

Biologiske Skrifter
udgivet af
Det Kongelige Danske Videnskabernes Selskab
Bind 10, nr. 2

Biol. Skr. Dan. Vid. Selsk. 10, no. 2 (1958)

EXPERIMENTAL
AND CYTOLOGICAL STUDIES ON PLANT
SPECIES

IV. FURTHER STUDIES IN SHORT-LIVED HERBS

BY

TYGE W. BÖCHER AND KAI LARSEN



København 1958

i kommission hos Ejnar Munksgaard

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Selskabets sekretariat og postadresse: Dantes Plads 5, København V.

The address of the secretariate of the Academy is:

*Det Kongelige Danske Videnskabernes Selskab,
Dantes Plads 5, København V, Denmark.*

Selskabets kommissionær: EJNAR MUNKSGAARD's Forlag, Nørregade 6, København K.

The publications are sold by the agent of the Academy:

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Synopsis.

Experimental cultivations of 13 annual or biennial species revealed that very many of these species vary in a number of characters affecting the life-form. When grown as summer-annuals southern races have a normal development while northern races of the same species have a retarded flowering or do not proceed beyond a vegetative stage, this, however, in particular being the case when the germination takes place late. In *Trifolium arvense* fifty strains from various European countries were cultivated, thus making a mapping of the distribution of the characters involving delay or inhibition of flowering possible. In most of the cultivated strains the chromosome number was determined. Intraspecific variation in the chromosome number was not found, but in the case of the two genera *Arenaria* and *Moehringia* differences in number and size of the chromosomes may justify a distinction between these closely related genera.

Introduction.

BÖCHER, LARSEN & RAHN (1955) proposed the term pauciennial to cover all plants with a very limited duration of life and without any power of vegetative reproduction. Pauciennials may be hapaxanthic or not (e.g. flowering more than one year or twice the same year). The results of cultivations of species like *Trifolium arvense* and *Kohlruschia prolifera* made a study of other short-lived herbs desirable. In the present paper our experiences with a number of European species are summarized. It appears that many of these species show a parallel heritable variation and a parallel geographical distribution of races or genes. The most important variability is expressed in different degrees of retardation or inhibition of flowering, which probably reflects different reactions to the temperature-daylength complex of factors.

The plants used for the experimental work were raised from seeds collected in nature. They were cultivated in the Copenhagen Botanical Gardens in pots which were placed together in frames. Some few were further or only cultivated in the experimental field west of Copenhagen. The batches used for comparison consisted of 10—15 plants. In most cases the chromosome counts were made in root tip sections from pot-grown plants. Fixative: MÜNTZING'S modification of NAVASHIN-KARPECHENKO'S fluid.

1. *Aira praecox* L.

Material: See Table 1.

Cytology: $2n = 14$ counted by HAGERUP 1939 (plants of unknown origin), MAUDE 1939, 1940 (English material), and by the present writers (Cult. Nos. 4258 (Fig. 4 a), and 3651).

Life-form: In Denmark found as seedlings in the autumn and undoubtedly most frequently winter-annual as is the case in Gotland (according to JOHANSSON 1899).

Exp. Cultivations (Table 1):

(1) Seed lots of three strains were sown in March and April 1954. The two batches germinated about the 14th and 30th of April. The first batch had during the first days been exposed to frost. Already in July the differences between the two batches became conspicuous. In all three strains the number of flowering culms were much greater in the March batch (see Fig. 1). In cult. Nos. 3639 and 3640 the plants in the two batches reached almost the same heights, but in the southern strain

(No. 3651) the late April batch was much higher than the March batch (Table 1). Heritable differences between the strains concerned the height and the habit. No. 3459 had erect and Nos. 3511 and 3651 spreading culms, whereas Nos. 3639—3640 (Fig. 1) were intermediate. All plants died after flowering even if they sometimes had very few culms and continued to grow until late in the summer (April batches).

(2) Cult. No. 3459 was sown partly in the spring of 1954, partly in September 1953. Late in October the autumn batch had formed vigorous tufts which came into flower in May 1954. The plants had 3—11 cm long widely spreading culms and were thus entirely different from the plants sown in March, which flowered in August and had erect culms.

(3) In 1955 No. 4258 from a dry field at Lovrup Krat in Jutland was cultivated. Two batches germinated on April the 20th and May the 2nd. Only two plants of the early batch got some few culms. In all the other plants flowering was inhibited and they began to wither in August.

2. *Aira caryophyllea* L.

Material: See Table 1.

Cytology: $2n = 14$ and 28, counted by WULFF (1937) and HAGERUP (1939). The tetraploid number was further found by us in the material from France, Portugal, and Denmark mentioned in Table 1 as well as in plants from Vemb in West Jutland and Rørvig in Zealand.

HAGERUP refers his tetraploid material to *A. multiculmis* Dum., which occurs in Southern Europe, but has been introduced to Northern Europe by man. Our material from Denmark belonged to typical *A. caryophyllea*, which thus contains diploid as well as tetraploid races. This is in agreement with TUTIN (in CLAPHAM, TUTIN & WARBURG 1952), who ascribes both chromosome numbers to *A. caryophyllea* and does not mention *A. multiculmis*. The latter may be difficult to separate from *A. caryophyllea*. It is possible, however, that future emendations may alter the limitation between the species and unite the tetraploids which at present are referred to *A. caryophyllea* and *multiculmis*.

Life-form: As *A. praecox* mostly winter-annual. HAGERUP (*loc. cit.*) states that diploid plants die after fructification in the beginning of the summer, whereas tetraploids (*A. multiculmis*) after the first flowering develop numerous new culms, and that this post-floration continues until late in the autumn. In his opinion polyploidy has thus been accompanied by a prolongation of life. Unfortunately no diploids were cultivated together with our tetraploid strains, but none of the latter had any prolonged flowering when they were grown as summer-annuals, and flowered normally.

Exp. Cultivations (Table 1, Fig. 1): As in *A. praecox* the number of flowering culms was much reduced in No. 3641 from France when the germination took place late. A similar reduced flowering occurred in No. 3469 from Denmark. In this case, how-

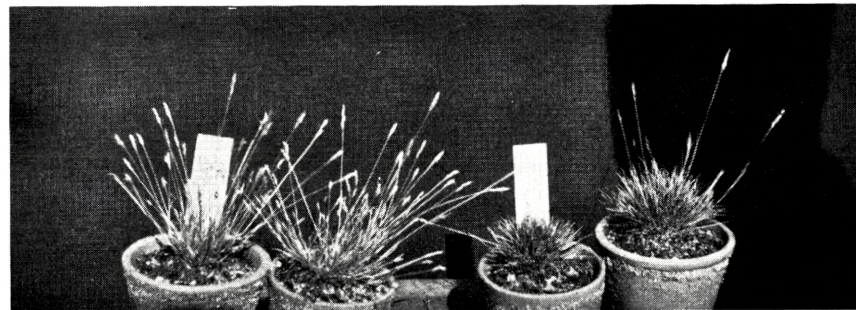
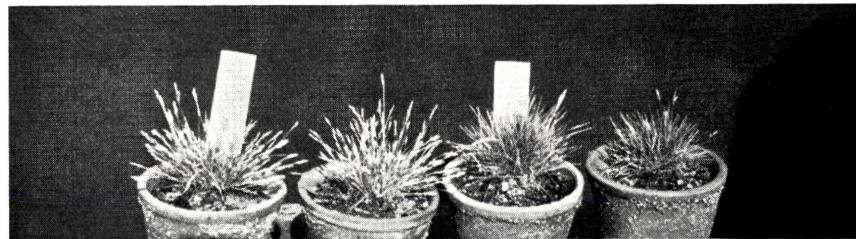
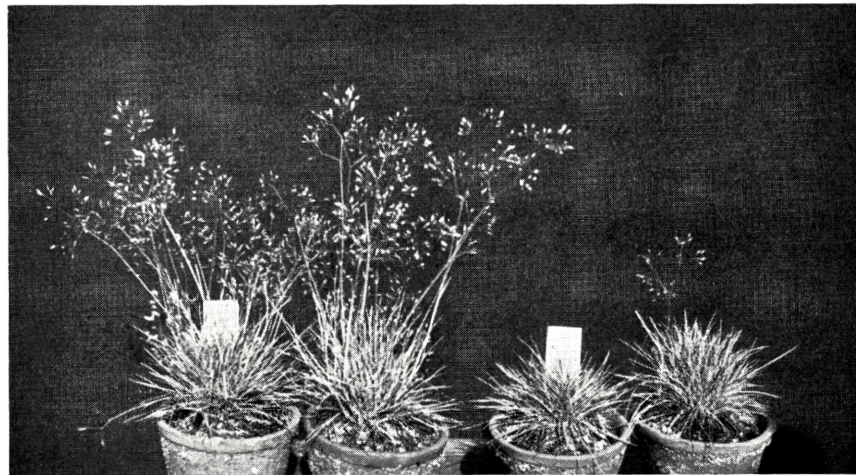
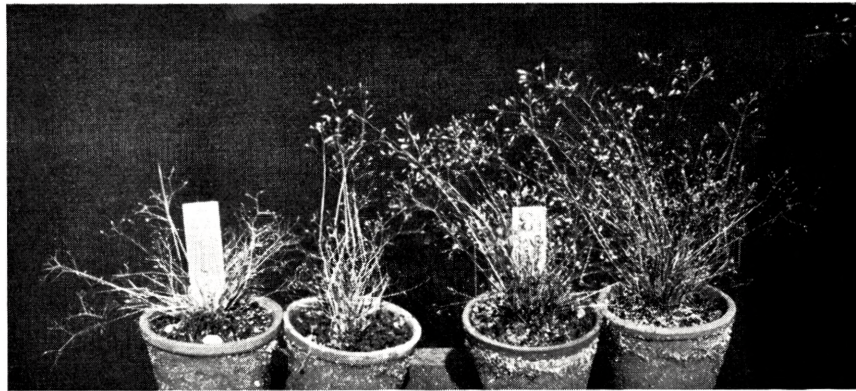


Fig. 1. Two pots from the early batches (left) and two from the late batches (right) of *Aira caryophyllea* (No. 3652, uppermost, No. 3641, the second from the top) and *Aira praecox* (No. 3640, the second from the bottom, No. 3639, at the bottom). TWB phot., Aug. the 14th, 1954.

Table 1. *Aira praecox* and *A. caryophyllea*.

Species	Cult. No.	Origin	Germination Date in April 1954	Stage of development in the first days of		Length in cm. of longest ripe culms.	
				August	September	Mean	Range
<i>Aira praecox</i>	3459	Denmark, Anst, C. Jutland	17	flowering	flowering or fructifying	17	(12—22)
	3511	Sweden, Kullen	17	almost withered	withered	16	(12—22)
	3639	Norway, Bergen	17	almost withered	withered, ¹ but with postfloration	15	(12—19)
			30	forming flow. culms	green basal leaves and few culms ²	12	(7—12)
	3640	France, Rouen	17	fructifying	fructifying, many culms	8	(6—10)
			30	green basal leaves. Forming flow. culms	green basal leaves, very few culms	8	(6—12)
	3651	Portugal, Coimbra	17	withered	withered	6	(5— 8)
			30	green basal leaves, incipience of culms	green basal leaves, very few culms	11	(7—17)
<i>Aira caryophyllea</i>	3469	Denmark, Hillerød	17	only basal leaves or with few culms	with very few culms		(4—22)
	3641	France, Rouen	14	flowering	fructifying	24	(20—27)
			30	only basal leaves	only basal leaves or with few culms	11	(4—14)
	3652	Portugal, Coimbra	14	withered	withered	15	(7—22)
			27	fructifying leaves green	almost withered	22	(17—29)

¹ Up to 50 culms per plant.² Up to 16 culms per plant.

ever, the plants germinated 13 days earlier. The southern strain, No. 3652 from Portugal, had a very rapid development. The late April batch was retarded, but without any inhibition of flowering, and reached greater heights (Fig. 1 on the right in the uppermost picture).

3. *Phleum arenarium* L.

Material: See Table 2; further Nos. 3308 (dunes in SE. Eire), 3510 (dunes at Tisvilde, N. Zealand), 4337 (dunes at Hirtshals, N. Jutland), and 4319 (Brittany, France).

Cytology: $2n = 14$ according to WULFF (1937, material from Schleswig-Holstein). The same number found in the strains investigated by us, Fig. 4c.

Life-form: RAUNKJÆR (1899, p. 598) says that the species is ephemeral-annual dying between April and June; in his manual as well as in ASCHERSON & GRÄBNER (1898—99) it is classified as a summer-annual. JOHANSSON (1899, p. 87) on the other hand regards it a summer- or winter-annual. Especially in places where the sand may be relatively moist in paths or tracks, it is winter-annual and forms small tufts.

Exp. Cultivations: Four experiments in the years 1953—1955:

(1) 1953. Two strains from W. Europe, Nos. 3308 and 3267, were cultivated as summer-annuals (germination in the first days of April) in pots as well as in the exp. field. In both environments only the plants from Jersey came into flower, whereas those from Eire produced vigorous tufts, which all, however, withered in October. In such vegetative plants as were unable to survive the winter no incipient formation of panicles in the leaf sheaths could be detected. See further Fig. 2 at the top.

(2) 1953—54. Nos. 3267 and 3460 were cultivated as winter- and summer-annuals. Both produced vigorous plants in the autumn, but only those from Jersey (No.

Table 2. *Phleum arenarium*.

Cult. No.	Origin	2n	1	Batch A			Batch B		
				Height ²	Panicle ²	³	Height	Panicle	³
3460	Fanø Isl., Jutland	14	fl	23 (19—26)	2.7 (2.5—3.0)	0	no plants	no plants	—
3267	Jersey Isl.		fl	12 (9—15)	1.9 (1.4—2.2)	0	13 (11—18)	1.9 (1.6—2.2)	0
3521	Tværsted, N. Jutland	14	b	15 (10—20)	3.1 (2.2—4.0)	7	13 (8—19)	2.9 (2.5—3.8)	13
3519	Skallerup, N. Jutland	14	(b)	7 (6— 9)	2.4 (2.2—3.0)	50	8 (5— 9)	2.6 (2.2—3.0)	40
3520	Hornbæk, Zealand	14	v	(3.5—6)	(? —2.6)	86	All plants vegetative		100

¹ Earliness conditions in July. fl = flowering, b = forming panicles, v = vegetative.

² Height and longest panicle in cm, mean and range (in brackets).

³ Percentage of plants without panicles.

3267) survived and flowered late in May 1954 at the same time as the other batch from the spring was in a vegetative stage (see Exp. (3)). The autumn plants reached heights between 9 and 21 cm and withered in July.

(3) 1954. Five strains cultivated as summer-annuals (Table 2); in four of the

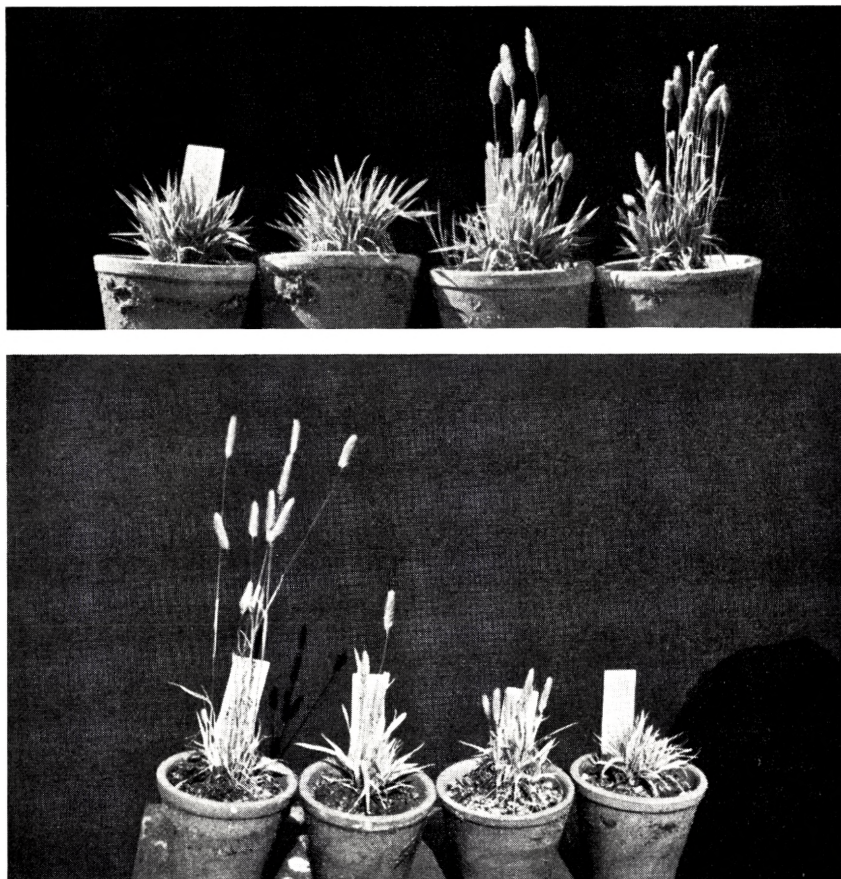


Fig. 2. *Phleum arenarium*. At the top two plants of No. 3308 from Eire (left) and two of No. 3267 from Jersey (flowering), photographed on August the 11th 1953 (Exp. 1). Below, one plant from four strains cultivated simultaneously and showing increasing inhibition of flowering. From the left, Nos. 3460, 3521, 3519 (all from the dunes in W. or N. Jutland) and No. 3520 from Zealand, photographed on August the 14th 1954 (Exp. 3).

strains two batches were sown in March and April and germinated on the 8th (A) and 27th of April (B), respectively. The two batches did not differ much from one another, although in No. 3520 only the early batch included two plants with some panicles. Otherwise the strains differed very much in height, length of panicle, earliness and development, No. 3520 from the dunes at Hornbæk resembling No. 3308 (1) by continuing in a purely vegetative stage (Fig. 2).

(4) 1955. Nos. 3267, 3519, 3520, 3521, 4319, and 4337 were cultivated as summer-annuals. In two cases half of the seed sample before sowing was treated for 8 days with cold (-2°C). Two samples were divided and sown in March the 17th and April the 13th (germination April the 14th—16th and May the 2nd). In July not a single plant had panicles, and most were withering in a vegetative stage except for the strains Nos. 3519 and 3521 from Jutland, which were green. Late in August four plants of No. 3519 had some few panicles, whereas the rest as well as all plants of No. 3521 were vegetative or mostly died in a vegetative stage. The deviating behaviour of the plants in this experiment could not be explained; perhaps the very dry and hot summer may have had some influence. The cold treatment had no effect on the development, but the rather late or very late germination in connection with the weather conditions may have inhibited flowering.

4. *Bromus mollis* L.

Material and Cytology: Two strains, No. 3788 from a heath at Hilversum in Holland and No. 4230 from a *Quercus pubescens* wood at Sorrento Peninsula, southern Italy, were cultivated in 1955—56. Both had $2n = 28$, a number which has also been reported by several previous workers.

Table 3. *Bromus mollis*.

Cult Nos.	Summer 1955		Spring 1956		Summer 1956	
	3788	4230	3788	4230	3788	4230
Batch A Germination April 14th—16th	2 out of 11 plants with a single culm	7 out of 11 plants with 1—several culms	Vegetative with withered leaves	Vegetative, but with many new green shoots	Flowering (1 dead, 5 weak plants)	Flowering (2 of the plants weak)
Batch B Germination May 2nd	11 plants, all vegetative	11 plants, all vegetative	As in the batch A outdoors in winter	As in the batch A	Weak and vegetative or dying in a vegetative stage	All flowering
			Forming culms 15 cm high. Rather few culms greenhouse in winter	Flowering; 30—40 cm high. Many culms		

Life-form: According to JOHANSSON (1899 p. 64) mostly winter-annual, but biennial according to MOE (1867).

Experimental Cultivations: (Table 3). Two batches with early and late germination (A and B). Only plants from the A batches succeeded in flowering the first summer, in particular those from Italy. The plants in the B batches were divided so that 5 plants were moved into a greenhouse during the winter. It appeared that the plants of southern origin (No. 4230) were much earlier, but during the summer those from the north caught up with them. All plants died after flowering in 1956. When sown early, the species may be summer-annual or pauciennial with flowering in two subsequent summers. When sown late in spring, it may develop as biennial or, if it is sown in the summer, as winter-annual.

5. *Arenaria serpyllifolia* L.

Material: See Table 4.

Cytology: $2n = 40$. A tetraploid species, $2n = 40$ being found by GRIESINGER (1937) in material from 10 different places in the Tyrol, ROHWEDER (1939) in plants probably from Schleswig-Holstein, v. WOESS (1941) in material from many parts of Germany and the Alps, and POLYA (1949) from Konyar in Hungary. The present writers likewise counted $2n = 40$ in plants from Denmark, Holland, Austria, Hungary, and Yugoslavia; see Table 4 and Fig. 4 d.

Life-form: According to JOHANSSON (1899, p. 61) and SYLVÉN (1906) normally germinating in the autumn and winter-annual; may sometimes be able to winter in a floral stage. If spring-sown it is summer-annual and gets very few branches. ASCHERSON & GRÄBNER (1913—19) also classify it as mostly winter-annual, sometimes summer-annual, and rarely with a tendency towards perenniality; they have cultivated it in sunny and shady places and state that the plants grown in different environments look so different that they might be taken as belonging to different species ("ganz verschiedenen Formenkreisen").

Exp. Cultivations:

(1) 1953—54. Nos. 3414 and 3427 were sown in August 1953; late in October vigorous plants of both strains were available, but under the given conditions in pots in a frame none of the plants were able to winter.

(2) 1954. 10 different strains were cultivated as summer-annuals, Nos. 3551—3327, see Table 4 and Fig. 3. They belonged to two very different types, one in the beginning with a more or less caespitose habit, short internodes, and generally late flowering (Nos. 3551—3414), and another with slender growth, longer internodes, and early flowering (Nos. 3715—3327). Nos. 3414 and 3715 formed the transition between the two types. The strains from the most northerly regions (Denmark) all belonged to the late, at first compact type. This, however, was not uniform, containing very late (No. 3551, Fig. 3) as well as relatively early races (No. 3414).

(3) In 1955 6 strains grown as summer-annuals. With the exception of No. 4229 the seed lots were divided and one part (A) sown early, on March the 17th, and exposed to frost outdoors, whereas the other part (B) was treated with low temperature (-2 for 8 days) before sowing, which was put off until April the 13th. In the cases of Nos. 3860, 3969, and 4123 the two batches germinated almost simultaneously in the first days of May. The germination of the A batches was poor, but in all cases the few plants resembled those of the corresponding B batch so much that they were almost identical. In Nos. 3861 and 4162, however, the A batches germinated plentifully on April the 14th and 20th, and the B batches on April the 28th and May the 2nd.



Fig. 3. *Arenaria serpyllifolia*, Exp. 2. From the left, No. 3327 from Budapest, No. 3712 from Termignon, No. 3545 from Eire, and No. 3551 from Jutland, photographed 14.8.1954. No. 3551 still quite vegetative and caespitose.

In both cases the two batches appeared to be very different, the B batches being retarded. In No. 4162 flowering was completely inhibited.

In nature the late caespitose type, which also includes a strain like No. 4162, will most frequently be winter-annual (or summer-annual if germination takes place early enough), whereas the more diffuse and early type may frequently develop as summer-annual or be winter-annual, especially towards the south. Late germination can change the habit from diffuse to caespitose. In no case caespitose, non-flowering specimens could winter and behave as biennials. Even plants placed in a greenhouse died during the winter.

6. *Arenaria leptoclados* (RCHB.) GUSS.

Taxonomy: Closely related to *A. serpyllifolia*, which it resembles, especially as a young plant. It is more slender and diffuse, with longer inflorescences and smaller flowers and seeds. It also differs in qualitative characters, e. g. the conical, straight-sided capsule (see figure in CLAPHAM, TUTIN & WARBURG 1952).

Material: See Table 4.

Cytology: $2n = 20$. According to TISCHLER (1950) this diploid number was reported by three authors, viz. GRIESINGER (1937), F. v. WETTSTEIN (1940), and v. WOESS (1941), all working with the same strain from Bolzano (Runkelstein). About this

Table 4. *Arenaria serpyllifolia* and *A. leptoclados*.

	Cult. No.	Origin	2n	Earliness ¹		Height in cm		Breadth in cm	
				5.8 1954	14.9 1954	Mean	Range	Mean	Range
A. serpyllifolia	3551	Jutland, Tværsted (sand dunes)			v	b, (fl)	about 1—2	11 (8—14)	
	3427	Zealand, Frederikssund (dry slope)			v	v-b, (fl)	about 1—2	10 (8—12)	
	3445	Zealand, Rørvig (sandy field)			v	fl, (fr)	4.1 (1—7)	15 (9—18)	
	3444	Bornholm, Lilleborg (dry rocks)			v	fl, (fr)	3.2 (2—6)	13 (9—17)	
	3457	Jutland, Fanø Isl. (dune grassland)			v	fl, (fr)	3.8 (3—6)	14 (12—18)	
	3414	Zealand, Selsø (dry slope)			b, fl	fl, fr	4.7 (1—9)	14 (8—17)	
	3715	Poland, Puszczykowo Poznan distr.			b, fl	fl, fr	8.0 (5—11)	19 (14—25)	
	3545	Eire, Curracloe House (sand dunes)			fl	fl, (fr)	7.0 (6—10)	16 (13—19)	
	3712	France, Termignon, Savoie (1300 m above the sea)			fl	fl, fr	11.9 (10—14)	19 (13—24)	
	3327	Hungary, Budapest*	40		fl	fl, fr	9.3 (6—12)	25 (17—34)	
	A. leptoclados	4162	Zealand, Lammefjord (dry slope of dike) . . .	40	B A	22.7 1955	31.8 1955		
						v	v, (b)	1.9 (1.5—3)	10 (6—19)
		4123	Austria, Seewinkel, Neusiedlersee (dry field)	40	B A	v, (b)	b, fl	7.4 (5—10)	20 (15—27)
v, (b)						b, fl, fr	² (1.5—3)	² (9—11)	
3969		Yugoslavia, Avala at Belgrade (dry slope)	40	B A	v, (b)	fl, fr	2.6 (1.5—5)	10 (7—16)	
					b	fl, fr	² (2—4)	² (9—14)	
3861		Yugoslavia, Sarajevo, Trebevic (400 m above the sea)	40	B A	b, (fl)	fl, (fr)	3.2 (2—7)	13 (10—16)	
					fl	fl, fr	7.1 (5—10)	17 (14—19)	
3860	Yugoslavia, Sarajevo, Trebevic (1200 m above the sea)	40	B A	(b), fl	fl, fr	3.0 (2—5)	10 (7—15)		
				b, fl	fl, fr	² (2.5—3)	² (12—13)		
4229	Holland, Kruisberg (dune grassland) ³	40		fl	fl, fr	² (about 6)	² (about 22)		
A. leptoclados	4227	Italy, Sorrento Peninsula, Minuto (on walls)	20	B A	fl	fr	10.5 (8—14)	24 (15—33)	
					fl, fr	fr, d	10.0 (8—12)	30 (25—38)	
	4226	Italy, Paestum, S. of Salerno (on walls)	20	A	fl, fr	fr, d	8.5 (6—10)	22 (14—28)	
					b, fl	fr	9.4 (8—11)	24 (20—29)	
3817	Yugoslavia, Lapad (rocks on the Adriatic)	20	B	fl	fl, fr	3.4 (3—4)	11 (9—13)		

¹ v = vegetative, b = with flowering buds, fl = flowering, fr = fruiting, d = dead.

² Few plants available.

³ Very broad-leaved race.

GRIESINGER says that "Die Pflanze . . . hat äusserlich durchaus keinen besonders artabweichenden Habitus," whereas v. WOESS states that it resembled var. *leptoclados*. Our material included 5 strains from Italy and Yugoslavia (the four mentioned in Table 4 and a strain from another station near Lapad on the Adriatic). They were all diploid with $2n = 20$ (Fig. 4 e).

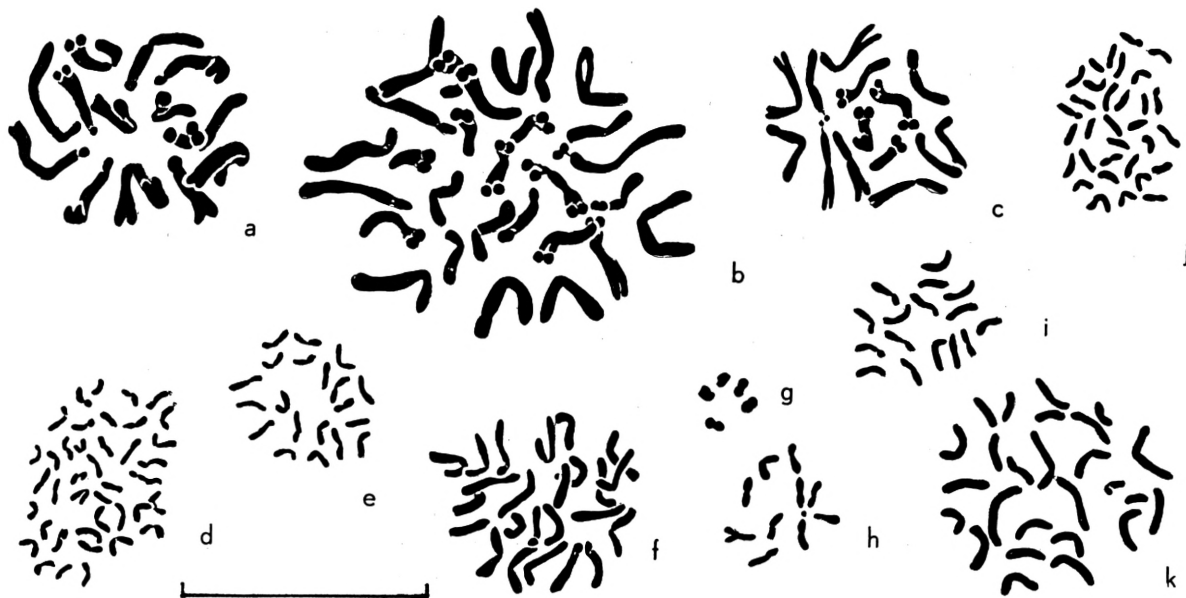


Fig. 4. Mitoses from root tips (g: Metaphase I of meiosis) — a: *Aira praecox* (No. 4258), b: *Aira caryophyllea* (No. 3641), c: *Phleum arenarium* (No. 3460), d: *Arenaria serpyllifolia* (No. 4162), e: *Arenaria leptoclados* (No. 4226), f: *Moehringia trinervia* (No. 3438), g—h: *Arabidopsis thaliana* (No. 3648), i: *Alyssum campestre* (No. 3846), j: *Alyssum alyssoides* (No. 3876), k: *Geranium molle* (No. 3952). Scale 10μ .

A. marschlinsii Koch is another diploid in the *A. serpyllifolia* complex. GRIESINGER and v. WOESS (*loc. cit.*) have counted $2n = 20$ in plants from nine different stations in the high Alps.

Life-form: ASCHERSON & GRÄBNER (1913—19) is of opinion that *A. leptoclados*, as compared with *A. serpyllifolia*, is more frequently biennial or at least winter-annual. Our strains, which all were from Southern Europe, were easy to cultivate as summer-annuals.

Exp. Cultivations: 4 strains were cultivated 1955 together with *A. serpyllifolia* (Exp. 3), see Table 4. They were generally very early and surpassed corresponding strains of *A. serpyllifolia* in height and diameter, only the Yugoslav strain (3817) being of the same size as most individuals of *A. serpyllifolia*. This and a very similar one also from Yugoslavia (No. 3830) of which only a single plant had germinated, belonged to typical *A. leptoclados*, whereas the three Italian strains were very glandular, matching the Mediterranean var. *viscidula* Rouy & Fouc.

7. *Moehringia trinervia* CLAIRV.

Taxonomy: The genus *Moehringia* differs from *Arenaria* by the seeds, which in the former are smoothly arilled. To this may be added important differences in the basic chromosome number and the length of the chromosomes.

Material: Three strains from Denmark and one from Småland (Sweden).

Cytology: $2n = 24$ counted by ROHWEDER (1939) in plants from Schleswig-Holstein, DE LITARDIÈRE (1948) in plants probably from Corsica (where furthermore a tetraploid subspecies was reported), and MATTICK (in TISCHLER 1950) in plants probably from the Alps. The same number was further found by us. As appears from Fig. 4 d-f, the chromosomes in *Moehringia* are significantly longer than those in *Arenaria*.

Life-form: Most Scandinavian authors, thus e.g. BRUNDIN 1898, p. 19, JOHANSSON 1899, p. 61, and SYLVÉN 1906 regard the species as being a winter-annual or biennial, which tallies with our results. According to ASCHERSSON & GRÄBNER (1898-99) and RAUNKJÆR (1934) also summer-annual, which may be exceptional. RAUNKJÆR even classifies it as sometimes perennial, a statement which needs corroboration.

Exp. Cultivations: The Danish strains (Nos. 3437, Randkløve, 3436, Jomfruberget, 3438, Korshage) were sown partly in August (germination in September) partly in March of the following year (germination in April). The autumn plants were during the winter divided into two batches, one of which kept in pots in a frame out of doors, the other in pots in a greenhouse. No. 3650 from Småland was sown early and late in the spring, and the two batches germinated on April the 17th and 30th, respectively.

All plants sown in the autumn developed as typical winter-annuals and flowered in the middle of April (greenhouse plants) or late in May (out-of-door plants). All spring-sown plants were biennial, forming many shoots the first summer, but no flowers. The plants of different origin were almost identical, not exceeding 6-10 cm in height, except for those of No. 3437 originating from the rocky woods at Randkløve on the isle of Bornholm. In this strain the habit was more crowded owing to short internodes, the plants reaching only 5-7 cm in height the first summer.

8. *Alyssum alyssoides* L.

(further *A. campestre* L. and *A. montanum* L. coll.)

Material: See Exp. Cultivations.

Cytology: $2n = 32$ according to countings by JARETZKY (1928) and MANTON (1932) and recent countings by us (Fig. 4 j, and exp. cultiv.).

Life-form: According to BRUNDIN (1898), JOHANSSON (1899), and RAUNKJÆR (1907) winter-annual; however, as pointed out by BRUNDIN (*loc. cit.*) it belongs to a special type that in the autumn produces short prostrate or ascending shoots, which persist during the winter and continue growing the next spring. In Denmark observed with

several wintering shoots issuing from the base and 1—4 cm long. Small unbranched flowering specimens have in the autumn one shoot or some few among which only one is able to persist. In culture all strains are easy to grow as summer-annuals. It is a Mediterranean-Central European species which was introduced into Denmark with grass or clover seed in the last century. Strains from Denmark did not differ in development from those of southern origin.

Exp. Cultivations: In 1955 three southern strains (Nos. 3876, Trebević, 700 m above the sea, Yugoslavia, 3970, Avala, dry slope, Yugoslavia, 4394, Languedoc, Mediterr. France), and two Danish ones (Nos. 4161, Hestbjerg, 4276, Frederiksbund) were grown together. They were all tetraploids ($2n = 32$). The seeds were sown early and late and germinated in the middle of and late in April. In all cases the two batches flowered normally and the plants died in August—September after the pods had ripened. The flowering stems of the late batches were some few centimetres longer than those of the early batches. In other respects the strains were not quite identical and might be referred to three types, viz. a southern type (Nos. 3970, 4394) with early flowering, a montane type (No. 3876) with prostrate-ascending reddish stems, short leaves and late flowering, and a northern type (Nos. 4161, 4276) with green stems, longer leaves, and rather late flowering. In most cases the diameters of the flowers were about 1.5 mm, only in No. 3970 it was about 1.7—2.0 mm.

In 1956 No. 4276 was grown again, this time together with a strain from Vienna (No. 4623). The latter was also tetraploid, but deviated much by showing segregation in normal plants with early flowering and ripening of the pods and very late plants which did not flower until the middle of August and formed many small buds or leaf-rosettes in the axils of the stem leaves in almost just the same manner as described by LAIBACH (1951 Figs. 9—10) in winter-annual races of *Arabidopsis thaliana*. None of the late plants of *Alyssum alyssoides* were able to persist during the following winter.

Two other species of *Alyssum* were cultivated in 1955 together with *A. alyssoides*, viz. *A. campestre* L. (material collected as seeds at Cavtat in Yugoslavia on the Dalmatian Coast), and *A. montanum* L. (material from wild sources sent to us under the name of *A. alyssoides* from Vacratat in Hungary). The first, *A. campestre*, appeared to be diploid ($2n = 16$, Fig. 4 i), the second, *A. montanum*, tetraploid ($2n = 32$), which is interesting because both JARETZKY (1932) and MANTON (1932) have counted $2n = 16$ in this species.

The seedlings of *A. campestre* were twice as large as those of *A. alyssoides* and the diameter of the flowers 2—3 mm. The pods were also longer. Late in August they were ripe and all plants died the next winter. The seedlings of *A. montanum* deviated by developing more slowly than those of the two other species. The plants did not begin to flower until late in July, about one month later than those of *A. alyssoides* or *A. campestre*, and they continued flowering until late in September. The diameter of the flowers was about 7 mm. Only a single plant was able to survive the

following winter. In Denmark this race thus behaved almost as an annual. Undoubtedly *A. montanum* L. is a complex species, which deserves special attention as it contains diploid and tetraploid as well as perennial and short-lived races.

9. *Teesdalia nudicaulis* (L.) R. BR.

Material: See Table 5.

Cytology: $2n = 36$, JARETZKY (1932), MANTON (1932), both in material of unknown origin. This number was also found by us in four strains from Denmark (Table 5).

Life-form: Very frequently regarded as more or less exclusively winter-annual (e.g. WARMING 1891, p. 15, BRUNDIN 1898, p. 24) or rarely also summer-annual (JOHANSSON 1899, p. 98, ASCHERSON & GRÄBNER 1898—99). In Denmark according to our own observations undoubtedly mostly winter-annual.

Exp. Cultivations: See Table 5. It could be demonstrated that some strains which by germination in the autumn did not produce many vigorous rosettes, were unable to persist during the winter (Nos. 2867, 3431), whereas others producing vigorous rosettes persisted and flowered early, almost at the same time as the plants found in nature.

Table 5. *Teesdalia nudicaulis*.

Cult. No.	Origin	n 2n	Germination	Developments of plants 1954				Habit
				May	August	Septbr.	Dec.	
2867	Rørvig, Zealand (sandy field)	18	Sept. 1953 April 8th, 1954	d r ₁	d fr ₁ ; r ₂ -b ₂	d fl ₂	d d	Few ± erect scapes
3431	Slotslyngen, Bornholm, (dry rocks)		Sept. 1953 April 10th, 1954	d r ₁	d fr ₁ ; fl ₂	d fr ₂ ; r ₃	d d	Many ascend- ing scapes
3432	Sandflugtskoven, Bornholm (sand dunes)	36	Sept. 1953 April 8th, 1954	fl ₁ r ₁	(fr ₁)-d fr ₁ ; r ₂ -b ₂	d fl ₂ ; r ₃	d d	Many ± erect and high scapes
3466	Salten Profil, Jutland (acid sand)	18	Sept. 1953 April 8th, 1954 April 20th, 1954	d; fl ₁ r ₁ r ₁	fr ₁ , fl ₂ fl ₁ -fr ₁ b ₁ -fl ₁	fr ₂ -d fl ₂ ; r ₃ fl ₂ ; (r ₃)	d d d	Many ascend- ing and high scapes
3541	Hovborg, Jutland (sandy roadside)	36	April 5th, 1954, April 27th, 1954	r ₁ r ₁	fl ₁ -fr ₁ r ₁ (-b ₁)	fl ₂ r ₁ -b ₁	d d	Many ascend- ing scapes
3708	Porto*, Portugal		April 17th, 1954	r ₁ -b ₁	(fr ₁)-d	d	d	Many ascend- ing high scapes

d = dead, r = rosette stage, b = with flower buds, fl = flowering, fr = fruiting. — 1, 2, 3 = first, second, or third flowering or rosette formation.

If germination takes place early in the spring, all strains are able to develop normally as summer-annuals and they very frequently had two separate periods of flowering (July and August—September) and even produce a late-autumn rosette (r_3) which, however, did not continue growing in culture. In nature in Denmark *Teesdalia* is sometimes found flowering in the autumn; such plants may have had a summer-annual development. If, as indicated by the third rosette formation, they occasionally are

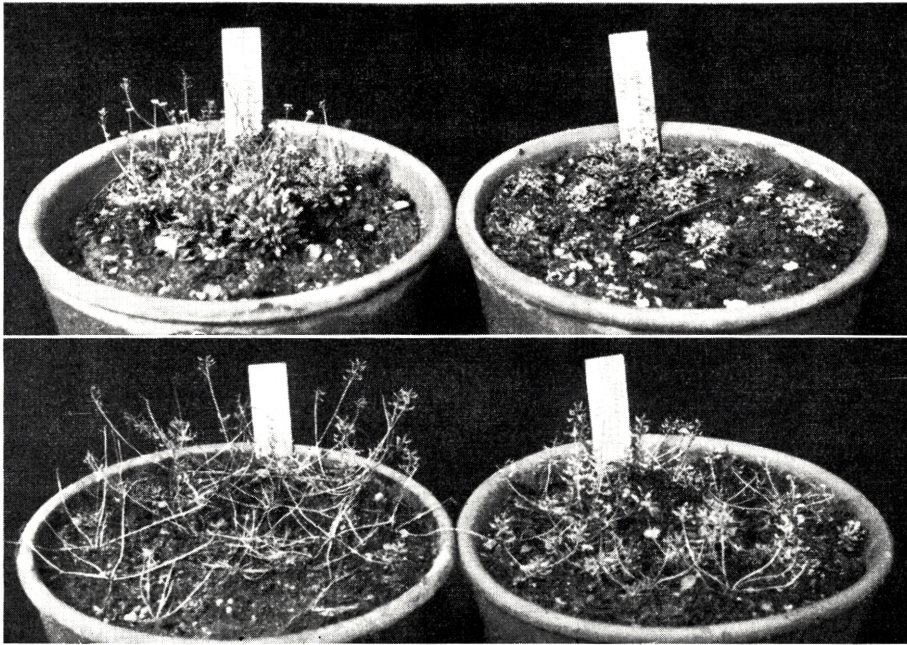


Fig. 5. Above: Early and late sown batches of *Teesdalia nudicaulis* from Jutland (No. 3541). Only plants sown in March (on the left) are able to flower. Below: *Teesdalia* No. 3708 from Portugal (to the left) and No. 3431 from Bornholm cultivated as summer-annuals. The plants from Portugal are dead whereas those from Bornholm produce some new flowering scapes. Photographed 14.8.1954.

able to survive the winter, the development may be classified as biennial-two year flowering.

Some strains may be very sensitive to the temperature-day length conditions during the germination. Thus two seed lots of No. 3541 were sown in March and April and the two batches were later very unlike, the plants of the late batch keeping their primary rosettes the whole summer and dying before the buds came out (Fig. 5). The retardation of this batch was very striking as the other batch flowered already in July—August and had another flowering in September. All northern strains, however, were late as compared with No. 3708 from Portugal, which in spite of comparatively late sowing flowered in June and had finished its life in July. It never formed new rosettes or scapes with a second flowering. Its behaviour resembled that of true summer-annuals.

10. *Capsella bursa pastoris* (L.) MED.

Cytology and life-form: The polymorphy of this species has been thoroughly treated by ALMQUIST (1907, 1921) and SØRENSEN (1954). Most races seem to be tetraploid, but in the Mediterranean area diploids have been reported; see literature in TISCHLER (1950). In nature the species according to many observers is summer- or winter-annual.

Exp. Cultivations: Our cultures comprise three strains which all proved to be tetraploids ($2n = 32$) in spite of two of them being from southern Europe (Nos. 3804, the Lido at Venezia, 4443, Lisbon). The southern strains were cultivated together in 1955. No. 3804 differed from the other by flowering a week later and by its radical leaves, which were lobate-pinnatifid, entire at the base, while in No. 4443 they were almost entirely toothed. Finally the pods were larger in No. 4443. In 1956 No. 3804 was repeated and grown together with No. 4592 from Kandestederne in the dune areas of northernmost Jutland. The latter had pinnatifid radical leaves. Germination took place late in April. Already in the first days of June the Lido-strain flowered and late in June the plants had ripe pods and reached heights of about 20 cm. The Jutland dune race deviated very much by being quite vegetative until late in June when only four out of 15 plants flowered. The flowering specimens were few or 10 cm high. The rest were clearly checked and did not flower. In nature a race like this may generally be winter-annual. It is probably related to the very late Rømø-race mentioned by SØRENSEN. It also came from natural vegetation in a dune area and under certain conditions many plants did not develop beyond the vegetative stage. On the other hand the majority of SØRENSEN's strains were from cultivated fields, waste places, or roadsides and did not show any sign of flower retardation when cultivated as summer-annuals.

11. *Arabidopsis thaliana* (L.) HEYNH.

Material: Six strains, two from Denmark (Nos. 3434, Korshage N. Zealand; 3435, Hammershus, Bornholm), one from Dijon, France (No. 3648) and three from Portugal (Nos. 3656, Coimbra; 3709, Lisbon; 3710, Porto).

Cytology: $2n = 10$ counted by LAIBACH (1907), WINGE (1925), JARETZSKY (1928), and MATTICK (according to TISCHLER 1950). All six strains mentioned above also had this number (Fig. 4 g-h). The number $2n = 6$ reported by TITOVA (1935) may therefore be in need of confirmation.

Life-form: Recorded as summer- or winter-annual (e.g. BRUNDIN 1898, JOHANSSON (1899), which corresponds to our observations in nature and to the experimental results.

Experimental investigations.

Earlier experimental results. The investigations carried out by LAIBACH (1951), KUGLER (1951), ZENKER (1955) and NAPP-ZINN (1955, 1957) have made this species

one of the best known annuals. Of special interest in connection with the main problem discussed in the present paper is LAIBACH's statement of winter-annual as well as several summer-annual races with different degrees of earliness. According to LAIBACH the species is mostly summer-annual. Only two strains, which both originated from Northern Europe (Copenhagen and Stockholm), were winter-annuals. Their flowering was completely inhibited or much retarded, thus approaching the late-flowering summer-annuals.

Own cultivations: The two above-mentioned Danish strains were cultivated in 1953—1954 as winter-annuals and summer-annuals. In both cases plants which had wintered, were very early as compared with the spring-sown plants. In No. 3434 they were higher, whereas in No. 3435 they were dwarfish. In August the winter batch of No. 3434 was withered, whereas the plants grown as summer-annuals had produced small new basal rosettes, which remained vegetative, but did not survive the next winter.

In 1954 Nos. 3648 and 3656 were sown early and late (in the middle of March and April). The two strains flowered normally, but differed from one another in the colour of the plants (dark- or pale green) and in the development, No. 3648 when sown late being able to produce new rosettes of radical leaves and new flowering stems in August.

Two seed lots from Portugal (Nos. 3709, 3710) were sown late in March 1954. The two strains resembled each other much and in September all plants were quite withered, but in the pots of No. 3710 numerous seedlings were growing up and reached a flowering stage, whereas in the pots of No. 3709 no seedlings were observed.

These unpretending experiments seem to strengthen the view of LAIBACH that true winter-annuals are rare in this species. Both Danish strains were easily grown as summer-annuals, but only No. 3434 approached the behaviour of true winter-annuals by receding into a vegetative stage when cultivated as a summer-annual.

12. *Geranium molle* L.

Material: Five strains from very different parts of Europe, see below, Exp. 1—2.

Cytology: $2n = 26$ (GAUGER 1937 in material from Schleswig-Holstein, WARBURG 1938 in material from the British Isles). This number could be corroborated in all the five strains, see Fig. 4 k (No. 3952).

Life-form: In Gotland regarded as almost exclusively winter-annual (JOHANSSON 1899, p. 76), in Germany as summer-annual and probably also winter-annual (ASCHERSON & GRÄBNER 1898—99) or even biennial (HEGI). Observed as winter-annual (or biennial), at several Danish stations.

Exp. Cultivations: In 1953—54 two strains, Nos. 3448—3449 (see Table 6), were sown in August and March. The autumn plants formed rosettes, but were unable to persist in pots out of doors during the winter. The spring batches were cultivated together

with plants from Coimbra (No. 3657), which also had germinated in the spring. The results appear from fig. 6 and Table 6. No. 3448 formed vigorous rosettes, but only 3 plants out of 15 produced a short flowering stem and in no cases the rosettes withered. In appearance such rosettes with a large central bud corresponded to those found in nature in late summer; however, they were unable to winter in pots in the Botanical Gardens. In nature a race like No. 3448 undoubtedly will proceed as a biennial or winter-annual. The other extreme was constituted by No. 3567, which very soon passed the rosette stage and had many fruiting stems in August; in no case the



Fig. 6. Plants of three strains of *Geranium molle* grown as summer-annuals in 1954 (Table 6), photographed on August the 14th. From the left: No. 3657 from Portugal, Nos. 3449 and 3448, both from Denmark.

rosette leaves were retained. In nature this race probably is summer-annual. No. 3449 was clearly intermediate, keeping the rosette leaves, but in late summer producing a small number of rather long flowering stems.

In 1955 a strain from Huizen in Holland (No. 3789) and another from a plantation of pines on Mt. Avala near Belgrade (No. 3952) were grown together as summer-annuals. The Dutch plants grew rather slowly, forming rosettes with adpressed leaves and flowering in late July (stems 16–21 cm long). The plants from Avala deviated very much by having more or less erect petioles of the radical leaves and getting flowers already in late June. They had shorter stems (11–16 cm) and died in August–September.

Table 6. *Geranium molle*.

Cult. No.	Origin	2n	Earliness ² Aug. 6th	Longest petioles (cm) ¹	Diameter of largest radical leaf (cm) ¹	Longest flowering stem (cm) ¹
3448	Rorvig, Zealand.....	26	v (fl)	11.3 (7–20)	4.0 (3.1–6.0)	See text
3449	Lilleborg, Bornholm.....	26	fl (v)	7.6 (5–12)	3.1 (2.5–3.8)	25 (20–36)
3657	Coimbra*, Portugal.....	26	fr (fl)	short	ca 2.2 (1.7–3.0)	17 (11–26)

¹ Mean and range (in brackets).

² v = vegetative, fl = flowering, fr = fruiting.

13. *Trifolium arvense* L.

Earlier investigations: In BÖCHER, LARSEN & RAHN (1955) experimental cultivations of 37 diploid and a single tetraploid strain were mentioned. A delay or inhibition of flowering was found in several strains of northern origin when cultivated as summer-annuals. An artificial shortening of the photoperiod involved a delay or inhibition while normal flowering occurred in the same strains when the photoperiod was unaltered.

New Exp. Cultivations: In 1955 12 strains, all diploid with $2n = 14$, were cultivated. The seeds germinated between April 24th and May 7th, and the plants were measured late in August (Table 7). With the exception of one strain from Rømø Island (No. 4255) which was very late and had reduced flowering and retained the radical leaves, all the other strains had a normal development and flowering and were without radical leaves when they were measured. The experiment comprised several discrete races which may be described as follows:

- (1) No. 3525. Very small size; extremely rapid development; see also BÖCHER *et al.* (1955, p. 12).
- (2) No. 4177. Heads very narrow, with open spaces between the flowers; sepals spreading; early flowering.
- (3) Nos. 4107 and 3972. Further probably No. 3828. Heads very long.

Table 7. *Trifolium arvense*.

Cult. No.	Origin	2n	Height in cm		Breadth in cm		Size index ²	Length of heads, cm		Stage of development, August 31th ⁴
			Mean	Range	Mean	Range		Mean	Range	
3525	Princes Isl., Turkey ¹ . . .	14	17 (15–22)	23 (19–31)	4	3.0 (2.5–4.0)	fr			
4177	Jalta ¹	14	22 (17–28)	49 (41–62)	11	2.5 (1.5–3.0)	fr (fl)			
3828	Mokosika, Dubrovnik, Yugoslavia . . .	14	³ (23–24)	³ (24–33)	(6)	³ (3.5–4.0)	fl-fr			
4107	Seewinkel, Austria . . .	14	30 (26–36)	44 (35–56)	13	4.9 (3.5–6.0)	fr (fl)			
3972	Avala I, Yugoslavia . . .	14	34 (22–43)	49 (32–63)	17	4.0 (3.5–4.5)	fr			
4425	Vácratát, Hungary . . .	14	43 (28–58)	65 (46–105)	28	2.6 (1.5–3.5)	fl-fr			
4016	Samobor, Yugoslavia . . .	14	42 (30–52)	73 (49–92)	31	2.9 (2.5–3.5)	fl-fr			
4278	Frushka, Gora, Yugoslavia	14	40 (24–53)	80 (53–98)	32	2.0 (1.5–2.5)	fl (fr)			
3964	Avala II, Yugoslavia . . .	14	31 (24–34)	87 (72–102)	27	1.5 (1.0–2.5)	fl (fr)			
3926	Doboj, Yugoslavia . . .	14	42 (31–59)	95 (68–129)	40	2.1 (1.5–2.5)	fl (fr)			
3978	Smederevo, Yugoslavia	14	48 (33–58)	111 (101–132)	53	2.5 (2.0–3.0)	fl (fr)			
4255	Lakolk, Rømø, Denmark	14	—	—	—	(ca. 1.5)	v-b (fl)			

¹ Seeds collected by Professor MORTEN LANGE.² Height × Breadth divided by 100.³ Very few plants available.⁴ v = vegetative, b = with flower buds, fl = flowering, fr = fruiting.

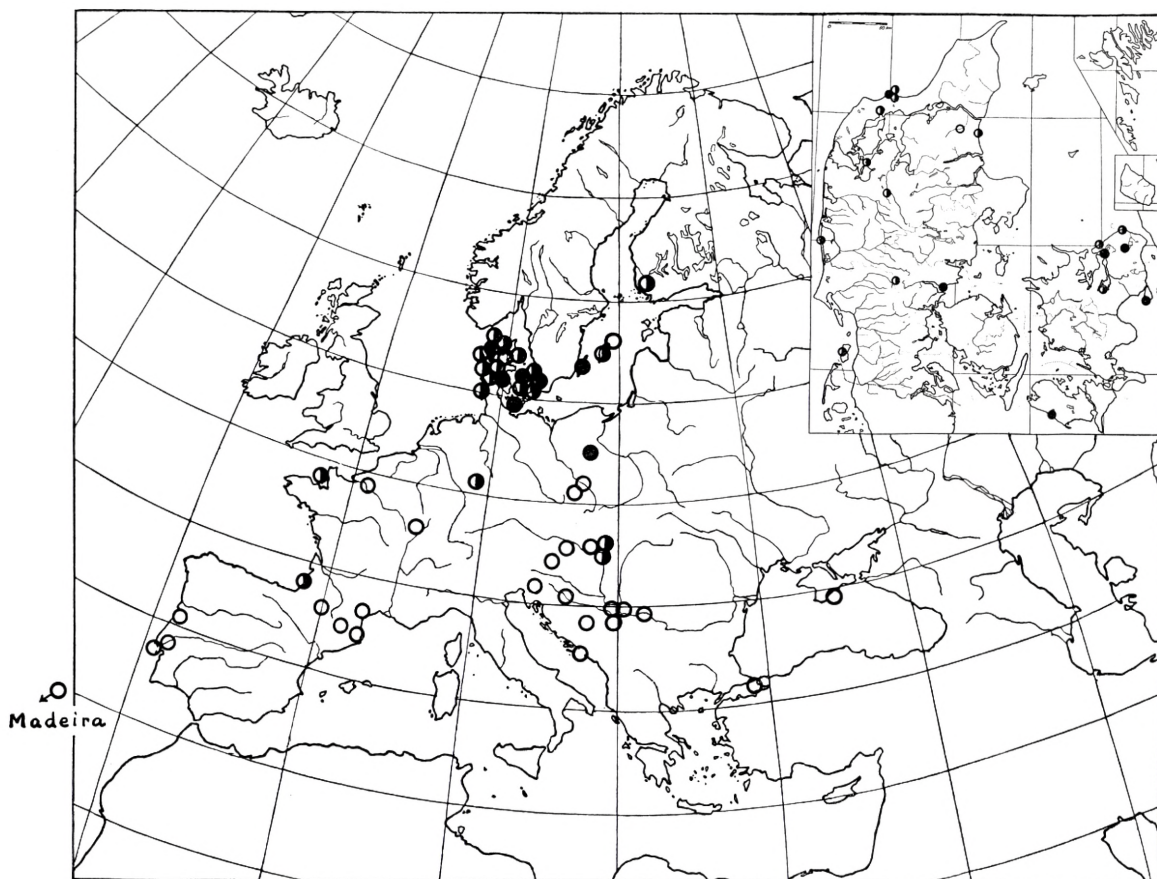


Fig. 7. Map showing the position of the fifty strains of *Trifolium arvense* which were cultivated in the years 1950—1955. — Rings: No retardation of flowering. Half-filled rings: Weak or distinct retardation of flowering. Solid black dots: Flowering inhibited or almost so.

- (4) Nos. 4016, 4278, and 4425. Heads rather short, but thick. Size index about 30. Leaflets very narrow and reddish in No. 4425.
- (5) No. 3964. Very coarse stems and narrow, conduplicate leaflets.
- (6) Nos. 3926 and 3978. Large or very large plants with narrow leaflets; heads rather thick, but not long. No. 3978: stems and leaves green, stems forming zigzag-lines; No. 3926: leaves reddish, only two of the plants with zigzag-lined stems.
- (7) No. 4255. Very late; flowering retarded. Late in August with few procumbent stems terminating several short heads just reaching a flowering stage.

The map Fig. 7 shows the location of the stations in Europe from which cultures of *Trifolium arvense* have been studied. It appears that genes responsible for a delayed or prevented flowering accumulate towards the north. In Denmark only one strain behaved as a true summer-annual, while no strains from the south showed any signs of retardation of the flowering.

In the earlier experiments 1950—54 mentioned in BÖCHER *et al.* (1955) very few strains attained size-indexes of more than 20. Unfortunately it is not possible to compare the sizes found in different experiments, but the results in particular of the cultivations in 1955 suggest that plants which genotypically are very large occur with great frequency in continental parts of the Balkan Peninsula.

Summary.

Cultivation experiments with 13 annual or biennial species have revealed that the majority of these species besides a moderate or great variation in morphological characters and size vary in a number of physiological characters which affect the life-form. When grown as summer-annuals in Denmark some races have a normal development while others of the same species have a retarded flowering or do not proceed beyond a vegetative stage, this, however, in particular being the case when the germination takes place in late spring. The latter type of races in all cases is of northern origin. Northern races which are difficult or impossible to grow as summer-annuals are found in *Aira praecox*, *A. caryophyllea*, *Phleum arenarium*, *Arenaria serpyllifolia*, *Teesdalia nudicaulis*, *Capsella bursa-pastoris*, *Arabidopsis thaliana*, *Geranium molle*, and *Trifolium arvense*. Of the last-mentioned species fifty strains have been studied, thus making a mapping of the distribution of the characters involving delay or inhibition of flowering possible. In nature races which possess such characters are probably winter-annual.

Alyssum alyssoides is an example of an annual species which in spite of being winter-annual in nature (at least in Denmark and Sweden) always develops normally if it is grown as a summer-annual. A somewhat similar case seems to be that of *Arenaria leptoclados*, but in this case we need experiences with plants of northern origin.

Moehringia trinervia seems in the north to be winter-annual or biennial; no races with a summer-annual development have been found. The same is also applicable to the two strains of *Bromus mollis* although in this species early germination in the spring enables some plants to flower already in the first summer. Such plants may be summer-annuals or more often two-year flowering biennials. A flowering in two subsequent summers may also occasionally occur in *Teesdalia nudicaulis*. This species as well as *Arabidopsis thaliana* also comprises races which are able to flower two (or three) times in the same summer, because they produce new rosettes of radical leaves from which new flowering scapes or stems issue.

Acknowledgment.

Financial support for the work of seed gathering and the chromosome countings was granted by the Carlsberg Foundation, for which the authors offer their sincere thanks.

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(For literature on chromosome numbers see TISCHLER (1950) and DARLINGTON & WYLIE (1955), *Chromosome Atlas of Flowering Plants*, London).

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