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Does plant performance under stress explain divergent life history strategies? The effects of flooding and nutrient stress on two wetland sedges

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ABSTRACT

Novel hydrology and nutrient loads are common environmental filters in disturbed wetlands. These filters impact plant growth and influence the composition and productivity of wetland plant communities by selecting for flooding-tolerant species that can efficiently acquire and use nutrients. We performed a factorial greenhouse trial to elucidate how nutrients and flooding affect the growth and morphology of *Carex obnupta* and *Carex stipata*, two wetland sedges with divergent life history strategies. Individual seedlings of each species were exposed to a combination of flooding (deep or shallow) and fertilization (low or high) treatments. These treatment combinations create a stress gradient from high fertilization and shallow flooding (lowest stress) to low fertilization and deep flooding (highest stress). Plant biomass accumulation and allocation were measured after 77-days. Total biomass, leaf area, and shoot biomass were greatest in high fertilizer treatments, regardless of flooding treatment. There was an initial plant size effect in *C. obnupta*: small plants accumulated less biomass than large plants under high flooding. *C. stipata* had higher biomass and specific leaf areas than *C. obnupta* in all treatments. *C. obnupta* had higher net assimilation rates per unit biomass and leaf area than *C. stipata*. These stress responses illustrate that each species has a distinct life history strategy. *C. obnupta* is a stress tolerator that can persist across a range of flooding conditions. *C. stipata* is a ruderal species that outgrows flooding stress by allocating carbon to leaf growth. These species' niches likely diverge based on how each species grows and allocates biomass under environmental stress

1. Introduction

Plant communities arise as products of biotic and abiotic environmental filters that shape plant species' growth and reproduction that drive interspecific competition (Keddy, 1992; Woodward and Diament, 1991). Environmental filters are any non-random process that shapes species assembly in a given environment (Díaz et al., 2007). Plant community composition shifts across environmental gradients based on species' functional capacities to acclimate to local environmental conditions (Cornwell and Ackerly, 2009; Wright and Westoby, 1999). As soil resources and/or environmental stress change across space or time, species that cannot acclimate to local conditions become less competitive and eventually fail to successfully reproduce and maintain their place in a community (Díaz et al., 1998). This theory of community assembly dictates that a species' life history strategy must correspond to the local physical, chemical and biotic environments for it to persist (Keddy, 1992). The traits that comprise the life history strategies that govern community assembly may be most easily elucidated across strong environmental gradients, such as those found in wetland ecosystems.

Wetland vascular plants have evolved functional strategies to tolerate environmental stress and acquire the resources required to persist, grow, and reproduce under suboptimal conditions. Accordingly, wetland plant communities often assemble across hydrologic gradients (Keddy, 1992; Shaffer et al., 1999; van Eck et al., 2004), as the depth, duration and timing of flooding stress select for wetland plant species with morphological and physiological adaptations that match a given environment (Keddy, 2000; Kozlowski, 1984; Magee and Kentula, 2005). To not be "filtered" out of a community, wetland plant species must be able to not only tolerate flooding stress, but also effectively acquire environmental

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resources such as nutrients and light. While general plant strategies have been classified based on functional traits that allow individual plant species to thrive and compete in different environmental settings (Grime, 2001; Kahmen and Poschlod, 2004) many species' life history strategies and their corresponding functional traits have not been assessed. Within this study we assess the abilities of two common wetland species, *Carex obnupta* and *Carex stipata*, to acclimate to persistent stress by quantifying how their functional traits—physiological and morphological characteristics that govern growth and reproduction–respond to the common wetland stressors and subsidies, flooding and nutrients.

To understand how each species will respond to wetland stress-subsidy dynamics, it is important to understand how each stressor (flooding and low nutrition) and subsidy (high nutrition) influences plant performance. Flooding reduces the oxygen available to submerged plant tissues and inhibits aerobic root respiration and active metabolic processes including nutrient and water uptake (Laanbroek, 1990). Plant responses to flooding are determined by belowground tissue oxygen acquisition and the expansion of leaf area relative to overall growth (Evans and Poorter, 2001). For many plants, including *Carex* species, flooding triggers the formation of aerenchyma–porous tissues that allow oxygen to diffuse within plant tissues (Chen et al., 2002; Visser et al., 2000). Within *Carices*, aerenchyma occurs predominantly by lysigenous processes where root tissues die and are replaced by new aerenchymous tissues (Visser et al., 2000). Proportional increases in root allocation to form aerenchyma may occur at the expense of plant growth because as relative photosynthetic tissue biomass decreases, so do photosynthetic carbon gain (Mielke et al., 2003).

Flooding not only changes plant allocation patterns, but also reduces leaf-level photosynthesis in many species (Kozlowski, 1984; Mielke et al., 2003). However, whole-plant photosynthesis may remain high due to high pre-stress specific leaf areas, the unit leaf area per unit leaf mass (SLA;(Shipley et al., 2005). High SLA allows fast-growing plants to maintain growth during flooded conditions, even when leaf-level photosynthesis is reduced (Bailey-Serres and Voesenek, 2008; Mommer et al., 2006). When an additional environmental stress, like low soil fertility, is paired with flooding, stressors may exacerbate flooding stress (Pezeshki, 2001; Pezeshki et al., 1999), selecting against species unable to build and maintain tissues under multiple stressors.

In contrast to flooding stress, nutrient enrichment is a common anthropogenic impact on wetlands (Verhoeven et al., 1993) and may increase plant nutrient uptake, photosynthesis and growth (DeLaune et al., 1998; McJannet et al., 1995). Wetland plant performance is enhanced by nutrient enrichment when plants are able to acclimate to the anoxic environment and essential nutrients do not occur exclusively as toxic, reduced compounds (Johnson and Leopold, 1994; Laanbroek, 1990; Merino et al., 2008; Rey Benayas and Scheiner, 1993). Fertile conditions are associated with high total productivity in wetlands at the expense of plant diversity as fast-growing, resource-efficient species outcompete stress-tolerant species (Bedford et al., 1999; Grime, 1977; Moore et al., 1989). This trade off between productivity and diversity in enriched environments may be explained by enhanced physiological performance (Laanbroek, 1990; McJannet et al., 1995) or biomass allocation strategies that allow plants to escape stress and continue to grow (Voesenek et al., 2004, 1992). In this way soil nutrition filters species that cannot use extra soil resources, favoring ruderal species that can quickly turn these resources into biomass.

Plants growing in flooded and nutrient-limited environments may allocate more biomass to roots, increasing root surface area to acquire nutrients (Morris and Ganf, 2001; Rubio et al., 1995) and oxygen. Anaerobic conditions created by flooding limit roots' ability to acquire nitrogen (N), specifically nitrate (NO_3), decreasing tissue nitrogen content and photosynthesis (Willby et al., 2001). Aerenchyma allows oxygen to diffuse into the soil, providing an oxidized buffer where nitrate remains soluble for plant uptake, enabling continued aboveground growth and photosynthesis. Building aerenchymous roots that acquire oxygen allows for continued plant growth facilitates a "low oxygen escape syndrome" life strategy (Bailey-Serres and Voesenek, 2008; Colmer and Voesenek, 2009). Low oxygen escape syndrome can occur rapidly in enriched, flooded conditions where sufficient photosynthesis maintains rigid stem architecture, expedites aerenchyma formation and allows leaf growth to continue (Blom and Voesenek, 1996). This rapid leaf expansion strategy in response to prolonged flooding has been shown to enhance the survival and growth of wetland plants in numerous settings (Pierik et al., 2008; Voesenek et al., 2004). However, differences in low oxygen escape strategy have not been evaluated among species known to occupy different environmental niches (Merino et al., 2008; Morris and Ganf, 2001).

C. stipata and *C. obnupta* occupy distinct niches in wetland environments and we anticipate that their functional responses to stress will explain these differences. While both species occur in wetlands, the types of wetlands they're capable of occupying (potential niche) may differ based on their ability to acclimate to stress and subsidy. We ask the question, does each species' performance under environmental stress explain its potential niche? To define how each species responds to flooding stress and nutrient susbsidy, we addressed intraspecific and interspecific hypotheses on plant biomass accumulation and allocation. Intraspecific hypotheses compare individual species' performance across the range of treatments:

Environmental stress from high flooding and low nutrients will shape plant allocation and biomass accumulation. We anticipate that flooded plants or nutrient-stressed plants will accumulate less total biomass, have lower leaf areas and specific leaf area, and allocate a greater proportion of total biomass to roots than in unflooded and well fertilized plants.

Specifically, we expect that plants experiencing shallow flooding and high fertilization will accumulate more total biomass than plants experiencing deep flooding and high fertilization or deep flooding and low fertilization and accumulate high leaf area, and show high specific leaf area, leaf mass ratio and leaf area ratio. We also anticipate that high flooding may be overcome by high fertilization that allows plants to outgrow environmental stress.

The interspecific hypotheses address differences in the growth and allocation of the two species based on their life-history strategies:

Deciduous *C. stipata* will exhibit low oxygen escape syndrome-like properties when flooded, rapidly growing leaves and producing more total biomass than *C. obnupta*, with higher specific leaf area and leaf area ratios. The evergreen *C. obnupta* will be more flood-tolerant than *C. stipata*, growing slowly and thriving under high nutrient conditions required to produce long-lived, evergreen leaves with high leaf mass ratios and low specific leaf areas. Specifically, we anticipate that *C. stipata* will have higher leaf area ratios and specific leaf areas and a lower leaf mass ratio than *C. obnupta*. We anticipate that *C. stipata* will photosynthesize less per unit leaf area and per unit total biomass, but have greater total leaf areas than *C. obnupta*.

2. Materials and methods

2.1. Plant species and experimental rationale

To evaluate the stress responses of two wetland sedges under a combination of flooding and fertilization treatments, we established a greenhouse experiment in June 2009 at the University of