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Germination of 14 freshwater wetland plants as affected by oxygen and light

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ABSTRACT

Oxygen and light are factors that can affect seed germination of wetland plants. We selected seeds from 20 plant species found in temperate eastern North American marsh and wet meadow wetlands, ranging from obligate wetland (OBL), facultative wetland (FAC) and upland (UPL) species. In growth chambers we tested germination success under controlled manipulations of O_2 concentration (low [<1%] and atmospheric [~20%]) and light levels (full light, half light and dark). Our objective was to (1) determine whether oxygen, light and their interaction facilitate germination of wetland seeds; (2) whether timing of germination is affected by oxygen and light; and (3) whether germination is related to wetland functional groups. Six species did not germinate. Of the 14 species that did germinate, a non-native ruderal (*Echinochloa crus-galli*) had the greatest germination success. However, we found that low O_2 reduced germination success of all but three species (*Rudbeckia triloba*, *Sagittaria latifolia* and *Typha latifolia*). Reduction in light levels only reduced germination success of *S. latifolia*. We conclude that the physiological constraints that control germination operate independently for oxygen and light. It is important to know and anticipate oxygen and light levels when designing a wetland restoration project so that the proper species can be sown that can germinate under the specific conditions. Restoration planners should be aware that anoxic and hypoxic conditions seem to promote the germination of weedy and potentially invasive native and non-native species.

1. Introduction

Wetland plants have adapted to the stressful anaerobic environment imposed by flooding and the resulting consequence of hypoxic and anoxic soil conditions. Much research has been done to study how wetland plants cope with submergence, with the principle mechanism being the evolution of air spaces or lacunae formed within plant tissue (Crawford, 1992, 1996; Kozlowski, 1984; Crawford and Brandle, 1996; Voesenek et al., 2006; Mitsch and Gosselink, 2007). However, it has been shown that life-history strategies of mature freshwater marsh plants do not necessarily reflect the strategies of seeds and seedlings (Shipley et al., 1989). The strategy of seeds is important because hydrologic changes often leave large areas of unvegetated soils open to colonization (van der Valk and Davis, 1978; Keddy and Reznicek, 1986). Without regeneration from surviving individuals (e.g., Grubb, 1977), seed banks and dispersal are responsible for the establishment of new plant communities (Leck, 1989; Baskin and Baskin, 1998; Fenner and Thompson, 2005). Since seed banks of freshwater wetlands often differ substantially from the plant community (van der Valk, 1981; Leck, 1989), disturbances have the potential to result in dramatic changes in vegetation. Species-specific germination responses will depend on site-specific environmental conditions such as hydrology, hypoxic soil conditions, and shade from remnant vegetation or litter.

Generally, seeds of plants that grow on well-drained soil have higher germination rates under ambient atmospheric O_2 concentrations than with reduced O_2 levels (Heichel and Day, 1972; Côme et al., 1991). However, wetland plant seeds can often germinate under hypoxic conditions, with some requiring hypoxia or anoxia (Leck, 1996). Lorenzen et al. (2000) found an increased germination percentage of *Typha domingensis* at low concentration of O_2 (4.34%) compared to atmospheric O_2 levels. Wijte and Gallagher (1996) found that *Phragmites australis* can germinate under hypoxic conditions of 2.5% O_2, but not under anoxic conditions; whereas *Spartina alterniflora* was able to germinate under anoxic conditions thereby giving that species a competitive advantage over *P. australis* in poorly drained marshes.

The effect of light on germination of wetland plant seeds may either promote or inhibit germination (Leck, 1989; Kettenring et al., 2006). Emergence from the seed bank of species requiring light for germination is triggered by a disturbance, such as lowering

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of water level or gaps in the plant canopy (Leck, 1989). There is often a connection between light levels and O_2 concentration on hydric soils with water level fluctuations such that a decline in water depth can increase light levels and O_2 on wetland soils. However, a physical disturbance, such as grazing, can increase light levels with little or no effect on the concentration of O_2 in the soil. We could not find any studies that investigated the interaction between O_2 concentration and light levels on wetland plant seed germination. Understanding species-specific germination requirements, and the potential interaction between light levels and O_2 concentration, is necessary for predicting how wetland species respond to disturbance.

With an understanding of how O_2 and light affect seed germination, revegetation efforts can be improved in freshwater wetland restorations. Wetland functional groups have been used as a predictive tool for restoration and management. Boutin and Keddy (1993) categorized wetland marsh plants into three groups based on 27 traits relating to adult and seedling growth and physiology: 'ruderals' flower in the first year, 'interstitials' are perennial plants with a clumped growth form, and 'matrix' species are perennial plants with a robust clonal growth form. Ruderals allocate a greater proportion of their resources to reproduction, rather than growth or storage, compared to interstitials and matrix species (Grime, 1979; Boutin and Keddy, 1993). Matrix species allocate most of their resources to growth, while interstitials allocate most resources to storage, and the least amount of resources to reproduction (Grime, 1979; Boutin and Keddy, 1993). Based on these findings, we might expect that germination success is related to functional group (Shipley and Parent, 1991).

Our study examined the effects of O_2 and light on twenty freshwater marsh species. The objective was to (1) determine whether oxygen, light and their interaction facilitate germination of wetland seeds; (2) whether timing of germination is affected by oxygen and light; and (3) whether germination is related to wetland functional groups. We hypothesized that low oxygen concentration and low light levels would inhibit germination success. We could find no published research that manipulates the interaction between oxygen and light, but it would be reasonable to expect that the combination of low oxygen and low light would have the greatest negative effect on germination. Finally, we hypothesized that ruderals would have the highest rate of germination, followed by matrix and then interstitial.

2. Materials and methods

Twenty species were selected to represent a broad range of plant life forms typically found in temperate eastern North American marsh and wet meadow wetlands (Crow and Helquist, 2000) (Table 1). Most of the species are commonly used in wetland restoration projects (Hammer, 1996; Cronk and Fennessy, 2001), while others are non-native (*Echinochloa crus-galli*, *Festuca ovina* and *Agrostis stolonifera*) and *Phalaris arundinacea*, while native, is highly invasive. *Typha latifolia* and *Leersia oryzoides* are also native, but can be invasive. The selected species represent three functional groups (matrix, interstitial, and ruderal). Seeds were either purchased through Ernst Seed Company (Meadville, PA) or collected in the field. The seed source from Ernst Seed Company is a combination of field-collected and cultivated plants that are bulk processed so that there is genetic variability. Field-collected seed were taken from multiple individuals and from at least three sites in northeast Ohio, which were then combined by species. Seed was placed in mesh bags, buried in containers of damp sand and stored in a refrigerator at 5 °C for at least two months but no longer than one year (Shipley et al., 1989). Immediately prior to setting up the experiment, seed viability was measured by placing 100 seeds of each species on moist filter paper in separate petri dishes exposed to a 14-h photoperiod provided by two 1000 W, High Pressure Sodium bulbs for thirty days (Table 1).

The experiment was a two by three factorial design with oxygen and light as treatments, and with three replicates. A single experimental unit was a 'pot' (a 20.3 cm diameter PVC pipe with a length of 16 cm). The bottom was sealed and three 18.5 cm Whatman™ general purpose filter papers were layered inside. Each pot had two 2 cm holes in the side, drilled 3 cm from the top and equidistant from each other. One hole was plugged with a rubber stopper containing an inflow tube. The other hole was plugged with a rubber stopper containing two small diameter holes for the constant release of air, for the sampling of air inside the pots, and for the occasional addition of water to ensure the filter papers remained saturated. The top of the pot was covered with one of three materials depending on the light treatment.

The oxygen treatment included an ambient atmospheric O_2 concentration and a N_2, anoxic treatment. A regulated constant flow of N_2 or ambient air was provided to each of the 36 pots. The light treatment included full, half light, and dark. For the full light treatment we used Tufflite IV™, 6 mil, 0.152 mm thick plastic (Tyco Plastics and Agricultural Films, Monroe, LA, USA), with 93% PAR transmission. For the half light treatment we used a layer of the same Tufflite as used in full, plus a layer of red Saran™ Premium Wrap. A red filter was used as a neutral shade because while it reduces general PAR transmission, the red-light spectrum is transmitted, which has been shown to be more responsive to germination (Shinomura et al., 1996). For the dark treatment we used the same Tufflite plus a layer of 0.024 mm aluminium foil.

A set of six pots, two of each light treatment, was placed within a single plastic container (80 cm long by 40 cm wide by 15 cm deep); the plastic container was used to facilitate handling of the pots. Each pot could contain seeds from only ten species when using 50 seeds per species, so two paired treatment pots were needed to accommodate the 20 species. Three of the six containers received the ambient oxygen treatment while the other three received the anoxic N_2 treatment. The arrangement of containers, pot position within each container, and seeds of species' groups within each pot were randomized at the beginning of the experiment.

Seeds from each species were arranged in separate species groups on saturated filter paper. A daily, 14-h photoperiod was provided by two 1000 W, High Pressure Sodium bulbs providing an average photosynthetically active radiation (measured with a LiCor LI-250 light metre) of 140.5 $\mu mol\ s^{-1}\ m^{-2}$ ($\pm$8.2 SD) on the experimental plants. Windows in the room were covered to prevent incident solar radiation. Temperature was maintained at 22 ± 2 °C. Humidity ranged between 40 and 50% and was self-maintained due to the evaporation of the water from the saturated filter paper. Filter paper was watered to maintain saturation when needed.

The experiment ran for 30 days and was monitored at least every second day to ensure adequate N_2 and air supplies. Light was measured twice, day 1 of the experiment and day 30, within each pot. Atmospheric oxygen concentration within each pot was measured every second day. Date of germination was recorded throughout the experiment. During monitoring of germination, the only light source was UV-A black light; all growth lights and room lights were turned off. At the end of the experiment, percent germination was calculated for each species within each pot.

A one-way ANOVA by species was done to test overall germination success, followed by a post hoc Tukey's HSD test. A two-way, fixed-effects ANOVA was conducted for the oxygen and light treatment effect on percent germination of all species that had any germination. Percent germination was arcsine square root transformed to meet assumptions of normal distribution. Tukey's HSD test was run to determine statistical significance between means. A Bonferroni correction was applied in order to adjust for the number of simultaneous tests (Rice, 1989). A three-way ANOVA was done