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ENVIRONMENTAL EFFECTS ON GERMINATION OF *CAREX UTRICULATA* AND *CAREX NEBRASCENSIS* RELATIVE TO RIPARIAN RESTORATION

Kimberly L. Jones[1], Bruce A. Roundy[1,3], Nancy L. Shaw[2], and Jeffrey R. Taylor[1]

[1] *Department of Integrative Biology*
401 WIDB
Brigham Young University
Provo, Utah, USA 84602

[2] *Aquatic Sciences Laboratory*
U. S. Department of Agriculture, Forest Service
Rocky Mountain Research Station
316 E. Myrtle
Boise, Idaho, USA 83702

[3] *Corresponding author*

Abstract: Seasonal riparian seedbed temperatures were measured and germination of *Carex utriculata* and *C. nebrascensis* seeds was tested in relation to chilling, perigynia removal, incubation temperature, and light to help guide propagation and direct seeding of these species for riparian restoration. Diurnal temperatures of riparian seedbeds at two sites in Strawberry Valley, Utah, USA ranged from 3.1 to 11.2° C in May to 9.5 to 24.1° C in August when water was generally available for seed germination. Pre-incubation treatments of chilling at 5° C for 7 to 150 days and perigynia removal increased germination of 2-year-old seeds of these species but were not necessary for high germination percentages (>89%) when seeds were incubated in light under a summer temperature regime (10 to 24° C). Seeds aged 0.5 and 1.5 years had lower germination percentages than 2-year-old seed but also had adequate germination percentages (> 20%) for greenhouse propagation without pre-treatments when incubated in light at the summer temperature regime. After 5.5 years of storage at room temperatures, germination of *C. utriculata* was negligible, but that of *C. nebrascensis* was > 35%. Seeds of both species that were overwintered in seed bags in riparian microsites had high germination percentages (>80%) when retrieved the following summer and incubated at a summer temperature regime in light. Although direct seeding in fall would allow natural chilling and potentially high germination percentages the following spring or summer, the risk of seed loss or excessive burial is great during high spring stream flows. A better strategy is to surface-seed wet seedbeds in early summer after peak flows have receded and temperature and light conditions are conducive to high germination percentages.

Key Words: seed dormancy, sedge, revegetation, wetlands, chilling, perigynia, temperature, light, overwintering

INTRODUCTION

Carex species are commonly reintroduced in wetland and riparian restoration by transplanting sod plugs, rhizomes, or intact plants from an adjacent area or planting greenhouse-propagated seedlings (Ratliff 1985, Nelson and Williams 1986, Hoag et al. 2001). For large areas, direct seeding is potentially more cost-effective and less disruptive than transplantation. However, revegetation to restore *Carex* meadows and wetlands by direct seeding has failed due to lack of seed viability, low germination, or seedling failure (van der Valk et al. 1999). *Carex utriculata* Boott (now recognized as distinct from *C. rostrata* Stokes) and *C. nebrascensis* Dewey are commonly used to restore riparian and wetland areas in the Intermountain area, USA (Frandsen 1995, Dearden 1998). Determination of their germination requirements would better guide both nursery propagation and direct seeding strategies for these species.

Pre-incubation treatments required to break dormancy, incubation conditions that maximize germination, and the effects of seed age on germination must be understood to guide efficient greenhouse propagation (Table 1). Propagators can then weigh the necessity, costs, and returns of specific treatments. For direct seeding, germination responses can guide the pre-treatments necessary, the season in which to seed, and method of seeding (Table 1). Direct seeding is most

Table 1. Research questions and experiments to determine strategies for propagation or field seeding of two *Carex* species.

Experiment number	Question	Effects tested
	Greenhouse Propagation	
2, 5	Are pre-incubation treatments necessary to break seed dormancy?	Chilling and perigynia removal on germination
2, 3, 5	What incubation conditions enhance germination?	Incubation temperatures and light on germination
2, 3, 5	How does seed age affect germination?	Chilling, incubation temperatures, and light on different seed ages
	Field Seeding	
1	What are the seasonal diurnal temperatures of riparian seedbeds when water is available? Should we seed in the fall?	Seasonal temperatures and water potential in riparian seedbeds
2, 5	1. Is chilling necessary for germination?	Chilling on germination
2	2. After chilling, how does incubation temperature affect germination?	Spring and summer incubation temperatures on germination with or without chilling
4	3. How does overwintering in riparian seedbed microsites affect germination?	Over wintering on germination of seeds in seed bags buried and retrieved from different microsites
2, 3, 5	Can we seed after peak flow in summer? Practical considerations	Summer seedbed temperatures on germination
2, 4, 5	1. Should we bury seeds or surface sow?	Light on germination, burial of overwintered seeds on in-place germination
2	2. Should we remove the perigynia?	Perigynia removal on germination
2, 3, 5	3. What seed ages can we use?	Seed age on germination

efficient for wetland species if pretreatments are not required and germination requirements can be met when conditions are optimal for seedling establishment.

Germination of some *Carex* species is increased by chilling, light, removal of the sac-like perigynia covering the seed, specific alternating incubation temperatures, and certain combinations of these factors (Budelsky and Galatowitsch 1999, van der Valk et al. 1999, Schütz 2000, Hoag et al. 2001). If chilling is required for germination, either fall seeding or chill treatments prior to spring or summer sowing are necessary. Fall- sowing when stream flows are low can potentially cover a larger area of exposed seedbed than in spring when flows are high. Fall-sown seeds have the advantage of being in place when water is available as temperatures warm sufficiently in spring for germination. However, fall-sown seeds are at risk of washing away in spring floods or being buried too deep for seedling emergence. Seeding in early summer when stream flows have stabilized could avoid seed and seedling loss and increase direct seeding success, if germination requirements are met. If these *Carex* species germinate at spring and summer riparian seedbed temperatures, restorationists can weigh the advantages and risks of fall versus spring or summer seeding for their particular sites. Seasonal riparian seedbed temperatures when water is available for germination have not been reported.

For direct seeding, seed burial is preferred to increase the time of available water to seeds and to avoid seed loss by predation or flowing water. However, a light requirement for germination necessitates surface sowing. Surface-sown seeds would be less at risk of washing away if sown in summer rather than fall, but the area of seedbed where water is available for germination may be restricted. Seeds could be surface-sown repetitively over riparian seedbeds that become exposed in spring as flows diminish. If seeds can germinate without light, broadcasting them and burying them by raking or harrowing might reduce the number of seeds that wash away in spring and allow sowing in fall over a potentially larger area than in summer. Germination responses to light under different seasonal temperature regimes are required to suggest direct seeding options.

Because wildland seed production and harvest can vary annually, seed vendors store *Carex* seed for revegetation projects for 1 to 5 years prior to sale. van der Valk et al. (1999) recommended that fresh seed be used in restoration of *C. atherodes* Spreng., *C. lacustris* Willd., and *C. stricta* Lam. based on reduced germinability and viability after 6 to 18 months of storage. However, the moisture and temperature environment of storage affects germination of various *Carex* species differently (Budelsky and Galatowitsch 1999), and some species have increased germination after storage, presumably due to after-ripening loss of dor-

mancy (Schütz 2000). Our purpose was to determine germination responses of *C. utriculata* and *C. nebrascensis* to guide strategies for restoration.

METHODS AND MATERIALS

We conducted five experiments to address specific questions relevant to greenhouse propagation and field sowing of *C. utriculata* and *C. nebrascensis* (Table 1). First, we measured actual riparian seedbed temperatures and water potentials (Experiment 1). We then tested germination of 2-year-old seed in response to chilling, perigynia removal, light, and incubation temperatures based on field or commonly used propagation temperatures (Experiment 2). Next, we tested germination of 2.5-year-old seed when incubated at a constant temperature and then exposed to alternating temperatures (Experiment 3). At the same time, we tested germination of 2.5-year-old seed that had been overwintered in riparian seedbeds (Experiment 4). We finally tested germination of 0.5, 1.5, and 5.5-year-old seed in relation to chilling and light (Experiment 5).

Seed Materials

Carex utriculata and *C. nebrascensis* seed was donated by Lone Peak Nursery (Draper, Utah, USA). *Carex utriculata* seed was collected in 1994 at an elevation of 1925 m on a meadow that is now submerged under the north arm of Jordanelle Reservoir, Utah. *Carex nebrascensis* seed was also collected in 1994 at an elevation of 2305 m on the Indian Creek drainage near Strawberry Reservoir, Utah. The seed was germinated and seedlings planted in small ponds at Lone Peak Nursery (elevation 1370 m). Seed subsequently produced from these plantings was harvested in August 1995 and stored at room temperature at $<9\%$ moisture content in sealed plastic bags until used for experiments commencing in 1997.

Germination Test Protocol

For controlled germination tests, 32 seeds were placed in petri dishes (diameter = 9 cm) with a double layer of blotter paper. Blotter papers were wetted with unfiltered tap water at the onset of experiments, and seeds were kept moist for the duration of the experiments. Germination was defined as emergence of the shoot and radicle. Viability was determined on all ungerminated seeds by assessing firmness with a cut test. A prior test indicated that firm seeds were viable as tested by tetrazolium (Yaklich 1984). Germination percentage was calculated using total number of germinated seeds relative to total firm seeds. Days to 50% germination (Thomson and El-Kassaby 1993) were calculated for the population of seeds that germinated in each petri dish.

Field Study Sites

Two stream sites differing in geomorphology—Co-op Creek and Trail Hollow Creek in the Strawberry Basin, Utah were selected for soil moisture and temperature measurements (Experiment 1) and an overwintering experiment (Experiment 4). The two different streams were chosen to measure a range of temperature regimes and germination responses after exposure to riparian seedbed microsites. Co-op Creek is located on the north side of Strawberry Reservoir (2680 m) and is dominated by *C. utriculata*, *Agrostis stolonifera* L., and several *Salix* species. The stream occurs in a broad alluvial delta. It has fast running water and shifting gravel bars during peak flow in the spring. Based on the Rosgen (1996) stream classification system, the stream is an E4 type—slightly entrenched, with very low width/depth ratio, very high sinuosity, and gravel as the predominant channel material with lesser amounts of cobble, silt, and clay.

Trail Hollow Creek is located at the south end of Strawberry Reservoir. The stream occurs on a moderately steep, fluvial dissected valley. The study site included several ponds with sloped banks created by porous rock check dams installed by the U. S. Department of Agriculture, Forest Service in an effort to rehabilitate streambanks damaged by severe gully erosion. The prominent riparian species is *C. utriculata* while the upland is dominated by *Artemisia tridentata* Nutt. var *vaseyana* (Rydb.) Bovin. The porous rock check dams allowed flow through the ponds during most of the year and especially during peak spring runoff when bank-full levels exceeded the height of the dam spillways. The stream was visually estimated as a G6 type—entrenched with low width/depth ratio, moderate sinuosity, and silt and clay as the predominant channel material (Rosgen 1996).

Experiment 1: Field Seedbed Temperatures and Water Potential

To determine the seasonal soil temperatures and water potentials of riparian seedbeds, copper-constantan thermocouples and gypsum blocks were installed at both study sites at three depths (1, 3, and 6 cm) in each of three bank positions. Two subsamples or sensors were buried at each bank position at each depth. At the Co-op Creek site, sensors were installed at the water's edge (in October 1996 at minimum flow) and at the highest point of a gravel point bar, as well as on a small mid-bank landing of the stream (0.3 and 1.5 m above minimum flow, respectively). At Trail

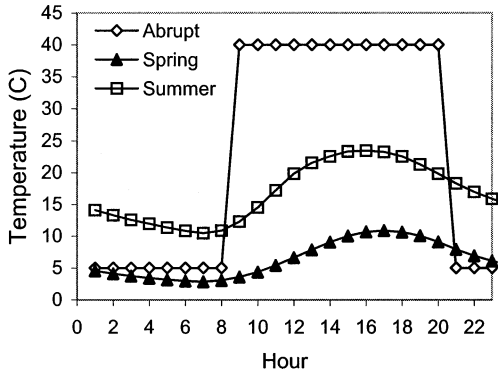

Figure 1. Abruptly alternating and gradually fluctuating spring and summer temperature regimes used to test germination of *Carex utriculata* and *C. nebrascensis*. Spring and summer regimes were composed of average hourly temperatures for May and July measured with thermocouples in riparian seedbeds at Co-op and Trail Hollow Creeks, Utah, USA.

Hollow, sensors were buried at the water's edge of the pond at minimum flow and at mid-bank and upper bank areas, 1 and 2 m above minimum flow, respectively. Temperature and water potential data were recorded at 1-minute intervals and averaged hourly by Campbell Scientific, Inc., CR-10 microloggers, Logan, Utah from September 1996 through July 1999. Temperatures from all depths were used to calculate hourly near-surface averages, which were then used to calculate diurnal hourly averages for each month of the year for each site.

Experiment 2: Effects of Chilling, Light, and Perigynia Removal on 2-Year-Old Seed

Design. Germination experiments were conducted on 2-year-old seed using a randomized block, split-plot design in three incubators, each programmed for a different temperature regime. Separate petri dishes, as described above, were the basic experimental unit, with one dish of 32 viable seeds for each combination of two species, four pre-incubation chill durations, light or dark exposure, and perigynia removed or left intact for each of four blocks (n = 4 petri dishes for each treatment combination) for each temperature regime. Dishes for each combination of species, chill duration, and perigynia treatment were placed randomly within clear (light) or black (dark) plastic bags (whole plot) placed on each of four shelves (blocks) within each incubator. Seeds were incubated for 36 days, with germination counted every 2 to 3 days.

Temperature. The three temperature regimes (Figure 1) were 1) abrupt: an abruptly alternating 5/40° C (a traditional temperature regime used in incubation to germinate seeds prior to growing seedlings in the greenhouse), 2) spring: gradually fluctuating temperatures from 4 to 11° C (an average May field temperature), and 3) summer: gradually fluctuating temperatures from 10 to 24° C (an average July field temperature). The average hourly temperatures for the 1-cm depth for May and July from experiment 1 were used as the spring and summer temperature regimes.

Light. All treatments exposed to light were incubated under a light regime of 12 hours light followed by 12 hours dark, with cool-white fluorescent lighting corresponding to the higher temperatures of the regimes. Photon flux in all chambers was at least 140 μmoles m^{-2} s^{-1} in the 400 to 700 nm wavelength range as measured by a quantum sensor. Germination of seeds in dark treatments was scored under a green light. The green light was a General Electric GE 540G green fluorescent light filtered by two layers of green (Roscolux 95 1.8 mil) and one layer of blue (Roscolux 90 2.3 mil) plastic light filters (VanDerWoude and Toole 1980) to produce an irradiance in the 500 nm range of least photoreactive light (Bewley and Black 1985). Germination was similar for seeds viewed under green light and seeds kept in darkness until final counting, according to a pilot study reported by Jones (1999).

Chilling and Perigynia Removal. The effect of chilling on germination of each species was tested by exposing seeds to moist incubation at 5° C for 0, 7, 30, and 150 days, with and without perigynia. Perigynia were removed by tumbling batches of seeds in a cylindrical tube (Fosberg) scarifier lined with sandpaper for 30 to 50 seconds. Seeds were then transferred into a seed blower to separate seeds from the empty perigynia.

Experiment 3: Effects of Constant and Alternating Temperatures

Germination experiments were conducted on 2.5-year-old seed. All seeds were moist-chilled at 5° C for 7 days prior to incubation. Seeds were then incubated for 44 days at six constant temperature regimes: 10, 15, 20, 25, 30, and 35° C. Four petri dishes containing at least 32 viable seeds of each species were placed randomly in six incubators programmed for each of the six temperatures, with cool-white fluorescent lights for 15 hours followed by dark for 9 hours. Germination was counted every 1 to 3 days. Seeds were then transferred to one incubator programmed for the gradually-fluctuating summer temperature regime described above for an additional 38 days, with germination scored every 3 days.

Experiment 4: Field Overwintering and Microsite Effects on Germination

A randomized block, split-plot design was used to test the effect of overwintering in the natural environment on germination. At each of the two field sites and for each of four blocks or stream reaches, three subsamples (seed bags) for each of the two *Carex* species were buried approximately 0.3 m apart in each of three microsites for each of two retrieval dates. Microsite was the whole plot, with retrieval date and species combination as the subplot. Seed bags were made of mosquito netting mesh and were approximately 5 cm^2 in area and contained 50 seeds. Each seed bag was securely fastened just underneath the head of a 30-cm-long spike by wrapping each seed bag around the spike with metal wire and covering it with 1 to 2 cm of soil or gravel. The spikes were color-coded and each block mapped for ease of retrieval.

Blocks were located within 100 m of the site where temperature and soil moisture were measured, but the actual microsites for seed burial and bank positions for soil temperature and moisture sensors were not the same. On Co-op Creek, microsites included the water's edge of a gravel bar (during minimum flow in September), the water's edge of a sediment beach, and the *Carex* community 2 m above the water's edge.

On Trail Hollow Creek, two blocks were located on an east-facing aspect, and two blocks were located on a west-facing aspect. Microsites were located in sediment along the water's edge, at mid-bank 1 to 2 m above the water in bare sediment and at mid-bank in a *Carex* community 1 to 2 m from the water. Seed bags were installed 9 September 1997 at Co-op Creek and 10 September 1997 at Trail Hollow Creek when the streams were at minimum flows. Seed shatter normally occurs at this time in the natural environment. Seeds were 2 years old when buried. The first retrieval was after high water had receded on 7 July 1998 for Co-op Creek and 30 July 1998 for Trail Hollow Creek. The second retrieval was one month later on 7 and 27 August 1998 for each respective creek.

Within one day of retrieval, germinated seeds were counted and ungerminated seeds placed on a double layer of blotter paper in disposable petri dishes and watered with tapwater as described above. Dishes were immediately placed in a growth chamber set at the summer temperature regime of gradually fluctuating from 10 to 24° C. Seeds were exposed to a 12-hour light/12-hour dark daily cycle corresponding to the high/low temperature fluctuations of the temperature regime. Germination was scored every 2 to 4 days for 30 days.

Experiment 5: Seed Age

In 2002, seeds harvested in fall 2001 (0.5 years old), fall 2000 (1.5 years old), and fall 1997 (5.5 years old) from Lone Peak Nursery were tested for germination responses to chilling and light. All seeds had been stored at room temperature. Seeds with intact perigynia were chilled for 0, 7, and 30 days and incubated in a 12 hours light, 12 hours dark regime or no light for 36 days at the gradually fluctuating summer temperature regime (Figure 1). This experiment was a randomized complete block with a split-plot design. All combinations of each species, age, and chilling time were randomized within clear (light) or black (dark) bags as the whole plot on each of four blocks or shelves within the incubator.

Statistical Analyses

Split-plot randomized block analyses of variance were performed for laboratory experiments. For 2-year-old seed (Experiment 2), the effects of chilling, light, and perigynia removal for the two species were analyzed separately for each temperature regime. Data for experiments 3 and 5 were also analyzed using analysis of variance. For the overwintering experiment (Experiment 4), germination data from each site were analyzed separately using general linear model analysis of variance. Different kinds of microsites and different sowing and retrieval dates precluded including site as a factor in this analysis. Missing data due to loss of one set of seed bags for one microsite on one block at Coop Creek necessitated the use of the general linear models analysis. Time to 50% germination (D50) was calculated as a percentage of total germinating seeds in a petri dish, not total seeds tested. The arcsin square root transformation was applied to germination percentage data prior to analysis as recommended by Steel and Torrie (1980) for percentages that cover a wide range of values. Single degree-of-freedom contrasts or Fisher's L.S.D. test were used to compare appropriate means. All analyses were conducted using Statistical Analysis System version 6.12 (PROC ANOVA or PROC GLM).

RESULTS

Experiment 1: Field Seedbed Temperatures and Water Potential

Riparian seedbeds had diurnal temperature curves with the greatest magnitude of fluctuation during warmer summer months (Figure 1, Table 2). Average hourly temperatures by month across both field sites ranged from 3.1 to 11.2° C in May, 6.6 to 15° C in June, 10.7 to 23.1° C in July, and 9.5 to 24.1° C in

Table 2. Average daily maximum and minimum temperatures and the diurnal difference in temperature for 1 to 10-cm soil and gravel depths for three different riparian bank positions at Co-op Creek and Trail Hollow Creek, Strawberry Valley, Utah, USA.

	Maximum (°C)			Minimum (°C)			Diurnal fluctuation (°C)		
Co-op Creek Month	Water's edge (Oct)	Gravel bar	Mid bank	Water's edge (Oct)	Gravel bar	Mid bank	Water's edge (Oct)	Gravel bar	Mid bank
Dec.	−0.1	0.3	−0.1	−0.4	−0.2	−0.5	0.4	0.5	0.4
Mar.	0.3	0.5	0.3	−0.3	−0.1	−0.3	0.5	0.6	0.5
May	9.1	8.1	8.7	3.1	3.9	3.5	6.0	4.2	5.2
June	13.4	14.1	15.0	6.7	7.6	6.6	6.8	6.5	8.4
July	23.0	22.3	19.8	11.6	14.1	12.2	11.4	8.1	7.6
Aug.	23.3	21.3	17.0	11.2	13.5	11.3	12.2	7.8	5.7
Sept.	18.9	17.0	14.2	9.1	10.9	9.5	9.8	6.2	4.7
	Maximum (°C)			Minimum (°C)			Diurnal fluctuation (°C)		
Trail Hollow Creek	Water's edge (Oct)	Mid bank	Upper bank	Water's edge (Oct)	Mid bank	Upper bank	Water's edge (Oct)	Mid bank	Upper bank
Dec.	0.0	0.6	0.4	−0.8	−0.0	−0.3	0.8	0.7	0.7
Mar.	0.2	0.7	0.2	−0.6	−0.3	−0.2	0.8	1.0	0.4
May	11.2	8.3	10.0	5.9	5.9	3.8	5.4	2.5	6.2
June	13.4	11.1	12.4	10.1	9.4	7.6	3.3	1.7	4.9
July	19.5	17.0	23.1	15.0	14.5	10.7	4.5	2.5	12.4
Aug.	24.1	17.9	22.7	10.5	14.9	9.5	13.6	3.0	13.2
Sept.	19.8	14.9	20.2	8.5	12.9	8.7	11.3	2.0	11.6

August. Temperatures from different depths were similar for most bank positions. Some temperature and water potential sensors moved during the course of the study, and some sensors were buried deeper than their original depth. For example, lower temperature fluctuations during summer months for the gravel bar compared to the other bank positions at the Co-op Creek site may have been associated with greater thermocouple burial as the bar accumulated more gravel during spring flow (Table 2). Temperature data in Table 2 are representative of the upper 10 cm of *Carex* seedbeds, rather than the original 1-, 3-, and 6-cm burial depths.

Although temperatures were generally similar for both sites and bank positions, maximum temperatures were higher at the October water's edge than on the upper bank at Trail Hollow, while the inverse was true at Co-op Creek (Table 2). This difference was associated with differences in aspect. Sensors were buried on the west side of the stream at Co-op Creek and on the east and sunnier side of the stream at Trail Hollow. Diurnal temperatures near the water's edge fluctuated more at Co-op Creek than at Trail Hollow, while temperatures on the upper bank fluctuated more at Trail Hollow than Co-op Creek. Sensors at Trail Hollow originally buried near the water's edge in October were probably immersed in the stream most other months.

Water potential was >-1.5 MPa at all microsites at Co-op Creek from spring through September. At Trail Hollow, water potential was >-1.5 MPa from May through early August and dropped to <-1.5 MPa at mid- and upper bank locations starting in mid-August. The water potential sensors were buried at least 1 cm deep and may not indicate availability of water to seeds on or near the surface. However, the data in Table 2 and Figure 1 show the temperature regimes that seeds may be exposed to when water generally is available for germination in spring and summer.

Experiment 2: Effects of Chilling, Light, and Perigynia Removal on 2-Year-Old Seed

For total germination percentage, all of the main effects were significant (Table 3) for each of the temperature regimes. The two-way interactions of light/chill duration, species/chill duration, and light/perigynia removal were significant (Table 3) for some of the temperature regimes. Germination was greater in light than darkness for both species and all temperature regimes, except for *C. utriculata* in the abrupt temperature regime (Figure 2). *Carex nebrascensis* germination in darkness was low for all temperature regimes, while *C. utriculata* had high germination percentages in darkness under the abrupt temperature and some germination in darkness under the summer tempera-

Table 3. Analysis of variance of seed treatments on the arcsin $\sqrt{\ }$ of germination percentage for 2-year-old seeds of *Carex utriculata* and *C. nebrascensis* under abruptly alternating and gradually fluctuating spring and summer incubation temperatures (MS = Mean square for error term).

	Abrupt		Spring		Summer		
Source	df	F	Prob > F	F	Prob > F	F	Prob > F
Block (B)	3	0.43	0.7482	2.27	0.2593	0.81	0.5655
Light (L)	1	12.45	0.0387	353.68	0.0003	286.13	0.0004
Error A = B*L	3	MS = 0.2467		MS = 0.0232		MS = 0.13	
Species (S)	1	282.1	<.0001	20.17	0.0015	132.18	<.0001
Chill (C)	3	51.99	<.0001	12.32	0.0015	6.71	0.0113
Perigynia (P)	1	71	<.0001	7.4	0.0226	37.83	0.0002
L*S	1	178.86	<.0001	22.1	0.0011	90.25	<.0001
L*C	3	0.1	0.9577	5.48	0.0203	3.23	0.0749
L*P	1	7.88	0.0205	2.65	0.1378	7.33	0.0241
L*S*C	3	3.53	0.0616	0.9	0.4784	1.1	0.3984
L*S*P	1	1.09	0.3239	4.14	0.0722	5.02	0.0519
L*C*P	3	0.07	0.9765	0.6	0.633	2.05	0.1772
L*S*C*P	3	0.64	0.6069	0.12	0.9446	0.02	0.9958
S*C	3	11.59	0.0019	0.59	0.6383	1.4	0.3042
S*P	1	0.03	0.8666	3.88	0.0803	1.73	0.2204
S*C*P	3	1.16	0.3772	0.11	0.9523	0.36	0.7853
C*P	3	3.38	0.0678	0.76	0.5429	0.32	0.8127
Error B = B*L*C*P	9	MS = 0.0199		MS = 0.0729		MS = 0.01	

ture. The effect of chilling was strongest on seeds of both species in light under the spring temperature regime. Chilling slightly increased germination percentages under the abrupt temperature but had little effect under summer temperatures (Figure 2). These results suggest that chilling may increase germination of seeds in the spring but not during the summer in natural seedbeds. Perigynia removal increased germination of seeds in the light for all temperature regimes but only increased germination in the dark in the abrupt temperature regime (Figure 3).

Time to 50% germination of germinated seeds (D50) was significantly affected by chill duration for the abrupt ($F_{3,9}$ = 12.2, $P < 0.002$) and spring ($F_{3,9}$ = 4.5, $P < 0.03$) temperature regimes. Perigynia removal decreased D50 for all three regimes (abrupt: $F_{1,9}$ = 64.6, $P < 0.0001$; spring: $F_{1,9}$ = 6.6, $P < 0.03$; summer: $F_{1,9}$ = 16.8, $P < 0.003$). The interaction of light and species was significant for D50 under the abrupt ($F_{1,9}$ = 23.4, $P < 0.001$) and summer ($F_{1,9}$ = 56.0, $P < 0.0001$) temperatures. Light decreased D50 for *C. nebrascensis* under all three temperature regimes but had little effect on *C. utriculata* (Figure 4).

Experiment 3: Effects of Constant and Alternating Temperatures

Germination of *C. nebrascensis* was limited (< 10%) except at 25° C, while that of *C. utriculata* was limited at all constant temperatures (Figure 5). Germination for both species increased dramatically when

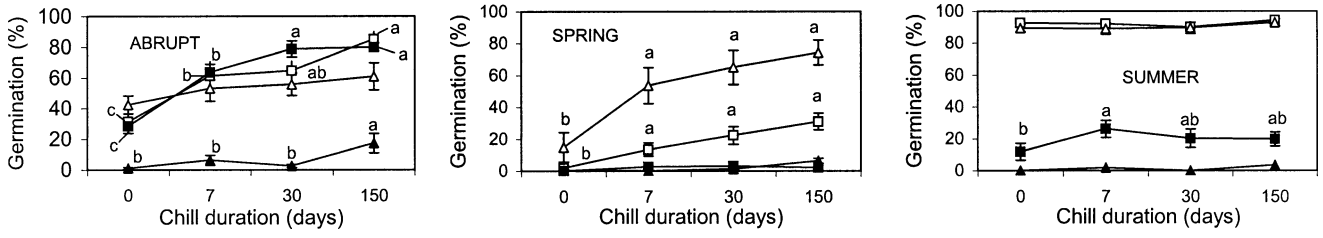

Figure 2. Total germination (%) after 36 days for 2-year-old seeds of *Carex utriculata* (boxes) and *C. nebrascensis* (triangles) in light (open symbols) and darkness (black symbols) for four chill durations and incubated under three temperature regimes (Figure 1). Error bars are ± 1 standard error of the mean (n = 8). Germination was greater in light than darkness except for *C. utriculata* at the abrupt incubation temperature. Different letters for a given species and light treatment indicate significant differences in germination for different chill durations according to Fisher's L.S.D. (p = 0.05). No letters for a line indicate no significant differences in germination associated with chill duration.

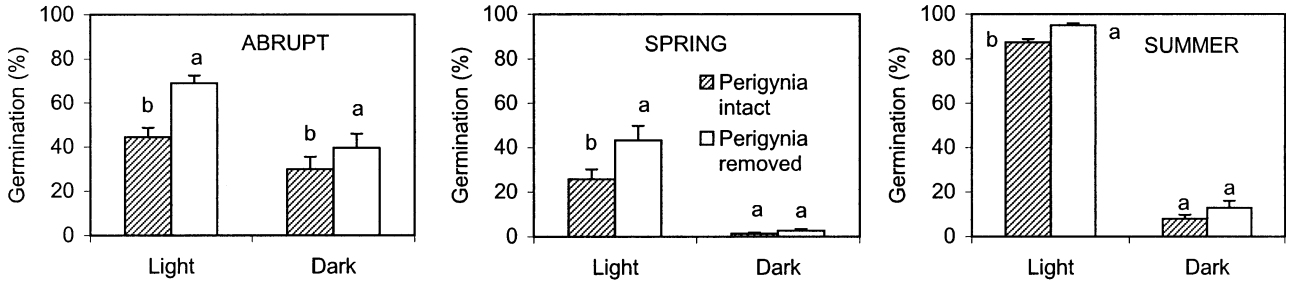

Figure 3. Average total germination (%) after 36 incubation days for 2-year-old seeds of *Carex utriculata* and *C. nebrascensis* with perigynia intact or removed and incubated in light or darkness under three incubation temperature regimes (Figure 1). Error bars = 1 standard error of the mean (n = 32). Different letters for a light treatment and temperature regime indicate significant differences in germination associated with perigynia removal (p = 0.05).

seeds were exposed to the summer fluctuating temperature regime.

Experiment 4: Overwintering and Microsite Effects on Seed Germination

Very few seeds germinated in seed bags in the field. After incubation in the laboratory, total germination varied by block, species, and microsite for seeds retrieved from the Co-op Creek site and by species, retrieval date, and the interaction of microsite and retrieval date for seeds from the Trail Hollow site (Table 4). Days to 50% germination of germinating seeds varied by block at Co-op Creek and by retrieval date and the interaction of microsite by retrieval date at the Trail Hollow site (Table 4). The total germination percentage was high for seeds retrieved from both sites and for both species (> 80%), but that of *C. utriculata* was greater than that of *C. nebrascensis* at both sites (Figure 6). Germination of seeds from most microsites and retrieval dates generally occurred within 9 days. Although seeds retrieved from Co-op Creek varied statistically in total germination and days to 50% germination among blocks (Table 4), differences were small (94 to 96% and 7.8 to 9.7 days). Likewise, differences in days to 50% germination for seeds from different blocks at the Trail Hollow site were small (9.3 to 12.6 days).

At Trail Hollow, seeds from the mid-bank *Carex* microsites had 13% lower germination percentage when retrieved 27 August than those retrieved earlier on 30 July (Figure 6). Seeds retrieved from the mid-bank sediment and mid-bank *Carex* microsites at the later date took 3.6 to 5.8 days longer to reach 50% germination than seeds retrieved the end of July.

Small differences in germination percentages and germination rates may have been associated with subtle environmental differences among blocks and microsites. For example, lowest and slowest germination was from seeds retrieved from mid- bank sediment and *Carex* microsites at Trail Hollow in late August (Figure 6). Soils at these microsites were drying out by then. Drying may have started to induce secondary dormancy in some seeds.

Experiment 5: Seed Age

Germination of 2-year-old seed was compared with germination for 0.5-, 1.5-, and 5.5-year-old seed for the summer incubation temperature and for light and chill treatments. All main effects of age, species, chilling, and light were significant (Table 5) for final germination percentage. The three-way interactions of age, light, and chill duration, as well as that of light, species, and chill duration were significant (Table 5). Germination of both *C. utriculata* and *C. nebrascensis*

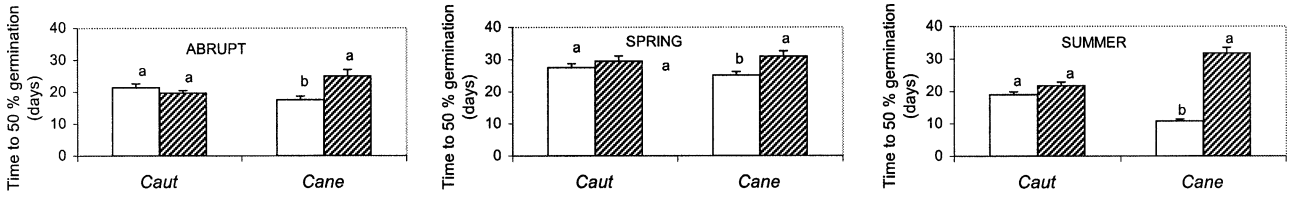

Figure 4. Time to 50% germination of germinating seeds after 36 days incubation under three incubation temperature regimes (Figure 1) in light (open bars) and darkness (cross-hatched bars) for 2-year-old seeds of *Carex utriculata* (*Caut*) and *C. nebrascensis* (*Cane*). Bars representing *C. nebrascensis* in darkness and *C. utriculata* under spring temperatures had <20% total germination, whereas total germination was > 50% for all other bars. Error bars = 1 standard error of the mean (n = 32). Different letters for a species and temperature regime indicate significantly different germination associated with light treatment (p = 0.05).

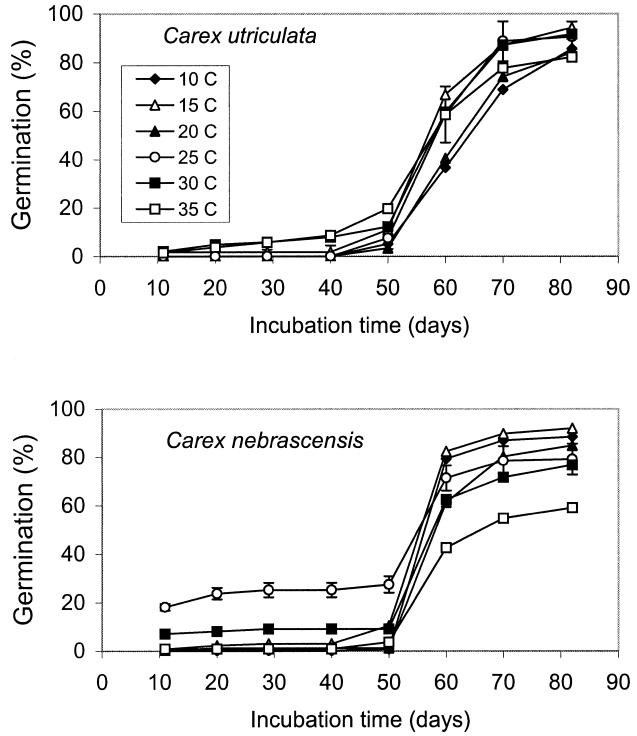

Figure 5. Cumulative germination (%) of 2.5-year-old seeds of *Carex utriculata* and *C. nebrascensis* incubated under six constant temperature regimes for 44 days followed by incubation under a gradually fluctuating summer temperature regime (Figure 1) for an additional 39 days. Error bars on the line for 25° C are ± 1 overall standard error of the mean for each day of measurement (n = 24).

in light was greatest at 2 years and lower for the other seed ages (Figure 7). Germination of *C. utriculata* was negligible at 5.5 years of age (Figure 7). For *C. utriculata*, germination was similar in light or darkness for all ages, except that it was greater in light for 2-year-old seed ($F_{1, 3} = 320.7$, $P < 0.001$). Germination was not significantly different for different chill durations for a given age, species, and light treatment, except that chilling increased germination of *C. nebrascensis* in the dark for 0.5-year-old seed ($F_{2, 6} = 7.8$, $P < 0.02$) and in the light for 1.5 year-old seed ($F_{2, 6} = 6.7$, $P < 0.03$, Figure 7). Germination of unchilled *C. nebrascensis* seed was greater in light than darkness at 0.5 years ($F_{1, 3} = 24.0$, $P < 0.02$) and 2 years ($F_{1, 3} = 251.1$, $P < 0.0001$) of age (Figure 7). Germination of *C. nebrascensis* was also increased by light for 0.5 ($F_{1, 3} = 21.6$, $P < 0.02$) and 1.5-year old seed ($F_{1, 3} = 81.1$, $P < 0.01$) when chilled 7 days (Figure 7).

DISCUSSION

Implications for Greenhouse Propagation

Chilling and perigynia removal increased germination of *C. utriculata* and *C. nebrascensis* for some incubation temperatures, as Hoag et al. (2001) also found for *C. nebrascensis*. However, these pre-treatments are not necessary for propagation because high germination percentages are possible under light and abruptly alternating or summer temperatures. Seeds could be germinated in an incubator that produces alternating temperatures of 5/40 or 10/24° C and germinants then transferred to the greenhouse. The abruptly alternating 5/40° C regime will even promote the germination of *C. utriculata* in the dark. *Carex nebrascensis* should be germinated in light. When seeds of *C. utriculata* are stored at room temperature, they should be used before they lose germinability between 2.5 and 5.5 years of age (Figures 5 and 7).

Implications for Direct Seeding

Water was available and temperatures were adequate for germination for *C. utriculata* and *C. nebrascensis* from spring into mid-August or September for the riparian seedbeds that we measured. Although overwintered seeds had high germination percentages and chilling increased germination in some cases, fall seeding is not necessary for these species. Our study confirms that the widely fluctuating warm temperatures that produce high germination percentages in these and other *Carex* species (Schmid 1984, Galinato and van der Valk 1986, Haggas et al. 1987, Baskin et al. 1989, Baskin et al. 1993, Schütz and Milberg 1997, Budelsky and Galatowitsch 1999) do occur in riparian seedbeds in the summer. Sowing after peak spring flows, but when riparian seedbeds are still wet, should allow high germination percentages.

Chilling effects varied with seed age, light, and incubation temperature and were more effective in increasing germination for seeds in darkness or at suboptimal temperatures, such as occur in spring. For most of the 32 species of *Carex* that they tested, Schütz and Rave (1999) found that chilling for 6 months and exposure to light during incubation substantially increased germination compared to freshly-harvested seed only exposed to light or similarly chilled seed incubated in the dark. Natural chilling of *C. nebrascensis* could enhance germination in the spring if seeds are exposed to light (Figure 2). Sowing in fall on upper banks and natural chilling over winter may allow germination of seeds in microsites that are wet with spring flows but are too dry for germination later in summer. The amount of seedbed exposed in spring and potential for loss of unburied seeds would have to be considered in planning fall sowing on upper banks. Also, seedling survival could be reduced if root growth does not keep pace with the decline of the water table, or if resources are reduced by competing species.

Table 4. Analyses of variance for the arcsin $\sqrt{}$ of germination percentage (GS) and days to 50% germination of germinating seeds (D50) of *Carex utriculata* and *C. nebrascensis* from seed bags overwintered at two riparian sites in Strawberry Valley, Utah, USA and retrieved the following July or August (MS = Mean square for error term).

		Co-op Creek			
		GS		D50	
Source	df	F	Pr > F	F value	Pr > F
Block (B)	3	12.71	0.0089	5.99	0.0414
Microsite (M)	2	7.91	0.0283	1.68	0.277
Error A = B*M	5	MS = 0.0031		MS = 3.527	
Species (S)	1	19.79	0.0021	3.5	0.0982
Retrieval date (R)	1	1.07	0.3308	4.37	0.0699
M*S	2	0.42	0.669	0.78	0.4912
M*R	2	0	0.9991	0.4	0.6841
M*S*R	3	0.71	0.5734	2.61	0.1237
Error B = B*M*S*R	8	MS = 0.02677		MS = 2.334	
		Trail Hollow Creek			
		GS		D50	
Source	df	F	Pr > F	F Value	Pr > F
Block (B)	3	0.82	0.5298	4.72	0.0508
Microsite (M)	2	0.67	0.547	0.61	0.572
Error A = B*M	6	MS = 0.1185		MS = 17.122	
Species (S)	1	45.71	<.0001	1.51	0.251
Retrieval date (R)	1	8.46	0.0174	18.44	0.002
M*S	2	2.24	0.1624	3.17	0.0907
M*R	2	7.45	0.0123	6.2	0.0203
M*S*R	3	1.99	0.1856	2.26	0.151
Error B = B*M*S*R	9	MS = 0.0209		MS = 17.195	

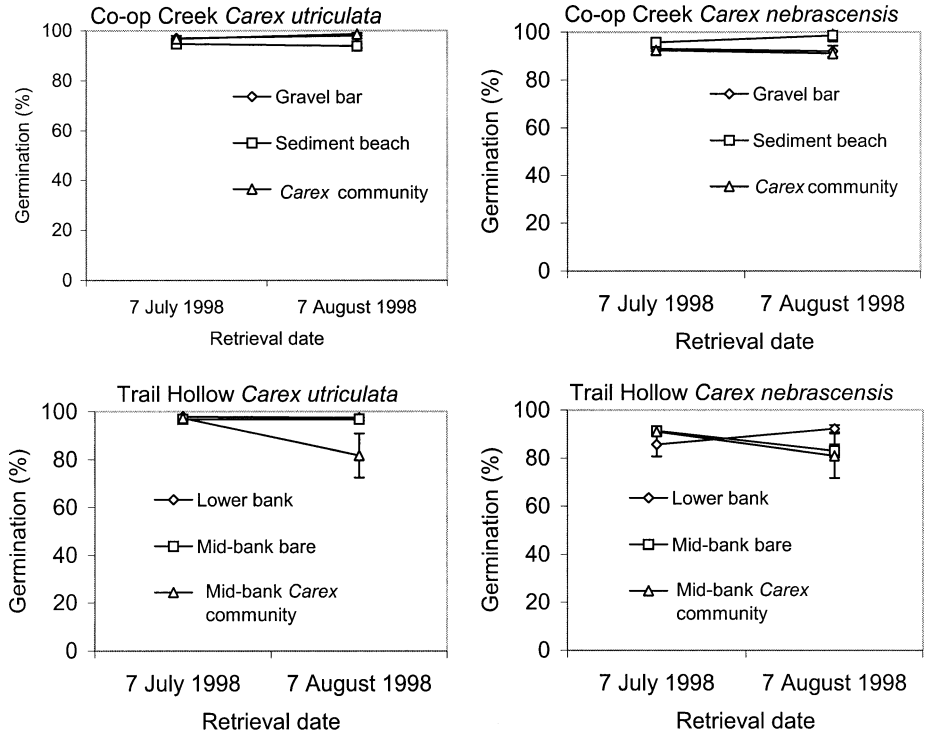

Figure 6. Germination (%) of seeds of two *Carex* species from seed bags overwintered and retrieved from various microsites at Co-op and Trail Hollow Creeks, Strawberry Valley, Utah, USA. Error bars are ± 1 standard error of the mean (n = 9 to 12).

Table 5. Analyses of variance of the effects of seed treatments on the arcsin $\sqrt{\ }$ of germination percentage of seeds of *Carex utriculata* and *C. nebrascensis* (MS = Mean square for error term).

	Seed ages 0.5, 1.5, 2, 5.5 years			Seed ages 0.5, 1.5, 5.5 years		
Source	df	F	Pr > F	df	F	Pr > F
Block (B)	3	1.13	0.4624	3	0.94	0.5181
Light (L)	1	47.55	0.0062	1	5.59	0.099
Error A = B*L	3	MS = 0.139		3	MS = 0.161	
Age (A)	3	57.54	<.0001	2	74.04	<.0001
Species (S)	1	56.25	<.0001	1	161.1	<.0001
Chill (C)	2	12.91	0.0003	2	17.23	0.0003
A*L	3	143.5	<.0001	2	11.0	0.0019
S*L	1	56.55	<.0001	1	42.27	<.0001
L*C	2	6.12	0.0094	2	10.92	0.002
A*S*L	3	2.7	0.0763	2	4.16	0.0423
A*L*C	6	3.32	0.0222	4	2.39	0.1092
L*S*C	2	5.92	0.0106	2	7.88	0.0065
A*S*L*C	6	1.32	0.3002	4	1.09	0.4041
A*S	3	125.99	<.0001	2	121.7	<.0001
A*C	6	2.32	0.0781	4	1.28	0.3304
S*C	2	1.17	0.3339	2	1.01	0.3942
A*S*C	6	1.83	0.149	4	2.82	0.0731
Error B = B*A*L*S*C	18	MS = 0.16		12	MS = 0.015	

Neither chilling nor fluctuating temperatures adequately compensated for the light requirement of *C. nebrascensis*. This stricter light requirement may be associated with the smaller seed size of *C. nebrascensis* as compared to *C. utriculata*. Thompson and Grime (1983) suggested that many small seeds have an absolute light requirement, with medium-size seeds having a variable requirement. *Carex nebrascensis* germination was always increased by light, while that of *C. utriculata* was most increased by light for 2-year-

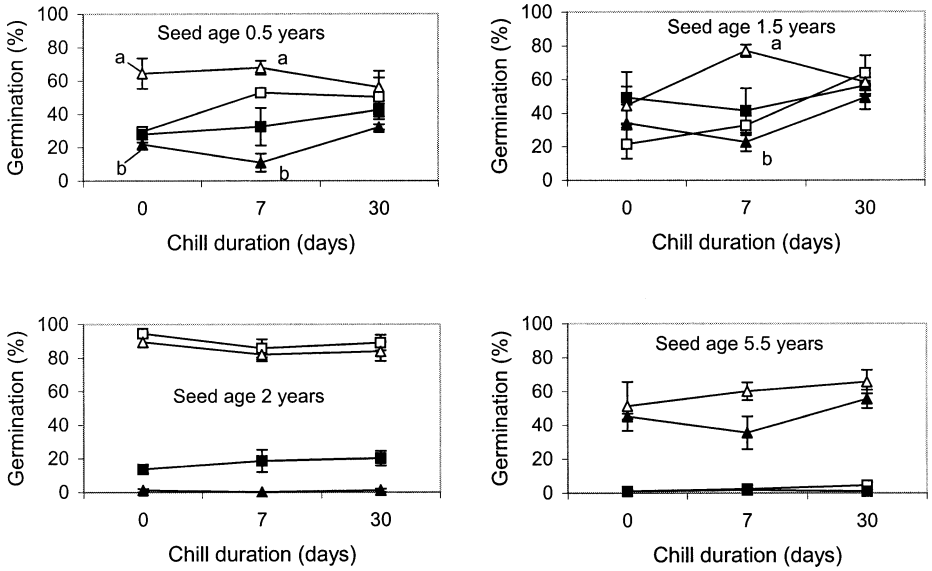

Figure 7. Total germination (%) after 36 incubation days for four seed ages of *Carex utriculata* (boxes) and *C. nebrascensis* (triangles) in light (open symbols) and darkness (black symbols) incubated under summer riparian seedbed temperatures (Figure 1). Error bars are ± 1 standard error of the mean (n = 4). Germination was not significantly different for different chill durations for a given age, species, and light treatment, except that chilling increased germination of *Carex nebrascensis* in the dark for 0.5-year-old seed and in the light for 1.5-year-old seed. Different letters for *C. nebrascensis* at 0.5 and 1.5-years old indicate a significantly higher germination percentage in light than in darkness. Germination of both species was significantly greater in light than darkness at 2 years but not 5.5 years of seed age.

old seeds incubated under spring or summer temperatures (Figures 2 and 7). Over-wintered, imbibed, and buried seeds in seed bags had limited germination when retrieved from riparian microsites but had high germination percentages under light exposure in the laboratory. This also suggests a need for light to maximize germination of these species. Broadcast-seeding these species and leaving them exposed on the soil surface would be expected to produce more germination than seed burial. The risk is that broadcast seeds may be lost to predation, desiccation, or flooding. To minimize potential seed loss, these species could be seeded on moist surfaces in mid-summer when seedbed temperatures favor more rapid germination (Figure 4).

Greater germination of these species in light compared to darkness after perigynia removal, especially for *C. nebrascensis*, suggests that the perigynium reduces light reception. Time to 50% germination of germinating seeds was 4 to 9 days shorter under all temperature regimes for both species with perigynia removed. Seeds with a strict light requirement may be sensitive to light absorbed by the dark-colored perigynium. *Carex utriculata* has a light colored perigynium compared to that of *C. nebrascensis*. Although scarification to remove the perigynia will increase germination percentage and rate of these species, moderate germination and successful direct seeding should be expected even with the perigynia left intact. Scarification to remove the perigynia to increase germination rate might be worth the effort if the risk of predation or seed loss is especially high.

The limited germination of *C. utriculata* after 5.5 years of dry storage agrees with the reports that many *Carex* species begin losing viability under dry storage conditions (Comes et al. 1978, Schmid 1984, Budelsky and Galatowitsch 1999, van der Valk et al. 1999). Storage under wet, cold conditions, such as occurs in the natural environment, conserves viability in many *Carex* species (Schmid 1984, Budelsky and Galatowitsch 1999). Budelsky and Galatowitsch (1999) found that fresh *Carex rostrata* seeds had higher germination percentages than stored seeds, but germination after 6 and 10 months under wet-cold or dry-warm storage conditions was comparable. In their study, germination decreased after 14 months under warm, dry storage conditions, and after 2.5 years, only 22% of the remaining seed was viable. In contrast, we found high germination percentages of *C. nebrascensis* after 5.5 years of dry storage. Because *C. utriculata* grows in wetter environments and its seeds are more likely to be dispersed into standing water or moist environments than those of *C. nebrascensis*, it may be less tolerant of dry seed storage conditions.

Germination of freshly harvested *Carex* seed can be low due to primary dormancy (Schütz 2000). Germination of the two species we tested after 0.5-year storage was generally moderate (>20%) when incubated with light and under summer temperatures. Our results suggest that seeds of these species harvested in fall could be sown the following summer. Use of *C. utriculata* seeds over 2.5-years-old is not recommended.

Our results suggest that maximum field germination of *C. utriculata* and *C. nebrascensis* will be achieved by broadcasting seeds on moist soil surfaces in summer after high water has receded and temperatures are warm, as has been recommended by Baskin et al. (1989) for *Cyperus odorata* L. and *Scirpus lineatus* Michx. A direct seeding field study is needed to test the success of this approach.

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