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ROLE OF TEMPERATURE, LIGHT AND DATE SEEDS WERE EXHUMED FROM SOIL ON GERMINATION OF FOUR WETLAND PERENNIALS

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ABSTRACT

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Seeds of the four wetland perennials *Cyperus odoratus* L., *Gratiola viscidula* Pennell, *Penthorum sedoides* L. and *Scirpus lineatus* Michx. were buried in soil and exposed to yearly seasonal temperature cycles. At monthly intervals for 30.5 or 31 months, seeds were exhumed and tested at daily alternating (12/12 h) temperature regimes of 15/6, 20/10, 25/15, 30/15 and 35/20°C in light (14 h photoperiod) and darkness. Seeds of all species had an absolute light requirement for germination. Freshly matured seeds of *C. odoratus* and *P. sedoides* were conditionally dormant, while those of *G. viscidula* and *S. lineatus* were dormant. Seeds of all species became non-dormant during winter; however, those of *C. odoratus* and *G. viscidula* never gained the ability to germinate at 15/6°C. Buried seeds of *C. odoratus* and *P. sedoides* remained non-dormant during the remainder of the study, while those of *G. viscidula* and *S. lineatus* exhibited an annual conditional dormancy/non-dormancy cycle.

INTRODUCTION

Studies of the seed banks in marshes, swamps and at the edges of lakes reveal that many emergent aquatic plant species form persistent seed banks (van der Valk and Davis, 1978, 1979; Leck and Graveline, 1979; Keddy and Reznicek, 1982, 1986; Leck and Simpson, 1987). It has been suggested that species growing in unpredictable habitats such as those where water levels fluctuate will have seeds that remain non-dormant during burial (Baskin and Baskin, 1988). Thus, seeds could germinate at any time during the growing season, if they are exposed to light and soil moisture is non-limiting.

Dormancy is not an all-or-nothing phenomenon. That is, seeds are not merely dormant or non-dormant. Instead, as seeds pass from the dormant to the non-

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dormant state, or from non-dormancy to dormancy, they exhibit a continuum of changes in their physiological responses to various factors such as light and temperature.Thus, the terms dormant, non-dormant and conditionally dormant are used to describe the full range of physiological states that seeds may exhibit as they come out of, or re-enter, dormancy (Vegis, 1964; Baskin and Baskin, 1985a). Dormant seeds will not germinate under any set of normal environmental conditions, while non-dormant seeds will germinate over the widest range of environmental conditions possible for the taxon or ecotype. Conditional dormancy (sensu Vegis, 1964) is the dynamic state between dormancy and non-dormancy. Conditionally dormant seeds germinate under a limited range of environmental conditions which widen as the seeds come out of dormancy (afterripen) or narrow as they go back into dormancy.

In 1985, studies were initiated on seeds of *Cyperus odoratus* L., *Gratiola viscidula* Pennell, *Penthorum sedoides* L. and *Scirpus lineatus* Michx. to determine if buried seeds undergo seasonal changes in their germination requirements or if they remain non-dormant after they have lost their initial dormancy. This study was mentioned by Baskin and Baskin (1988), but at that time it was incomplete. In this paper, we compare germination of the four wetland perennials.

MATERIALS AND METHODS

Mature, ripe seeds of *S. lineatus* were collected in Davidson County, TN, U.S.A. on 27 May 1985, and those of *C. odoratus, G. viscidula* and *P. sedoides* were collected in Scioto County, Ohio, U.S.A., on 5 October 1985. Seven days after collection of the *S. lineatus* seeds, about 3000 were placed in each of 31 fine mesh (average area of openings was 0.13 mm^2) nylon bags, and 9 days after collection of seeds of *C. odoratus, G. viscidula* and *P. sedoides* about 3000 seeds of each species were placed in each of 30 bags. Each bag was buried to a depth of 7 cm in potting soil (3:1 v/v mixture of limestone-derived topsoil and river sand) in 15-cm-diameter clay pots (volume=1700 ml) with drainage holes, and the pots were placed under a bench in a non-temperature-controlled glasshouse (no heating or air-conditioning and windows kept open all year). Mean daily maximum and minimum monthly temperatures in the glasshouse for the duration of the study were calculated from continuous thermograph records (Table 1). The soil in the pots was watered to field capacity once each week during summer (1 May–31 August) and each day during the remainder of the year, except on winter days when it was frozen.

Germination tests were conducted on freshly matured seeds of each species. Seeds of *S. lineatus* were exhumed on the first day of each month (except as noted below) until January 1988, and seeds of the other species were exhumed on the first day of each month (except as noted below) until May 1988. Seeds of the four species were not exhumed on 1 August 1986, those of *S. lineatus*

TABLE 1

Mean daily maximum and minimum monthly air temperatures (°C) in the non-temperature-controlled glasshouse in Lexington, Kentucky, U.S.A. for the duration of the study

Month	Maximum				Minimum			
	1985	1986	1987	1988	1985	1986	1987	1988
January		8.0	5.2	5.7		−2.4	−2.2	−1.5
February		8.6	9.4	8.2		1.1	0.2	−2.1
March		17.2	17.7	16.4		4.2	4.8	4.4
April		23.9	20.7	24.4		9.2	7.2	9.4
May		27.7	29.8			17.6	15.5	
June	29.6	30.7	31.2		17.2	18.9	19.0	
July	30.4	31.1	32.7		18.2	20.5	21.3	
August	28.3	29.3	31.8		18.8	17.6	19.8	
September	28.1	27.6	27.0		15.2	18.1	15.0	
October	21.6	21.3	20.7		12.0	11.6	9.4	
November	15.7	11.3	14.9		9.2	5.5	5.6	
December	4.2	6.8	8.5		−2.0	0.1	0.8	

were not exhumed on 1 October 1986 and those of *C. odoratus* and *P. sedoides* were not exhumed on 1 December 1987. Germination tests were done in light- and temperature-controlled incubators at a 14-h daily photoperiod (20 μmol m^{-2} s^{-1}, 400–700 nm, cool white fluorescent light) or in continuous darkness at alternating (12/12 h) temperature regimes of 15/6, 20/10, 25/15, 30/15 and 35/20°C. These thermoperiods approximate the mean daily maximum and minimum monthly temperatures in central Tennessee and southern Ohio (Wallis, 1977) during the growing season: March, 15/6; April, 20/10; May, 25/15; June, 30/15; July and August, 35/20; September, 30/15; October, 20/10; November, 15/6°C. At each thermoperiod, the photoperiod extended from 1 h before the daily high temperature period began to 1 h after it ended.

Seeds were incubated in 5.5-cm Petri dishes on two sheets of Whatman No. 1 filter paper moistened with distilled water. For dark-incubated seeds, three replications of 50–75 seeds each were placed at each thermoperiod, and for light-incubated seeds three replications of 50 seeds each were used. All dishes were wrapped with plastic film, and those to be incubated in darkness were also wrapped with two layers of aluminium foil. All manipulations of dark-incubated seeds were carried out in complete darkness; thus, these seeds were not exposed to any light from the time they were buried until the germination tests were terminated. In darkness, the bag of seeds was removed from the pot of soil, cut open and the seeds poured into a dish. A small "pinch" of seeds then was placed in each Petri dish to be incubated in darkness, and the dishes were wrapped with plastic film and aluminium foil. Seeds incubated in light were counted into replicates of 50 seeds each using fluorescent room light, and the dishes were wrapped with plastic film. Final germination was determined after 15 days of incubation; emergence of the radicle was the criterion for germination. Data were transformed to percentages, and standard errors were calculated.

RESULTS

Regardless of the length of the burial period, seeds of *C. odoratus, G. viscidula, P. sedoides* and *S. lineatus* did not germinate in the bags during burial nor in the Petri dishes in darkness over the range of thermoperiods.

Freshly matured seeds of *C. odoratus* germinated to 35, 100 and 100% in light at 25/15, 30/15 and 35/20 °C, respectively, but they did not germinate at 15/6 and 20/10 °C (Fig. 1a). By February seeds germinated to 100% at all thermoperiods, except at 15/6 °C where no seeds germinated. Seeds never gained the ability to germinate to high percentages at 15/6 °C. From February 1986 to May 1988, seeds germinated to 76–100% at 20/10, 25/15, 30/15 and 35/20 °C.

Fresh seeds of *G. viscidula* germinated to only 0–7% in light over the range of thermoperiods (Fig. 1b). By April 1986, seeds germinated to 76–90% at 20/10, 25/15 and 30/15 and to 5 and 45% at 15/6 and 35/20 °C, respectively. By

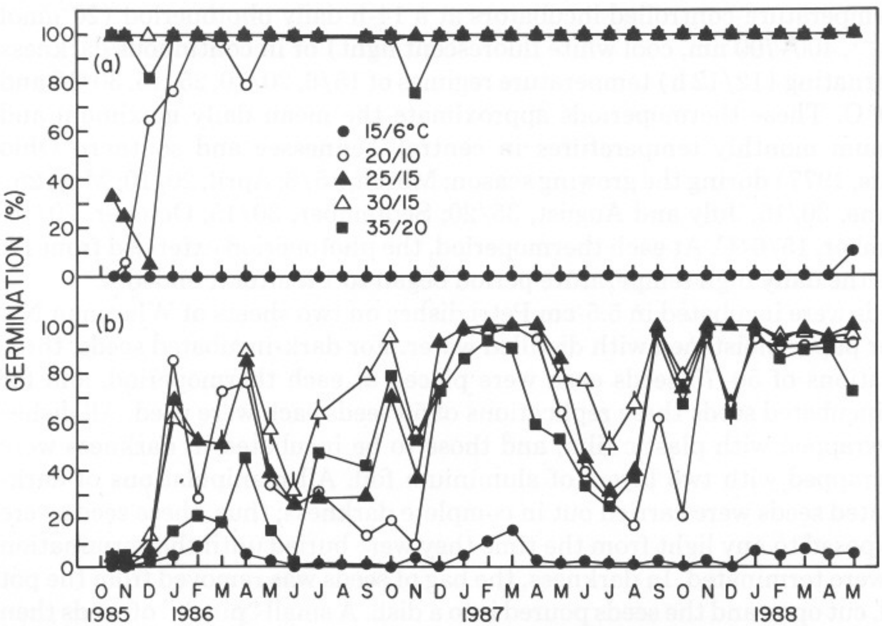

Fig. 1. Germination percentages (mean ± SE, if ⩾5%) of seeds incubated for 15 days in light at 15/6, 20/10, 25/15, 30/15 and 35/20 °C following 0–30.5 months of burial in soil (symbols as shown on figure). (a) *Cyperus odoratus*; (b) *Gratiola viscidula*.

June, however, germination had declined to 25–33% at 20/10, 25/15 and 30/15 and to 0 and 2% at 15/6 and 35/20 °C, respectively. By March 1987, seeds germinated to 90–100% at all thermoperiods, except 15/6 where they germinated to only 15%. By June 1987, germination had declined again, but during the subsequent autumn it increased.

Freshly matured seeds of *P. sedoides* germinated to 0, 49, 78, 98 and 93% at 15/6, 20/10, 25/15, 30/15 and 35/20 °C, respectively, in the light (Fig. 2a). After 2 weeks of burial, seeds germinated to 100% in light at all five thermoperiods. During the remainder of the study, seeds germinated to 88–100% at all thermoperiods in light each time they were exhumed.

Fresh seeds of *S. lineatus* did not germinate at any thermoperiod (Fig. 2b), but by March 1986 they germinated to 95–100% in light at all five thermoperiods. During summer, seeds lost the ability to germinate at 15/6 and 35/20 °C, and germination at the other three thermoperiods declined to 15–39% in July 1986. However, by April 1987 seeds germinated to 95–100% at all five thermoperiods. During the second summer of burial, seeds lost the ability to germinate at 15/6 and 35/20 °C, and germination at the other thermoperiods declined. During the subsequent autumn and winter, seeds exhibited increases in germination percentages at all thermoperiods.

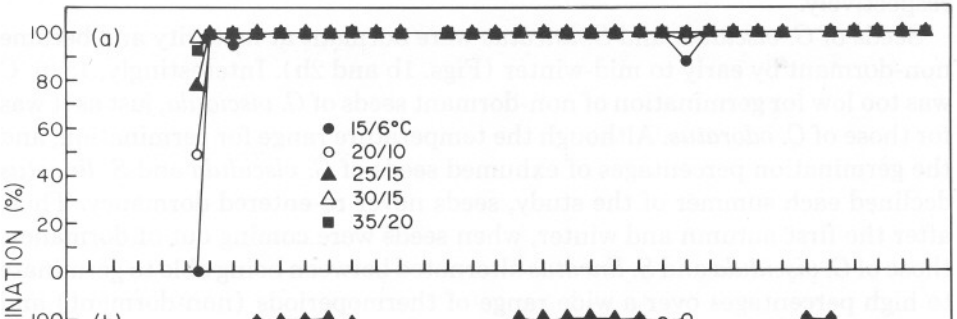

Fig. 2. Germination percentages (mean ± SE, if ⩾5%) of seeds incubated for 15 days in light at 15/6, 20/10, 25/15, 30/15 and 35/20 °C following 0–30.5 or 31 months of burial in soil (symbols as shown on figure). (a) *Penthorum sedoides*; (b) *Scirpus lineatus*.

DISCUSSION

Seeds of *C. odoratus* and *P. sedoides* were conditionally dormant at maturity and thus germinated to near 100% only at high temperatures in light (Figs. 1a and 2a). The inability of freshly matured seeds to germinate at 20/10 and 15/6°C would prevent germination of newly dispersed seeds in temperate regions in autumn.

Seeds of *C. odoratus* and *P. sedoides* became non-dormant during autumn and winter. In spring, they germinated to near 100% in light over the range of thermoperiods, except for seeds of *C. odoratus* at 15/6°C, which is below the temperatures required for germination of non-dormant seeds of this species. After seeds of two species lost their initial conditional dormancy, they did not exhibit seasonal declines in germination percentages. In the herbaceous weedy perennial *Rumex crispus* L. (Baskin and Baskin, 1985b), buried seeds lost their conditional dormancy after 4 months and then remained non-dormant for the remaining 18 months of the study. Thus, seeds of these three herbaceous perennials potentially can germinate to high percentages at any time during the growing season, if they are exposed to light. However, seeds of *C. odoratus* probably would not germinate well in early spring in temperate regions until mean daily maximum and minimum temperatures exceed 15 and 5°C, respectively.

Seeds of *G. viscidula* and *S. lineatus* were dormant at maturity and became non-dormant by early to mid-winter (Figs. 1b and 2b). Interestingly, 15/6°C was too low for germination of non-dormant seeds of *G. viscidula*, just as it was for those of *C. odoratus*. Although the temperature range for germination, and the germination percentages of exhumed seeds of *G. viscidula* and *S. lineatus* declined each summer of the study, seeds never re-entered dormancy. Thus, after the first autumn and winter, when seeds were coming out of dormancy, those of *G. viscidula* and *S. lineatus* alternated between being able to germinate to high percentages over a wide range of thermoperiods (non-dormant) and germinating to moderate percentages over a restricted range of thermoperiods (conditional dormancy).

Annual conditional dormancy/non-dormancy cycles such as those found in *G. viscidula* and *S. lineatus* have not been reported in other herbaceous perennials, but they have been found in winter annuals such as *Lamium amplexicaule* L. (Baskin and Baskin, 1981) and *Veronica arvensis* L. (Baskin and Baskin, 1983). However, in buried seeds of these winter annuals the period of conditional dormancy occurs earlier in the growing season (April–June) than it does for those of *G. viscidula* and *S. lineatus*.

The best time for germination of *G. viscidula* and *S. lineatus* seeds, as far as their responses to temperature are concerned, is spring. However, seeds of *G. viscidula* never gained the ability to germinate to high percentages at the simulated March (15/6°C) temperatures, so high germination percentages in early spring when mean daily maximum and minimum temperatures are about 15 and 5°C, respectively, are unlikely. Even if seeds are in light on wet mud, they may not germinate in summer because of conditional dormancy. Exhumed seeds of *S. lineatus* did not germinate at the simulated July and August (35/20°C) thermoperiod during July and August, and those of *G. viscidula* only germinated to 25–47% at 35/20°C during July and August.

The fact that buried seeds of *C. odoratus, G. viscidula, P. sedoides* and *S. lineatus* were still viable after 30.5 or 31 months suggests that these species have the potential to form persistent seed banks (sensu Grime, 1981). Seeds of various other species of *Scirpus* (van der Valk and Davis, 1978; Keddy and Reznicek, 1986; Leck and Simpson, 1987), *Gratiola* (Leck and Graveline, 1979; Schneider and Sharitz, 1986) and of *Cyperus odoratus* (van der Valk and Davis, 1978, 1979) and *Penthorum sedoides* (van der Valk and Davis, 1979; Schneider and Sharitz, 1986) have been found in seed banks of marshes, swamps and edges of lakes and ponds. An absolute light requirement for germination such as that found in *S. lineatus, G. viscidula, C. odoratus* and *P. sedoides* contributes to longevity of buried seeds because it prevents germination of seeds during burial. Salisbury (1970) reported that most "mudflat" species with small seeds do not germinate, or germinate poorly, in darkness, while those with large seeds germinate well. Of the 38 mudflat species that he studied in Britain, only seven germinated well in darkness. Seeds of *S. lineatus, G. viscidula, C. odoratus* and *P. sedoides* are small (Baskin and Baskin, 1988).

Various factors including the amount and quality of light, low daily temperature fluctuations and low oxygen concentrations probably interact to prevent germination of seeds under water. After the water recedes, seeds will not germinate unless they are on the soil surface where they are exposed to light. The ability of mudflat species to germinate at any time during the growing season is an adaptation to the unpredictable timing of the lowering of the water level in these aquatic habitats, assuming that plants can become established and set seeds regardless of when they germinate. Based on data obtained in this study, it appears that freshly exposed seeds of *C. odoratus* and *P. sedoides* could germinate to high percentages throughout the growing season, whereas those of *G. viscidula* and *S. lineatus* would germinate to higher percentages in spring than in summer.

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