

# Germination strategies of two dominant *Carex* species in a swamp alder forest: implications for restoration

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**Abstract:** Germination strategy is an essential mechanism that determines plant survival in previously established populations or newly colonised sites. *Carex* is a group of species that has shown difficulties to germinate experimentally and also many of them failed in order to use in restoration projects. Our aim was to determine whether *Carex elata* and *C. elongata* that dominate in vegetation of Central European swamps differ in their germination strategy. We conducted germination experiments with stratified and unstratified seeds of both species to determine: 1) if they are able to germinate fresh, 2) if they exhibit a cyclic dormancy pattern, and 3) if they will germinate from a seed bank. We demonstrate fresh seed germination and no evidence of cyclic dormancy in either species. Stratification did not enhance final germination but it did accelerate germination. Seed bank seeds of both species germinate sparsely. We demonstrate that these coexisting *Carex* species differ with respect to final germination. The higher germination percentages of the fresh seeds compared to buried and seed bank seeds of both species probably reflect adaptation to fluctuating water-level conditions. In summary, these findings support a strategy of fresh germination in a highly-variable environment. Our study indicates that both *C. elata* and *C. elongata* are suitable for restoration projects. Successful establishment and revegetation with *C. elongata* may result simply from sowing fresh seeds. In contrast, seed sowing, combined with vegetatively produced seedling transplants is essential for the successful restoration of *C. elata*.

**Key words:** burial experiment; fresh germination; sedges; seed bank; seed dormancy; stratification.

## Introduction

The coexistence of species within communities is possible only if species that occupy the same place share a preferred life strategy and functional traits, allowing long-term survival in a stress-induced environment (*habitat filtering effect*; Keddy 1992). Species with an un-preferred strategy are excluded because they cannot cope with local environmental stress or competition (Mayfield & Levine 2010). On the other hand, species that differ in their life strategies may coexist due to complementarity of resource use in space and time (*limiting similarity*; Silvertown 2004), which decreases the intensity of inter-specific competition (Gross et al. 2007).

Germination strategy is one of the mechanisms that determine how species respond to their environment (Angevine & Chabot 1979; Narbona et al. 2013). It affects the probability of plant survival and plays a key role in the successful colonisation of new sites (Keddy et al. 1989). The probability of successful recruitment of species individuals in recently released patches is closely dependent on the seasonal timing of germination (Schütz & Rave 1999; Fernández-Pascual et al. 2013). Seed dormancy and germination ecol-

ogy can differ considerably, even for congeneric species (Grime et al. 1981; Schütz & Rave 1999; Kettenring & Galatowitsch 2007). However, it is still not well understood whether plant species inhabiting the same habitats have the same or different germination behaviours (Baskin et al. 1993). This variation in seed germination behaviour and dormancy pattern may contribute to plant population persistence and the maintenance of community diversity (Grime et al. 1981). At the same time, this variation often limits the revegetation success of anthropogenically damaged habitats, which is the main challenge in the restoration process (Cochrane et al. 2002).

Sedge species (*Carex* L.) are by far the most diversified groups of Cyperaceae. They occur in various types of wetlands where they often dominate (Hegi 1980). Many *Carex* species supply a large number of ecological services such as indication of recent environmental change at the ecosystem and landscape levels (Fojt & Harding 1995). Not surprisingly, populations of many *Carex* species are associated with extensive and abandoned wetland habitats due to decline of recent agricultural management practices (Van der Valk & Pederson 1989). Knowledge of germination strategy of species is required to predict successful revegetation

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after restoration (Kettenring & Galatowitsch 2011a). However, *Carex* is a group of species that experience has shown to be very difficult to germinate *ex situ*. Until recently, little attention has been paid to this behaviour (Schütz 2000). Hence, germination studies are urgently needed to increase our ability to manage *Carex* species in restoration projects.

Recent studies indicated that several groups of wetland *Carex* L. species differ with respect to their germination strategies: 1) The first group is represented by species with physiologically dormant seeds that are not able to germinate even when appropriate environmental conditions are present (Baskin & Baskin 1998). Due to natural winter stratification under moist and cold conditions, strict dormancy may be broken and the majority of seeds are consequently able to germinate under the full range of conditions possible in spring. In some species, the remaining ungerminated seeds fall back into dormancy in late summer (cyclic dormancy pattern; Baskin & Baskin 1998; Schütz 2000). 2) The seeds of the species in the second group are conditionally dormant at maturity. Seeds do not require stratification to germinate but they are initially able to germinate only within a narrow range of conditions, mostly under diurnally fluctuating or constant high temperatures and exposure to light (Budelsky & Galatowitsch 1999; Schütz & Rave 1999; Schütz & Rave 2003; Kettenring & Galatowitsch 2007). Conditional dormancy is the most common type of dormancy that is present in the seeds of wetland species and is typical for wetland sedges (Schütz 2000).

The germination strategy of *C. elongata* has been studied previously by Schütz (1997a,b, 1999) and Schütz & Rave (1999, 2003). They found annual non-dormancy/conditional dormancy cycles in seeds subjected to outdoor conditions. Information on the germination strategy of *C. elata* is scarce. Schütz (2000) reported, that fresh seeds of *C. elata* germinate in dark conditions at high temperature, which should predispose *C. elata* to regenerate from seed banks.

In European swamp forests, which are strongly endangered habitats that host many protected plant and animal species, *Carex* species often dominate or make up an important part of the vegetation (Hegi 1980; Schütz 2000). In this study, we focused on the germination of *C. elata* and *C. elongata*, potentially suitable for restoration projects. Preferring the same habitat, these may differ in their regeneration strategies. Our aim was to determine whether these *Carex* species differ in their germination strategies. First, comparing the germination differences between fresh and stratified seeds, we attempted to determine if seeds of each species are able to germinate fresh. This would enable us to include them among species suitable for restoration. Second, we carried out a burial experiment that simulated the possible cyclic dormancy (seeds able to germinate fresh, do not germinate under unfavourable conditions and so fall into dormancy at the end of the growing season to minimise seedling mortality in winter). Cyclic dormancy was tested for, based on the germination of seeds

buried in wet sand (i.e., to simulate the natural conditions in swamp alder forests during late summer and early autumn). We also examined the germination of seeds from the alder swamp forest soil bank to detect the formation of a seed bank. These enable species to spread the germination of their seeds in time and so cope with long periods of unfavourable conditions.

## Material and methods

### Species

*Carex elata* and *C. elongata* are associated with alder carr throughout Europe where they frequently dominate the herbaceous layer (Douda et al. 2016a). Both are long-living clonal sedges that produce densely tufted shoots (Hegi 1980). However, they can also produce short underground rhizomes (Douda et al. 2016b). In addition, they spread sexually by achenes. *C. elongata* is medium-sized sedge with a high production of seeds that ripen from the middle to the end of June (Schütz & Rave 2003). A high proportion of the seeds are well developed, and empty perigynia and mouldy seeds are rare (Schütz 1997b). *C. elata* seeds ripen in June.

### Study area

The seed material of *Carex elata* and *C. elongata* was collected from an old-growth swamp forest in the Vrbenské rybníky Nature Reserve located in southern Czech Republic. The collection site is dominated by black alder [*Alnus glutinosa* (L.) Gaertn.]. Sedges and perennial grasses dominate the understorey vegetation (Douda et al. 2009, 2012). The average annual precipitation ranges from 550 to 650 mm; the mean annual temperature is 8.5°C and the average temperature in June, when *C. elata* and *C. elongata* ripen, is 16°C (Tolasz et al. 2007).

### Seed collection

Seeds were collected from 12 *Carex elata* plants and 12 *C. elongata* plants in July 2012. The seeds of both species were collected from plants that were at least 10 metres distant each other to ensure there was no doubt about their individuality. Fully matured seeds were identified by a brownish colour and the fact that they could easily be detached from the mother plant. All mouldy seeds were discarded. Seeds were air dried after collection, cleaned and stored together at room temperature (20°C, 40–60% RH) in paper bags for 10 days.

### Seed bank sampling

Seeds from the soil seed bank of *Carex elata* and *C. elongata* were collected from 12 randomly established sites in the same location in August 2012. At each of these sites, five sediment cores (5-cm depth) were collected from the perimeter of a 60-cm diameter circle. These soil samples contained seeds that matured at the beginning of summer of this year and seeds that were stored in the seed bank. The collected soil samples were placed in plastic bags and transported to a cold (13°C) dark room where they remained until the extraction of the seeds. All seeds were extracted from wet soil samples using the flotation method (Thompson et al. 1997). A 950-mL volume of each soil sample was dispersed in 20 L of water. Coarse fractions of disintegrated necromass in the humic soil were removed from the water surface using a coarse sieve (4 × 4-mm cell diameter) to ensure that all seeds passed through. The seeds that were dispersed in the water were collected from the entire water column using a fine sieve (0.212 × 0.212-mm cell diameter)

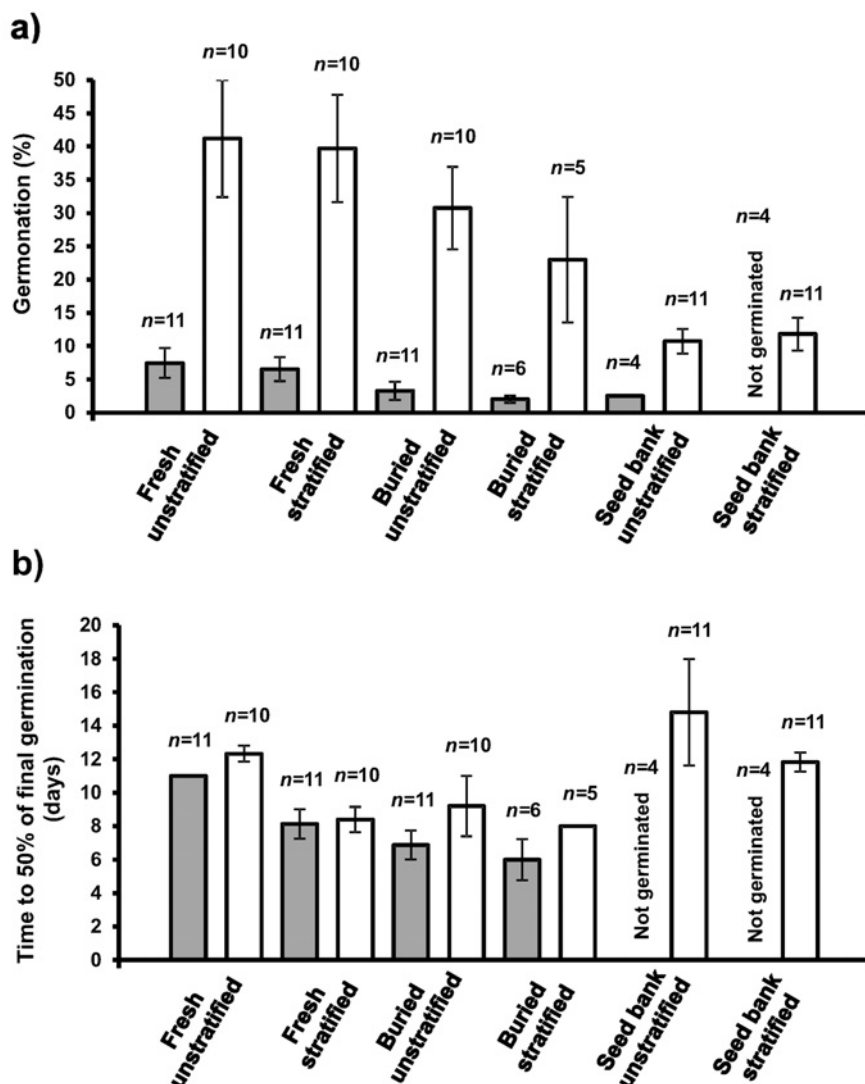


Fig. 1. Differences in (a) the final germination percentage and (b) the germination rate of unstratified and stratified seeds of *Carex elata* (grey-shaded column) and *C. elongata* (white-shaded column) of fresh, buried and seed bank seeds incubated under a 22/10°C temperature regime and 16 h of light per day (means  $\pm$  SE if  $> 5\%$ ). Cold, wet stratification was carried out at 4°C for six weeks. For the differences between seed origin and stratification treatment see Table 1; *n* indicates the number of Petri dishes used for the treatments in the germination experiments.

after the fine organic sediment settled on the bottom. The collected seeds were stored in permeable plastic bags placed in wet sand for the time necessary to extract all the seeds from the soil samples.

To determine the presence of both species in the seed bank we also collected seed bank seeds from samples taken from 60 sites at the same location.

#### Burial

Fifty seeds of each of 12 individuals of *Carex elata* and *C. elongata* were placed in fine-mesh, permeable plastic bags and buried in darkness to a depth of 5 cm in wet, fine-grain river sand in a wooden box. To mimic unfavourable conditions during late summer and autumn, the seeds were stored in a wet basement (80–90% RH) at a constant temperature of 13°C for 4 months preceding germination. During burial none of the *C. elata* or *C. elongata* seeds germinated.

#### Germination experiments

The experiments were of factorial design with two factors: seed origin (fresh/buried/seed bank) and seed pre-treatment

(stratified/unstratified). To analyze germination strategy of *Carex* species, fresh, buried and seed bank seeds were subjected to one of the following pretreatments: (1) no stratification, where seeds were incubated immediately without stratification or (2) stratification, where seeds were stratified prior to incubation.

Due to limited availability of seeds, the base number of repetitions was 11 for *Carex elata* and 10 for *C. elongata*. We were forced to reduce the number of repetitions in two cases: (1) the stratified, buried seeds of both species because of a low number of fertile plants in the location where the seeds were collected, and (2) the seed bank of *C. elata*, which was only sparsely present in the soil in the location where the samples were collected. For full numbers of repetitions see Fig. 1.

Fifty seeds of each species were placed on a single layer of filter paper in each 90-mm diameter Petri dish and moistened with distilled water. The seeds were then incubated at 22°C under a 16-h light period (warm white light, photon irradiance of 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , R:FR ratio of approximately 11.5) and at 10°C under an 8-h dark period each

Table 1. Results of the GLMs comparing the effects of different seed origin and stratification on final germination percentage and germination rate of seeds of *Carex elata* and *C. elongata*.

Effect	Final germination percentage			Germination rate		
	df	F ratio	p-value	df	F ratio	p-value
Species	1, 102	382.56	< <b>0.0001***</b>	1, 81	5.86	<b>0.018*</b>
Seed origin	2, 100	110.80	< <b>0.0001***</b>	2, 79	5.64	<b>0.0053**</b>
Stratification	1, 99	1.88	0.1708	1, 78	9.35	<b>0.0031**</b>
Species*seed origin	2, 97	0.70	0.4963	2, 76	2.07	0.1334
Species*stratification	1, 96	0.63	0.4271	1, 75	0.02	0.8797
Seed origin*stratification	2, 94	0.61	0.5451	2, 73	1.26	0.2898
Species*seed origin*stratification	2, 92	1.53	0.2159	1, 72	0.33	0.5691

Significant differences are indicated in boldface. \* ( $P < 0.05$ ); \*\* ( $P < 0.01$ ); \*\*\* ( $P < 0.001$ ).

day, corresponding to environmental conditions in central Europe during June (Schütz & Rave 1999, 2003). Distilled water was added to the dishes every 1 to 2 d to maintain moist conditions. The germinated seeds were counted and removed at 2-d intervals for 45 d. A seed was considered to have germinated when the radicle visibly emerged from the seed coat by approximately 1 mm. All infected seeds were excluded from the calculation of germination percentages and the statistical analyses. After the germination experiments we opened the non-germinated seeds with razor blade to check for the viability. Empty or undeveloped seeds were identified as unviable. The stratification treatment was conducted with seeds moistened with distilled water and placed on Petri dishes that were wrapped in aluminium foil and stored in a climabox at 4°C for 6 weeks prior to germination (Budelsky & Galatowitsch 1999).

#### Data analysis

The effects of seed origin and pretreatments on the final germination percentage and rate of germination were analysed using generalised linear models (GLMs). For each species, germination and germination rate were considered as dependent variables, whereas seed origin and pre-treatment were considered as predictor variables (Crawley 2012). Because seed germination follows a binomial distribution (probability ranging from 0 to 1), we used a logit link function (Venables & Ripley 1998). The inverse function of time (in days) to 50% of final germination ( $t_{50}$ ) was used to express the rate of germination ( $r_{50} = 1/t_{50}$ ). The rate of germination follows a normal distribution, therefore, we used the identity link function (McCullagh & Nelder 1989). Multiple comparisons were made using Tukey's *post-hoc* tests. GLMs were carried out using the function *glm*. Tukey's *post-hoc* tests were carried out using the function *glht* in the package *multcomp* (Hothorn et al. 2013). Differences in the mean numbers of *C. elata* and *C. elongata* seeds present in the soil seed bank were carried out using the Wilcoxon rank sum test with continuity correction. All analyses were carried out using R (R Core Team 2015).

## Results

### Germination

We found a significant effect of seed origin (fresh/buried/seed bank) on final germination percentage of both *C. elongata* and *C. elata* (Table 1). The fresh seeds of *C. elongata* and *C. elata* had the highest germination percentages (Fig. 1a). Significant differences were in the final germination percentages of fresh compared with buried ( $Z = -6.805$ ,  $P < 0.001$ ,  $n = 74$ ; Fig. 1a)

and fresh compared with seed bank ( $Z = 7.416$ ,  $P < 0.001$ ,  $n = 72$ ; Fig. 1a) seeds. However, differences in final germination percentages of buried compared with seed bank seeds were not significant ( $Z = 1.486$ ,  $P = 0.294$ ,  $n = 62$ ; Fig. 1a).

Cold, wet stratification did not enhance the germination of *C. elongata* or *C. elata* seeds in any of the fresh, buried or seed bank treatments (Table 1). Final germination percentages of fresh seeds differed between species. The final mean germination percentage of *C. elongata* was almost six-times higher than that of *C. elata* (mean  $\pm$  S.E. =  $40 \pm 7\%$  and  $7 \pm 5\%$ , respectively; Fig. 1a).

### Germination rate

We found significant effects of seed origin on germination rate of both *C. elongata* and *C. elata* (Table 1). Based on the  $r_{50}$  values, rapid germination occurred in the buried compared with the fresh seeds of both *C. elongata* and *C. elata* ( $Z = 3.091$ ,  $P = 0.006$ ,  $n = 74$ ; Fig. 1b). No significant differences were found in the germination rate of the fresh compared with the seed bank seeds ( $Z = -0.813$ ,  $P = 0.694$ ,  $n = 72$ ; Fig. 1b) or buried compared with seed bank seeds ( $Z = 1.898$ ,  $P = 0.138$ ,  $n = 62$ ; Fig. 1b).

The effect of the stratification treatment on germination rate was significant in both *C. elongata* and *C. elata* (Fig. 1b, Table 1). A higher germination rate was detected in the stratified compared with the unstratified seeds ( $Z = 2.283$ ,  $P = 0.022$ ,  $n = 208$ ; Fig. 1b).

## Discussion

We found highly significant effects of seed origin on final germination percentage of both, *C. elongata* and *C. elata*. Specifically, the fresh seeds had the highest germination percentages. Fresh seed germination has been reported for annual plants that occur in highly variable environments (Baskin et al. 1993) and has been confirmed in several studies of *Carex* species from wetlands. Even though stratification usually significantly enhances germination, more than 50% of seeds of *C. canescens*, *C. paniculata* and *C. pseudocyperus* germinated without any stratification (Schütz 1997b). In a study conducted on 14 *Carex* species from North Amer-

ica, 8 species required little or no stratification to germinate readily over a broad range of temperatures (Kettenring & Galatowitsch 2007). Schütz & Rave (1999) found that more than 60 % of fresh seeds of *C. elongata* germinated without any stratification after exposure to light. Similarly, Fernández-Pascual et al. (2013) stated that the majority of seeds of *C. echinata* and *C. diandra* germinated without any stratification. We agree that temperature and light regime set in climabox which allow us to compare the results with other authors cannot faithfully simulate the environmental conditions in the field.

The fresh germination in both *C. elata* and *C. elongata* probably reflects the fluctuating water conditions. In swamp forests, the ground water level fluctuates substantially during the growing season (Czerepko et al. 2007). We detected such fluctuations in two consecutive years 2014 and 2015 (Fig. 3). In such variable environment, it could be beneficial for species to remain non-dormant or conditionally dormant, even buried in the sediment during the period of flooding. It has been shown that for wetland species with conditionally dormant seeds, requirement of high diurnal or high constant temperatures for germination serve as a mechanism for the recognition of decreasing water levels in spring at the beginning of the growing season (*temperature germination niche*; Grime et al. 1981; Fernández-Pascual et al. 2013). Baskin & Baskin (1998) state that such a mechanism enables seeds to lose their dormancy at the end of the flooded winter season and to germinate as soon as the water recedes. This strategy enables seeds to start germinating in the growing season when the water level decreases to approximately the same level as the soil (Baskin & Baskin 1988, 1993). Such a strategy could represent the *window of opportunity* for regeneration of swamp forest species.

To simulate the delay in germination under unfavourable conditions in late summer and early autumn, we conducted a burial manipulation experiment with seeds of both *C. elongata* and *C. elata* (Baskin et al. 1989, 1996). We expected that burying the seeds for four months in moist sand would result in induced dormancy. Contrary to our expectations, stratification of buried seeds did not enhance final germination percentages, indicating that buried seeds did not fall into dormancy at all. The possibility of cyclic dormancy was therefore ruled out. Cyclic dormancy does not occur in

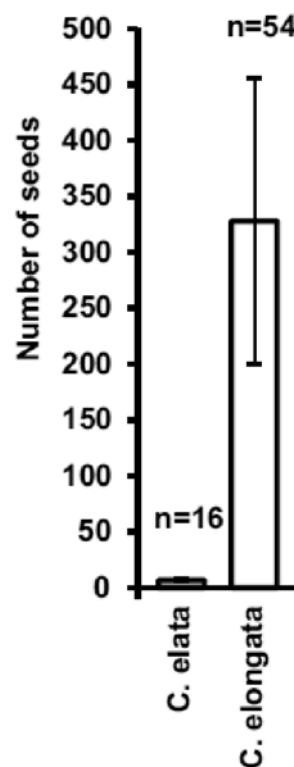


Fig. 2. Differences in the mean number of *Carex elata* and *C. elongata* seeds present in one sample of the soil seed bank (means  $\pm$  SE if  $> 5\%$ ). Differences were significantly different according to the Wilcoxon rank sum test with continuity correction ( $W = 588$ ,  $P < 0.001$ ,  $n = 60$ ). Seeds of *C. elongata* were found in 54 seed bank samples, seeds of *C. elata* were found in 20 seed bank samples.

all temperate plant species (Baskin et al. 1989, 1993). The loss of cyclic dormancy patterns in *Carex* species from wetlands may reflect a strategy of coping with fluctuations in water level (Baskin et al. 1996). For these species, it is important to be able to germinate at any time during the growing season providing the water level is suitable (Baskin et al. 1989, 1993).

Several burial experiments have indicated the presence of a transient seed bank for many *Carex* species, including *C. elongata* and *C. elata* (Schütz 2000). Contrary to our expectations, we found only a few *C. elata* seeds in the seed bank. In addition, a small fraction of these seeds was viable and germinated successfully. Repeated collections of seed bank samples from 60 sites in

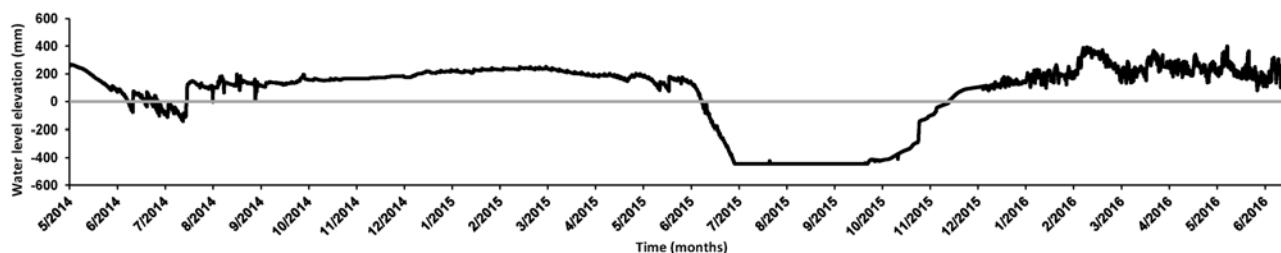


Fig. 3. The amplitude of the water level fluctuations from an old-growth swamp forest in the Vrbenské rybníky Nature Reserve since May 2014 to June 2016. The water level was measured at one hour interval.

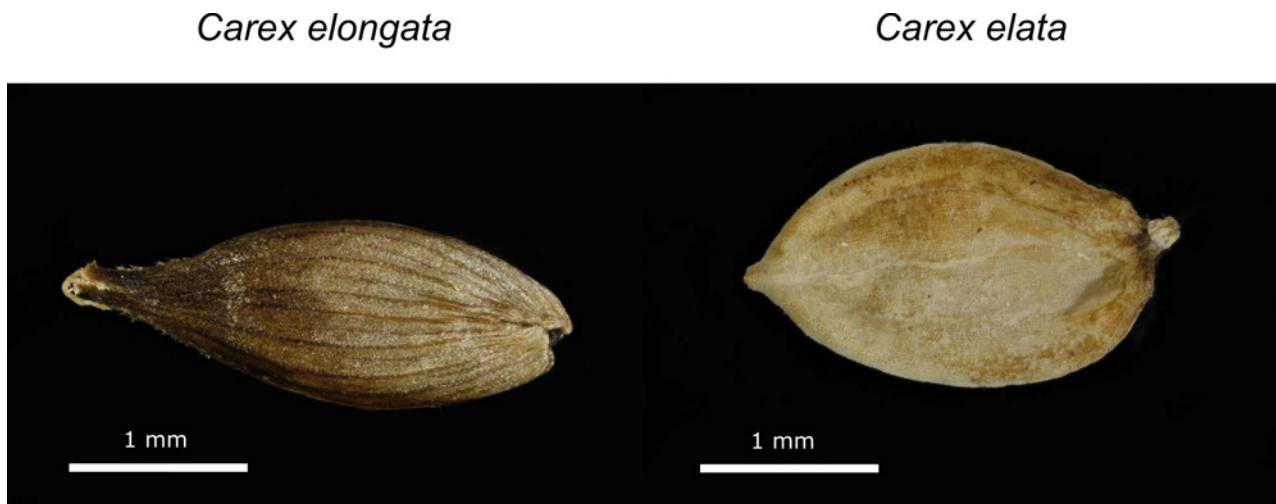


Fig. 4. Front view of the seed coat shape of *Carex elongata* and *C. elata* seed.

this location confirmed the lack of *C. elata* seeds in the seed bank (Fig. 2). This indicates *C. elata* is probably not able to regenerate successfully from a seed bank.

We found that stratification had no significant effect on final germination percentage, however, rapid germination was found in seeds of both *C. elongata* and *C. elata*. It has been shown, that cold wet stratification is suitable for breaking dormancy in many species with physiological dormancy, and that it both accelerates and synchronises germination (Baskin & Baskin 1998). We recognise that six weeks of stratification (used in this study) is a short period with which to represent the overwintering stratification of seeds in the field. However Kettenring & Galatowitsch (2007) note that most of the 14 wetland *Carex* species they studied required only eight weeks stratification at 5°C for successful germination. More usefully, Brändel (2005) states that four weeks stratification was sufficient for almost 100% germination under 5, 11, 13 or 15°C for *C. remota* and *C. pendula* seeds. Lastly, short, cold stratifications periods of only two or three weeks at 5°C consistently led to 90–100% germination in seeds of *C. elongata* (Schütz & Rave 2003). Therefore, we reasonably conclude that our somewhat abbreviated six-week stratification period is likely to have had a negligible effect on our final germination results. Instead, it has been demonstrated that germination success may be most strongly influenced by the viability of the seeds (Baskin & Baskin 1998; van der Valk et al. 1999; Emrani et al. 2013). Generally, *Carex* species, which have a cespitose growth form, tend to produce a high number of viable seeds in contrast to other species, which spread through the production of long rhizomes, and tend to produce a low number of viable seeds (Leck & Schütz 2005). Interestingly, we recorded considerable differences in the viability of the seeds of the studied species, even though both species have a cespitose growth form. Regardless of the high production of *C. elata* seeds, they had low viability.

Final germination percentages differed between species. *C. elongata* had a relatively high germination percentage of fresh seeds, i.e., greater than 40% com-

pared with *C. elata*, which exhibited low germination, just over 5% on average. We repeated germination experiments from different locations within the region. These results confirmed the generally high final germination of *C. elongata* (over 60%) and the low final germination of *C. elata* (less than 5%). It has been shown that environmental limitations may strongly influence reproductive-vegetative allocation in clonal plants (van Kleunen et al. 2002; Douda et al. 2016b). Because seed recruitment of plants in areas with perennial vegetation is often only associated with vegetation gaps created after disturbance (Eriksson & Fröberg 1996), clonal species may have restricted generative reproduction in some cases. Thus, it is possible that *C. elata* allocated more resources to vegetative reproduction and consequently may produce seeds of low viability, which is generally more typical for *Carex* species that usually spread clonally through rhizomes (Schütz 2000; Douda et al. 2016b). Juvenile fruiting and the presence of abnormally inflated seeds with missing embryos, which we found in several plants in this location, may prevent germination in this species (Hulík et al., personal observation).

#### *Application of C. elata and C. elongata in restoration projects*

Previous studies have demonstrated that active revegetation of plant species in wetlands is an important component of restoration practices (Kettenring & Galatowitsch 2007). Active revegetation via seed sowing may help ensure species diversity in decaying wetlands or may maintain species in restoration projects (Kettenring & Galatowitsch 2011a). A problem arises because seed dormancy restricts the restoration success of many *Carex* species (Kettenring & Galatowitsch 2011b). To maximise the return on the investment of time and cost in active revegetation, it is critical to ensure maximum seed germinability. Based on species-specific seed viability and responses of seeds of different origins to similar simulated conditions, we assume that after flooding disturbances, *C. elongata* regenerates readily via



seeds in open gaps when the water subsequently recedes. Other species with low seed viability such as *C. elata*, or species with deep dormancy or specific temperature requirements for germination are likely to produce seedlings less frequently and so may be difficult to revegetate in wetland restorations.

Our study highlights some of the factors restoration workers should consider for revegetation. For many plant species, more than just a seed dormancy breaking treatment is essential for successful restoration. We demonstrate fresh seed germination of *C. elata* and *C. elongata*. This indicates they are suitable for restoration projects. Consequently, successful establishment and revegetation with these species may be achieved by sowing fresh seeds. The seeds that are able to germinate fresh can be used for seeding immediately after ripening. Time consuming storage and overwintering stratification of seeds is not needed in this case. Particular attention should be paid to species showing low seed viability, such as *C. elata*, that generally occupy constantly high water-level habitats, and where they reproduce clonally. In some cases, the transplanting of vegetatively produced seedlings may be necessary for effective revegetation if establishment from seed in the field is insufficient. Seed sowing combined with seedling transplants may not only achieve the successful restoration of a range of target communities but may also help to prevent incursion by many invasive species, that frustrate many attempts at wetland restoration.

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## References

- Angevine M.W. & Chabot B.F. 1979. Seed germination syndromes in higher plants, pp. 188–206. In: Solbrig O.T., Jain S., Johnson G.B. & Raven P.H. (eds), *Topics in Plant Population Biology*, Columbia University Press, New York.
- Baskin C.C. & Baskin J.M. 1988. Germination ecophysiology of herbaceous plant species in a temperate region. *Am. J. Bot.* **75**: 286–305.
- Baskin C.C. & Baskin J.M. 1993. Seed germination ecophysiology of four summer annual mudflat species of *Cyperaceae*. *Aquat. Bot.* **45**: 41–52.
- Baskin C.C. & Baskin J.M. 1998. *Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, 665 pp.
- Baskin C.C., Chesson P.L. & Baskin J.M. 1993. Annual seed dormancy cycles in two desert winter annuals. *J. Ecol.* **81**: 551–556.
- Baskin C.C., Chester W.E. & Baskin J.M. 1996. Effect of flooding on annual dormancy cycles in buried seeds of two wetland *Carex* species. *Wetlands* **16**: 84–88.
- Brändel M. 2005. The effect of stratification temperatures on the level of dormancy in primary and secondary dormant seeds of two *Carex* species. *Plant Ecol.* **178**: 163–169.
- Budelsky R.A. & Galatowitsch S.M. 1999. Effects of moisture, temperature, and time on seed germination of five wetland *Carices*: implications for restoration. *Restor. Ecol.* **7**: 86–97.
- Cochrane A., Kelly A., Brown K. & Cunneen S. 2002. Relationships between seed germination requirements and ecophysiological characteristics aid the recovery of threatened native plant species in Western Australia. *Ecol. Manage. Restor.* **3**: 47–60.
- Core Team R. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org/>.
- Crawley M. J. 2012. *The R book*, 2nd edition. John Wiley & Sons, Inc., Chichester, 1076 pp.
- Czerepko J., Boczon A., Pierzgałski E., Sokolowski A.W. & Wróbel M. 2007. Habitat diversity and spontaneous succession of forest wetlands in Białowieża primeval forest, pp. 37–43. In: Okruszko T., Maltby E., Szatylowicz J., Mirosław-Swiątek D. & Kotowski W. (eds), *Wetlands: Modeling, Monitoring and Management*, Taylor and Francis, London.
- Douda J., Boublík K., Slezák M., Biurrún I., Nociar J., Havrdová A., Doudová J., Aćić S., Brisse H., Brunet J., Chytrý M., Claessens H., Csiky J., Didukh Y., Dimopoulos P., Dullinger S., FitzPatrick Ú., Guisan A., Horchler P.J., Hrivnák R., Jandt U., Kącki Z., Kevey B., Landucci F., Lecomte H., Lenoir J., Paal J., Paternoster D., Pauli H., Pielech R., Rodwell J.S., Roelandt B., Svenning J.C., Šibík J., Šilc U., Škvorec Z., Tsiropidis I., Tzonev R.T., Wöhlgemuth T. & Zimmermann N.E. 2016a. Vegetation classification and biogeography of European floodplain forests and alder carrs. *Appl. Veg. Sci.* **19**: 147–163.
- Douda J., Čejková A., Douda K. & Kochánková J. 2009. Development of alder carr after the abandonment of wet grasslands during the last 70 years. *Ann. For. Sci.* **66**: 1–13.
- Douda J., Doudová-Kochánková J., Boublík K. & Drašnarová A. 2012. Plant species coexistence at local scale in temperate swamp forest: test of habitat heterogeneity hypothesis. *Oecologia* **169**: 523–534.
- Douda J., Hulík J. & Doudová J. 2016b. Vegetative sprouting as an additional pathway for a seed size-number trade-off: a field-parameterised simulation approach. *Community Ecol.* **17**: 205–215.
- Emrani S.N., Arzani A. & Saeidi G. 2013. Seed viability, germination and seedling growth of canola (*Brassica napus* L.) as influenced by chemical mutagens. *Afr. J. Biotechnol.* **10**: 12602–12613.
- Eriksson O. & Fröberg H. 1996. “Windows of opportunity” for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Can. J. Bot.* **74**: 1369–1374.
- Fernández-Pascual E., Jiménez-Alfaro B. & Díaz T.E. 2013. The temperature dimension of the seed germination niche in fen wetlands. *Plant ecol.* **214**: 489–499.
- Fojt W. & Harding M. 1995. Thirty years of change in the vegetation communities of valley mires in Suffolk, England. *J. Appl. Ecol.* **32**: 561–577.
- Grime J.P., Mason G., Curtis A.V., Rodman J., Band S.R., Mowforth M.A.G., Neal A.M. & Shaw S. 1981. A comparative study of germination characteristics in a local flora. *J. Ecol.* **69**: 1017–1059.
- Gross N., Suding K.N., Lavorel S. & Roumet C. 2007. Complementarity as a mechanism of coexistence between functional groups of grasses. *J. Ecol.* **95**: 1296–1305.
- Hegi G. 1980. *Illustrierte Flora von Mitteleuropa*, Band 2, Teil 1, *Cyperaceae, Typhaceae incl. Sparganiaceae, Araceae, Lemnaceae, Juncaceae*, 3rd edition. Parey, Berlin.
- Hothorn T., Bretz F. & Westfall P. 2013. Package “multcomp”. <http://cran.stat.sfu.ca/web/packages/multcomp/multcomp.pdf> (accessed 18.8.2013).
- Keddy P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**: 157–164.
- Keddy P.A., Wisheu I.C., Shippley B. & Gaudet C. 1989. Seed banks and vegetation management for conservation: toward predictive community ecology, pp. 347–365. In: Leck M.A., Parker V.T. & Simpson R.L. (eds), *Ecology of Soil Seed Banks*. Academic Press, San Diego.
- Kettenring K.M. & Galatowitsch S.M. 2007. Temperature requirements for dormancy break and seed germination vary

- greatly among 14 wetland *Carex* species. *Aquat. Bot.* **87**: 209–220.
- Kettenring K.M. & Galatowitsch S.M. 2011a. Seed rain of restored and natural prairie wetlands. *Wetlands* **31**: 283–294.
- Kettenring K.M. & Galatowitsch S.M. 2011b. *Carex* seedling emergence in restored and natural prairie wetlands. *Wetlands* **31**: 273–281.
- Leck M.A. & Schütz W. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. *Perspect. Plant Ecol. Evol. Syst.* **7**: 95–133.
- Mayfield M.M. & Levine J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* **13**: 1085–1093.
- McCullagh P. & Nelder J. A. 1989. *Generalized Linear Models*, 2nd edition. Chapman & Hall, London, 532 pp.
- Narbona E., Delgado A., Encina F., Miguez M. & Buide M.L. 2013. Seed germination and seedling establishment of the rare *Carex helodes* Link depend on the proximity to water. *Aquat. Bot.* **110**: 55–60.
- Schütz W. 1997a. Are germination strategies important for the ability of cespitose wetland sedges (*Carex*) to grow in forests? *Can. J. Bot.* **75**: 1692–1699.
- Schütz W. 1997b. Primary dormancy and annual dormancy cycles in seeds of six temperate wetland sedges. *Aquat. Bot.* **59**: 75–85.
- Schütz W. 2000. Ecology of seed dormancy and germination in sedges (*Carex*). *Perspect. Plant Ecol. Evol. Syst.* **3**: 67–89.
- Schütz W. & Rave G. 1999. The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecol.* **144**: 215–230.
- Schütz W. & Rave G. 2003. Variation in seed dormancy of the wetland sedge, *Carex elongata*, between populations and individuals in two consecutive years. *Seed Sci. Res.* **13**: 315–322.
- Silvertown J. 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* **19**: 605–611.
- Thompson K., Bakker J.P. & Bekker R.M. 1997. *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge university press, Cambridge, 288 pp.
- Tolasz R., Míková T. & Valeriánová A. 2007. *Climate atlas of Czechia*. ČHMÚ, Praha & UP, Olomouc.
- Van der Valk A.G., Bremholm T.L. & Gordon E. 1999. The restoration of sedge meadows: seed viability, seed germination requirements, and seedling growth of *Carex* species. *Wetlands* **19**: 756–764.
- Van der Valk A.G. & Pederson R.L. 1989. Seed banks and the management and restoration of natural vegetation, pp. 329–346. In: Leck M.A., Parker V.T. & Simpson R.L. (eds), *Ecology of Soil Seed Banks*, Academic Press, San Diego.
- Van Kleunen M., Fischer M. & Schmid B. 2002. Experimental life-history evolution: selection on the allocation to sexual reproduction and its plasticity in a clonal plant. *Evolution* **56**: 2168–2177.
- Venables W.N. & Ripley B.D. 1998. *Modern Applied Statistics with S-Plus*. Springer-Verlag, New York, 447 pp.

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