Hybridization in Ajuga populations

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Hybridization in Ajuga populations

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RÉSUMÉ

LÜÖND, B. & R. LÜÖND (1980). Hybridation dans des populations d'Ajuga. *Candollea* 35: 87-109. En anglais, résumé français.

La morphologie de deux espèces, très répandues en Suisse, du genre *Ajuga, A. reptans* et *A. genevensis,* a été étudiée dans douze localités. Ces espèces, généralement bien définies, forment des colonies hybrides polymorphes dans des stations dégradées. La cohérence des caractères dans les populations a été analysée avec la méthode graphique du diagramme de dispersion (pictorial scatter diagram) et comparée aux distributions correspondantes de l'indice d'hybridation. Les différents facteurs sélectifs responsables de la structure de la population sont discutés. La réaction, extrêmement sensible des populations aux facteurs sélectifs biotiques et abiotiques, est mise en évidence. Les modifications de la structure des populations peuvent survenir déjà après trois ans. Les différences morphologiques sont confirmées par les résultats des analyses génétiques et chromatographiques.

ABSTRACT

LÜÖND, B. & R. LÜÖND (1980). Hybridization in Ajuga populations. *Candollea* 35: 87-109. In English, French abstract.

Two widespread Swiss *Ajuga* species, *A. reptans* and *A. genevensis* were morphologically investigated at twelve localities. The generally well defined species produce polymorphic hybrid swarms in disturbed habitats. The character coherence in the populations was analysed with the pictorial scatter diagram method and compared with the corresponding hybrid index distributions. The different selective factors, which are responsible for the structure of the populations, are discussed. It is shown, that the populations react very sensitively to biotic and abiotic selective factors. Such changes in the population structure can occur within only three years. Results of chromatographic and genetic investigations support the morphological evidence.

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INTRODUCTION

Two widespread species of *Ajuga* were chosen for this work. *Ajuga reptans* is frequent and *A. genevensis* is somewhat rarer in Switzerland. Both species are well-defined and can be recognized by several characters. In the course of a doctorate on *Ajuga* (LÜÖND & LÜÖND, 1979), the authors collected information on different aspects of the biology of these two species. *Ajuga reptans* is a good competitor and grows chiefly on cultivated nutrient rich pastures, that are regularly cut or grazed. It propagates vegetatively by runners. *Ajuga genevensis* prefers sunny places with loose and poor soil. This species is therefore often found in south-exposed poor meadows and other places with weak competitive pressure. Vegetative propagation is effected by root buds.

During the work, the specific identity of many individuals was found to be difficult at certain sites. Morphologically, intermediate plants are particularly frequent at the edges of gravel pits, on excavated soil and at similar places. The variability of populations from twelve sites was investigated by morphological and thin-layer-chromatographic methods. Genetic investigations were undertaken to clarify questions of the origin of the variability and to supply information on the evolutionary state of these species.

MORPHOLOGICAL VARIABILITY IN POPULATIONS WITH A. REPTANS AND A. GENEVENSIS

Method

The features used for the characterization were listed in data tables. All measurements and observations were made on fresh plant material. The natural sites, which supplied the material for the following investigations, are given in Fig. 1 (for more precise information, see LÜÖND & LÜÖND, 1979). The following characters were included in the data tables:

a) rosette leaves: total length, length and width of the blade of 2-3 leaves of each plant. To record the shape, an index was calculated as quotient of blade length and width, which was averaged for each plant. This index will be called "index of rosette leaves";

b) pubescence of the main shoot, called "pubescence of the stem";

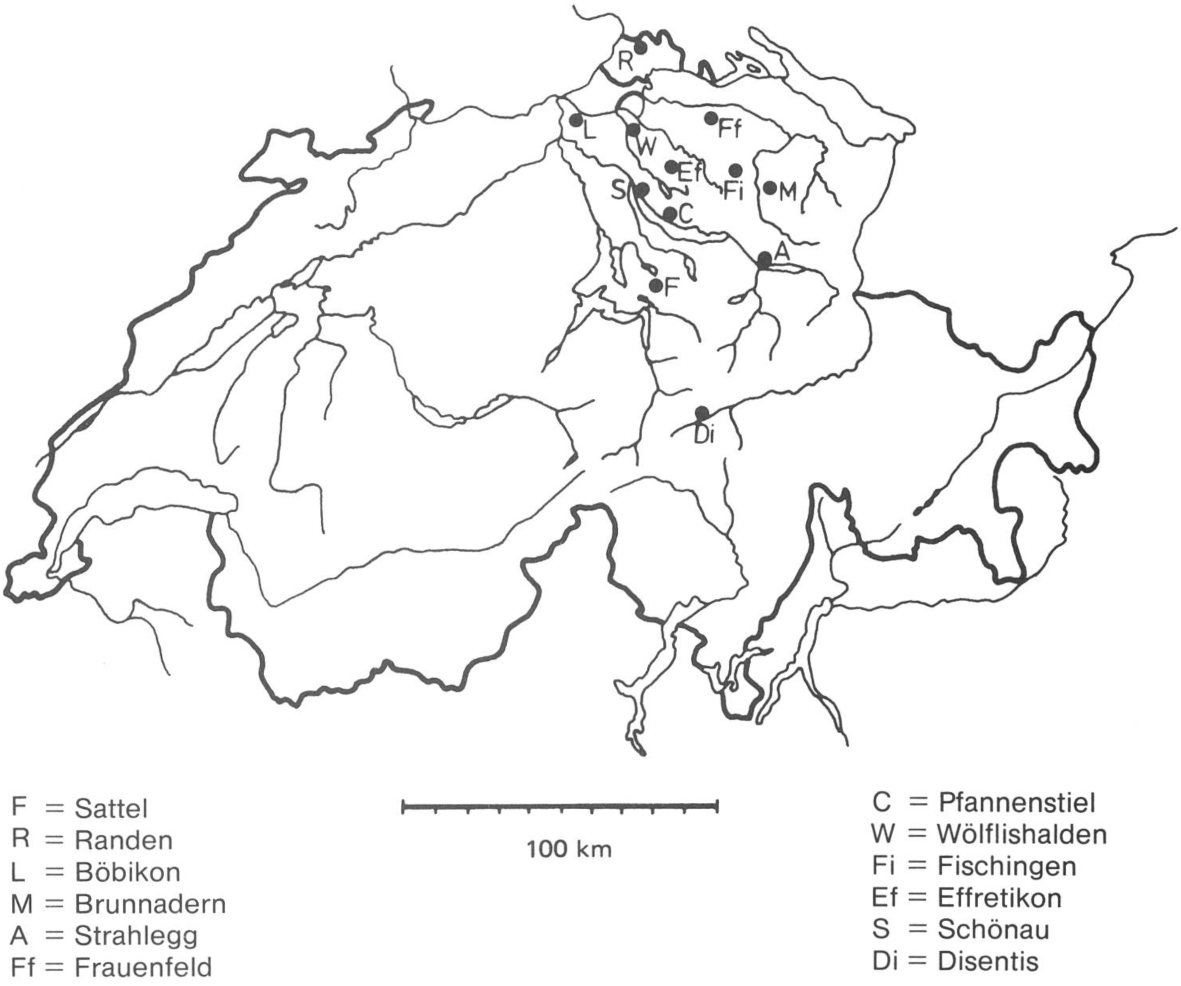


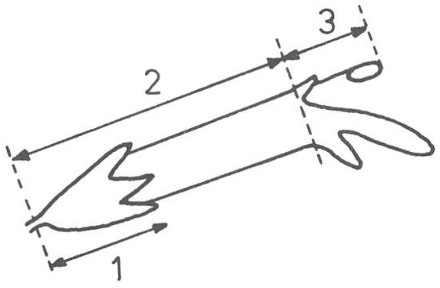
Fig. 1. — Geographical positions of the sites in Switzerland.

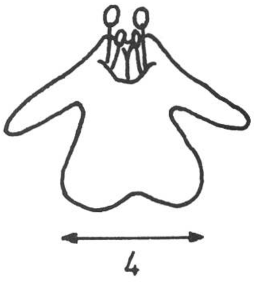
c) shape of the cauline leaves;

d) shape and pubescence of lateral shoots;

e) mode of vegetative production;

f) floral characteristics.





1 = calyx length
2 = length of corolla tube
3 = length of the protruding part of the stamens, called "protruding stamen length"
4 = width of the middle lobe of the lower lip, called "width of middle of LL"

Two flowers from each plant were measured and then averaged.

Means and standard deviation of the metric characters were calculated for the population samples of *A. reptans* and *A. genevensis*. It must be remembered though, that the recorded figures for the standard deviation are not very reliable, because as a result of the sampling method the intermediates are often overrepresented. Accordingly, the scatter diagrams do not reflect the exact proportions of the different morphs in the populations.

The overall variation of populations, which vary simultaneously in several characters, is most conveniently presented by the pictorial scatter diagram method of ANDERSON (1949). This method provides additional information on correlations between characters.

Together with the scatter diagrams, the frequency distribution of the hybrid index is recorded.

For calculating the hybrid index of a plant, the measurements and observations of all characters were valued by a three- or fourgraded index. A character expression, typical of *A. genevensis*, got the index number 3 or 2; an expression, typical of *A. reptans,* the number zero. The hybrid index of a plant is the sum of the indices of the individual characters. In table 1, the character expressions and the corresponding index values are recorded together with their signatures in the scatter diagrams. A typical *A. reptans* plant therefore has the index value 0 and the signature ○ , a typical *A. genevensis* plant, the hybrid index 18 and the signature ●.

Phenotypic plasticity

Plants from two populations of *A. genevensis* and two populations of *A. reptans* were cultivated in pots with standard soil in the experimental part of the Zürich Botanic Garden. These plants were then compared with population samples from the original natural sites. On the whole, the measured characters proved to be sufficiently stable for them to be used for the investigation of genetic variability (LÜÖND & LÜÖND, 1979).

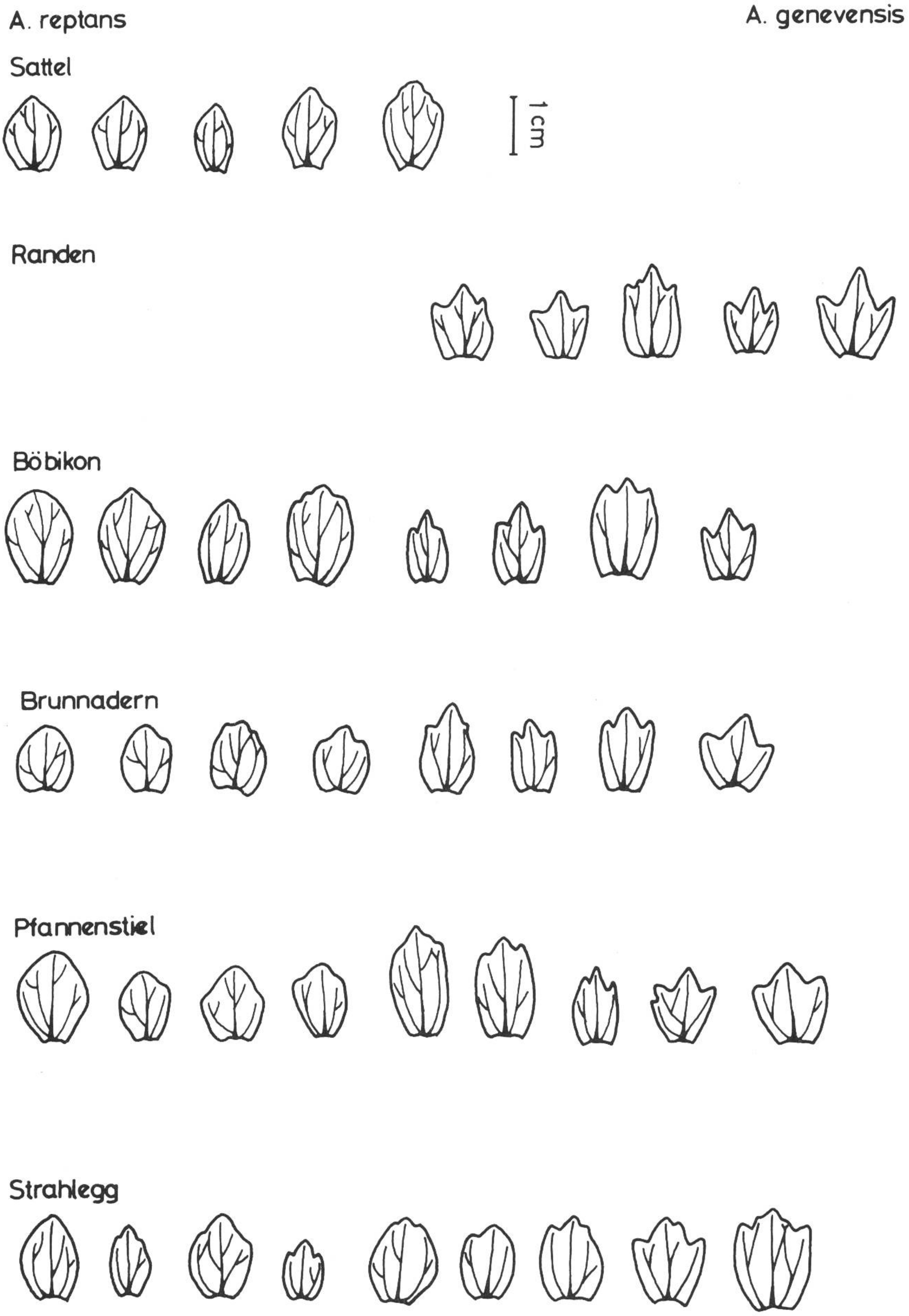


Fig. 2. — Variability of cauline leaves in different populations (third leaf from base).

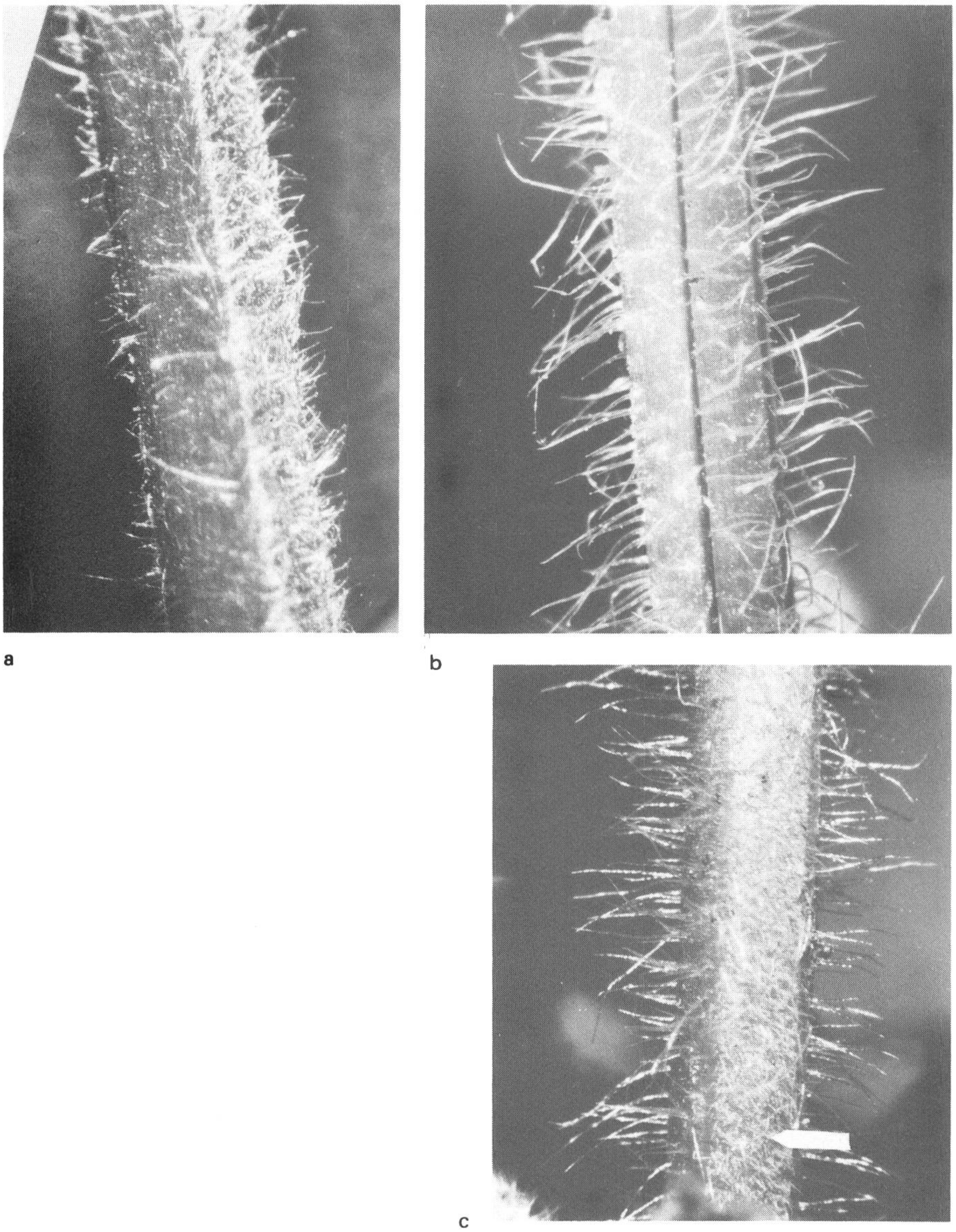


Fig. 3. — Pubescence of the stem. F_1 (c) between *A. reptans* (a) and *A. genevensis* (b). Arrow: ground pubescence.

Variability in natural populations

Variability of single features

- Cauline leaves. Fig. 2 shows third cauline leaves (subtending inflorescences) of plants from several sites. At the sites "Randen" and "Sattel" only *A. genevensis* resp. *A. reptans* occur. No intermediate plants are found. At the other sites, the two species are sympatric. In these mixed populations, some plants of both species vary in the direction of the other species. Especially in the populations "Strahlegg" and "Brunnadern", the species are linked by a complete series of intermediate forms.
- Pubescence of the stem. Fig. 3 shows several kinds of pubescence of *Ajuga* plants. Artificial F_1 hybrids and many natural intermediates show a combination of the parental characters. All four sides of the stem are covered with long hairs as in *A. genevensis.* In addition, two opposite sides are covered with a rather dense coat of short hairs, typical of *A. reptans.* This ground-pubescence is variable in appearance on intermediate plants; usually, it is dense and very short, but in many plants, it is longer and less dense. For simplification, all plants with a higher density of shorter hairs on opposite sides were classed as having a ground-pubescence.
- Growth form. The lateral shoots of *A. reptans* develop into glabrous or almost glabrous runners, which normally develop terminal rosettes (Fig. 4). As a rule, each rosette produces one inflorescence. *Ajuga genevensis* produces few erect lateral inflorescences or hibernating rosettes. Intermediate plants often have runners as well as side rosettes and lateral flowering spikes. The runners of such plants are generally rather hairy and thicker than normal *A. reptans.* The stems of the often numerous lateral inflorescences are creeping at the base and then ascending (Fig. 4). Intermediate plants are often conspicuous and vigorous with numerous flowering shoots.

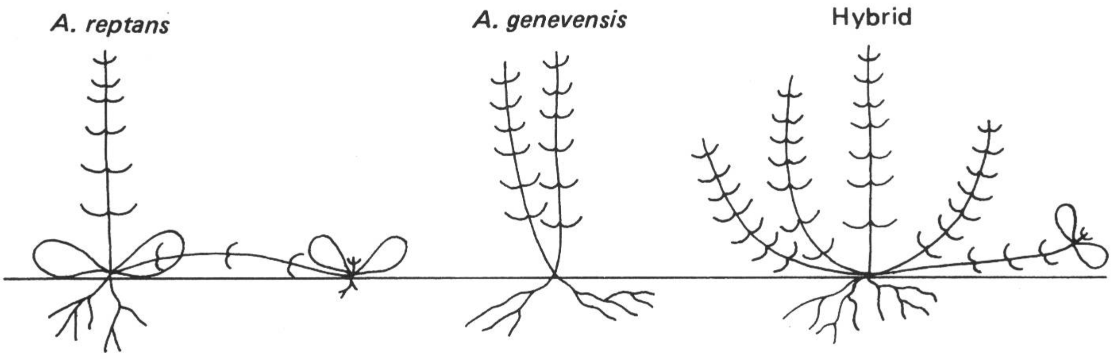


Fig. 4. — Growth forms of *Ajuga.*

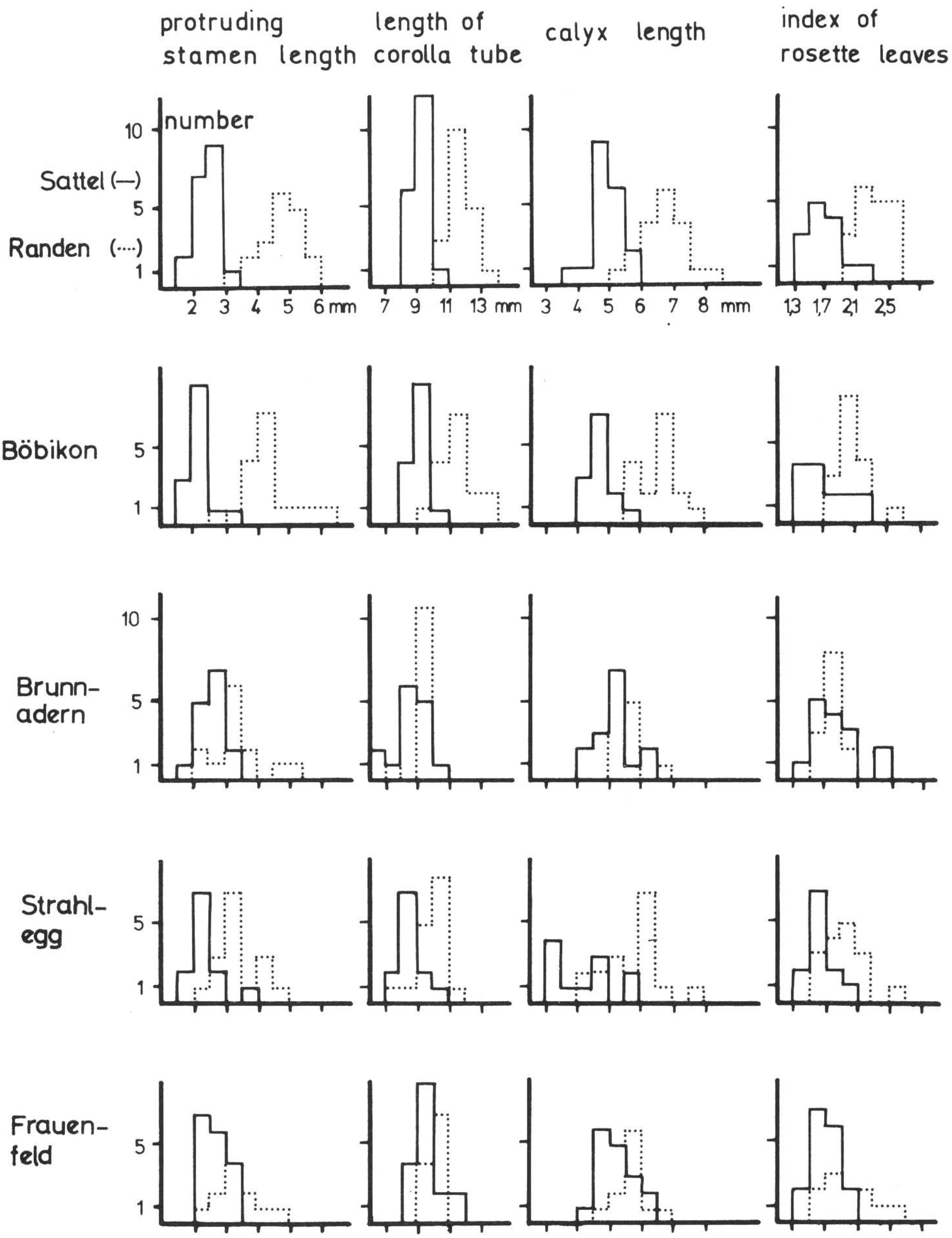


Fig. 5. — Frequency distribution of metrical characters of 5 populations of *A. reptans* (—) and *A. genevensis* (.....).

Character		*Index*	*Signature*
Index of rosette leaves	up to 1.7	0	○
	1.71-1.99	1	⚲
	from 2	2	♀
Pubescence of the stem	alternating on opposite sides	0	○
	long on all sides with additional ground pub. on opposite sides	1	◐
	long on all sides	2	●
Form of cauline leaves	elliptic-ovate	0	○
	with traces of coarse teeth	1	ό
	weakly trident-pointed	2	♁
	strongly trident-pointed	3	**♁**
Length of corolla tube	up to 9.2 mm	0	○
	9.3-10.9 mm	1	┄○-
	from 11 mm	2	┆┄○┤
Protruding stamen length	up to 2.5 mm	0	ordinate
	2.6-3.24 mm	1	
	3.25-3.9 mm	2	
	from 4 mm	3	
Width of middle of LL	up to 6 mm	0	abscisse
	6.1-6.9 mm	1	
	from 7 mm	2	
Calyx length	up to 5 mm	0	
	5.1-6 mm	1	
	from 6.1 mm	2	
Form and pubescence of lateral shoots	glabrous stolons	0	not included in scatter diagrams
	hairy stolons or ascending flowering spikes	1	
	straightly upright flowering spikes	2	

Tab. 1. — Index values and signatures.

Site	Species	n	Index of rosette leaves		Corolla tube length (mm)		Calyx length (mm)		Protruding stamen length (mm)		Width of middle of LL (mm)	
			$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Randen	G	19	2.31	0.19	11.5	0.88	6.55	0.67	4.54	0.66	7.61	1.09
Sattel	R	19	1.64	0.22	9.09	0.47	4.79	0.44	2.32	0.4	5.61	0.56
Böbikon	G	16	2.06	0.22	11.28	1.13	6.42	0.62	4.3	0.78	7.54	1.43
	R	14	1.73	0.29	9.13	0.66	4.64	0.38	2.11	0.39	5.56	0.62
Pfannenstiel	G	12	2.14	0.23	11.3	0.79	6.45	0.78	4.12	0.62	7.6	0.97
	R	10	1.72	0.21	8.48	0.97	4.78	0.32	2.78	0.58	5.68	0.88
Wölflishalden	G	10	2.3	0.32	10.33	0.74	6.4	0.29	3.55	0.51	7.01	0.67
	R	11	1.59	0.11	8.35	0.98	4.5	0.27	2.32	0.39	5.03	0.53
Strahlegg	G	16	1.95	0.25	9.71	0.95	5.6	0.92	3.37	0.68	6.71	0.95
	R	12	1.65	0.17	8.65	0.71	4.1	0.93	2.28	0.49	5.5	0.92
Brunnadern	G	13	1.77	0.17	9.37	0.6	5.4	0.4	3.32	0.78	6.84	0.79
	R	15	1.82	0.3	8.62	1.05	5.02	0.6	2.57	0.39	5.74	0.72
Frauenfeld	G	11	1.99	0.32	9.96	0.51	5.52	0.52	3.26	0.69	6.66	1.19
	R	17	1.67	0.24	9.45	0.89	5.13	0.58	2.51	0.43	6.11	0.91
Fischingen	G	10	1.8	0.2	10.3	0.68	5.95	0.72	3.17	0.67	7.22	0.59
	R	13	1.75	0.32	9.28	0.46	5.22	0.74	2.54	0.45	6.03	0.73
Effretikon	G	16	—	—	10.22	0.99	6.41	0.68	4.34	0.64	7.59	1.27
	R	10	—	—	9.54	0.97	5.07	0.62	2.53	0.48	6.28	0.61
Schönau	R	17	1.65	0.14	9.21	0.64	4.41	0.43	2.09	0.26	4.99	0.69
Disentis	G	19	—	—	9.42	1.02	5.78	0.87	3.88	0.4	6.64	1.02

Tab. 2. — Mean values ($\bar{x}$) and standard deviations (s) of characters in different populations (G = *A. genevensis*; R = *A. reptans*).

- Means and standard deviations of the metric characters (Tab. 2). Putative hybrids were allocated to the species which they most resembled. The general impression of resemblance is determined mainly by the vegetative parts. Male sterile plants of *A. reptans* were not included in the calculations of means and standard deviation, because they have much smaller flowers with partly missing or transfigured (petaloid) stamens. The histograms, in Fig. 5, show the frequency distribution of the measurements of a not hybridized population of *A. reptans* (Sattel) and *A. genevensis* (Randen) and four mixed populations. The ranges of the two monospecific populations "Sattel" and "Randen" are rather clearly separated. In the mixed populations "Brunnadern", "Strahlegg" and "Frauenfeld", the ranges usually overlap much more; the maxima are approximated and even identical in some instances. This shifting of the feature ranges is almost exclusively the result of changes in the *A. genevensis* part of the populations. In all mixed populations, the ranges of *A. genevensis* are more or less clearly displaced in the direction of the range of *A. reptans.* The ranges of *A. reptans* do not show any such displacement.

Overall variation

Scatter diagrams allow a comparison of the extent and kind of variability in populations from several sites. The *A. reptans* population from Sattel (Fig. 6) appears relatively homogenous. Width of the middle of the lower lip and the protruding stamen length are not correlated. *A. genevensis* does not occur in the neighbourhood of this population, which precludes hybridization. The marked coordinates 2.3/5.6 denote the means for protruding stamen length and width of the lower lip. The population of Randen (Fig. 7) consists of *A. genevensis* only. The nearest known population of *A. reptans* was found at a distance of 0.6 km. It is separated from the site Randen by a forest belt. Isolated plants of *A. reptans* were also found along the road cutting through the forest. EHRLICH & RAVEN (1969) stated in a survey on the importance of gene flow for speciation, that gene flow as a factor controlling variation is efficient only over very short distances. It can be assumed therefore, that hybridization at Randen was not taking place during the investigations. Nevertheless, a considerable number of plants show a trend in variation towards *A. reptans.* The standard deviation of the population is high. Correlations between characters cannot however be detected. The population of Randen is the one showing the least variation of all examined populations of *A. genevensis* in the direction of *A. reptans.* The means of protruding stamen length and width of the lower lip are indicated in the scatter diagram. The two coordinates of these not hybridized populations at Sattel and Randen are included for comparing the diagrams of the other populations.

The *Ajuga* population of Brunnadern (Fig. 8) is very polymorphic. It includes *A. reptans,* a complete series of intermediates and very few more or

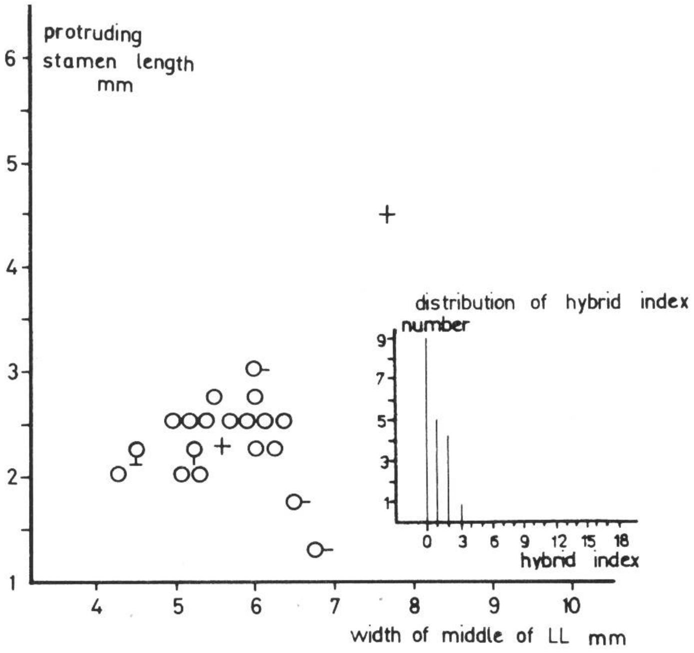


Fig. 6. — Population Sattel (explanation of signatures s. Tab. 1).

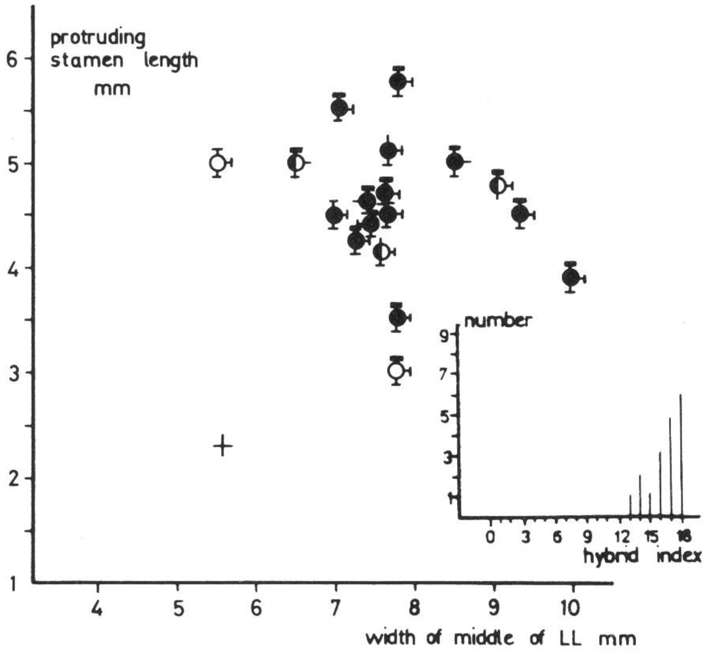


Fig. 7. — Population Randen.

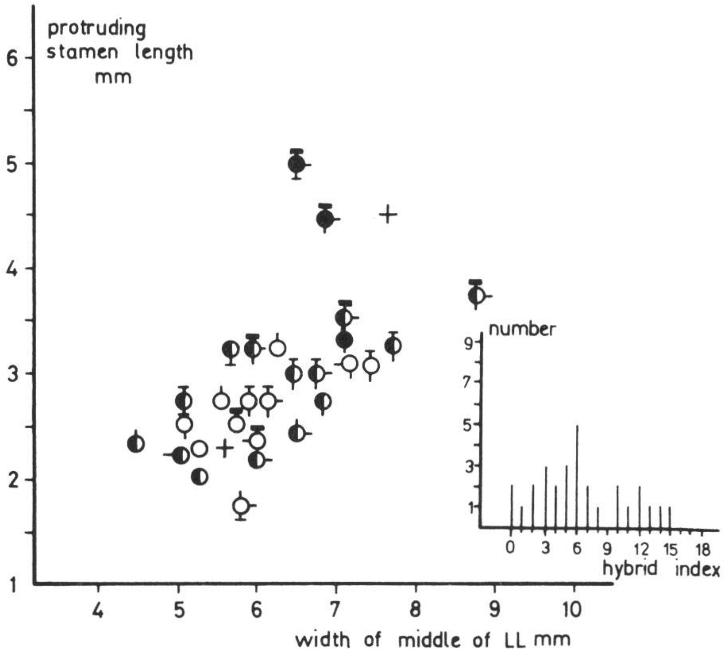


Fig. 8. — Population Brunnadern.

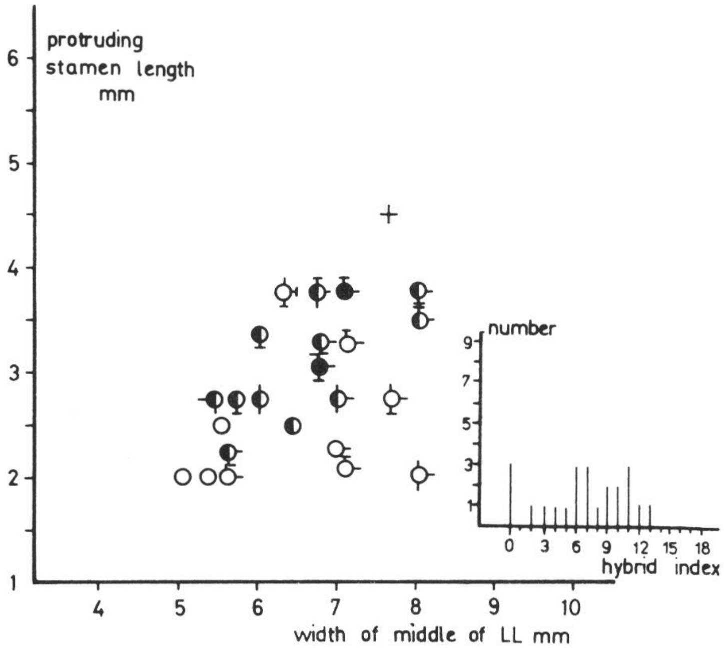


Fig. 9. — Population Fischingen.

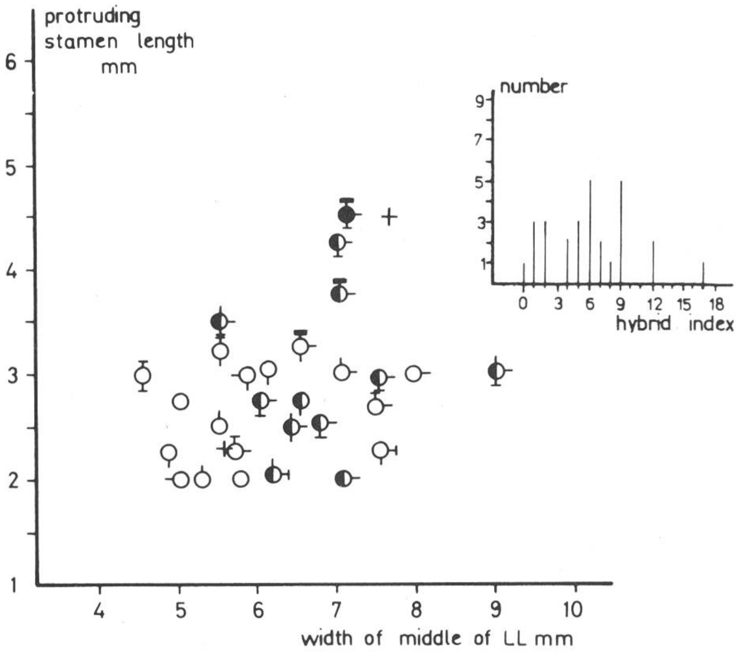


Fig. 10. — Population Frauenfeld.

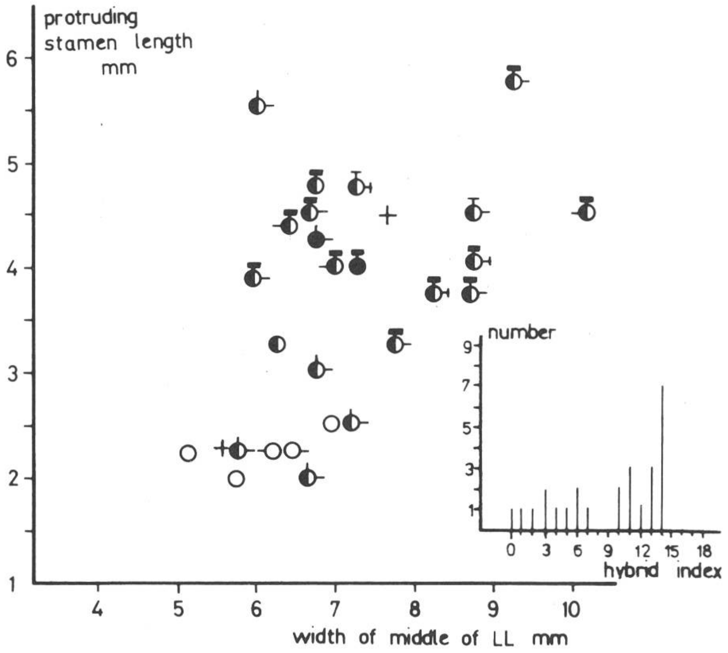


Fig. 11. — Population Effretikon (without index of rosette leaves).

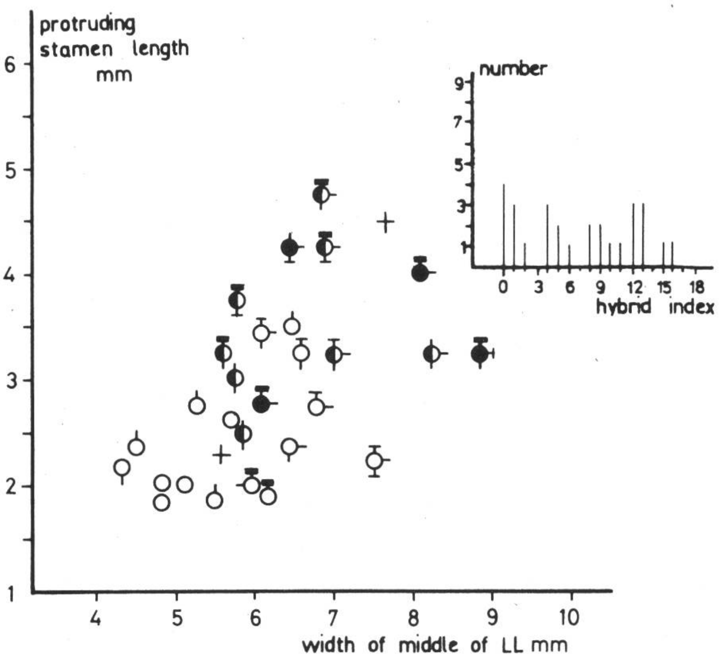


Fig. 12. — Population Strahlegg.

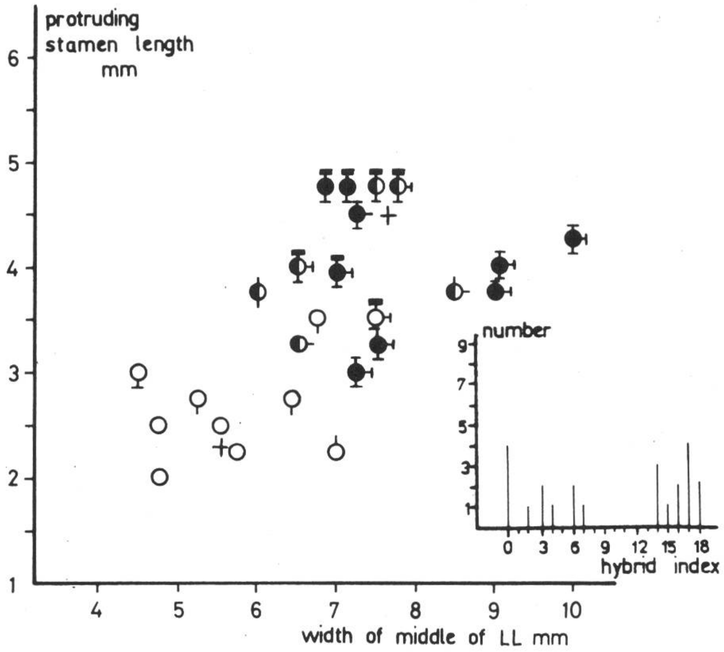


Fig. 13. — Population Pfannenstiel.

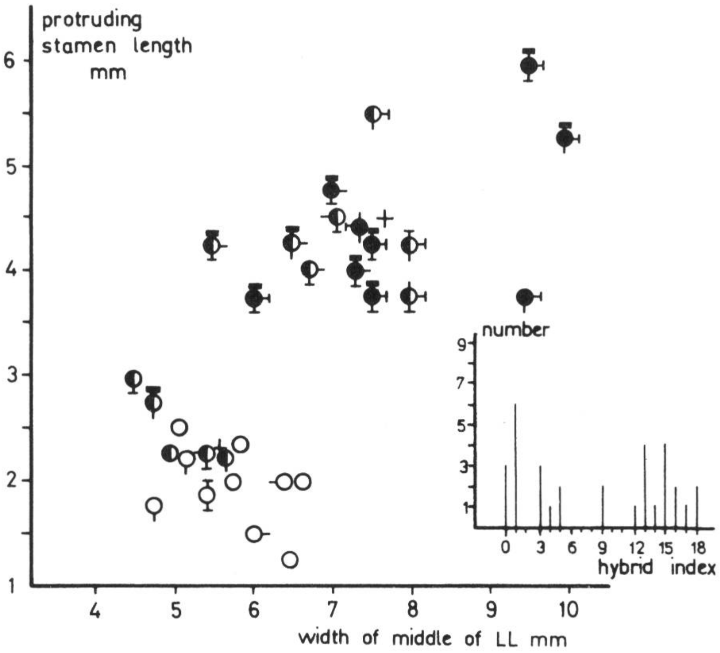


Fig. 14. — Population Böbikon.

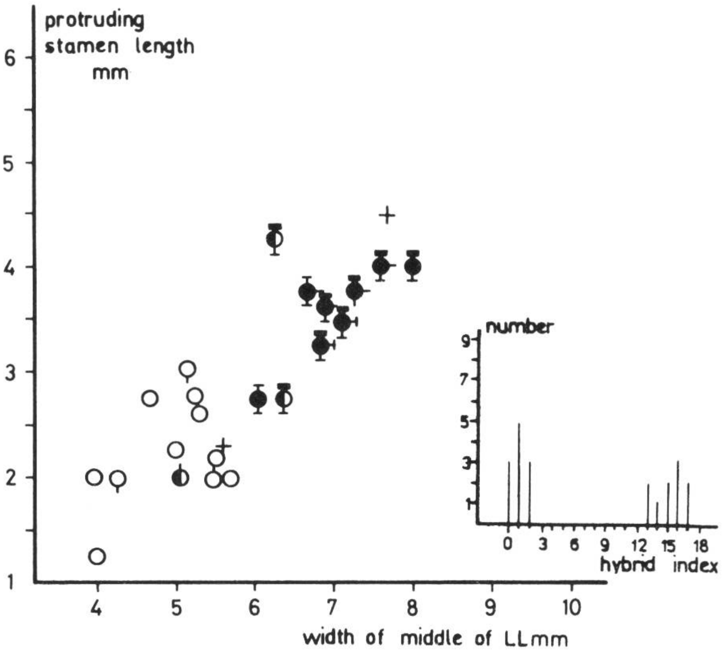


Fig. 15. — Population Wöflishalden.

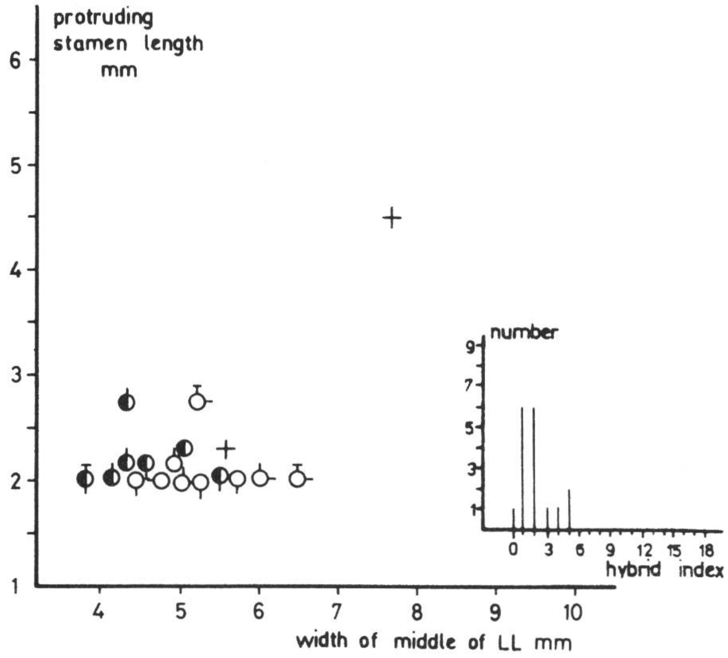


Fig. 16. — Population Schönau.

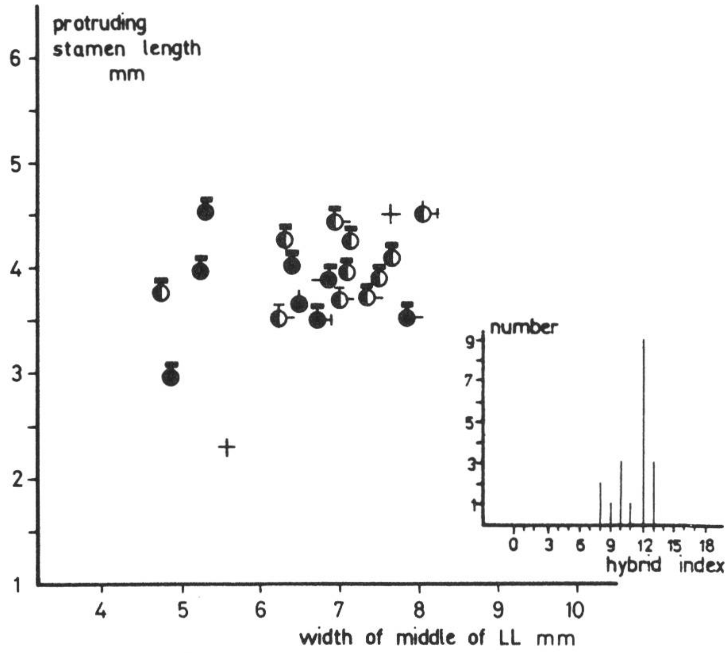


Fig. 17. — Population Disentis (without index of rosette leaves).

less typical *A. genevensis* plants. The scatter diagram shows clearly, that the various characters of *A. reptans* resp. *A. genevensis* are loosely correlated. Thus, plants with rather broad lower lip also have rather long stamens, more hairy stems and narrower rosette leaves. The distribution of plants, resembling *A. reptans* or *A. genevensis* at the site, is of special interest. The south-exposed slope is a pasture. The rather poor soil of its upper part is covered with a closed sward. In the lower part of the pasture, the fertility of the soil is increasing, and the grass sward is interrupted by steps with bare places caused by the tread of the grazing cattle. *Ajuga genevensis*-like plants are found especially in the upper part of the pasture. At the base of the slope, *A. reptans*-like plants are abundant. Intermediates grow particularly on the bare spots of the steps.

Similarly composed populations, with a large proportion of intermediate plants, are found at other sites under a variety of environmental conditions. In the following four examples, typical *A. genevensis* plants are largely missing.

The sites Fischingen (Fig. 9) and Frauenfeld (Fig. 10) are old gravel pits, and on their edges, *Ajuga* populations grow in an open habitat. In spite of the weak competitive pressure, *A. genevensis* is missing, because of unfavourable exposition in both cases (Fischingen is north-east-exposed, Frauenfeld is situated in a rather shady plain). *Ajuga reptans*-like plants are abundant, particularly at Frauenfeld. Correlations between characters are not clear at Frauenfeld and scarcely detectable at Fischingen. The features seem to be distributed at random in the populations.

The site Effretikon (Fig. 11) is a clearing at the edge of a forest, brought about by a storm two years before the investigation (in 1976). At the time of the examination, the clearing was gradually being colonized by woody plants. The competitive situation and the eastern exposition are unfavourable for *A. genevensis.* On the other hand, numerous fairly large clones of *A. genevensis*-like intermediates are found on the overturned trunks, and sometimes also on even places. *Ajuga reptans* and intermediate plants are found especially at the edges of the clearing and along the road.

Strahlegg is a meadow with a closed turf on fairly nutrient poor soil (Fig. 12). It is rarely influenced by grazing and manuring. As the cattle avoid the steep slope, baretrodden places scarcely occur. Liquid manure flows off. The competitive situation is unfavourable for *A. genevensis;* intermediate plants similar to it are abundant however. Correlations of the typical characters of the species are evident in the scatter diagram.

At the three following sites, there are typical *A. genevensis* plants in addition to *A. reptans* and intermediates. In all three cases, fairly typical representatives of the two species predominate, whereas intermediates are sparingly represented.

Pfannenstiel is a partly pastured site with southern exposition (Fig. 13). The upper part of the site is covered by a scanty dry meadow. The lower part, a dry steep slope, is manured and intensively grazed, and bears a nutrient rich pasture with numerous baretrodden patches. *Ajuga genevensis* occurs in poor meadow and in the bare patches of the fertile pasture. Intermediate plants are found especially in the nutrient rich pasture.

The site Böbikon is an abandoned gravel pit surrounded by forest. It was filled up and levelled about three years before the time of investigation. At the beginning of the inquiry, the loamy soil was almost without vegetation. The most frequent plant accompanying *Ajuga* was *Tussilago farfara* L. During the following two years, a more or less closed cover of vegetation developed very quickly. This process was already fairly well advanced at the time of the data-collecting. The numerous intermediates are clearly divided into an *A. reptans*- and an *A. genevensis*-like group (Fig. 14).

At the site Wölflishalden (Fig. 15), the two species are most clearly separated. Intermediate plants, resembling either species, occur only in very small numbers. The lower part of the east-exposed slope, which is situated in a hollow protected against the wind, is grazed and covered by a closed, moist, nutrient rich pasture, which contains only *A. reptans.* In the dry, poor meadow on the upper slope, there are almost exclusively *A. genevensis.*

The two last populations are from sites, where only one of the two species occurs.

The site Schönau (Fig. 16) is a nutrient rich meadow in the Botanic Garden Zürich, which contains *A. reptans.* For the most part, the investigated plants vary in one or few characters in the direction of *A. genevensis.* No correlations between the deviating characters can be found. From numerous observations taken from herbarium specimens it can be seen, that *A. genevensis* was present in Zürich at the beginning of our century, e.g. in the immediate neighbourhood of the investigated site. Some of the plants identified as *A. genevensis* in the herbaria clearly show hybrid characters.

The population Disentis (Fig. 17) is exclusively *A. genevensis.* The nearest known population of *A. reptans* is reported from about 18-20 km down the Rhine valley, between Tavanasa and Waltensburg (BRAUN-BLANQUET & RÜBEL, 1936). Nevertheless, all plants vary for the most part in several characters in the direction of *A. reptans.* Correlations between the deviating characters cannot be detected. They seem to be randomly distributed in the population. At Disentis, *A. genevensis* grows partly in densely closed nutrient rich pastures.

SUMMARY AND DISCUSSION

Highly variable populations of *Ajuga* were found in many places. Every population has its own history, and the selective pressure from the abiotic and vegetational environment is different in every place. Genuine hybrid swarms preferentially occur at sites open or disturbed by man, so called "hybridized habitats" (ANDERSON, 1949). The gravel pits at Fischingen and Frauenfeld are disturbed sites. It is difficult to judge, whether the small competitive pressure or the occurrence of various new niches is the more important reason for the survival of the hybrid plants. *Ajuga* populations subject to high competitive pressure (Wölflishalden, Pfannenstiel) can contain hybrids, but these are generally similar to one of the parental species. Morphologically intermediate hybrids are mostly lacking.

In the population "Brunnadern", *A. genevensis*- and *A. reptans*-like plants are separated in the pasture along a cline of nutritive salt and moisture contents. This population as a whole gives the misleading impression of a polymorphic hybrid swarm. But here, different ecological conditions obviously select different hybrid types. A similar situation was found by BENSON & al (1967) in Californian oaks, which are linked by a continuous spectrum of hybrids. At the natural (undisturbed) sites however, different hybrid types are selected, according to the exposition of the site.

At the sites Brunnadern and also at Strahlegg, some plants resemble *A. genevensis* very closely, but support the competition of pasture plants much better than not hybridized *A. genevensis.*

Here, hybridization has produced, beside the amplification of the morphologic variability, an increase of the ecological tolerance of the species. HEISER (1949) has also found in *Helianthus bolanderi* A. Gray a hybridized race with new ecological preferences. Hybridized genotypes can survive after the not hybridized parents have died out at the site. Accordingly, *A. genevensis* is missing at Fischingen and Strahlegg, whereas hybrids similar to it have probably survived for a long time. A similar case is reported by GRANT (1952), who has investigated hybridization in two *Aquilegia* species in an overlapping area in the southern Sierra Nevada of California. Pure *Aquilegia pubescens* dit not occur in this region. The site Fischingen, a gravel pit in the middle of a forest, bears a small, isolated and probably rather old hybrid population. The gravel pit was worked in connection with the construction of a forest road about 30 years ago. This *Ajuga* population is very variable; however, the characters are hardly correlated. This old hybrid population has probably reproduced in isolation for a considerable number of generations. The correlations between the parental characters have therefore gradually disappeared. Increasing blurring of the character correlations in older, isolated hybrid populations were also observed by ROLLINS & SOLBRIG (1973) in *Lesquerella* and by DANESCH & al. (1975) in *Ophrys.*

A different situation is found with the population "Strahlegg". This hybrid population is in continuous contact with not hybridized *Ajuga reptans.* The *Ajuga*-species are mainly crossbreeders, and their hybrids mainly reproduced by backcrossing. Thereby, new intact groups of linked parental genes are continuously introduced to the hybrid population. This gene flow is probably the reason, why the caracter correlations are conserved in this old hybrid population, which is in close contact with *A. reptans.*

In some cases, hybridization has only short-term effects on the genetic structure of the concerned populations. It allows the quick production of a great number of genotypes, which are adapted to various ecological niches of new hybridized habitats. During the normally occurring reversion of such sites to more stable conditions with stronger competitive pressure, these genotypes mostly disappear. In a clearing near the site Böbikon, which was nearly bare at the beginning, a hybrid swarm disappeared almost completely within only two years. After the place was overgrown by bramble, raspberry-bushes etc., few plants of *A. genevensis* survived on still bare spots, and *A. reptans* survived along the road. Change in the conditions of natural selection made the hybrids disappear. Similarly, STEBBINS & DALY (1961) stated, that the genotypic composition of a *Helianthus*-hybrid swarm had considerably changed with time by transformation of the environmental conditions.

At certain sites like Randen and Schönau, there are beside *A. genevensis* resp. *A. reptans* plants which vary rather weakly towards the other species, although it does not occur at the site at present. Considering the extensive hybridization between the species at many other sites, it can be supposed, that these plants are products of introgression in the sense of ANDERSON (1949). At these sites, repeatedly backcroossed individuals, which are morphologically and physiologically only slightly different from one species, can survive under the prevailing selective conditions, whereas more strongly hybridized plants have no chance of survival.

The population of Disentis is somewhat difficult to interpret. It is a variable population, strongly shifted towards *A. reptans.* Correlation between characters are not visible. The population shows biochemical deviations from both species. Possibly, this population is a former hybrid swarm, which has been stabilized and developed into a new selective norm. Examples of differential development of isolated hybrid swarms are also described for other plants (EHRENDORFER, 1959, in *Achillea;* LEVIN & SMITH, 1966 in *Phlox;* DANESCH & al., 1975, in *Ophrys*).

Several of the polymorphic populations (at Brunnadern, Strahlegg, Pfannenstiel, Frauenfeld) show clear correlations between characters, which are not correlated in allopatric populations of the parental species (Sattel, Randen). There are several lines of argument, which indicate, that these highly variable populations are hybrid swarms. A main point is the distribution of the variability within the population. CLAUSEN & HIESEY (1958) investigated the genetic structure of ecological races of *Potentilla glandulosa* Lindl. They stated, that the polygenic inheritance of the characters separating races leads to a restriction of the recombination in the F_2 and further hybrid generations, and promotes the resegregation of parental character combinations. This tendency towards correlated occurrence of parental characters in hybrid descendants is called genetic coherence by Clausen and Hiesey. CLAUSEN (1967) stated in a survey of the importance of coherence mechanisms, that genetic coherence exists not only at the race level but at every level of evolutionary development. Conversely, as ANDERSON (1949) emphasized commenting on his pictorial scatter diagram method, correlated occurrence of the supposed parents in polymorphic populations can be valued as strong evidence for their hybrid origin. Accordingly, DANESCH & al. (1975) used the character coherence to prove the hybrid origin of populations and tribes between mediterranean *Ophrys* species. ANDERSON & GAGE (1952) found, by the method of extrapolated correlates, the second parent of a supposed hybrid swarm between two *Phlox* species. Therefore, it is very probable, that hybridization is the cause of the increased variability of the investigated *Ajuga*-populations. This assumption is also supported by the results of experimental crossbreedings. The examined *Ajuga* species can be crossed and produce fertile offspring. Among the artificial hybrids there are plants, which are morphologically almost identical with putative hybrids from natural populations. The total experimental F_1 plants were far from uniform (LÜÖND & LÜÖND, 1979) and gave the impression of a hybrid swarm rather than of a first generation from a cross between good species. Such a wide variation in an F_1 can only be explained by the asumption of hybridity in the parents.

The hypothesis of the hybrid origin of polymorphic *Ajuga*-populations is further supported by work on chromatography and pollen fertility reported by LÜÖND & LÜÖND (1979). The results of thin-layer-chromatography generally agreed quite well with those of morphological investigations. By both methods, the allopatric population of *A. reptans* from Sattel was recognized as not hybridized. In *A. genevensis,* this was never the case in any of the examined populations. All the populations, which were considered as hybridized on the basis of morphological investigations (Pfannenstiel, Böbikon, Disentis), also showed hybrid character in the chromatographic spot patterns.

The lower pollen fertility of the polymorphic populations, the values of which lie between those of the not or little hybridized populations and the experimental F_1, also indicates their hybrid character.

Alternative explanations of these facts are unlikely. Correlated variation of several characters could also be brought about by gradual changes of selective environmental factors. Such a parallel selection ought to produce individuals that show an absolute correlation between the concerned characters. Such plants are however very rare in the examined populations of *Ajuga.* Most plants have a mosaic of strongly, weakly and not deviating characters. Such loose correlative relations between species characters are best explained by reduced recombination of adaptive gene complexes of the parents following hybridization.

Although *A. genevensis* has vanished from many sites, its genetic material has been saved in the gene pool by means of hybridization with *A. reptans.* An enlarged gene pool permits the production of a wider variety of genotypes by recombination. Thus, the evolutionary potential of the genus is largely conserved, even if *A. genevensis* should eventually become extinct in some regions, as is in fact the case.

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