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Influence of environmental factors on *Vallisneria americana* seed germination☆

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Abstract

Over the course of a growing season (April–October) water quality (water temperature, light, salinity, dissolved oxygen) and reproductive phenology (biomass, production of flowering shoots and seed pods, seed bank densities) were quantified in three *Vallisneria americana* beds in Nanjemoy Creek, MD, a tributary to the Chesapeake Bay. Clonal production of *V. americana* biomass increased at all sites when water temperatures rose above 25 °C. Flowering occurred during peak biomass (August–September) and resulted in the production of up to 16,000 seeds m^{-2} at the end of the growing season. However, observed seed bank densities represented <1% of seed production. Laboratory experiments quantified the effects of dissolved oxygen (0.29–8.00 mg l^{-1}), light (0–160 μmol m^2 s^{-1}), temperature (13–29 °C), salinity (0.1–17.4 psu), sediment composition (3–86% sand; 0.9–8.3% sediment organic content), and burial depth (0.2–10 cm) on *V. americana* seed germination. Germination of *V. americana* seeds was enhanced (greater overall germination and shorter time to germination) under oxygenated conditions (8.00 mg l^{-1}), temperatures >22 °C, salinities of <1 psu, and in sediments composed of ≤3% organic content and >40% sand. Light (<160 μmol m^{-2} s^{-1}) and burial depth (0.2–10 cm) had no significant effects on germination. Temperatures most favorable for seed germination (>22 °C) occurred in June, 2 months in the growing season just prior to development of peak vegetative standing stock. Seedlings were therefore at a distinct disadvantage to plants developed from over wintering buds. A lack of viable seed retention and inadequate environmental conditions at critical times in the growing season may be limiting seed germination success and subsequent seedling establishment within *V. americana* beds in the Chesapeake Bay. However, ungerminated seeds were found to maintain high viability, especially at salinities of 10 psu that can have significant negative effects of shoot growth survival. This suggests that seeds may serve as a source of reproductive material for bed recovery after periods of drought or other stressful conditions in estuarine systems.

Keywords: Submerged aquatic vegetation; Seeds; Germination; Viability

1. Introduction

Vallisneria americana Michx. (wild celery) populations are primarily maintained inter-annually through clonal reproduction with a minimal observed contribution from seeds (Sculthorpe, 1967; Stevenson, 1988; McFarland, 2006). However, seeds have been found to provide important functions for submerged macrophyte communities through the establishment of new genotypes in existing populations (Kimber et al., 1995; McFarland, 2006), movement of populations into new regions (Arnold et al., 2000; Figuerola and Green, 2002; Harwell and Orth, 2002), and re-establishment of populations after episodic declines (McMillan and Jewett-Smith, 1988; Titus and Hoover, 1991; Preen et al., 1995). Due to the apparent dominate role of clonal reproduction, there is a lack of information concerning the timing and success of *V. americana* seed germination (Lokker et al., 1997) and the ability of germinated seeds to become established as seedlings under *in situ* conditions (Sculthorpe, 1967).

Influences of environmental factors, specifically temperature and salinity, on sexual reproduction and seed germination have been documented for many submerged macrophyte species (Muenscher, 1936; Barko et al., 1986; Moore et al., 1993). For example, in the Chesapeake Bay flower production of *Zostera marina* is initiated when water temperatures are >14 °C, pollen is released after temperatures reach 16 °C, and seeds are released when temperatures are >25 °C (Silberhorn et al., 1983). In freshwater communities, temperatures of 15 °C

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have been associated with the initiation of germination of *Myriophyllum spicatum* seeds (Hartleb et al., 1993) and temperatures of 23–28 °C initiated seed germination within a week of exposure for *Hydrilla verticillata* (Lal and Gopal, 1993). French and Moore (2003) found that *V. americana* plants exposed to salinities of 10 and 15 psu survived but did not flower, but other effects of increased salinity on seed germination are largely unknown.

Light, oxygen, burial depth, and sediment composition can also affect submerged macrophyte seed germination (Muenscher, 1936; Rybicki and Carter, 1986; Koch, 2001). Kimber et al. (1995) found that *V. americana* seeds collected from the top 5 cm of the substrate germinated when exposed from 2 to 25% of total surface irradiance. Sediment hypoxia (dissolved oxygen (DO) < 1.0 mg l^{-1}; EPA, 2003) has been documented to increase germination of seagrasses *Z. marina* and *Z. capricorni*, seeds (Moore et al., 1993; Brenchley and Probert, 1998). However, high organic content of sediments (>6%), with potentially low DO and negative oxidation–reduction potential (Eh), was found to delay *V. americana* germination 3–5 weeks compared to seeds exposed to less organic sediments (Hoover, 1984). Despite the apparent influence of environmental factors on reproductive phenology and timing and success of submerged macrophyte seed germination, there has been little research on the effects of these factors, especially on many species of freshwater submerged macrophytes (Barko et al., 1986).

In the present study we have quantified environmental conditions and reproductive phenology (biomass, flower production, seed production, seed bank densities) in three established *V. americana* beds over a growing season (April–October) and have quantified the effects of dissolved oxygen (0.29–8.00 mg l^{-1}), light (0–160 μmol m^2 s^{-1}), temperature (13–29 °C), salinity (0.1–17.4 psu), sediment composition (3–86% sand; 0.9–8.3% sediment organic content), and burial depth (0.2–10 cm) on *V. americana* seed germination under controlled laboratory conditions. We hypothesized that seed germination and seedling production in established beds will be highest during the beginning (April–May) of the growing season (providing the longest period for seedling growth), and environmental conditions similar to those observed during that period would result in the greatest overall germination and shortest time to germination under controlled laboratory conditions.

2. Methods

2.1. Field sampling

2.1.1. Site selection

In 2004 three *V. americana* beds were selected for study in Nanjemoy Creek, MD based on historical data and aerial photography. In addition, these sites served as the locations for seed collection for subsequent experiments. Nanjemoy Creek is a 14 mile long tidally influenced tributary to the Potomac River where submerged macrophyte populations have been stable over 15 years (Orth et al., 2004). Site A (38°25.9′N, 77°07.2′W) was located along the western bank of Nanjemoy Creek and contained the largest bed of the three sites. In addition to *V. americana* *Najas* sp., *Myriophyllum spicatum*, and *Hydrilla verticillata* were also observed although they were not considered dominant or co-dominant. All species were found throughout the bed to a maximum depth of 78 cm below mean lower-low water (MLLW). Site B (38°25.9′N, 77°06.4′W) was located along the eastern shoreline of Nanjemoy Creek. In addition to *V. americana*, *Najas* sp. and *H. verticillata* were observed to a maximum depth of 65 cm below MLLW. Site C (38°26.4′N, 77°07.1′W) was the northern most sampling site and contained only *V. americana* distributed to a maximum depth of 48 cm below MLLW. Mean tidal range in the study area during 2004 was approximately 0.45 m (National Oceanic and Atmospheric Administration, National Water Level Observation Network, Silver Spring, MD, USA).

2.1.2. Species description and seed pod collection

A member of the family Hydrocharitaceae, *V. americana*, is a clonal, dioecious, perennial characterized by distinct mid-veined leaves that grow from a basal meristem (Wilder, 1974; Korschgen and Green, 1988; Catling et al., 1994). Adult shoots are able to live in sandy to soft clay substrates (Rybicki and Carter, 1986; Adair et al., 1994), moderate to low light environments (minimums of 5–25% total surface irradiance; Meyer et al., 1943; Carter and Rybicki, 1985; Doyle and Smart, 2001), median temperatures ranging from 19 to 36 °C (Barko et al., 1982; Kraemer et al., 1999) and in moderate salinities (0–5 psu; French and Moore, 2003).

Seed pods of *V. americana* were collected by hand in October 2003 and 2004 in Nanjemoy Creek. Intact pods were transferred to containers, sealed, and stored in de-ionized water at 4–6 °C until analysis and use (Baskin and Baskin, 1998). The total number of seeds within 50 randomly selected seed pods were counted and tested for viability using the tetrazolium staining method (Lakon, 1949; Grabe, 1970; Leist and Krämer, 2003). Seed embryos were removed from their seed coats and soaked in a 1% tetrazolium chloride (tetrazolium) solution for 24 h before examination on a dissecting scope at 10× magnification. Positive tests (live embryos) occurred when >50% of the embryo was stained red (Leist and Krämer, 2003).

2.1.3. Vegetation characterization

To characterize *V. americana* at each site percent cover, shoot density, and flowering shoot density were recorded along one 100 m long transect running perpendicular to the shoreline once a month from April to October 2004. Along each transect a 0.5 m^2 PVC square was randomly tossed within a 2 m^2 area three times every 10 m. Percent cover within the square was estimated visually. Density of shoots, flowering shoots, and seed pods were quantified within a 20 cm diameter ring placed within the PVC square. The number of seeds per seed pod were counted from a subset of seed pods from each site and tested for viability using the tetrazolium method (Lakon, 1949; Grabe, 1970; Leist and Krämer, 2003).

Biomass was quantified at each site using a 22 cm diameter core that was inserted into the sediment to a maximum depth of