



Effect of temperature and nutrient manipulations on eelgrass *Zostera marina* L. from the Pacific Northwest, USA



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ABSTRACT

Global climate change will impact the three dominant drivers of estuarine seagrass productivity, temperature, light and nutrients. The response of Pacific Northwest (PNW) *Z. marina* to interactive effects of temperature and nitrogen conditions was experimentally evaluated. Experimental manipulations were conducted hydroponically in acrylic chambers. Preliminary single factor experiments were conducted to evaluate physiological tolerances to temperature and nitrogen concentrations. Eelgrass exhibited a statistically significant linear increase in relative growth with increasing NH_4 concentration (range from 5 to 1000 μM); in contrast, there was no relationship between relative growth rate and increasing NO_3 concentration. After 14 d there were no indications of plant mortality associated with NH_4 or NO_3 . Leaf growth metrics exhibited strong statistically significant linear relationships with increasing water temperature (temperature range 4–25 °C), indicating broad thermal tolerance. In the factorial experiment, triplicate plants were exposed to 3 temperatures (10, 18 and 25 °C) and 3 nitrate concentrations (10, 30 and 100 μM). Most metrics (leaf elongation, growth, relative growth, wasting index) exhibited a statistically significant temperature effect but no nutrient concentration effect, indicating the importance of temperature on metabolic rates. Plants at 18 and 25 °C had significantly more wasting disease than plants at 10 °C. Tissue $\delta^{15}\text{N}$ and C:N values exhibited significant nutrient concentration and temperature effects, indicating that both factors influenced how much NO_3 was incorporated into the tissues. Whole plant non structural carbohydrate content exhibited no significant response to either temperature or nitrate concentration. Temperature played a dominant role controlling *Z. marina* response to nutrients; nitrogen toxicity was not observed, and in general the effects of temperature and nutrients were not synergistic. This work highlights the complex nature of *Z. marina* response to environmental conditions; additional multifactor experiments will be required to tease apart these interactions.

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1. Introduction

It is generally accepted that the three “master variables” of seagrass health and productivity are light, temperature and nutrients. Although other factors influence seagrasses (e.g. wave and desiccation exposure, salinity, sediment type, geochemistry), these three variables exert the strongest control over production and survival (Koch, 2001). Light availability controls photosynthetic production by the plants, temperature influences all metabolic processes, and nutrients (C, N and P) provide the basic building blocks required for life.

Global climate change (GCC) is projected to have profound impacts on terrestrial and marine environments of North America. In the Pacific Northwest (PNW) region of North America (Northern California, Oregon and Washington, USA), these changes are predicted to alter air and water temperatures, sea-level, storm frequency and intensity, as well as timing and magnitude of precipitation (Mote et al., 2005). Consequently, GCC is expected to directly impact the master variables

controlling *Zostera marina* L. productivity and survival (Short and Neckles, 1999).

Thermal tolerance is considered a dominant factor controlling the distribution of many organisms and is a major driver of altered distributions associated with climate change (Chen et al., 2011). The southern range of *Z. marina* (North Carolina USA and Baja Mexico for North America) is a result of environmental temperatures regularly exceeding the plants tolerance (Koch and Orth, 2003). At the physiological level, increased temperatures increase metabolic rates and requirements. For example, seagrass respiratory rates increase faster than photosynthetic rates with increased temperature, which can lead to negative carbon balance (Lee et al., 2007; Moore and Short, 2006). Temperature also influences nutrient uptake, growth rates, and may be a trigger for sexual reproduction (Lee et al., 2007; Moore and Short, 2006). Extreme temperatures can lead to cellular and organismal death (Kaldy and Shafer, 2012; Phillips, 1984; Thayer et al., 1984). Additionally, warm water temperatures favor the occurrence and spread of “wasting disease” (Rasmussen, 1977) caused by the pathogen *Labyrinthula zosterae* (Muehlstein et al., 1991; Short et al., 1987). Wasting disease has been implicated in the large scale loss of *Z. marina* in North

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America and Europe (Rasmussen, 1977; Short et al., 1988; Vergeer et al., 1995).

Although the influence of temperature on physiological rates is relative well understood, the impact of thermal change on plant growth is more complicated; since growth is the integration of nutrient availability, uptake and partitioning along with carbon balance (Lee et al., 2007). Worldwide *Z. marina* tolerates temperatures between -1.5 and 30 °C but has an optimum temperature of 15.3 ± 1.6 °C for growth and 23.3 ± 1.8 °C for photosynthesis (Lee et al., 2007). Regional experimental work found that PNW *Z. marina* was healthiest at 5 – 8 °C and at temperatures above 15 °C plants exhibit physiological stress (Thom et al., 2003). In Oregon, *Z. marina* maximum plant growth was observed during summer when water temperatures were lowest due to upwelling and light levels were saturated (Kaldy and Lee, 2007). Consequently, *Z. marina* can be considered eurythermal but responds to local or regional environmental conditions (e.g. carbon limitation, light availability, etc.).

Nutrient effects (limitation and over-enrichment) on seagrass have been a topic of intense research for several decades with some of the earliest studies going back to the 1970s (Hemminga and Duarte, 2000; Romero et al., 2006; Touchette and Burkholder, 2000). Several recent studies in North America have focused on how seagrasses respond to nutrients using factorial experiments where more than one independent variable is manipulated at a time. Results from manipulative and observational studies have led to development of two dominant hypotheses regarding *Z. marina* response to nutrient loading. Numerous researchers (Duarte, 1995; Moore and Wetzel, 2000; Nixon et al., 2001; Short et al., 1995) have concluded that seagrass decline is an indirect response to nutrient loading mediated through algal blooms. Light limitation caused by algal blooms results in decreased seagrass abundance (Hauxwell et al., 2003). Other researchers (Bird et al., 1998; Brun et al., 2002; Burkholder et al., 1992, 1994; Invers et al., 2004; Touchette and Burkholder, 2007; van Katwijk et al., 1997) suggest that seagrass decline can be a direct response to nutrient loading, causing negative carbon balance via a physiological mechanism. These researchers hypothesize that the lethal effects are related to carbon starvation because all available C is used for N uptake and assimilation (Invers et al., 2004; Touchette and Burkholder, 2007). Other recent work suggests that pH, shoot density, and time of year can mediate lethal N impacts (Brun et al., 2002; van der Heide et al., 2008). These hypotheses are the result of research conducted along the Atlantic Coast of North America and Europe and have not been evaluated for PNW *Z. marina* populations, which experience high ambient nutrient loads, cold water temperatures and rapid flushing (Brown and Ozretich, 2009; Lee and Brown, 2009).

One reason to believe that these hypotheses may not apply in the PNW is that nitrogen loading is very high relative to many other estuarine systems due to natural nitrogen sources. In the PNW, coastal ocean processes are dominated by nearshore upwelling and nitrogen fixing red-alder trees (*Alnus rubra* Bong.) are an important component of estuarine watersheds (Lee and Brown, 2009). For example, in the ocean dominated portion of Yaquina Bay, OR, $\text{NO}_2 + \text{NO}_3$ concentrations commonly reach or exceed 30 μM during summer upwelling, while in the riverine dominated portions winter values in excess of 100 μM $\text{NO}_2 + \text{NO}_3$ are routine (Brown and Ozretich, 2009; Lee and Brown, 2009). Average annual NH_4 concentrations are often less than 4 μM , and as a result $\text{NO}_2 + \text{NO}_3$ accounts for 70–90 % of the dissolved inorganic nitrogen pool (Brown and Ozretich, 2009). Consequently, annual nitrogen loads are on the order of 4.6×10^5 mols DIN d^{-1} exceeding even the most eutrophic systems, but these systems are also characterized by short residence times (Brown and Ozretich, 2009; Lee and Brown, 2009; Nixon et al., 2001). Despite very high nitrogen loadings and seasonal macroalgal blooms, the distribution of eelgrass within Yaquina Bay has remained stable for at least 30 years (compare maps in Cortright et al., 1987 and Lee and Brown, 2009). The long-term survival of *Z. marina* with these high nutrient stress levels suggests that PNW systems may not respond the way we might predict based on work from other parts of the world.

The goal of this work was to experimentally evaluate *Z. marina* response to a factorial exposure of temperature and nutrient conditions expected to be stressful to the plant in order to evaluate the growth and physiological response to these stressors. In order to successfully attain this goal, there were two objectives: (1) conduct single factor experiments to determine the physiological tolerances of PNW *Z. marina*, (2) conduct a fully crossed factorial experiment to assess plant response to multiple stressors. The response of *Z. marina* to high nutrient concentrations is expected to be influenced by temperature in a synergistic manner. The results of these experiments will be important for mechanistic modeling of seagrass–stressor interactions as well as providing insight to the response of eelgrass to global climate change.

2. Methods

2.1. Study area

All seagrass material used in this study was collected from Yaquina Bay, Newport, OR, USA (Kaldy, 2012; Kaldy and Lee, 2007). During field collections, care was taken to excavate the rhizome/root complex with minimal damage. Senescent leaf material was removed, rhizomes were trimmed to five internodes and blades were wiped clean of epiphytes. For each experiment, plants were collected, cleaned and held in the dark in flowing seawater for <24 h prior to initiating the treatments. Only healthy plants with no visible evidence of wasting disease (e.g. no brown/black lesions) were used for the experiments.

Dual-compartment chambers were used to hydroponically (no sediments) incubate *Z. marina* plants under experimental treatments (Kaldy, 2012). A small piece of tubing was used to facilitate exchange of water between the upper and lower chamber compartments. Each chamber was randomly assigned to treatment cabinets that contained a 1000 W metal halide light and a polycarbonate tank (60 cm \times 60 cm \times 90 cm) that was used as a water bath to control temperature. Lights were on a 14:10 L:D cycle and irradiance was >400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, which is above saturation for *Z. marina* (Lee et al., 2007). Temperature conditions for each experiment are detailed below. Air was continuously bubbled through each chamber to mix the water. In all experiments an artificial seawater media (AFSW) consisting of Red Sea Salt (Red Sea Fish Pharm Inc., Eilat, Israel) and Milli-Q water made to salinity 20 was used as the incubation media (Kaldy, 2012). In all experiments the AFSW media was exchanged daily for each chamber. NO_3 is used to represent measured concentrations of $\text{NO}_2 + \text{NO}_3$.

2.2. Single factor nutrient experiment

Fifteen dual-compartment chambers were used in the single factor nutrient experiment (February 2008). Each chamber contained a single plant with a leaf length of 50 to 80 cm, an average total biomass of 0.8 ± 0.2 gdw and an average root:shoot of 1.1 ± 0.4 . Each chamber was assigned a treatment; NO_3 exposure ($n = 7$), NH_4 exposure ($n = 7$), or control without a plant ($n = 1$). Chambers were randomly assigned to two experimental cabinets. AFSW was amended with reagent grade KNO_3 or NH_4Cl to produce treatment concentrations of 5, 30, 100, 250, 500, 750 and 1000 μM of either NO_3 or NH_4 . All AFSW was amended with KH_2PO_4 to a final concentration of 10 μM PO_4 . Chamber temperatures were maintained at 13 ± 0.5 °C by the seawater flowing around the chambers. Prior to being placed into a chamber, plants were marked with a needle to assess leaf production and relative growth rates (RGR; Kaldy and Lee, 2007). Additional metrics included leaf and rhizome + root ($r + r$) biomass.

2.3. Single factor temperature experiment

In March 2008, fifteen dual-compartment chambers were used in the single factor temperature experiment. Each chamber contained a single plant with a leaf length of 50 to 110 cm and an average leaf

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