Studies on competition between closely related species of *Scabiosa columbaria* L.s.l.
II. Differentiation of hybrid populations under different temperature, water and nutrient conditions

Konkurrenzuntersuchungen zwischen nah verwandten
Arten von *Scabiosa columbaria* L.s.l.
II. Differenzierung von Bastardpopulationen unter
verschiedenen Temperatur-, Feuchtigkeits- und
Nährstoffbedingungen

by

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CONTENT

1. INTRODUCTION

In the winter of 1966/1967, a study was started at the Geobotanical Institute ETHZ (SFIT) in Zürich on the evolution of closely related species of *Scabiosa columbaria* s.l. under different temperature, fertilization and water conditions. The intention was to follow up the morphological differentiation of populations grown under different conditions as a result of free crossing between the different species. The question was, if for each condition tested a population with specific properties would develop.

After four years the first part of the investigations dealing with the response of the pure species to different conditions was completed and the results published (LANDOLT et al. 1975). The study of the greenhouse containers was discontinued in 1985, and that of the plots of differing water table levels in 1983. Thus the experiments lasted for 18 and 20 years, respectively.

2. MATERIAL AND METHODS

2.1. The species investigated

The species group of *Scabiosa columbaria* is of southeuropean- westasiatic origin and consists of about 30 species. In the area of the Alps about a dozen species occur. Three widely distributed species have been choosen for the investigations:

a. *Scabiosa gramuntia* L. (*S. triandra* L.). The species has a southwesteuropean distribution and grows in regions with a submediterranean climate. In the Alps it is restricted to the warmest central and southern alpine valleys. The distribution in Switzerland is shown in Fig. 1.

b. *Scabiosa columbaria* L. The species has a central european distribution north
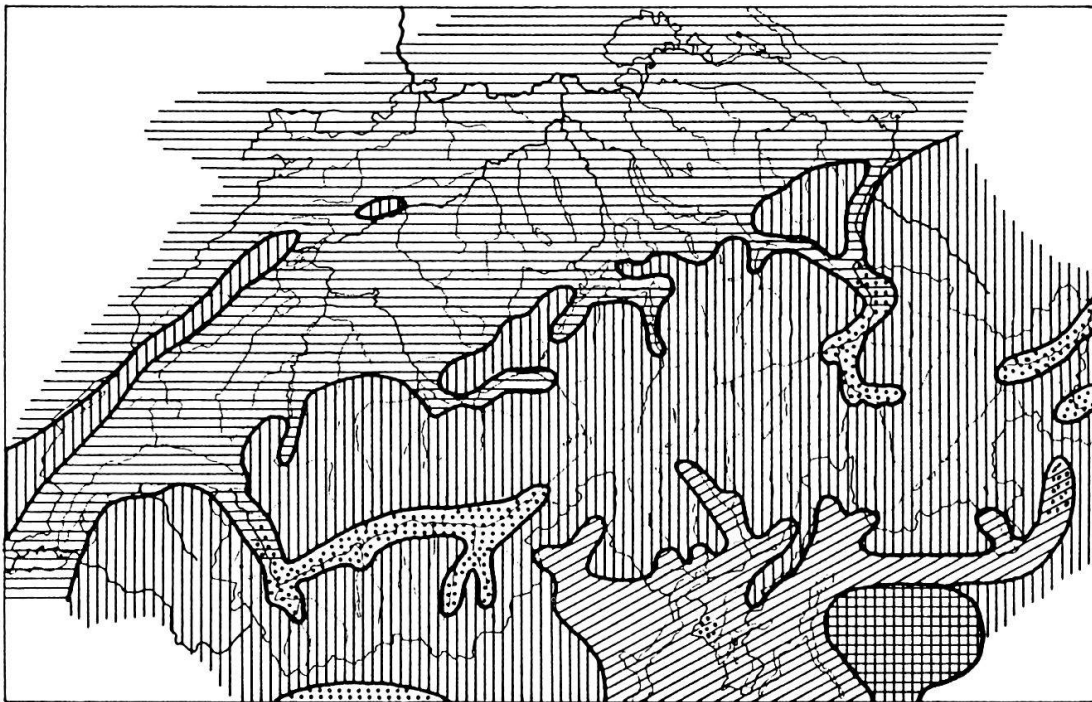
Fig. 1. Distribution map of species of *Scabiosa columbaria* s.l. in Switzerland and surroundings (according to LANDOLT 1971).
Verbreitungskarte von Scabiosa columbaria s.l. in der Schweiz und Umgebung (nach LANDOLT 1971).

| S. columbaria | S. lucida | S. gramuntia | S. portae | S. dubia |
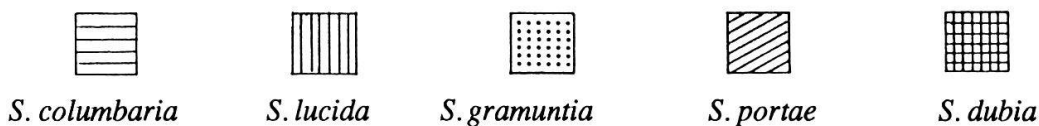
of the Alps from central France to western Russia and north to southern Scotland and southern Scandinavia. In Switzerland it is widely distributed at lower altitudes north of the Alps (Fig. 1). However, it is becoming more and more rare as a result of intensive fertilization of the meadows.

Table 1. Origin and original habitat of the species studied.
Herkunft und Standort der untersuchten Arten.

1 from SCHÜEPP (1960) for the stations Davos-Schatzalp, Zürich and Martigny-Bourg
2 from UTTINGER (1965) for the stations Davos-Schatzalp, Boppelsen and Martigny-Ville
3 from MÖRIKOFER (1932) for the stations Davos-Platz, Zürich and Sion. Sunny days are days with less than 2/10 cloudiness
4 from SCHÜEPP (1962) for the stations Davos-Platz, Zürich and Sion
5 from KUHN (1973) for the stations Rigi, Zürich and Sion. The length of the dry period is defined as the number of days with less than 5 mm precipitation.
Remarks on the climate stations : The stations Davos-Platz and Davos-Schatzalp are situated in a more continental climate than the collection locality of *S. lucida* (Davos-Parsenn). The precipitations are about 25% higher. On the other hand, the station Rigi is more oceanic having a somewhat lower value of length of dry periods than Davos-Parsenn. However, all three stations show the tendency towards the habitat conditions of *S. lucida*. The other stations (Martigny and Sion for *S. gramuntia* and Zürich and Boppelsen for *S. columbaria*) show only minor differences in the actual climate at the habitat station.

Species	*S. lucida*	*S. columbaria*	*S. gramuntia*
Canton	Grisons	Zürich	Valais
Locality	Davos	Boppelsen	Martigny
Exposition	SE	SSE	ESE
Slope (°)	30	25	40
Altitude (m a.s.l.)	1950	560	500
pH of the upper soil	6.4	7.2	7.5-8.0
Mean temperature (°C) (April to October)[1]	6.7	12.7°	14.9
Mean precipitation (cm) (April to October)[2]	76	74	45
Mean of sunny days (April to October)[3]	39	39	64
Hours of sunshine (April to October)[4]	1162	1336	1484
Most frequent extreme value of dry periods in days (April to September)[5]	12.3	17.1	32.6
Most frequent extreme value of dry periods multiplied by the mean July temperature	121	303	626

c. *Scabiosa lucida* Vill. *S. lucida* is distributed in the mountains of central Europe: viz. Alps, Carpathians, northern Apennins and Jura. In Switzerland it occurs at higher altitudes (above 1500 m a.s.l.) (Fig. 1).

The origin and habitat of the investigated populations is shown in Table 1. For more details see LANDOLT et al. (1975, p. 88). $CaCO_3$ is present in all three types of soil, the nitrogen content being rather low (1.7-3.2 mg/100 g soil after incubation of six weeks). The most characteristic differences in climate are the amount of precipitation and the temperature. *S. gramuntia* grows in a dry climate with warm summers, *S. lucida* in a humid one with cool summers. *S. columbaria* has intermediate climatic demands. The climatic differences of the habitats of the three species are also shown in the ecological indicator values of the different species (Table 2). The values for temperature and continentality are highest in *S. gramuntia* and lowest in *S. lucida*. The humidity value is lowest in *S. gramuntia*.

Table 2. Indicator values of the species investigated (from Landolt 1977).
Zeigerwerte der untersuchten Arten.

Species	F	R	N	H	D	L	T	K
S. gramuntia	1	3	2	3	3	4	5	4
S. columbaria	2	4	2	3	4	4	4	3
S. lucida	2	4	2	3	4	4	2	3

Table 3. Some characteristics of the species investigated.
Einige typische Eigenschaften der untersuchten Arten.

Characteristics	*S. gramuntia*	*S. columbaria*	*S. lucida*
Length of calyx setae (mm)	1-3	3-5	5-8
Width of calyx setae (mm)	0.08-0.15	0.10-0.20	0.20-0.40
Colour of setae	light brown	dark brown	black
Number of hairs per mm^2 on the lower surface of upper rosette leaves	4-8	0-2	0-2
Width of lobes of cauline leaves (mm)	0.5-1.8	1-3	2-8
Height of stems (cm)	20-100	20-60	10-35
Length of stalks of flower heads (cm)	20-50	20-50	10-25
Length/width ratio of terminal lobe of upper cauline leaves	12-25	8-16	4-8
Number of flower heads per stem	5-70	5-30	1-10

Typical morphological characteristics of the three species are put together in Table 3 and *S. columbaria* has morphologically and ecologically an intermediate position between *S. lucida* and *S. gramuntia*.

Best characteristics to distinguish the species are the length and width of calyx setae and the number of hairs on the lower leaf surface.

2.2. Experimental conditions

The experimental conditions are described in detail in LANDOLT et al. (1975). During winter season the plants were cultivated in the Institute's garden, all under the same conditions. The soil consisted of one part Löss loam, poor in nutrients, and three parts quartz sand. After the first part of the experiment (1970) half of the plants were harvested for measurements. The remainder stayed in the plots for the second part of the experiment. Since 1968 the plants were cross-pollinated and set numerous seeds. Weeds were removed periodically but the seedlings of *Scabiosa* were left in the experimental plots.

Two groups of experiments were carried out :

a. Greenhouse experiments

From the beginning of April to the end of October the plants stayed under two different temperature conditions in the greenhouse (Table 4).

The mean cool temperature of 11 °C is two degrees lower than the mean temperature of April to October of the habitat of *S. columbaria* and only slightly higher than the warmest month of Davos/Parsenn (origin of *S. lucida*). The mean warm temperature of 24°C is by far higher than the summer temperature at the habitat of *S. gramuntia*. It is five degrees warmer than the warmest month in Martigny (origin of *S. gramuntia*).

Plants of the three species *S. gramuntia, S. columbaria* and *S. lucida* were grown in culture containers (45x45x45 cm). At the beginning of the experiment six

Table 4. Temperature conditions in the greenhouse experiment.
Temperaturbedingungen im Gewächshausexperiment.

Series	day temperature (10 hours) (°C)	night temperature (14 hours) (°C)
warm conditions	30	20
cool conditions	17	7

plants were planted either in pure cultures of each of the three species or in mixtures of two or all three species. Four replicates of each combination were made in the warm chamber but only two in the cool chamber (on account of limited available space).

Pollination: Since no insects were allowed in the greenhouse, the pollination had to be done with a small brush. Twice a week every flower was pollinated at random.

b. Experiments in the garden

During the vegetation period the following conditions were established in twelve directly adjacent basins with controlled water table level in the garden (Table 5). Only two species (*S.gramuntia* and *S. columbaria* were used in this experiment. The basins (4.25x1.20 m) were divided into three plots and planted with *S. gramuntia*, *S. columbaria* and a mixture of both species, respectively.

The fertilizer used, contained constant amounts of nitrogen, phosphorus and potassium as well as some trace elements. The yearly fertilization corresponded to a supply of 30, 3 and 0 g nitrogen per squaremeter, respectively. The fertilization of

Table 5. Conditions in the plots of different ground water tables.
Bedingungen in den Grundwasserbecken.

Conditions	Water table level in cm below surface	Yearly supply of each N, P, K in g/m^2	Dry periods in days between watering
$G_{45}D_0$	45	0	natural
$G_{45}D_3$	45	3	natural
$G_{45}D_{30}$	45	30	natural
$G_{145}D_0$	145	0	natural
$G_{145}D_0$	145	3	natural
$G_{145}D_{30}$	145	30	natural
B_7G_{45}	45	3	7
B_7G_{95}	95	3	7
B_7G_{145}	145	3	7
$B_{28}G_{45}$	45	3	28
$B_{28}G_{95}$	95	3	28
$B_{28}G_{145}$	145	3	28

3 g nitrogen corresponds to about the natural conditions in the habitat of the two *Scabiosa* species. In addition the plots with natural rain conditions receive 3106 g/m² nitrogen yearly with the rain.

Dry periods of 28 days are very uncommon in the distribution area of *S. columbaria* (in Switzerland) but not too rare in the central alpine valleys (origin of *S. gramuntia*)(see also Table 1).

The pollination was achieved by the insects in the garden. Cross-pollination between plants of different conditions was possible.

The climatic conditions during the study period are summarized in Table 6. Relatively cool years were: 1972, 1980 and 1974.Warm years: 1983, 1971 and 1982. 1971 was also a very sunny year whereas 1980 and 1981 received little sunshine. Wet years were 1975 and 1970, dry years 1983 (dry July) and 1985 (dry Fall). Longer dry periods occurred in 1976 from March to June, and in 1969 and 1972 during the Fall.

Table 6. Mean temperatures, precipitation, and sunshine hours during the study period (from Ann.Schweiz.Meteorol.Anst. 1968-1985).
Mitteltemperaturen, Niederschläge und Sonnenscheindauer während der Untersuchungsperiode.

Year	Temperature °C	Precipitations mm	Sunshine hours
1985	13.8	571	1306
1984	13.0	683	1091
1983	14.5	540	1123
1982	14.0	810	1143
1981	13.5	848	986
1980	12.4	681	966
1979	13.0	637	1064
1978	12.3	754	1032
1977	12.8	721	1013
1976	13.9	684	1370
1975	13.4	918	1134
1974	12.6	751	1256
1973	13.4	806	1258
1972	12.1	715	1127
1971	14.2	693	1500
1970	13.0	887	1231
1969	13.5	662	1305
1968	13.3	805	1280
1968-1985	13.3	731	1177

2.3. The investigated characteristics

The following characteristics have been scored (Fig. 2):

1) Hair density (number of hairs per mm^2) on lower surface of the uppermost rosette leaves

   The hair density was described by classes. Class 0: no hairs; class 1: 1-2 hairs/mm^2; class 2: 2-4 hairs/mm^2; class 3: 4-8 hairs/mm^2; class 4: 8-16 hairs/mm^2; class 5: 16-32 hairs/mm^2; class 6: 32-64 hairs/mm^2.

2) Length of calyx setae

   The length was measured in mm.
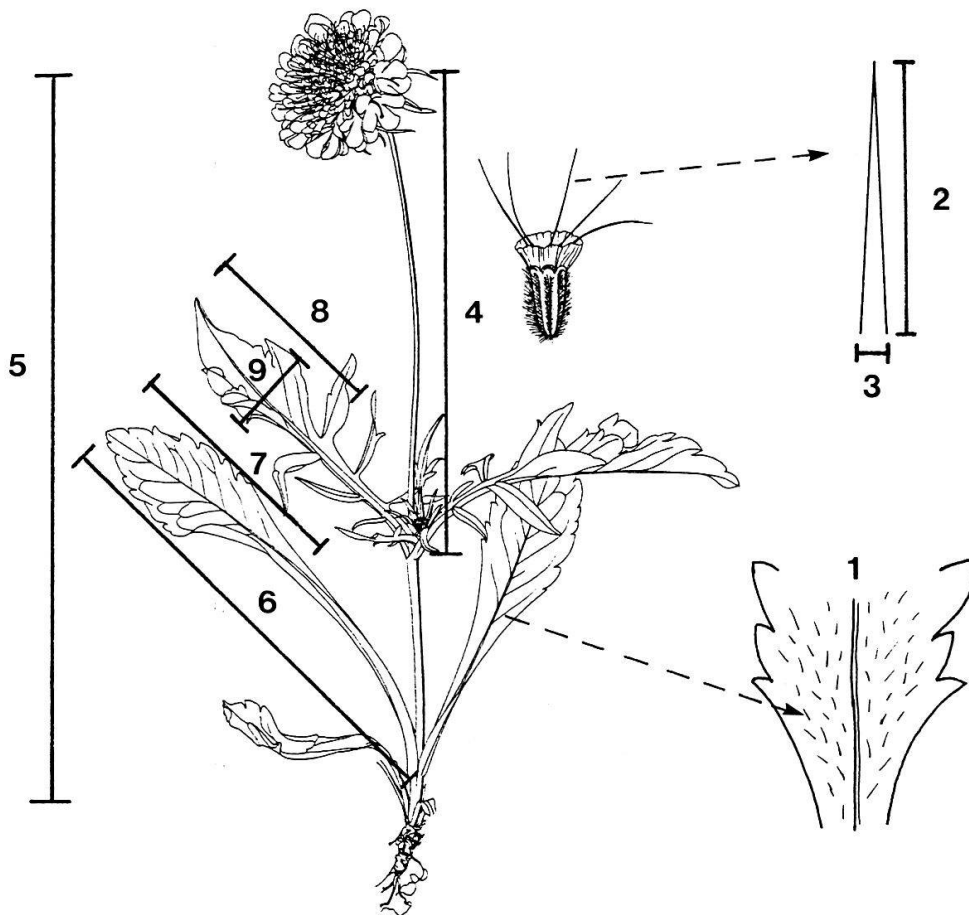
Fig. 2. Characteristics of *Scabiosa* used in the present study (see chapter 2.3.). The Figure represents *S. lucida* (from HESS et al. 1972, slightly modified).
In der vorliegenden Untersuchung berücksichtigte Eigenschaften von Scabiosa. Die Figur zeigt S. lucida (aus HESS et al. 1972, abgeändert).

3) Width of calyx setae

The width was characterized by classes. Class 1: 0.05-0.10 mm; class 2: 0.10-0.15 mm; class 3: 0.15-0.20 mm; class 4: 0.20-0.25 mm; class 5: 0.25-0.30 mm.

4) Length of stalk of flower head

The length of stalk was measured in cm.

5) Height of stems

The height of stems was measured in cm.

6) Length of the uppermost rosette leaves

The length was measured in mm.

7) Length of terminal lobe of the uppermost rosette leaves

Distance from the leaf to the point where the margin of the leaf blade reaches first as near as 1.5 mm to the middle nerve.

8) Length of the terminal lobe of the uppermost cauline leaves

The length was measured in mm.

9) Width of the terminal lobe of the uppermost cauline leaves

The width was measured in mm.

In addition some ratios of different characteristics were used, e.g. 2/3, 5/4, 7/6, 8/9.

It was supposed that characteristics 1) to 3) were only slightly modified by environmental conditions whereas the characteristics 4) to 8) seemed to be rather strongly influenced.

The characteristics of 20 plants of each plot or container were measured at the beginning. Later the number of full grown individuals was sometimes much smaller (down to 4). Measurements were made in the following years : 1968, 1969, 1970, 1971, 1973, 1975, 1979. The last measurements occurred in 1983 for the ground water plots and 1985 for the greenhouse containers.

2.4. Evaluation methods

The mean and single values of the measured characteristics (see Chapter 2.3.) have been plotted versus time.This representation allows a good overview not only of the tendencial development of the characteristics of the different species, but also shows scatter and distribution of the single values within every species under given conditions (see Figs. 5 to 31). Because the hair density on the uppermost rosette leaves is given only as classes, small random values have been added to every single value, thus making visible the cases where more than one indi-

vidual lies within the same hair density class.

Additionally, the differences of the characteristics between the final populations and the original species have been tested by Fisher's t-test (Tables 7 and 8).

To show general tendencies of the different species considering all characteristics, a multivariate analysis of the data has been done. Every measured plant is considered as an individual and described with the nine attributes listet in Chapter 2.3. These individuals have been classified into n groups according to species, environmental conditions and year of measurement (e.g. *S. columbaria*, in ground water table plots with a water level at 145 cm below the ground and well fertilized, in 1968). With this classification, discriminant analysis has been performed. This algorithm creates $n - 1$ new "attributes" (called discriminant axis) by linear combination of the measured characteristics in a way that the given groups are best separated on the first one or two axes. Thus, the main information of the data set is concentrated on two dimensions and can easily be represented as a scattergram. Because the investigated characteristics are of different kinds, the attribute vectors have been transformed to unit length, i.e. every attribute is considered an m-dimensional vector formed by the values of the given attribute of all m chosen individuals; the measured values are divided by the length of this vector before the analysis:

$$\mathring{a}_j = \frac{1}{\sqrt{\sum_m a_j^2}}$$

$\mathring{a}_j$ ... transformed value of a given attribute of individual j
a_j ... measured value of a given attribute of individual j
m ... number of individuals

The contribution of every attribute to the scores ist characterized by the discriminant coefficient, which equals the cosine of the angle α between the attribute coordinates and the discriminant axis. All multivariate analysis has been done with the program package (now called MULVA-4) of WILDI and ORLOCI (1983 and 1988). Some results are shown as ordination plots in Figs. 41 to 43.

3. SUMMARY OF THE RESULTS OF PART I

Results on the behaviour of pure species have been published by LANDOLT et al. (1975). A short summary of those investigations follows below.

3.1. General results

- The three species responded in different ways to the various experimental conditions, some aspects being taxonomically important, some others being only of statistical value.
- The number of flower-heads is strongly correlated to the dry weight of the shoot. In all three species the average of 3.5 g shoot dry weight corresponds to one flower-head. The height of the shoot and the root dry weight do not show a similar pattern. The diameter of the rosette varied greatly, both individually and seasonally; consequently, differences between the various treatments could only partially be evaluated.
- Under warm conditions in the greenhouse the dry matter production of three plants per culture container was about the same as that of six plants per container (under the same conditions).
- *Scabiosa columbaria*, *S. gramuntia* and *S. lucida* root down to an the average depth of almost 130 cm within one vegetation period (at low ground water table). The roots of some plants even reached a depth of more than 150 cm.

3.2. Influence of fertilization

- The various fertilizer treatments influenced particularly the number of flower-heads and the dry weight of the shoots. With *S. columbaria* and *S. gramuntia* at high ground water table the relative numbers of flower-heads of high, low and no fertilizer treatments were like 9:2:1 (Fig. 3).
- At high fertilizer treatment the flowering began on the average four to eight days earlier than in the other treatments.
- The life-span of plants at high fertilizer treatment was shorter than that of poorly or not at all fertilized ones, particularly in *S. columbaria*.
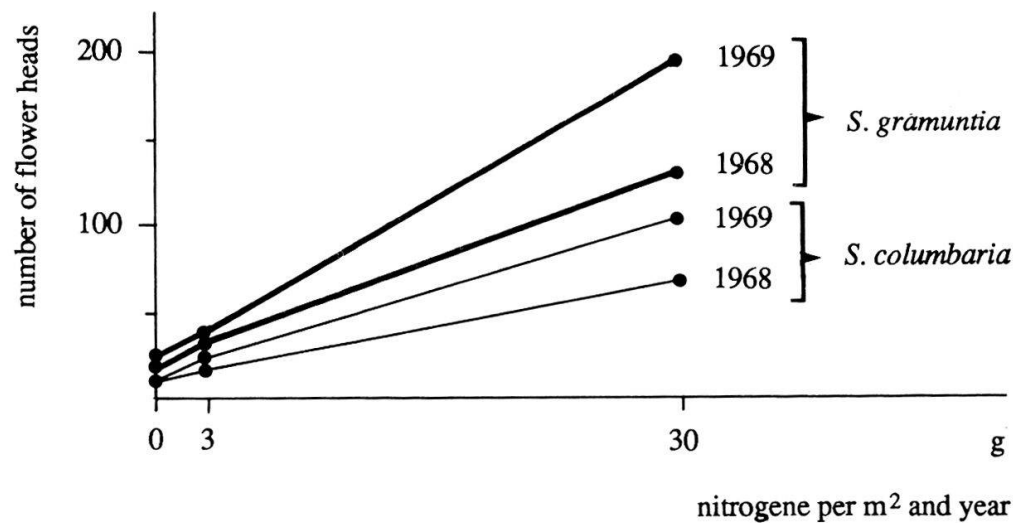
Fig. 3. Number of flower heads at different stages of fertilizer treatment and high ground water level.
Köpfchenzahl bei verschiedenen Düngungsstufen und hohem Wasserstand.

3.3. Influence of ground water table and irrigation

- The effects of the ground water table were influenced by irrigation and fertilizer treatment.
- A high water table level reduced the rooting space and was particularly unfavourable for *S. gramuntia.*
- A low water table level inhibited the growth of *S. columbaria,* in particular within the series irrigated at 28 day intervals.

3.4. Influence of temperature

- At high temperature the shoot weights of *S. columbaria* and *S. gramuntia* were nearly twice those at low temperature. With *S. lucida* hardly any differences could be observed (Fig. 4).
- With all three species the root weight under cool conditions was about twice that under warm conditions (Fig. 4).
- The root/shoot ratio is larger under cool conditions than under warm conditions. It increases in the following order: *S. gramuntia - S. columbaria - S. lucida* (Fig. 4).
- With *S. columbaria* and *S. gramuntia* the flowering began two to three

months later under cool conditions than under warm conditions. With *S. luci-da* the respective delay was only about one month.
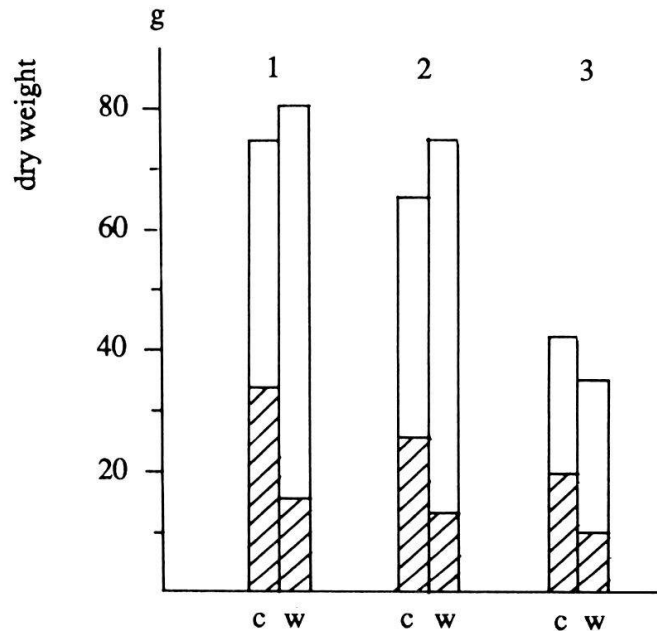
Fig. 4. Influence of temperature on weight of shoots and roots.
Einfluss der Temperatur auf das Spross und Wurzelgewicht.

1	*S. columbaria*	c	cool temperatures (17°C /7°C)		shoot weight
2	*S. gramuntia*	w	warm temperatures (30°C /20°C)		root weight
3	*S. lucida*				

3.5. Competition experiments

- In mixed culture all three species were most competitive under those conditions, where they showed the best relative growth in pure culture.
- Because of its strong growth, *S. gramuntia* was vegetatively the most successful competitor under nearly all experimental conditions.
- The competitive potential of *S. gramuntia* versus *S. columbaria* was particularly strong under conditions with a low water table level and simultaneously a strong fertilizer treatment or irrigation intervals of 28 days; under these conditions *S. gramuntia* produced five to seven times more flower-heads than *S. columbaria* (in the respective pure cultures it was only two or three times more).

- *S. gramuntia* grown in mixed culture with a high water table level and low fertilizer treatment produced about twice as many flower-heads as *S. columbaria*; in pure culture it was only about 11/2 times as many.
- Differences occurring between mixed cultures and pure cultures in the greenhouse were not very pronounced and in general statistically insignificant. However, under these same conditions a correlation seems to exist between the growth in pure culture and the vegetative competition; accordingly, the following sequence of the competition potential can be established: *S. gramuntia* ≥ *S. columbaria* ≥ *S. lucida*.
- Under cool conditions *S. lucida* has an advantage over the other two species in so far as its fruit comes to maturity, whereas a large proportion of that of the other species do not ripen.

4.   RESULTS OF PART II

The results of part II are summarized in the Figs. 32 to 40.

4.1. Variability of the characteristics under identical and differing conditions

The variability is shown for each characteristic under warm and cool conditions and from the ground water table experiment under the combination of low water table level and high fertilization. These examples are also representative for other conditions.

4.1.1. Hair density (Figs. 5 to 7)

Variability of hair density is in all three species not very high. Within the first three years hair density remains quite stable. Also under differing conditions there is not much variation within each species. Only *S. columbaria* and *S. lucida* show a slightly higher density under warm conditions compared with cool ones. But the difference is insignificant (Tables 7 and 8).
After 1970 the first generation of crossings were fully grown. Therefore the measurements included this mixed generation as well as the pure species. The total variability is very high, as expected. It reduces after 1973 to the smallest levels in 1985 (for the greenhouse conditions) and in 1979 (for the ground water plots). The higher variability in 1983 for these populations is probably due to the matu-

classes
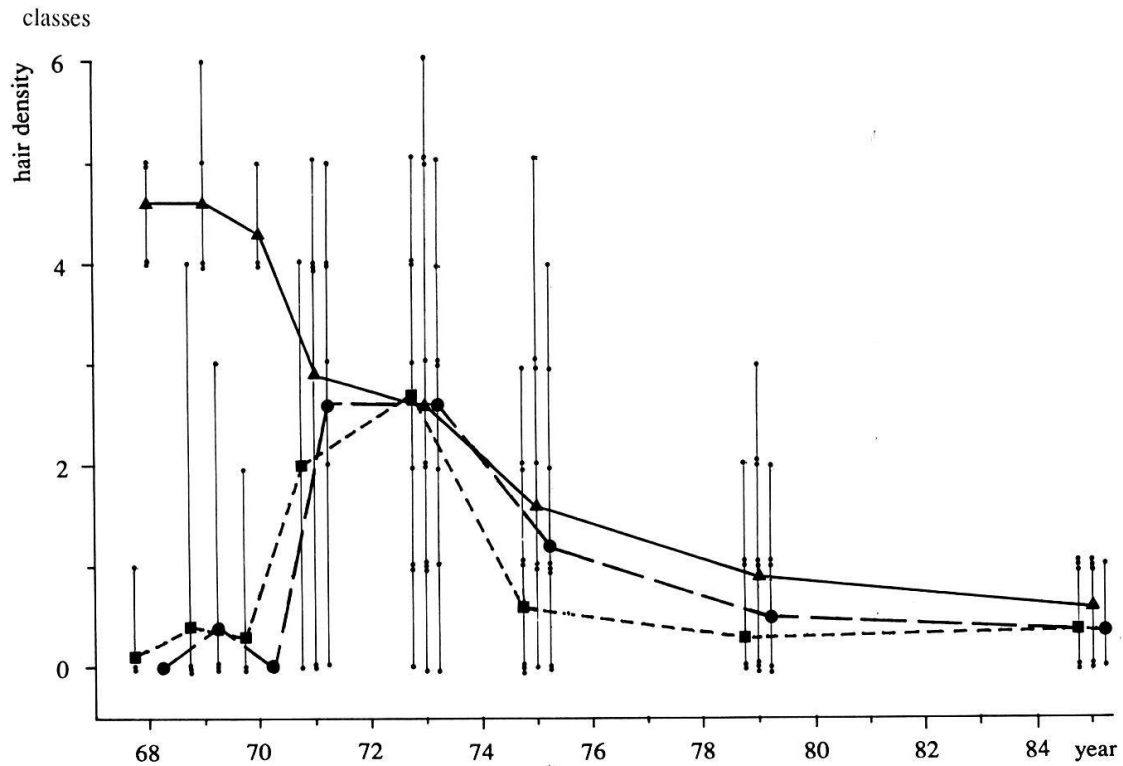
Fig. 6. Cool conditions - *kühle Bedingungen*
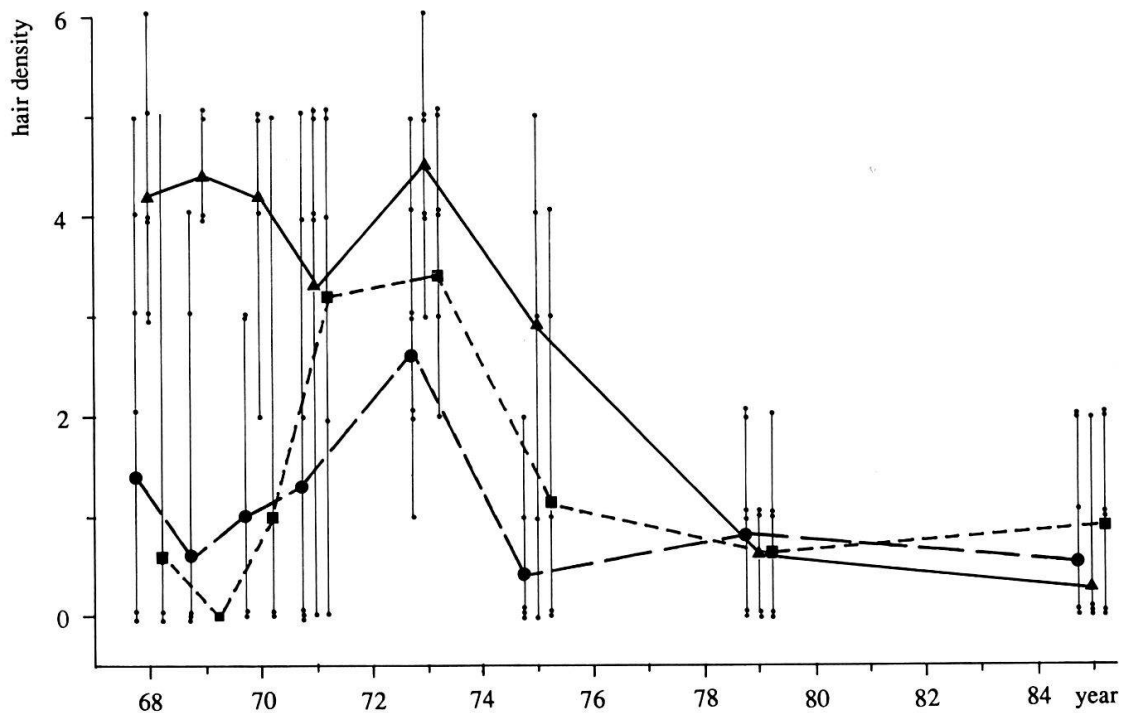
Fig. 6. Warm conditions - *warme Bedingungen*

Figs. 5-7. Hair density on rosette leaves of *Scabiosa* populations
Haardichte der Rosettenblätter von Scabiosa-Populationen
■ *S. lucida*   ● *S. columbaria*   ▲ *S. gramuntia* | total variation with individual values
★ mixed population
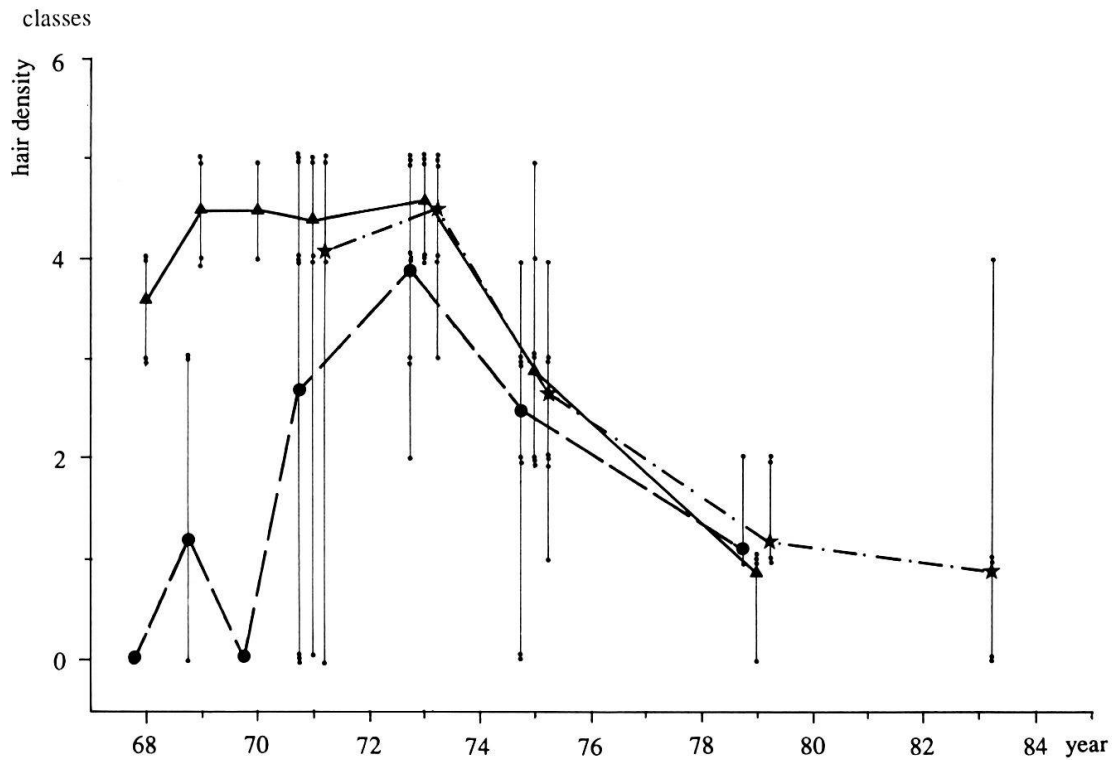
Fig. 7. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

ration of young plants of a new generation which did not yet undergo full selection. In 9 out of 14 different conditions the change of the mean values within the last 3 (respectively 5) years is still higher than 10%.

Table 7. Significant differences between the measured characteristics of *S. lucida* 1968 (luc) *S. columbaria 1968* (col), *S. gramuntia* 1968 (gram) and the final populations in 1985 (M) respectivley under warm (30°/20°C) and cool (17°/7°C) conditions in the greenhouse and between the species and the final populations under warm conditions and cool conditions respectively.
Gesicherte Unterschiede in den gemessenen Merkmalen von S. lucida 1968 (luc), S. columbaria 1968 (col), S. gramuntia 1968 (gram) und den Mischpopulationen 1985 (M) unter warmen (30°/20°C) bzw. kühlen Bedingungen (17°/7°C) im Gewächshaus sowie zwischen den Ausgangsarten und den Endpopulationen je unter warmen und kühlen Bedingungen.

Significance level *Signifikanzniveau*: 1 = 95%, 2 = 99%, 3 = 99.9%, - = insignificant
a = hair density - *Haardichte*
b = length of calyx setae - *Kelchborstenlänge*
c = width of calyx setae - *Kelchborstenbreite*
d = stalk length - *Blütenstiellänge*
e = stem length - *Stengellänge*
f = length of the uppermost rosette leaf - *Länge des obersten Rosettenblattes*
g = length of terminal lobe of cauline leaf - *Länge des Endabschnittes des obersten Stengelblattes*
h = length / width of terminal lobe - *Länge / Breite des Endabschnittes des obersten Stengelblattes*
i = length of terminal lobe / rosette leaf - *Länge des Endabschnittes / Länge des letzten Rosettenblattes*

Conditions and populations in comparison	Characteristics								
	a	b	c	d	e	f	g	h	i
Temperature									
S. lucida 1968 warm/cool	-	1	-	-	-	-	-	-	-
S. columbaria 1968 w/c	-	-	1	-	-	-	-	1	-
S. gramuntia 1968 w/c	-	-	2	3	-	-	3	3	1
Final population 1985 w/c	-	3	3	2	3	3	-	-	3
warm									
luc/col	-	2	3	-	-	-	-	1	-
luc/gram	3	3	3	-	3	2	-	3	3
col/gram	3	2	3	-	3	2	-	-	3
luc/M	-	3	3	2	3	1	3	2	-
col/M	-	2	3	-	3	-	3	-	-
gram/M	3	-	-	1	-	-	3	-	3
cool									
luc/col	-	2	-	-	-	-	1	1	-
luc/gram	3	3	2	3	3	3	3	3	-
col/gram	3	-	1	-	3	3	-	1	2
luc/M	-	3	-	3	2	-	3	1	-
col/M	-	2	-	-	1	-	3	3	3
gram/M	3	3	3	1	3	3	-	3	3

Table 8. Significant differences between the measured characteristics of *S. columbaria 1968* (col), *S. gramuntia* 1968 (gram) and the final populations in 1985 (M) respectively under different conditions and between the species and the final populations under all conditions and strong fertilization (D_{30}) respectively.

Gesicherte Unterschiede in den gemessenen Merkmalen von S. columbaria 1968 (col), S. gramuntia 1968 (gram) und den Mischpopulationen 1985 (M) unter je verschiedenen Bedingungen sowie zwischen den Ausgangsarten und den Endpopulationen unter allen Bedingungen bzw. unter starker Düngung (D_{30}).

Significance level - *Signifikanzniveau*: 1 = 95%, 2 = 99%, 3 = 99.9%, - = insignificant
B_x, D_x, G_x see Table 5.; a to i see table 7. B_x, D_x, G_x *vgl. Tab. 5.; a - i vgl. Tab. 7.*

| Conditions and populations in comparison	Characteristics								
	a	b	c	d	e	f	g	h	i
Fertilization (D)									
S. gramuntia 1968 D_{30}/D_3	-	1	-	-	-	3	-	-	2
S. columbaria 1968 D_{30}/D_3	-	-	-	-	-	3	-	-	-
Final population 1983 D_{30}/D_3	3	-	1	-	3	3	1	-	2
S. gramuntia 1968 D_{30}/D_0	-	2	-	2	-	3	-	-	1
S. columbaria 1968 D_{30}/D_0	-	-	-	1	-	3	-	-	-
Final population 1983 D_{30}/D_0	3	-	-	3	3	3	1	-	3
S. gramuntia 1968 D_3/D_0	-	-	-	1	-	-	-	-	-
S. columbaria 1968 D_3/D_0	-	-	-	-	-	-	-	-	-
Final population 1983 D_3/D_0	-	1	-	3	1	3	-	-	-
Water table (G)									
S. gramuntia 1968 G_{45}/G_{145}	-	-	3	-	-	-	-	-	-
S. columbaria 1968 G_{45}/G_{145}	-	-	-	-	-	-	-	-	-
Final population 1983 G_{45}/G_{145}	-	-	-	-	-	-	-	-	-
Watering interval (B)									
S. gramuntia 1968 B_{nat}/B_7	3	-	1	-	-	1	-	-	-
S. columbaria 1968 B_{nat}/B_7	1	-	3	-	-	2	-	-	1
Final population 1983 B_{nat}/B_7	-	-	-	2	3	3	3	-	-
S. gramuntia 1968 B_7/B_{28}	-	-	-	-	1	2	-	1	-
S. columbaria 1968 B_7/B_{28}	-	-	-	-	-	-	-	-	-
Final population 1983 B_7/B_{28}	1	2	-	-	3	-	-	-	-
S. gramuntia 1968 B_{nat}/B_{28}	-	-	1	3	1	3	-	2	2
S. columbaria 1968 B_{nat}/B_{28}	-	-	3	-	-	3	-	-	-
Final population 1983 B_{nat}/B_{28}	3	2	1	3	1	3	3	-	-
All conditions									
col/gram	3	3	3	3	3	3	3	3	3
col/M	3	3	3	3	3	-	-	2	3
gram/M	3	-	1	3	1	1	3	2	-
D_{30}									
col/gram	3	-	3	-	3	1	1	-	3
col/M	3	3	3	-	3	3	1	-	3
gram/M	3	-	-	-	3	2	-	-	-
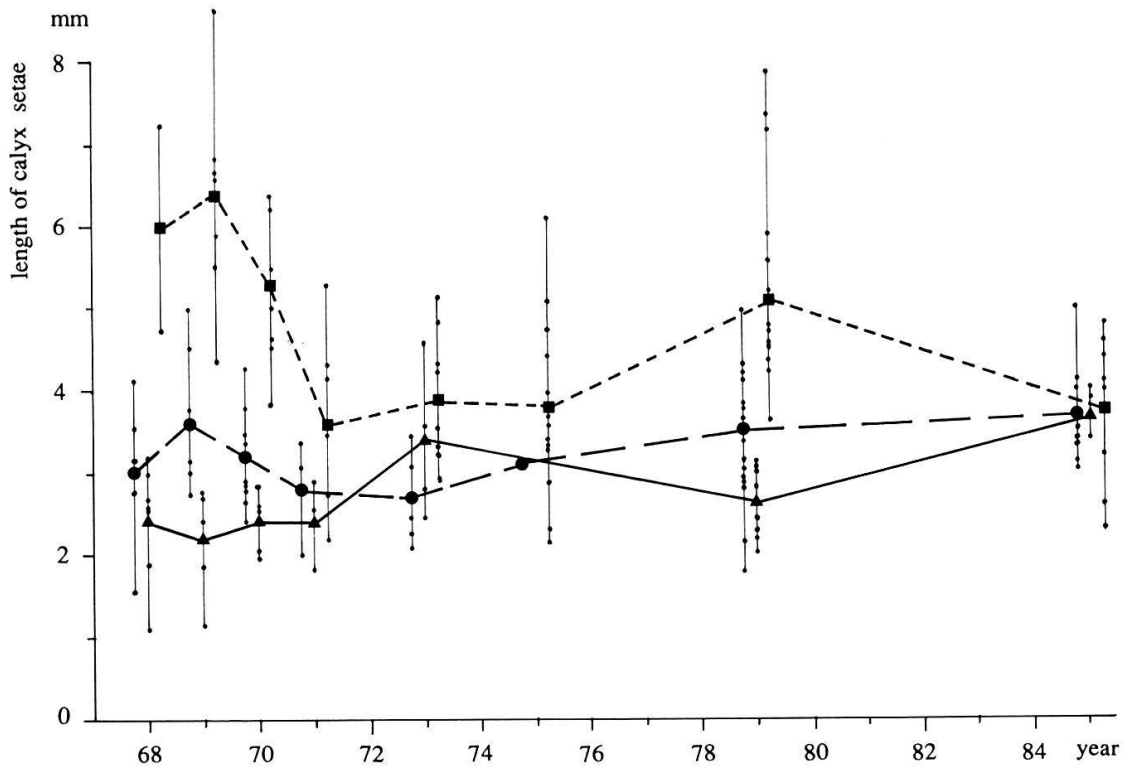
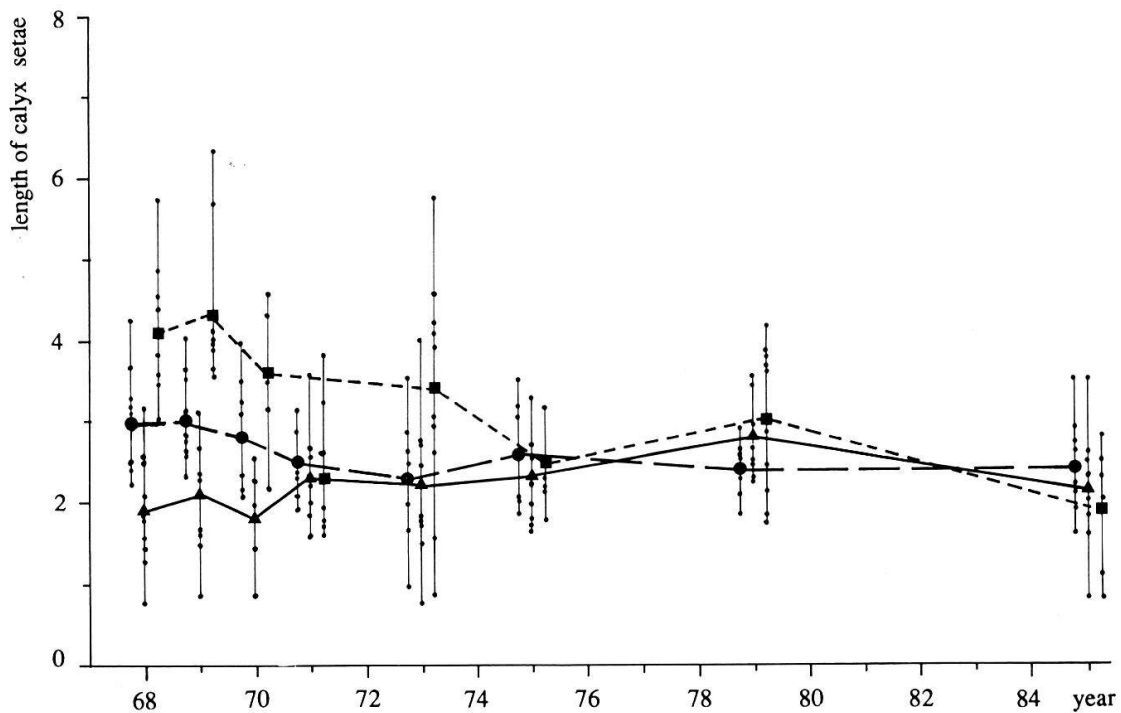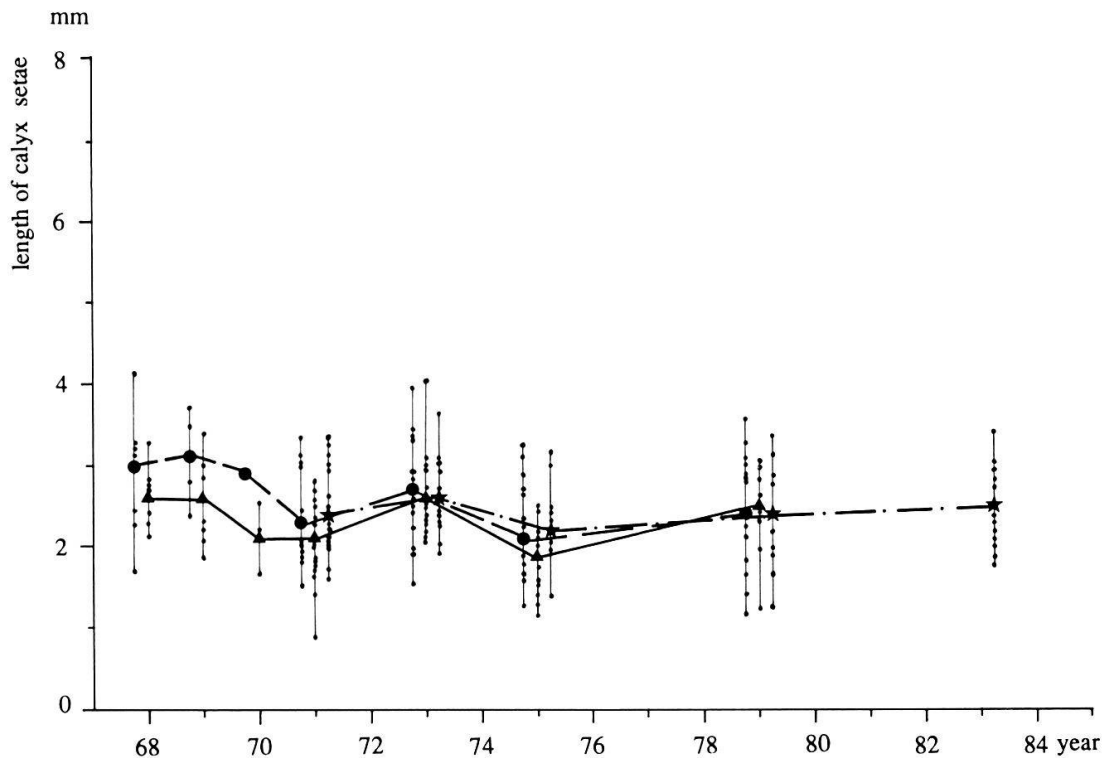**Fig. 8.** Cool conditions - *kühle Bedingungen*

Fig. 9. Warm conditions - *warme Bedingungen*

Figs. 8-10. Length of calyx setae of *Scabiosa* populations
Kelchborstenlänge von Scabiosa-Populationen

■ *S. lucida*　● *S. columbaria*　▲ *S. gramuntia*　│ total variation with individual values
★ mixed population

Fig. 10. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.2. Length of calyx setae (Figs. 8 to 10)

The variability of the length of calyx setae is medium. The deviations are sometimes more than 20% from the mean. The yearly variability (during the first three years) is about 10% around the mean.

Warm conditions tend to cause shorter setae. However, the difference is only significant for *S. lucida* (Tables 7 and 8). No other variance was observed which could be attributed to the different environmental conditions, except longer setae for *S. gramuntia* under low fertilization.

The variability during the first years after maturation of crossings (1971 and later) is rather high and contains the whole variability of all three species. Toward the end of the experiments (1985 and 1983) variability became much smaller. The difference between the two mean values of the last three years is mostly less than 10%.

4.1.3. Width of calyx setae (Figs. 11 to 13)

The width of calyx setae is more variable than the length. The variability is rather high within one species and between different years (considering the first three years).

In warm conditions the setae are narrower than in cold ones (the difference is significant for *S. columbaria* and *S. gramuntia*, Table 7). The same is true under dry conditions.

The variation of the mixed populations is highest in 1971 and lowest toward the end of the experiment (1985 and 1983). Except for cool conditions the mean values decreased somewhat within the last three years.
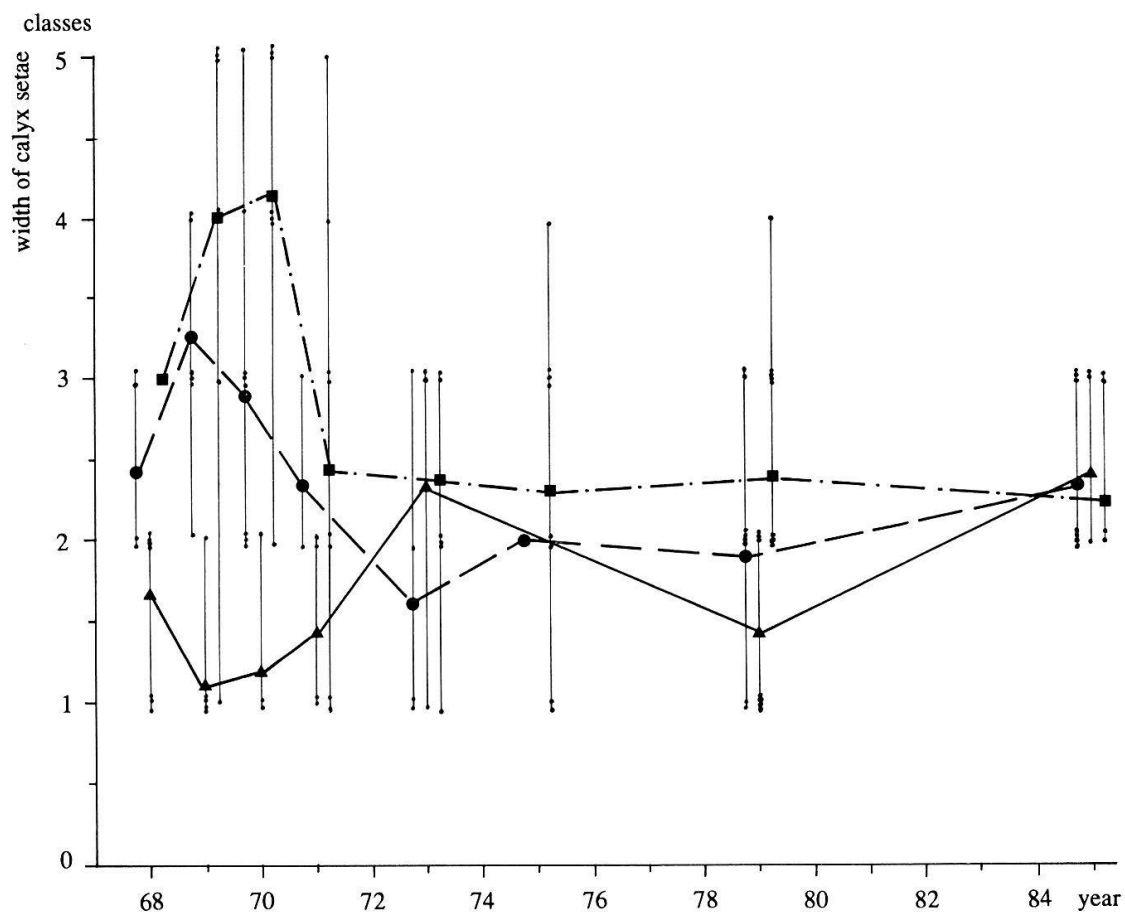
Fig. 11. Cool conditions - *kühle Bedingungen*

Figs. 11-13. Width of calyx setae of *Scabiosa* populations
Kelchborstenbreite von Scabiosa-Populationen
■ *S. lucida*   ● *S. columbaria*   ▲ *S. gramuntia*   ⁞ total variation with individual values
★ mixed population

Fig. 12. Warm conditions - *warme Bedingungen*

Fig. 13. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt
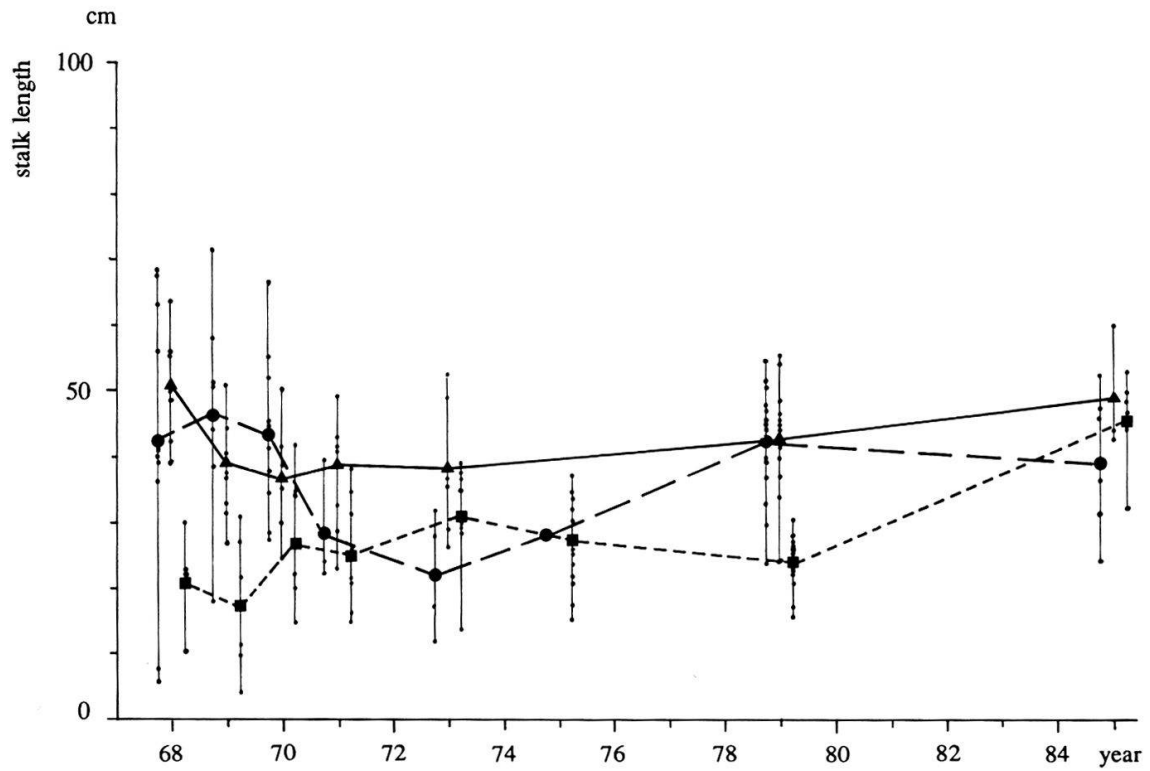
Fig. 14. Cool conditions - *kühle Bedingungen*
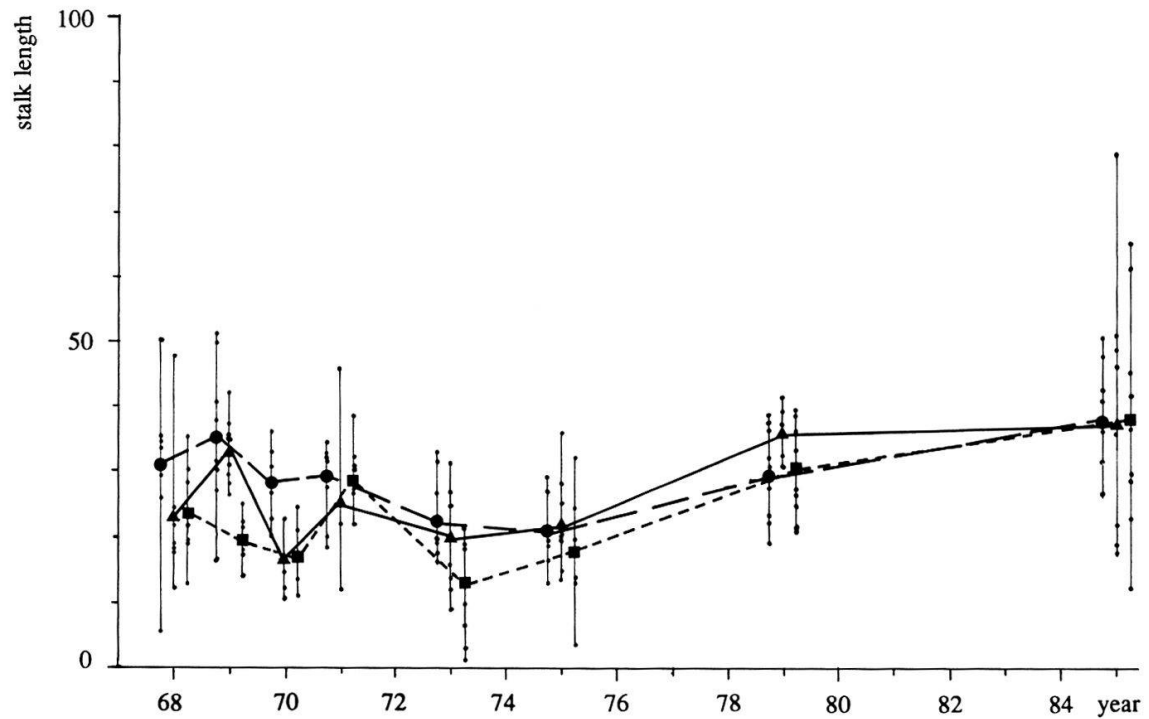
Fig. 15. Warm conditions - *warme Bedingungen*

Figs. 14-16. Stalk length of flower heads of *Scabiosa* populations
Länge des Blütenkopfstiels von Scabiosa-Populationen

■ *S. lucida*   ● *S. columbaria*   ▲ *S. gramuntia* | total variation with individual values
★ mixed population
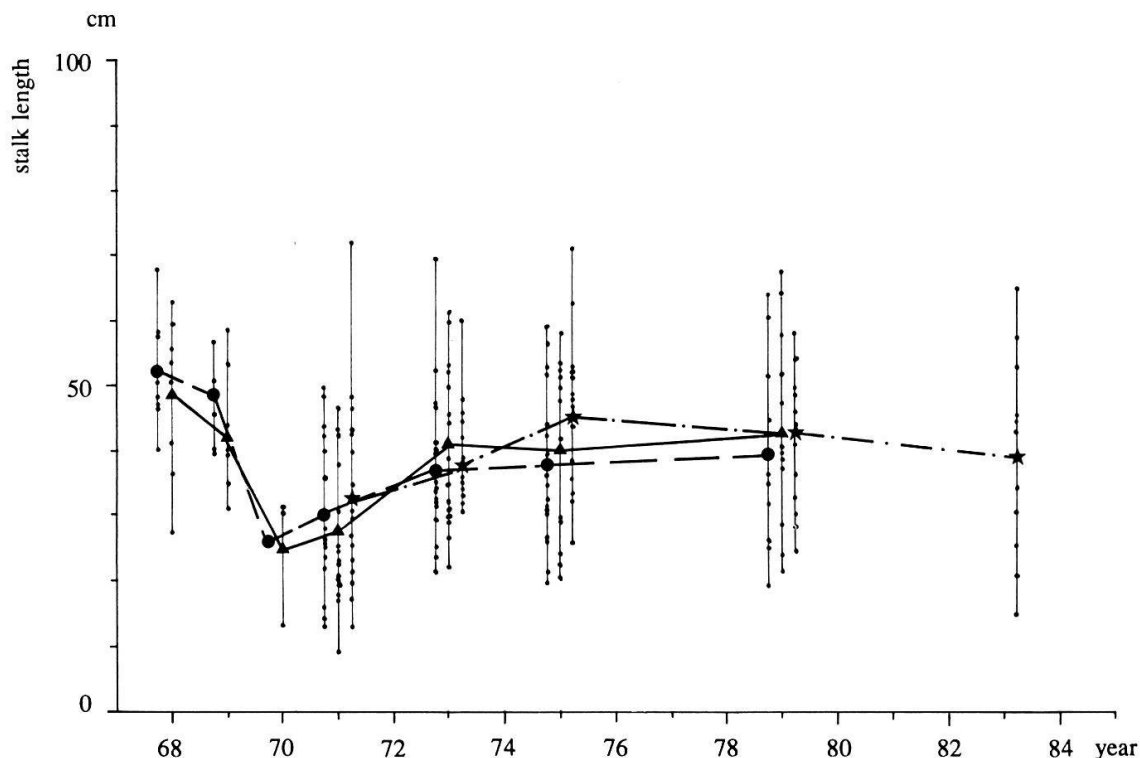
Fig. 16. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.4. Stalk length of flowering heads (Figs. 14 to 16)

The stalk length varies widely, especially in *S. columbaria*. Also the yearly variation (1968 to 1970) is rather high (deviating up to 20% from the mean). The variation of the mixed population (from 1971 to 1985 and 1983 , resp.) stays on a high level during the whole experiment.

The variation between different conditions is quite pronounced in *S. gramuntia* and a little less in *S. columbaria*. No variance was observed between the two temperature conditions of *S. lucida*. For *S. gramuntia* significant differences occur between cool (longer stalks) and warm conditions (Table 7), and for *S. columbaria* and *S. gramuntia* between well fertilized (longer stalks) and slightly fertilized or unfertilized conditions (Table 8). Within the last three years the mean values hardly changed anymore.
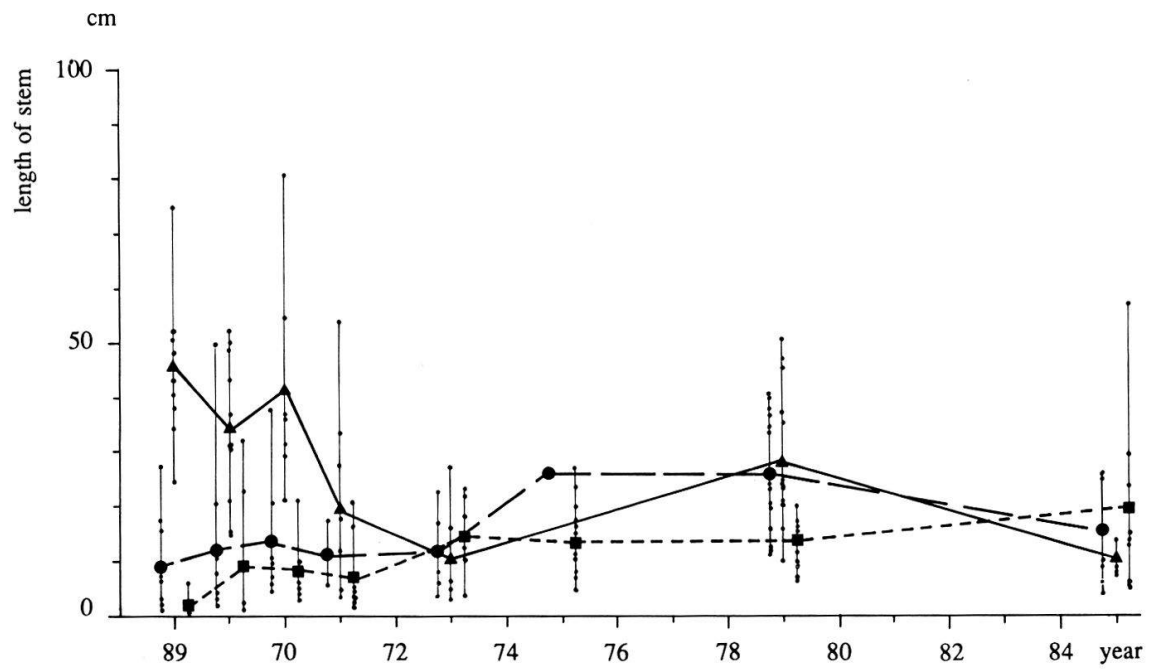
Fig. 17. Cool conditions - *kühle Bedingungen*
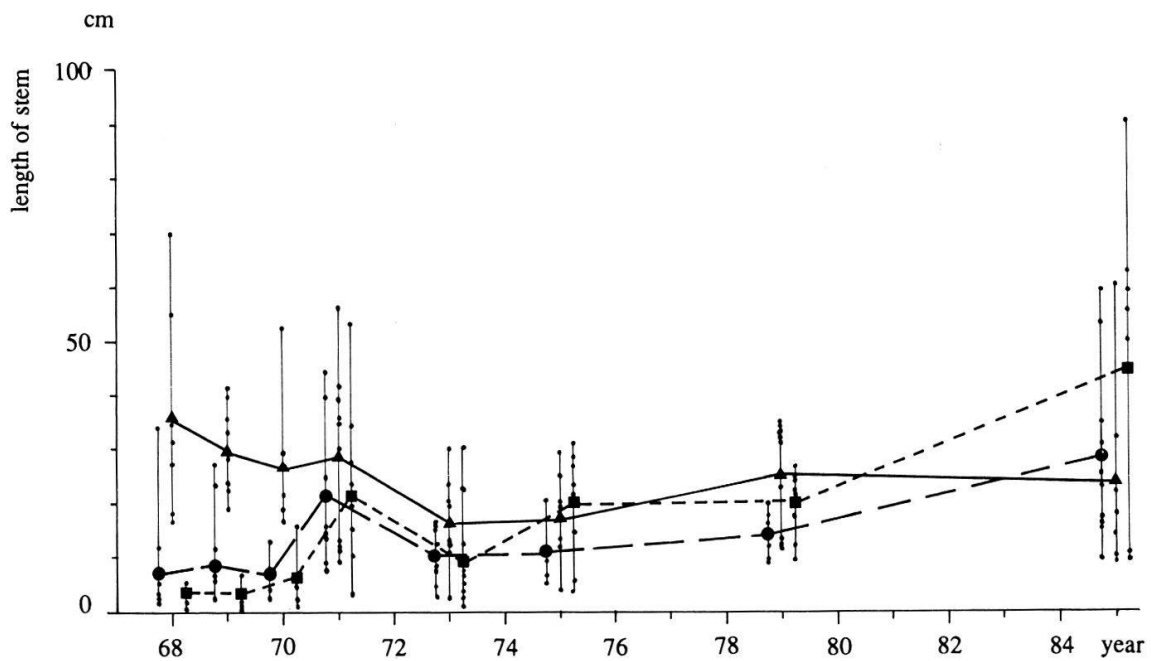
Fig. 18. Warm conditions - *warme Bedingungen*

Figs. 17-19. Length of stem of *Scabiosa* populations
Stengellänge von Scabiosa-Populationen
■ *S. lucida*   ● *S. columbaria*   ▲ *S. gramuntia*   ⏐ total variation with individual values
★ mixed population
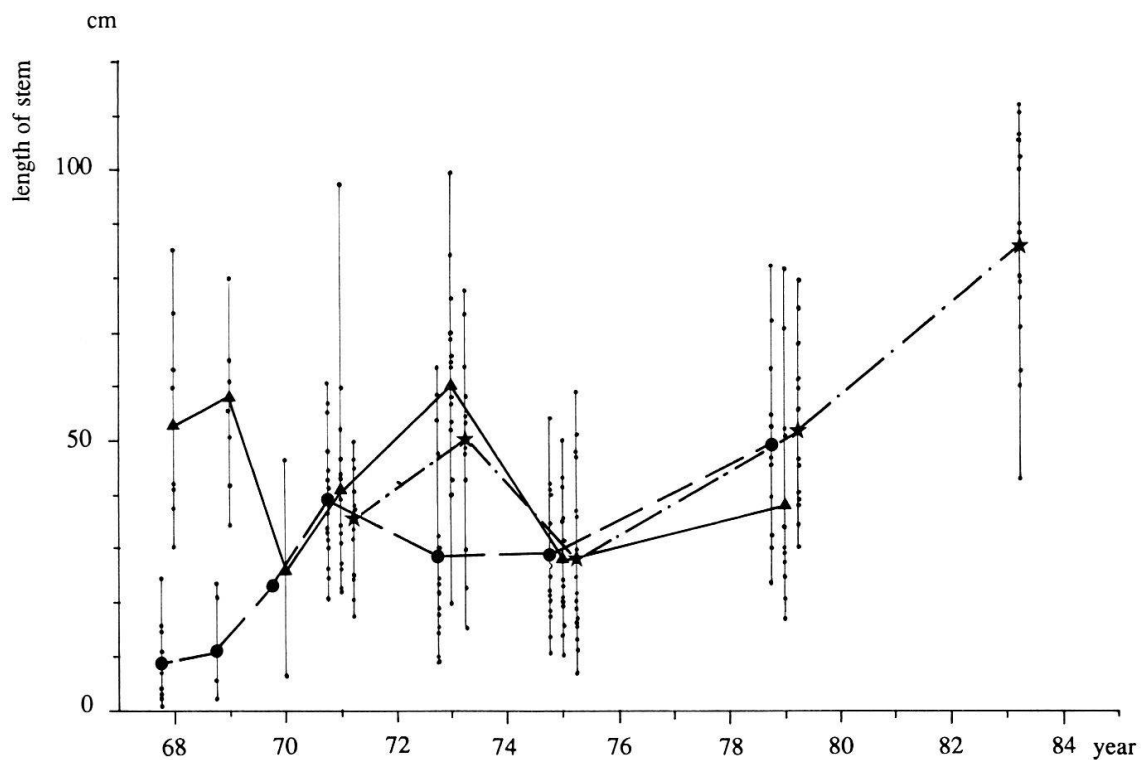
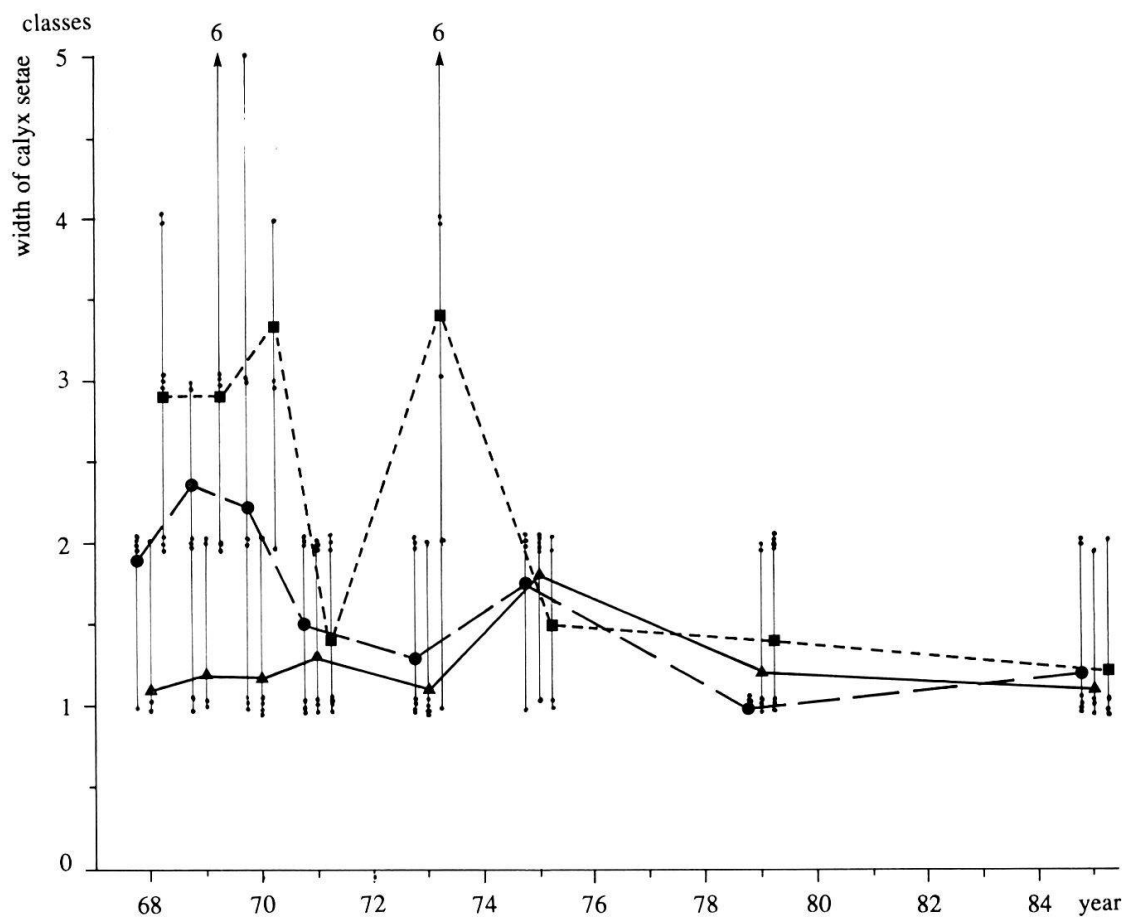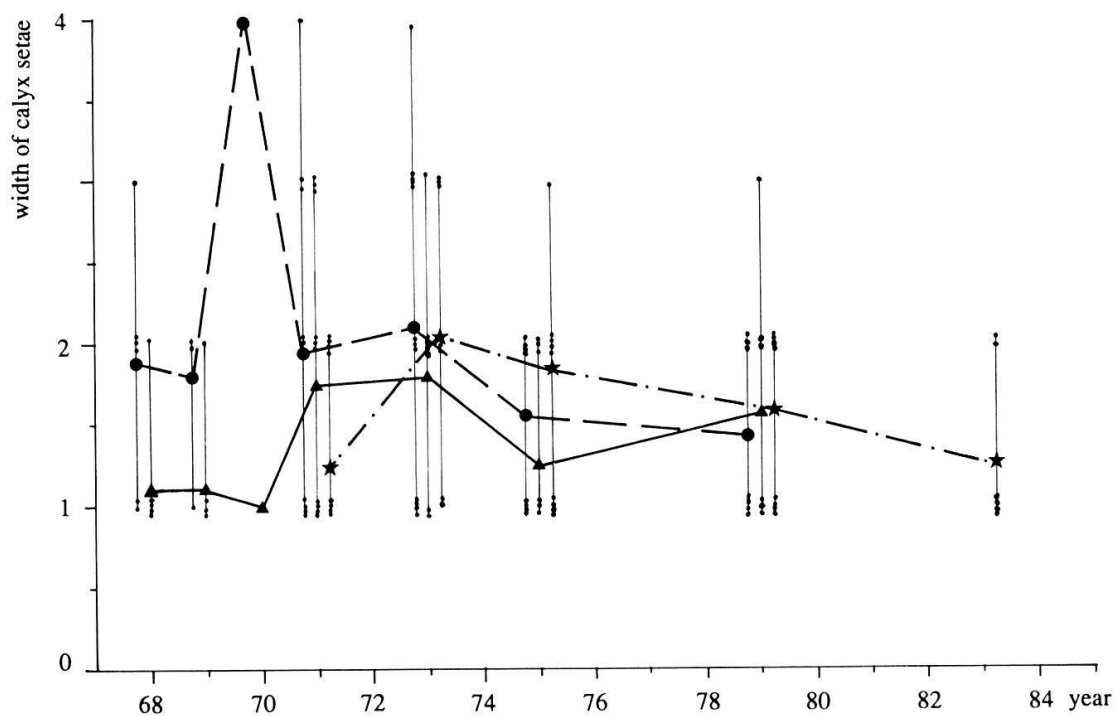**Fig. 19.** Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.5. Length of stem (Figs. 17 to 19)

The stem length varies widely under all but cool conditions. This concerns the individuals within a population as well as the mean values for different years. The stem heights of *S. lucida* and *S. columbaria* in the greenhouse are nearly the same under both cool and warm conditions. On the other hand, the stem of *S. gramuntia* is longer under cool than under warm conditions.

There is still a pronounced difference between the two mean values of the last three years.
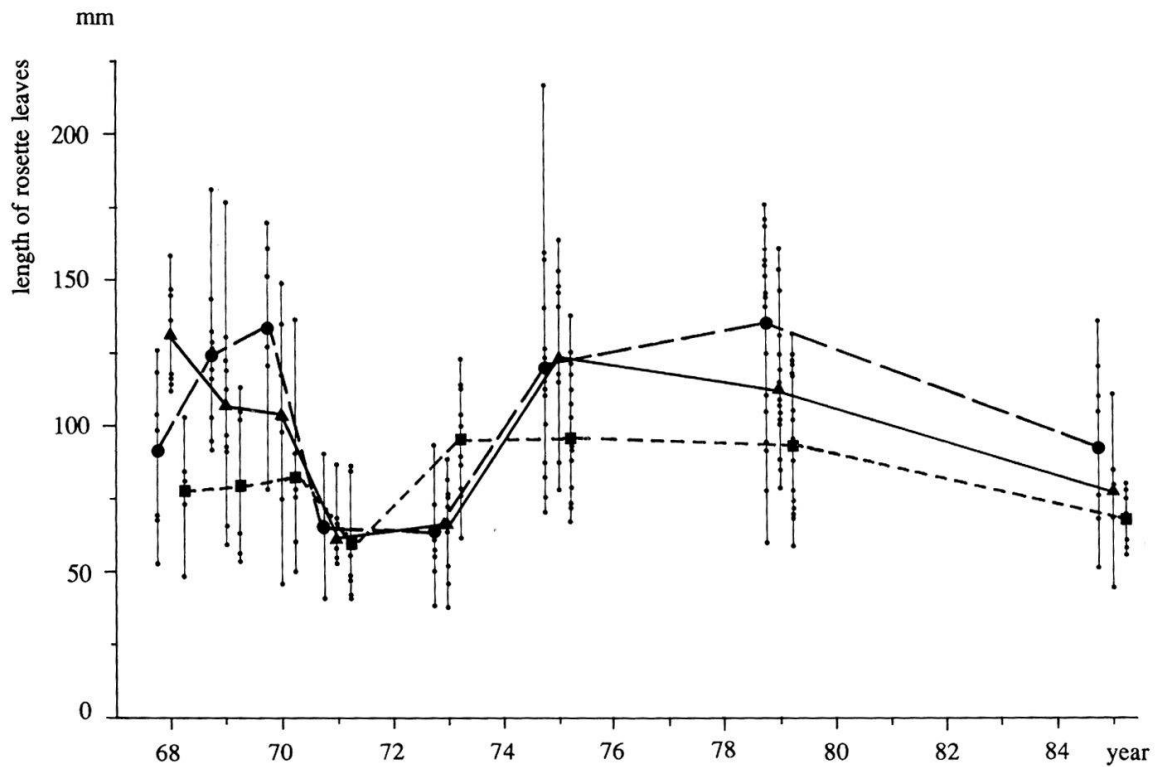
Fig. 20. Cool conditions - *kühle Bedingungen*
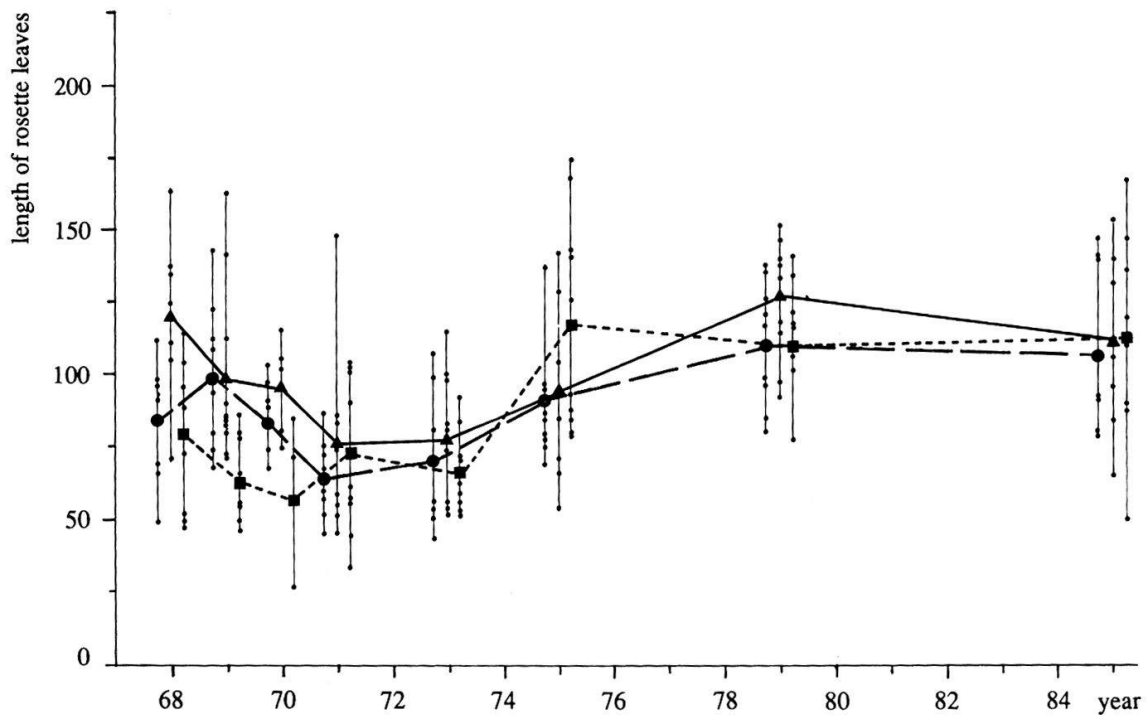
Fig. 21. Warm conditions - *warme Bedingungen*

Figs. 20-22. Length of rosette leaves of *Scabiosa* populations
Länge der Rosettenblätter von Scabiosa-Populationen
■ *S. lucida* ● *S. columbaria* ▲ *S. gramuntia*   total variation with individual values
★ mixed population
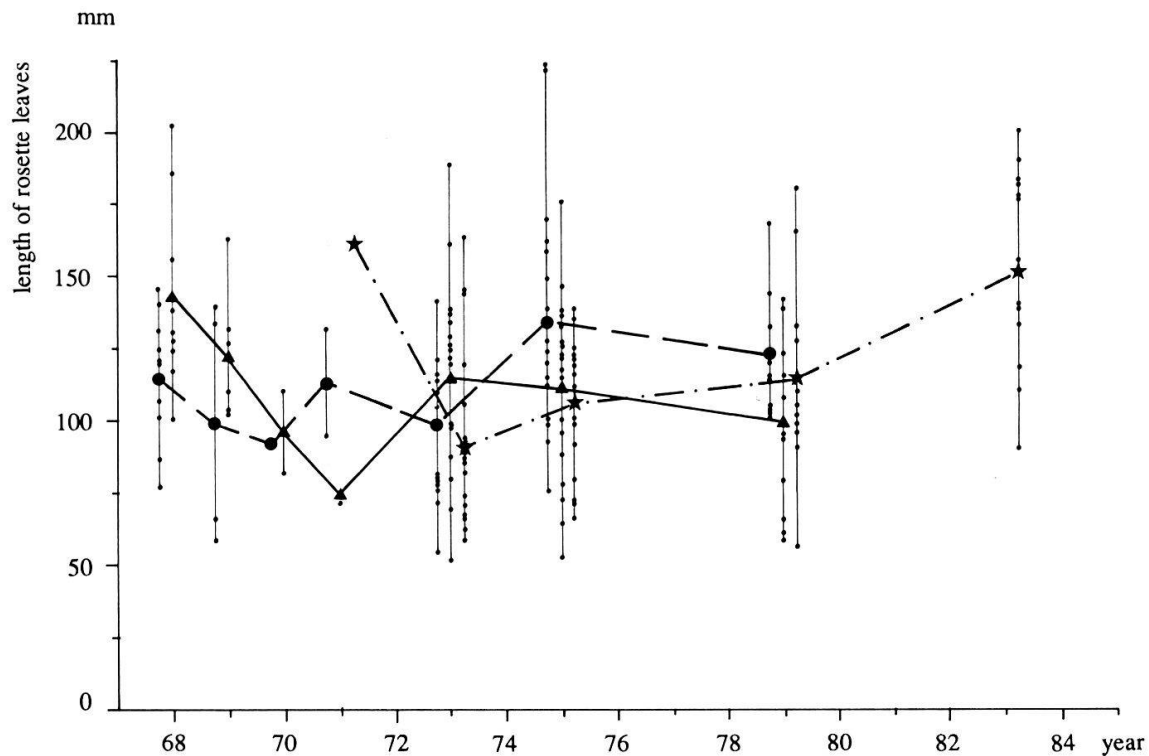
Fig. 22. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.6. Length of rosette leaves (Figs. 20 to 22)

The variation of the leaf length is rather high in all three species reaching up to 50% deviation from the mean value. Also the yearly variation (1968 to 1970) is high.

Due to this high variation the differences in length between different conditions are statistically not always significant, though the tendency is clear : The leaves of *S. columbaria* and *S. gramuntia* are shorter under warm conditions than under cool ones, they are longer in well fertilized plots than in slightly or unfertilized ones. A watering interval of seven days also produces longer leaves than a 28 day interval.

The variability within the mixed populations is high and does not diminish during the experiment. Also the difference of the mean values between the last three years is remarkable, the values being higher under normal rain watering and lower under all experimental watering conditions.

Fig. 23. Cool conditions - *kühle Bedingungen*
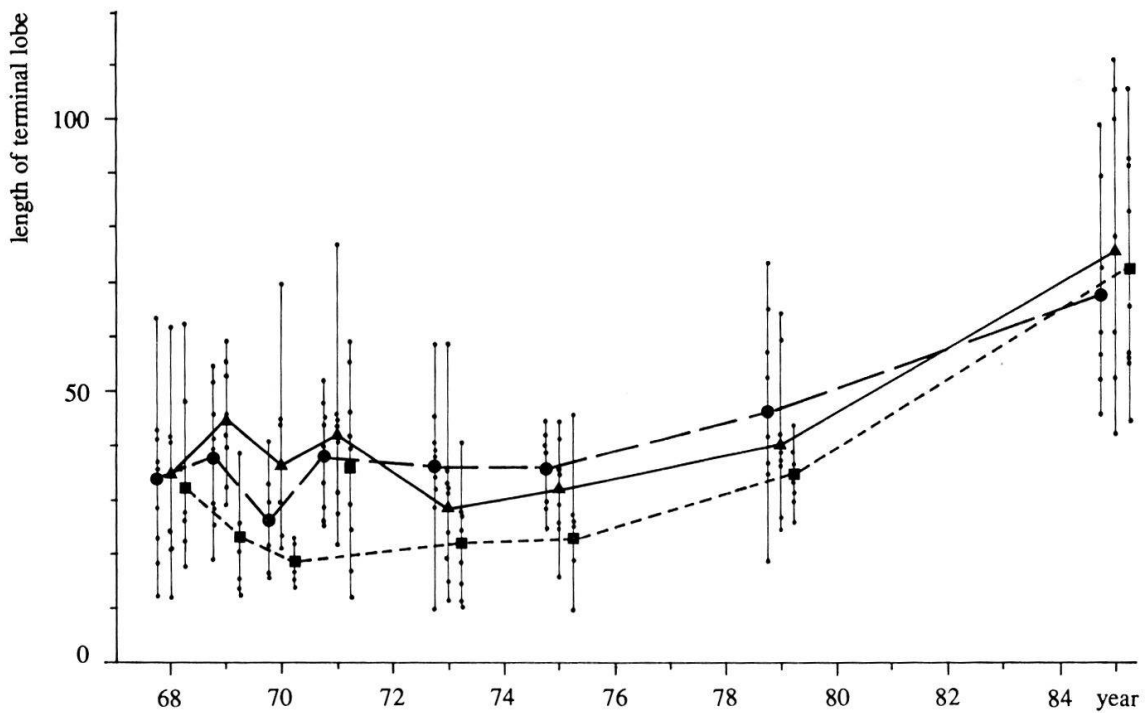
Fig. 24. Warm conditions - *warme Bedingungen*

Figs. 23-25. Length of the terminal lobe of the uppermost cauline leaf of *Scabiosa* populations - *Länge des Endabschnittes des obersten Stengelblattes von Scabiosa-Populationen*
■ *S. lucida* ● *S. columbaria* ▲ *S. gramuntia* ⎸ total variation with individual values
★ mixed population
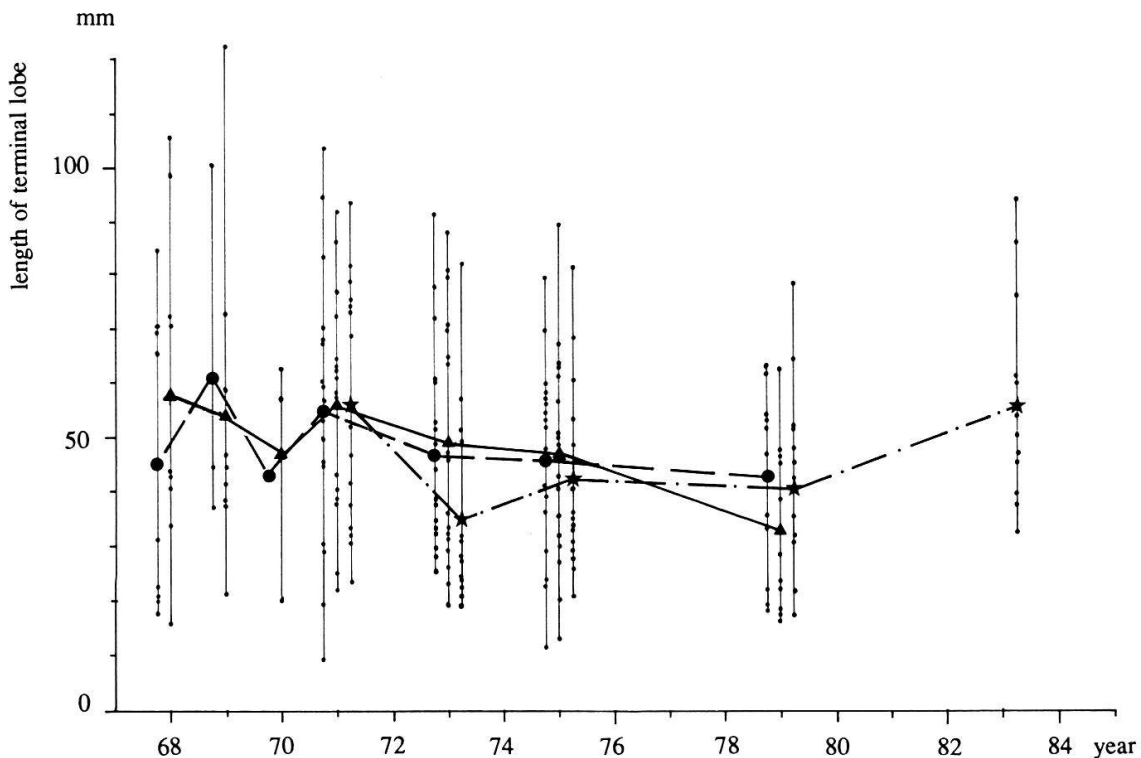
Fig. 25. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.7. Length of the terminal lobe of upper cauline leaves (Figs. 23 to 25)

The variation of the length of the terminal lobe is high within the same species as well within different years (up to 100% deviation from the mean value).

Under warm conditions the lobe is shorter for *S. columbaria* (insignificant) and for *S. gramuntia* than under cool conditions. Contrary, *S. lucida* develops longer leaves under warm conditions (difference insignificant). In the well fertilized plots the lobe is longer than in slightly or unfertilized ones.

The variability at the beginning of the experiment was slightly higher than at the end. A pronounced difference between the mean values of the last three years can be observed in the greenhouse..
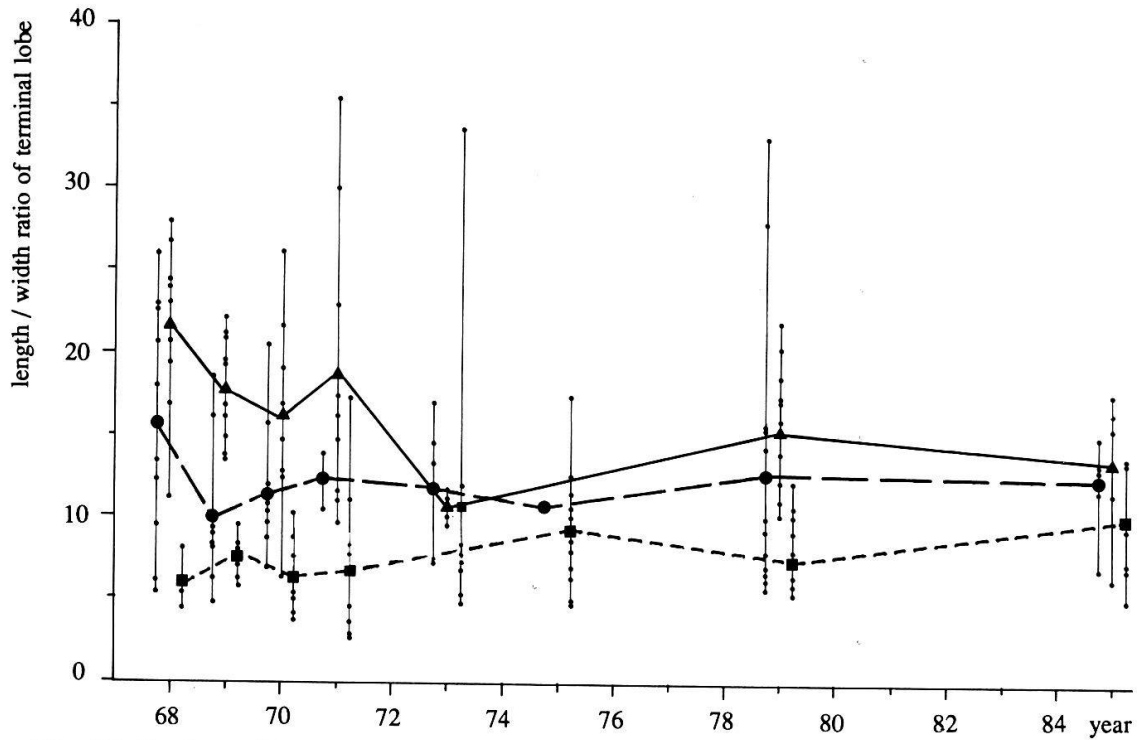
Fig. 26. Cool conditions - *kühle Bedingungen*
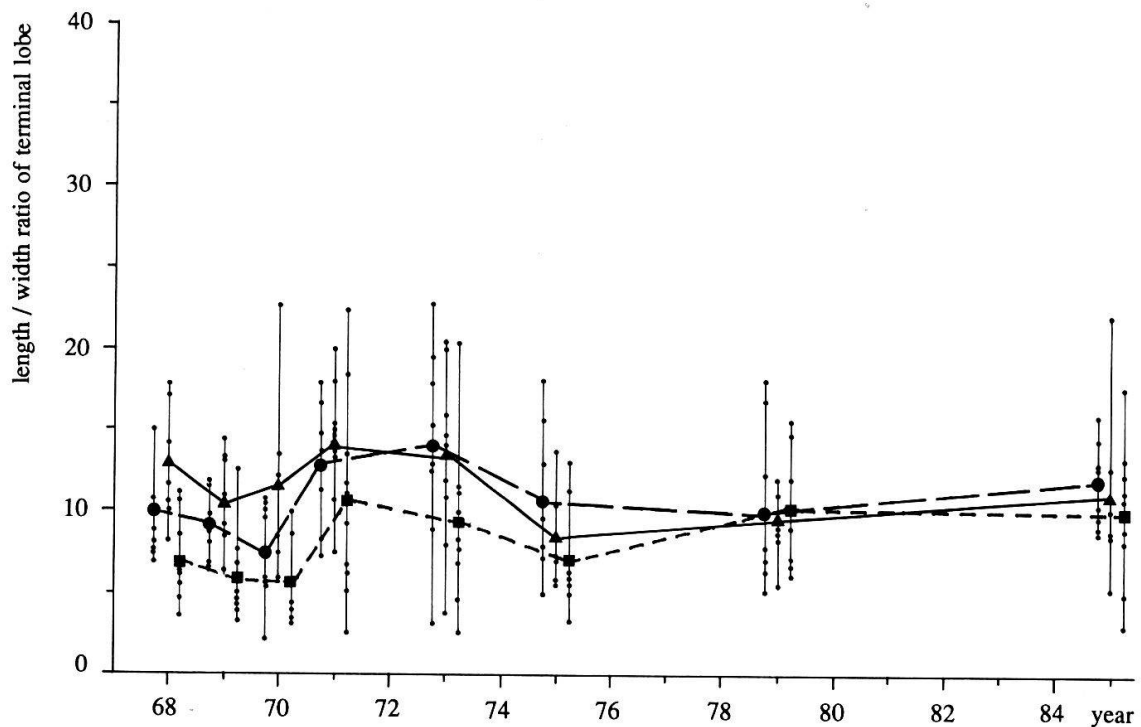
Fig. 27. Warm conditions - *warme Bedingungen*

Figs. 23-25. Length/width ratio of the terminal lobe of the uppermost cauline leaf of *Scabiosa* populations - *Längen/Breitenverhältnis des Endabschnittes des obersten Stengelblattes von Scabiosa-Populationen*

■ *S. lucida*　● *S. columbaria*　▲ *S. gramuntia*　│ total variation with individual values
★ mixed population
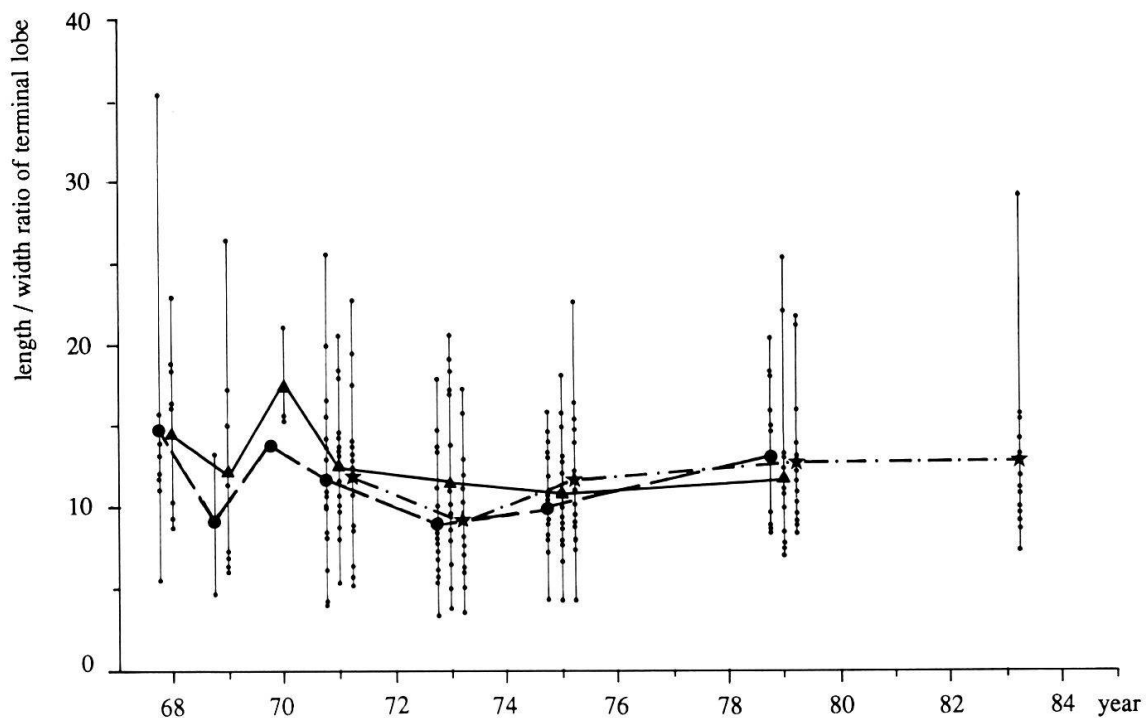
Fig. 28. Ground water plots with a water table level at 145 cm below the surface and well ferti-
lized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.8. Length/width ratio of the terminal lobe of the uppermost cauline leaf
(Figs. 26 to 28)

There is a rather high variability under each condition within a species. Also the
yearly variation is remarkable. *S. columbaria* and *S. gramuntia* show a clearly
lower ratio under warm than under cool conditions. No other variation between
different conditions is recognizable.

The variability of the mixed populations was slightly higher at the beginning of
the experiment than at the end. The difference between the mean values of the last
three years is rather small even where the difference of the lobe length is pro-
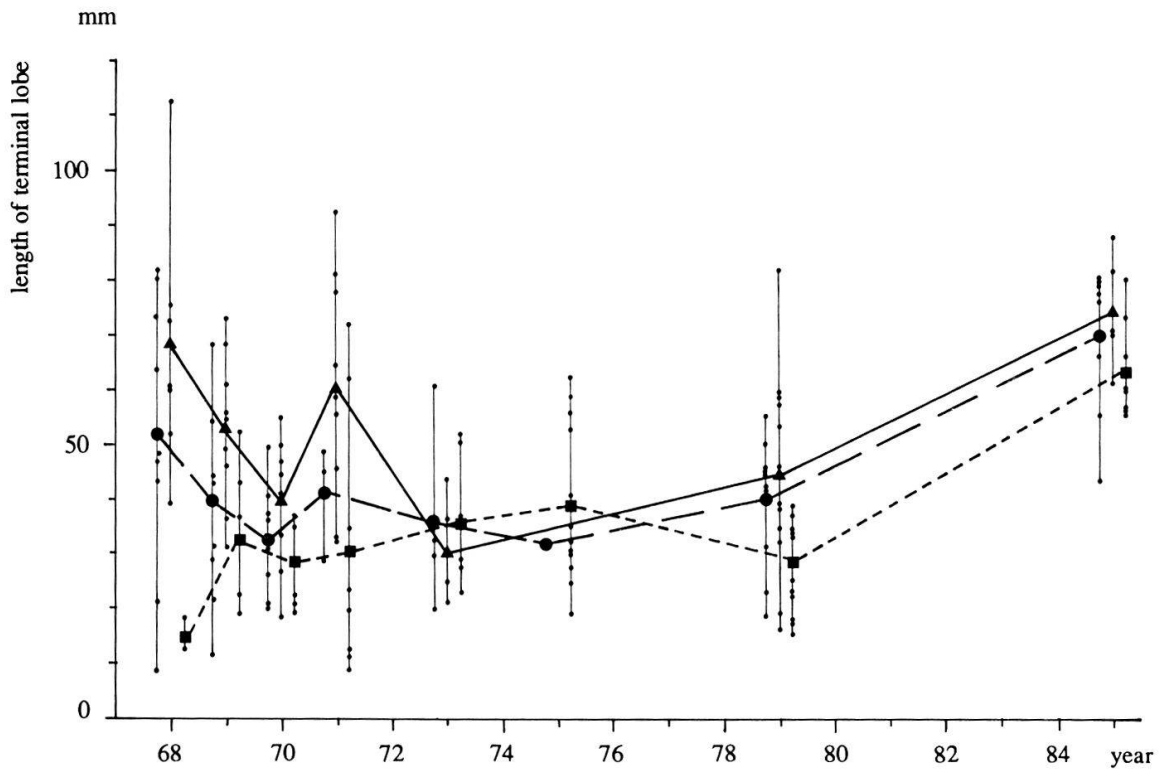nounced.
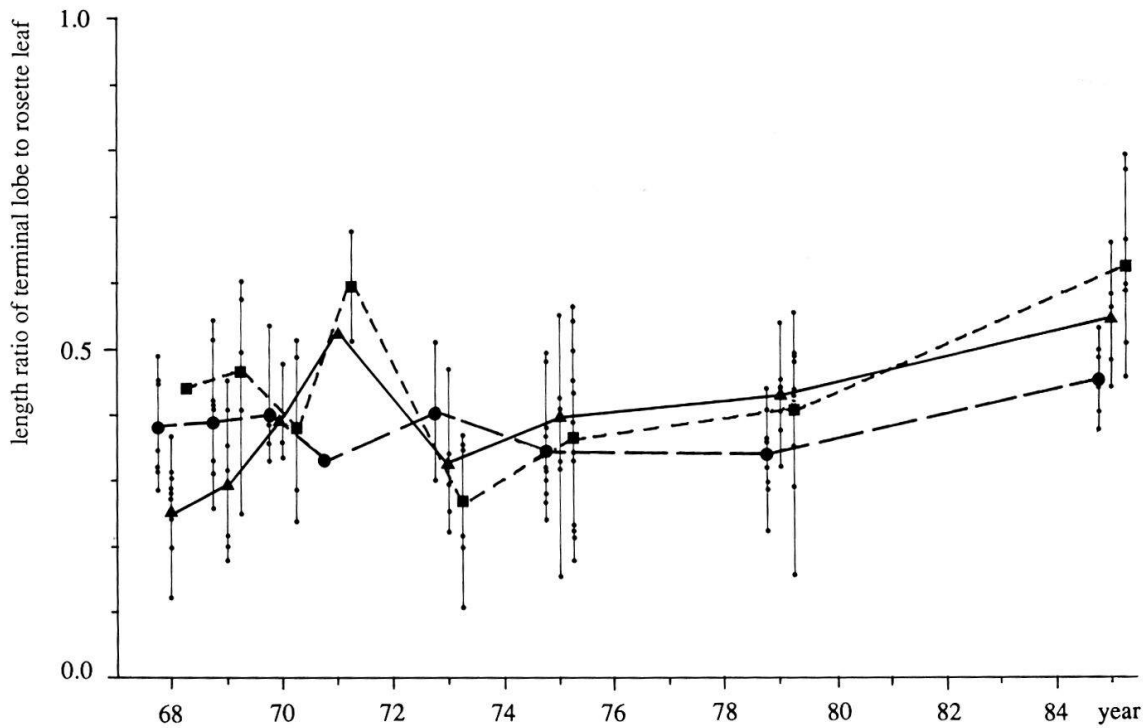
Fig. 29. Cool conditions - *kühle Bedingungen*
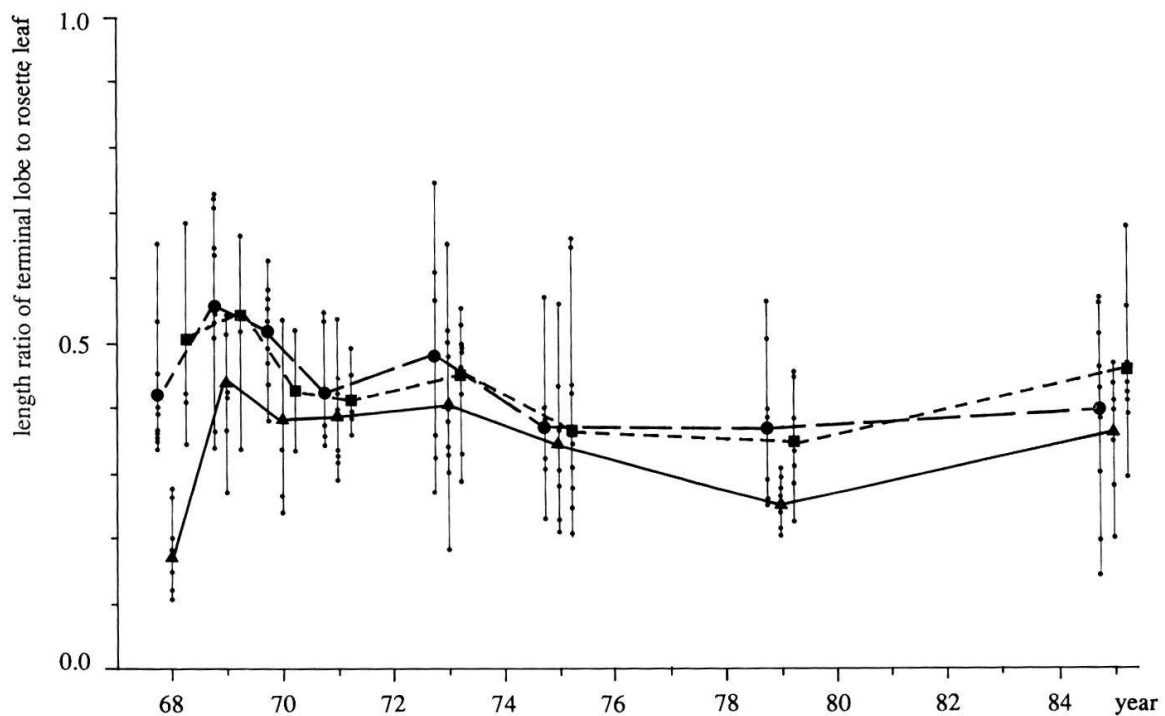
Fig. 30. Warm conditions - *warme Bedingungen*

Figs. 29-31. Length ratio of the terminal lobe of the uppermost rosette leaf to the rosette leaf of *Scabiosa* populations - *Längenverhältnis des Endabschnittes des obersten Rosettenblattes zum Rosettenblatt von Scabiosa-Populationen*

■ *S. lucida*   ● *S. columbaria*   ▲ *S. gramuntia*   │ total variation with individual values
★ mixed population
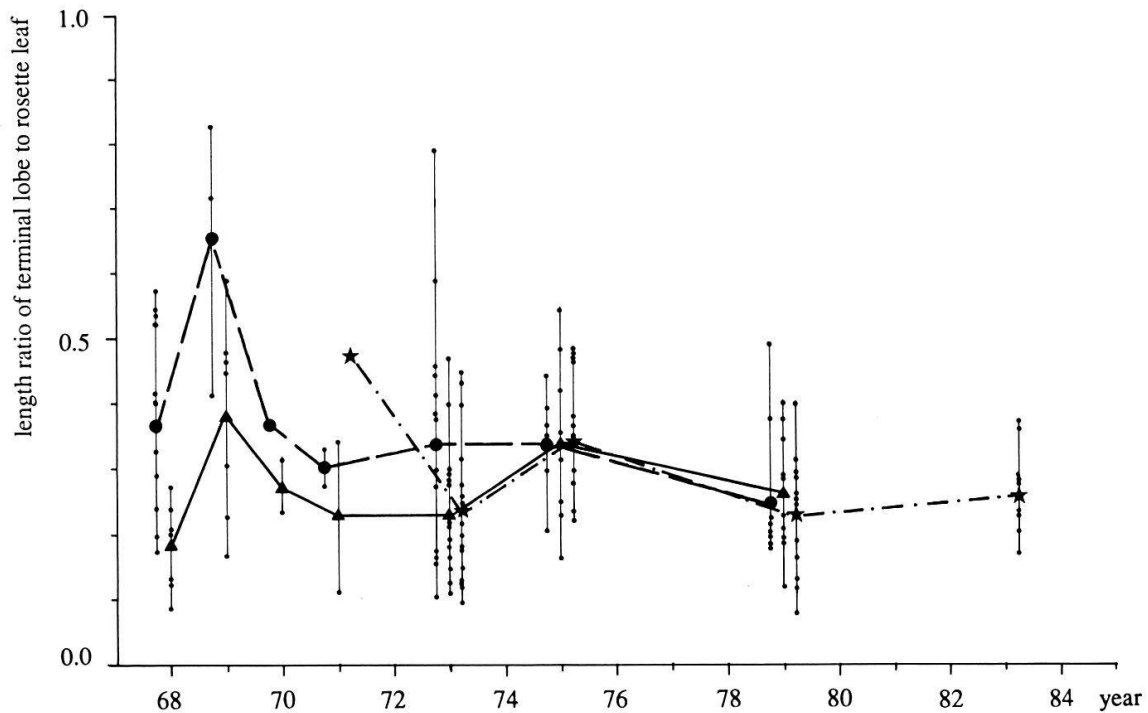
Fig. 31. Ground water plots with a water table level at 145 cm below the surface and well fertilized.
Grundwasserbecken mit einem Wasserstand von 145 cm unter Flur und stark gedüngt.

4.1.9. Length ratio of the terminal lobe of the uppermost rosette leaf to the rosette leaf (Figs. 29 to 31)

The individual variation of the ratio within the species as well as between the years is rather high.

The ratio is smaller for *S. gramuntia* under warm than under cool conditions, under well fertilized than under unfertilized conditions, and under normal watering conditions than under watering intervals of 28 days.

The variability of the mixed populations scarcely decreased during the experiment.

4.2.   Morphological differentiation under different conditions

4.2.1. Hair density (Fig. 32)

Under most conditions the hair density at the end of the experiment is similar to *S. columbaria*. The values are distinctly higher under well fertilized conditions and under controlled watering.
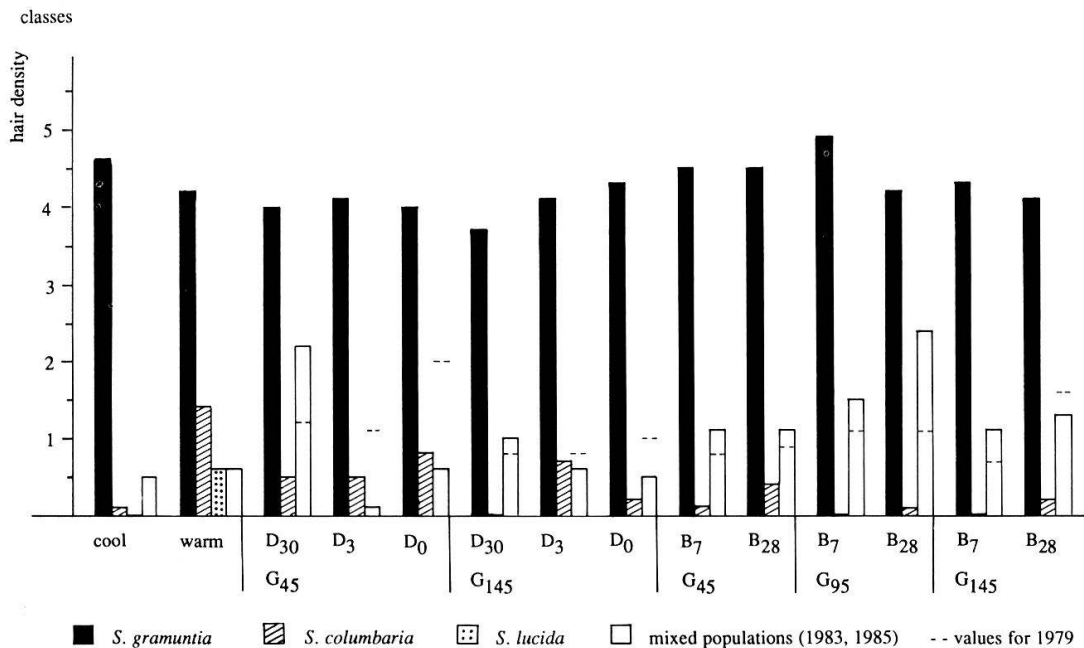
Fig. 32. Hair density on rosette leaves of *Scabiosa* populations under different conditions. *Haardichte der Rosettenblätter von Scabiosa-Populationen unter verschiedenen Bedingungen.*
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.2. Length of calyx setae (Fig. 33)

The length of calyx setae is under most conditions intermediate but nearer to *S. gramuntia* than to *S. columbaria*. The only clear exception is observed under cool conditions in the greenhouse where the setae are even longer than in *S. columbaria*.

Fig. 33. Length of calyx setae of *Scabiosa* populations under different conditions.
Kelchborstenlänge von Scabiosa-Populationen unter verschiedenen Bedingungen.
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.3. Width of calyx setae (Fig. 34)

Similarly to the length of calyx setae the width is mostly intermediate but nearer to *S. gramuntia*. Also, as with the length of setae, the width is similar to *S. columbaria* under cool conditions. In plots with a low water table level and long watering intervals the setae are even narrower than in *S. gramuntia*.

Fig. 34. Width of calyx setae of *Scabiosa* populations under different conditions.
Kelchborstenbreite von Scabiosa-Populationen unter verschiedenen Bedingungen.
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.4. Stalk length of flowering heads (Fig. 35)

In the ground water plots towards the end of the experiment the stalk is always shorter than either *S. columbaria* or *S. gramuntia* in 1968. Under warm conditions it is longer than in the original populations of all three species, under cool conditions it is similar to *S. columbaria*.

Fig. 35. Stalk length of flower heads of *Scabiosa* populations under different conditions.
Länge des Blütenkopfstiels von Scabiosa-Populationen unter verschiedenen Bedingungen.
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days
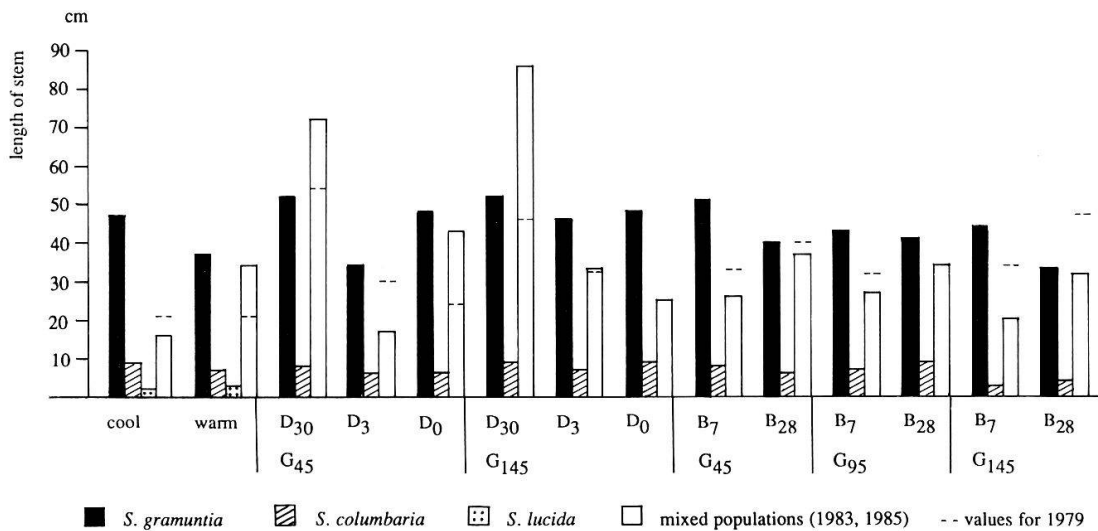
Fig. 36. Length of stem of *Scabiosa* populations under different conditions.
Stengellänge von Scabiosa-Populationen unter verschiedenen Bedingungen.
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.5. Length of stem (Fig. 36)

The stem length of the final populations is under most conditions somewhere between *S. columbaria* and *S. gramuntia*. Under dry and warm conditions it is nearer to *S. gramuntia*, under cool and moist conditions it is more similar to *S. columbaria*. Under well fertilized conditions the stems become even higher than in *S. gramuntia*.

4.2.6. Length of rosette leaves (Fig. 37)

Under most conditions the leaf length is similar to that of *S. columbaria*. Under very dry conditions (low water table and long watering intervals) the leaf is longer than in *S. columbaria*. The same is true under well fertilized conditions. In the warm greenhouse the length is similar to *S. gramuntia*, in the cool one similar to *S. lucida*.
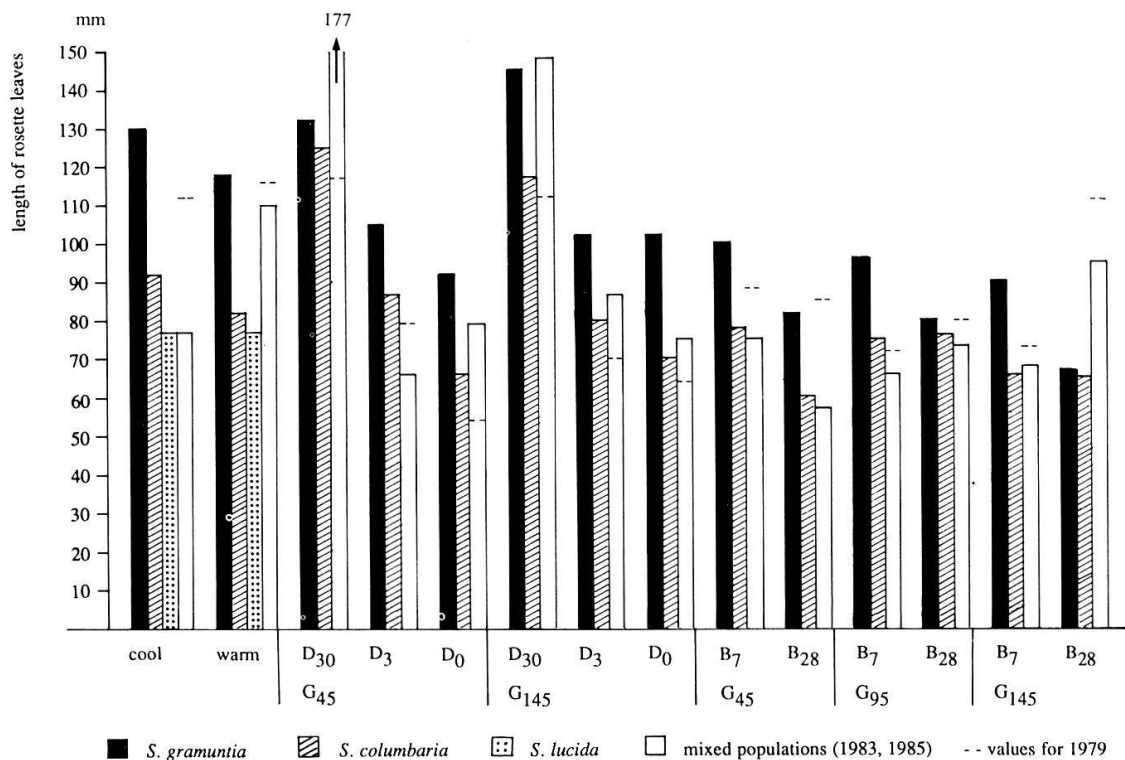
Fig. 37. Length of rosette leaves of *Scabiosa* populations under different conditions.
Länge der Rosettenblätter von Scabiosa-Populationen unter verschiedenen Bedingungen.
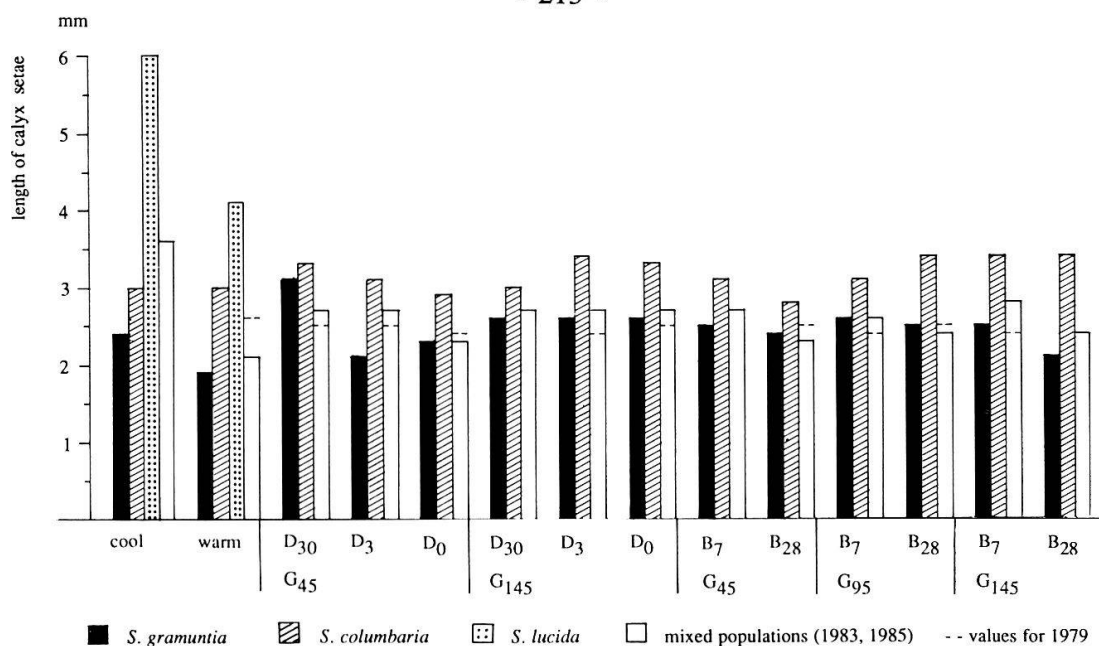D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.7. Length of terminal lobe of the uppermost cauline leaf (Fig. 38)

The lobe length of plants from dry and from unfertilized plots is similar to *S. columbaria* or even shorter. In well fertilized plots and under cool conditions in the greenhouse it is similar to *S. gramuntia*. In the warm greenhouse it became much longer than in all the original populations of the three species.
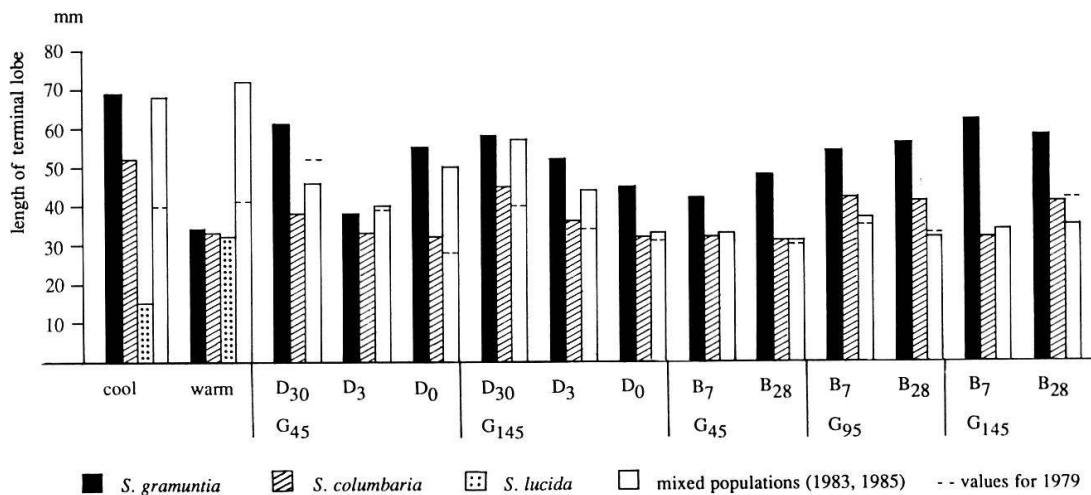
Fig. 38. Length of the terminal lobe of the uppermost cauline leaf of *Scabiosa* populations under different conditions.
Länge des Endabschnittes des obersten Stengelblattes von Scabiosa-Populationen unter verschiedenen Bedingungen.
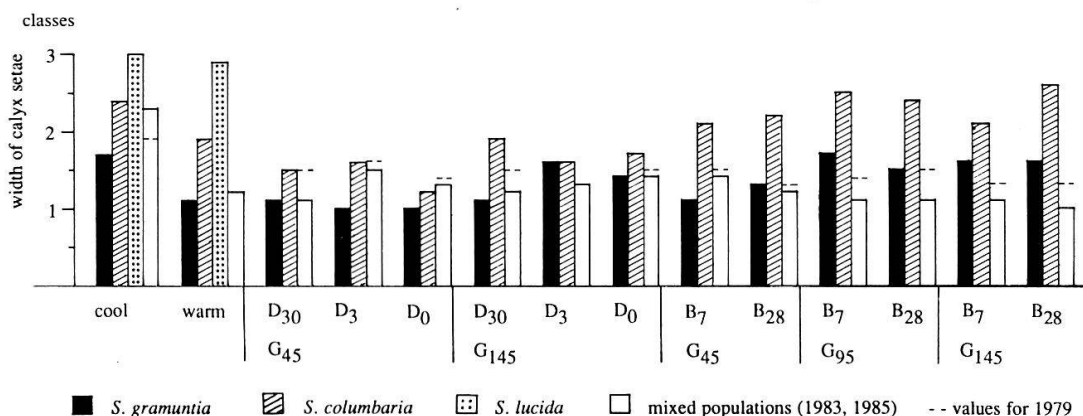D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.2.8. Length/width ratio of the terminal lobe of the uppermost cauline leaf (Fig. 39)

The length/width ratio of the final population lies in most series between *S. columbaria* and *S. gramuntia*. In well fertilized plots it is similar to *S. gramuntia*. In the cool greenhouse it is even lower than for *S. lucida*.

4.2.9. Length ratio of terminal lobe of the uppermost rosette leaf to rosette leaf (Fig.40)

The ratio in the final populations is mostly between *S. columbaria* and *S. gramuntia* except under long watering intervals where it is lower than in *S. gramuntia*. In the cool greenhouse the ratio is about the same as in *S. lucida*.
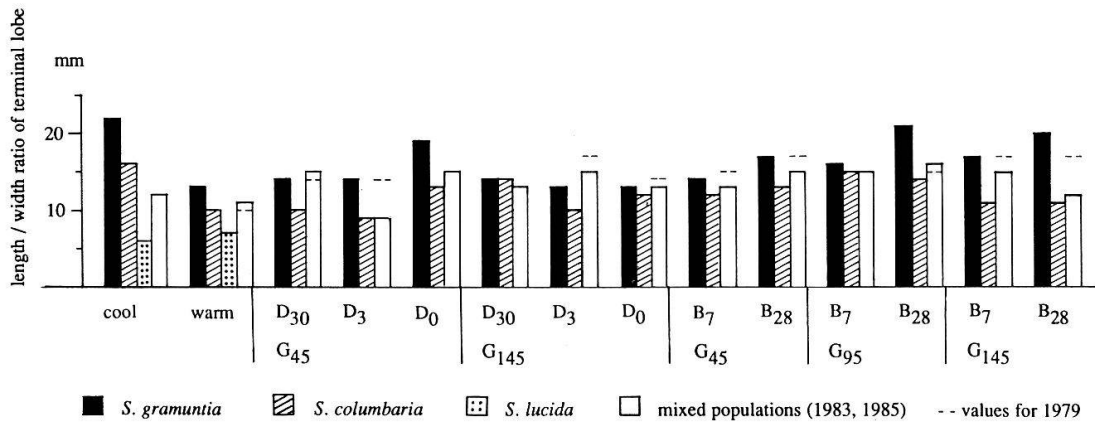
Fig. 39. Length/width ratio of the terminal lobe of the uppermost cauline leaf of *Scabiosa* populations under different conditions.

Längen/Breitenverhältnis des Endabschnittes des obersten Stengelblattes von Scabiosa-Populationen unter verschiedenen Bedingungen.
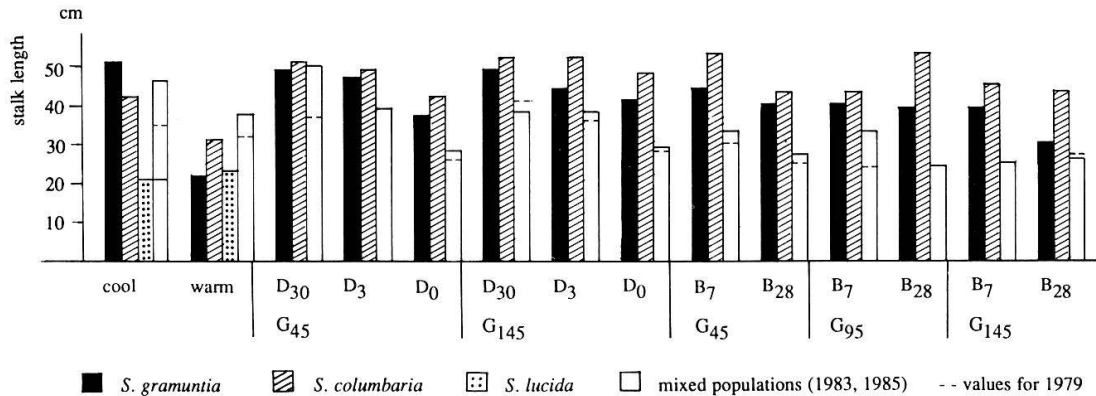
D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days
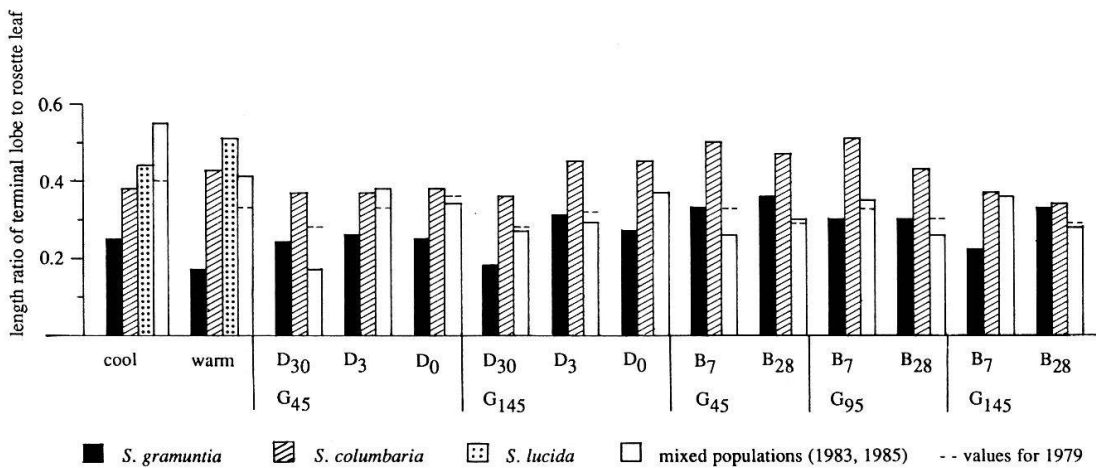
Fig. 40. Length ratio of the terminal lobe of the uppermost cauline leaf to the rosette leaf of *Scabiosa* populations under different conditions.

Längenverhältnis des Endabschnittes des obersten Stengelblattes zum Rosettenblatt von Scabiosa-Populationen unter verschiedenen Bedingungen.

D = intensity of fertilization corresponding to g nitrogen per m^2 and year
G = depth of water table level in cm
B = watering intervals in days

4.3.   The influence of different conditions

4.3.1. Temperature

The combinations of characteristics of the plants of the final populations (1985) under warm and cool conditions compared with the original species populations are shown in Table 9.

The plants of the final population in the cool greenhouse chamber have two characteristics (out of nine tested) similar to *S. lucida,* two intermediate between *S. lucida* and *S. columbaria,* two similar to *S. columbaria,* two intermediate between *S. columbaria* and *S. gramuntia* and one similar to *S. gramuntia* . Under warm conditions two characteristics of the plants are similar to *S. columbaria,* three intermediate between *S. columbaria* and *S. gramuntia* and two similar to *S. gramuntia.* Two characteristics are outside of the range of the three species.

Table 9. Characteristics of the final populations under different temperature conditions compared with the original (parent) species.
Eigenschaften der Endpopulationen unter verschiedenen Temperaturen verglichen mit den ursprünglichen Elterarten.

col   = *S. columbaria*   col-gram = between *S. columbaria* and *S. gramuntia*
gram = *S. gramuntia*   col-luc   = between *S. columbaria* and *S. lucida*
luc   = *S. lucida*

Characteristics	Temperature conditions	
	cool	warm
hair density	col (= luc)	col (= luc)
length of calyx setae	col-luc	col-gram
width of calyx setae	col-gram	gram
stalk length of flower heads	col	different
length of stem	col-gram	gram
length of rosette leaves	luc	col-gram
length of terminal lobe	gram	different
length/width ratio	col-luc	col-gram
terminal lobe/rosette leaf	luc	col

4.3.2. Fertilization

In Table 10, the morphological characteristics of the final populations are compared with the original populations of the different species.

Table 10. Morphological characteristics of the final populations of *Scabiosa* under different conditions compared with the original populations of the studied species.
Morphologische Eigenschaften der Endpopulationen unter verschiedenen Bedingungen, verglichen mit den ursprünglichen Populationen der untersuchten Arten.

col	=	*S. columbaria*	col-gram	= between *S. columbaria* and *S. gramuntia*
gram	=	*S. gramuntia*	gram +	= more extreme than *S. gramuntia*
luc	=	*S. lucida*		

Characteristics	Conditions	
	well fertilized	unfertilized
hair density	col-gram	col
length of calyx setae	gram	gram
width of calyx setae	gram	gram
stalk length of flower heads	gram +	gram +
stem length	gram +	col-gram
length of rosette leaves	gram	col-(gram)
length of terminal lobe	col-(gram)	col
length/width ratio of terminal lobe	gram	gram
length ratio of terminal lobe to rosette leaf	(col)-gram	col-(gram)

In fertilized plots most characteristics of plants of the final populations tend to *S. gramuntia*. Three characteristics are intermediate between *S. columbaria* and *S. gramuntia*, three are similar to *S. gramuntia* and three are even more extreme (gram+) than in *S. gramuntia*. In unfertilized plots the characteristics of the final populations approach *S. columbaria* somewhat more: two are similar to *S. columbaria*, three are intermediate between *S. columbaria* and *S. gramuntia* and three are similar to *S. gramuntia*; only one is more extreme than *S. gramuntia*.

4.3.3. Ground water table (Table 11)

There is not much difference between the morphological characteristics of the plants of the final populations in plots with different water levels. Generally the characteristics are intermediate between *S. columbaria* and *S. gramuntia*.

4.3.4. Watering intervals (Table 12)

The characteristics of the final populations are mostly intermediate between *S. columbaria* and *S. gramuntia*. Some characteristics are even more extreme than in *S. gramuntia*. Under dry conditions (28 day intervals) they show a more pro-

nounced tendency to evolve characteristics of *S. gramuntia* compared with the less dry conditions.

Table 11. Morphological characteristics of the plants of the final populations of *Scabiosa* under differing water table levels compared with *S. columbaria* and *S. gramuntia*.
Morphologische Eigenschaften von Pflanzen der Endpopulationen von Scabiosa unter verschiedenen Bodenwasserständen , verglichen mit S. columbaria und S. gramuntia.

col   =   *S. columbaria*   col-gram = between *S. columbaria* and *S. gramuntia*
gram =   *S. gramuntia*   gram +   = more extreme than *S. gramuntia*

Characteristics	Conditions	
	high water table	low water table
hair density	col	col
length of calyx setae	gram	gram
width of calyx setae	col	gram
stalk length of flower heads	gram+	gram+
stem length	gram	col-gram
length of rosette leaves	col	col
length of terminal lobe	col-gram	col-gram
length/width ratio of terminal lobe	col-gram	col-gram
length ratio of terminal lobe to rosette leaf	col-gram	col-gram

Table 12. Morphological characteristics of plants of the final populations of *Scabiosa* under different watering intervals compared with *S. columbaria* and *S. gramuntia*.
Morphologische Eigenschaften von Pflanzen der Endpopulationen von Scabiosa unter verschiedenen Bewässerungsintervallen, verglichen mit S. columbaria und S. gramuntia.

col   =   *S. columbaria*   col-gram = between *S. columbaria* and *S. gramuntia*
gram =   *S. gramuntia*   gram +   = more extreme than *S. gramuntia*

Characteristics	Watering intervals	
	7 days	28 days
hair density	col-(gram)	col-gram
length of calyx setae	col-gram	gram
width of calyx setae	gram+	gram+
stalk length of flower heads	gram+	gram+
stem length	col-gram	gram
length of rosette leaves	col	gram
length of terminal lobe	col	col
length/width ratio of terminal lobe	col-(gram)	col-(gram)
length ratio of terminal lobe to rosette leaf	col-gram	gram+

4.4. A synthetical approach to the experimental differentiation by discriminant analysis

The layout of **greenhouse experiments** allowed the formation of ten groups within each condition, i.e. three original species in 1968, the tree descendants of these species within the same containers in 1985 and the descendants of the four combinations of the species originally planted in the same container under cool and warm conditions respectively (Figs. 41 and 42). These ten groups lead to 9 discriminant axis. All the descendants of the pure species and of the mixed populations have developped in the same direction and cannot be distinguished from
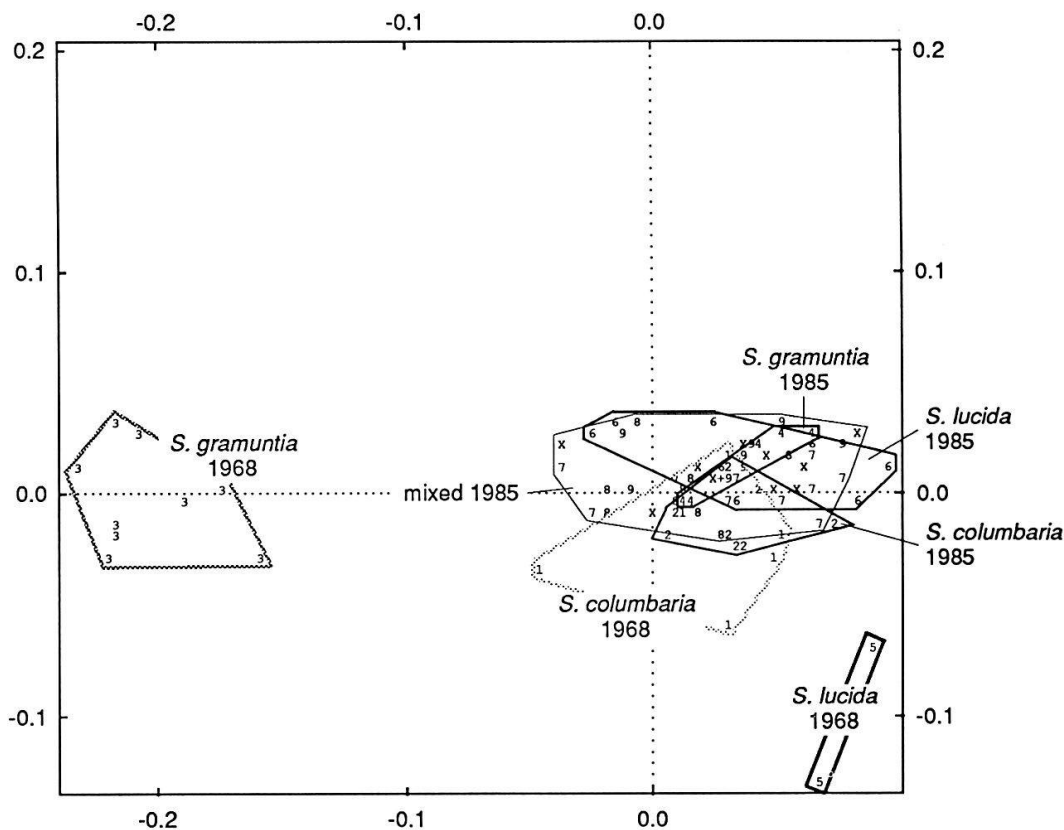
Fig. 41. Discriminant analysis of *Scabiosa* populations under cool conditions in the greenhouse, based on the nine characteristics listed in Chap. 2.3, first and second axis. *Diskriminanzanalyse aufgrund der neun Merkmale nach Kap. 2.3 von Scabiosa-Populationen unter kühlen Bedingungen im Gewächshaus, 1. und 2. Achse.*

1 = *S. columbaria* 1968	6 = *S. lucida* 1985
2 = *S. columbaria* 1985	7 = *S. columbaria / S. gramuntia* 1985
3 = *S. gramuntia* 1968	8 = *S. lucida /S. columbaria* 1985
4 = *S. gramuntia* 1985	9 = *S. lucida /S. gramuntia* 1985
5 = *S. lucida* 1968	X = *S. lucida / S. columbaria / S. gramuntia* 1985

each other anymore.Therefore, the areas of the four groups of the mixed populations in 1985 are not marked separately in the figures, only one line surrounding all individuals of the mixed population has been drawn.

Under cool conditions (Fig. 41), the first two axes express almost 75% of the total variance. The group structure, therefore seems to be well represented by these two axes. However, *S. gramuntia* in 1968 being very different from all other groups, has the most extreme values on the first axis. For the same reason, this axis expresses 66% of the between-group variance, the second axis only 17%. The three original species are clearly separated. It should be noted that *S. lucida* is represented only by two individuals, the other eight individuals not having
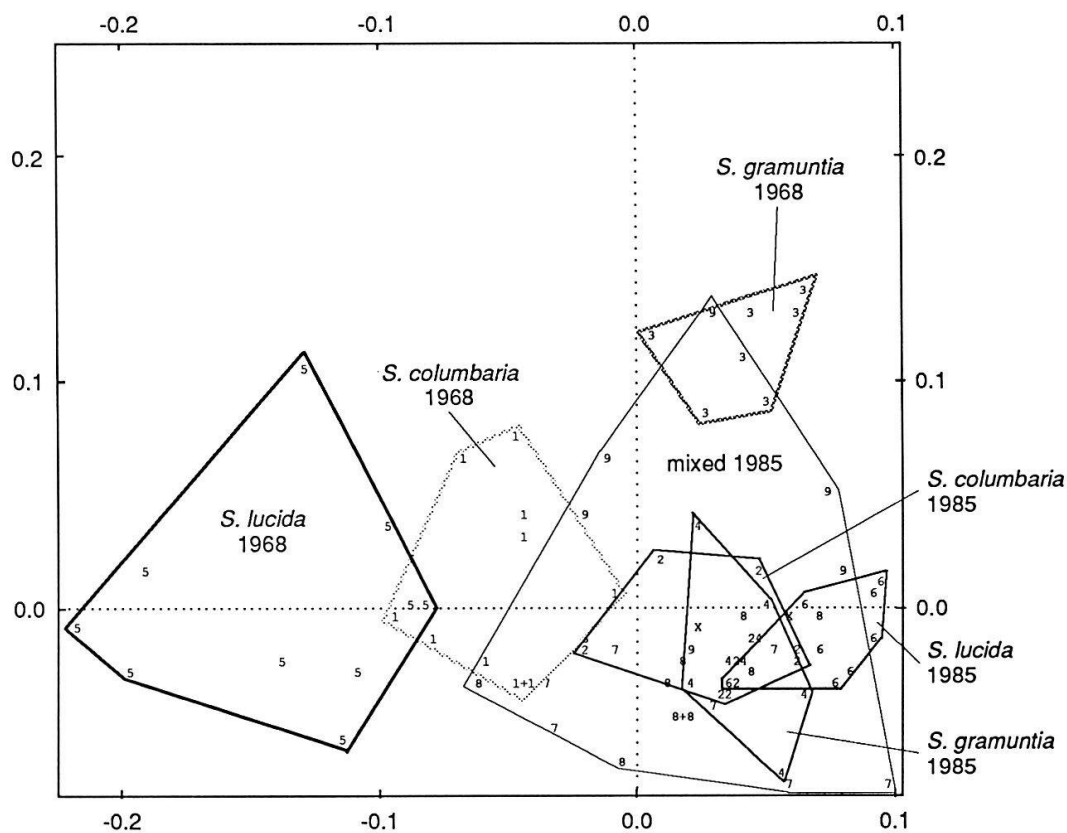
Fig. 42. Discriminant analysis of *Scabiosa* populations under warm conditions in the greenhouse, based on the nine characteristics listed in Chap. 2.3, first and second axis. *Diskriminanzanalyse aufgrund der neun Merkmale nach Kap. 2.3 von Scabiosa-Populationen unter warmen Bedingungen im Gewächshaus, 1. und 2. Achse.*

1 = *S. columbaria* 1968	6 = *S. lucida* 1985
2 = *S. columbaria* 1985	7 = *S. columbaria / S. gramuntia* 1985
3 = *S. gramuntia* 1968	8 = *S. lucida /S. columbaria* 1985
4 = *S. gramuntia* 1985	9 = *S. lucida /S. gramuntia* 1985
5 = *S. lucida* 1968	X = *S. lucida / S. columbaria / S. gramuntia* 1985

reached flowering stage in 1968. The populations of the descendants of pure species and of the mixed populations form a very compact pool in 1985. On the first axis, all populations in 1985 lie within the range of *S. columbaria* and *S. lucida* of 1968 whereas on the second axis the range of the final populations is almost identical to the range of *S. gramuntia* in 1968. What characteristics are mainly represented by the first two axes? The negative values on the first axis are mainly due to the hair density of the rosette leaves ($\cos\alpha = -0.51$) and the length of the upper rosette leaves ($\cos\alpha = -0.42$). The minus sign only indicates the sense of direction of the axis, meaning that high attribute values correspond to negative scores. Positive correlations exist between the second axis and the length of the the the terminal lobe of the upper rosette leaves ($\cos\alpha = 0.44$) and the length of the terminal lobe of the uppermost cauline leaves ($\cos\alpha = 0.42$), respectively.

Under warm conditions (Fig. 42), the first two axes express almost 70% of the total between-group variance (52% and 29%, respectively). Because there is no outlying group similar to *S. gramuntia* under cool conditions (Fig. 41), the group structure of the individuals under warm conditions is more regular and thus well represented by the first two discriminant axes plotted in Fig. 42. The three original species are almost completely separated by the first axis. *S. lucida* and *S. columbaria* differ less from each other than from *S. gramuntia*, a fact which is accentuated by the second axis, separating *S. gramuntia* from the two other species even more distinctly than the first. In 1985, the populations of the descendants of pure species are clearly spearated from the original populations but considerably overlap each other. It is noticeable that the descendants of *S. lucida* have moved almost to the opposite position compared with 1968. *S. columbaria* has changed least. Regarding the first axis, the three final populations are quite similar to *S. gramuntia*, on the second axis the values cover almost the same range as *S. lucida* and *S. columbaria*, the variability being somewhat reduced. The individuals of the desendants of the mixed populations cover a wider area than the descendants of the pure species in 1985, the range is enlarged in the directions of *S. columbaria* and *S. gramuntia* 1968. Considering the relations between the discriminant axes and the characteristics, we note the strongest correlation between the width of calix setae and the first axis ($\cos\alpha = -0.80$) followed by the length of calix setae with $\cos\alpha = -0.37$. Positively correlated with the first axis is also the length of the terminal lobe of the uppermost cauline leaves ($\cos\alpha = 0.35$). The second axis is most correlated with the length of the upper rosette leaves ($\cos\alpha = 0.67$) and much weaker with the hair density of rosette leaves ($\cos\alpha = 0.33$). It is negatively correlated with the length of the terminal lobe of the uppermost cau-

line leaves (cos α = -0.44) and with the length of the terminal lobe of the upper ro-
sette leaves (cos α = -0.34).

From the *Scabiosa* populations in the **garden**, only one example is chosen (low
water table level, well fertilized, natural watering conditions). The scattergram
(Fig. 43) of the first two discriminant axes shows three clearly distinct groups: the
two original species of 1968 and the final population measured in 1983. Because
there are only three groups all variance between the groups is expressed by the
first two axes (57% and 43% resp.). On the first axis, the final population is totally
different from either species of 1968 whereas the values of the final population on
the second axis are almost the same as for *S. gramuntia*. The height of the stem
has the highest discriminant coefficients to both of the axes, 0.66 and -0.67. We
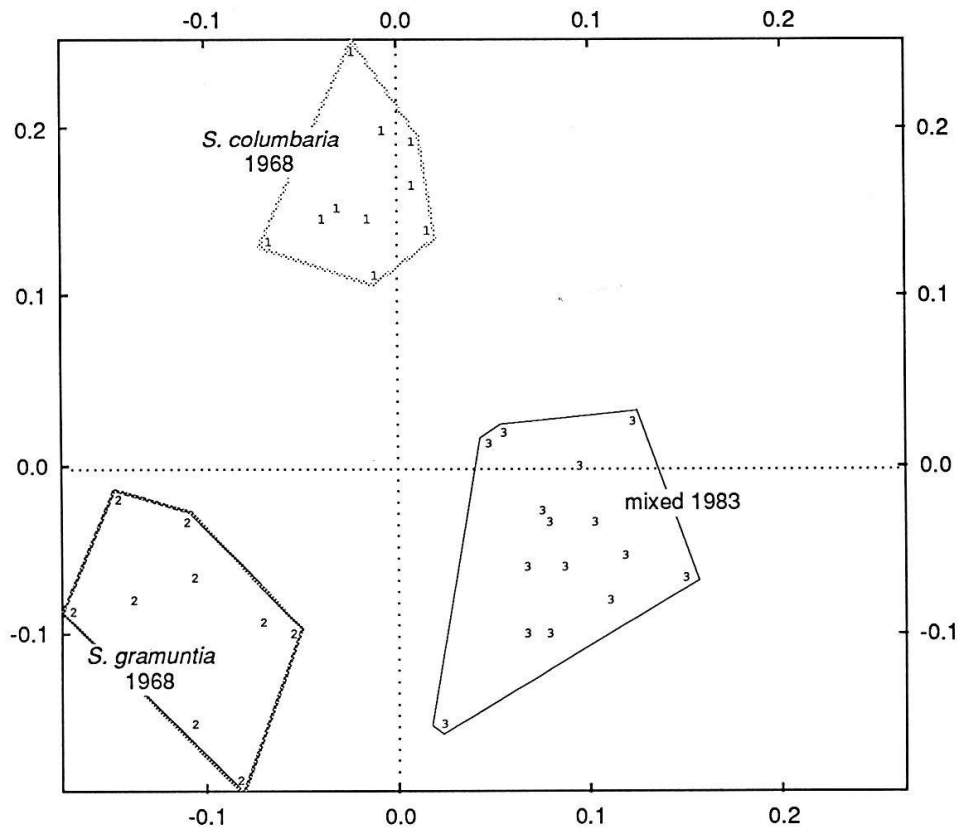
Fig. 43. Discriminant analysis of *Scabiosa* populations in ground water plots with a water
level at 145 cm below the ground and well fertilized, based on the nine characteristics list-
ed in Chap. 2.3, first and second axis.
*Diskriminanzanalyse aufgrund der neun Merkmale nach Kap. 2.3 von Scabiosa-Popula-
tionen in Grundwasserbecken mit einem Grundwasserstand von 145 cm unter Flur und
stark gedüngt, 1. und 2. Achse.*

1 = *S. columbaria* 1968, 2 = *S. gramuntia* 1968, 3 = *S. columbaria / S. gramuntia* 1983

can therefore imagine both discriminant axes standing at an angle of a little more than 45° to the stem height coordinate. The second most important attribute for axis 1 is the hair density ($\cos\alpha = -0.54$), the third is the length of the calyx setae ($\cos\alpha = -0.37$). The second axis, separating *S. columbaria* from the two other groups is furthermore determined by the width of calyx setae ($\cos\alpha = 0.46$), the hair density ($\cos\alpha = -0.35$) and the length of terminal lobe of the upper rosette leaves ($\cos\alpha = 0.33$).

5. DISCUSSION

The aim of the present study was to find out if it is possible to develop different ecotypes from a given genetical pool consisting of three (and two, respectively) species under different environmental conditions. Four factors have been varied in adjacent plots: temperature, nutrient content, water table and watering intervals. Temperature was studied separately in conditioned greenhouse chambers with the other factors left identical. Water table and nutrient content as well as water table and watering intervals were varied in different combinations in the garden. One of the first questions which arises is: How long does it take to get stable populations which are adapted to the new given conditions? Or with other words: Is the study period of 15 years long enough to reach the final stage of selected combinations of characteristics in each population under the different conditions? Only if a certain stability is reached, can a statement on the possible development of new ecotypes under different conditions be made.

5.1. Stability of the characteristics of the final populations

Taking into account, that the average life-time of an individual *Scabiosa* plant is between three and five years, we can suppose that most of the plants at the end of the study period represent the third or the fourth generation. This is obviously a very low number if the selection pressure is not high. However, at least the hair density and calyx setae of the descendants of the original three (resp. two) species developed under most conditions to an average which was in 1985 (resp. 1983) for all plants not very different for a single species from that in 1979. The other characteristics showed more variation within this time-span. In addition, some differences occurred between the plots of different descendants. However, these differences are not statistically significant. The more variable characteristics also showed a more pronounced phenological plasticity and already varied to a great

extent in the parental species. Therefore it is difficult to decide if the variations observed are due to different weather conditions in different years or to an adaptation still in progress. Even if we assume that a slight change of characteristics still might be possible, an ecological differentiation cannot be denied.

5.2. Ecological meaning of the characteristics investigated

If we do not know the selective advantages of the characteristics investigated (under the different studied conditions), it is not possible to decide whether the selection of a certain characteristic is the result of successful adaptation to the given conditions, or if it is linked with another unknown adaptive characteristic. Unfortunately, knowledge of the ecological meaning of plant characteristics is poor and little experimental data is available.

The assessment given below is therefore rather specultative.

Hairs. Hairs seem to be of value as a protection against high radiation and rapid transpiration. In humid air hairs might be able to screen out humidity usable by the plants. It is possible that they are also effective in preventing herbivore damage, but this was not studied in our experiments. On the other hand, a hairy leaf costs more energy to form than a hairless leaf.

Calyx setae. Calyx setae play a role in long-distance dispersal. The size of the setae is probably positively correlated with the size of the fruit. Should the setae become too small compared to the fruit, they are not able anymore to stick with the fruit to animal furs. In the present study the long-distance dispersal had no importance. However, many small seeds are likely to be more successful under favourable conditions than a few large seeds. If the size of setae is strongly connected with the size of fruit we might expect also small setae if small fruits are of advantage.

Length of stems and stalks (of flowering heads). A positive selection advantage of these characteristics can be supposed in a better competition ability for light. On the other hand, long stems and stalks are more costly since they need not only more energy than short ones but also a good nutrient supply. Both characteristics have a large phenotypical plasticity.

Length of rosette leaves. The length of rosette leaves is roughly proportionate to the assimilation area on the ground. Long leaves are clearly advantageous if they get enough light. In dense stands they might not be efficient enough compared with the energy and nutrient need.

Length of terminal lobe of uppermost cauline leaf. The length of the terminal lobe is a measure of assimilation area in the upper part of the plant provided that

the length/width ratio is similar. Long lobes are of advantage in dense stands of *Scabiosa*.

Length/width ratio of the terminal lobe of uppermost cauline leaf. Under conditions of water stress a large ratio might be advantageous because the water supply for transpiration is easier if the leaf area is situated near the vascular bundle of the nerve. Therefore in dry regions the average length/width ratio of the leaves of vegetation is larger than in humid regions.

Length ratio of terminal lobe (of uppermost rosette leaf) to rosette leaf. A large ratio means that the assimilation area in higher layers is relatively large. Therefore it is favourable in dense stands of *Scabiosa* (with high competition for light). A small ratio is of advantage where competition is low.

5.3. Effect of selection

In the following sections the effect of the different environmental factors investigated is discussed, taking into account the considerations of Chap. 5.2. In Table 13 the characteristics of the final *Scabiosa* populations are classified according to their similarity to the three species studied: 1 means similar to *S. lucida*, 3 similar to *S. gramuntia*. Most characteristics of *S. columbaria* are somewhat intermediate and therefore typified with 2. A plant which is typical in all characteristics for *S. lucida* receives the score 9, one typical for *S. gramuntia* the score 27.

Table 13. Scale for classifying the investigated *Scabiosa* species. Morphological characteristics of typical *S. lucida* are classified by 1, of typical *S. gramuntia* by 3.
Skala für die Klassifizierung der untersuchten Scabiosa-Arten. Morphologische Eigenschaften für typische S. lucida erhalten eine 1, für typische S. gramuntia eine 3.

Morphological characteristics	*S. lucida*	*S. columbaria*	*S. gramuntia*
Hair density	1	1	3
Length of calyx setae	1	2	3
Width of calyx setae	1	2	3
Stalk length	1	2	3
Stem length	1	2	3
Length of rosette leaves	1	2	3
Length of terminal lobe	1	2	3
Length/width ratio of terminal lobe	1	2	3
Length ratio of terminal lobe to rosette leaf	1	2	3
Total	9	17	27

5.3.1. Effect of temperature

As is shown in chapter 4.3.1. under cool conditions the final populations developed most like *S. columbaria,* the total score being 16 compared with 17 for typical *S. columbaria.* This was expected because the temperature conditions in the cool chamber correspond roughly to those at the original habitat of *S. columbaria:* average temperature during vegetation period in the cool chamber 11°C (compared to 24°C in the warm chamber), at the habitat of *S. lucida* 6.7°C, of *S. columbaria* 12.7°C and of *S. gramuntia* 14.9°C. However, some of the characteristics differ clearly from *S. columbaria* (Tables 7 and 9): the terminal lobe length is similar to *S. gramuntia,* the length/width ratio of the terminal lobe as well as the rosette leaf length approaches *S. lucida.* The length ratio of terminal lobe to rosette leaf even surpasses the ratio of *S. lucida* (but not statistically significant). Apparently the relatively humid conditions in the greenhouse chambers cause high competition, giving the large cauline leaves the advantage: long terminal lobe as in *S. gramuntia* but much wider. The final populations under warm conditions have the total number of 22.5 (compared to 27 for *S. gramuntia* and 17 for *S. columbaria*). They stay morphologically between *S. columbaria* and *S. gramuntia.* In the length and width of calyx setae and in the stem length they are very similar to *S. gramuntia,* in the hair density and in the length ratio of terminal lobe to rosette leaf they approach *S. columbaria.* The terminal lobe length and the stalk length exceed the values of all three original species not differing much from each other. Though the average temperature of the warm chamber is much higher than at the original habitat of *S. gramuntia,* the final populations have some characteristics of *S. columbaria.* This is probably due to the relatively humid conditions, in contrast to the original conditions of *S. gramuntia,* which grows in very dry places. In the final populations mostly those characteristics prevailed which seem to enable the plant to survive high light competition. In nature the plants of all species avoid light competition. They grow in rather dry soils of low nutrient content surrounded by narrow leafed grasses.

5.3.2. Effect of water table and watering intervals

If we compare the final populations which developed under different water table levels, no statistically significant morphological differences can be observed (Table 8). As can be seen from Table 14, the plants grown at low water table tend towards *S. gramuntia.* The relatively low effect of the water table might be explained by the fact that probably in none of the basins the plants had to endure

high water stress. As it is shown in section 3.1. the roots of *Scabiosa* grow down
to 130 cm within the first vegetation period. Therefore they reach relatively early
even the deepest water table. The mature plants are able to procure enough water
from any investigated water level. Only young plants might endure certain selec-
tion pressure in basins with low water level if long periods without rain or water-
ing occur. That's the reason why the watering interval shows a clear effect on
some characteristics in contrast to the water table. If the plots are watered only
every 28th day the hair density is significantly higher, the length of calyx setae
shorter, and the length of terminal lobe of cauline leaf shorter than under normal

Table 14. Total score of morphological characteristics (cf. Table 13) of the different popula-
tions under the investigated conditions.
*Gesamtzahl (s. Tab. 13) für die verschiedenen Populationen unter den untersuchten Bedin-
gungen.*

S. lucida 9, *S. columbaria* 17, *S. gramuntia* 27

Conditions	Total number of morphological characteristics
$G_{45} D_{30}$	26.5
$G_{45} D_3$	21.0
$G_{45} D_0$	21.5
$G_{145} D_{30}$	27.0
$G_{145} D_3$	24.0
$G_{145} D_0$	23.0
$G_{45} B_7$	22.0
$G_{45} B_{28}$	24.5
$G_{95} B_7$	22.5
$G_{95} B_{28}$	24.5
$G_{145} B_7$	22.5
$G_{145} B_{28}$	27.0
warm	22.5
cool	16.0

watering conditions. There is also a difference for other characteristics. But the same difference could already be observed for the original species populations. In these cases the difference is mainly caused by modification. Under long watering intervals the final populations are very similar to *S. gramuntia* populations. Only hair density, length of terminal lobe and length/width ratio of the terminal lobe do not reach the values of *S. gramuntia*. On the other hand, length and width of calyx setae are even more extreme than in *S. gramuntia*.

5.3.3. Effect of nutrient content

As seen from Table 8 the nutrient content has a great selection effect on the morphological characteristics of *Scabiosa*. Generally, populations grown under low nutrient conditions more closely resemble *S. columbaria,* whereas populations from well fertilized sites tend towards *S. gramuntia*. This concerns nearly all measured characteristics.The score of populations from plots with high nutrient content is similar to that of *S.* gramuntia (Table 14). Only the hair density does not reach values of *S. gramuntia*. On the other side, the values of stem length exceed *S. gramuntia*. Under conditions of high nutrient content the populations grow in dense stands and the competion for light is very high. Apparently many characteristics of *S. gramuntia* (e.g. long stems , long leaves) are better fitted for growth under high competition.In particular, the long stems of plants from well fertilized plots (40-50% higher than in *S. gramuntia*) demonstrate the high effect competition has on genetically based characteristics.

In our experiments three levels of nutrient content were investigated, corresponding to a yearly supply of 0 g, 3 g and 30 g nitrogen, phosphorus and potassium per squaremeter. The most significant difference of the selection effect for hair density, stem length, length of rosette leaves, length of terminal lobe and length ratio of terminal lobe to rosette leaf developed between the high and the medium (resp. high and low) level of nutrients, whereas the difference between length of stalk is biggest between populations of low and medium nutrient content (Table 8).

5.4. The formation of new ecological races

It is generally assumed that " each species represents a unique set of adaptive gene combinations fitting it for a particular niche or habitat in nature. The speciation process produces a diversity of such adaptive gene combinations correlated with the diversity of environments ". (GRANT 1981). If environmental conditions

change, a new adaptive gene combination will be selected, leading possibly to a new ecological race. The existence of ecological races in plants is known since the classical works of TURRESSON (1922, 1930), CLAUSEN, KECK and HIESEY (1940, 1948), BÖCHER (1949) and many others. Many species from different habitats were compared and the morphological, physiological and genetical relationship established. A review of work done so far on ecological races is given by HESLOP-HARRISON (1964), HIESEY and MILNER (1965) and LANGLET (1971). Also there are many examples known of microdifferentiations of populations occurring a few meters or less apart with either a steep environmental change (BRADSHAW 1959 in *Agrostis tenuis*, BREESE and CHARLES 1962 in *Lolium perenne*, SNAYDON 1970, SNAYDON and DAVIES 1978 and ANTONOVICS et al. 1971 in *Anthoxanthum odoratum*, WU et al. 1975 in *Agrostis stolonifera*, LOWETT DOUST 1981 in *Ranunculus repens*, GRACE and WETZEL 1981 in *Typha latifolia*, VERLEJ et al. 1985 in *Silene cucubalus*, VERNET et al. 1987 in *Arrhenatherum elatius*) or a more gentle gradient (EHRENDORFER 1953 in *Galium pumilum*, LINHARD 1974 in *Veronica peregrina*, GRANT and ANTONOVICS 1978 in *Anthoxanthum odoratum*, TURKINGTON and HARPER 1979 in *Trifolium repens*). Substantial genetic change can occur within one or a few generations and be related to various factors , e.g. temperature, soil humidity, nutrient and heavy metal content , use of herbicides, type of management, progressing succession, etc.). Ecotypic variation is also possible without barriers to gene flow (JAIN and BRADSHAW 1966, EHRLICH and RAVEN 1969, BRADSHAW 1972).

An experimentally caused differentiation of a known genetical pool of plants under different environmental conditions is to the best of our knowledge so far unknown. The results of the present study confirm the findings of other authors that it is possible to get an ecological differentiation within relatively few generations regardless of genetical isolation. As can be seen from Figs. 41 and 42 it is not important for the results if the randomly pollinated seed plants at the beginning belong to one of the original species in pure culture or in a mixture. Therefore the intermixing of genes and the selection of special gene combinations is astonishingly fast. At different temperatures in the greenhouse (ca. 13°C difference in summer, the same conditions in winter) within 17 years (two to four generations) two distinct ecological races developed which are in six out of nine measured characteristics significantly different from each other (Table 7). The relatively high difference in temperature must give rise to a high selection pressure. Interestingly, the race is most similar to *S. columbaria* at cool temperatures (Table 9) which correspond to those of the natural habitat (two degrees cooler in the mean) . It differs significantly in five out of nine measured characteristics from *S. columba-*

ria, in five from *S. lucida* and in eight from *S. gramuntia*. The race which developed under warm conditions (in the mean 9°C warmer than at the natural habitat of *S. gramuntia*, 11°C than that of *S. columbaria* and 17°C than that of *S. lucida*) is most similar to *S. gramuntia* (Table 9), but in some characteristics quite different from all original species. It differs significantly from *S. gramuntia* in four characteristics, from *S. columbaria* also in four and from *S. lucida* in seven. In the garden the ecological races are not quite so clear-cut . However , under extreme conditions (high nutrient content , long watering intervals) distinct ecological races developed (Fig. 43) which are not only intermediate between the parent species but have also developed partly distinct morphological characteristics. In spite of the opportunity in the garden of high levels of gene flow, the selection pressure (possibly by disruptive selection) seems to be adequate to overcome it's homogenizing effect. The evolution of isolating factors (different flowering time) between neighbouring populations forming clines takes a very long time (hundreds of generations) (CAISSE and ANTONOVICS 1978). Therefore it is not astonishing that no tendency towards different flowering times between different populations under the given conditions could be observed. Although in 1968, there was a difference in flowering time between the populations on well fertilized soils and all the other populations (flowering begins 4 to 8 days earlier), the difference at the end of the experiment was not significantly higher. Since *S. columbaria* is strictly self-incompatible, an exchange of genes is always granted. Nevertheless the pollination done mostly by bees and flies is not purely accidental. The insects prefer to visit neighbouring flowers and change less often from one plot to another.

It is interesting to note that the newly formed ecological races contain not only new combinations of characteristics of the original species, but developed also some quantitative characteristics which are outside of the range of the original species. This concerns especially the length of stem and the length of rosette leaves under well fertlized conditions, and the length of terminal lobe of the uppermost cauline leaf under warm conditions. In all cases the average length exceeds that of *S. gramuntia*. The temperatures in the warm greenhouse are 9°C warmer than those at the natural habitat of *S. gramuntia* in Martigny (Valais). Under well fertilized conditions the soil contains by far more nutrients than at the natural habitat of all species (LANDOLT et al. 1975). In nature, *Scabiosa* does not grow in well fertilized soils because it becomes overgrown by faster growing plants. It would be interesting to observe if populations of *S. gramuntia* from warmer regions (e.g. Southern France) look similar to the new ecological races in the warm greenhouse. Long stems and rosette leaves are only possible if enough

nutrients are available. These characteristics are probably selected by competition for light in the densely grown stock of *Scabiosa* within well fertilized plots.

SUMMARY

Between 1968 and 1985 the evolution of mixed populations of three (resp. two) species of *Scabiosa columbaria* was investigated under different culture conditions and the development of the populations towards new ecotypes was observed. Nine morphological characteristics were measured. The new populations which had formed under different conditions were compared with the populations of the pure parent species investigated earlier (see chapter 3). Thus, a distinction could be made between genetically based differences and those which were caused by modification.

Two series of experiments were performed:

a. Greenhouse experiments (1968-1985). *Scabiosa lucida*, *S. columbaria* and *S. gramuntia* grew in greenhouse chambers under two different temperature conditions (cool: day 17°C, night 7°C; warm: day 30°C, night 20°C) during the summer half-year. The plants were cross-pollinated weekly by hand and at random.

b. Experiments in adjacent basins in the garden (1968-1983). *Sabiosa columbaria* and *S. gramuntia* were cultivated in the garden under differing ground water table levels (145 cm, 95 cm, 45 cm under surface), watering intervals (natural rains, 7 day and 28 day intervals) and nutrient supply (0 g, 3 g, 30 g per sqm and year of each nitrogen, phosphorus and potassium). Insects cross-pollinated the flowering plants. Therefore crossings between plants grown under different conditions were possible.

Results:

1. After 15 years (resp. 17 years) duration of the experiments, relatively stable combinations of morphological characteristics could be observed in the populations grown under the investigated conditions. This is valid especially for the characteristics which do not vary much in the parental species (e.g. hair density, length of calyx setae).

2. Under each investigated condition a population developed which was significantly different from the neighbouring populations in some characteristics.

3. In particular the difference between the final populations grown under cool and under warm conditions was remarkable. Under cool condition the population was similar to *S. columbaria*, under warm conditions it was morphologically somewhere between *S. columbaria* and *S. gramuntia*. Some characteristics (length of stalks of flower heads, length of terminal lobe of cauline leaves) surpassed even *S. gramuntia*.

4. Low ground water table and particularly long watering intervals caused an approximation of the populations towards *S. gramuntia* (Table 11).

5. High nutrient supply affected a differentiation of the populations in the direction of *S. gramuntia*. Some characteristics even exceeded *S. gramuntia* grown under the same conditions (Table 10).

ZUSAMMENFASSUNG

Zwischen 1968 und 1985 wurde das Verhalten von Mischpopulationen von drei (bzw. zwei) Arten von *Scabiosa columbaria* L. s.l. unter verschiedenen Kulturbedingungen untersucht

und die Entwicklung der Populationen zu neuen Oekotypen verfolgt. Neun verschiedene morphologische Merkmale wurden gemessen (Kapitel 2.3).

Die neu entstandenen Populationen unter den verschiedenen Bedingungen wurden mit den in einer früheren Arbeit dargestellten Untersuchung mit den reinen Elterarten verglichen (s. Kapitel 3) und so genetische und modifikatorische Unterschiede auseinandergehalten.

Zwei Serien von Experimenten wurden durchgeführt:

a. Gewächshausexperimente (1968-1985) : *S. lucida*, *S. columbaria* und *S. gramuntia* wurden im Sommerhalbjahr unter zwei verschiedenen Temperaturregimes im Gewächshaus gehalten (kalt: Tag 17°C, Nacht 7°C; warm: Tag 30°C, Nacht 20°C, s. Tab. 4). Die Pflanzen wurden zur Blütenzeit in jeder Kammer wöchentlich nach Zufallsprinzip von Hand bestäubt.

b. Experimente in benachbarten Becken im Garten (1968-1983): *S. columbaria* und *S. gramuntia* wuchsen unter verschiedenem Grundwasserstand (145 cm, 95 cm und 45 cm unter Flur), verschiedenen Bewässerungsintervallen (natürliche Regenintervalle, 7 Tage, 28 Tage), verschiedenem Nährstoffangebot (je 0 g, 3 g, 30 g N, P, K pro m^2 und Jahr) (s. Tab. 5). Die Kreuzungen der blühenden Pflanzen erfolgten durch Insekten. Kreuzungen zwischen Pflanzen, die unter verschiedenen Bedingungen wuchsen, waren deshalb möglich.

Resultate:

1. Nach 15 (bzw. 17) Jahren Versuchsdauer haben sich unter den einzelnen Bedingungen relativ stabile morphologische Merkmalskombinationen eingestellt, zumindest für die auch bei den Elterarten relativ wenig variablen Merkmale (Haardichte, Kelchborstenlänge).

2. Unter jeder Bedingung entstand eine Population, die sich durch bestimmte morphologische Merkmale signifikant von Nachbarpopulationen unter anderen Bedingungen unterschied.

3. Die Endpopulationen unter kalten und warmen Bedingungen unterschieden sich besonders deutlich. Unter kalten Bedingungen war die Population ähnlich wie *S. columbaria*, unter warmen Bedingungen stand sie morphologisch zwischen *S. columbaria* und *S. gramuntia* (Tab. 9). Blütenkopfstiellänge und Länge des Endlappens der Stengelblätter waren sogar extremer (länger) als bei *S. gramuntia*.

4. Tiefer Grundwasserstand und besonders längere Bewässerungsintervalle bewirkten eine Angleichung der Populationen an *S. gramuntia* (Tab. 11).

5. Die starke Düngung hatte eine Differenzierung der Populationen in Richtung *S. gramuntia* zur Folge. Einzelne Merkmale übertrafen sogar jene von *S. gramuntia* unter gleichen Bedingungen (Tab. 10).

REFERENCES

ANTONIVICS J. , 1976: The nature of limits to natural selection. Ann.Mo.Bot.Garden *63*, 224-247.

ANTONIVICS J., BRADSHAW A.D. and TURNER R.G., 1971: Heavy metal tolerances in plants. Adv.Ecol Res. *7*, 1-85.

ASTON J.L. and BRADSHAW A.D., 1966: Evolution in closely adjacent populations. II. *Agrostis stolonifera* in maritime habitats. Heredity *21*, 649-664.

BÖCHER T.W., 1948: Racial divergences in *Prunella vulgaris* in relation to habitat and climate. New Phytol. *48*, 285-314.

BRADSHAW A.D., 1959: Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differentiation. New Phytol. *58*, 208-227.

BRADSHAW A.D., 1972: Some of the evolutionary consequences of being a plant. Evol.Biol. *5*, 25-47.

BREESE E.L. and CHARLES A.H., 1962: Population studies in ryegrass. Rep.Welsh Pl.Breed. Stat. 1961, 30-34.

CAISSE M. and ANTONIVICS J., 1978: Evolution in closely related plant populations. IX. Evolution of reproductive isolation in clinal populations. Heredity *40*, 371-384.

CLAUSEN J., KECK D.D. and HIESEY W.M., 1940: Experimental studies on the nature of species. I. Effect of varied environments on Western South American plants. Carnegie Inst.Wash. Publ. *520*, 452 pp.

CLAUSEN J., KECK D.D. and HIESEY W.M., 1948: Experimental studies on the nature of species. II. Environmental responses of climatic races of *Achillea*. Carnegie Inst.Wash.Publ. *581*, 129 pp.

CRAWDORD R.M.M., 1989: Studies in plant survival. Ecological case histories of plant adaptation to adversity. Blackwell Sci.Publ.Oxford. 296 pp.

DAVIES M.S. and SNAYDON R.W., 1976: Rapid population differentiation in a mosaic environment. III. Measures of selection pressures. Heredity *36*, 59-66.

EHRENDORFER F., 1953: Ökologisch-geographische Mikro-Differenzierung einer Population von *Galium pumilum* Murr. (Sect. *Leptogalium* Lange). Österr.Bot.Z. *100*, 670-672.

EHRLICH P.R. and RAVEN P.H., 1969: Differentiations of populations. Science *165*, 1228-1232.

GRACE J.B. and WETZEL R.G., 1981: Phenotypic and genotypic components of growth and reproduction in *Typha latifolia*: Experimental studies in marshes of differing successional maturity. Ecology *62*, 789-801.

GRANT M.C. and ANTONOVICS J., 1978: Biology of ecologically marginal populations of *Anthoxanthum odoratum*. I. Phenetics and dynamics. Evolution *32*, 822-838.

GRANT V., 1981: The genetic goal of speciation. Biol.Zbl. *100*, 473-482.

GROSSMANN F., 1975: Morphologisch-ökologische Untersuchungen an *Scabiosa columbaria* L. s.l. im mittleren und westlichen Alpengebiet.Veröff.Geobot.Inst.ETH,Stiftung Rübel, Zürich *25*, 125 pp.

HARPER J.L., 1977: Population biology of plants. Acad.Press London. 892 pp.

HAYWARD M.D., 1985: Adaptation, differenciation and reproductive systems in *Lolium perenne*. In: JACQUARD P., HEIM G. and ANTONIVICS J. (eds.), Genetic differentiation and dispersal in plants. NATO ASI Series G: Ecologiocal Sciences *5*, 83-93.

HESLOP-HARRISON J., 1964: Forty years of genecology. Adv.Ecol.Res. *2*, 159-247.

HESS H.E, LANDOLT E. and HIRZEL R., 1972: Flora der Schweiz und angrenzender Gebiete. *Scabiosa*. Birkhäuser, Basel. *3*, 350-358.

HIESEY W.M. and MILNER H.W., 1965: Physiology of ecological races and species. Ann.Rev. Plant Physiol. *16*, 203-216.

JAIN S.K. and BRADSHAW A.D., 1966: Evolutionary divergence among adjacent plant populations. I. The evidence of its theoretical analysis. Heredity 21, 407-441.

KUHN N., 1973: Frequenzen von Trockenperioden und ihre ökologische Bedeutung. Viertelj.schr.Naturf.Ges.Zürich *118*, 257-298.

LANDOLT E., 1971: Oekologische Differenzierungsmuster bei Artengruppen im Gebiet der Schweizer Flora. Boissiera *19*, 129-148.

LANDOLT E., 1977: Oekologische Zeigerwerte zur Schweizer Flora. Veröff.Geobot.Inst.ETH, Stiftung Rübel,Zürich *64*, 208 pp.

LANDOLT E., GROSSMANN F., GIGON A. and MEYER M., 1975: Konkurrenzuntersuchungen zwischen nah verwandten Arten von *Scabiosa columbaria* L. s.l. I. Verhalten der Arten unter verschiedenen Temperatur-, Feuchtigkeits- und Nährstoffbedingungen. Ber.Geobot.Inst. ETH,Stiftung Rübel,Zürich *43*, 83-142.

LANGLET O., 1971: Two hundred years of genecology. Taxon *20*, 653-722.

LINHARD Y.B., 1974: Intra-population differentiation in annual plants. I. *Veronica peregrina* L. raised under non-competitive conditions. Evolution *28*, 232-243.

LOVET DOUST L., 1981: Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). II. The dynamics of leaves, and a reciprocal transplant-replant experiment. J.Ecol. *69*, 757-768.

SNAYDON R.W., 1970: Rapid population differentiation in a mosaic environment. I. The response of *Anthoxanthum odoratum* populations to soils. Evolution *24*, 257-269.

MÖRIKOFER W., 1932: Zur Bioklimatologie der Schweiz 2: Die Strahlungsverhältnisse. Schweiz.Mediz.Jahrb. *1932*, 1-11.

SchÜEPP M., 1960 : Klimatologie der Schweiz . C. Lufttemperatur 1. Beih.Ann.Schweiz.Meteorol.Zentralanstalt *1959*, 1-14.

SchÜEPP M., 1962: Klimatologie der Schweiz. I. Sonnenscheindauer 1. Beih.Ann.Schweiz. Meteorol.Zentralanst. *1961*, 1-36.

SNAYDON R.W., 1970: Rapid population differentiation in a mosaic environment. I. The response of *Anthoxanthum odoratum* populations to soils. Evolution 24, 257-269.

SNAYDON R.W. and BRADSHAW A.D., 1962 : Differences between natural populations of *Trifolium repens* L. in response to mineral nutrients. I. Phosphate. J.Exp.Bot. *13*, 422-434.

SNAYDON R.W. and BRADSHAW A.D., 1969: Differences between natural populations of *Trifolium repens* L. in response to mineral nutrients . II. Calcium, magnesium and potassium. J.App.Ecol. *6*, 185-202.

SNAYDON R.W. and DAVIES M.S., 1976: Rapid population diferentiation in a mosaic environment. IV. Populations of *Anthoxanthum odoratum* at sharp boundaries. Heredity *37*, 9-25.

TURESSON G., 1922: The genotypical response of the plant species to the habitat. Hereditas *3*, 211-350.

TURESSON G. , 1930: The selective effect of climate upon the plant species. Hereditas *14*, 99-152.

TURKINGTON R. and HARPER J.L., 1979: The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. J.Ecol. *67*, 245-254.

UTTINGER H., 1966: Klimatologie der Schweiz . E. Niederschlag 1.,. Beih.Ann.Schweiz.Meteorol.Zentralanst. *1965*, 125-170.

VERKLEIJ J.A.C., BAST-CRAMER W.B. and LEVERING H., 1985: Effects of heavy-metal stress on the genetic structure of populations of *Silene cucubalus*. In : HAECK J. and WOLDENDORP J.W. (eds.), Structure and functioning of plant populations 2. Phenotypic and genotypic variation in plant populations. North-Holland Publ. Co. Amsterdam . 355-365.

VERNET P., DUCOUSSO A., PETIT D. and VALERO M., 1987: Genetic structure and diversity patterns in adjacent populations: *Arrhenatherum elatius* (L.) Beauv. In : URBANSKA K.M. (ed.), Differentiation patterns in higher plants. Acad.Press London. 131-152.

WILDI O. and ORLOCI L., 1983: Management and multivariate analysis of vegetation data. (2nd revised ed.). Eidg.Anst.Forstl.Versuchswesen, Birmensdorf, Ber. *215,* 139 pp.

WILDI O. and ORLOCI L., 1988: MULVA-4, a package for multivariate analysis of vegetation data. Eidg.Anst.Forstl.Versuchswesen, Birmensdorf. (Polycopy).

WU L., BRADSHAW A.D. and THURMAN D.A., 1975: The potential for evolution of copper tolerance in plants. III. The rapid evolution of copper tolerance in *Agrostis stolonifera*. Heredity *34*, 165-185.

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