Vol. 11: 169–177, 2010
doi: 10.3354/ab00300

AQUATIC BIOLOGY
Aquat Biol

Seed germination of 14 wetland species in response to duration of cold-wet stratification and outdoor burial depth

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ABSTRACT: Effects of cold-wet stratification periods (0, 5, and 10 wk) and temperature fluctuation at different outdoor burial depths (0, 5, and 10 cm) on seed germination were examined in 14 wetland species from the temperate region of central China, with the aim of improving germination for rehabilitation. Prior to cold-wet stratification, only seeds of 1 species, *Eclipta prostrata*, germinated to a high percentage (>90 %), and a few seeds (<20 %) germinated in 10 species. Five wk of stratification significantly promoted germination in 6 species, but only 2 species germinated ≥50 %. Ten wk of stratification significantly promoted germination in 11 species, and 6 species germinated ≥50 %. In general, seeds of perennials required longer stratification periods than those of annuals to come out of dormancy. Burial significantly enhanced germination percentages in 7 species. Time to 50 % of germination (t_{50}) values indicated that 11 species germinated much faster after burial treatments than after stratification treatments. During 1 wk of continuous monitoring, the mean amplitude of daily temperature fluctuations at 0 cm was much higher than that at the other 2 depths. Even though 8 species differed significantly in germination percentages at different burial depths, their optimal germination varied in relation to burial depth. The results suggest that cold-wet stratification for 10 wk or outdoor burial for 5 wk could significantly improve seed germinability of most temperate wetland plants.

KEY WORDS: Amplitude · Seed dormancy · Temperature fluctuation · Rehabilitation

INTRODUCTION

Understanding the requirements for seed dormancy break and germination is crucial to the management and rehabilitation of ecosystems. Sowing seeds of appropriate species has been proven to accelerate vegetation restoration effectively (Dixon & Hambler 1984, Pywell et al. 2002, Lindborg 2006, Wallin et al. 2009). However, seeds of many wetland species are dormant at maturity (Baskin et al. 1989). In the natural environment, only a small proportion of seeds are recruited as seedlings from the soil seed bank in any given season (Baskin & Baskin 2001). However, if seeds are collected at dispersal and stored *ex situ* prior to use in rehabilitation projects, the storage conditions may be the key to dormancy loss. Understanding how to accelerate dormancy release in stored seeds can be useful for facilitating effective rehabilitation projects based on seed sowing.

Some water-permeable seeds in temperate regions that mature in late summer are dormant or conditionally dormant (Baskin & Baskin 2006), and they may come out of dormancy during exposure to cold stratification or to alternating temperatures during winter (Taylorson 1970, Baskin & Baskin 1985, Baskin et al. 1996). Cold stratification is regarded as the most important way to break dormancy in seeds of most northern temperate plants (Thompson & Grime 1983, Baskin & Baskin 1988, Schütz & Rave 1999). Previous studies have shown that germination responses to cold stratification depend on habitats, life history traits, and phylogenetic relationships (Grime et al. 1981, Thompson & Grime 1983, Baskin & Baskin 1988, Probert 1992, Schütz & Rave 1999).

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Temperature fluctuation is regarded as another important way to break dormancy. Germination of seeds of many wetland species is stimulated by fluctuating temperatures (Thompson & Grime 1983, Schütz & Rave 1999, Baskin & Baskin 2001). The germination of 42% of 66 aquatic species was promoted under alternating temperature controls (Thompson & Grime 1983). In the field, diurnal temperature fluctuations vary significantly among different soil depths (Stoller & Wax 1973). Thus, the dormancy patterns of seeds at different burial depths could be dissimilar.

In the temperate regions of China, 2 gigantic dam projects, the Three-Gorges Dam and the Danjiangkou Dam, were completed on the Yangtze River and its main tributary, the Han River, in 2009 and 2010, respectively. The 2 dam projects will form the Three-Gorges Reservoir (29° 16′ to 31° 25′ N, 106° to 111° 10′ E; 1080 km^2) and the Dianjiangkou Reservoir (32° 36′ to 33° 48′ N, 110° 59′ to 111° 49′ E; 1050 km^2). Due to the water regulation, the area of emergent reservoir margins will be 340 to 370 km^2 from May to October. With the change of the hydrology regime, most of the pre-existing vegetation will lose its natural habitat in the reservoir margins. Hence, there are critical concerns about the success of rapid rehabilitation of these margins with native species in order to reduce bank collapse and reservoir sedimentation. An understanding of seed biology is essential to enable rehabilitation procedures. The present study focuses on 14 native wetland species from diverse plant habitats, that are common in the vegetation of the reservoir margin area. We hypothesized that cold-wet stratification would promote germination. More specifically, we tested how (1) the duration of cold-wet stratification and (2) diurnal amplitudes of temperature fluctuation affect the germination percentage and rate.

MATERIALS AND METHODS

Seed material. Seeds were collected from natural populations in central China in September to November 2007 (Table 1). The inflorescences of mature plants were harvested by hand. Orthodox seeds of mudflat and emergent species (*Caldesia parnassifolia*, *Cyperus difformis*, *C. iria*, *Eclipta prostrata*, *Monochoria korsakowii*, *Oenanthe javanica*, *Polygonum lapathifolium*, *Pycreus globosus*, *Sagittaria trifolia*, *Scirpus triqueter*) were stored under laboratory conditions (15–20°C, 40–60% relative humidity). Recalcitrant seeds of submerged and free-floating species (*Hydrocharias dubia*, *Ottelia alismoides*, *Vallisneria natans*, *V. spinulosa*) were submerged in water. All seeds were stored until late January 2008, when the experiments began.

Climate overview of the seed collection area. Lying in a northern subtropical monsoon climate zone, central China has 4 distinct seasons with an annual average temperature of 15 to 17°C and an annual average precipitation of 800 to 1600 mm. The coldest month is January, with a mean temperature of 2 to 4°C, and the warmest month is July, with a mean temperature of 27 to 29°C. In the season of seed collection, mean air temperature is 22 to 24°C in September and 10 to 12°C in November, and mean precipitation is 80 to 110 mm in September and 30 to 60 mm in November, respectively (data from the meteorological bureau of Hubei Province).

Cold-wet stratification trials. Cold-wet stratification trials were conducted to learn more about differences in the germination percentages between 2 treatment durations. Seeds of each species were placed in 1 Petri dish (10 cm diameter) containing 2 layers of filter

Table 1. Wetland species used in this study. Life form: A: annual; P: perennial; M: mudflat species; E: emergent; F: free-floating; S: submerged

Species	Family	Class	Life form	Seed maturation	Collection location	Collection habitat
Caldesia parnassifolia (Bassi ex L.) Parl.	Alismataceae	Monocot	PM	Mid-September	32° 46′ N, 111° 32′ E	Permanent marsh
Cyperus difformis L.	Cyperaceae	Monocot	AM	Mid-August	32° 44′ N, 111° 36′ E	Cropland
Cyperus iria L.	Cyperaceae	Monocot	AM	Mid-August	32° 31′ N, 111° 08′ E	Cropland
Eclipta prostrata (L.) L.	Asteraceae	Dicot	AM	Early September	32° 44′ N, 111° 36′ E	Reservoir margin
Hydrocharis dubia (Bl.) Backer	Hydrocharitaceae	Monocot	AF	Early October	30° 11′ N, 114° 33′ E	Lakeshore marsh
Monochoria korsakowii Regel et Maack	Pontederiaceae	Monocot	PM	Early October	30° 21′ N, 114° 27′ E	Wet meadow
Oenanthe javanica (Blume) DC.	Umbelliferae	Dicot	PM	Mid-August	32° 31′ N, 111° 08′ E	Wet meadow
Ottelia alismoides (L.) Pers.	Hydrocharitaceae	Monocot	AS	Early October	30° 11′ N, 114° 33′ E	Lakeshore marsh
Polygonum lapathifolium L.	Polygonaceae	Dicot	AM	Early October	30° 11′ N, 114° 33′ E	Wet meadow
Pycreus globosus (All.) Reichb.	Cyperaceae	Monocot	PM	Early September	32° 31′ N, 111° 08′ E	Cropland
Sagittaria trifolia L.	Alismataceae	Monocot	PE	Early October	32° 44′ N, 111° 36′ E	Cropland
Scirpus triqueter L.	Cyperaceae	Monocot	PE	Mid-October	32° 46′ N, 111° 32′ E	Wet meadow
Vallisneria natans (Lour.) Hara	Hydrocharitaceae	Monocot	PS	Mid-September	30° 17′ N, 114° 34′ E	Shallow-water lake
Vallisneria spinulosa Yan	Hydrocharitaceae	Monocot	PS	Mid-September	30° 17′ N, 114° 34′ E	Shallow-water lake

paper moistened with distilled water. Petri dishes were stored in a refrigerator (ca. 4°C) in darkness on 29 January 2008 for 5 and 10 wk. Distilled water was added periodically to keep the seeds moist but not submerged.

Burial trials. Burial trials were conducted to learn more about differences in germination percentages in response to different diurnal amplitudes of temperature. The sediment for burial trials was excavated to a depth of 40 cm in a seasonal pond. Organic content, particle size distribution, and pH of sediment were roughly determined. A sediment sample was dried in a drying cabinet at 80°C for 48 h. The dry sample was burned in a muffle furnace at 600°C for 6 h to remove the organic matter. Clay was separated from silt and sand in the upper suspension by centrifugation at 750 rpm for 3 min (Chu & Johnson 1985). Sand was separated from silt by wet sieving under a water stream though a 200 mesh sieve (mesh size 0.065 mm). The sediment contained 8% sand, 35% silt, 48% clay, and 9% organic matter, with a pH of 6.7. One hundred seeds per species were enclosed in an 80 mesh nylon bag (mesh size 0.2 mm) to allow for free movement of air, water, and microorganisms around the seeds in the burial experiments. One seed bag for each species was placed randomly on the surface and at burial depths of 5 and 10 cm in a plastic box (75 × 50 × 50 cm). The bottom of the box was covered with 3 cm of sediment to prevent the lower seed bags from touching the bottom of the box. The treatments were replicated 5 times (i.e. 5 boxes). The boxes were placed on the roof of the research building of the Wuhan Botanical Garden (30° 33′ N, 114° 25′ E) on 30 January 2008 and covered by a stainless steel net (mesh size 1.5 × 1.5 mm) to prevent accidental dislocation and loss by flooding or from the activities of small animals. Seeds were exhumed after 5 wk. After counting and removing the germinated seeds, the rest were cleaned and prepared for the germination experiment. The data of germination percentage in the germination experiment were based on the ungerminated seeds after burial.

This burial treatment system did not allow us to accurately simulate natural soil temperature conditions. Compared to the natural habitat, it was expected to produce different diurnal amplitudes of temperature. We hypothesized that seeds lying on the surface of the soil would experience the greatest temperature fluctuations due to their direct exposure to air. Seeds at 10 cm burial depths would experience moderate temperature fluctuations due to the bottoms of the boxes being directly in contact with the concrete roof; and seeds at 5 cm burial depth would experience the least temperature fluctuations because soils tend to be buffered from the extreme variation in air temperature. Temperature probes were placed at corresponding seed positions, and temperatures were recorded hourly from 07:00 to 23:00 h each day during the last week of the burial experiment. Daily air temperatures during the seed burial period were acquired from the automatic meteorological monitoring station of Wuhan (30° 32′ N, 114° 23′ E).

Germination experiments. Tests were conducted on seeds without cold-wet stratification on 29 January. On 7 March, we tested seeds that were cold stratified for 5 wk and those that were buried for 5 wk, and on 9 April, we tested seeds that were cold stratified for 10 wk. Germination experiments were carried out in 3 growth chambers at a constant temperature of 25 ± 1°C, using a 12 h photoperiod and a photon irradiance of 25 µmol m^{-2} s^{-1} provided by warm white fluorescent lamps. Thirty seeds were placed in 7 cm diameter Petri dishes containing 2 layers of filter paper moistened with distilled water. Petri dishes were placed at random in growth chambers, and each species was replicated 5 times. Distilled water was added to the dishes every 1 to 2 d to maintain a moist substrate. Germinated seeds were counted daily for 30 d. Any seeds that had germinated were removed from the dishes at each counting. A seed was considered to have germinated when the radicle emerged from the seed coat.

Statistical analysis. The results were analyzed for statistical significance with a general linear model ANOVA using SPSS 16.0. Germination percentage data were arcsine square root transformed prior to analysis. Multiple comparisons of means were made with Tukey tests. The time (in days) to 50% of final germination (t_{50}) was used to express the rate of germination (Keeley 1987, Escudero et al. 1997). For each species, t_{50} data were compared using ANOVA and Tukey HSD tests.

RESULTS

Cold-wet stratification

Except for seeds of *Eclipta prostrata*, which germinated to a high percentage without stratification, seeds of all species either did not germinate or germinated to only a low percentage prior to cold-wet stratification. Germination percentages of 6 species were significantly enhanced by a 5 wk period of stratification, but only 2 species, *Cyperus difformis* and *Hydrocharias dubia*, germinated ≥50%. After a 10 wk period of stratification, germination percentages of 11 species were enhanced significantly compared to germination prior to stratification, and 6 species reached more than 50% germination (Fig. 1).

Burial

Seeds of 11 species germinated during burial. For most species, germination percentages of seeds placed on the soil surface were significantly higher than those buried at 5 and at 10 cm depths. All buried seeds either did not germinate or germinated with a low percentage, with the exception of *Monochoria korsakowii* (Fig. 2).

Compared to cold-wet stratification, burial significantly enhanced the germination percentages of 7 species (Fig. 3). Five species had significantly higher germination percentages at depths of 0 cm, at 0 and 5 cm, or at 0 and 10 cm. *Hydrocharias dubia* and *Ottelia alismoides* had the highest germination percentages at 0 cm, *Cyperus difformis* and *Oenanthe javanica* at 0 and 5 cm, and *Sagittaria trifolia* at 0 and 10 cm. Conversely, 3 species had significantly higher germination percentages at 5 or 10 cm depths (*Polygonum lapathifolium* and *Pycreus globosus* at 5 cm and *Cyperus iria* at 10 cm). Overall, the results showed that the optimal germination conditions of wetland plants are species dependent.

Based on t_{50} values, 11 out of 14 species germinated significantly faster after burial than after cold stratification (Table 2).

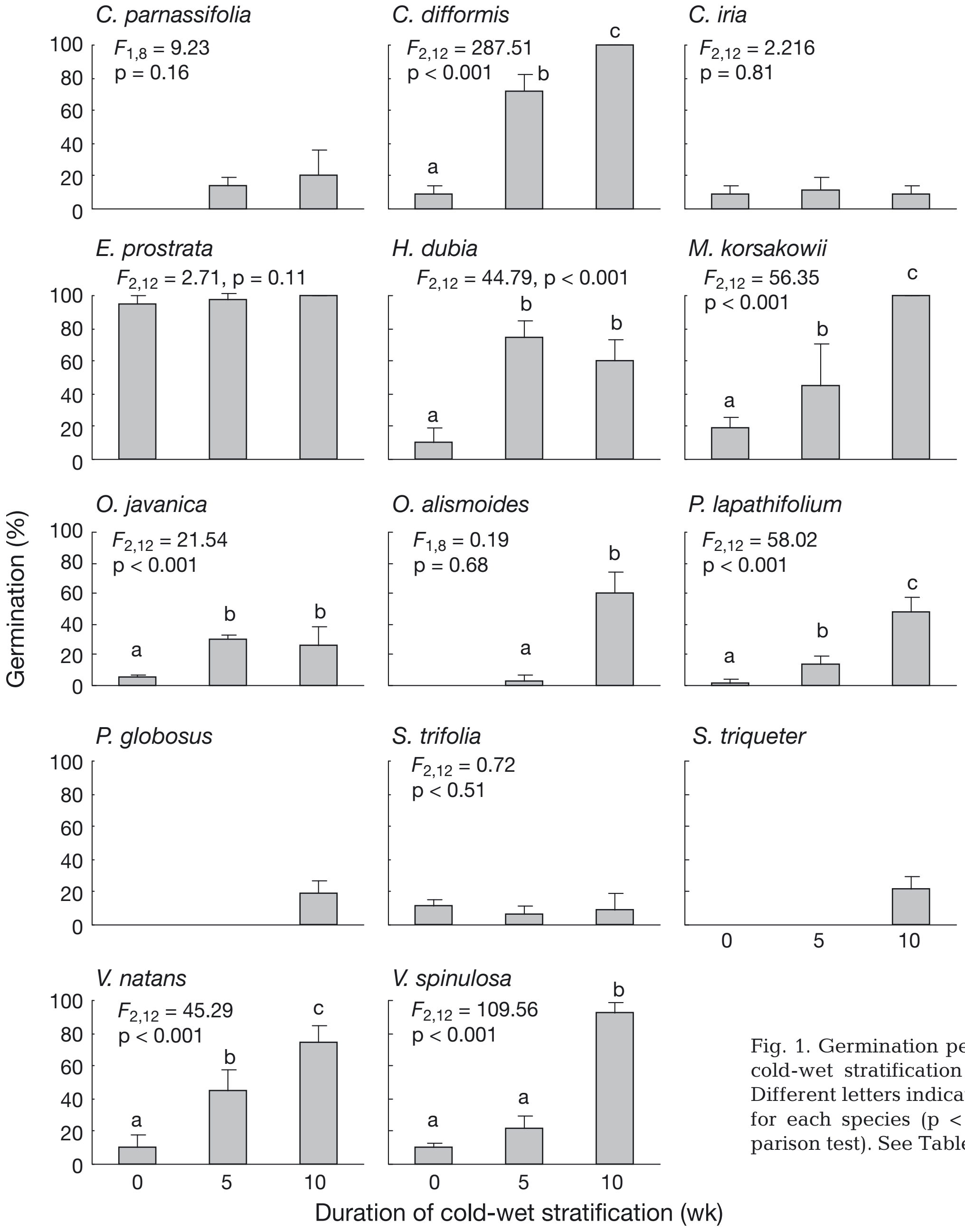

Fig. 1. Germination percentages of seeds after cold-wet stratification in 14 wetland species. Different letters indicate significant differences for each species ($p < 0.05$; Tukey HSD comparison test). See Table 1 for full species names

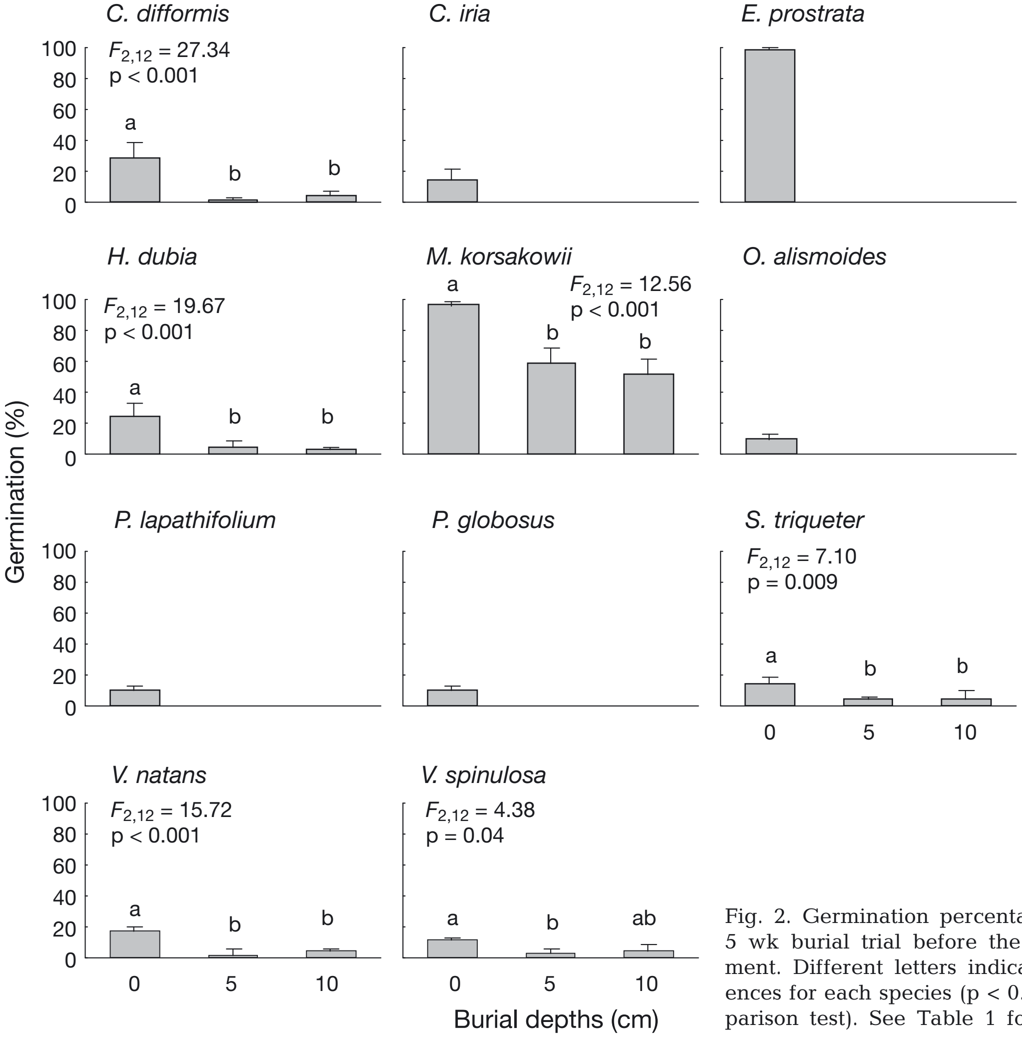

Fig. 2. Germination percentages of seeds after a 5 wk burial trial before the germination experiment. Different letters indicate significant differences for each species ($p < 0.05$; Tukey HSD comparison test). See Table 1 for full species names

Temperature fluctuation

Daily air temperature and precipitation during seed burial periods fluctuated considerably (Fig. 4). The absolute maximum and minimum air temperatures were 20.1 and –5.2°C, and the highest and lowest daily temperature amplitudes were 9 and 1.4°C, respectively. Although the cumulative precipitation was not high, the soil surface never dried.

The amplitude of daily temperature fluctuation differed markedly among burial depths (Fig. 5). Within 1 wk of monitoring, the mean temperature maxima were 23.2°C at 0 cm, 24.3°C at 5 cm, 18.9°C at 10 cm, and 18.6°C in air, and corresponding mean temperature minima were 7.8°C at 0 cm, 21.3°C at 5 cm, 12.0°C at 10 cm, and 7.7°C in air. The mean amplitude of daily temperature fluctuation at 0 cm burial depth (15.4°C) was much higher than that at the other 2 burial depths (3°C at 5 cm and 6.9°C at 10 cm) and air temperature (8.7°C; $F_{3,24}$ = 12.119, $p < 0.01$).

DISCUSSION

We investigated dormancy loss in seeds of temperate wetland species under stratification and outdoor burial conditions. Seeds of all species examined had primary dormancy at maturity, with the exception of *Eclipta prostrata*. Dormancy can be broken by natural cold stratification either in the field or laboratory. This study also indicates that manipulation of the seed storage environment can affect the rate of dormancy loss and improve germination performance of diverse temperate wetland species. Since stratification and outdoor burial did not effectively break dormancy in several species, it is clear that low temperature and moisture are not the only 2 environmental cues to break dormancy, and thus other environmental cues need to be identified.

It is well established that the dormancy of many species from temperate regions can be broken by cold-wet stratification (0 to 8°C) (Grime et al. 1981, Washitani &

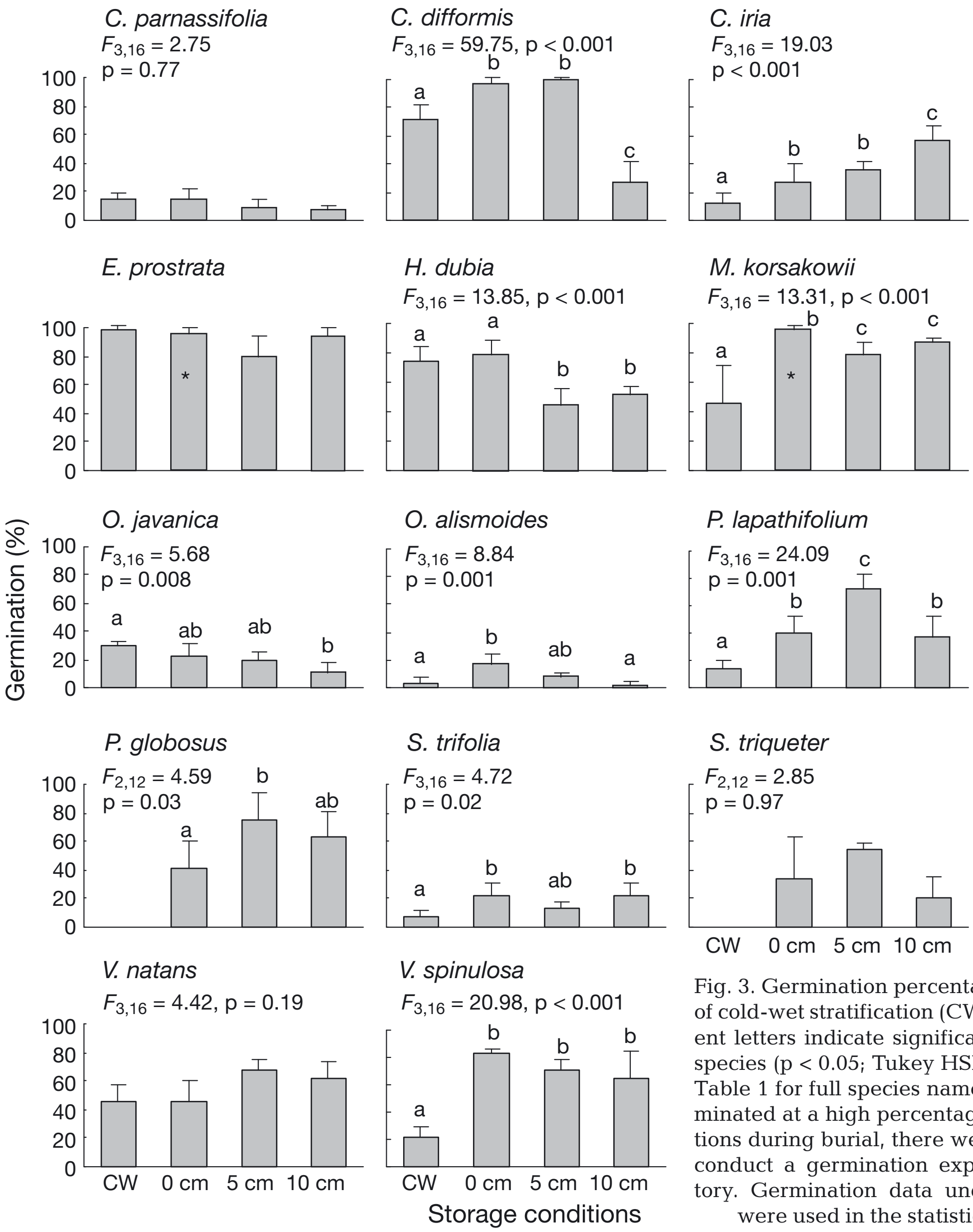

Fig. 3. Germination percentages of seeds after 5 wk of cold-wet stratification (CW) or after burial. Different letters indicate significant differences for each species ($p < 0.05$; Tukey HSD comparison test). See Table 1 for full species names. *Because seeds germinated at a high percentage under outdoor conditions during burial, there were not enough seeds to conduct a germination experiment in the laboratory. Germination data under outdoor conditions were used in the statistical analysis instead

Masuda 1990, Schütz 2000, Nishihiro et al. 2004, Wilson et al. 2006, Kettenring & Galatowitsch 2007). However, sufficient duration of stratification to break dormancy varies widely among species. For instance, a 10 wk stratification period is enough to remove dormancy for most species (Grime et al. 1981, Baskin et al. 1992, Bewley & Black 1994). However, several sedges require at least 2 to 6 mo of stratification before any germination occurs (Schütz 2000, Esmaeili et al. 2009). In the present study, 6 species exhibited significantly higher germination percentages after 5 wk of stratification. However, compared with germination prior to stratification, only 2 annuals (*Cyperus difformis* and *Hydrocharias dubia*) germinated to more than 50%. After a 10 wk stratification period, 8 species reached more than 50% germination. Five of the other 6 species with less than 50% germination were perennials, except *Polygonum lapathifolium*. This implies that the dormancy traits of wetland plants could be related to their life cycles. For instance, for the purpose of weed control, the dormancy releases from the dormant seed bank were more effective for annual species than for perennial species (Davis 2006). Moreover, in the present study the duration of stratification had a minimal effect on the germination rates of 4 species: *Caldesia parnassifolia*, *Cyperus iria*, *Oenanthe javanica*, and *Scirpus triqueter*. The low germination rate and long stratification duration requirement are typical charac-

Table 2. Average t_{50} (time to 50% of germination) values (± SE, days) recorded for seeds cold-wet stratified for 5 wk (CW) and for those buried for 5 wk at 0, 5, and 10 cm depths. $^{**}p < 0.01$; $^{***}p < 0.001$. Same letters indicate no significant differences for each species by Tukey HSD comparison test. Dash corresponds to absence of germination. See Table 1 for full species names

Species	CW	0 cm	5 cm	10 cm	$F_{3,16}$
C. parnassifolia	13.6 ± 1.4^{a}	9.6 ± 0.4^{b}	10.0 ± 0.0^{b}	10.0 ± 0.8^{b}	4.99*
C. difformis	8.6 ± 0.6^{ab}	6.4 ± 0.4^{a}	5.0 ± 0.3^{a}	10.8 ± 1.7^{b}	7.07**
C. iria	15.4 ± 1.5^{a}	11.6 ± 0.7^{b}	6.4 ± 0.4^{c}	6 ± 0.5^{c}	23.90***
E. prostrata	4.6 ± 0.2^{a}	4.4 ± 0.2^{ab}	3.8 ± 0.4^{ab}	3.4 ± 0.2^{b}	3.79*
H. dubia	8.4 ± 0.4^{a}	6.6 ± 0.5^{ab}	6.0 ± 0.8^{b}	6.8 ± 0.5^{ab}	3.33*
M. korsakowii	6.6 ± 0.4^{a}	1.0 ± 0.0^{b}	3.0 ± 0.0^{c}	3.0 ± 0.3^{c}	83.69***
O. javanica	10.6 ± 0.2^{ab}	9.8 ± 0.6^{a}	7.4 ± 0.2^{a}	14.3 ± 2.1^{b}	8.05**
O. alismoides	14.5 ± 3.5^{a}	11.2 ± 1.8^{a}	10.0 ± 0.8^{a}	10.5 ± 0.9^{a}	1.11
P. lapathifolium	5.6 ± 0.2^{a}	5.0 ± 0.0^{a}	4.8 ± 0.4^{a}	5.2 ± 1.2^{a}	0.28
P. globosus	–	7.8 ± 0.6^{a}	9.0 ± 0.6^{a}	9.0 ± 0.0^{a}	1.95
S. trifolia	10.5 ± 1.0^{a}	6.0 ± 0.0^{b}	5.6 ± 0.6^{b}	6.2 ± 0.2^{b}	15.90***
S. triqueter	–	8.5 ± 0.3^{a}	7.8 ± 0.2^{a}	11.0 ± 2.7^{a}	1.38
V. natans	11.2 ± 1.0^{a}	10.2 ± 1.3^{a}	7.8 ± 0.4^{ab}	6.6 ± 0.2^{b}	6.24**
V. spinulosa	11.0 ± 0.3^{a}	7.0 ± 0.0^{b}	6.8 ± 0.6^{b}	7.9 ± 0.5^{b}	29.58***

teristics of most species in the Cyperaceae. For example, 3 carices, *Carex demissa*, *C. davalliana*, and *C. flava*, showed a positive response to a stratification period of 6 mo, whereas a stratification period of 6 to 8 wk was too short to release dormancy (Schütz 2000). Seed germination of *C. granularis* required at least 2 mo of stratification (Kettenring & Galatowitsch 2007); *Scirpus lacustris* and *S. maritimus* reached high germination after 80 wk of stratification (Clevering 1995). These studies suggest that a 10 wk stratification period is too short to break dormancy in the seeds of some species.

Effects of temperature fluctuations on seed germination have been widely discussed (Thompson 1974, Totterdell & Roberts 1980, Pons & Schröder 1986, Benech-Arnold et al. 1990, Van Assche & Van Nerum 1997, Ekstam & Forseby 1999, Zhang et al. 2007). Our results showed that 9 species had a higher germination percentage and a lower t_{50} at 1 or more burial depths after a 5 wk burial, compared to the same period of stratification (Table 2). Although results obtained so far clearly show evidence that soil temperature is an overriding factor governing dormancy changes of wetland seed banks, it has been hypothesized that light, soil moisture, and oxygen concentration could also affect the dormancy level of buried weed seeds (Benvenuti & Macchia 1995, Benech-Arnold et al. 2000, Batlla & Benech-Arnold 2004). Our experimental design did not evaluate these effects.

It should be noted that 11 species germinated prior to the germination experiment, especially on the soil surface. Germination during outdoor burial would be wasteful of seeds. With the aim of storing seeds for rehabilitation, the seeds of these species should be kept buried below 5 cm. Interestingly, seeds of *Monochoria korsakowii* germinated massively during burial at all 3 depths, whereas seeds of *Eclipta prostrata* germinated only on the soil surface. This result reflects the finding that the germination of *E. prostrata* seeds

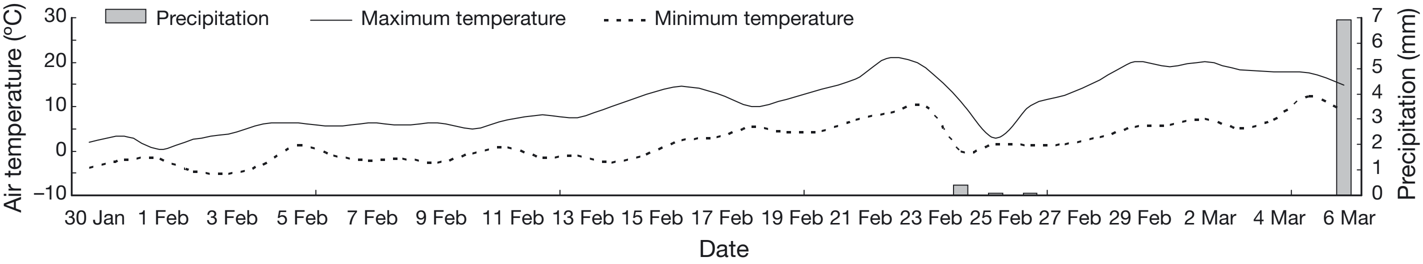

Fig. 4. Daily air temperature and precipitation during the seed burial period

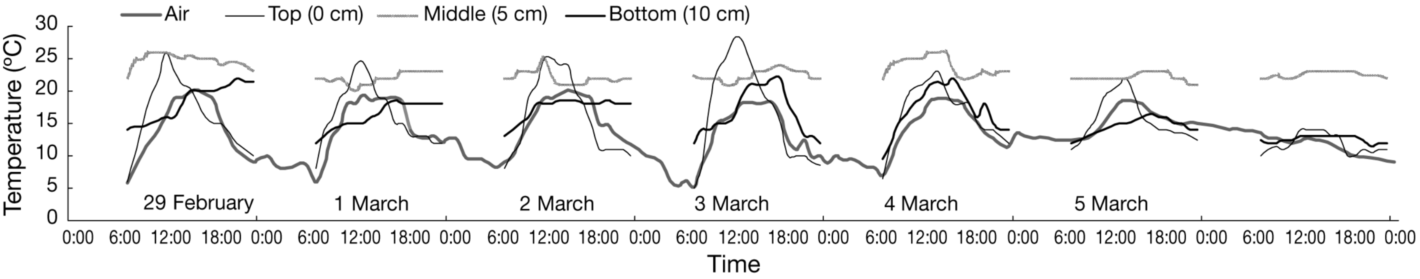

Fig. 5. Diurnal amplitude of temperature fluctuations in air and at burial depths of 0, 5, and 10 cm during 1 wk of monitoring (29 February to 6 March 2008)

is highly dependent on light (Altom & Murray 1996). Previous research has indicated that the light requirements for germination contribute to the formation of persistent seed banks in some light-dependent species such as *Carex* spp. (Kettenring et al. 2006). As a consequence, most of the species in the present study have the potential to form persistent seed banks, an exception being *M. korsakowii.*

In conclusion, seeds of 14 wetland species reached relatively high germination by manipulation of the seed storage environment. The present study has increased our understanding of dormancy loss in these species by demonstrating that most of them respond to cold-wet stratification and diurnal amplitudes of temperature through outdoor burial. To improve germinability, this study indicates that seeds should be stored at cold-wet stratification for at least 10 wk or buried outdoors for 5 wk. A longer storage period is recommended for some sedge species. In addition, *Monochoria korsakowii* is not recommended for outdoor burial, and *Eclipta prostrata* should be buried at least 5 cm deep. These findings show that seed dormancy can be overcome between the time of seed collection in spring and the time of seed sowing in summer, which has direct implications for the rehabilitation of the degraded wetland. The results of the present study may also be applicable to other wetland species in temperate regions.

Acknowledgements. We thank 4 anonymous reviewers for critical comments and helpful suggestions, and H. Goon for correcting the English. This study was supported by the National Science Foundation of China (30970469) and the National S & T Major Project (2008ZX07102-005).

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Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: January 18, 2010; Accepted: October 13, 2010
Proofs received from author(s): December 9, 2010