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Ecology of seed dormancy and germination of *Carex divisa* Huds.: Effects of stratification, temperature and salinity

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Abstract

Carex divisa is a patrimonial rhizomatous species and acts as an important component of grazed wet permanent grassland on the French Atlantic coast. This study treated three storage regimes (wet-cold, dry-cold and dry-warm), burial in soil, fluctuating temperature and salinity on seed germination of *C. divisa*. The seeds were dormant at maturity. No seed germinated after 2 and 6 weeks of dry storage under laboratory conditions prior to the onset of the stratification treatment. Thus, the effect of after-ripening was not evident in *C. divisa*. Germination rate of 11.3% started only in the wet-cold stratification treatment after 2 months. Seeds that had been stored under wet-cold conditions for 8 months had a higher germination than seeds stored under dry-cold and dry-warm treatments for the same length of time. Seeds of *C. divisa* tested at 10-20 °C in light had no marked dormancy cycle, but in darkness under a fluctuating temperature regime (10-20 °C), *C. divisa* seems to exhibit annual dormancy cycles. There were no differences in germination between fluctuating temperatures 10-20 °C and 15-25 °C after 12 months in the wet-cold treatment. No germination occurred at fluctuating temperatures 0-10 °C. The highest percent germination was observed in distilled water, followed by 50 mM L^{-1} NaCl. The highest NaCl concentration (250 mM L^{-1}) was found to inhibit seeds germination.

Keywords: After-ripening; Burial experiment; Poitevin Marshland; Sedges; Wet-cold

Introduction

Carex is one of the most important genera in the Cyperaceae. It includes at least 1800 species extending throughout the world, with most occurring in northern-temperate zones (Jermy and Tutin, 1968). *Carex* species are found in a wide range of habitats (Schütz, 2000). C*arex divisa* Huds. is able to spread laterally by rhizomatous growth and as a result, large clonal patches may be formed in wet permanent grasslands (Bouzillé, 1992). Germination is initiated or regulated by many internal and external processes, such as seed coat texture, temperature, light and salinity (Khan and Ungar, 1984; Khan and Gulzar, 2003). An understanding of the timing of germination in a species requires information about environmental temperature conditions as well as the dormancy state of seeds at various time of the year (Baskin et al., 1996).

Dormancy characteristics of a species, or of a particular population, are often assumed to be the result of adaptation to the particular habitat where the species occurs (Schütz, 2000). *Carex* species from moderate and dry habitats show severe or strong conditional primary dormancy, possibly as a result of high seed mass (Schütz, 2000). The observed differences in dormancy seem to be related to the thickness and hardness of the seed coat (Schütz, 2000). These characters are usually more prominent in sedges with large seeds (Schütz, 2000). Low germination rates of fresh seeds were considered as typical for *Carex* species (Amen and Bonde, 1964; Grime et al., 1981).

The dormancy of many species in temperate regions, and especially those exhibiting physiological dormancy, can be broken by stratification at temperatures of 0–8 °C (Grime et al., 1981; Baskin and Baskin, 1988, 1998; Washitani and Masuda, 1990; Probert, 1992). Cold-wet stratification was also beneficial for germination at 10/22 °C in 28 of 32 temperate *Carex* species (Schütz and Rave, 1999). In all studies, stratification at low temperatures had a positive effect on the capacity of *Carex* seeds to germinate. A comparison of freshly matured seeds with those incubated after four and eight weeks of dry storage at room temperature revealed an increase of germination in three out of six wetland *Carex* species (Schütz, 1997b). Germination percentages were significantly higher in four of six wetland Carices after a six-week period of stratification (Maas, 1989), and in three sedges investigated by Grime et al. (1981). Some species (*C. demissa* Hornem., *C. davalliana* Sm. and *C. flava* L.) responded positively to a stratification period of six months, whereas a stratification period of 6–8 weeks proved to be too short to release dormancy (Schütz, 2000). Six weeks of stratification was not sufficient to relieve strict primary dormancy in seeds of *C. nigra* (L.) Reichard and *C. hostiana* Tawny., while seeds of *C. lepidocarpa* (Tausch) Nyman. were able to germinate under fluctuating, but not at constant temperatures (Patzelt and Pfadenhauer, 1998).

Further evidence for a positive effect of cold stratification on *Carex* germination comes from burial experiments (Baskin et al., 1996; Schütz, 1997b). Seasonal changes in dormancy have been investigated in burial experiments in which seeds were buried in the field in batches (Schütz, 1997b; Schütz, 2000). Seeds came out of dormancy in late autumn or winter and entered dormancy in late spring or early summer (Schütz, 1997b). This process represents a natural mechanism which ensures that germination occurs in spring (Probert, 1992). Primary dormancy can be an important mechanism influencing germination timing, as it may increase the likelihood that germination coincides with conditions favorable for seedling survival (Silvertown and Lovett-Doust, 1993; Baskin and Baskin, 1998).

Temperature and salinity have different effects on seed germination (Badger and Ungar, 1989; Khan and Gulzar, 2003). Germination at constant temperatures was below that obtained at 10/22 °C in every treatment of 34 temperate *Carex* species (Schütz and Rave, 1999). A significant positive effect of daily temperature fluctuation on germination was observed for some wetland sedges (Maas, 1989). Grasses differ in their upper limit of salinity tolerance and an increase in salinity concentration usually delays and reduces seed germination (Perez et al., 1998; Gulzar and Khan, 2001; Khan and Gulzar, 2003).

There have been many studies, using various methods, on the germination ecology of the genus *Carex* (Schütz and Rave, 1999; Schütz, 2000). There is a remarkable difference in C*arex* species which exhibit a physiological dormancy (Schütz, 2000). Information on seasonal dormancy patterns and stratification methods are mostly available for temperate *Carex* species. Although dormancy-breaking and the ecology of germination for many sedges are well documented (Schütz, 2000), there is no scientific information on seed germination ecology of *C. divisa.* This species is an important plant of mesophilous communities in grasslands along the French Atlantic coast. Knowledge about germination ecology of *C. divisa* is necessary for inducing/managing regeneration by seed in gaps created by perturbation.

The main objectives of this study were to determine: (1) germination capacity of newly matured seeds of *C. divisa*, (2) the influence of wet-cold stratification, dry-cold stratification and dry-warm storage on dormancy level, (3) the behavior of newly matured seeds when buried in the soil, and (4) the effects of fluctuating temperature and salinity on germination.

Materials and Methods

Species

Carex divisa is a perennial species, originally regarded as a Mediterranean plant, that propagates clonally and grows to heights of 30-70 cm, along the French Atlantic coast (46°28′N and 1°13′W), a large wetland area (120 000 ha). The topography of this grassland consists of depressions, higher-level flats and intermediate slopes, with a maximum altitude of 70 cm. This wet grassland was reclaimed from tidal salt-marshes in the 10th century and has since been subjected to mixed grazing by cattle and horses from about April to December each year. Specific plant communities occur at each level. The plant communities are mesophilous on the high level flats, meso-hygrophilous on the intermediate slopes and hygrophilous in the depressions, which are flooded in winter and early spring. *C. divisa* appears in all three communities in these grasslands. The climate is a mild Atlantic type, with an excess of precipitation over evapotranspiration in winter and an almost equal deficit in summer of about 300–350 mm (Amiaud et al., 1998).

Seed collection

Newly matured fruits, referred to here as seeds, were collected from nearly 50 individual plants of *C. divisa* at the end of June 2005 (first cohort) and in June 2006 (second cohort) from the Marais Poitevin on the French Atlantic coast. *C. divisa* is abundant in this region, flowering and fruiting occurs from May until July. After collection, seeds were air dried (2 weeks), hand separated from the article walls pods and stored in paper bags at room temperature (15–25 °C) under laboratory humidity conditions. Average seed weight (including the perigynium) was 1.17 ± 0.14 mg, and average size was 2.7 ± 0.4 mm long and 1.8 ± 0.2 mm wide.

Germination tests

Primary tests were applied to newly-matured seeds at 2 and 6 weeks after collection. Germination tests were performed on sub-samples of approximately 150 seeds for each treatment in light at a daily alternating temperature of 10-20 C°. The period of minimum and maximum temperature were kept constant for 12h. Illumination was provided on a 12 light/dark cycle by a bank of 6 W cool-white fluorescent tubes in the germination incubator. Seeds were placed in 9-cm Petri-dishes on filter paper moistened with distilled water. All tests were performed in triplicate on 40-50 seeds. Approximately every 2-3 months from October 2005 to November 2006, percent seed germination from one bag of each treatment was determined. The dishes were checked during 45 days and every 2 days the number of seeds/embryos germinated was recorded. A seed was considered to have germinated when the radicle had elongated by at least 1 mm. Seeds that had not germinated at 45 d were opened to determine if the embryo had aborted or if the seed was empty. If so, they were considered dead and excluded from calculation of germination percentages (Basking and Basking, 1998). Seeds were checked for germination after 45 d and results were compared with mean percentage of seeds germinated after 6 weeks.

Storage and stratifications condition

Seeds used for the stratification experiment were stored dry in the laboratory for 6 weeks before the beginning of the stratification treatment on 1 September 2005. Three different storage regimes were applied. 1- Seeds stored in the plastic bags and kept in a laboratory drawer at 15-25°C, (dry – warm). 2- Seeds placed in sealed plastic bags and kept in the refrigerator at 4°C (cold-dry). 3- Seeds wrapped in 2 layers of sterile filter paper, wetted with distilled water, placed in sealed plastic bags and stored in a refrigerator at 4°C for 1 year (cold-wet).

Burial experiment

In order to study the effect of the duration of seed burial in soil, 10 batches of 500 seeds were placed into fine-mesh nylon bags and buried at a depth of 5 cm in 18-cm diameter pots with holes at the base (in September, 2005). The pots were filled with soil and placed in the garden of the University of Rennes 1. At intervals of approximately 3 months a single pot was exhumed and transferred to the laboratory where the contents of the bag was spread onto 6 Petri-dishes and the percent germination determined in both light and dark conditions at 10-20 °C. Light was reported to be a germination requirement for a number of *Carex* species, including *C. stricta* Lamarck. and *C. comosa* Boott. (Johnson et al., 1965; Larson and Stearns, 1990; Baskin et al., 1996). Dark conditions were provided by wrapping the Petri dishes in 2 sheets of tinfoil and black plastic. Germination in darkness was determined only during the middle and end of the experiment, because light stimulation can occur during evaluation (Grime and Jarvis, 1975; Blom, 1979).

Effect of fluctuating temperatures

The germination was evaluated with 4 regimes of fluctuating temperature chosen on the based average temperatures at the study site (Amiaud et al., 2000). A separate germination incubator was used for each temperature regime: 0-10, 5-15, 10-20 and 15-25 °C (11 h at each temperature with one hour transition between temperature extremes), with a 12 h, daily alternation of light and darkness. After 12 months of cold-wet stratification, germination was determined. This experiment was directed in triplicate with 50 seeds at each condition.

Effect of salinity

Seed germination was tested under different concentrations of salinity: 0, 0.05, 0.10, 0.2, and 0.25 mol NaCl L^{-1} in both light and dark at 10-20 °C. Germinated seeds were counted every 2 days for 6 weeks. Seeds used in the experiment had been cold-wet stratified at 4°C for one year. Levels of salinity were similar to those found at the study site (Amiaud et al., 2000).

Statistical analysis

Two-way analysis of variance (ANOVA) was used to determine differences among treatments of stratification periods and storage regimes, and in the burial experiment, the effects of the burial period and light regime. One-way ANOVA was applied to determine the statistical significance of differences among levels of salinity and fluctuating temperature treatments. Differences between treatment means were tested using Fisher's LSD *post hoc* test (Zar, 1996). Percent germination data were arcsine-transformed prior to analysis in order to stabilize variances. The statistical analyses were conducted using MINITAB 13.31 software.

Results

Effect of stratification conditions

No germination was recorded on fresh seeds, (2 and 6 weeks old seed after collection) prior to the onset of stratification (first cohort in 2005, second cohort in 2006) and was thus dormant. Germination was 11.3% after two months of the wet-cold stratification. Maximum germination for the wet-cold and dry-cold stratification treatments occurred after 8 month of storage and had declined by 11 months (Figure 1).

The two-way ANOVA on the percent germination indicated a significant difference among storage conditions, duration and the combination of stratification treatments (Table 1). Seeds stored wet-cold had significantly higher germination rates than seeds stored dry-cold or dry-warm under all storage durations. Dry-warm storage conditions resulted in the lowest germination rates of the 3 storage regimes. The optimum condition for germination of *C. divisa* was the wet-cold stratification regime maintained for 8 months (60.7%).

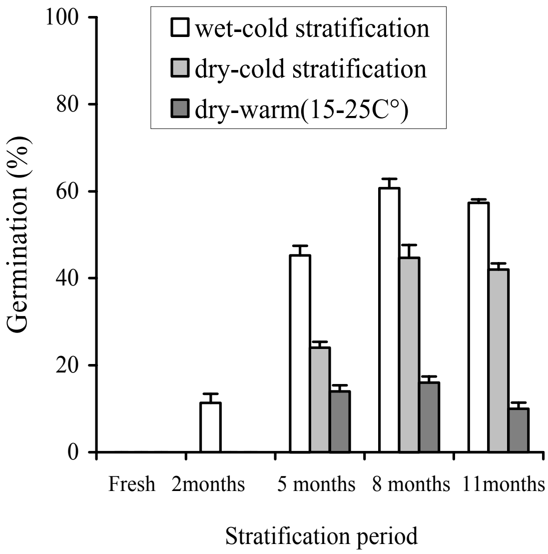

Figure 1. Seed germination percentages (means ± S.E.) of *C. divisa* incubated under three stratification treatments from 0 to 11 months.

Table 1. Result of two-way ANOVA on the effects of storage conditions (stratification), storage duration and combinations of these treatments on germination of *C. divisa.*

Effect	DF	F	P
Stratification	2	61.19	<0.001
Duration	3	59.23	<0.001
S*D	6	17.65	<0.001

Effect of burial

Seeds of *C. divisa* tested at 10-20 °C in light showed no marked dormancy cycle, but in darkness, it seems to exhibit an annual dormancy cycle (Figure 2). However, germination of *C. divisa* had a seasonal cycle with somewhat lower values in summer. In the burial experiment only a very few *C. divisa* seeds germinated after 2 months in light and none germinated under dark conditions (Figure 2). Percent seed germination differed significantly between light ($P \leq 0.001$) and dark ($P \leq 0.001$) treatments and there was significant interaction between sampling date and light treatment at all burial times ($P \leq 0.007$). Seeds that had been germinated in the light had higher germination rates than those germinated in darkness. After 15 months of burial, percent germination was somewhat higher in light than in darkness. No germination occurred while seeds were buried in the soil. Nearly 15% of the buried seeds were observed to be infected by saprophytes or pathogens in December 2006.

Effect of fluctuating temperatures

The seeds of *C. divisa* were found to germinate well (>50%) to 2 alternating temperature regimes (15-25 and 10-20 °C) under a 12 h light/dark regime (Figure 3). The effect of fluctuating temperature on seed germination was also influenced by the difference between daily maximum and minimum temperature when diurnally fluctuating germination temperatures were applied. For seeds stored 12 months under a cold-wet stratification the highest germination (≥ 55%) occurred at fluctuating temperatures of 15-25 °C (Figure 3). Temperatures of 15-25 °C led to greater germination in *C. divisa* than 10-20 °C. No germination occurred at fluctuating temperatures of 0-10 °C. Our results indicated that non-dormant seeds did not germinate at low temperatures, thus fluctuating temperatures greater than 5-15 °C were required for seed germination in *C. divisa*. There was no difference in percent germination between temperatures of 10-20 °C and 15-25 °C after 12 months under cold-wet stratification ($P \leq 0.001$). Seed germination was significantly lower under fluctuating temperatures of 5–15 °C (Figure 3).

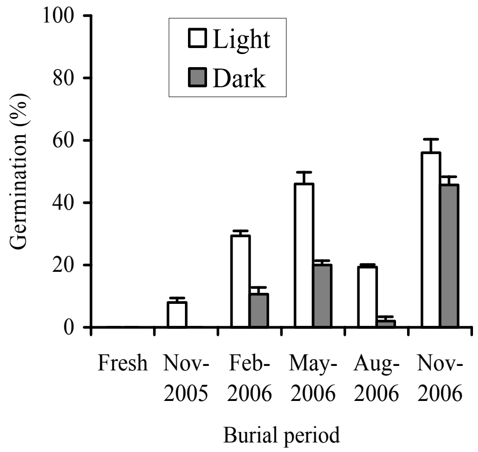

Figure 2. Seed germination percentages (means ± S.E.) of *C. divisa* incubated in light and darkness at 10-20 °C following burial periods from 0 to 15 months.

Effect of salinity

The one-way ANOVA showed that the mean germination rate of *C. divisa* was significantly affected ($P \leq 0.001$) by NaCl (Figure 4). The highest germination was obtained in distilled water, followed by 50 mM NaCl. The highest NaCl concentration (250 mM NaCl) completely inhibited seed germination.

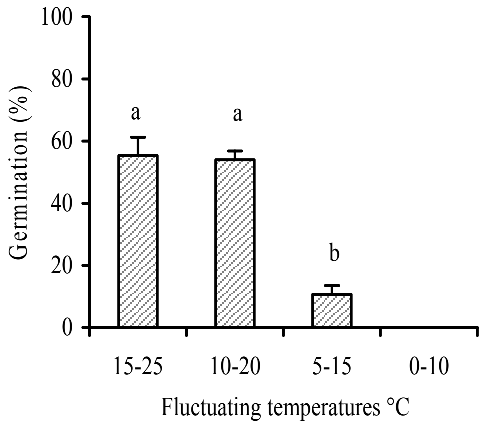

Figure 3. Seed germination percentages (means ± S.E.) of C. divisa after 12 months of cold-wet stratified at four fluctuating temperatures. Values followed by the same letter are not significantly different ($P \geq 0.05$).

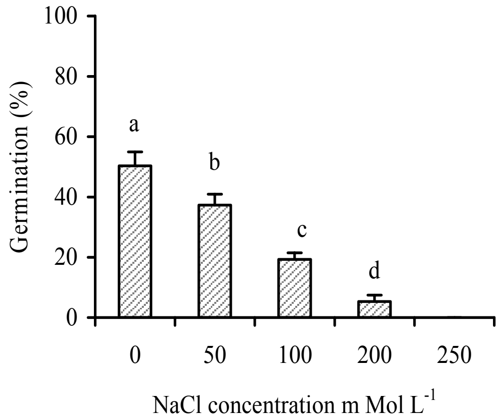

Figure 4. Seed germination percentages (means ± S.E.) of *C. divisa* after a 12 month cold-wet stratification treatment under increasingly saline conditions. Values followed by the same letter are not significantly different ($P \geq 0.05$).

Discussion

Stratification requirements

Ripe mature seeds of *C. divisa* did not germinate 2 and 6 weeks after collection, indicating innate dormancy. Seed germination did not occur after 6 weeks of dry storage under laboratory conditions, indicating that after-ripening did not occur in *C. divisa*. Low germination rates of fresh seeds have been reported previously for *Carex* species (Amen and Bonde, 1964; Grime et al., 1981). Low percent germination prior to stratification was also observed in *Carex* species of various habitat types in other studies (Schmid, 1984;

Baskin et al., 1996; Schütz, 1997a, b). Seeds of both species were conditionally dormant at maturity and germinate under a very limited range of environmental conditions, as shown by Schütz and Rave (1999), appropriate conditions for them include combinations of fluctuating temperatures, storage conditions and light regimes. Our study showed that the response of *C. divisa* to cold-wet and cold-dry treatments was similar to other wetland *Carex* species (Budelsky and Galatowitsch, 1999). Dormancy of *C. divisa* was broken following wet-cold and dry-cold stratification, which supports the hypothesis that the species requires cold stratification to alleviate physiological dormancy (Martin, 1946).

In this study, germination rates of *C. divisa* seed after 8 months of storage were: 61% for the wet-cold treatment, 45% for the dry-cold, and 16% for the dry-warm. Germination rates for *C. stricta* Lamarck. after 10 months of wet-cold (37%), dry-cold (19%) and dry-warm (13%) storage were similar to the rates observed by Budelsky and Galatowitsch (1999). The current study showed that the combined effects of storage conditions and storage duration significantly affected seed germination; particularly that dry-warm storage did not stimulate germination of seeds.

Dormancy of *C. divisa* can be broken by cold-wet stratification (4 °C) after storage for 2 months, although these conditions were not sufficient to relieve severe primary dormancy. Maximum germination occurred after 6-8 months of cold-wet stratification, which is similar to the conditions where the species occurs on the French Atlantic coast. The breaking of dormancy under these experimental conditions is similar to the conditions in the field, which ensures that germination occurs in late spring.

According to Grime et al. (1981) there are two categories of positive responses to stratification. The first category is characterized by rapid germination at low temperature and in darkness. These species normally produce large, populations of seedlings in early spring, which colonize spaces among other plants. In the second category, a requirement for chilling is often associated with a need for exposure to light and/or high or diurnally fluctuating temperatures. *C. divisa* obviously belongs to the second category according to Grime et al. (1981), because a significant positive effect of stratification, light and fluctuating temperatures was evident on seed germination of *C. divisa*.

Pattern of seasonal dormancy

Seasonal changes in dormancy can be investigated with burial experiments (Schütz, 1997b; Schütz, 2001). It seems that a cyclical change in dark germination condition was observed the first 2 years of burial (Fig 2). The percent germination was high in seeds exhumed in May but very low in August. Seeds of *C. divisa* had a high germination rate from mid-autumn to early summer and a low one in late summer. A high germination rate in spring is presumably a consequence of the low winter temperature and humidity in the soil.

The seeds of *C. divisa* exhibited dormancy cycles in darkness and showed a seasonal response as most *Carex* species found in wet habitats (Schütz, 2000). Of the *C. divisa* seeds examined in the second year none become completely dormant in the light, because a fraction of these seeds were still capable of germination in warm-storage conditions. Inadequate germination in summer can be avoided by the induction of secondary dormancy in response to gradually increasing temperatures (Bouwmeester and Karssen, 1993).

For 6 species of sedges, the temperature for secondary dormancy was reported to be close to 15°C, since germination was high in seed batches removed from burial in June when soil temperatures were between 10 and 12 °C, but low in seed batches removed in August 1994, when soil temperatures were between 15 and 20°C (Schütz, 1997b). The results from this study suggest that a positive effect of light on germination is a common phenomenon in seeds. Moreover, similar results have been reported for *Carex* species (Grime et al., 1981; Baskin and Baskin, 1988; Schütz, 2000). Light was a particularly important germination cue, confirming previous report on *Carex* species (Grime et al., 1981; Pons, 1992; Baskin and Baskin, 1998; Schütz, 2001). *C. divisa* showed a marked seasonal pattern of germination, the seeds were able to germinate at the end of autumn and in the spring, but not in summer. In general *Carex* species from mesic and dry habitats show strong conditional primary dormancy, perhaps because these species often have a rather high seed mass (Schütz, 2000). Germination in *Carex* species with seeds >0.9 mg was significantly lower than in species with lighter seed weights (Schütz and Rave, 1999). Seed mass of *C. divisa* is approximately 1.17 mg per seed, which is perhaps a factor affecting in germination rate.

Effect of fluctuating temperatures

Fluctuation of temperature between 15 and 25 °C was conducive to germination of *C. divisa* as was temperatures of 10-20 °C. A significant positive effect of daily temperature fluctuations on germination was also shown for some wetland sedges (Maas, 1989). Germination of *C. divisa* seeds occurred equally well at fluctuating temperatures of 15-25 and 10-20 °C. These temperature regimes correspond to mid-spring mean temperatures in the natural habitat. It has been shown that different habitat conditions do not have as great an influence on germination as fluctuating temperatures (Schütz, 1999). An increase in temperature was associated with increased germination of *C. divisa* seeds. Wetland sedges and plants, in general, were found to respond positively to large diurnal temperature fluctuations (Thompson and Grime, 1983; Schiitz, 1997b; Schlitz and Milberg, 1997), but the ecological significance of the response varies (Thompson and Grime, 1983). Germination of *C. divisa* seed did not occur at fluctuating temperatures of 0-10°C. Therefore, it is possible that low temperature fluctuations are part of the mechanism that prevents germination.

One of the treatments was 5-15 °C, a fluctuating temperature regime with the lower temperature occurring at night. However, seeds of *C. divisa* germinated to only 10.7 % after 12 months at 5-15 °C. Hence, we conclude that a low night temperature had only a small positive effect on germination level of *C. divisa.* A requirement for relatively high minimum temperatures for germination is typical of wetland plants (Grime et al., 1981; Baskin and Baskin, 1998), but seems to be a characteristic of sedges in general (Schütz, 1997b; Schütz and Rave, 1999).

The capability to respond to daily temperature fluctuations in light was almost exclusively restricted to seeds of wetland and ruderal species growing in moist sites (Thompson et al., 1977), whereas in species from other habitats (e.g. grasslands and heath) temperature fluctuations had either no effect or an effect only in darkness. By contrast in another study, the response of sedges to fluctuating temperature regimes was relatively uniform (Schütz, 1999), indicating that different habitat conditions are hardly reflected in the response to fluctuating temperatures. That is, sedges from dry and mesic habitats were on average equally sensitive to increasing temperatures as those occurring in wetlands. Similarities in germination rates between our study and other studies indicate that different populations of these species respond in a similar manner to similar stratification conditions and germination temperatures. The optimum temperature of seed germination of *C. divisa* was 15-25 °C followed by 10–20 °C (Figure 3).

Effect of salinity

C. divisa has been reported to grow under non-saline conditions on high level flats that have mesophilous plant communities characterized by species such as *Cynosurus cristatus* L., *Lolium perenne* L., *Elytrigia repens* L. (Bonis et al., 2005). The pattern of distribution of this species in the field and the germination tests indicated that it is not adapted to a wide range of soil salinity. *C. divisa* has not been reported as a halophytic plant (Bonis et al., 2005). Our results showed that the highest percent germination occurred in distilled water, and decreased as salinity increased. Little germination was observed at 200 mM NaCl. The inhibitory effects of NaCl on seed germination could be due to its direct effect on the growth of the embryo, or may increase the osmotic potential of the media causing inhibitory effects on seed imbibition (Waisel, 1972; Poljakoff-Mayber et al., 1994). *C. divisa* showed a similar pattern of increase in the salinity concentration in delays and reduction of seed germination that is similar to the results of Khan and Gulzar, (2003) in some grass species.

The present germination studies have identified the environmental parameters required for germination of *C. divisa*. Cold-wet stratification (4 °C) for 6-8 months increased germination at 10-20 and 15-25 °C under a light/dark photoperiod. Seed germination of *C. divisa* may be attributed to the combined influence of intermediate fluctuating temperatures, light and moisture storage conditions. A fraction of seed has the potential to germinate throughout the year. Therefore, it is possible that germination can occur in autumn when suitable moisture and temperature conditions are present. This study clearly illustrates that the germination of *C. divisa* was enhanced under non-saline conditions compared to saline, although a small percentage of seeds under saline conditions may still germinate.

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