factors of the TDL complex. There are, however, also great differences which follow the earliness differences mentioned above and are unaffected by the winter conditions. Very short life was found e. g. in *Kohlruschia* no. 1700 and *Galium aparine* nos. 2482 and 3080. In a species like *Calamintha acinos*, which is not strictly annual, the variation in the duration of life is very great and

there the material strongly suggests a geographical distribution similar to that found in *Prunella vulgaris*. The southern races of *Calamintha* are strictly annuals, whereas the northern live 2—3 years. Finally, presumably as a result of introgression from *C. alpina*, some plants from montane stations are perennial.

(3) **Hereditary life-form vacillation.** Experiences with life form vacillation in species like *Viola tricolor* (CLAUSEN 1922) *Prunella vulgaris* (BÖCHER 1949), *Gossypium hirsutum* (HUTCHINSON 1951), *Arabis holboellii* (BÖCHER 1954), and *Calamintha acinos* render it necessary to discuss the life-form concept and some of the life-form classes used most. We must first accept that such species which consist of races with different life-forms cannot be placed within one class of life-form, but should in all phytogeographical statistics of life-forms be placed in those life-form classes to which they can belong unless it is shown that the flora or vegetation in question has only one race belonging to a single life-form class. A consequence of this may be that the life-form concept can always be used in connection with races, but in the case of species only when these are rigid and do not vary with regard to their life-form.

Two life-form classes which are generally accepted and much used may here be discussed, viz. the so-called winter annual and biennial life-form. The material presented in Tables 4 and 8 shows that the influence of the factors of the TDL complex need not be long. Only a few days' exposure to cold and short days may suffice for bringing about a normal development and flowering. Early germination in the spring, therefore, may frequently give almost the same result as germination in the autumn. Consequently we must redefine the concept of winter annuality so that it concerns only such plants the normal development of which depend on the winter effect.

The biennial life-form class is generally defined as plants which in the first year form a rosette on the ground and do not flower, but which next year flower and die after the ripening of their fruits. We have found several cultures of *Calamintha* and *Arabis holboellii* which are biennial, but which flower in both growing seasons. In *Arabis* the most luxuriant flowering is in the first year, in *Calamintha* in the second year because a comparatively long time is spent the first year in a vegetative "reinforcement stage". In *Calamintha* even three-year-flowering specimens were observed. This species cannot be classed as a hapaxanthic herb, neither is it a perennial. In RAUNKJÆR's life-form system it belongs to at least three classes, the therophytes, the hemicryptophytes, and the chamaephytes. Thus it is impossible to place it in one of the generally accepted life-form classes.

It is to be expected that the experimental methods now so much used in botanic research will soon bring about a recasting of the life-form classes. As a contribution to such a renewed treatment we have introduced the term *pauciennial* as a superior life-form class covering all plants with a very limited duration of life and without any vegetative power of production. Pauciennials can be hapaxanthic (flowering only once) or not (two- or three-year flowering).

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