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Herbivore damage increases methane emission from emergent aquatic macrophytes

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ABSTRACT

Wetlands are the largest natural methane (CH4) source and the vegetated littoral areas are the major contributors for CH₄ release from sediment to the atmosphere. Although the effects of herbivores on biomass removal, growth and reproduction of emergent macrophytes have been well documented, their effect on plant-mediated CH₄ fluxes, especially by insects, remains unknown. We performed a mesocosm experiment in which we simulated the damage caused by herbivorous insects and manipulated the density of damaged culms of *Eleocharis equisetoides* (4 levels -0, 20, 50 and 100%) measuring the corresponding CH₄ emission, concentration and potential production in the sediment. We hypothesized that an increased percentage of culms with simulated herbivory would be associated with increased CH₄ fluxes from sediment toward the atmosphere. Simulated herbivory positively affected CH₄ emissions, but only under high herbivory pressure. The average CH₄ flux from mesocosms with 50% and 100% damaged culms was 3.5 higher than those with intact or low levels of damage. These results indicate that physical damage on macrophytes affects gas transport within the plants. A field survey in our studied system revealed that plant biomass consumed by herbivores is relatively low. This result highlight that insects may have a disproportional effect on CH₄ emissions, i.e., a very small damage (low biomass removal), when performed in many culms (50% and 100% of damaged culms treatments), may substantially increase CH₄ fluxes. In summary, our findings bring a new perspective to the influence of herbivory on CH₄ and carbon cycling, especially regarding the role insects might play.

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1. Introduction

Among global ecosystems, wetlands are one of the most important organic matter (OM) degradation sites, and are the largest natural source of atmospheric methane (CH₄) (Bridgham et al., 2013). Average CH₄ emissions from wetlands are 217 Tg yr⁻¹ (Ciais et al., 2013). Within wetlands, the littoral zones are major sources of CH₄ emissions. Aquatic macrophytes dominate the littoral zone (Bergstrom et al., 2007) and participate in all three fundamen-

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http://dx.doi.org/10.1016/j.aquabot.2015.07.003 0304-3770/© 2015 Elsevier B.V. All rights reserved. tal processes of CH₄ dynamics: production (Petruzzella et al., 2013), oxidation (Jespersen et al., 1998) and, particularly, emission (Laanbroek, 2010).

The contribution of plant-mediated CH₄ to the atmosphere can be very variable, ranging from 30 to 100% of the total CH₄ flux (Bridgham et al., 2013). Several studies have shown that, compared with other life forms (e.g., floating-leaved and submerged), emergent aquatic macrophytes are the greatest contributors to CH₄ fluxes from wetlands (Duan et al., 2005; Bergstrom et al., 2007). However, CH₄ emission rates by emergent macrophytes are influenced by a variety of factors, including sediment CH₄ concentration and production (Ding et al., 2003); the presence or absence of morphological features (aerenchyma structures) (Sorrell and Boon, 1994); the mechanisms by which gas flows within aerenchyma tissues (Dacey, 1980; Armstrong et al., 1992; Brix et al., 1992) and, recently investigated, herbivory (Dingemans et al., 2011).





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Emergent aquatic macrophytes are adapted to oxygen-limited conditions. Their roots and rhizomes form a permanent connection that acts as a conduit between sediment and atmosphere, providing oxygen to their underground parts. Following the opposite pathway, CH₄ produced in the sediment enters the roots and is transported directly to the atmosphere (see Laanbroek, 2010 for a review). Thus, any physical harm to the plants could affect the rate or the magnitude of gas transport, as shown in some previous studies (Ding et al., 2003, 2005). Studying the effects of herbivorous birds on aquatic macrophytes, Dingemans et al. (2011) demonstrated that CH₄ emissions from stands subjected to herbivory could increase approximately 5 times compared with non-affected macrophyte stands. However, plants species vary in their capacity to transport CH₄ from the sediment to the atmosphere (Bhullar et al., 2013). Because their study focused on only one plant-bird interaction, a research priority is to assess grazing effects on other plant species and by other herbivorous species. Additionally, artificial and natural shoot clipping experiments have generally been used to demonstrate gas transport through macrophytes (Ding et al., 2005; Laanbroek, 2010; Dingemans et al., 2011). Despite the well-documented effects of herbivores on biomass removal, plant growth, reproduction, species composition and diversity of aquatic macrophytes (Van Eerden et al., 1997; van den Wyngaert et al., 2003; Gauthier et al., 2005; Bakker et al., 2006; Hidding et al., 2009), the effect of herbivory, and especially by insects, on potential CH₄ emissions has not been studied.

According to dos Santos and Esteves (2002), the net annual aboveground primary production loss due to herbivory by grasshoppers (Order: Orthoptera) in *Eleocharis interstincta* (Vahl) Roem. and Schult. was relatively low ($\approx 2\%$). However, the plants were always damaged in the apical part of the culms which did not reduce the culms' survival. Thus, damaged culms can act as an open conduit for CH₄ release to the atmosphere, potentially resulting in higher CH₄ emission rates.

While there are indications that tropical lakes and reservoirs emit up to 400% more CH₄ than similar environments in boreal and temperate biomes, direct measurements are still scarce (Bastviken et al., 2010). Previous investigations have been conducted in the tropics (Bastviken et al., 2011), but the contribution of vegetation to the CH₄ emissions is arguably the least well understood (Carmichael et al., 2014). Despite the potential importance of herbivory in modulating CH₄ emission rates (Schimel, 1995; Kelker and Chanton, 1997; Dingemans et al., 2011), no study was developed to examine the role that herbivorous insects might play in the CH₄ dynamics. Understand these insect–plant interactions could be very important, mainly, in highly vegetated tropical ecosystems such as shallow lakes and coastal lagoons, which suffers high herbivory pressure (Cyr and Pace, 1993; Lodge et al., 1998; Franceschini et al., 2010).

Eleocharis equisetoides (Elliott.) Torr. is abundant and often cooccur with *E. interstincta* in many coastal lagoons and inland lakes in the tropics (Kissmann and Groth, 1997). These species are morphologically similar and are one of the main components of the orthopteran diet in these ecosystems (dos Santos and Esteves, 2002; Bove and Paz, 2009). The presence of grasshoppers of the genus *Stenacris* (Family: Acrididae) are recorded in our study system. Biological information on *Stenacris* is scanty but they appeared throughout the year, as well as damaged culms of *E. equisetoides* (A.R. Gripp, Personal communication; dos Santos and Esteves, 2002). They do not occur only during the period of new culm growth after a sudden decrease in water level due to sandbar breaching events, indicating great influence by water level fluctuations on their population dynamics (dos Santos and Esteves, 2002; Capello et al., 2013).

In the present investigation, we used an experimental approach within mesocosms to simulate grasshopper herbivory. We manipulated the percentage of damaged culms using the aquatic macrophyte *E. equisetoides* and measured the corresponding CH_4 flux, concentration and potential CH_4 production (PMP) in the sediment. Thus, we hypothesized that an increased percentage of culms with damage from simulated herbivory would be associated with increased CH_4 fluxes.

2. Methods

2.1. Experimental design

The mesocosm experiment was conducted in the northern region of the State of Rio de Janeiro, Brazil ($22^{\circ}32'S$ and $41^{\circ}73'W$). The region has a tropical sub-humid to humid climate condition. The annual precipitation is 1165 mm, and there is a pronounced seasonal distribution with a minimum precipitation occurring in June (40 mm) and maximum precipitation occurring December (190 mm). The annual mean temperature is 22.6 °C with a mean summer temperature of 25 °C, an average winter temperature of 19 °C, while the annual mean relative humidity is approximately 83% (Caliman et al., 2010).

We established twenty-four mesocosms in an open field and exposed them to full sunlight and ambient temperature and precipitation. Sediment, water and plants used to construct the mesocosms were taken from two lagoons located in the Restinga de Jurubatiba National Park (22°-22°30'S and 41°15′-42°W). In Jurubatiba lagoon, we collected water from the limnetic region, while sand and E. equisetoides shoots were collected at the margins. We also sampled organic sediment from the bottom of Amarra Boi lagoon, located near Jurubatiba lagoon. We used sediment from different lagoons because of the high OM content of the Amarra Boi lagoon (~74%). A previous experimental assay demonstrated that the mesocosms produced no detectable CH₄ emission. This was probably due to the low availability of labile organic carbon in the sand of Jurubatiba lagoon. Thus, we added organic sediment from a different lagoon to ensure that the system was not carbon limited.

The mesocosms were constructed using plastic cylinders (27 cm diameter and 45 cm deep). Each mesocosm was filled with a bottom layer of a homogenized mixture of sand and organic sediment using a 10:3 ratio (8550 cm³/15 cm). Followed by a second layer containing only organic sediment $(1150 \text{ cm}^3/2 \text{ cm})$. Then, five plant shoots were carefully transplanted into the mesocosms. We also added leaf fragments from aquatic macrophytes (30g wet weight per mesocosm) to the mesocosms, which mimics the natural input of OM observed along the margins of coastal lagoons. The mesocosms were filled with water from the Jurubatiba lagoon only during the assembly process. After this, they were watered with tap water maintained at a depth of 6.5 cm during the whole experiment. It is important to note that at the time of transplanting, shoots had different number of culms, but there was no difference in the number of E. equisetoides culms (n = 44 in average) among mesocosms after a three-month growth period (ANOVA $F_{3,20} = 1.04$, P = 0.3; n = 24), right before experimental manipulation started.

We assigned the twenty-four mesocosms to four treatments with six replicates each in a random design. We manipulated the percentage of damaged culms in the mesocosms as follows: (1) 0% (all culms intact), (2) 20% (damage to twenty percent of culms), (3) 50% (damage to fifty percent of culms), and (4) 100% (damage to all culms). We used a razor blade to simulate damage on the culms of each corresponding treatment level (except 0%). The simulated culm damage was always performed in the apical part, above the water line and on a longitudinal section of the culms, and their size ranged between 5 and 10 cm. It is important to note that we did not manipulate the size of the damage, but their density in relation to

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