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Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe

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ABSTRACT

In forested wetlands, hydrology exerts complex and sometimes compensatory influences on tree growth. This is particularly true in semi-arid ecosystems, where water can be both a limiting resource and a stressor. To better understand these relationships, we studied hydrologic and edaphic controls on the density, growth, tree architecture and overall productivity of forested wetlands dominated by the tree species *Alnus glutinosa* and *Salix atrocinerea* in Southern Europe. We sampled 49 plots set within 21 stands in the Atlantic coastal zone of the Iberian Peninsula, and quantified woody composition, size structure (diameter and height), and radial growth using dendrochronology. Plots were grouped into three saturation classes to compare tree growth characteristics (tree density, degree of sprouting, live basal area and productivity) across levels of saturation. We used Principal Component Analysis (PCA) to create integrated explanatory factors of hydrology, soil nutrient status and soil texture for use in linear mixed models to predict stand characteristics. Increased site saturation favoured a shift in species dominance from *Alnus* to *Salix* and resulted in a higher degree of multi-stemmed tree architecture ('shrubbiness'), particularly for *Alnus*. Radial growth was negatively correlated with long-term soil saturation; however, annual productivity on a per-tree basis varied by species. *Alnus* growth and tree density were negatively correlated with waterlogging and fine-textured soils, possibly due to anaerobiosis in the rooting zone. In contrast, *Salix* growth was more influenced by nutrient limitation. Overall site productivity as measured by annual basal area increment decreased with prolonged saturation. In summary, soil saturation appears to act as a chronic stressor for tree species in this ecosystem. However, these species persist and maintain a dominant canopy position in the most permanently flooded patches through increased sprouting, albeit at a reduced rate of overall biomass accumulation relative to well-drained sites. The diversity in functional responses among wetland forest species has important implications for the conservation and management of these ecosystems. The sustainable management of these ecosystems is directly tied to their vulnerability to changing hydrological conditions. Non-equilibrium modifications to the hydrologic regime from land use and climate change, which are particularly severe in semi-arid regions, may further decrease productivity, integrity and resilience in these stress-adapted communities.

1. Introduction

The growth and functional response of plants to resource availability and stressors is a long-standing research focus in ecology and agriculture (Chapin, 1980; Grime, 2002). In wetlands, water can be both a limiting resource and a chronic stressor (Mitsch and Gosselink, 2007). This is particularly the case for wetlands in semi-arid or transitional climates (Gasith and Resh, 1999), where sharp ecological gradients exist between upland communities and those dominated by wetland specialists that tolerate a wider range of disturbance and hydrologic conditions (Mouw, 2003; Sieben et al., 2009). Odum et al. (1979) characterized the opposing effects of perturbations such as flooding as ends of a "subsidy-stress" gradient, and predicted that ecosystem function/performance is highest at intermediate levels along the gradient. The effects of seasonal or permanent flooding can be envisioned as influencing both individual plants as well as whole ecosystems. Flooding can create a subsidy of high water and nutrient availability to individual terrestrial plants. Conversely, long-term soil saturation induces soil anoxia, which limits nutrient availability and gas exchange for

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plants (Mitsch and Gosselink, 2007), and soil toxicity due to reducing conditions. In addition, flooding in dynamic riparian settings can scour the soil substrate disturbance or induce local sedimentation (Kozlowski and Pallardy, 2002). These negative effects are mitigated to some degree by plants' adaptive responses to prolonged flooding, including tissues to facilitate oxygen exchange such as aerenchyma and lenticel development (Blom and Voesenek, 1996; Rood et al., 2003; Walls et al., 2005). Much of the research on physiological responses to flooding is based on laboratory experiments (Gill, 1975; Pereira and Kozlowski, 1977; Conner et al., 1997; Lopez and Kursar, 2003; Li et al., 2005; Day et al., 2006; Ewers et al., 2007; Wikberg and Ögren, 2007), with less emphasis on field studies (but see Megonigal et al., 1997; Eschenbach and Kappen, 1999; Tardif and Bergeron, 1999).

Though flooding generally has negative effects on individual tree function, its effects on overall stand productivity are less clear. Understanding the net integrative effects of flooding on species and whole stands is difficult because plants may exhibit compensatory responses across the hydrological gradient (e.g., shifts between sexual and clonal reproduction), and these are generally species-specific (Tardif and Bergeron, 1999). Increased inundation frequency and duration can have various effects on aboveground net primary productivity (ANPP), ranging from negative (e.g., Mitsch et al., 1991; Megonigal et al., 1997) to slightly positive (Burke et al., 1999; Clawson et al., 2001; Hanson et al., 2001). Many factors affect productivity, including stand age (Ryan et al., 1997), growth rate (Burke et al., 1999, Anderson and Mitsch, 2008), density (Szaro, 1990), and degree of sprouting (Bellingham, 2001; Francis, 2007; Opperman et al., 2008). In recent years, there has been a growing appreciation for the role of vegetative growth in allowing woody plants to persist in a diversity of ecosystems, particularly where stressful abiotic conditions may limit organism size, lifespan, and/or recruitment opportunities (Odum et al., 1979; Klimesová and Klimeš, 2007; Nzunda et al., 2007). Sprouting may be an important strategy in particular for species that do not maintain a seed bank (Karrenberg et al., 2002; Stella et al., 2006).

The question of whether flooding is primarily a subsidy or a stress in woodlands is of particular interest in drought-prone areas, where water is limiting to the surrounding upland ecosystem for long periods of the year (Eriksson, 1996; Megonigal et al., 1997). Many studies have been conducted in flooded bottomland forests of the mesic Southeastern U.S. (Conner et al., 1997; Mitsch et al., 1991; Megonigal et al., 1997; Burke et al., 1999; Anderson and Mitsch, 2008). Studies in arid and semi-arid climates tend to focus on drought and/or water regulation impacts to riparian communities (e.g., Scott et al., 1999; Shafroth et al., 2002; Northcott et al., 2007), and dendroecological studies generally consider growth of individual trees (e.g., Stromberg and Patten, 1990). However, whole-stand productivity studies in the wetland forests of drought-prone areas are less common. In Southern Europe, where few forested wetlands remain because of intensive land use and extensive hydrologic alteration, wetland tree sensitivity to flooding is not well-understood. A large portion (86%) of wetland forests in Portugal and western Spain are dominated by *Salix atrocinerea* Brot. and/or *Alnus glutinosa* (L.) Gaertn. (Rodríguez-González et al., 2004, 2008). Though growth and yield have been studied extensively for some North American species of both *Alnus* and *Salix* (Johnson, 2000; Schaff et al., 2003; Balian and Naiman, 2005; Hultine et al., 2007; Johnston et al., 2007), studies of European wetland trees are relatively rare (but see Iremonger and Kelly, 1988; Johansson, 1999) and are non-existent for Southern Europe. The *Salix* and *Alnus* stands of Portugal and Western Spain show distinct patterns of stand structure and relative dominance by each species, but the drivers of these patterns are largely unknown. Given the importance of the remaining wetlands in semi-arid regions -for wildlife habitat, ecosystem productivity, and the regulation of biogeochemical cycles, studying the controls on tree composition and structure is critical to developing a comprehensive understanding of these ecosystems' dynamics.

Our study examines the influences of hydrology and soil properties on tree species dominance, growth, and aboveground stand biomass across the natural range of wetland hydrology within the Ibero-Atlantic region of Portugal and Western Spain. This study represents the first attempt to quantify net aboveground wood production in Southern European wetland forests. Specifically, we compared tree density, shrubbiness (single versus multi-stemmed architecture), growth rate, and stand health (proportion of dead standing aboveground biomass) along the natural hydrological gradient. We hypothesized that high soil saturation and correlated edaphic factors exert differential responses based on species' flood-tolerance, resulting in shifts in woodland stand composition, structure, and aboveground biomass. Furthermore, we assessed whether the correlated trends in basal area, density, shrubbiness, and growth rate along the hydrological gradient were consistent with a stress response (i.e., lower aboveground growth and productivity with higher soil saturation), or alternatively, a positive growth response to increased resource subsidies (Odum et al., 1979).

2. Materials and methods

2.1. Tree sampling

The field sampling was carried out during the summer of 2003 and 2004 in 21 freshwater wetland forest stands along the Atlantic coastal belt of the Iberian Peninsula, from north-western to southern Portugal and western Andalusia in Spain (between 6° and 9°W longitude and 42° to 38°N latitude; Fig. 1). Sampling years were representative of long-term hydrologic conditions across the Ibero-Atlantic coastal belt, with annual precipitation during the sampling years generally falling into the middle two quartiles of annual precipitation totals since 1960 (Appendix A). Criteria for stand selection included dense tree cover (>70%), and sufficient permanence of soil water for the development of wetland species. Forests were mainly lentic systems located in depressional areas, on soils subject to frequent flooding and saturation, or with markedly impeded drainage with different levels of connectivity with the fluvial network. Thus their geomorphic position

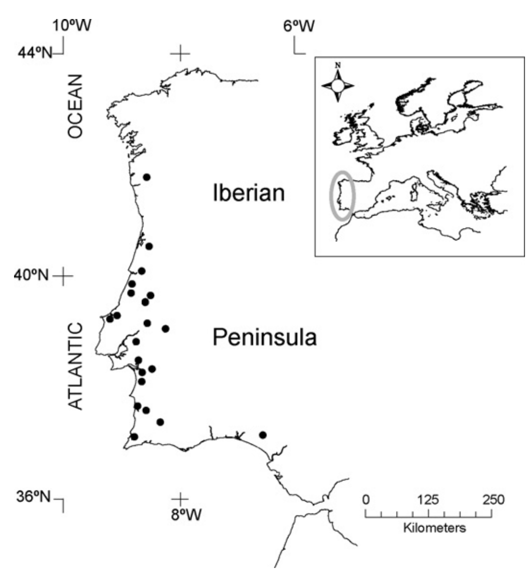

Fig. 1. Location of the sampled wetland forests along the Atlantic coastal belt of the Iberian Peninsula in Southern Europe.