

Zeitschrift:	Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel
Herausgeber:	Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel
Band:	55 (1989)
Artikel:	Studies on competition between closely related species of <i>Scabiosa columbaria</i> L.s.l. Part 2. Differentiation of hybrid populations under different temperature, water and nutrient conditions = Konkurrenzuntersuchungen zwischen nah verwandten Arten von <i>Scabiosa columbaria</i> L.s.l. : Teil II. Differenzierung von Bastardpopulationen unter verschiedenen Temperatur-, Feuchtigkeits- und ...
Autor:	Landolt, Elias / Binz, Hans-Rudolf
Kapitel:	5: Discussion
DOI:	https://doi.org/10.5169/seals-377754

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 11.01.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

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 speculative.

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	<i>S. lucida</i>	<i>S. columbaria</i>	<i>S. gramuntia</i>
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 selection pressure in basins with low water level if long periods without rain or watering 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 populations under the investigated conditions.

Gesamtzahl (s. Tab. 13) für die verschiedenen Populationen unter den untersuchten Bedingungen.

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 competition 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 its 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 fertilized 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). *Scabiosa 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 m² 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.
- CRAWFORD 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, differentiation 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: Ecological 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 differentiation 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 THURMAND.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.

Address of the authors: Prof. Dr. Elias Landolt
Dr. Hans-Rudolf Binz
Geobotanisches Institut ETH
Stiftung Rübel
Zürichbergstrasse 38
CH-8044 Zürich