

## SEED DORMANCY CYCLES AND GERMINATION PHENOLOGIES IN SEDGES (*CAREX*) FROM VARIOUS HABITATS

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**Abstract:** Seeds (nutlets) of four temperate-zone perennial *Carex* species from various habitats and with different growth forms were investigated to identify seasonal germination patterns. In the first experiment, freshly matured seeds were sown in summer 1994 on the soil surface and at a depth of 1 cm at a sun-exposed site and under a leaf canopy in an experimental garden. In the second experiment, seeds were exhumed after various periods of burial (7-cm depth) for up to 30 months and tested for germination in both light and darkness at 15°, 25°, and 22/10°C. In the first experiment, freshly-matured seeds of the four sedges did not germinate during summer or autumn 1994. Almost all surface-sown seeds of the four species germinated from late spring to summer in 1995 at the sun-exposed site. Most buried seeds of three species germinated in the soil, but germinants died prior to emergence. In *Carex flacca*, however, about 50% of the buried seeds germinated and emerged until 1997, and the ungerminated seeds remained viable. At the shaded site, seeds of *C. acutiformis* and *C. flacca* did not germinate, whereas a small percentage of the buried and surface-sown seeds of *C. arenaria* and *C. extensa* emerged in the second year. Seeds of *C. acutiformis* and *C. flacca* were dormant, and those of *C. arenaria* and *C. extensa* were conditionally dormant at the beginning of the second experiment. All four species had annual dormancy cycles at 22/10°C in light and in darkness and at 25° and 15° in light. Seeds came out of dormancy in late autumn or winter and re-entered dormancy or conditional dormancy in late spring or early summer. Very few seeds of any of the four species germinated at constant temperatures in darkness. No seeds germinated during burial in soil at a depth of 7 cm. These field germination patterns indicate that the four sedges have the potential to form a persistent seed bank but that losses due to germination in the seed bank are dependent on temperature amplitudes, mean temperatures, and red:far red ratios under a leaf canopy.

**Key Words:** *Carex*, dormancy, germination, dormancy cycles, seedling emergence

### INTRODUCTION

Seedling emergence shows a marked seasonality in many species of temperate regions (Kinzel 1915, Roberts 1986, Baskin and Baskin 1988, Masuda and Washitani 1990, Vleeshouwers 1997). This is a consequence both of species-specific germination traits and of environmental signals, of which temperature is the most important (Baskin and Baskin 1988). Germination characteristics important for the control of seasonal emergence may include primary dormancy, a subsequent requirement for a period of high and/or low temperatures to break dormancy, changing sensitivities to light (Pons 1992), and sometimes a requirement for fluctuating temperatures (Thompson and Grime 1983, Schütz 1998).

In temperate regions, spring and early summer are regarded as the most appropriate seasons for seedling emergence of most species (Probert 1992). Germina-

tion in summer, however, has several disadvantages for seedling survival (e.g., a higher risk of drought periods, shading by leaf canopies and a reduced length of the growing period (Baskin and Baskin 1985a, Guterman 1993, Schütz 1997b)). Thus, the majority of species in temperate regions are adapted to avoid summer conditions for germination (Roberts 1986, Baskin and Baskin 1988, Olf et al. 1994).

The avoidance of germination in summer can be mediated by the induction of a conditional or absolute secondary dormancy by high (Washitani and Masuda 1990) or by gradually increasing temperatures (Baskin and Baskin 1980, Bouwmeester and Karssen 1993). This secondary dormancy is removed during winter by cold stratification (Roberts 1986, Baskin and Baskin 1988). Annual dormancy/non-dormancy cycles are the result, provided that seeds persist for a year or longer in the soil (Baskin and Baskin 1985a).

Since the late 1960s, dormancy cycles have been demonstrated in numerous annual weeds (summary in Baskin and Baskin 1985a, Bouwmeester and Karssen 1993, Milberg and Anderson 1997, Vleeshouwers 1997), in some annuals and perennials of wetlands (Baskin et al. 1989, 1993a 1993b, 1994, 1996a, 1996b, Schütz 1997b), grasslands (Pons 1991b, Milberg 1994a,b) and ruderal habitats (e.g., Baskin and Baskin 1981, VanAssche and Vanlerberghe 1989, Meyer and Kitchen 1992). By contrast, buried seeds of a few species do not undergo dormancy/non-dormancy cycles and thus remain non-dormant after losing their initial dormancy. Among them are the perennials *Rumex crispus* L. (Baskin and Baskin 1985b), *Potentilla recta* L. (Baskin and Baskin 1990), *Cyperus odoratus* L., *Penthorum sedoides* L. (Baskin et al. 1989), and a small number of annual species (e.g., Baskin et al. 1987, 1993a). Among these, there is only one winter annual, the aquatic species *Hottonia inflata* Elliott (Baskin and Baskin 1996b).

In a study on the germination ecology of sedges, seasonal changes in dormancy were investigated in six perennial wetland sedges with an obligate cespitose growth form (Schütz 1997b). Cespitose sedges are not clonal and thus are dependent on dispersal by seed and effective germination-timing mechanisms, including dormancy cycles, for the long-term maintenance of their populations (Schütz 1997b). However, it is not known if annual dormancy cycles also occur in sedges that spread primarily by clonal growth. To answer this question, a burial experiment was conducted on one cespitose and three clonal species. Simultaneously, freshly-matured seeds of the four sedges were sown on the soil surface and at a soil depth of 1cm in a garden experiment at an open, unvegetated site and under a leaf canopy.

The present study was conducted to determine (1) whether buried seeds show annual dormancy cycles or remain nondormant after they have lost their initial dormancy, (2) if seasonal dormancy patterns found in these germination experiments coincide with the season of seedling emergence under field conditions, and (3) if dormancy-breaking and seed-germination requirements differ under shaded and open site conditions.

## METHODS

### Study Species

The four species are polycarpic perennials with an apparently long life-span and occur in cool-temperate regions of Europe. *Carex extensa* Good. is a small, tufted sedge restricted to coastal areas near saltwater; it occurs on both sandy and muddy estuarine or littoral

flats. *Carex acutiformis* Ehrh. is the largest of the three clonal sedges, and it often forms extensive stands by rivers, ditches, and ponds. However, it also occurs in fens, wet meadows, and wet carrs. In contrast to the three other sedges, production of viable seed in *C. acutiformis* is low, probably due to genetic constraints favoring clonal reproduction. *Carex flacca* Schreber has loosely-tufted shoots and widely-creeping rhizomes and is a common species in limestone and chalk grasslands, where it occurs in locally-wet sites. *Carex arenaria* L. has widely-creeping rhizomes, and it usually produces single shoots. This species is primarily a coastal plant that is often dominant on fixed sand dunes (Jermy and Tutin 1968, Hegi 1980).

### Seed Collection and Storage

Freshly matured fruits, consisting of a nutlet and a perigynium (hereafter called seeds), were collected in the vicinity of Kiel, northern Germany (N54°, E10°) during summer 1994: seeds of *Carex acutiformis* in a riverine wetland (14 July); *C. flacca* in an extensively-used grassland (15 July); *C. extensa* in a littoral flat at the Baltic Sea (20 August); *C. arenaria* in an adjacent dune system (20 August). After five days of drying in the laboratory (20–22°C), seeds were separated from other plant parts and either used in a garden experiment (see below) or stored in paper bags at ambient laboratory temperatures (18–22°C and 40–60% RH) until October 1994. No loss of viability in the four species had occurred during dry storage after a period of 7 to 8 months under these conditions (unpublished data). It may be concluded from studies of Grime et al. (1981) and Schütz (1997b) on dormancy loss in sedges, however, that germinability has increased during dry storage.

### Garden Experiment

Freshly matured seeds of the four sedges were sown in an experimental garden at a sun-exposed site and in an adjacent small woodlot to simulate open habitat conditions and those occurring under a vegetation canopy, respectively. Dates of sowing were 20 July 1994 for *Carex flacca* and *C. acutiformis* and 25 August 1994 for *C. extensa* and *C. arenaria*. None of the investigated species occurred in the vicinity of the experimental garden. Three replicates of 100 seeds for each of the four species were sown in 8-cm plastic pots (50:50 mixture of peat and sand) on the soil surface and at a soil depth of 1cm. The pots were placed randomly in trays in which the water level was kept at 2–3 cm. The trays were covered with fine mesh nylon netting to prevent predation by animals and placed within a wooden frame equipped with a plex-

iglass roof to protect the pots from uncontrolled flooding or damage by rain or hail. Seedlings were counted and removed once or twice a week until germination had ceased in autumn 1996. Regular counting was terminated in autumn 1996, but emerged seedlings also were counted in June 1997. In August 1997, the pots were transferred to the laboratory, and the soil layer above the buried seeds was removed. The pots were transferred to a refrigerator, kept in darkness at 4°C for two weeks, and were then incubated for three weeks at 22/10°C in light. Most of the remaining viable seeds had germinated at the end of this treatment due to a loss of conditional dormancy by cold stratification (Murdoch and Ellis 1992).

Then, the remaining seeds were extracted from the pots under a binocular microscope and scored as viable, germinated in the soil, or dead. Dead seeds were identified by their softness and brownish color. Seeds that germinated in the soil could be distinguished from dead ones by a characteristic opening in the empty seed coat. Seeds were recorded as viable when the contents were firm and white.

Final germination percentages achieved until the cessation of the experiment in August 1997 (not counting two weeks and three weeks incubation in the laboratory) were arcsin-transformed and compared within species using a t-test at the 5% level of significance. Comparisons were made between surface-sown seeds at the sun-exposed and shaded site, and between surface-sown and buried seeds at the shaded site. No comparisons were made in *C. acutiformis* and *C. flacca*, because there was substantial germination of these species only in one treatment.

Temperature on the soil surface and at 1-cm depth in the pots was monitored every half hour during the study period with a temperature sensor (Pt 100) connected to a data-logger (Squirrel 1200, Grant Instruments, Cambridge, Great Britain).

### Burial Experiment

At the beginning of October, 24 batches of 300 seeds of each of the four species were placed separately into fine mesh nylon bags and buried in a 50:50 mixture of sand and peat at a depth of 7 cm in 12-cm-diameter pots with a drainage hole in the bottom. Each pot contained two bags of each species. Pots were sunk into the ground under the canopy of deciduous shrubs and trees in an experimental garden. During prolonged periods with or without little rainfall, the pots were watered weekly to field capacity. Additional watering was started when there was no rainfall for at least one week. No watering was done when the soil was frozen.

Retrieval of buried seeds began in January 1995 and

ended in April 1997. At intervals of two or three months, one pot was transferred to the laboratory. Bags were exhumed in dim green light, and seeds were distributed in 9-cm-diameter Petri dishes on filter paper moistened with distilled water. Germination tests were conducted in both light and darkness at constant temperatures of 15 and 25°C and at an alternating temperature regime of 22/10°. At 22/10°C, the maximum temperature period was kept constant for 8 h each day and the minimum temperature for 12 h. Heating and cooling periods lasted 2 h each, resulting in a mean temperature of 15°C. Incubators (Rubarth Apparatebau, Hannover, Germany) equipped with warm white fluorescent lights (Philips TL 20 W/29 RS) provided approximately 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at seed level for 12 h per day. Seeds to be incubated in darkness were wrapped in a double layer of aluminium foil under dim green light (Philips TLD 18 W/17) covered with "medium blue" and "yellow" filters (LEE Filters, Andover, UK). Two replicates of approximately 50 seeds were used for each treatment. Germination tests also were conducted on laboratory-stored seeds of each species at the beginning of October, a few days before the onset of burial.

Germinated seeds were counted twice a week in light treatments and weekly in dark treatments using dim green light. Seeds were scored as germinated if the radicle and at least 1 mm of the green coleoptile, which appeared a few hours after the onset of radicle growth, were visible. In the calculation of germination percentage, dead seeds, identified by their softness and brownish color, were excluded. The experiments were terminated after germination had ceased for at least one week. Length of germination tests ranged from four to seven weeks, but few seeds germinated after four weeks. To test for germinability, seeds that had failed to germinate in darkness at 15°C and 22/10°C were exposed to light at 22/10°C. Of the remaining seeds, 80–100% consistently germinated after such a treatment. Ungerminated seeds were opened with forceps and considered to be viable if the content was white and firm. Temperature at 7-cm depth was monitored at the site of burial using the same equipment as for the garden experiment.

## RESULTS

### Garden Experiment

*Sun-Exposed Site.* Very few seeds of the four sedges germinated in 1994. Germination of seeds sown on the soil surface began in late April 1995 in *Carex extensa* and *C. flacca*, when daily mean temperatures were higher than 10°C. For *C. arenaria*, germination began in early May, when the mean temperature was between

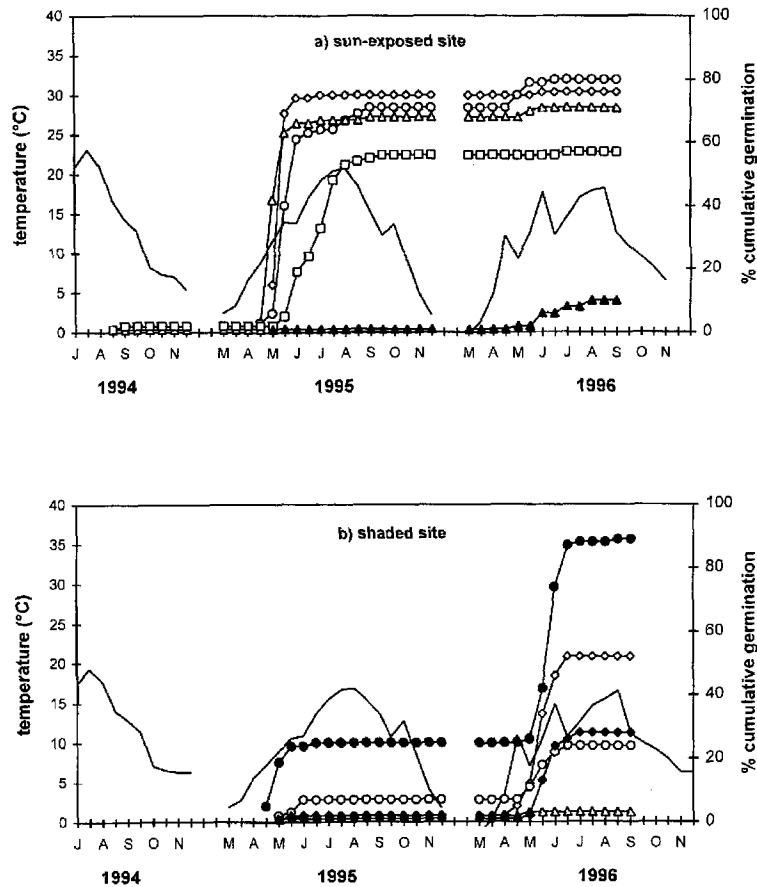


Figure 1. Biweekly mean temperatures (solid line without symbols) and cumulative percentage of emergence in seeds of four temperate *Carex* species at a sun-exposed site (A) and at a shaded site (B) over a period of 2.5 years. Seeds were sown on the soil surface and at 1-cm depth. Open symbols: emergence of seeds on the soil surface; solid symbols: emergence of seeds from 1 cm depth; ○—*C. extensa*, □—*C. acutiformis*, ◇—*C. arenaria*, Δ—*C. flacca*.

11° and 15°C, and for *C. acutiformis* at the end of May, when mean temperature was higher than 15°C. Average daily temperature amplitudes increased rapidly and steadily from early to late spring (e.g., in 1995 from 4.4° in February to 11.9°C in May (Figure 1a)). Daily differences between 1-cm soil depth and the soil surface in mean temperatures remained below 0.5°C, and those in amplitude of temperature fluctuations below 2°C. Hence, buried and sun-exposed seeds experienced almost the same temperature conditions.

The germination period lasted until mid-June in *C. flacca* and *C. arenaria*, but it peaked at the beginning of May for *C. flacca* and in mid-May for *C. arenaria*. Germination in *C. extensa* lasted almost until the end of June, and the peak of germination was in late May. Emergence of *C. acutiformis* seeds continued until the end of July, with the peak in mid-June. A small number of seeds of all species germinated in August and September. Most surface-sown seeds germinated in 1995, and only in *C. extensa* was there a second flush of seedlings, in spring 1996. Between 58% and 80% of the initially-sown seeds had emerged by August

1996 (Figure 1a). Very few seedlings emerged from buried seeds of three species. Only in *C. flacca* did as many as about 10% of the seedlings emerge in 1996, after a period of high temperatures at the end of May; another 41% of the seedlings emerged in 1997. Monthly mean temperature 1995–1997 amplitudes on the soil surface ranged between 11.0° and 14.1°C from April to October.

About 60% of the exhumed seeds of *C. acutiformis* and of *C. arenaria* and 100% of those of *C. extensa* were empty; apparently they had died during or shortly after germinating. Forty-two percent of the seeds of *C. acutiformis* and 35% of those of *C. arenaria* were dead, although they had not germinated. Only a few viable seeds were found in *C. flacca* and *C. arenaria*.

**Shaded Site.** No seeds of the four sedges germinated in 1994 at the shaded site, and very few seedlings of *C. flacca* and *C. acutiformis* emerged from the surface or from 1-cm depth during the 3-year period of the investigation. In 1995, 24% of the buried seeds of *C. extensa* and 7% of those on the surface emerged, most of them at the beginning of May (Figure 1b).

Table 1. Monthly mean temperature amplitudes (°C) at the soil surface and in 7-cm soil depth in two successive years in the experimental garden at the shaded site.

	1995				1996			
	March	April	May	June	March	April	May	June
Surface	3.9	5.8	4.3	3.2	2.5	7.7	4.9	4.5
7 cm	2.0	2.7	1.8	1.6	0.1	1.5	1.6	1.7

In 1996, germination began in both surface-sown and buried seeds of *C. extensa* and *C. arenaria* between the end of April and the beginning of May, and it continued until 20 June. Ninety percent of the buried seeds of *C. extensa* and 25% of those sown on the soil surface had emerged by the end of summer. However, in *C. arenaria*, 56% of the surface-sown seeds and 26% of the buried seeds had emerged by this date. There were significant differences in final germination percentages between buried and surface-sown seeds in *C. arenaria* (t-test, df = 4, p = 0.04) and in *C. extensa* (t-test, df = 4, p = 0.0001). There were also significant differences between germination percentages of surface-sown seeds of *C. arenaria* (t-test, df = 4, p = 0.05) and *C. extensa* (t-test, df = 4, p = 0.0004) at the shaded and the sun-exposed site.

Mean temperature at the beginning of the emergence period (16 April–4 May) was 8.0°C in 1995 and 10.3°C in 1996. In both years, temperature amplitude was greatest in April, but it decreased markedly in May due to the development of the leaf canopy (Table 1). During the growing period, monthly mean temperatures were 3.0–3.5°C lower under the leaf canopy than those at the sun-exposed site.

In 1995, the leaf canopy at the shaded site started to develop at the end of April, and it was fully developed around the 15th of May. Bud break occurred at the beginning of May in 1995 and in mid-May in 1996. Red:far red under the leaf canopy was 0.2–0.3 at the end of May. However, in 1996, the leaf canopy developed sparsely during the growing period due to severe damage of the shrub (*Sambucus nigra* L.) caused by a long drought and low winter and spring temperatures; thus, the red:far red ratio was 0.4–0.6 at the end of May. Between 90 and 100% of the ungerminated seeds of all species were viable at the final counting, regardless of their position in the soil.

#### Burial Experiment

Prior to burial, very few seeds germinated in darkness for any species except *C. arenaria*, where 25% of them germinated at 22/10°C. Germination in light was >50% in seeds of *C. arenaria* and *C. flacca* at 22/10° and for *C. arenaria* at 25°C.

After burial, the four sedges showed marked dormancy cycles at all temperatures, with high dormancy levels in summer and autumn and low levels from winter to early spring. Germination percentages were highest in all four species at 22/10°C in light, a temperature regime representing early summer conditions in northern Germany. Germination percentages were low or nil for all species in darkness at constant temperatures. In darkness and at constant temperatures in late spring, seeds of all four species came out of dormancy later and re-entered dormancy earlier than at 22/10°C in light (Figure 2).

*Carex arenaria* was the least dormant species, and it germinated to high percentages at 22/10°C in light regardless of season. Germination percentages of this species were also high at the constant temperatures in light and in darkness at 22/10°. However, germination percentages were cyclic in darkness at 22/10° (Figure 2a) and in light at 15° and 25°C (Figure 2b). Seeds of *C. extensa* germinated in darkness almost as well as they did in light, but germination at constant temperatures was low and restricted to spring. As in *C. arenaria*, a dormancy cycle was apparent in *C. extensa* at 22/10°C in 1995 but not in 1996 (Figure 2a).

From winter to early summer, 20 to 100 % of the *C. acutiformis* seeds germinated at 22/10° and at 25°C in light, and at 22/10°C in darkness (Figure 2a, 2b). Almost no seeds germinated in summer and autumn in this species. Germination percentages of *C. flacca* were between 80 and 100 % during winter and spring, and they showed a marked dormancy cycling at 22/10° in light. However, germination percentages never exceeded 25 % at the constant temperatures in light (Figure 2b) or at 22/10°C in darkness. Overall, germinability can be ranked in the following order: *C. arenaria* > *C. extensa* > *C. acutiformis* = *C. flacca*.

In 1995, mean temperatures at the 7 cm depth at the site of burial were rarely below 0°C. In 1996, however, below-zero temperatures lasted from the beginning of January to mid-April. Mean temperatures in summer rarely exceeded 17°C. Mean monthly temperature fluctuations were low, ranging from 0.1° to 2.9°C throughout the period of investigation (Table 1). No seeds germinated in the soil during burial.

## DISCUSSION

### Germination in Light

Very few freshly matured seeds germinated in summer and autumn 1994 in the garden experiment (Figure 1) despite the fact that constantly moist soil, high mean temperatures, and large diurnal temperature amplitudes provided optimal germination conditions (Schütz 1995, 1998). In *Carex acutiformis* and *C. flacca*

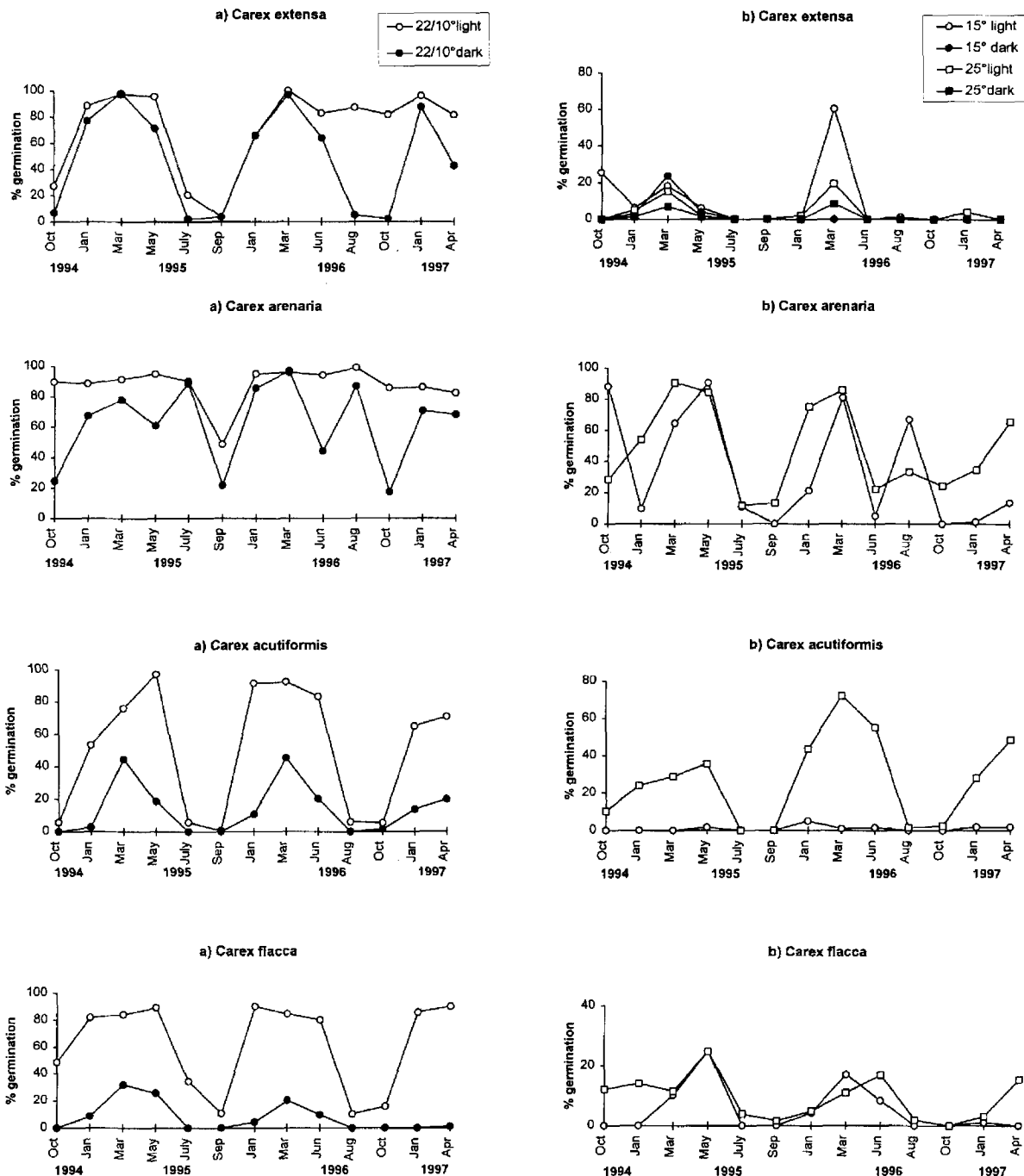


Figure 2. Final germination percentages in four *Carex* species incubated in light and darkness at a fluctuating temperature regime (a) and at two constant temperatures (b) following 0–30 months of burial in an experimental garden. Seeds of *C. acutiformis* and *C. flacca* tested in October had been stored dry in the laboratory for seven weeks and those of *C. arenaria* and *C. extensa* for 11 weeks.

*ca*, which were sown in mid-summer, lack of germination is clearly a sign of primary dormancy. When exposed to a range of constant and fluctuating temperatures, recently harvested seeds of these species germinated only at a high average temperature (22°C) combined with amplitudes > 12°C (Schütz 1998). Late shedding or late ripening of *C. arenaria* and *C. extensa*

seeds, which are less dormant at maturity than those of *C. acutiformis* and *C. flacca* (Schütz 1998), effectively prevents them from germinating, since temperatures at this time are below those required for germination. However, some germination occurred in batches of dry-stored seed of *C. acutiformis* and *C. flacca* in October, shortly before the burial experiment

was began. Breaking of primary dormancy during 1 month of dry storage at 20°C was observed in *C. acutiformis* and in *C. flacca* by Grime et al. (1981). Hence, a prolonged period of dry storage at room temperatures might have increased the germinable fraction of seeds of these species in the present study.

When exposed to seasonal changes in temperature, the four sedges showed clear seasonal dormancy patterns (Figure 2). In a number of studies, it has been shown that temperature changes are responsible for the relief of dormancy in winter and spring and for the induction of a secondary dormancy in summer and autumn in spring-germinating species (Baskin and Baskin 1980, 1985a, Bouwmeester and Karssen 1993). There is also strong evidence in the present study that temperature regulated germination in seeds of the four sedges in the garden experiment. Large diurnal temperature fluctuations (> 11°C) and high mean temperatures (10–20°C) experienced by the seeds at the sun-exposed site in late spring and early summer exceeded the temperature requirements for germination of non-dormant seeds of all species, and it triggered germination in almost all seeds in the second year. Seeds located on the soil surface showed a different germination behavior at the shaded than at the sun-exposed site. *Carex flacca* and *C. acutiformis* did not germinate at all, and germination in *C. extensa* and *C. arenaria* was delayed two years (Figure 1b). It is likely that mean temperatures (ca. 8°C) and temperature amplitudes (5.8°C in April) at the shaded site were too low to trigger germination before closure of the leaf canopy. A low red:far red ratio, which prevents germination in seeds of many temperate species (Pons 1992), inhibited germination in seeds of six wetland sedges placed under a dense leaf canopy (Schütz 1997b). However, considerable germination occurred in *C. extensa* and *C. arenaria* seeds in 1996, when the canopy developed weakly, and thus, the red:far red ratios were relatively high. Moreover, mean temperatures and temperature amplitudes at the beginning of the growing season in 1996 were about 2°C higher in 1996 than they were in 1995, and thus, a fraction of the *C. extensa* and *C. arenaria* seeds germinated. Requirements for relatively high minimum temperatures and slow germination (Schütz 1998) probably prevented most seeds of *C. acutiformis* and *C. flacca* from germinating at the shaded site (Figure 1b).

Seeds frequently retain the ability to germinate at alternating but not at constant temperatures due to the induction of dormancy by increasing or high ambient temperatures (Baskin et al. 1989, Van Assche and Vanlerberghe 1989, Schütz 1997b). This was most conspicuous in *C. arenaria* and *C. extensa*, which germinated to 85–100% at 22/10°C from March 1996 until the end of the burial experiment in April 1997 at 22/

10°, but not at constant temperatures in light (Figure 2). On the other hand germination in *C. acutiformis* and *C. flacca* seeds decreased from 80–100% in May 1995 and June 1996 to 0–30% in July 1995 and August 1996, respectively. In the garden experiment, secondary dormancy apparently was strong enough to prevent germination of seeds during summer at the shaded site, despite a relatively high red:far red ratio and high summer temperatures. Seeds of six cespitose wetland *Carex* species exposed to seasonal temperature changes showed little temporal difference in germination percentages at 22/10°C, but they were conditionally dormant at 15°C constant temperature (Schütz 1997b). The beneficial effect of temperature amplitudes on germination is obvious in many temperate species (Thompson and Grime 1983), but it is most pronounced in sedges. Germination in recently harvested seeds of 33 of 34 temperate *Carex* species tested was enhanced by fluctuating temperatures (Schütz 1998). Large diurnal temperature amplitudes, coupled with mean temperatures above 20°, may have enabled conditionally dormant seeds of *C. acutiformis* to germinate in July and August at the sun-exposed site.

#### Germination in Darkness

Germination in darkness occurred in non-dormant seeds of many sedges at high mean temperatures and/or at high amplitudes (Schütz 1995, 1997a, 1998, Baskin et al. 1996). In the burial experiment, germination of exhumed seeds at 22/10°C in darkness ranged from 25 to 100% in non-dormant seeds (Figure 2). However, no seeds germinated during the 30 months of burial at 7-cm depth, although seeds of two species emerged at the shaded site and seeds of all species germinated at the sun-exposed site at 1-cm depth (Figure 1). Since soil type and moisture conditions were the same for seeds buried at depths of 7 cm and at 1 cm, it is likely that different temperature regimes were responsible for differences in seed germination at these two depths.

VanAssche and Vanlerberghe (1989) concluded from field and laboratory experiments with *Rumex obtusifolius* L. that a season-sensing mechanism enables seeds buried in the soil to respond to short-term temperature shifts. In the present study, a rapid increase in temperature amplitudes at the beginning of the growing period occurred both at the shaded and sun-exposed site at a depth of 1 cm, but not at 7 cm (Table 1).

The timing of germination in buried seeds varied not only between sites and species but also between years. Germination of buried seeds began in *C. extensa* in spring 1995, but it peaked in spring 1996, when mean temperatures and temperature amplitudes at the

end of April were greater than in 1995. *Carex extensa* is one of the few sedges in which non-dormant (cold-wet stratified) seeds germinate in darkness almost as well as in light, even at constant temperatures (Schütz, unpublished data). Temperatures in spring 1996 were more favorable for germination of *C. arenaria* than those in spring 1995, and thus, about 30 % of the buried seeds of this species germinated (Figure 1b). However, 1996 temperatures were unfavorable for germination of buried seeds of *C. acutiformis* and *C. flacca*. Germination at the sun-exposed site of a fraction of buried seeds of *C. acutiformis* and *C. flacca*, and in almost all seeds of *C. extensa* and *C. arenaria*, apparently was triggered by a combination of temperature amplitudes  $>10^{\circ}\text{C}$  and mean temperatures of  $1.5\text{--}3.5^{\circ}\text{C}$  higher than those at the shaded site. The germination response in the garden experiment mirrors the laboratory germination response of the four species to various temperature regimes in darkness. This not only was obvious in the present study, but also in laboratory experiments, where recently-harvested seeds of *C. extensa* and *C. arenaria* germinated to 23 and 12 %, respectively, over a range of temperature amplitudes and those of *C. acutiformis* and *C. flacca* to only 4 % (Schütz 1998).

#### Timing of Germination and Field Emergence

In contrast to most other spring germinating species (e.g., Lauer 1953, Baskin and Baskin 1985a, Roberts 1986, Thompson and Baster 1992, Bouwmeester and Karssen 1993, Vleeshouwers 1997), which have their emergence peak in March or April, the four sedges germinated fairly late in spring (May), probably due to a requirement for high mean temperatures. A requirement for high minimum temperatures for germination is widespread in the Cyperaceae (Grime et al. 1981) and apparently is an inherent character of the genus *Carex* (Schütz 1997a). The late emergence date in the garden experiment agrees with data from the laboratory experiments, where stratified seeds of *C. flacca* and *C. acutiformis* did not germinate at a constant temperature of  $10^{\circ}\text{C}$  and germination percentages of *C. extensa* and *C. arenaria* seeds were low. Only a small proportion of the seeds of *C. extensa* germinated at  $7^{\circ}\text{C}$  constant temperature (Schütz, unpublished data). The late onset of seed emergence in the field coincides with the temporal course of the seasonal dormancy cycles, whereby the *Carex* species reentered dormancy or conditional dormancy in early summer (Schütz 1997b). The cessation of non-dormancy in most other spring germinating species frequently occurs earlier in the year (e.g., Courtney 1968, Baskin and Baskin 1985a, Pons 1991a, Bouwmeester and Karssen 1993) and it seems to be correlated with the

ability to germinate at low temperatures. In contrast, the temporal dormancy patterns of other, mostly wetland species, (e.g., Baskin and Baskin 1985a, Baskin et al. 1994, Milberg 1994a), apparently corresponds to a requirement for high minimum temperature for germination; consequently, they resemble the cycles shown by *Carex* species. High temperature requirements and dormancy cycles seem to prevent germination in autumn more effectively in sedges than in species of many other genera. Thompson et al. (1996) observed autumn-emergence in artificially created gaps in a limestone grassland in England in almost all species with long-living seeds, but not in the various *Carex* species occurring there.

Despite the commonness in several vegetation types of three of the sedges investigated in the present study, field data on seedling emergence are scarce. No seedling emergence was observed for *C. flacca* in artificially created gaps in field sites in which this species occurred (Thompson et al. 1996). No observations are known to the author on field germination of *C. extensa*, *C. arenaria*, or *C. acutiformis*. Long-term changes in dormancy and viability of seeds are important in determining survival in the seed bank (Pons 1991b). Since almost no seed germinated or died during the 30 months of burial under suboptimal conditions, and little germination under optimal temperature conditions, the ability to form long-persistent seed banks is obvious. Indeed, results from seed bank studies indicate high longevity of seeds in many *Carex* species. Seeds of *C. acutiformis* were concentrated below the top of the 5-cm soil layer under intensively-used forage meadows, indicating the former existence of a fen community (Maas and Schopp-Guth 1995), and those of *C. flacca* emerged from soil samples collected in afforested sites prior to a clearcut (Poschlod and Jordan 1992). Due to a lack of seed bank studies encompassing their habitats no information is available on *C. extensa* and *C. arenaria*.

#### Dormancy Cycles versus Non-dormancy

Clonal growth and the occurrence of unpredictable habitat conditions may be regarded as means favoring the maintenance of non-dormancy in buried seeds of a species. Germination syndromes can be rather simple in species that maintain their populations mainly by clonal growth (Eriksson 1989). Hence, dormancy cycles may be lacking in clonal species. The ability of species growing in unpredictable habitats to germinate at any time during the growing season is an adaptation to the unpredictable timing of conditions favorable for germination (Baskin et al. 1989). Not surprisingly, species with seeds retaining the ability to germinate over a range of temperatures after they had come out



of primary dormancy were found primarily, but not exclusively, in unpredictable habitats, particularly on mudflats (Baskin et al. 1989, 1993a).

All 12 *Carex* species previously investigated showed marked dormancy cycles (Baskin et al. 1996a, Schütz 1997b). Growth form and habitat type had no effect on seasonal dormancy patterns. Even *C. acutiformis*, a species with a permanent low production of viable seed and a strong bias on clonal spreading to maintain its populations, shows dormancy cycles. Thus, there likely is no trade-off between the existence of complex seed germination timing mechanisms involving seasonal dormancy patterns and the prevalence of clonal growth in *Carex* spp. The effect of habitat type, however, is less clear. The degree and duration of flooding can vary considerably across years at the growing sites of the ten wetland sedges that have been investigated, but lowering of the water level occurs normally between spring and early summer. The same is true for the water supply in the seasonally wet habitat of *C. flacca* and the prevailing dry habitat of *C. arenaria*. The annual amount and distribution of rainfall also may vary considerably in these environments, but within the distribution area of these species, the probability of the occurrence of wet or moist conditions is fairly high in spring (Walter and Breckle 1986). Therefore, the habitats of the 12 *Carex* spp. investigated thus far may be characterized as moderately predictable (Schütz 1997a). It is likely that dormancy cycles are a common trait of *Carex* spp. growing in habitats that indeed encompass a wide range of environmental conditions important for germination and establishment of seedlings, but also show a certain seasonal predictability of these conditions. However, buried seeds of *Carex* spp. growing in unpredictable habitats might well be non-dormant during the growing season. Further investigations, especially on true mudflat *Carex* spp. and on those of rock outcrops, another unpredictable habitat type, are needed to confirm the significance of seasonal dormancy patterns in the genus *Carex*.

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