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Niche width and variation within and between populations in colonizing species (*Carex flava* group)

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Summary. Taxa of the *Carex flava* group in Switzerland show a trend towards increased colonizing ability (*r*-selection). High colonizing ability is correlated with a large fundamental but a small and discontinuous realized niche. It is argued that *r*-selected species with wide niches should be monomorphic with generalists rather than polymorphic with specialists since they have small effective population sizes in which high genetic variability cannot be maintained. The most *r*-selected taxon of the group, *C. viridula* ssp. *viridula*, has indeed the lowest genetic variability within populations but, in ecologically important characters, expresses the highest plasticity. The taxonomically important characters (inflorescences) have high heritability and differences between populations of *C. viridula* ssp. *viridula* are probably much affected by genetic drift.

Introduction

The success of colonizing species depends upon their ability to grow under a wide range of habitat conditions. Species in unsaturated environments, where density-dependent regulation is low, often have wide, overlapping niches (Miller 1964, Pianka 1975, Diamond 1975, Suchanek 1981, Parrish and Bazzaz 1982a, b). Populations capable of occupying wide niches may be monomorphic with generalists, expressing large within-phenotype variability, or they may be polymorphic with specialists, expressing large between-phenotype variability (Roughgarden 1974). While all of the within-phenotype variability is plasticity, the between-phenotype variability has a genetic as well as a plastic component. However, in considering whether generalists or specialists will be favoured in a particular habitat by natural selection, we are only interested in the genetic component of the between-phenotype variability.

The question then is whether the wide niches of colonizing species reflect high genetic variation within populations or high plasticity. Since populations of colonizing species fluctuate in size and usually remain small and isolated from each other they are likely to be affected by genetic drift. This leads to an increase in genetic variation between but a decrease in genetic variation within populations (Hamrick et al. 1979, Barrett and Wilson 1981, Oka 1983). If the genetic variability for resource utilization cannot be maintained within populations the evolution of general purpose genotypes with the ability to respond to varying environmental conditions by plasticity seems to be the only alternative.

To investigate this hypothesis the niche relations of sedges from the *Carex flava* group were examined. Detailed observations on the biology of the species revealed a trend towards increased colonizing ability within the group (Schmid 1980, 1982, 1984). Results from these studies are summarized in Table 1 in which the taxa are placed along the *r*-*K* continuum. Karyological evidence (Schmid 1982)

Table 1. *r*- and *K*-correlates of taxa of the *Carex flava* group placed along the *r*-*K* continuum (comparisons are relative within the group)

Trait	*C. flava* (two varieties)	*C. viridula* ssp.		
		brachyrrhyncha	*oedocarpa*	*viridula*
	⟶	increasingly *r*-selected		⟶
Development (genets and tillers)	slow	intermediate		fast
Size (genets and tillers)	large	intermediate		small
Life span (genets and tillers)	long	intermediate		short
Reproduction	delayed	delayed	early	early
Seed and seedling number	low	low	intermediate	high
Population size	large and constant, near carrying capacity	intermediate		small and variable, well below carrying capacity
Mortality	density-dependent	intermediate		density-independent

suggests that the best colonizer, *C. viridula* ssp. *viridula*, is the most recent member of the group, presumably derived from *C. flava* by speciation processes including strong *r*-selection. The hypothesis can be reformulated in the following way:

(i) *r*-selected species have large and overlapping niches.

(ii) *r*-selected species have high genetic variability between populations but within populations genetic variability is low and plasticity high.

Materials and methods

In Switzerland the *Carex flava* group consists of the five taxa *C. flava* var. *flava* and var. *alpina*, *C. viridula* ssp. *brachyrrhyncha*, *C. viridula* ssp. *oedocarpa*, and *C. viridula* ssp. *viridula* (for nomenclature see Schmid 1983). Where more than one taxon occurs at a single site F_1-hybrids and backcrosses are commonly also present; but ecological differences almost always prevent complete intermixing. Populations from thirty-seven sites representing a maximal range of climatic and edaphic conditions (described in Schmid 1984) were observed in the field and under uniform cultivation in outdoor plots at the Botanic Garden of the University of Zürich.

Each site was visited on the average five times from 1977 to 1979. Species lists were constructed using Braun-Blanquet's cover-abundance values (Mueller-Dombois and Ellenberg 1974). Twenty environmental variables were recorded as well: latitude, longitude, altitude, microtopography, trampling, soil compaction, organic matter, lime, pH, water condition, higher plant cover, management, moss cover; indices for light, temperature, continentality, soil water, soil reaction, and nitrogen calculated from floristic data (Ellenberg 1974). For natural populations, up to 103 morphological characters were recorded on usually five to ten sedge tillers from different tussocks (genets) and for cultivated populations thirty-three characters on usually five tillers.

The BMDP-77 programme package was employed for data analyses (Dixon and Brown 1977) along with some small programmes for data preparation written in PL/I. Details about methods of sampling and analysis are given in Schmid (1980).

Results and discussion

Niche width

The floristic similarities between sites were evaluated with two types of cluster analyses. One was block clustering (Hartigan 1972, BMDP-programme 3M) for cover-abundance values and the other was agglomerative procedures based on a similarity index for presence/absence data (Mountford 1962). Results were similar with the exception that main groups were better separated if only the presence/absence of species at the sites was considered. Five more or less equally sized clusters of sites could be recognized. About 75% of the sites with *Carex viridula* ssp. *viridula* made up one single group whereas pure *C. flava* sites were distributed over the remaining four groups. Sites with *C. viridula* ssp. *brachyrrhyncha* or ssp. *oedocarpa* were intermediate in floristic similarity.

The sites were also classified according to ecology as measured by twenty environmental variables. Euclidean distances were calculated for each pair of sites and the matrix of distances rearranged using cluster analyses (BMDP-programme 2M; Fig. 1). Four sets of sites are specially marked in Figure 1:

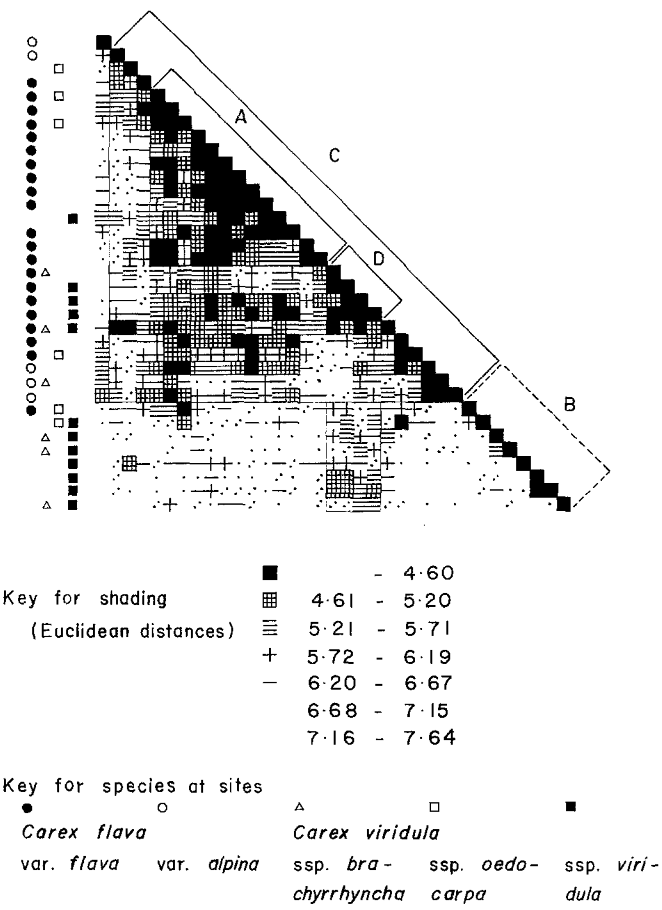

Fig. 1. Matrix of Euclidean distances between sites of the *Carex flava* group; data from 20 environmental variables (for explanation of group labels see text)

Group A is a tight cluster of pure *C. flava* var. *flava* sites. The majority of the *C. viridula* ssp. *viridula* sites (B) are very different from all other sites (C) and also amongst each other. All they have in common is to be the least different from four of the five remaining *C. viridula* ssp. *viridula* sites (D).

The high ecological diversity between sites of *Carex viridula* ssp. *viridula* suggests that this taxon has a large fundamental niche (Hutchinson 1957). Unfortunately, the width of fundamental niches could not be measured directly in the present study (this could be done if the taxa were grown without competitors on resource gradients in cultivation, *cf.* Parrish and Bazzaz 1982b).

Niche widths were examined graphically by projecting the multidimensional niche space onto different planes using principal component analysis on the twenty environmental variables. Subsequent axis rotation allowed the extraction of factors of which the first three accounted for 46% of the total variability in the data. An ordination of sites is shown in Fig. 2. The first factor stands for disturbance, closed sites (*C. flava* present, but no other taxa of the group) have low and open sites (*C. viridula* ssp. *viridula* present) high scores. Where *C. flava* occurs together with

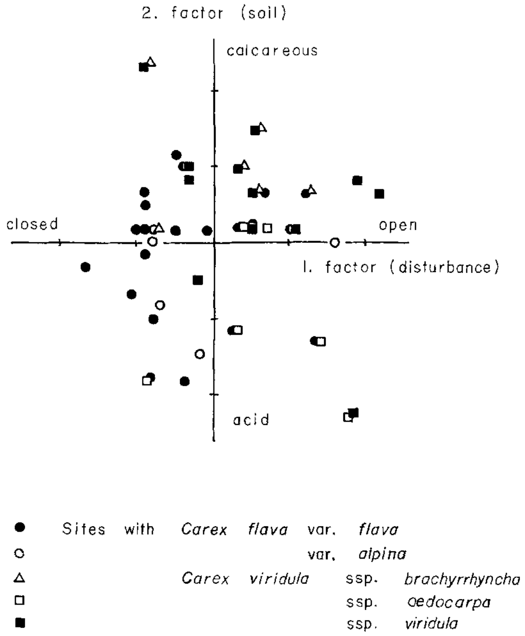

Fig. 2. Ordination of sites of the *Carex flava* group (principal component analysis with subsequent rotation of axes)

other taxa of the group its abundance was lowest and individual growth least vigorous (Schmid 1980). Reciprocal transplant experiments indicated that *C. flava* dies under high disturbance, e.g. on foot paths and that, in contrast, *C. viridula* ssp. *viridula* is outcompeted in moderately dense vegetation (Schmid 1980). The second factor represents soil conditions (pH, soil reaction index, organic matter, lime). *C. viridula* ssp. *viridula* sites are more spread along this axis than *C. flava* sites (Fig. 2), that is, *C. viridula* ssp. *viridula* grows on more different kinds of soil than does *C. flava*. *Carex viridula* ssp. *brachyrrhyncha* is restricted to calcareous soils and *C. viridula* ssp. *oedocarpa* to acid soils.

From the results of different ordinations it appears that the niche of *C. flava* is included (Hutchinson's (1978) terminology) in that of *C. viridula* ssp. *viridula*. Since *C. viridula* ssp. *viridula* is the weakest competitor of the *C. flava* group it is excluded from moderate and predictable habitats by *C. flava* and other taller growing plants and occurs only in *different* extreme or unpredictable habitats such as footpaths or small depressions that are flooded or dry out at irregular intervals. *Carex viridula* ssp. *brachyrrhyncha* and ssp. *oedocarpa* are intermediate in competitive ability. There are not enough sites for these two taxa to investigate their niche relationships within the group in detail. The surprising floristic similarity between sites with *C. viridula* ssp. *viridula* finds its explanation in that, as a colonizing species, it grows often together with the same set of other pioneer plants, all of which have wide ecological tolerances but are forced by competitors to live at the margins of their niches. Thus, for the *Carex flava* group, the hypothesis that *r*-selected species have large (and overlapping) niches is supported by the field data. This applies for the fundamental (Hutchinson 1957) niche. The realized niche of *C. viridula* ssp. *viridula*, however, is small and discontinuous.

Variation within and between populations

It could be argued that populations of *Carex viridula* ssp. *viridula* experiencing particular environmental conditions would become locally adapted ecotypes with narrower niches than that of the whole taxon. Such evolutionary specialization would be disadvantageous if environmental conditions changed over time, as they typically do in habitats of *r*-selected species. Populations which respond to their environment by plasticity would then be favoured by long term selection because they are less likely to evolve locally adapted ecotypes than populations which are genetically variable.

Plants of the five investigated taxa of the *Carex flava* group collected in the field showed significantly ($P<0.05$) different within-taxon variances in 74% of the recorded morphological characters. The variances usually decrease from *C. flava* var. *flava*> *C. flava* var. *alpina*, *C. viridula* ssp. *brachyrrhyncha*, *C. viridula* ssp. *oedocarpa*> *C. viridula* ssp. *viridula* (Fig. 3). As could be shown by ecological and karyological studies (Schmid 1980, 1982), the higher variability of the more *K*-selected *C. flava* var. *flava* in Switzerland is in part due to larger population sizes and high occurence of introgression at many of their field sites. The other taxa, especially *C. viridula* ssp. *viridula*, have a population structure which is exactly opposite; in Switzerland they grow in smaller and genetically more isolated populations.

The within-taxon and between-population variation of *C. flava* var. *flava* and *C. viridula* ssp. *viridula* are compared in Table 2 for some of the taxonomically most important characters. Although the overall variability is larger in *C. flava* var. *flava*, differences between field populations are more pronounced in the *r*-selected *C. viridula* ssp. *viridula*. It follows that the within-population variation under natural conditions is smaller in the *r*-selected taxon.

In cultivation *Carex flava* var. *flava* was significantly ($P<0.05$) less variable in most characters than in nature

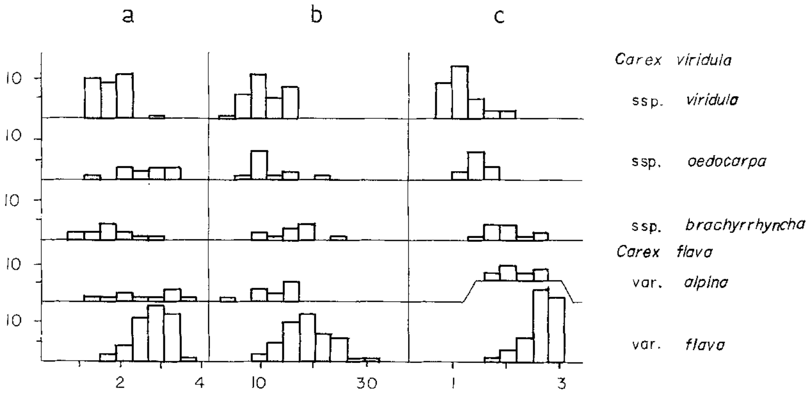

Fig. 3a–c. Frequency distributions of three morphological characters for five taxa of the *Carex flava* group (material from natural populations). **a** Leaf width (mm), **b** Stem height (cm), **c** Beak length (mm)

Table 2. Variability of *Carex flava* var. *flava* and *C. viridula* ssp. *viridula* in nature and under cultivation

Character	Within taxon variances different (*C. flava* var. *flava* – *C. viridula* ssp. *vir.*)	Between population differences			
		C. flava var. *flava*		*C. viridula* ssp. *vir.*	
		nature (10 pop.)	cultiv. (9 pop.)	nature (10 pop.)	cultiv. (6 pop.)
Leaf:					
width	+ +	**	*	**	·
ligula length	+ +	**	*	·	·
Stem:					
height	+ +	**	**	*	·
width	+	*	*	**	·
♂ spike:					
length	+	**	·	**	*
peduncle length	+ +	·	·	**	·
glume length	·	**	·	**	*
glume width	·	·	**	**	·
♀ spikes:					
length	+	**	·	**	·
utricle length	+ +	*	**	**	**
utricle width	+ +	·	·	*	**
beak length	+ +	·	·	**	**
beak bristles	+ +	·	*	**	**

+ ($P<0.05$) and + + ($P<0.01$) indicate that variances are significantly larger in *C. flava* var. *flava* (*F*-test)

* ($P<0.05$) and ** ($P<0.01$) indicate that population means are significantly different (analysis of variance)

whereas overall variability in *C. viridula* ssp. *viridula* was not affected by cultivation. The decreased between-population variability in some characters of this taxon in cultivation (Table 2) must therefore have been compensated by an increase in the within-population variability. Most characters which show such a shift are related to the life history (leaf width, stem height and width). Therefore between-population differences in life history of *C. viridula* ssp. *viridula* at the field sites are not genetic but are due to different plastic responses in different environments. The ecologically presumably less important characters of the inflorescences (utricle length and width, beak length, beak bristles) are more constant and differences between populations heritable. These differences may be the result of genetic drift in small, ephemeral populations of the *r*-selected *C. viridula* ssp. *viridula* rather than of local adaptations (Schmid 1980).

Considering all five taxa of this study, the second part of the hypothesis posed in the Introduction can now be tested. Within the *Carex flava* group the variability between populations increases with increasing *r*-selection and decreasing effective population sizes from *C. flava* var. *flava* > *C. flava* var. *alpina, C. viridula* ssp. *brachyrrhyncha, C. viridula* ssp. *oedocarpa* > *C. viridula* ssp. *viridula.* For the more *r*-selected taxa with smaller effective population sizes the genetic component of the between-population variability is large in characters with no obvious ecological importance, low however in characters which can be assigned high ecological importance. Here, within a group of closely related taxa, *r-selection* is indeed correlated with increased plasticity.

Conclusion

In the introduction I have argued that colonizing (*r*-selected) species with wide niches are probably more often monomorphic with generalists than polymorphic with specialists, since it will be difficult to maintain high genetic variability within the typically small populations of such species. A similar proposal was made by Glasser (1982), whose model predicts high within-phenotype variability for populations living in variable environments.

Results obtained with the *Carex flava* group, which consists of a series of increaingly *r*-selected taxa, support these hypotheses. The most *r*-selected taxon, *C. viridula* ssp. *viridula,* has the largest fundamental niche and shows, within populations, the highest plasticity in characters of obvious ecological significance. Genetic variation within populations increases with increasing population size and decreasing *r*-selection. Other plant species, such as *Cannabis sativa* (Small et al. 1976), *Bellis perennis* (Warwick and Briggs 1980), *Athyrium filix-femina* (Schneller and Schmid 1982), have particularly high overall within-population variability and build very large populations.

Another hypothesis regarding the success of colonizing species can be made if the problem is viewed only as one of optimization (i.e. what 'strategy' should be employed by an ideal organism in a 'colonizing' habitat). Clearly, in theory, genetic variation within a population should facilitate establishment into new habitats. Martins and Jain (1979) founded new colonies of *Trifolium hirtum* from seed populations of known genetic variability and observed that highly polymorphic populations were more successful colonizers than less polymorphic populations. But in real situations high rates of genetic drift and natural selection in the small populations of *r*-selected species may be constraints too strong for genetic variation to be maintained within populations. Indeed, Martins and Jain (1979) report that in nature polymorphism is lower the smaller the colony size.

A promising approach to the question of whether species capable of occupying wide niches are monomorphic with generalists or polymorphic with specialists lies in the use of reciprocal transplant experiments. Antonovics and Primack (1982) showed in such a study with seedlings of *Plantago lanceolata* that individual genets of this species have an all-purpose genotype and are very flexible phenotypically.

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