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Effects of sediment and salinity on the growth and competitive abilities of three submersed macrophytes

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ABSTRACT

Submersed macrophytes are generally found in multispecies beds, with the dominance of individual species varying in both space and time. In estuarine environments, these plants can grow across a range of environmental conditions which may alter species interactions. Three species common to the Chesapeake Bay region, *Vallisneria americana* (wild celery), *Heteranthera dubia* (water stargrass), and *Stuckenia pectinata* (sago pondweed), were planted in a microcosm designed to test their growth and interactions (relative yielding) under a range of conditions of salinity (0, 5, or 10), sediment type (mud or sand), and species combinations. *H. dubia* was most sensitive to elevated salinity, while sediment type impacted only *V. americana,* performing better in mud compared with sand. *V. americana* and *H. dubia* were strong competitors, overyielding in many treatments when grown in mixture, while *S. pectinata* never overyielded and frequently underyielded. Interspecific competition was only strong between *H. dubia* and *S. pectinata* under 0 salinity, regardless of sediment type. *V. americana* on the other hand, showed strong interspecific competition with *S. pectinata* across multiple salinity and sediment types, indicating that this species is able to compete well across a wider range of environmental conditions. Our results suggest that *H. dubia* and *V. americana* are strong candidates for multi-species restoration, as positive interactions were observed when grown together. This measure of complementarity provides evidence for increased mixed bed plant performance under environmental conditions that would typically be more stressful to each growing alone.

1. Introduction

Submersed aquatic vegetation (SAV) growing in low-salinity and freshwater systems are typically not found in monotypic communities, but in multispecies beds, with the dominance of individual species varying in both space and time (Moore et al., 2000; Chambers et al., 2008; Orth et al., 2009; Arthaud et al., 2013). This suggests that there is a range of suitable environmental conditions among the diversity of species in these beds. This may allow for greater natural survival or restoration under a wider range of environmental conditions when compared to monotypic communities.

Changing environmental conditions may alter the competitive advantage of one species over another, because each species may have different requirements for their growth or tolerate a different range of conditions. Within an estuarine system such as the Chesapeake Bay, parameters related to light, temperature, nutrients, salinity, and sediment may all play roles in the SAV community dynamics (Kemp et al., 2004). Historically, light availability has been a primary focus when studying SAV habitat requirements (Carter and Rybicki, 1990; Korschgen et al., 1997; Moore et al., 1997; Moore and Wetzel, 2000). Salinity and sediment requirements have not received as much attention, but are likely to be very important in estuarine environments due to their variability in both space and time and their differing effects on individual SAV species.

SAV communities in the Chesapeake Bay are typically distributed by salinity, with *Zostera marina* and *Ruppia maritima* occurring in meso and polyhaline regions, and a variety of freshwater mixed species occurring in oligohaline and tidal fresh regions. Within the oligohaline and tidal fresh regions, over 15 species of SAV have been identified (Moore et al., 2000). Many of these species have been shown to have differing salinity tolerances (Teeter, 1965; Haller et al., 1974; Kantrud, 1990; Twilley and Barko, 1990; French and Moore, 2003; Bergstrom et al., 2006; Frazer et al., 2006) as well

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as a range of suitable sediment conditions for their growth (Barko and Smart, 1983, 1986; Hoover, 1984; Chambers and Prepas, 1990; Batiuk et al., 2000; Jarvis and Moore, 2008).

It is not well understood how different local sediment composition and salinity levels might affect SAV bed growth or how these conditions might affect SAV restoration success when species are planted both singly and in competition with other species. Typically, restoration of SAV has been conducted using a single species approach, while the potential positive interactions of planting multiple species together has generally been overlooked (Halpern et al., 2007). Previous work has determined that there is considerable potential for SAV restoration in the major Chesapeake Bay tributaries including the James River using both whole plants and seeds (Moore and Jarvis, 2007; Moore et al., 2010). It is still poorly known if mixed plantings would be more successful by providing a broader range of bed tolerance when subject to varying environmental conditions. It has been reported that in many regions experiencing re-growth of SAV that *Vallisneria americana* can be found growing in combination with other SAV, including *Hydrilla verticillata*, *Myriophyllum spicatum*, *Heteranthera dubia*, and *Ceratophyllum demersum* (Moore et al., 2000; Rybicki and Landwehr, 2007). This suggests that mixed plantings may improve restoration success through complementarity among species in resource utilization.

Plants exhibit positive complementarity when their combined performance is greater than what would be expected from them individually (Loreau and Hector, 2001). This is due to resource partitioning and facilitative interactions, and has been observed in SAV communities (Salo et al., 2009; Gustafsson and Boström, 2011; Hao et al., 2013). On the other hand, multi-species assemblages may not increase overall productivity, bed resilience or restoration success due to interspecific competition, which has been shown to be strong in both temperate and tropical SAV communities (Titus and Stephens, 1983; Moen and Cohen, 1989; Van et al., 1999; Spencer and Ksander, 2000; Barrat-Segretain and Elger, 2004).

Here we present results from a microcosm that was designed to test the growth and competitive abilities of low-salinity and freshwater SAV under varying conditions of salinity and sediment type. We address the following research questions: a) what effect will different salinity and sediment types have on plants growing separately in monoculture? b) How will the different treatments alter species interactions when plants are grown in combination? Our goals were to examine the degrees of competition and complementarity among three different species exposed to variable environmental conditions, and to improve the site selection criteria and success of restoration efforts of freshwater and low-salinity tolerant SAV.

2. Methods

An outdoor microcosm was used for the experiment which was conducted in the summer and located at the Virginia Institute of Marine Science, Gloucester Point, Virginia (37°14.8′N, 76°30.3′W). 20-liter white translucent containers with a height of 37 cm and diameter of 30 cm were used for each individual experimental unit, and all the containers were housed in a shallow nursery tank approximately 8.5 m × 3 × 0.5 m filled with freshwater to allow for consistent temperatures among the experimental units. Three main treatments were established. Sediment type consisted of two levels (mud and sand), salinity consisted of three levels (0, 5, 10) and species combinations included all combinations of three species (three monocultures, three bicultures, one triculture) for a total of 42 treatments. Each treatment was replicated three times for a total of 126 experimental units. *H. dubia* (water stargrass) and *V. americana* (wild celery) plants were taken from adjacent outdoor nursery tanks grown from local Chesapeake Bay stock, and *Stuckenia pectinata* (sago pondweed) was harvested from two outdoor ponds located on the Chesapeake Bay at the University of Maryland Center for Environmental Science Horn Point Laboratory, Cambridge, Maryland (38°35.5′N, 76°08.8′W). These were brought back to Virginia and planted in an outdoor SAV restoration nursery pond next to other ponds containing the other species. Prior to the start of the experiment, oligohaline estuarine sediment was collected from the Chickahominy River, Virginia. Sediments were obtained from two sites where SAV occur, with target organic content of > 8% for the muddy site (37°17.5′N, 76°51.8′W) and < 2% for the sandy site (37°15.5′N, 76°52.4′W). At the time of collection, percent organic content was determined through loss on ignition (Erftemeijer and Koch, 2001). NH_4^+ concentrations were determined using a Lachat auto analyzer (Liao, 2001, revised 2002) and PO_4^{3-} concentrations were determined spectrophotometrically at 880 nm (VIMS, 1991).

Sediment was homogenized, and each container was filled approximately 10 cm deep with sediment, and then filled with filtered freshwater. Plants were sorted within species to a similar length (*V. americana* 16.8 cm ± 1.2; *H. dubia* 17.6 cm ± 1.4; *S. pectinata* 44.3 cm ± 2.2). A subset of 30 plants from each species was sampled for dry weight measurements of above and belowground biomass (*V. americana* 0.068 gDW; *H. dubia* 0.042 gDW; *S. pectinata* 0.074 gDW per plant). A total of 12 plants were planted in each container in a replacement series design. With this design, the total number of plants in each container was kept constant, but the number of plants per species was altered according to their species combination treatment. For example, in biculture, six plants of each species were used, and in triculture four plants of each species were used. This planting density was chosen based on a literature review of densities of natural plant populations of these species (Moen and Cohen, 1989; Van et al., 1999; Jarvis and Moore, 2008).

After planting, each container was placed in the tank in a randomized design. The tank was filled with freshwater, and a drain pipe ensured the water level in the tank never rose above the rim of the containers. This served as a water bath to help keep temperature constant in the containers. The containers were allowed to sit for two days to allow sediment settlement, and then individual air bubblers and aquarium foam/floss, carbon, and zeolite filters were connected to each container. These filters were routinely rinsed and were replaced halfway through the experiment. Clear plexiglass sheets were placed over each container to minimize evaporation and to protect the containers from rain. A neutral density (50% light reduction) shade cloth was placed over the top of the tank to minimize algal growth and to better mimic natural field light availability.

The experiment started on 17-June and ran for 11 weeks. Plants were kept in freshwater until 10-July, when salinity treatments began, in order to allow the plants to recover from any transplant stress. Salinity was elevated in increments over the course of the next 19 days using Forty Fathoms© Crystal Sea® salt. This was done to parallel rates of salinity change which have been observed under natural field conditions in the region (Shields et al., 2012). The 5 salinity treatments were increased by 1 and the 10 salinity treatments were increased by 2 every 3–4 days during the 19 days until the final concentrations were reached. Salinity was monitored every 3–4 days during this period using a handheld YSI 6000 (Yellow Springs Instrument, Inc.). Additionally, temperature, dissolved oxygen, and pH were also monitored biweekly throughout the experiment.

At the end of the experiment prior to harvesting, sediment was sampled for percent organic content and NH_4^+ and PO_4^{3-}. All plant material was harvested and brought to the lab for measurements of maximum shoot length, shoot density, and above and belowground biomass. Biomass was determined by drying the plants at 60 °C until a constant weight was obtained.