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Germination and dormancy studies of *Pontederia cordata* L.[1]

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WHIGHAM, D. F. (Chesapeake Bay Center for Env. Stud., Smithsonian Instn., P.O. Box 28, Edgewater, MD 21037) and R. L. SIMPSON, (Biol. Dept., Rider Coll., Lawrenceville, NJ 08648). Germination and dormancy studies of *Pontederia cordata* L. Bull. Torrey Bot. Club 109: 524-588. 1982.—*Pontederia* rootstocks do not require low temperature treatment to produce shoots and the lack of a required stratification period enables established *Pontederia* plants to have the longest possible growing season. Seeds are dormant at time of dispersal in late summer and autumn and will not germinate until they have been stratified for 6-8 weeks. After stratification, seeds germinate best at constant or alternating temperatures greater than 20°C. Germination requirements keep seeds from germinating in the fall and permit stratified seeds to germinate in habitats where seedling competition is minimal.

Key words: *Pontederia cordata*; seed germination; dormancy; freshwater tidal wetland.

To survive in temperate climates, aquatic macrophytes have evolved various mechanisms similar to other temperate species. Several types of perennating vegetative structures have been described and most produce seeds that are dormant when they are shed (Hutchinson 1975; Sculthorpe 1967). Dormant seeds not only provide for future generations (Angevine and Chabot 1979) but they are also particularly important in the dynamics of vegetation in freshwater wetlands where dormant seeds in the soil appear to provide a reserve for when environmental conditions change (van der Valk 1981; van der Valk and Davis 1977; van der Valk and Davis 1979).

Leck and Graveline (1979) have studied the buried seed bank of a freshwater tidal wetland and found that buried seeds were dispersed more uniformly than were established plants. Whigham *et al.* (1979) studied the distribution of seeds of *Peltandra virginica* in the same wetland and also found that established plants were more restricted in their distribution than were seeds and seedlings. In this paper we report results of studies of *Pontederia cordata* in the same freshwater tidal wetland in an effort to correlate distribution patterns with seed germination and root stock growth requirements.

Pontederia is a common macrophyte in eastern North American wetlands (Sculthorpe 1967; Hutchinson 1975). Aspects of its biology have been examined including its growth and nutrient allocation patterns (Garbisch and Coleman 1978; Hazen 1918; Ornduff 1966; Laing 1940; Cowgill 1974; Riemer and Toth 1968; Bayley and Shibley 1978), but little information is available on mechanisms that control dormancy of seeds or vegetative plants (Garbisch and Coleman 1978). It was known, however, that *Pontederia* seeds required five to seven months of cold storage before they would germinate (Muenscher 1936). The specific purposes of this study were to determine: (1) the duration of cold storage required

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for seeds to germinate, (2) the influence of temperature on seed germination, and (3) the dormancy-breaking requirements of *Pontederia* rootstocks.

Methods. Seeds and seedlings were collected in September and October from the Hamilton marshes, a freshwater tidal wetland located near Trenton, N.J. (Whigham and Simpson 1975; Whigham *et al.* 1979).

Because preliminary studies showed that freshly collected seeds were dormant and did not survive if stored for a year under moist conditions at room temperatures, germination tests were initiated to determine the stratification time required before germination occurred. Freshly collected fruits were stored moist in plastic bags in a cold room at 4 C or in the laboratory at temperatures that varied from 15 to 27 C. At two week intervals thereafter, seeds were removed from the fruits and placed on moist filter paper in petri dishes. Triplicate samples of 25 seeds were then placed in an incubator which had a thermoperiod of 12 h at 30 C and 12 h at 20 C which had previously been found to elicit high germination. Since preliminary tests also showed that stratified seeds germinated equally well in the dark and light, all tests in incubators were conducted with illumination of 640 microeinsteins m^{-2} sec^{-1} during the 12 h and 30 C thermoperiod. Seeds were examined daily and the filter paper was kept moist with distilled water. The tests, run for a minimum of 7 weeks, were conducted using cold stored seeds only in 1979 and both cold stored and laboratory stored seeds in 1980.

Other preliminary tests showed that *Pontederia* seeds germinated best under alternating temperature conditions. Accordingly, additional tests were initiated using seeds that had been freshly collected and then stratified for 22 weeks. Tests using four replicates of 25 seeds were conducted in incubators in the dark at the following thermoperiods: (1) constant temperatures: 5, 10, 15, 20, and 30 C; (2) alternating temperatures (12 h thermoperiods): 10/15 C, 5/20 C, 10/20 C, 15/20 C, 5/30 C, 10/30 C, 15/30 C, and 20/30 C.

Intact samples of substrate with rootstocks of *Pontederia* were collected near the end of the growing season in September and transplanted into five gallon plastic pots that were lined with plastic bags. The pots were saturated with water and stored out of doors until the plants were dormant and then transferred to a cold room at 2/4 C. On the same day, five pots were placed in the greenhouse to serve as controls. After 8, 10, 12, 14, and 16 weeks in the cold room, ten pots were transferred to the greenhouse. The plants were observed for the onset of growth 5, 10, 15 days after they had been placed in the greenhouse. Dormancy was considered to be broken when the first leaf lamina began to unfold.

Results. Table 1 shows the effects of cold storage on *Pontederia* rootstocks. No innate dormancy was observed and almost all plants had initiated growth within 15 days after they were moved from cold storage to the greenhouse.

Seeds, however, were dormant at the time of collection and very few unstratified seeds germinated during the 4 months that they were placed in incubators. Seeds collected in both 1979 and 1980 began to germinate after 8 weeks of cold stratification (Fig. 1), and the germination patterns were very similar for tests performed in both years.

Results of the other germination tests are shown in Table 2. Although low germination percentages were recorded in 1982 tests, the effects of temperature

Table 1. Percent of rhizomes that broke dormancy after cold stratification. Values are averages for 10 plants except for the control which is a mean of 5 samples.

Stratification period (weeks)	Days after transfer to greenhouse 5	10	15
none	0%	60%	80%
8	0	70	90
10	20	70	80
12	10	50	60
14	10	50	80
16	50	60	90

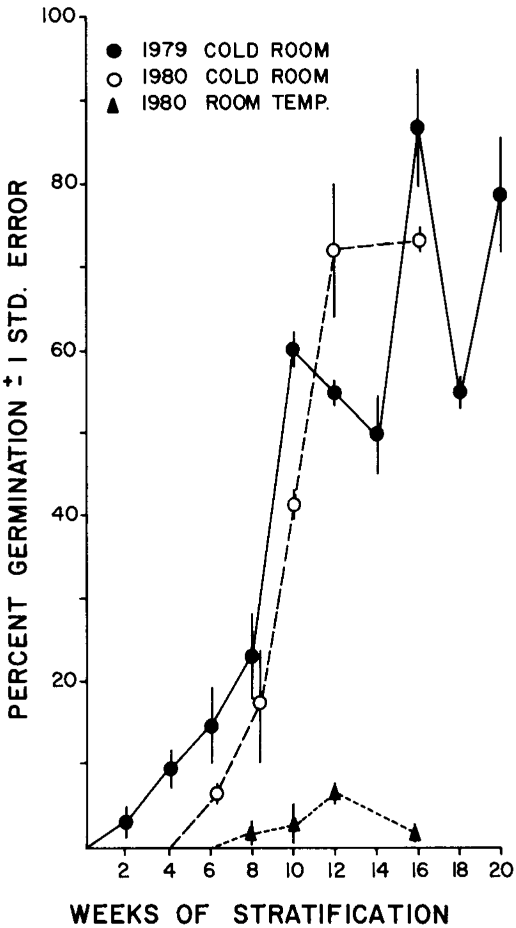

Fig. 1. Germination of *Pontederia* seeds after between 2 and 20 weeks of stratification. Stratification and experimental conditions are described in the METHODS section. All values are means (%) ± 1 standard error.

on germination were often significant ($F = 8.99$; df = 12, 39; $P \leq 0.0001$).

The average percent germination of seeds held at constant temperatures was significantly less than the average percent germination of seeds germinated at varying temperatures ($F = 16.315$; df = 1, 39; $P \leq 0.0002$). At constant temperatures, significantly fewer seeds germinated at 5, 10, and 15 C, compared to 20 and 30 C ($F = 27.386$; df = 1, 39; $P \leq 0.0001$). There were no significant differences between germination at 5, 10, and 15 C, compared to the 10/15, 5/20, or 10/20 C alternating temperature treatments ($F = 0.017$; df = 1, 39; $P \leq 0.980$). The germination at 15/20 C was, however, significantly greater than germination at 5, 10, and 10/15 C. Germination at 20 and 30 C was significantly greater than at 10/15 C ($F = 14.538$; df = 1, 39; $P \leq 0.0005$).

There was no significant difference between alternating temperatures of 10/15 C and 5/20 C, but germination percentages were significantly greater at 10/20 C and 15/20 C ($F = 4.996$; df = 1, 39; $P \leq 0.0312$). There was no significant difference between germination at 5/20, 10/20, and 15/20 C ($F = 1.400$; df = 1, 39; $P \leq 0.24$). Significantly different germination percentages occurred at temperatures that alternated between 5 C and 30 C than temperatures alternating between 10/15 C ($F = 34.026$; df = 1, 39; $P \leq 0.0001$). Germination percentages were not significantly different for the group of treatments with a maximum of 20 C and the group with a maximum temperature of 30 C. Germina-

Table 2. Mean percent germination (± 1 standard error) of *Pontederia* seeds at constant and alternating temperatures. Results of statistical comparisons are provided in the text.

CONSTANT TEMPERATURES (C)				
5 C	10 C	15 C	20 C	30 C
0	0	5.0 ± 1.9	17.5 ± 2.5	16.0 ± 5.9

ALTERNATING TEMPERATURES (C)			
10/15	15/20	10/20	15/20
2.0 ± 2.0	6.0 ± 1.2	10.0 ± 2.6	11.0 ± 4.1
5/30	10/30	15/30	20/30
25.0 ± 3.0	20.0 ± 1.6	16.0 ± 4.3	28.0 ± 4.6

tion at 5/20 C was, however, significantly less than germination at all of the 30 C alternating temperature groups.

There were significant differences within the group of alternating 30 C temperatures due to higher germination percentages at 5/30 C ($F = 4.200$; $df = 1, 39$; $P \leq 0.047$) and 20/30 C ($F = 7.468$; $df = 1, 39$; $P \leq 0.009$). Germination at 15/30 C was not different from 10/30 C, 30 C, and 20 C, but was significantly lower than at 5/30 C and 20/30 C ($F = 4.200$; $df = 1, 39$; $P \leq 0.0472$).

Discussion. Like other wetland macrophytes (Sculthorpe 1967), *Pontederia* rootstocks do not require cold treatment and can commence growth when temperatures of the wetland substrate are above freezing. Dormancy of the rootstocks is thus enforced rather than induced (Harper 1977). *Pontederia* seeds, however, require a period of moist cold storage before they will germinate. This is of survival value because *Pontederia*, which has a long flowering period (Ornduff 1966), sheds seeds over a long period of time (August until late October in New Jersey) and it is unlikely that seedlings which germinate in the fall would survive the winter because of ice scouring of the wetland surface. Ice scouring is especially characteristic of streambanks, the primary habitat of *Pontederia*, which are almost devoid of vegetation by spring (Simpson *et al.*, in press).

After seeds have been stratified, water and substrate temperatures may be important in controlling the germination of *Pontederia*. *Pontederia* seeds germinate best at higher temperatures (Table 2). Diurnal temperature fluctuation with high temperatures between 20 and 30 C seem to be able to overcome periods of lower temperatures. Generally, poorest germination occurred at temperatures between 5 and 20 C while significantly greater numbers of seeds germinated at temperatures above 20 C. With two exceptions, the highest germination occurred at temperatures which were at 30 C for part of the day, even though minimum temperatures were as low as 5 C.

Pontederia is primarily restricted to streambanks or pond-like areas and few individuals are found in high marsh plant communities (Whigham and Simpson 1975, Simpson *et al.*, in press). Seeds that germinate on the bare streambank, where surface temperatures are highest because there is very little litter coverage, would suffer less competition as only limited numbers of seedlings are present. On the high marsh, the surface is covered by litter and the underlying seeds would only rarely be exposed to temperatures that reach 20 or 30 C. Van der Valk (personal communication) has found that seeds of many other macrophytes germinate best at 30 C or higher. This appears to be an adaptation for species to colonize exposed areas such as streambanks, the edges of ponds which are subject to frequent water level changes, or areas where macrophytes have been removed through biotic and/or physical factors (Weller 1978).

Field data corroborate our results (Garbisch and Coleman 1978). Seeds were planted along a tidal gradient of a Chesapeake Bay wetland from near the low tide line (0 meters above mean low water) to the upper limit of tide (0.79 to 0.85 m above mean low water) which was near the litter line of the adjacent high marsh. Seed germination was primarily restricted to sites between the tidal limits where seeds would most often be exposed to the high and alternating temperatures needed for maximum germination rates. Temperature requirements, therefore, seem to be an adaptation to restrict germination primarily to seeds that had been dispersed to optimum sites for establishment. It does not appear that the high temperature requirements for germination are used in the maintenance of buried *Pontederia* seeds since seeds do not appear to remain viable for more than a year (Whigham and Simpson, personal observation). This was also verified by Leck and Graveline (1979) who found that no *Pontederia* seed germinated from sediments from streamside habitats in the same wetland.

In summary, established plants are capable of growth whenever substrate temperatures are above freezing. Seeds, which are mostly shed before the first killing frosts, will not germinate because they require approximately 8 weeks of stratification. Once stratified, seeds require rather high constant temperatures (20 or 30 C) or variable temperatures with maximum diurnal temperatures of 20 C or higher for optimum germination. The germination requirements assure that seeds germinate primarily on streambank sites where competition is minimal during seedling establishment.

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