



Effects of nutrient enrichment and crab herbivory on a SW Atlantic salt marsh productivity

Juan Alberti^{a,b,*}, Just Cebrian^{c,d}, Agustina Méndez Casariego^{a,b}, Alejandro Canepuccia^{a,b}, Mauricio Escapa^{a,b}, Oscar Iribarne^{a,b}

^a Laboratorio de Ecología, Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Rivadavia 1917, CP C1033AAJ, Ciudad de Buenos Aires, Argentina

^c Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, AL 36528, United States

^d Department of Marine Science, University of South Alabama, LSCB 25, 307 University Blvd., Mobile, AL 36688, United States

ARTICLE INFO

Article history:

Received 15 September 2010

Accepted 21 May 2011

Available online 12 June 2011

Keywords:

Crab herbivory

Leaf growth dynamics

Neohelice granulata

Nitrogen addition

Spartina densiflora

SW Atlantic

ABSTRACT

After intense debate it is now accepted that nutrients (a bottom-up process) and herbivores (a top-down process) are both important controls of plant productivity in many systems. Besides their direct effects, herbivores may also have profound positive or negative indirect effects that can be modulated by nutrients and time. The interactive relationships between time, nutrient availability and herbivore impacts (direct and indirect) on plant growth dynamics are an emerging research topic that merits further effort. Here we did several experiments in a SW Atlantic marsh to contribute towards that gap by focusing on the dominant plant, *Spartina densiflora*, and one of the dominant herbivores, the crab *Neohelice (Chasmagnathus) granulata*, in the marsh. Herbivory by the crab was highly seasonal, with most of the consumption occurring in fall. Even though crabs preferred nutrient enriched leaves, nitrogen content was not the driver of these seasonal variations. Crab herbivory had markedly indirect negative impacts on *S. densiflora* leaves, reducing their growth rates and increasing their senescence. These deleterious impacts may partially explain the seasonal decline in leaf growth and a net loss in leaf biomass observed in the fall. Fertilization did not seem to alter these processes. Adding nutrients increased leaf growth in the spring, where ambient herbivory was low, but it also increased herbivory in the fall, resulting in similar patterns as the ones observed under non-fertilized conditions. Herbivory by the crab also greatly affected the dynamics of *S. densiflora* stems. Increases in stem density in relation to initial conditions were larger in non-grazed than in grazed plots regardless of whether nutrients were added or not. Together, these results indicate that, in Southwestern marshes populated by *S. densiflora* and *N. granulata*, herbivory by the crab represents an important direct and indirect control of plant growth. Our results also emphasize the importance of considering impacts on growth rates and not only on biomass because not considering reduced growth after herbivory may lead to improper calculations of nutrient cycling or detritus production.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

After intense and long-lasting debate about whether top-down (i.e. herbivores and their predators) or bottom-up forces (i.e. nutrients and physical factors) regulate plant productivity (see Hunter and Price, 1992), there is increasing agreement that both forces commonly operate together and that their net balance often depends on local characteristics (i.e. species involved, abiotic conditions, and habitat productivity; Lotze et al., 2001; Moran and Scheidler, 2002; Russell and Connell, 2005; Borer et al., 2006; Burkepile and Hay, 2006; Gruner et al., 2008). Nutrients generally increase plant biomass while herbivores decrease it (e.g., Burkepile and Hay, 2006; Gruner et al., 2008). However, it is also

known that increased nitrogen availability may lead to more palatable plants and increased consumption rates on them (Cebrian et al., 2009; Mattson, 1980). A recent review, however, found that the interaction of nutrients and herbivory controlling the biomass of primary producers is uncommon (Gruner et al., 2008). Nevertheless, at least in salt marshes, nutrient-enhanced herbivory may become intense and override the positive impact of nutrients on plant biomass, leading to lower biomass in fertilized in comparison with unfertilized conditions (Bertness et al., 2008; Sala et al., 2008).

The impacts of herbivores on plants are highly variable, as the amount they consume depends on many abiotic and biotic conditions (e.g., Goranson et al., 2004). Herbivores may also interact with pathogens or mutualists, which may modify their impacts on plants. For example, herbivores may induce plant susceptibility (decreased resistance or tolerance to other herbivores or pathogens), which may magnify the negative effects of herbivore consumption *per se* (Nykänen and Koricheva, 2004; Silliman and Newell, 2003). Herbivores may also

* Corresponding author at: Laboratorio de Ecología, Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina. Tel.: +54 223 4753554; fax: +54 223 4753150.

E-mail address: jalberti@mdp.edu.ar (J. Alberti).

promote mycorrhizal colonization, increasing nutrient availability for plants and thus increasing their growth (Kula et al., 2005). Herbivores themselves may become mutualists by, for instance, triggering plant growth through moderate and partial consumption (i.e. overcompensation; see de Mazancourt et al., 1998; Agrawal, 2000; Hawkes and Sullivan, 2001). Overcompensation may occur through the promotion of nutrient cycling and enhanced photosynthetic activity due to removal of old, less productive tissues and increased light availability for basal parts of grasses (Tiffin, 2000; Yamauchi and Yamaura, 2004; Zieman et al., 1984). Plant nutritional quality and phenology influence herbivory and plant compensatory responses (Mattson, 1980; Yamauchi and Yamaura, 2004). Many studies have focused on nutrient–plant–herbivore interactions (Borer et al., 2006; Burkepille and Hay, 2006; Gruner et al., 2008; Mattson, 1980), but relatively fewer studies have explicitly addressed these issues through time (Lotze et al., 2001; Vinueza et al., 2006).

Salt marshes are vegetated intertidal areas where nitrogen availability has long been recognized as a major limiting factor for plant productivity (Dai and Wiegert, 1996; Pomeroy and Wiegert, 1981; Valiela et al., 1976). However, recent results show that herbivores can also limit marsh productivity by reducing plant density and/or height (Bortolus and Iribarne, 1999; Jefferies et al., 2006; Kuijper and Bakker, 2005; Silliman et al., 2005). Vast areas of Southwestern Atlantic salt marshes (located between southern Brazil and the northern Argentinean Patagonia) are vegetated by the cordgrass *Spartina densiflora* Brongn (Isacch et al., 2006). The productivity of this plant may be strongly limited by nutrients, as fertilizer supply may result in up to 6-fold increases in plant biomass (Alberti et al., 2010). These marshes are also characterized by the presence of the burrowing crab *Neohelice (Chasmagnathus) granulata* Dana (Alberti et al., 2007a; Iribarne et al., 2005). The crabs are mainly herbivorous in the marsh and herbivorous/detritivorous in the mudflat (Bortolus and Iribarne, 1999; Botto et al., 2005; Iribarne et al., 1997). Crab herbivory typically removes the top part of cordgrass leaves (J. Alberti unpubl. data), facilitating fungal infections (Daleo et al., 2009). However, evidence suggest that the relative importance of nutrients and herbivory might be seasonally variable given that growth as well as herbivory vary throughout the year (Alberti et al., 2008). The objective of the present study was to contribute to our understanding of the relationships between nutrient enrichment, herbivory by *N. granulata*, and the growth dynamics and mortality of *S. densiflora* through time. In particular, we evaluated (1) the effects of fertilization on herbivory and leaf growth rates, (2) the single and interactive short-term effects of fertilization and recent herbivory on length-specific leaf growth and senescence and, (3) the single and interactive effects of fertilization and herbivory on stem density dynamics.

2. Materials and methods

2.1. Study site

This study was carried out at the Mar Chiquita coastal lagoon (37° 45' S, 57° 26' W Argentina), an UNESCO Man and the Biosphere Reserve. This is a body of brackish water (salinity range between 0.5 and 34‰) with low-amplitude tides (≤ 1 m; Reta et al., 2001). The surrounding area is characterized by halophytic vegetation, dominated by *S. densiflora* and *Sarcocornia perennis* (Isacch et al., 2006). The burrowing crab *N. granulata* is one of the most important macro-invertebrates of SW Atlantic salt marshes and occurs in high abundance in the tidal flats and marshes of the Mar Chiquita coastal lagoon (Iribarne et al., 1997).

2.2. Effects of nutrient enrichment on leaf growth and herbivory

We conducted a 19-month experiment (from January 2006 through July 2007) to evaluate if fertilizer supply affected the growth rates of *S. densiflora* and herbivory by *N. granulata*. This experiment

consisted of two treatments (with and without nutrient addition) with 8 replicates each (75 × 75 cm open plots), located in the low marsh where crab herbivory is frequent (Alberti et al., 2007a). Nutrient additions started in January 2006 and consisted of doses of 60 g of a slow-release pelletized fertilizer (29% N, 5% P, and 5% K) per plot per month. Similar dosing has been used in other nutrient addition studies in salt marshes (Daleo et al., 2008; Emery et al., 2001; Levine et al., 1998).

Seven months after the beginning of fertilization (August 2006), we measured the length and width at the base of all live leaf blades (thereafter called “leaves”) in two stems chosen randomly in each plot. We considered live leaves those exhibiting some green length. The crab *N. granulata* consumes the leaves from the top, cutting their tips and rendering them trapezoidal in shape. Thus, if the leaf had been grazed by the crab, we also measured the width at the top of the leaf. In addition we made a small mark at the base of each leaf with a permanent fine point marker. Upon revisiting the plots the following month, in all marked leaves we measured the length from the base to the top of the leaf, the length from the base to the mark, and width at the base, mark, and top of the leaf if it had been grazed. We repeated this process monthly throughout the conclusion of the experiment (i.e. every month we marked and measured green leaves in two randomly-chosen new stems in each plot and measured them again 1 month later as previously explained).

From these measurements the area consumed by the crab on each leaf through the month (H, cm² per leaf per month) was quantified as:

$$H = \text{total leaf area in month } t \text{ (A) + leaf area grown from } t \text{ to } t + 1 \text{ (B)} - \text{total leaf area in month } t + 1 \text{ (C)} \quad (1)$$

where leaf areas were calculated using equations for triangular or trapezoidal areas. For instance, the leaf area grown from t to $t + 1$ corresponds to the area of the trapezoid with height = length from base to mark of the leaf, length of bottom side = width at the leaf base, and length of top side = width at the mark (see Fig. 1). Grazing by other herbivores, such as snails and the wild guinea pig *Cavia aperea* did not occur at our experimental units or were minimal and the marks left by those herbivores were different from the marks left by the crab and did not hinder calculation of the leaf area consumed by the crab.

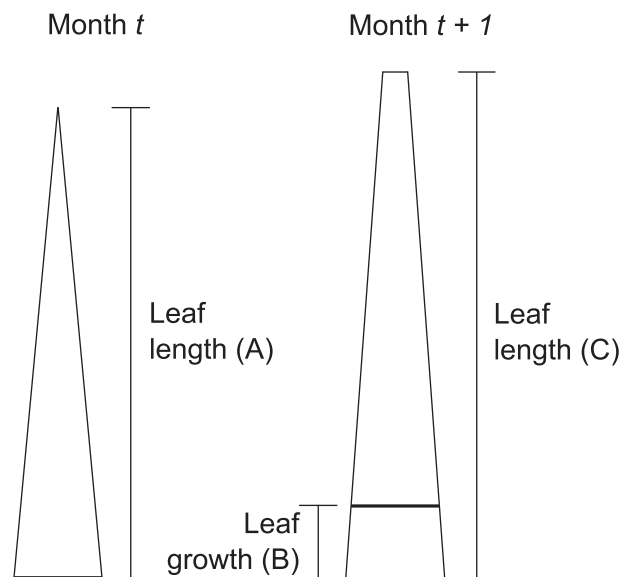


Fig. 1. Schematic representation of the measurements taken to estimate the leaf area consumed by the crab *N. granulata*. See text and Eq. (1) for details.

Download English Version:

<https://daneshyari.com/en/article/4396261>

Download Persian Version:

<https://daneshyari.com/article/4396261>

[Daneshyari.com](https://daneshyari.com)