



Morphological response of *Zostera marina* reproductive shoots to fertilized porewater



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ABSTRACT

Exposing *Zostera marina* to fertilized porewater has been shown to increase vegetative shoot density and leaf growth rates, and affect shoot morphology. However, aside from changes in shoot density, records of morphological changes to reproductive shoots are lacking. To address this, five replicate ambient and nutrient enriched patches, each between 0.5 and 2.0 m², were selected within a developing *Z. marina* meadow in Shinnecock Bay, NY. Fertilizer stakes, with a N:P:K of 15:3:3, were used to amend the sediments of a subset of patches in the late fall and early spring. In June, morphological measurements of reproductive shoots and stages of anthesis were recorded. We found significantly increased reproductive shoot height, number of rhipidia, and number of spathes on each rhipidium in response to fertilization. Nutrient enrichment also advanced the stage of ovary development in the first spathes at the time of sampling, indicating that the rate of development had been accelerated or the reproductive shoot had flowered earlier. Additionally, the number of normally developing ovaries, as determined by the size of the seed embryo, was significantly greater in enriched patches. We estimated that these changes acted to increase seed output per reproductive shoot, and may have enhanced pollen access by elevating receptive stigma above the local vegetative canopy.

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1. Introduction

Nutrient and light availability are considered to be the primary physical factors controlling seagrass growth (Short, 1987; Dennison, 1987). However, nutrients and light tend to be negatively correlated within the nearshore ecosystems where most seagrasses are found. For example, chronic nutrient loading has been shown to increase planktonic and epiphytic algal biomass, reducing light penetration (Orth and Moore, 1983; Short and Neckles, 1999) and, over time, restricting seagrasses to areas with relatively little bulk water nutrient concentrations. In contrast to most algae, however, seagrasses can acquire nutrients directly from the sediments using adventitious roots (Agami and Waisel, 1986), a capacity that often exceeds that of foliar uptake (Short and McRoy, 1984; Vonk et al., 2008). Because of this, altering porewater nutrients has been shown to have profound effects on vegetative shoot morphology. Typically, porewater amendments result in increased vegetative shoot density, number of leaves, leaf length, leaf area, leaf growth rate, and areal coverage of *Zostera marina* (Orth, 1977; Short, 1987; Kenworthy and Fonseca, 1992; Carroll et al., 2008; Peralta et al., 2003). Additionally, Roberts et al. (1984) reported that more shoots had sprouted from seedlings planted in areas of nutrient enrichment.

While the effect of porewater nutrients on *Z. marina* vegetative growth has been extensively studied, the impact of nutrient addition

on reproductive shoots remains unexplored. Short (1983) provided the only description of nutrient condition and *Z. marina* reproductive growth, quantifying their density along natural gradients of interstitial ammonia in the Alaskan archipelago. Although he did not directly manipulate porewater nutrients, Short (1983) found increased ammonia concentrations correlated with greater vegetative leaf area, length and width. He and others have interpreted the short-term, shoot proliferation by *Z. marina* as a positive response to nitrogen availability, while the long-term, negative effects associated with chronic eutrophication, such as reduced shoot density and productivity, are the combined result of water-column, epiphytic, macroalgal and self-shading (Short, 1983; Cabaco et al., 2013).

Given the dramatic and numerous impacts of nutrient availability on vegetative growth, we hypothesized that similar changes might occur among the anatomical structures comprising generative growth. In *Z. marina*, flowers consist of spathes nested within sympodial branching rhipidia (De Cock, 1981, Fig. 1). A spathe is the protective sheath surrounding the spike-like inflorescence or spadix (Churchill and Riner, 1978). In *Zostera*, the spadix consists of both male and female flowers (Fig. 2a). The reproductive shoot develops acropetally, causing the lowest rhipidium to be the oldest and the topmost rhipidium to be the youngest (De Cock, 1981). Spadices on each rhipidium develop acropetally, with the oldest spadix (closest to the stem) undergoing anthesis first and the youngest spadix (farthest from the stem) maturing last (Churchill and Riner, 1978; De Cock, 1981). The stages of anthesis are clearly identifiable with the first being the erection of the style to a

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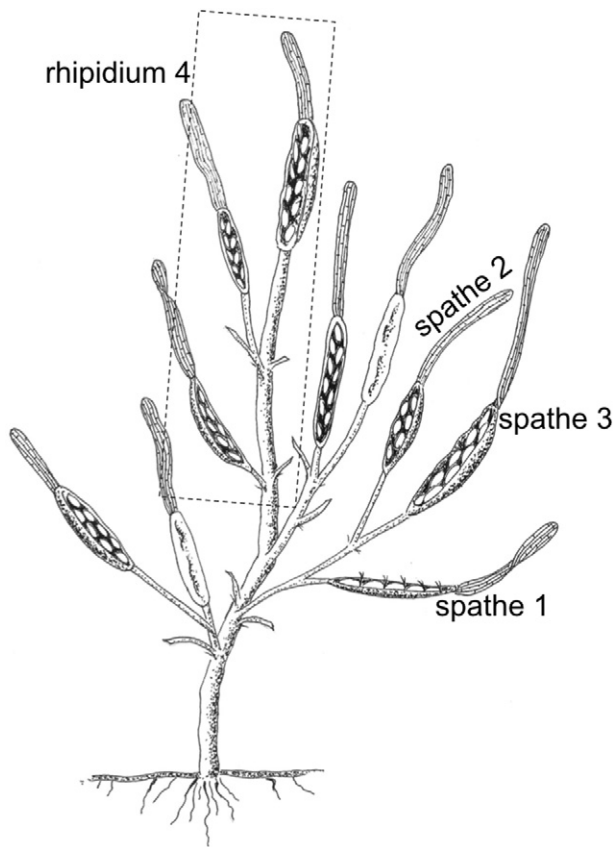


Fig. 1. Stylized representation of a *Zostera marina* reproductive shoot with 4 rhipidia. Spathes on the second rhipidium are numbered sequentially in order of development. The youngest, tallest rhipidium (the 4th) is identified by a dashed box.

90° angle with the ovary (De Cock, 1980). Pollen grains in the water column then contact one of two stigmata. Fertilization of the ovary marks the second stage of anthesis, visible as a dark abscission scar on the style (Fig. 2b). Next, the anthers release their pollen into the water column and dehisc from the plant, leaving the fertilized ovaries to mature into small seeds (De Cock, 1980, Fig. 2c and d).

Historically, studies of seagrass spatial expansion and persistence have focused primarily on vegetative growth, with attention to seagrass reproductive ecology occurring only for annual species (Orth et al., 2000), those with significant seed banks (Fonseca et al., 2008) or for denuded and disturbed areas (Orth and Moore, 1986; Lee et al., 2007; Peterson et al., 2002). Recently, this clonal-centric view has been challenged (Becheler et al., 2010; Zipperle et al., 2011; Buckel et al., 2012; Peterson et al., 2013), reinvigorating the discussion of sexual recruitment in meadow development and recovery (Macreadie et al., 2014).

In this study, we manipulated porewater nutrient concentrations within five seagrass patches to examine its effect on reproductive growth. We asked the following questions: (1) can fertilization alter the morphology of *Zostera marina* reproductive shoots, and (2) how will these changes affect seed production?

2. Materials and methods

2.1. Study site

The study area (250 m × 225 m) consisted of a patchily distributed *Zostera marina* meadow in Shinnecock Bay, Long Island, NY (40.857237° N, 72.450289° W; Fig. 3). Depth at the site ranged from 0.25–1.25 m (MLLW). Light penetration at the site was $143 \pm 9.2 \mu\text{mol s}^{-1} \text{m}^{-2}$, which was $46 \pm 2\%$ of surface incident light at a depth of 0.89 ± 0.04 m ($n = 5$; LI-COR underwater PAR sensor).

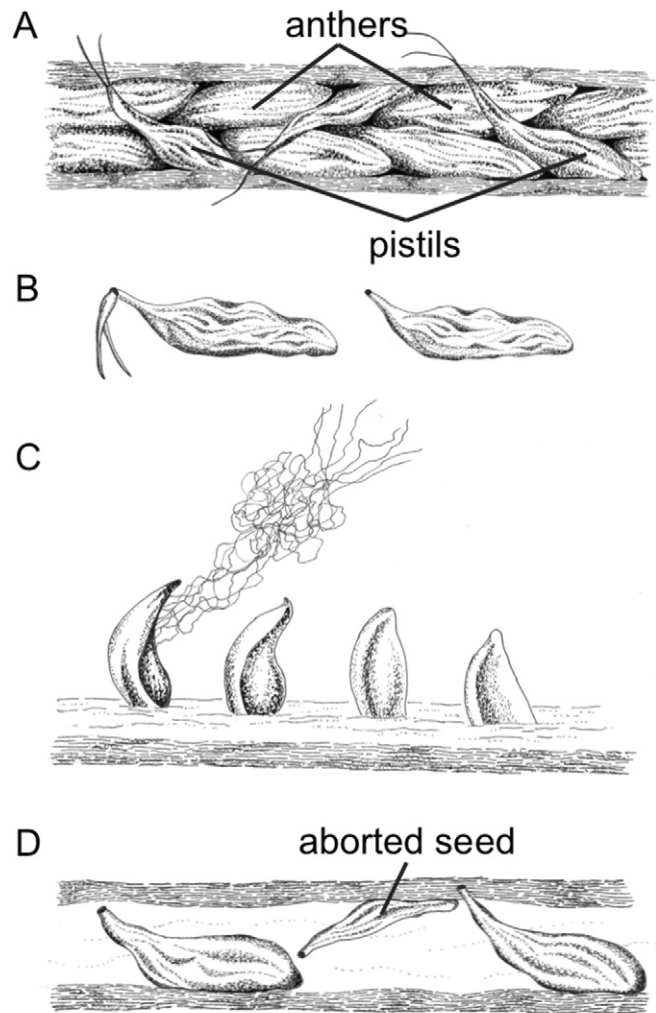


Fig. 2. A *Zostera marina* reproductive shoot spadix (a) contains both male flowering parts (anthers) and female flowering parts (pistils). Stages of anthesis include the erection of the styles to a 90° angle with the ovary, (b) the abscission of the stigmata, (c) the release of pollen by the anthers, and (d) the development of ovules into seeds.

Surficial sediments consisted of siliceous sands uniformly low in organic content (<1% loss on ignition at 500 °C for 5 h). In 2008, Carroll et al. found evidence for nutrient limitation in *Z. marina* growing within this portion of the bay. Flowering phenology in *Z. marina* varies by latitude and is strongly regulated by temperature; at the study site, primordial inflorescences first appear at 0.5–3 °C during winter, anthesis occurs mid-May at 15 °C and fruit maturation is completed by the end of June, after temperatures have reached 21 °C (Churchill and Riner, 1978; Silberhorn et al., 1983).

Seagrass was mapped using available aerial imagery beginning in 2001 and, via a balloon-mounted camera, bi-monthly since 2011 (Furman et al., 2015). These maps allowed for tracking of patch formation, expansion, loss, and the calculation of minimum age. Over 2200 patches were identified via ArcGIS, ranging in size from 0.01 to 20,000 m².

2.2. Experimental nutrient addition

Using a Trimble GeoXT unit with Arcpad 7 software, ten *Z. marina* patches between 0.5 and 2.0 m² were selected and field-located in the shallowest portion of the study site, (0.33–0.39 m MLLW). A 4-m² quadrat, divided into 100 cells (400 cm²), was placed over each patch. Permanent rebar markers secured three of four quadrat corners, ensuring exact replacement for sampling and fertilization. Five patches were

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