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Temperature requirements for dormancy break and seed germination vary greatly among 14 wetland *Carex* species

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Abstract

We evaluated dormancy loss in seeds of 14 *Carex* species (*C. atherodes*, *C. brevior*, *C. comosa*, *C. cristatella*, *C. cryptolepis*, *C. granularis*, *C. hystericina*, *C. lacustris*, *C. pellita*, *C. scoparia*, *C. stipata*, *C. stricta*, *C. utriculata*, *C. vulpinoidea*) under growing season and stratification conditions and determined the temperature requirements for germination. Seeds were germinated for 1 year at a diel temperature regime (5/1 °C, 14/1 °C, 22/8 °C, or 27/15 °C) or a seasonal regime (seeds moved among the four diel regimes to mimic seasonal temperatures). All species had conditionally dormant seeds at maturity. The optimal temperature for germination of most species was 27/15 °C. The 14 species were grouped by their seed viability, dormancy, and germination with a Seed Regeneration Index (SRI; range 0–1) using the results of this study and a previously published paper on stratification effects on *Carex* seed dormancy and germination. The eight species that had an SRI value >0.5 (*C. brevior*, *C. comosa*, *C. cristatella*, *C. cryptolepis*, *C. hystericina*, *C. scoparia*, *C. stipata*, *C. vulpinoidea*) had high seed viability (>60%) and required little to no stratification to germinate readily over a broad range of temperatures. The six species with an SRI value <0.5 (*C. atherodes*, *C. granularis*, *C. lacustris*, *C. pellita*, *C. stricta*, *C. utriculata*) generally had low seed viability (<50% and often <1%) and required stratification or particular temperatures (35/30 °C or 5/1 °C for *C. stricta*; 35/30 °C for *C. utriculata*; 27/15 °C for *C. atherodes*, *C. lacustris*, *C. pellita*; 5/1 °C for *C. granularis*) for germination ≥50%. These six species will require more attention from restoration practitioners to ensure that there are sufficient viable seeds to meet revegetation goals, that dormancy break is achieved, and that seeds are sown when temperatures are optimal for germination. The different seed germination syndromes that we found for these *Carex* species likely contribute to variable seed bank formation and emergence patterns, and species coexistence.

Keywords: Cold stratification; Germination temperature; Glacial wetland; Prairie pothole region; Sedge; Seed dormancy; Seed germination ecology

1. Introduction

As humans attempt to reverse trends of environmental degradation, ecosystem restoration is becoming increasingly important. Restoration efforts are often hampered by a lack of basic ecological information of the processes and species involved. For instance, attempts to restore plant communities are often limited by a dearth of knowledge of the life history of native species (Clewell and Rieger, 1997). Revegetation efforts focus on seeding target species directly into restoration sites or propagating plants for transplantation to restorations (Galatowitsch and van der Valk, 1994; Guerrant, 1996; Middleton, 1999). Understanding the requirements for dormancy break and germination of desired species is necessary to maximize the often limited native seed supply in many restoration efforts (Lippitt et al., 1994; Urbanska, 1997; Middleton, 1999). In nature, the requirements for seed dormancy break and germination may vary greatly within and among species (Baskin and Baskin, 1998). From a restoration perspective, breaking seed dormancy and providing suitable germination microsites can be relatively straightforward or very complicated depending on the species and its class of seed dormancy (i.e., physiological, morphological, morphophysiological, physical, or combinational) (Lippitt et al., 1994; Diboll, 1997; Baskin and Baskin, 1998; Cochrane et al., 2002). Seed dormancy and germination ecology can be quite different even for congeneric species (Grime et al., 1981; Shipley and Parent, 1991; Meyer et al., 1995; Schütz and Rave, 1999; Brändel,

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2004; Hölzel and Otte, 2004; Kettenring and Galatowitsch, 2007). These variations in seed dormancy break and germination requirements influence plant emergence patterns that can drive plant population persistence and plant community diversity (Harper, 1977; Thompson and Grime, 1979; Hutchings, 1997). At the same time, these variations and complexities often limit revegetation success and challenge restorationists (Clewell and Rieger, 1997; Diboll, 1997; Cochrane et al., 2002).

In the glaciated region of mid-continental North America, thousands of acres of wetlands have been hydrologically restored within the last 20–30 years to counteract the loss of this valuable natural resource and prized waterfowl habitat (Galatowitsch and van der Valk, 1996a). Little effort, however, has been placed on active revegetation; the assumption generally has been that the native species will recolonize rapidly from remnant seed banks or from seed source wetlands in the landscape (Galatowitsch and van der Valk, 1996c). Seed banks of sedge meadow species, however, are usually depleted because of the often lengthy period of wetland drainage (sometimes 50–100 years) prior to most restorations (Wienhold and van der Valk, 1989). In addition, while some species recolonize quickly from wetlands in the landscape, the characteristic *Carex* species, that are dominants of natural wetlands in this area, are noticeably absent (Galatowitsch and van der Valk, 1996b,c; Mulhouse and Galatowitsch, 2003). Recolonization by these species is seed limited (Kettenring, 2006), but two studies have found that seeds of at least some *Carex* species germinate readily if sown into restored wetlands (Bohnen and Galatowitsch, 2005; Kettenring, 2006). Without active revegetation efforts, these sites become dominated by the invasive species *Phalaris arundinacea* (reed canary grass), preempting the establishment of *Carex* species (Mulhouse and Galatowitsch, 2003). Future efforts to revegetate these wetlands will require knowledge of the dormancy and germination ecology of these key *Carex* species.

Seed production and seed viability vary considerably among *Carex* species (Leck and Schütz, 2005). Many species of *Carex* spread clonally through rhizomes, form large, dense mats, and tend to produce few seeds with low viability (Gleason and Cronquist, 1991; Schütz, 2000), while others have a cespitose growth form and generally have high production of viable seeds (Leck and Schütz, 2005). Despite these variations in growth habits and seed viability and production, propagation by seed in the wild is important for all species of *Carex* to recolonize new sites after disturbance and maintain gene flow among distant populations. Further, seeding is the most efficient method for revegetation in restorations but low production of viable seeds further challenges revegetation efforts and makes knowledge of the seed dormancy and germination ecology especially crucial.

Many species of *Carex* produce seeds with physiological dormancy (Schütz, 2000), the most common type of seed dormancy in plants (Baskin and Baskin, 1998). In species with physiological dormancy, nondormant seeds germinate under the full range of conditions possible for the species or that population, conditionally dormant seeds germinate under a narrower range of conditions than nondormant seeds, and dormant seeds are unable to germinate under any conditions usually suitable for germination (Baskin and Baskin, 1998). Physiological dormancy in nature may be broken during cold stratification, i.e. seeds are exposed to moist, cold conditions (0–10 °C). However, depending on the species, physiological dormancy also can be broken during exposure to the high temperature conditions of summer (Baskin and Baskin, 1998). To determine whether seeds are dormant or conditionally dormant, seeds are treated with conditions known to break dormancy to see if the range of conditions (e.g., light, inundation, and for our study, temperature) suitable for germination broadens.

While there have been numerous studies on seed dormancy and germination of many European *Carex* species (see Schütz, 2000 for a review), only a few studies have focused on the *Carex* species common in wetlands in mid-continental North America (Larson and Stearns, 1990; Baskin et al., 1996; Budelsky and Galatowitsch, 1999; van der Valk et al., 1999; Kettenring and Galatowitsch, 2007). For many species, it is not known whether freshly matured seeds are physiologically dormant and how this dormancy affects seed germination at different temperatures. From a restoration perspective, it is important to understand if, for instance, stratification is required for dormancy break and whether freshly matured seeds will germinate readily without stratification across different growing season temperatures.

The specific objectives of our study were to (1) evaluate the dormancy state in freshly matured *Carex* seeds of 14 species, (2) determine if cold, moist stratification is required to break physiological dormancy, and (3) determine what temperatures are suitable for germination of freshly matured *Carex* seeds and seeds that have been stratified. Our experimental approach was to use a ''move-along'' experiment (sensu Baskin and Baskin, 2004) where for 1 year *Carex* seeds are incubated at one of four diel temperature regimes or in the seasonal (move-along) treatment, seeds move through these four diel temperature regimes to mimic seasonal temperature changes in the field. By contrasting the performance of seeds incubated at a constant diel regime with seeds that transition through a winter stratification period, we can determine: (1) whether seeds are totally dormant or conditionally dormant at maturity and (2) whether dormancy breaks down with stratification (in seasonal regime) or under growing season temperatures (in diel regimes). We combined the results of our study with those of a previously published paper on *Carex* seed dormancy (Kettenring and Galatowitsch, 2007) in a Seed Regeneration Index (SRI) that predicts how readily seeds of these *Carex* species are likely to germinate in the field under diverse temperature conditions.

2. Materials and methods

2.1. Seed collection and viability tests

The 14 species used in this study occupy a range of wetland habitats in the glaciated mid-continental North America (Table 1). Seeds were collected at maturity from wetlands in Minnesota and Iowa during the summers of 2002–2004

Table 1
The 14 *Carex* species used in this study

Species	Seed maturation	Seed collection location	Seed viability	Habitat[a]
C. atherodes Sprengel.	Mid-August	(43°28′N, 95°8′W)$^{\beta}$	$^{\alpha}$15%$^{\beta}$	Marshes, shallow water
C. brevior (Dewey) Mackenzie.	Mid-July	(44°40′N, 93°37′W)$^{\beta\gamma}$	80%$^{\beta}$, 82%$^{\gamma}$	Usually in dry soil
C. comosa F. Boott.	Early September	(44°51′N, 93°36′W)$^{*\gamma}$	84*, 95%$^{\gamma}$	Swamps, wet meadows
C. cristatella Britton.	Early August	(44°51′N, 93°36′W)$^{*\gamma}$	63%*, 93%$^{\gamma}$	Open swamps, wet meadows, shores
C. cryptolepis Mackenzie.	Late October	(45°9′, 93°8′W)$^{\gamma}$	80%$^{\gamma}$	Wet meadows and shores
C. granularis Muhl.	Mid-July	(44°40′N, 93°37′W)$^{\beta\gamma}$	39%$^{\beta}$, 56%$^{\gamma}$	Wet meadows and swales
C. hystericina Muhl.	Mid-July	(44°51′N, 93°36′W)$^{*\gamma}$	69%*, 89%$^{\gamma}$	Swamps, wet meadows, shores
C. lacustris Willd.	Mid-August	(44°51′, 93°36′W)$^{\beta}$, (45°24′N, 93°12′W)$^{\gamma}$	$^{\alpha}$42%$^{\beta}$,14%$^{\gamma}$	Swamps, marshes
C. pellita Ehrh.	Late July	(44°40′N, 93°37′)$^{\beta}$	$^{\alpha}$22%$^{\beta}$	Bogs, marginal sedge-mats, shallow water
C. scoparia Schk.	Late July	(45°24′N, 93°12′W)$^{\gamma}$	90%$^{\gamma}$	Open swamps, wet meadows, shores
C. stipata Muhl.	Late June	(44°51′N, 93°36′W)$^{*\gamma}$	54%*, 71%$^{\gamma}$	Wet low ground
C. stricta Lam.	Mid-August	(45°24′N, 93°12′W)$^{\gamma}$	$^{\alpha}$3%$^{\gamma}$	Swales and marshes, especially where seasonally flooded
C. utriculata Stokes.	Mid-August	(45°24′, 93°12′W)$^{\gamma}$	$^{\alpha}$9%$^{\gamma}$	Wet soil, shallow water
C. vulpinoidea Michx.	Early August	(44°51′N, 93°36′W)$^{*\gamma}$	73%*, 82%$^{\gamma}$	Marshes, other wet low places

(α) Initial seed viability values for these species were <1% so seeds were sorted by hand or with an air column separator to remove empty seeds (i.e., unfilled achene in perigynia) to increase the proportion of viable seeds in the experiments. Seeds were collected at maturity from wetlands in Minnesota and Iowa, USA, in (*) 2002, (β) 2003, and ($^{\gamma}$) 2004. Seed viabilities of seed batches in the experiments are from different years of collection (*, 2002; β, 2003, γ, 2004).
[a] From Gleason and Cronquist (1991).

(Table 1). Prior to the start of the experiments, seeds were tested for viability using standard tetrazolium testing procedures (n = 200 seeds per species; Grabe, 1970). For a few species (*C. atherodes*, *C. lacustris*, *C. pellita*, *C. stricta*, C. *utriculata*), initial seed viability was <1% and seeds were sorted by hand or with an air column separator to remove empty seeds (i.e., unfilled achene in perigynia) to increase the proportion of viable seeds in the experiments (see Table 1).

2.2. Move-along experiment

Over 1 year, we observed the dormancy break and germination response of seeds incubated in growth chambers (Model GCW-15, Environmental Growth Chambers, Chagrin Falls, OH) set at one of four diel temperature regimes (5/1 °C, 14/1 °C, 22/8 °C, or 27/15 °C; 10:10 h of high and low temperature with a 2-h linear transition between temperature changes) or one seasonal (i.e., move-along) regime (Baskin and Baskin, 2004). Seeds were stored dry at room temperature for 2–3 weeks prior to the start of the germination experiment. Seed germination of four species (*C. cryptolepis*, *C. scoparia*, *C. stricta*, *C. utriculata*) also was evaluated at an additional diel temperature regime of 35/30 °C. For the other 10 species, the diel temperature germination trials were repeated in a subsequent year and 35/30 °C was added to this trial. In the seasonal regime, seeds moved among four chambers set at different seasonal temperatures (i.e., the diel temperature regimes not including 35/30 °C) to mimic field conditions. Depending on the time of seed maturation, seeds entered the seasonal regime in the summer (27/15 °C for a maximum of 12 weeks starting June 1, or proportionally fewer weeks if entering after June 1; *C. atherodes*, *C. brevior*, *C. cristatella*, *C. granularis*, *C. hystericina*, *C. lacustris*, *C. pellita*, *C. scoparia*, *C. stipata*, *C. stricta*, *C. utriculata*, *C. vulpinoidea*), early fall (22/8 °C for at most 4.5 weeks; *C. comosa*), or late fall (14/1 °C for at most 4.5 weeks; *C. cryptolepis*). Then, after the winter stratification period (5/1 °C for 21 weeks), seeds transitioned back to summer (27/15 °C) with 4.5 weeks at 14/1 °C (early spring) followed by 4.5 weeks at 22/8 °C (late spring).

The four diel temperature regimes in the seasonal cycle were chosen based on long-term temperature data (1961–1990) taken near Lake Park, Dickinson County, IA (43.45°N 95.31°W), archived by the National Climatic Data Center (acquired at www.worldclimate.com). The temperature regime 5/1 °C was chosen for winter conditions (rather than placing seeds in sub-freezing temperatures) to maximize the potential for seed stratification and dormancy loss; 5/1 °C is often suitable for breaking dormancy in many species with physiological dormancy (Baskin and Baskin, 1998). The 35/30 °C temperature regime represented an extreme temperature that a seed might encounter on the soil surface in a wetland with little to no vegetation, as in a new restoration.

All seeds were incubated in growth chambers illuminated with cool white fluorescent bulbs at PAR (photosynthetically active radiation, total irradiance between 400 and 700 nm) = 200 μmol m^{-2} s^{-1} at seed level as measured with the LI-189 quantum sensor (LICOR, Lincoln, Nebraska, USA). The lights turned on as the temperature increased to the high temperature and remained on for the 14 h until the temperature decreased to the low temperature. A single exposure to $\leq$14 h of white light (PAR = 200 μmol m^{-2} s^{-1}) is sufficient to trigger seed germination of at least eight of the study species (Kettenring et al., 2006); thus we assumed that light was not a limiting factor to seed germination.

Seed viability values were used to ensure that each treatment for each species had a sample size of at least 300 viable seeds, except for some species where seed supplies in the field were limiting (*C. atherodes*, *C. cryptolepis*, *C. lacustris*, *C. pellita*, *C. stricta*, *C. utriculata*). In these cases, the sample size was at

least 150 viable seeds per treatment. We used either 6 cm or 10 cm Petri dishes for each species with either 25 or 50 seeds per dish, respectively. Thus, the number of Petri dishes (d) required per species and number of seeds per dish (s/d) was different: *C. atherodes* (39 d, 25 s/d), *C. brevior* (15 d, 25 s/d), *C. comosa* (17 d, 25 s/d), *C. cristatella* (20 d, 25 s/d), *C. cryptolepis* (4 d, 50 s/d), *C. granularis* (34 d, 25 s/d), *C. hystericina* (17 d, 50 s/d), *C. lacustris* (15 d, 25 s/d), *C. pellita* (15 d, 25 s/d), *C. scoparia* (4 d, 50 s/d), *C. stipata* (21 d, 25 s/d), *C. stricta* (12 d, 50 s/d), *C. utriculata* (9 d, 50 s/d), and *C. vulpinoidea* (20 d, 25 s/d). We did not retest seed viability on ungerminated seeds at the end of the experiment. Thus, some ungerminated seeds may have no longer been viable, although seed viability loss under moist conditions is much lower than viability loss commonly associated with storage under dry conditions (Budelsky and Galatowitsch, 1999).

Seeds were incubated on saturated white silica sand in Petri dishes wrapped in two layers of plastic wrap to reduce water loss. Seeds were watered with deionized water every 1–2 weeks to maintain a moist germination substrate and checked for germination every 2 weeks. The 2-week interval for germination assessment was deemed suitable given our goal of comparing the broad patterns of germination across species and temperature regimes. Germination was defined as radicle or cotyledon emergence when visible without magnification.

2.3. Analysis

The data were graphically explored by plotting the cumulative germination curves for the diel and seasonal temperature regimes (SigmaPlot, Systat Software Inc., 2004). Germination percentages were corrected for seed viability by dividing germination percentage by the possible number of germinated seeds (i.e., number of viable seeds based on initial tetrazolium tests). From the cumulative germination data for each curve, maximum percent germination, the lag time to germination (in days), time to 50% germination (t_{50}), and the maximum germination rate (percent of seeds germinating per week) were determined. The lag time to germination was defined as the number of days between the start of the experiment and when germination first occurred. To calculate time to 50% germination (t_{50}) and maximum germination rate for each species for each temperature regime, logistic regression curves were fitted to the cumulative germination curves using the SSlogis function in R (R Development Core Team, 2005). A curve was determined as a proper fit by evaluating residual plots. If greater than 5% of the data points had a residual value of greater than 0.05, the curve fit was rejected. In this case, t_{50} and maximum germination rate were calculated manually by graphing the data in Excel (Microsoft Corporation, 2002) and, for the former, finding the point on the cumulative germination curve where 50% of maximum seed germination for that condition occurred. Maximum germination rate for each cumulative germination curve was calculated manually by determining the slope of the 1-week interval with the greatest germination. If a species did not achieve at least 10% maximum germination, then t_{50} and maximum germination rate were not calculated for a particular curve because they would be structurally correlated (Shipley and Parent, 1991).

We also used ANOVA and Tukey HSD to evaluate the effect of temperature on maximum percent germination for each species (Analytical Software, 2003). *P*-values of <0.05 were considered significant. All germination proportions were arcsine square root transformed prior to analyses to standardize the variance.

2.4. Seed Regeneration Index

In order for the findings of our study to be more meaningful to plant ecologists and restoration practitioners, an index that provides a relative measure of seed regeneration ability across species is necessary. A Seed Regeneration Index (SRI; range 0–1) for each species was calculated as a means of comparing all species with respect to their seed viability, dormancy, and germination based on the results of the initial seed viability estimates, the move-along experiment, and a previously published *Carex* seed stratification experiment (Kettenring and Galatowitsch, 2007) (Fig. 1). Species with a low SRI value are expected to regenerate via seed less frequently than those with a high SRI value.

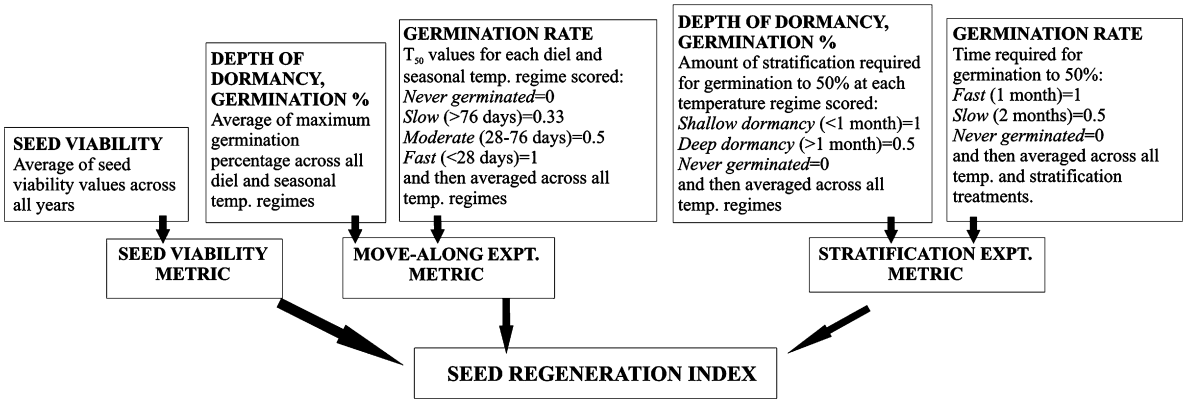

Fig. 1. How the Seed Regeneration Index (SRI) was calculated for each species.

Separate metrics from (a) seed viability, (b) move-along experiment, and (c) stratification experiment were averaged to calculate the SRI for each species. For (b) and (c), there were two components of the metric (depth of dormancy/germination % and germination rate); after these components were calculated, they were averaged for a single value for the metric.

In the seed stratification experiment, *Carex* seeds were stratified at 5/1 °C for 0 weeks (control), 2 weeks, or 1, 2, 3, 4, 5, or 6 months and then germinated at one of five diel temperature regimes: 5/1 °C, 14/1 °C, 22/8 °C, 27/15 °C, or 35/30 °C (see Kettenring and Galatowitsch, 2007 for a more detailed description of the methods). Differences in germination for each species were qualitatively compared across the stratification lengths and temperature regimes and the data are summarized in Fig. 2. Here, species were compared according to whether 50% germination had been achieved within 1 or 2 months. The 1-month versus 2-month distinction was used as an indicator of how quickly germination might occur under field conditions, as in a restoration. The response of "germination to 50%" was chosen as a convenient factor that could be compared for each species between the stratification and move-along experiments.

3. Results

3.1. Move-along experiment

Maximum percent germination for each of the 14 *Carex* species varied significantly by temperature regime (Figs. 3 and 4, Table 2). In the seasonal regime, all but one species (*C. utriculata*) germinated ≥50% (Table 2). The sequence of temperatures in the seasonal regime was particularly beneficial for six species (*C. comosa*, *C. cryptolepis*, *C. granularis*, *C. pellita*, *C. scoparia*, *C. stricta*); these species achieved greater germination in the seasonal regime than at any other temperature regime. Four species (*C. cryptolepis*, *C. scoparia*, *C. stricta*, and *C. utriculata*) germinated ≥50% at 35/30 °C. The optimal diel temperature regime for germination for most species was 27/15 °C; all but four species (*C. cryptolepis*, *C. granularis*, *C. stricta*, *C. utriculata*) germinated ≥50%. At 22/8 °C, seeds of *C. brevior*, *C. cristatella*, *C. scoparia*, and *C. stipata* germinated ≥50%. *Carex brevior* was the only species to germinate ≥50% at 14/1 °C. Seeds of five species responded strongly to constant cold stratification such that they eventually germinated ≥50% at 5/1 °C (*C. cristatella*, *C. granularis*, *C. scoparia*, *C. stricta*, and *C. vulpinoidea*) while germination was

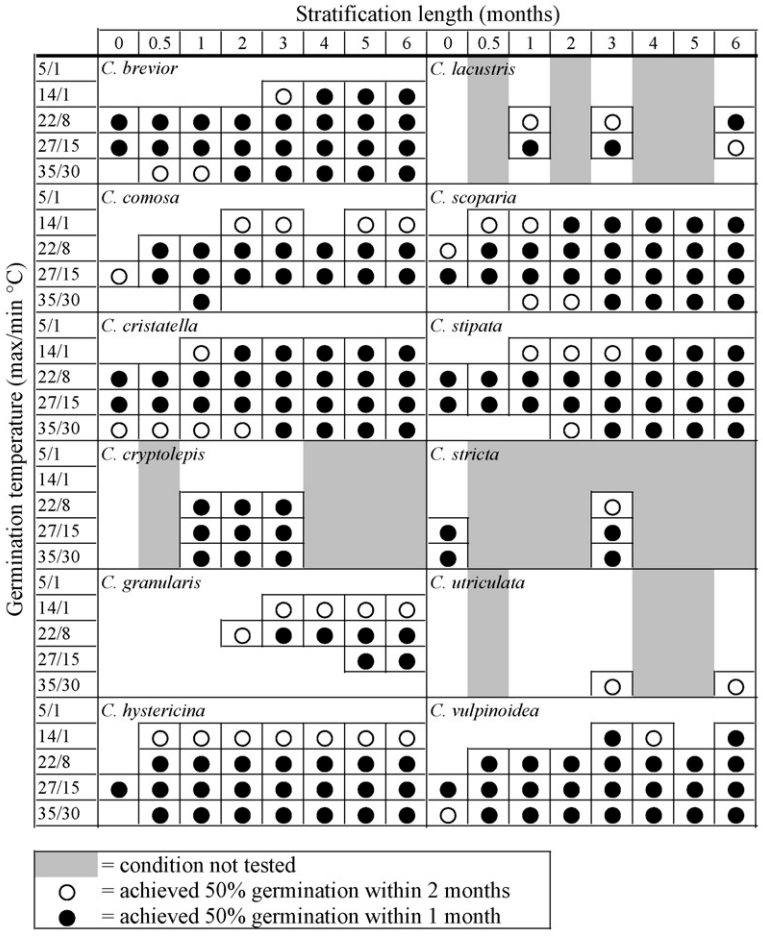

Fig. 2. *Carex* germination after different lengths of stratification. This figure is adapted from Kettenring and Galatowitsch (2007).

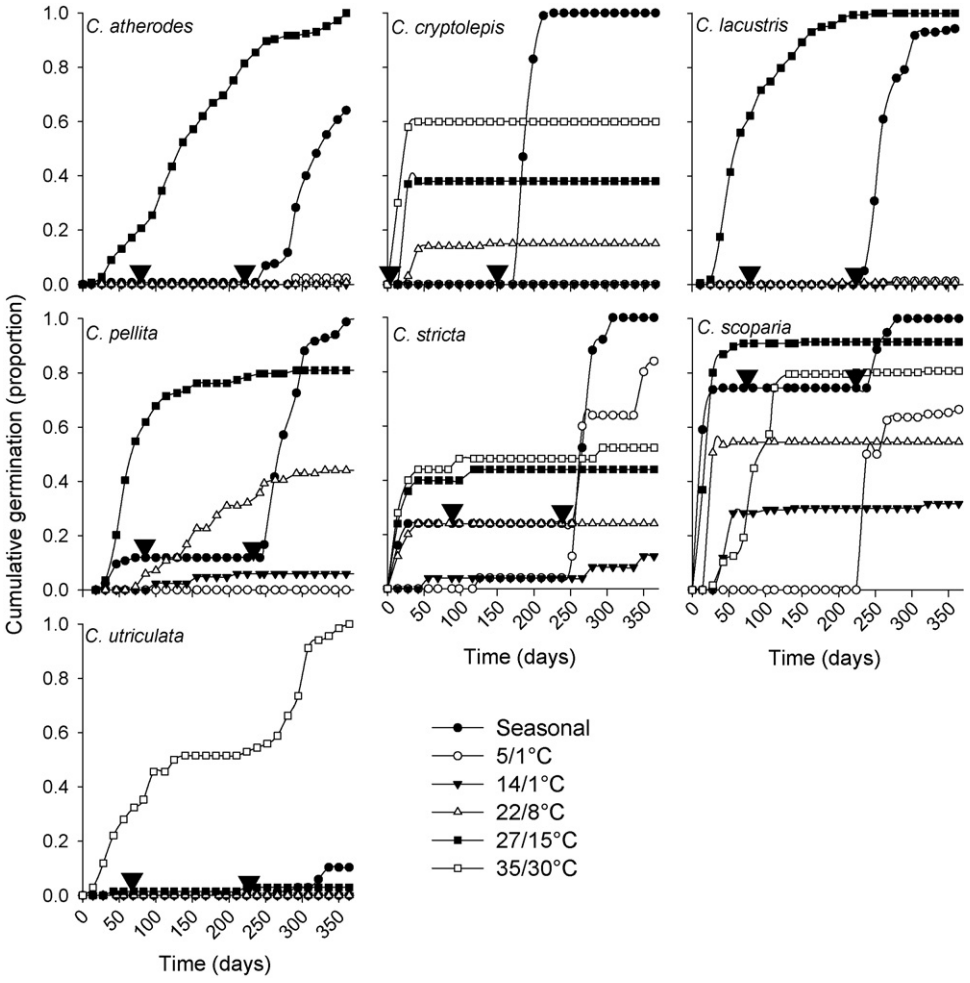

Fig. 3. *Carex* germination from the move-along experiment for seven species. (▼) This denotes the start and end of the period when seeds in the seasonal treatment were incubated at 5/1 °C for stratification.

Table 2
Maximum percent germination for the 14 *Carex* species in the move-along experiment at four diel and one seasonal temperature regime

Species	Mean percent germination ± 1 standard error				
	Seasonal	27/15 °C	22/8 °C	14/1 °C	5/1 °C
C. atherodes***	64 ± 1^{b}	100 ± 1^{a}	1 ± 0^{c}	0 ± 0^{c}	2 ± 0^{c}
C. brevior***	100 ± 2^{a}	100 ± 2^{a}	96 ± 2^{a}	63 ± 3^{b}	48 ± 4^{c}
C. comosa***	100 ± 2^{a}	75 ± 5^{b}	ND	4 ± 1^{c}	0 ± 0^{c}
C. cristatella***	96 ± 2^{a}	99 ± 2^{a}	100 ± 2^{a}	44 ± 2^{b}	86 ± 3^{a}
C. cryptolepis***	100 ± 14^{a}	38 ± 7^{b}	15 ± 3^{c}	0 ± 0^{d}	0 ± 0^{d}
C. granularis***	100 ± 2^{a}	21 ± 1^{b}	2 ± 0^{c}	0 ± 0^{c}	90 ± 2^{a}
C. hystericina***	87 ± 3^{a}	100 ± 3^{a}	ND	7 ± 1^{b}	0 ± 0^{c}
C. lacustris***	94 ± 3^{a}	100 ± 3^{a}	1 ± 0^{b}	0 ± 0^{b}	1 ± 0^{b}
C. pellita***	100 ± 3^{a}	81 ± 2^{a}	44 ± 2^{b}	6 ± 1^{c}	0 ± 0^{c}
C. scoparia***	100 ± 3^{a}	91 ± 4^{ab}	55 ± 7^{cd}	32 ± 9^{d}	66 ± 7^{bc}
C. stipata***	93 ± 3^{ab}	100 ± 3^{a}	81 ± 3^{b}	24 ± 2^{c}	1 ± 0^{d}
C. stricta***	100 ± 21^{a}	44 ± 13^{ab}	24 ± 11^{b}	12 ± 6^{b}	84 ± 19^{a}
C. utriculata*	10 ± 1^{a}	3 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
C. vulpinoidea***	95 ± 2^{a}	100 ± 3^{a}	ND	1 ± 0^{c}	84 ± 2^{b}

ND indicates no data are available for the species at 22/8 °C. Letters indicate results of a Tukey HSD comparison test for each species. Same letters indicate no significant difference between the pairs for $\alpha = 0.05$.

* $P < 0.05$.

*** $P < 0.001$.

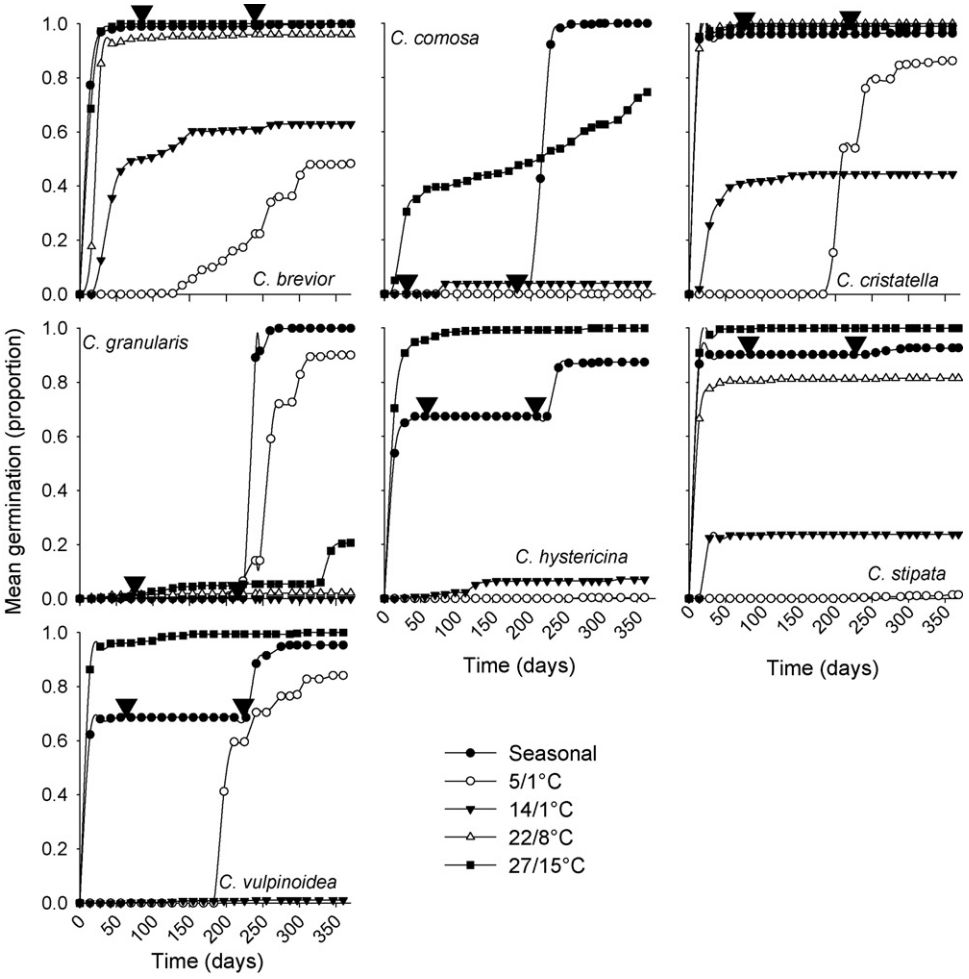

Fig. 4. *Carex* germination from the move-along experiment for seven additional species for which a second year of germination data are also available (see Fig. 5). (▼) This denotes the start and end of the period when seeds in the seasonal treatment were incubated at 5/1 °C for stratification.

≤50% at 14/1 °C for these species (i.e., most seeds remained conditionally dormant at this temperature).

The lag time to germination varied enormously by species and temperature regime (Figs. 3 and 4). In the seasonal regime, seven species (*C. brevior*, *C. cristatella*, *C. hystericina*, *C. scoparia*, *C. stipata*, *C. stricta*, *C. vulpinoidea*) began to germinate within 2 weeks and *C. atherodes* and *C. pellita* within 6 weeks. In the diel regimes, at 27/15 °C, seeds of most species started germinating within 2 weeks (*C. atherodes*, *C. brevior*, *C. comosa*, *C. cristatella*, *C. hystericina*, *C. lacustris*, *C. scoparia*, *C. stipata*, *C. stricta*, *C. vulpinoidea*), while the four species that did not (*C. cryptolepis*, *C. granularis*, *C. pellita*, *C. utriculata*), began within 6 weeks. At 22/8 °C, seeds of *C. brevior*, *C. cristatella*, *C. stipata*, and *C. stricta* began to germinate within 2 weeks and seeds of *C. cryptolepis*, *C. granularis*, and *C. scoparia* within 6 weeks. At 14/1 °C, the lag time to germination was 2 weeks for *C. cristatella* and ≤6 weeks for *C. brevior*, *C. hystericina*, *C. scoparia*, and *C. stipata*. At 5/1 °C, the lag time to germination was ≥14 weeks for all species.

The time to 50% germination (t_{50}) varied from ≤2 weeks at the more ideal conditions for most species (usually the seasonal regime, or the diel regimes 27/15 °C and 22/8 °C) to ≥28 weeks for all species at 5/1 °C (Figs. 3 and 4). t_{50} was ≤2 weeks in the seasonal regime for *C. brevior*, *C. cristatella*, *C. hystericina*, *C. scoparia*, *C. stipata*, and *C. vulpinoidea*; and in the diel regimes, at 27/15 °C for seven species (*C. brevior*, *C. cristatella*, *C. hystericina*, *C. scoparia*, *C. stipata*, *C. stricta*, and *C. vulpinoidea*); and at 22/8 °C for *C. cristatella*, *C. stipata*, and *C. stricta*. t_{50} was ≤8 weeks for *C. comosa*, *C. cryptolepis*, *C. lacustris*, and *C. pellita* at 27/15 °C; for *C. brevior*, *C. cryptolepis*, and *C. scoparia* at 22/8 °C; and for *C. brevior*, *C. cristatella*, *C. scoparia*, and *C. stipata* at 14/1 °C. t_{50} for all species was between 28 and 42 weeks at 5/1 °C. t_{50} was >14 weeks for *C. atherodes*, *C. granularis*, and *C. utriculata* at all conditions and >8 weeks at all conditions for *C. comosa*, *C. lacustris*, and *C. pellita*.

The maximum germination rate (percent of seeds per week) varied by species and treatment, and ranged from 1% to 68% per week, with many species having maximum germination rates of 30–50% per week (Table 3). For nine species (*C. atherodes*, *C. brevior*, *C. comosa*, *C. cryptolepis*, *C. granularis*, *C. lacustris*, *C. pellita*, *C. scoparia*, *C. utriculata*), the highest rate of germination was in the seasonal regime. For all other species, the highest rate of germination occurred in the diel regimes at 27/15 °C except for *C. stricta*, which had its highest germination rate at 5/1 °C.

Table 3
Maximum germination rate (percent of seeds per week) for the 14 species in the move-along experiment at four diel and one seasonal temperature regime

Species	Maximum germination rate (percent of seeds per week)				
	Seasonal	27/15 °C	22/8 °C	14/1 °C	5/1 °C
C. atherodes	14	5	[a]	[a]	[a]
C. brevior	38	32	36	11	5
C. comosa	36	1	ND	[a]	[a]
C. cristatella	47	48	45	12	19
C. cryptolepis	47	28	7	[a]	[a]
C. granularis	37	12	[a]	[a]	21
C. hystericina	27	35	ND	[a]	[a]
C. lacustris	23	12	[a]	[a]	[a]
C. pellita	13	12	4	[a]	[a]
C. scoparia	68	43	41	8	25
C. stipata	43	45	33	11	[a]
C. stricta	18	20	12	2	24
C. utriculata	3	[a]	[a]	[a]	[a]
C. vulpinoidea	31	43	ND	[a]	21

ND indicates no data are available for the species at 22/8 °C.
[a] No values are given for species that had <10% germination at a particular temperature.

The seven *Carex* species tested under the diel temperature regimes in multiple years exhibited differing germination responses, especially at 5/1 °C and 14/1 °C (Fig. 4 versus Fig. 5). For instance, maximum percent seed germination of *C. brevior* from 2003 was 25% higher at 5/1 °C and 55% higher at 14/1 °C than seed from 2004. At 14/1 °C, *C. comosa* seeds from 2004 germinated 50% higher than those from 2002. On the other hand, *Carex granularis* seed from 2003 and 2004 and *C. hystericina* seed from 2002 and 2004 germinated to very similar percentages at all temperatures (within 10% both years).

3.2. Seed Regeneration Index

The cold stratification treatments had a strong but variable effect on the ability of seeds to germinate to 50% and the rate of germination for all species, especially at 14/1 °C and 35/30 °C (Fig. 2) (see Kettenring and Galatowitsch, 2007 for additional results from the stratification experiment). When the results of the stratification experiment were summarized with the move-along experiment results and the seed viability data, we found that the 14 *Carex* species fell into two distinct groups: Group 1 included six species (*C. atherodes*, *C. granularis*, *C. lacustris*, *C. pellita*, *C. stricta*, *C. utriculata*) with an SRI <0.5 and Group

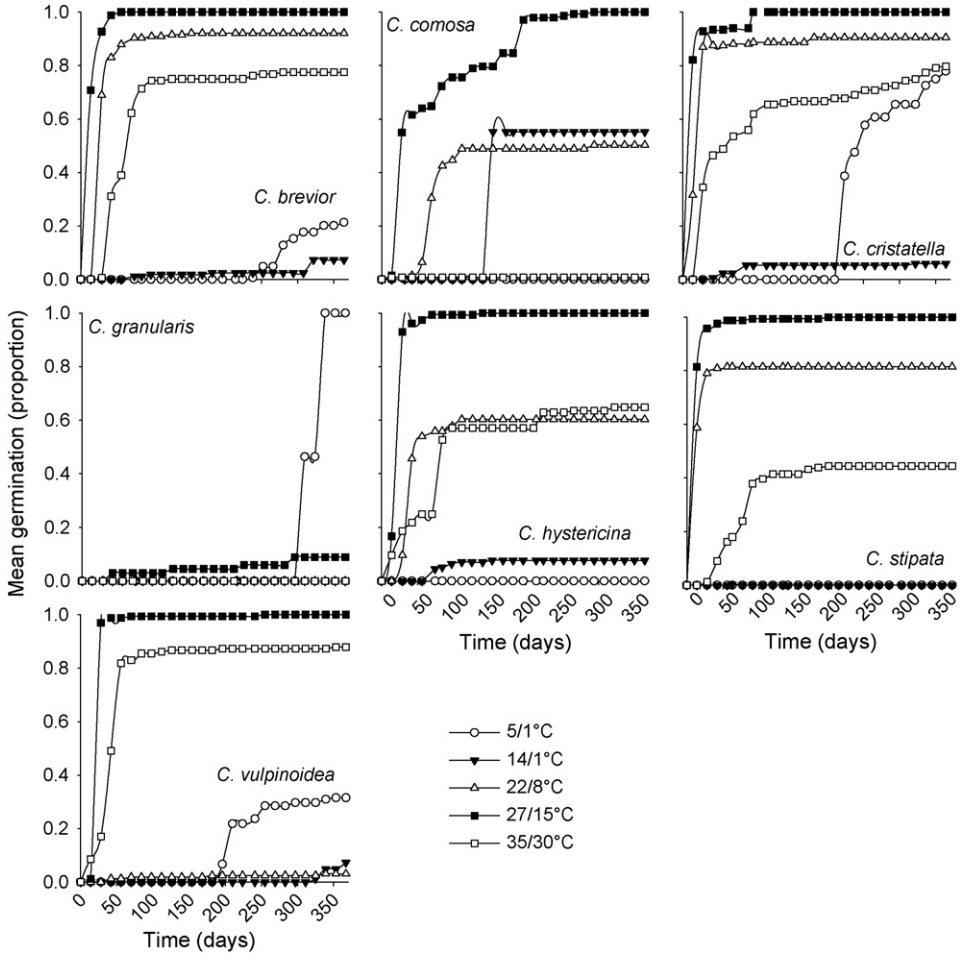

Fig. 5. Germination of seeds of seven *Carex* species at five diel temperature regimes for 1 year. Batches of seeds from a previous year were also incubated at the four cooler diel temperature regimes (data shown in Fig. 4).

Table 4
Seed Regeneration Index (SRI) values for each species and the different values from each experiment that contributed to the SRI

Species	Field seed viability	Move-along experiment		Stratification experiment		Seed Regeneration Index
		Dormancy depth, germination (%)	Germination rate	Dormancy depth, germination (%)	Germination rate	
Group 1						
C. utriculata	0.01	0.03	0.07	0.13	0.05	0.05
C. atherodes	0.01	0.33	0.13	ND	ND	0.12
C. pellita	0.01	0.46	0.20	ND	ND	0.17
C. lacustris	0.01	0.39	0.13	0.50	0.28	0.22
C. granularis	0.48	0.43	0.20	0.38	0.27	0.37
C. stricta	0.01	0.53	0.60	0.63	0.64	0.40
Group 2						
C. cryptolepis	0.80	0.31	0.40	0.75	0.56	0.60
C. comosa	0.90	0.45	0.25	0.88	0.55	0.65
C. stipata	0.63	0.60	0.80	0.75	0.78	0.70
C. hystericina	0.79	0.49	0.50	1.00	0.80	0.73
C. vulpinoidea	0.78	0.70	0.58	0.88	0.78	0.75
C. brevior	0.81	0.81	0.80	0.88	0.80	0.82
C. scoparia	0.90	0.69	0.80	0.88	0.83	0.83
C. cristatella	0.78	0.85	0.87	1.00	0.86	0.86

ND indicates no data are available for the species for the stratification experiment. Species with a high SRI value are expected to regenerate more readily by seed than those with a low SRI value. See Fig. 1 for further details on how the SRI was calculated.

2 included eight species (*C. brevior*, *C. comosa*, *C. cristatella*, *C. cryptolepis*, *C. hystericina*, *C. scoparia*, *C. stipata*, *C. vulpinoidea*) with an SRI >0.5 (Table 4). The species in Group 1 versus Group 2 differed greatly in their seed viability and depth of dormancy/germination % from the stratification experiment (i.e., Group 1 species had low seed viability and strong dormancy/low germination). Metrics for germination rate from both experiments and depth of dormancy/germination % from the move-along experiment were different between species in Group 1 with very low SRI values versus Group 2 with very high SRI values. However, for species with more intermediate SRI values, the germination rate and depth of dormancy/germination % metrics were overlapping.

4. Discussion

This study looks at two important aspects of seed dormancy and germination of wetland *Carex* species in North America: (1) dormancy loss in seeds under seasonal and stratification conditions and (2) the temperature requirements for germination of conditionally dormant and nondormant seeds. Seeds of all species examined in this study were conditionally dormant at maturity, a finding that is consistent with seed dormancy patterns in many other *Carex* species (Schütz, 2000). The optimal diel temperature regime for germination of conditionally dormant and nondormant seeds of most species was 27/15 °C. Based on these results we expect that nondormant *Carex* seeds, following either natural stratification in the field or lab stratification, can germinate early in the growing season and establish seedlings before the harsher conditions of midsummer.

Beyond the aforementioned similarities in dormancy and germination patterns, we found wide variation in dormancy breaking and germination requirements that demonstrates the diversity of life history strategies even for closely related species within a single genus from prairie wetlands of the midcontinental U.S. Approximately 60 species of wetland *Carex* are native to the prairie region of the U.S. (Barkley, 1986) and the variation in seed germination syndromes for species in the genus *Carex* likely contributes to variable seed bank formation and emergence patterns, and species coexistence. In our study, no two species had identical dormancy and germination patterns, although at certain temperatures, some species had similar germination and dormancy loss behaviors. These variations in dormancy and germination ecology will greatly influence *Carex* emergence from seed banks in wetlands. For instance, *C. granularis*, which required at least 2 months of stratification before any germination occurred and germinated optimally at a cooler temperature regime than most species (22/8 °C), is the most likely species to form a persistent seed bank and emerge from the seed bank at cool spring temperatures. On the other hand, seeds of *C. utriculata* are more likely to emerge in the hottest part of the summer because it germinates best at 35/30 °C, although the survival of seedlings at this temperature is not known. Seeds of *C. brevior* and *C. cristatella* likely emerge throughout the growing season because they germinate over a wide range of temperatures even without stratification.

Carex seed germination patterns varied widely between seed crops from different years, particularly at 5/1 °C and 14/1 °C. This is the first study to illustrate such variability in North American *Carex* species. However, variation in germination across years occurs in many species and is likely a result of the effect of the maternal environment during seed maturation. The position of the seed on the maternal plant, the age of the maternal plant, or environmental factors such as light quantity and quality, temperature, soil moisture, and mineral nutrition during seed maturation on the mother plant can cause this

variation in germination (Gutterman, 2000 and references therein). Any number of these factors could be responsible for the variation in germination patterns that emerged in these *Carex* species and further study is necessary to elucidate these patterns. Regardless of the mechanism driving this phenomenon, this variation has implications for restoration practice. Most of the variation between years for the study species occurred at 5/1 °C and 14/1 °C. Thus, restoration practitioners should expect more variable germination responses from different seed lots for seed emerging under late fall and early spring temperatures.

Although seed viability and germination can vary among years and populations, we found that our results reflect findings from other studies in North America of these same *Carex* species. van der Valk et al. (1999) documented low seed viability for *C. atherodes*, *C. lacustris*, and *C. stricta* from Iowa populations, as we found in the present study. Budelsky and Galatowitsch (1999) also found that stratification improved *C. comosa* seed germination from Minnesota populations. Baskin et al. (1996) germinated fresh seeds of *C. comosa* and *C. stricta* from Tennessee populations and found highest germination percentages under summer temperature conditions (35/20 °C), similar to our findings. These similarities suggest that the results from this study may be relevant to these same *Carex* species occurring in other regions although how widely (i.e., geographic distance) these results may be applied is unknown. Regional differences in the level of dormancy have been demonstrated among populations of *Carex canescens* from northern and southern Sweden and northern and southern Germany (Schütz and Milberg, 1997) but there is still a great need for understanding how seed viability, dormancy, and germination varies geographically.

The six *Carex* species with low Seed Regeneration Index (SRI) values (<0.5, Group 1) are less likely to propagate successfully from seed in the field than species with a higher SRI value. Interestingly, many of the species in Group 1 are some of the most dominant *Carex* in prairie wetlands. For instance, *C. atherodes*, *C. lacustris*, and *C. pellita* were both abundant and frequent in 10 natural prairie wetlands surveyed in 1991 (Galatowitsch and van der Valk, 1996c). This discrepancy between the low seed regeneration ability for these species in our study and their high vegetative cover in the field indicates that many *Carex* species must spread through clonal propagation to colonize new areas. *Carex atherodes*, *C. lacustris*, and *C. pellita* can form large stands in wetlands (S.M. Galatowitsch, pers. obs.) and all six species in Group 1 spread via rhizomes. A rare germination event and then clonal spread to cover larger areas is likely responsible for these species' colonization of gaps after a disturbance or new sites physically separated from current populations.

Ultimately, the usefulness of the SRI to predict plant emergence patterns and restoration efforts will depend on whether other species can be classified *a priori* into these designations without detailed dormancy and germination studies. The 14 wetland *Carex* study species represent 20% of the *Carex* flora of prairie wetlands of mid-continental North America (Barkley, 1986). The question is whether any of the other wetland *Carex* that share the same characteristics of the study species (e.g., rhizomatous spread, small seededness) have similar viability, dormancy, and germination patterns. In the present study, species with a tufted or clustered growth form had a higher SRI value than those with a more spreading growth habit such as *C. atherodes*, *C. lacustris*, *C. pellita*, and *C. utriculata*. Also, species that are found at higher elevations within wetlands (e.g., wet meadows) tended to have a higher SRI value than those that occupy shallow water areas of wetlands, like *C. atherodes*, *C. lacustris*, and *C. stricta* (elevation classification based on Galatowitsch and van der Valk, 1996b,c). We also found that four of the smallest seeded species (K.M. Kettenring, pers. obs.), *C. cristatella*, *C. scoparia*, *C. vulpinoidea*, and *C. brevior,* had the highest SRI value. Interestingly, three of these species – *C. brevior*, *C. cristatella*, *C. scoparia* – are in the same *Carex* tribe, Ovales (Gleason and Cronquist, 1991). Seeds of all four species germinated to high percentages without stratification or with <1 month stratification across all temperatures. It should be noted, however, that exceptions to these generalizations exist. In our study, *C. stricta*, a small seeded species, had a low SRI value. Schütz and Rave (1999) found no correlation between germinability and seed size in 18 *Carex* of open, wetland habitats from Germany, the Czech Republic, and southern Sweden. Plant community ecologists should evaluate regeneration patterns in prairie wetlands to determine if the generalizations we suggest hold true. At this stage, however, these generalities can at least provide guidance for restorationists who need to know where to focus efforts and what species may present extra challenges. Based on our study, particular attention should be paid to larger seeded species (like *C. atherodes* and *C. lacustris* compared with smaller seed species like *C. cristatella* and *C. vulpinoidea*), species that generally occupy lower elevations of wetlands (i.e., shallow water habitats compared with wet prairie inhabitants), and species that are mat forming and spread via rhizomes. In some cases, extra steps such as transplanting seedlings or rhizomes of these species may be necessary for effective revegetation if establishment from seed is unlikely (Yetka and Galatowitsch, 1999; Budelsky and Galatowitsch, 2004).

Our study illustrates the complexities of seed dormancy and germination patterns that can exist within a single genus from wetland habitats. We found that the 14 *Carex* study species vary widely in their seed dormancy and germination patterns. Based on species-specific seed viability and responses of seeds to simulated field temperatures, it is reasonable to assume that some species are likely to regenerate via seeds readily after natural disturbance in natural wetlands or in restorations. Others with low seed viability, deep dormancy, and strict germination temperature requirements, are likely to produce seedlings less frequently and may be difficult to revegetate in wetland restorations. Also, our study demonstrates the utility of autecological studies to informing plant community ecology and restoration science. In revegetation efforts, particular attention will need to be paid to the Group 1 species by adequately pretreating seeds with cold, moist stratification to

break seed dormancy and then sowing them at optimum temperatures for seed germination (especially for *C. granularis* and *C. utriculata*). With the findings from our experiments, we are closer to predicting wetland plant community development and to restoring the diversity of native *Carex* species in prairie wetlands.

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