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Effect of Light on Seed Germination of Eight Wetland *Carex* Species

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• *Background and Aims* In wetland plant communities, species-specific responses to pulses of white light and to red : far-red light ratios can vary widely and influence plant emergence from the seed bank. *Carex* species are the characteristic plants of sedge meadows of natural prairie wetlands in mid-continental USA but are not returning to restored wetlands. Little is known about how light affects seed germination in these species—information which is necessary to predict seed bank emergence and to develop optimal revegetation practices. The effects of light on germination in eight *Carex* species from prairie wetlands were investigated.
• *Methods* Non-dormant seeds of eight *Carex* species were used to determine the influence of light on germination by examining: (*a*) the ability of *Carex* seeds to germinate in the dark; (*b*) the effect of different lengths of exposures to white light on germination; (*c*) whether the effect of white light can be replaced by red light; and (*d*) whether the germination response of *Carex* seeds to white or red light is photoreversible by far-red light.
• *Key Results* Seeds of *C. brevior* and *C. stipata* germinated >25 % in continuous darkness. Germination responses after exposure to different lengths of white light varied widely across the eight species. *Carex brevior* required <15 min of white light for ⩾50 % germination, while *C. hystericina*, *C. comosa*, *C. granularis* and *C. vulpinoidea* required ⩾8 h. The effect of white light was replaced by red light in all species. The induction of germination after exposure to white or red light was reversed by far-red light in all species, except *C. stipata*.
• *Conclusions* The species-specific responses to simulated field light conditions suggest that (*a*) the light requirements for germination contribute to the formation of persistent seed banks in these species and (*b*) in revegetation efforts, timing seed sowing to plant community development and avoiding cover crops will improve *Carex* seed germination.

Key words: *Carex*, far-red light, seed germination ecology, photomorphogenesis, phytochrome, prairie wetland, red light, sedge, white light.

INTRODUCTION

Carex is a globally important genus with >2000 species worldwide (Bernard, 1990), and in many wetlands of the northern hemisphere, *Carex* species are the dominant vegetation. In the prairie pothole region of mid-continental North America, >60 species of *Carex* are found in wetland habitats (Barkley, 1986), especially sedge meadows, the seasonally flooded zone of prairie wetlands. Seed bank dynamics of prairie wetlands have been the focus of a number of studies (e.g. van der Valk and Davis, 1978; Welling *et al*., 1988; Seabloom *et al*., 1998). The specific factors that drive emergence from the seed bank and vegetation dynamics in sedge meadows, however, are not well understood in comparison to what is known about the dynamics of the emergent plant community (van der Valk and Davis, 1978; Kantrud *et al*., 1989; Murkin *et al*., 2000). In wetland plant communities, species-specific dormancy break and germination requirements influence emergence from the seed bank (van der Valk and Davis, 1978; Leck, 1989; Baskin and Baskin, 1998). Both the amount of light [length of exposure and photosynthetic photon flux density (PPFD)] and quality of light [especially the red : far-red light ratio (R : FR)] are environmental cues that signal conditions potentially suitable for seedling establishment and survival (Pons, 2000).

Many wetland species require light for germination compared with upland species (Grime, 1981). In wetland plant communities, emergence of light-requiring species from the seed bank is triggered by a disturbance when soil turnover, decline in water depth, or gaps in litter or the plant canopy (Leck, 1989) expose seeds to light or higher R : FR. Small-scale disturbances in sedge meadows include burrowing, trampling and grazing by mammals and waterfowl (Fritzell, 1989; Murkin, 1989; Swanson and Duebbert, 1989). What is the predicted response of *Carex* seeds to these disturbances in sedge meadows? For many *Carex* species from prairie wetlands it is not known whether seeds germinate readily in the dark or if their emergence from the seed bank is restricted to disturbances that expose seeds to adequate light. Schütz and Rave (1999), however, evaluated germination in light and dark of seeds of 18 *Carex* species from open, wetland habitats in Germany, the Czech Republic and Sweden. They found that seeds of two species required light for germination and 16 species germinated to higher percentages in light than in darkness when stratified and then incubated at 22/10 °C. Similar findings were reported by Baskin and Baskin (1998) who summarize published and unpublished studies on germination requirements of *Carex* species from aquatic environments. Seeds of four species required light for germination (*C. canescens*, *C. crinita*, *C. pseudocyperus* and *C. vulpinoidea*) and those of six

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TABLE 1. *The eight* Carex *species used in this study*

Species	Seed viability (%)	Seed collection location	Collection date (2004)
C. brevior (Dewey) Mackenzie.	82	Minnesota Valley State Park in Scott County, MN (44°40′N, 93°37′W)	19 July
C. comosa F. Boott.	95	Minnesota Landscape Arboretum in Carver County, MN (44°51′N, 93°36′W)	9 September
C. cristatella Britton.	93	Minnesota Landscape Arboretum	18 August
C. granularis Muhl.	56	Minnesota Valley State Park	16–19 July
C. hystericina Muhl.	89	Minnesota Landscape Arboretum	14–21 July
C. scoparia Schk.	90	Cedar Creek Natural History Area in Anoka County, MN (45°24′N, 93°12′W)	11 August
C. stipata Muhl.	71	Minnesota Landscape Arboretum	28–30 June
C. vulpinoidea Michx.	82	Minnesota Landscape Arboretum	18 August

Seed viability was based on initial tetrazolium tests and performance in germination trials.
Seeds were collected from wetlands in central and southern Minnesota.

species germinated to higher percentages in the light than dark (*C. comosa*, *C. elongata*, *C. nigra*, *C. paniculata*, *C. remota* and *C. stricta*). Further study is required to determine if similar patterns exist in seeds of *Carex* from prairie wetlands. Understanding species-specific germination requirements is the first step in predicting how plant communities may respond to disturbance (e.g. Stockey and Hunt, 1994) and would provide insight into plant community development in prairie wetlands.

Understanding the light requirements for seed germination is also important for *Carex* species revegetation efforts in freshwater wetland restorations. Even though *Carex* are the dominant vegetation of sedge meadows of natural prairie wetlands, they are absent or slow to return to hydrologically restored wetlands (Galatowitsch and van der Valk, 1996; Mulhouse and Galatowitsch, 2003) due to seed availability limitation (Kettenring, 2006). The introduction of propagules is necessary for *Carex* revegetation success. Knowledge of species-specific light requirements for germination could indicate whether restoration practitioners should time seed sowing efforts to plant canopy development or whether excess sedimentation common in new restorations in agricultural landscapes reduces *Carex* seed germination (Jurik *et al*., 1994; Gleason and Euliss, 1998). In addition, it is not known whether current practices such as mulching (van der Valk *et al*., 1999) or planting cover crops (Perry and Galatowitsch, 2003) may inhibit *Carex* emergence.

The light requirements for seed germination of eight North American wetland *Carex* species were determined to compare broad patterns of the light requirements for seed germination with what is known about *Carex* in wetlands from other parts of the world. Using non-dormant seeds (i.e. cold stratified), the following were evaluated: (*a*) the ability of *Carex* seeds to germinate in the dark; (*b*) whether germination patterns differ with different exposures to white light; (*c*) whether the effect of white light can be replaced by red light, and (*d*) whether *Carex* seed germination after exposure to white or red light is photoreversible by far-red light.

MATERIALS AND METHODS

Seed collection and preparation

Seeds of eight *Carex* species were collected at maturity from wetlands in central and southern Minnesota during the 2004 growing season (Table 1). Seeds were air dried at room temperature for 2 weeks and then tested for viability using standard tetrazolium procedures with 200 seeds per species (Table 1) (Grabe, 1970). At the same time, seeds were counted into batches of 50 seeds, wrapped in filter paper, and placed in a growth chamber (model GCW-15; Environmental Growth Chambers, Chagrin Falls, OH, USA) set at 5/1 °C (10 : 10 h of high and low temperature with a 2 h linear transition between temperature changes) for stratification. Seeds were buried in well-drained, sterilized wetland soil in pots and watered weekly to saturation. Seeds were stratified for a minimum of 4 months to fully break dormancy (Kettenring, 2006). In this study, the definition of seed dormancy, according to Baskin and Baskin (1998), as an inhibiting characteristic of the seed that prevents germination rather than unsuitable environmental conditions for germination, is used. Prior to the start of each experiment, seeds were excavated from the pots in the dark under dim green light; it is not believed that this exposure to dim green light triggered germination given the low germination percentages for seeds in the dark treatment (Fig. 1). Seeds were placed in Petri dishes on saturated silica sand for the germination trials. The perigynium for each seed was left intact. Sample size was at least 2×50 seeds per dish for each treatment (sometimes more for white light experiments when extra seeds were available).

White-light experiment

To determine the effect of white light on *Carex* germination, stratified seeds of eight species (Table 1) were exposed to a single pulse of 0·25, 1, 2, 4, 8 or 14 h of white light, 3 14-h days of white light, or 3 weeks of 14 h d^{-1} of white light. A dark control was also maintained. The white light was provided by cool white

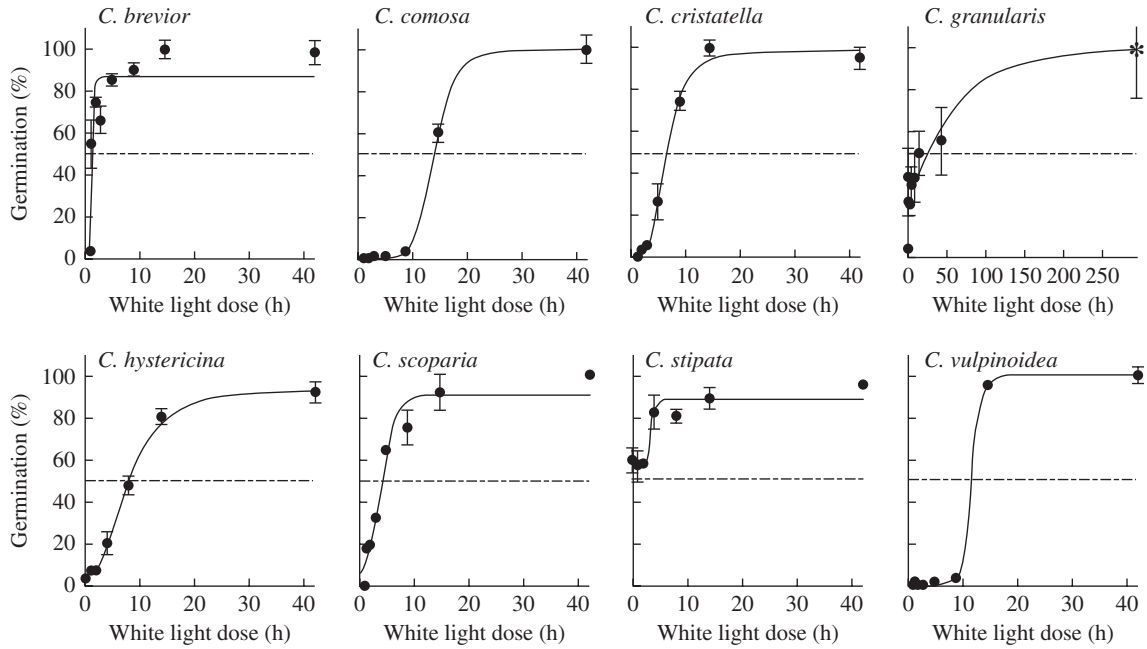

FIG. 1. The effects of different lengths of exposure to white light on *Carex* seed germination. PAR was 200 µmol m^{-2} s^{-1}. Three days of 14 h d^{-1} white light = 42 h. Values are means ± s.e. *Carex granularis* was the only species that did not germinate >90 % with 42 h of white light so germination after 3 weeks

fluorescent bulbs, photosynthetically active radiation (PAR; total irradiance between 400–700 nm) = 200 µmol m^{-2} s^{-1}, measured with the LI-189 quantum sensor (LICOR, Lincoln, NB, USA) and a R : FR of 10·3 : 1·0 measured with the SKR 110 660/730-nm sensor (Skye Instruments, Llandrindod Wells, UK) at seed level. Each Petri dish was covered with two layers of aluminium foil for the dark control or following the light exposure and stored at 27/15 °C for germination (10 : 10 h of high and low temperature with a 2 h linear transition between temperature changes). This temperature regime is suitable for seed germination for these *Carex* species (Kettenring, 2006). After 3 weeks, seeds were inspected in the light for germination. A seed was considered germinated if the cotyledon or radicle was visible without magnification.

Phytochrome experiment

To determine if phytochrome is involved in the photocontrol of *Carex* seed germination, stratified seeds were exposed to R or white light (light controls) or R followed by 1 h FR or white light followed by 1 h FR. A dark control was also maintained. The length of the R or white light exposure was chosen based on the results of the white light experiment (Fig. 1) by selecting a light exposure that resulted in a large increase in germination over the dark control. The white light was identical to that provided in the white-light experiment. The R source consisted of two R fluorescent lamps (Sylvania F48T12/2364/HO) filtered through an Encapsulite red tube guard (Lighting Plastics of Minnesota, Inc., St Louis Park, MN, USA) and a single layer of Roscolux cool blue filter (#66, Rosco Laboratories, Stamford, CT, USA). The FR light was provided by two FR fluorescent lamps (Sylvania F48T12/232/HO) filtered through an Encapsulite FR tube guard and a single layer of Lee deeper blue filter (#85, Lee Filters, Andover, Hampshire, UK). The red light (660 nm) was 2·97 µmol m^{-2} s^{-1} and the far-red light (730 nm) was 1·94 µmol m^{-2} s^{-1} as measured with the SKR 110 660/730 nm sensor. The spectra of these light sources are shown in fig. 1 of Howe *et al*. (1996); the R source has very little irradiance above 700 nm and the FR source has very little irradiance below 700 nm. Following the light exposure, seeds were covered with two layers of aluminum foil and stored at 27/15 °C for germination. All *Carex* species were evaluated in this experiment except *C. granularis*, which was omitted due to limited seed availability.

Analysis

For the white light experiment, mean percentage germination was graphically compared for each species at the different white light exposures (SigmaPlot 9·0; Systat Software Inc., 2004). In addition, time to 50 % germination (t_{50}) values were determined to compare the responses across species. Each germination curve was fitted with a logistic curve, $y = a/(1 + be^{-cx})$ (CurveExpert 1·3; Hyams, 2005), and t_{50} was determined as the point on the logistic curve that intersected the line for 50 % germination (Fig. 1).

For the phytochrome experiment, mean percentage germination was compared between dark-incubated seeds and seeds exposed to white or red light, and seeds exposed to white light versus white followed by FR or R versus R followed by FR using 2 × 2 contingency tables and chi-square tests (Statistix; Analytical Software, 2003). Germination percentages for each species presented in Fig. 1 and Table 2 were based on the number of viable seed taken as 100 % (Table 1). Seed viability was based on the

TABLE 2. *The photoreversibility of* Carex *seed germination*

Species	Length of red/ white light exposure	Quality of light exposure				
		Dark	White light	White + 1 h far-red	Red light	Red + 1 h far-red
C. brevior	1 h	25 ± 16	73 ± 4***	14 ± 5***	71 ± 8***	16 ± 5***
C. comosa	14 h	1 ± 1	100 ± 0***	0 ± 0***	77 ± 21***	0 ± 0***
C. cristatella	8 h	2 ± 2	92 ± 0***	14 ± 3***	68 ± 7***	14 ± 1***
C. hystericina	8 h	7 ± 0	35 ± 3***	8 ± 3***	18 ± 9*	6 ± 1**
C. scoparia	4 h	1 ± 1	76 ± 10***	7 ± 2***	54 ± 11***	8 ± 1***
C. stipata	4 h	29 ± 3	78 ± 4***	50 ± 6***	85 ± 15***	76 ± 6 NS
C. vulpinoidea	14 h	0 ± 0	100 ± 7***	36 ± 0***	100 ± 1***	53 ± 4***

Values are mean percent germination (± s.e.).

Seeds were exposed to either white, white followed by far-red, red or red followed by far-red light, or kept in the dark. The length of the red or white light pulse was chosen based on the white light exposure length that resulted in a distinct increase in germination over the dark control (near the estimated t_{50}; Fig. 1).

Differences in germination were compared with chi-square analyses for: (1) dark control *vs*. seeds exposed to white light; (2) white light *vs*. white followed by far-red light; (3) dark control *vs*. red light; or (4) red light *vs*. red followed by far-red light. For each comparison, significant differences were denoted: NS, Not significant; $*P < 0{\cdot}05$; $**P < 0.01$; $***P < 0{\cdot}001$.

results of the tetrazolium tests, unless seeds germinated to higher percentages during the 3-week incubation under white light. In this case, the value of the mean germination percentage was used as 100 % seed viability.

RESULTS

White-light experiment

Viable seeds of all species germinated to 100 % during 3 weeks incubation at a 14-h daily exposure to white light; however, seeds of each species responded differently to white-light exposures shorter than 3 weeks of 14 h d^{-1} (Fig. 1). In decreasing order of amount of light required for germination to 50 %, the species were *C. granularis* (t_{50} = 14·64 h) > *C. comosa* (t_{50} = 13·35) > *C. vulpinoidea* (t_{50} = 11·19) > *C. hystericina* (t_{50} = 8·37) > *C. cristatella* (t_{50} = 6·00) > *C. scoparia* (t_{50} = 3·15) > *C. brevior* (t_{50} = 0·23 h). *Carex stipata* was the only species with significant germination (>50 %) in the dark but its germination was increased with 4 h of white light.

Phytochrome experiment

Exposure to both white and R light significantly increased germination over the dark control for all species (Table 2); two species germinated to >25 % in the dark. The white light effect was greatest for seeds of *C. comosa*, *C. cristatella* and *C. vulpinoidea* that germinated to <5 % in the dark but >90 % in the light. *Carex vulpinoidea* was the only species whose seeds germinated to >90 % under R. Red light fully replaced the effects of white light on seed germination for three species (*C. brevior*, *C. stipata* and *C. vulpinoidea*). FR significantly reduced germination after exposure to white light for seeds of all species and for all species except *C. stipata* after exposure to R. The photoreversibility effect was greatest for *C. comosa* that germinated to 100 % under white light versus 0 % when exposed to white followed by FR light and to 77 % under R versus 0 % when exposed to R followed by FR.

DISCUSSION

White light triggered germination in all *Carex* species, and only two species germinated to >25 % in the dark. In the literature, *Carex* seed germination has been shown to be greater in the light than dark. It appears, however, that a greater proportion of the species from the present study were unable to germinate in the dark than what previous studies found. Schütz and Rave (1999), who studied 32 *Carex* species from different habitats, found that the probability of germination of stratified seeds increased after exposure to white light. However, contrary to the results of the present study, they found that 10 of 18 species from wet, open habitats germinated to >25 % in the dark at 22/10 °C after stratification. In another study, freshly matured seeds of six species germinated in the light but failed to germinate in the dark; all species, however, gained the ability to germinate to >25 % in the dark following stratification (Schütz, 1997*b*). Jensen (2004) found that germination of stratified seeds was significantly greater in the light versus the dark for two species at 25/15 °C and 15/5 °C but was not significantly different for two other species. Still, all three species germinated to >25 % in the dark. A previous study of *C. comosa* from a Kentucky population found that this species did not germinate in the dark (Baskin *et al*., 1996) as found in the present study. Stratified *C. stricta* seeds, however, did germinate to >50 % in the dark (Baskin *et al*., 1996). Finally, chilling had little effect on the ability of *C. nebrascensis* and *C. utriculata* from Utah sedge to germinate in the dark compared with germination in the light (Jones *et al*., 2004). A number of factors may have contributed to these different responses within and among *Carex* species from different parts of the world. Purely interspecific differences in seed ecology among species is likely to have the largest influence. It is also possible that the influence of environmental conditions during seed maturation on seed dormancy played a role (Gutterman, 2000). Finally, different experimental conditions among studies such as PAR levels and temperature regimes (*Carex* germination in the present study was evaluated only at 27/15 °C) could have affected experimental results.

Widely differing responses were found among the eight study species to varying lengths of exposure to white light. The variability of the response is interesting given that these species are from the same genus, were collected from a similar climatic region, and co-occur in the same type of habitat—sedge meadows; five of these species were collected from the same site. It is important to note, however, that these results are based on a single seed batch for these species. There was no obvious relationship between the light requirements for seed germination and either seed size or seed maturation time for the eight *Carex* species, results similar to Kettenring (2006). The largest-seeded species (*C. comosa*, *C. hystericina* and *C. stipata*) spanned the range for length of white light exposures required for 50 % germination. Similarly, some of the earliest-maturing species required the most and the least amount of white light for germination.

Seeds of most *Carex* species required much longer exposure to white light (in the order of many hours to days) to trigger high germination percentages than the pulses of a few seconds to minutes that have been found to trigger germination in other species (e.g. Sauer and Struik, 1964; Scopel *et al*., 1994; Milberg *et al*., 1996; Schütz, 2000; but see Steadman *et al*., 2004). For instance, Milberg *et al*. (1996), in a study of the effects of short duration light exposure (5 s of PAR = 210 μmol m^{-2} s^{-1}) on seed germination found that germination was stimulated in 24 of 44 species. Interestingly, this response was found in both summer and winter annuals and perennials and in small- and large-seeded species. However, *Carex* species appear to require longer white light exposures than many species that germinate after short duration light exposures (Schütz, 2000). Amen and Bonde (1964) found that at least 15 d of continuous white light was required for *C. ebenea* germination. In another study, a single exposure of 1 h of white light did not trigger germination in *C. canescens* (Schütz and Milberg, 1997). This requirement for longer exposures to white light for germination in many *Carex* species (e.g. in this study *C. hystericina*, *C. vulpinoidea*, *C. comosa* and *C. granularis*) implies that an adaptation exists for regeneration in long-lived gaps that exist for multiple days or weeks (i.e. a 'low-risk' germination strategy *sensu* Leck and Schütz, 2005). On the other hand, some species, like *C. stipata* and *C. brevior*, that require short exposures to white light, may be adapted to regeneration in fleeting gaps of sunlight that may exist for a few minutes or hours. Further evaluation of the adaptive significance of these germination light requirements for *Carex* regeneration and coexistence is important.

For some species, red light did not fully replace the effect of white light. One possibility for why this occurred is that the white light may have had an additional beneficial effect on germination beyond the phytochrome effect of R. Secondly, the fluence rate of the R treatment was 65 times lower than the white light. This may have resulted in lower seed germination in some species, although germination is known to be a low fluence response (Pons, 2000) and usually irradiance levels of 3 μmol m^{-2} s^{-1} (R treatment) are sufficient to trigger seed germination in most species.

Phytochrome is involved in the germination of six of the seven *Carex* species evaluated—far-red light reversed the effects of red light for all species except *C. stipata*. Additional testing at other FR exposures would indicate whether a different length exposure is necessary to reverse *C. stipata* germination and whether the 1-h FR treatment produced the maximum reversal of seed germination in all species. Nonetheless, the findings on the FR effect imply that germination of these six *Carex* species will be inhibited under plant canopies that have low R : FR. These findings are consistent with the results of a field study where seeds of five *Carex* species evaluated in the present study (*C. hystericina*, *C. comosa*, *C. stipata*, *C. vulpinoidea* and *C. cristatella*) germinated very poorly in natural wetlands with a well-established plant canopy and thick litter but germinated readily in the restored wetland sites that had little vegetation and litter (Kettenring, 2006). In that study, low R : FR was the most likely factor to prevent *Carex* seed germination in natural wetlands (e.g. soil moisture levels were more favourable in natural wetlands). In another study, Schütz (1997*a*) found that germination of six *Carex* species from open or forest wetlands was inhibited under a dense leaf canopy with a low R : FR. Also, for seeds incubated in the laboratory under a low R : FR (0·01), germination was 0 % for three of the species and <30 % for the other two species evaluated. Further investigation of the effects of different R : FR ratios on *Carex* germination is necessary to predict the response of *Carex* seeds to different light environments in the field.

Based on the white light germination requirements of the study species, the findings indicate that many of these species should be able to form a large persistent seed bank. Only *C. brevior* and *C. stipata* germinated >25 % in the dark. Seeds of any of the other study species (and most seeds of *C. brevior* and *C. stipata*) that are covered by a plant canopy, litter or soil are expected to remain in the soil until disturbed and exposed to adequate light. Further field tests of this phenomenon are necessary, as well as determining the absolute level of irradiance required for germination (e.g. can germination occur under the low light conditions just below the soil surface?). In addition, it is also necessary to determine the interaction between light/dark and temperature requirements for seed germination. The timing of natural seed dispersal or seed sowing for revegetation will influence seed germination because irradiance levels (along with other environmental factors) vary as plant canopies and litter accumulation change over the growing season. The germination of seven species was photoreversible with far-red light. Thus, germination of any seed falling under a plant canopy (e.g. cover crop) should be inhibited by low R : FR, which would also contribute to the formation of persistent seed banks in these species. Numerous studies from different habitats and regions of the world found that many, if not all, *Carex* species form persistent seed banks (for reviews, see Schütz, 2000; Leck and Schütz, 2005). The challenge now for ecologists is to understand how this persistence varies under different

environmental conditions, including light quantity and quality.

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