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Colonizing plants with persistent seeds and persistent seedlings (*Carex flava* group)

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Abstract

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Seeds or seedlings of the *Carex flava* group persist if environmental conditions are unfavourable for germination or growth. Buried seeds can remain viable in the soil for at least 6 years. Persistent seedlings are one to several years old yet only slightly larger than freshly germinated ones. Several (but not all) seedlings respond to the removal of close neighbours in the field or after transplanting to spaced garden trials with rapid growth. This response is faster in *C. viridula* than in *C. flava.* The importance of seed dormancy and persistent seedlings for the colonizing success of these sedges, particularly *C. viridula,* in open, disturbed habitats is discussed.

Introduction

The question of how an organism survives in a variable environment has stimulated the development of life history theory during the past few decades (cf. review in Stearns 1976). Environmental variability can be spatial or temporal. Many plants escape unfavourable conditions by surviving in a dormant state from which they can transform into growing stages of the life cycle when the environment improves. In higher plants the resting stages are usually seeds or buds, but seedlings may assume the same function in certain cases (Grime 1979).

Sedges of the *Carex flava* L. group grow in more or less open, wet habitats. Within the group *C. flava* is a better competitor (least 'r-selected') but tolerates less environmental variability than *C. viridula* Michaux (most 'r-selected'; Schmid 1984 a). Descriptive studies of field populations in Switzerland showed that both species have long-lived seeds and long-lived seedlings (Schmid 1984 b). The present study is an experimental investigation of the possible importance of these life history traits for population recruitment in variable habitats. In the first experiment I test how long seeds of the two species can survive under different conditions (including the simulation of natural conditions). In the second experiment I test if seedlings can respond to decreased competition within a single growing season.

Materials and methods

Study site

The nature reserve 'Neuweiher' near Kreuzlingen, Switzerland (47°38'N, 9°12'E; altitude 500 m) was once an artificial pond, but has remained empty since the early 1940s. It is now a heterogeneous mosaic of wetland and old-field communities. The two species *C. flava* and *C. viridula* are distributed in patches over the whole site (Schmid 1976, 1980). Estimates of tiller and seedling densities and of seed output in such patches are given in Table 1.

Seed longevity

Ripe seeds of both species were collected at Neuweiher on 10 September 1978 and stored under different conditions: (a) air dried, at room temperature (20 °C); (b) air dried, in a refrigerator (7 °C); and (c) buried in soil (40 cm deep) in outdoor plots at the Botanic Garden of the University of Zurich. The first two treatments were designed to test the potential longevity of seeds under artificial conditions whereas the third was used to mimic natural conditions. To prevent predation or loss, buried seeds were packed in fine Nybolt mesh (20 μm) and placed in inverted clay pots filled with soil.

Germination experiments were carried out during April and May 1984. In each germination test five random samples of fifty seeds were placed on wet filter paper in 9-cm diameter petri dishes and put in a growth cabinet (14-hour day, alternating temperature; see Schmid 1984 b for details). Percentage germination was recorded at 3- to 4-day intervals. Differences in mean percentage germination (arc-sin-transformed) between treatment (b) and (c) and the two species were tested with two-factor analyses of variance (no seeds germinated under treatment (a)).

Seedling Persistence, release from competition

Four sampling areas (two for each species), each of about 6 m², were selected within the Neuweiher site at the beginning of June 1984 for observation of seedling growth. Old, 'persistent' seedlings could be distinguished from young, 'freshly germinated' ones by the presence of brown leaves at their base. Since germination requires mean day-temperatures of about 15 °C (Schmid 1984 b) the maximum age of young seedlings at the beginning of June could be determined as less than one month. Old seedlings had germinated in the previous summer or earlier. Populations of ca. 3-month old seedlings of the *C. flava* group at Neuweiher, observed over a more than 2-year long census, show very slow depletion (50% dead after 16 months, i.e. at the age of ca. 19 months) yet no increases in the mean height and number of leaves of survivors (Schmid 1984 b).

To test for size differences at the beginning of the experiments random samples of twenty young and twenty old seedlings and twenty vegetatively produced tillers of an early developmental stage were harvested for each species from the sampling areas. The following characters were measured: (i) height, (ii) number of green leaves, (iii) maximum leaf width, (iv) dry weight of living above-ground material.

Tab. 1. Population characteristics of the *Carex flava* group at Neuweiher (Kreuzlingen, Switzerland). Values are means ± 1 standard error of mean; data from Schmid (1980)

	C. flava	*C. viridula*
Maximum tiller density (including seedlings; m^{-2})	1094 ± 149	2046 ± 294
% flowering or fruiting	22.8 ± 3.8	26.6 ± 3.6
% seedlings	15.4 ± 4.8	61.3 ± 15.0
Estimated seed rain (m^{-2} $year^{-1}$)	c. 30 000	c. 80 000

Young and old seedlings of *C. flava* and *C. viridula* from the four sampling areas were subject to five treatments simulating different degrees of release from competition:

(a) Control. Seedlings were marked in the field with split plastic rings around their base (n = 40).

(b) Above-ground competition reduced. Seedlings were marked in the field and the above-ground parts of neighbours (mostly different species) surrounding each seedling removed within a 10-cm diameter circle (subsequently repeated if necessary) (n = 20).

(c) Above- and below-ground competition reduced. Seedlings were transplanted into 10-cm diameter plastic pots with drainage holes filled with field soil and dug in level with the soil surface at the sampling areas in the field (n = 40).

(d) No competition. Seedlings transplanted in the same way as in (c) were dug in with a core of field soil (no pot) in an experimental bed at the Botanic Garden of the University of Zurich (n = 40).

(e) Simulated competition. Ten seedlings and young tillers from each sampling area were planted in pairs with the seedling in the centre and the tiller at the periphery of the core (distance between the two 5 cm) and cultivated in the same way as in (d) (n = 40). (Plants of treatments (d) and (e) were grown in a single plot using a completely randomized design.)

Seedling growth was recorded by measuring (i) height, counting (ii) the number of green and (iii) brown leaves, and (iv) the number of shoots of survivors at the beginning, middle and end of June, middle of July, and end of August 1984. For this final observation all plants were harvested and in addition to (i) – (iv), their (v) maximum leaf width and (vi) dry weight was determined. Effects of treatments, seedling age, species, replicate (sampling area), and interactions were estimated using univariate and multivariate analyses of variance. (Since all single characters measured at the final harvest are related to plant size, the multivariate analysis of variance is a combined test for differences in mean 'overall size' between groups.)

Results

Seed longevity

No seeds that had been stored dry at room temperature for 6 years germinated. However, some seeds subjected to low temperature (7 °C), and buried in soil, did germinate (Fig. 1). Germination was significantly lower among seeds stored in soil than among seeds stored at low temperature ($P < 0.001$) and was lower for *C. viridula* than for *C. flava* ($P < 0.01$). Microbial activity destroyed the utricles in the soil but left seeds intact.

Tab. 2. Size characteristics of young, freshly germinated and old, persistent seedlings and of young tillers produced vegetatively of the *Carex flava* group from Neuweiher (Kreuzlingen, Switzerland). Values are means of 20 individuals.

	C. flava			*C. viridula*		
	Height (cm)	Leaf width (mm)	Dry wt (mg)	Height (cm)	Leaf width (mm)	Dry wt (mg)
Freshly germinated seedlings	2.3	0.52	0.6	2.5	0.41	0.5
Persistent seedlings	2.8	0.59	1.8	3.0	0.53	2.0
Young tillers	7.6	2.35	32.5	7.5	1.82	24.0

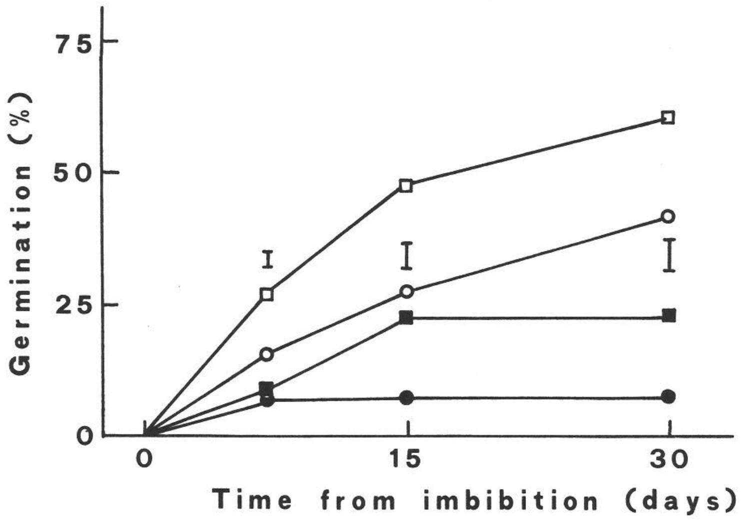

Fig. 1. Germination, with time, of 6-year old seeds of *C. flava* (squares) and *C. viridula* (circles) in petri dishes in a controlled growth chamber (light period: 14 h, 24 °C; dark period: 10 h, 15 °C). Open symbols are for seeds that had been stored in a refrigerator (7 °C), solid symbols are for seeds that had been buried in soil in an experimental garden (seeds stored at room temperature did not germinate and results from this treatment are not shown); bars indicate standard errors of differences between means, n = 5.

Sizes of naturally-occurring seedlings and tillers

The sizes of young and old seedlings, and of tillers of an early developmental stage at the beginning of the seedling-growth experiments are given in Table 2. Tillers had more and much larger leaves and were about ten to fifty times heavier than seedlings ($P < 0.001$ for all comparisons). Size differences between persistent and freshly germinated seedlings were small but still significant: persistent seedlings had larger mean values for height ($P < 0.05$), maximum width of leaves ($P < 0.01$), number of green leaves ($P < 0.001$), dry weight ($P < 0.001$, log-transformed) than freshly germinated ones. With the exception of leaf width ($P < 0.01$) differences between species were not significant ($P > 0.1$). Leaf width is an important taxonomic character for distinguishing adult plants of *C. flava* (wide leaves) from *C. viridula* (narrow leaves) (Schmid 1983).

Seedling development in competition experiments

Survival. – Survival of seedlings of *C. viridula* was high (96.6%) in all treatments during the course of the experiment (beginning of June until end of August 1984). In *C. flava* only 71.1% of all seedlings survived and most of the deaths in this species occurred among freshly germinated seedlings: the probability of a seedling dying during the first 3 months after emergence was about five times higher than that of a persistent seedling during this time ($P < 0.001$, χ^2-test).

Growth. – All seedlings grew very slowly during the first 7 weeks of the experiment and treatment effects were not significant ($P > 0.1$). After this time differences in growth rates became apparent and at the end of the experiment some seedlings had transformed into young plants with large leaves and started to produce tillers whereas

Tab. 3. Tables of means (a) and of multivariate (MANOVA) and univariate (ANOVA) analyses of variance (b) for size characteristics of plants of the *Carex flava* group from Neuweiher (Kreuzlingen, Switzerland). Freshly germinated ("Young") and persistent ("Old") seedlings of *C. flava* and *C. viridula* were grown under different competition treatments (see text). Means in (a) are only listed where at least two seedlings survived. Effects of replicates and most interaction terms are omitted from table (b); F-values are listed together with significance levels (***, P<0.001; **, P<0.01; *, P<0.05; ns, not significant).

(a) Means

	C. flava					*C. viridula*				
Treatment:	(a)	(b)	(c)	(d)	(e)	(a)	(b)	(c)	(d)	(e)
Height (cm):										
Young	–	–	4.1	2.3	3.0	2.1	–	5.2	3.3	6.2
Old	3.4	3.4	3.3	7.1	5.7	4.2	3.6	6.0	4.9	2.9
Leaf width (mm):										
Young	–	–	1.30	0.86	0.91	0.52	–	1.22	1.21	2.14
Old	0.74	1.10	0.93	2.44	2.07	0.74	0.97	1.44	1.83	0.84
Dry weight (mg)										
Young	–	–	8.2	2.2	2.1	1.6	–	11.3	5.6	25.3
Old	3.6	5.0	3.1	47.9	23.5	5.1	6.6	11.6	34.6	4.1

(b) Analyses of variance

Effect	MANOVA	ANOVA for				
		Height	No. of green lvs	No. of brown lvs	Leaf width	Dry weight (log)
Treatment	4.49***	2.59*	2.52*	6.48***	4.93**	6.24***
Age	7.44***	6.26*	2.92 ns	11.00**	3.73 ns	18.86***
Treat. × age	2.33**	2.60*	1.87 ns	1.03 ns	2.67*	5.64***
Species	5.89***	1.27 ns	0.22 ns	4.39*	0.15 ns	8.19**

others had still the size and thread-like leaves of seedlings. Results from the final harvest (12 weeks after the start of experiments) are shown in Table 3.

The largest differences in mean overall size were found among treatments (Fig. 2). In the control (a) all seedlings except one remained very small and had more dead (brown) leaves than plants of the other treatments. Removal of above-ground parts of close (≦ 5 cm) neighbours (b) stimulated growth, and if below-ground parts of neighbours were absent as well (c) growth was further increased. The largest plants were found in the experimental garden, regardless of whether they were planted singly (d) or in combination with tillers at a distance of about 5 cm (e). The mean biomass of plants in these two treatments was almost three times higher than in the control.

Although persistent seedlings at harvest were on average still larger than freshly germinated ones freshly germinated seedlings were larger in two of the five treatments (c, e; significant interaction term for treatment × age). Differences between the two species, although highly significant in the overall test (multivariate analysis of variance), were small and the reverse of those predicted from adult plant size: at

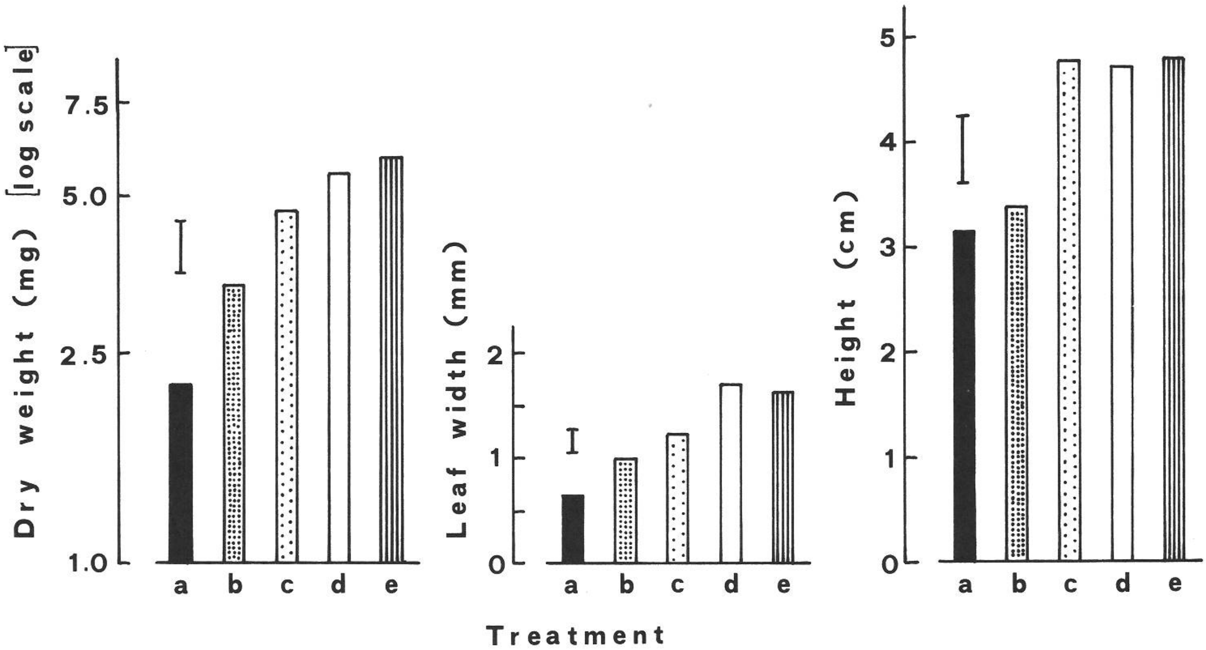

Fig. 2. Effects of 12 weeks of decreased competition on the growth of seedlings of the *C. flava* group (both species). Treatments (see text): a, control (n = 28 survivors); b, removal of above-ground parts of close neighbours (n = 18); c, removal of above- and below-ground parts of close neighbours (n = 33); d, no neighbours (experimental garden, n = 35); e, one young tiller as neighbour (experimental garden, n = 31). Bars indicate standard errors of differences between means.

harvest seedlings of the shortest taxon of the group, *C. virdula,* had accumulated more biomass than seedlings of the tallest taxon of the group, *C. flava.*

Discussion

Taxa of the *C. flava* group, particularly *C. virdula,* have a scattered distribution with many small and isolated populations (Davies 1956, Schmid 1980, 1981). They are pioneers in open, wet habitats but are quickly eliminated (Schmid 1980). In Switzerland *C. viridula* can be found at most newly disturbed sites as predicted (B. and H. Schmid, personal observation). Such colonizing success may be achieved by long-distance dispersal, by having life cycle stages which remain dormant for prolonged periods by the production of large numbers of propagules, or by some combination of these.

Davies (1956) suggested that seeds of *C. viridula* may remain viable in the soil for at least 20 years. This is in contrast with my observation that the percentage germination of both *C. flava* and *C. viridula* drops from about fifty to zero between year four and six for dry seeds stored at room temperature (Schmid 1980 and this study). However, seeds stored in the cold or buried in soil retain their ability to germinate for longer. It is conceivable that seeds are better preserved under low oxygen conditions in the wet, compacted soil typical of field sites of the *C. flava* group.

Slow-growing, persistent seedlings are known for several tropical and temperate tree species (see e.g. Grime 1979, Bazzaz & Pickett 1980, Bazzaz 1984) and some graminoids (Chippindale 1948, Gartner, Chapin & Shaver 1983). Detailed demographic observations indicate that the build-up of a large bank of persistent seedlings in populations of the *C. flava* group at Neuweiher is due to a combination of very slow growth and high survival probability of seedlings (Schmid 1984b; see Table 1). The present study confirms that very few naturally occurring seedlings develop into larger plants, even during the time from June to August when growth conditions are most favourable.

The removal and cultivation experiments show that competition of close neighbours, both above and below ground, maintains this seedling persistence: if the nearest neighbours grow at a distance of 5 cm or more the chances of a seedling to develop into a bigger plant are significantly increased (see Fig. 2). Some seedlings, however, remain small in all treatments suggesting that competition is not the only explanation of slow seedling growth in these sedges.

Both seed dormancy and seedling persistence as means of temporal dispersal increase the colonizing ability of species of the *C. flava* group and could therefore be interpreted as traits associated with r-selection. Furthermore, *C. viridula* should have an advantage over *C. flava* in temporally variable environments since it can recruit plants from the bank of persistent seedlings faster than *C. flava* (see p. 6). This is consistent with the ecological relations observed for the two species at Neuweiher (Schmid 1980). The described patterns of seed dormancy and seedling persistence in the *C. flava* group allow for an efficient and flexible demographic response to habitat disturbances. The contribution of seedlings to population growth may be important after minor disturbance events which remove competitors only and create small gaps. If disturbance events are more severe, killing seedlings of the *C. flava* group and competitors alike, the contribution of seeds to population growth may be most important. Such differences in the relative contributions of persistent seeds or seedlings in response to increasing severity of disturbance seem to be typical among tropical forest trees (Bazzaz 1984). However, whilst both modes of regenerative strategies can be employed by a single individual of the *C. flava* group, a single tree species usually has only one of the two (Bazzaz & Pickett 1980).

Zusammenfassung

Samen und Keimlinge der *Carex flava*-Gruppe können unter ungünstigen Umweltbedingungen mehrere Jahre überleben. Im Boden bleiben Samen während mindestens sechs Jahren keimfähig. Persistierende Keimlinge sind ein bis mehrere Jahre alt, unterscheiden sich aber in ihrer Größe kaum von frisch gekeimten Pflänzchen. Manche (nicht alle) Keimlinge zeigen stark gesteigerte Wachstumsraten, wenn am natürlichen Standort alle Nachbarpflanzen im Umkreis von 5 cm entfernt werden, oder nach Verpflanzung in einen Garten. *C. viridula* reagiert darauf schneller als *C. flava.* Die Fähigkeit, die Individualentwicklung auf zwei verschiedenen Stadien des Lebenszyklus unterbrechen zu können, ermöglicht es diesen Seggen, im Besonderen *C. viridula,* offene Habitate mit häufig wiederkehrenden ungünstigen Umwelteinflüssen erfolgreich zu besiedeln.

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References

Bazzaz F. A. 1984. Dynamics of wet tropical forests and their species strategies, 233–243. In: E. Medina, H. A. Mooney and C. Vásquez-Yánes [eds.], Physiological ecology of plants of the wet tropics, Dr. W. Junk, Publ. The Hague.
– and S. T. A. Pickett 1980. Physiological ecology of tropical succession: a comparative review. Ann. Rev. Ecol. Syst. 11: 287–310.
Chippindale H. G. 1948. Resistance to inanition in grass seedlings. Nature (London) 16: 65.
Davies E. W. 1956. The ecology and distribution of *Carex flava* and its allies in the British Isles. Bot. Not. 109: 50–74.
Gartner B. L., F. S. Chapin and G. R. Shaver 1983. Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. J. Ecol. 20: 965–980.
Grime J. P. 1979. Competition and the struggle for existence, 123–139. In: R. M. Anderson, B. D. Turner, and L. R. Taylor [eds.], Population dynamics, Blackwell, Oxford.
Schmid B. 1976. Floristische Untersuchungen im „Neuweiher“ bei Kreuzlingen. Mitt. Thurg. Nat. Ges. 41: 23–48.
– 1980. *Carex flava* L. s.l. im Lichte der r-Selektion. Ph.D. thesis, University of Zurich, Zurich, 360 pp.
– 1981. Die Verbreitung der Artengruppe *Carex flava* L. s.l. in der Schweiz. Bot. Helv. 91: 3–8.
– 1983. Notes on the nomenclature and taxonomy of the *Carex flava* group in Europe. Watsonia 14: 309–319.
– 1984a. Niche width and variation within and between populations in colonizing species (*Carex flava* group). Oecologia (Berlin) 63: 1–5.
– 1984b. Life histories in clonal plants of the *Carex flava* group, J. Ecol. 72: 93–114.
Stearns S. C. 1976. Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3–47.