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Alteration of the chemical composition of mangrove (*Laguncularia racemosa*) leaf litter fall by freeze damage

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Abstract

Resorption, the remobilization and subsequent transport of leaf constituents (e.g. N, C, and P) into the perennial structures of the plant prior to leaf abscission, may be interrupted or prevented by stressors that interfere with the normal course of leaf senescence. Mangroves that lie along the latitudinal extremes of their distribution are susceptible to freeze damage that may periodically disrupt the normal resorptive process. On January 24, 2003, the white mangroves (*Laguncularia racemosa*) in a northern portion of Tampa Bay, Florida were exposed to freezing temperatures for 8 h. The leaves of these trees were noticeably withered by this freeze event. Over a four-month period following the freeze, we compared the subsequent rate of leaf litter production at this site to that of two, apparently undamaged, fringing mangrove forests in Tampa Bay. We also examined the carbon and nitrogen concentrations of the leaf litter from the litter traps at these three sites and compared it to that of green, yellow (nearly senescent), and freeze-damaged leaves hand-picked from the mangroves. A pronounced pulse of leaf litter fall (maximum: 7 g dw m^{-2} d^{-1}) was found at the putatively freeze-damaged site but not at the two comparison sites. In addition, the leaf litter at the freeze-damaged site was richer in nitrogen and carbon, and had a lower C:N than litter collected at the comparison sites. Comparison of the elemental composition of this leaf litter with leaves hand-picked from the mangroves suggests that the freeze event killed the leaves of *L. racemosa*, interrupting the process of resorption. This perturbation to nutrient flow may have implications for mangrove forest structure and the entry of mangrove material into food webs.

Keywords: mangrove; freeze; *Laguncularia racemosa*; resorption; nitrogen; leaf litter; Florida

1. Introduction

The flow of nutrients within forest ecosystems is regulated, in part, by the nutrient resorption that accompanies the senescence of leaves on trees (Hörtensteiner and Feller, 2002). Resorption is accomplished via the remobilization of chemical constituents (e.g. N, C, and P) in leaves and the subsequent transport of these elements into the perennial structures of the plant prior to leaf abscission (Chapin et al., 1990; Killingbeck, 1996). Resorption has been identified as an important mechanism in the conservation of nutrient resources, and as most heterotrophs in forested systems are affected in some way by the quality of litter falling to the forest floor, resorption is described by some as a "keystone process" (Killingbeck, 1996). Thus, disturbances that interrupt resorption and divert nutrients that otherwise would have been retained by trees are processes of particular consequence.

Resorption may be reduced by biotic or abiotic stressors that cause either premature leaf senescence or loss of leaf material prior to complete senescence (May and Killingbeck, 1992). Pre-senescent leaf mass is commonly removed by herbivory (Farnsworth and Ellison, 1993; Stowe, 1995; Saur et al., 1999; Kathiresan, 2003) and forces of weather (e.g. wind, rain, hail, etc.) (Dagar and Sharma, 1991; Mackey and Smail, 1995; Wafar et al., 1997; Davis et al., 2001). Particularly notable, however, are more severe manifestations of these events

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that are difficult to study due to their unpredictable and variable nature (Houlton et al., 2003). For example, irregular outbreaks of the gypsy moth *Lymantria dispar* have caused widespread, complete defoliation and even mortality of trees in the United States (Davidson et al., 1999). Likewise, hurricanes routinely strip leaves of tropical (Koptur et al., 2002; Hirsh and Marler, 2002) and temperate forests (Conner, 1998; Hunter and Forkner, 1999). Studies of these and other defoliation events have shown potential system-wide consequences as litter quality and quantity (Findlay et al., 1996), nutrient mineralization rates (Houlton et al., 2003; Ayres et al., 2004), and nutrient export in drainage water (McDowell et al., 1996; Lovett et al., 2002; Townsend et al., 2004) have been altered.

Mangroves that lie along the latitudinal extremes of their distribution are susceptible to freeze damage that may interrupt resorption and normal senescence as they are evergreen and lack a seasonal dormancy (Hogarth, 1999). Resorption is an active process (Hörtensteiner and Feller, 2002); therefore it cannot be performed in leaves that have been killed due to the physical damage of freezing (Norby et al., 2000). Each year, mangroves around Tampa Bay, Florida (USA), may experience up to 10 days of freezing temperatures (U.S. National Weather Service). Mangroves, particularly *Laguncularia racemosa*, the white mangrove, which is less cold resistant than either *Rhizophora mangle* or *Avicennia germinans*, may suffer limited mortality during prolonged exposure to freezing temperatures. The white mangrove may also experience defoliation and loss of limbs under these conditions (Savage, 1972). Therefore, it is reasonable to expect that, around Tampa Bay, the flow of nutrients in forests containing *L. racemosa* will be perturbed by freezing temperatures that interrupt resorption.

On January 24, 2003, temperatures in some of the Tampa Bay area fell below freezing (minimum −2 °C) for approximately 8 h. Afterwards, the leaves of white mangroves in Upper Tampa Bay Park were found brown and wilted, apparently damaged by the freeze. This event presented an opportunity to test the following predictions: (1) the elemental composition of freeze-damaged leaves will differ from that of senescent leaves (i.e., %N of the freeze-damaged leaves will be greater than that of senescent leaves, whereas the %C and C:N will be relatively lower), (2) freeze damage to *Laguncularia racemosa* will result in a pulse of leaf litter fall, and (3) the elemental composition of the white mangrove leaf litter fall at the freeze site will differ from senescent leaves (i.e., %N of the litter will be greater than that of senescent leaves, whereas the %C and C:N will be relatively lower).

2. Methods

2.1. Study sites

Three fringing mangrove study sites were selected in Tampa Bay, Florida: one site in which freeze damage to the white mangrove (*Laguncularia racemosa*) was evident, and two comparison sites without apparent freeze damage. The noticeably freeze-damaged site, located at Upper Tampa Bay Park in northern Tampa Bay (Fig. 1), was a narrow fringing mangrove forest dominated by *L. racemosa* with lesser representation of *Rhizophora mangle* and *Avicennia germinans*. The two comparison sites, the Gateway Tract and Fort De Soto Park, located in central and southern Tampa Bay, respectively (Fig. 1), contained the same species complement but were not dominated by *L. racemosa.* Mangroves in the comparison sites were taller and less dense than at Upper Tampa Bay Park (Table 1). Air temperature, maximum wind speed, and rainfall data were obtained for the duration of this study from a National Weather Service Station at Tampa International Airport near Upper Tampa Bay Park.

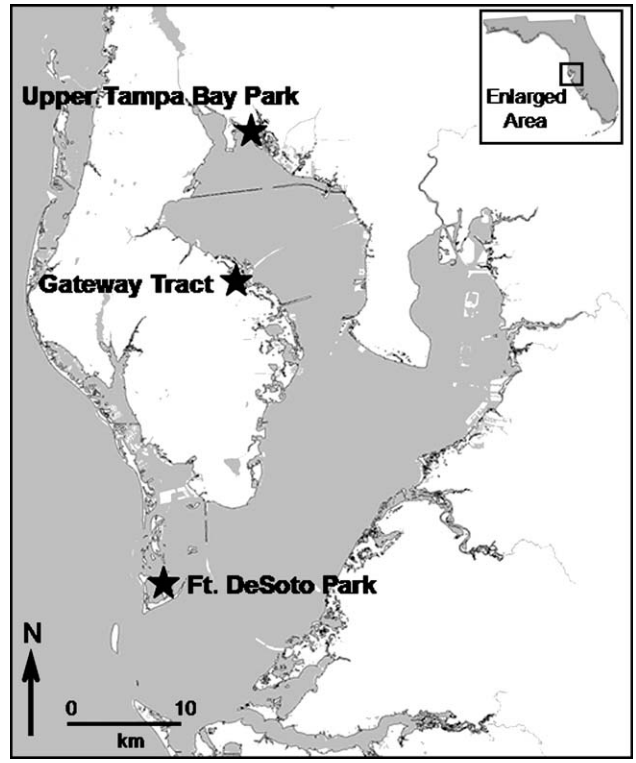

Fig. 1. Stars indicate the location of fringing mangrove study sites in Tampa Bay, Florida. Freeze damage was apparent at Upper Tampa Bay Park, but not at Gateway Tract or Fort De Soto Park (modified from Tampa Bay Estuary Atlas, an edition of wateratlas.org).

2.2. Litter fall

On January 30, 2003, five days after the freeze, eight 0.25 m^2 (3 mm mesh) litter traps (Twilley et al., 1986) were placed at each study site under white mangrove trees that were within 3 m of the waterward edge of the fringing forests. The traps were spaced at least 3 m from each other in a line parallel to the shoreline. All material was collected from these traps weekly from February 5, 2003 to April 9, 2003, and thereafter biweekly until May 21, 2003 ($n = 13$). The collected litter was dried in an oven (60 °C) for a minimum of 48 h, sorted into components [i.e., leaves (by species), wood, and reproductive structures], and subsequently weighed. Because *Laguncularia racemosa* was the only species obviously damaged by the freeze, we limited our analysis to its leaves. These