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Multilevel responses of emergent vegetation to environmental factors in a semiarid floodplain

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Abstract

Wetland emergent vegetation of Tablas de Daimiel National Park (Central Spain), mainly composed by *Cladium mariscus*, *Phragmites australis* and *Typha domingensis*, was studied to test if population responses to environmental factors were invariant to scaling-up conditions from the single plant to the entire wetland. While the significance of the main controlling, abiotic factors (wetland location, sedimentary and water nitrogen and phosphorus, water level, duration of flooding) was that of earlier studies, the importance of them changed along with the level of plant organization. Our study showed that multiple effects occurred in the responses of helophyte populations to abiotic factors, and that these responses appeared to depend upon the level of observation involved, showing positive (*Typha* biomass and sedimentary phosphorus), negative (*Cladium* biomass and sedimentary phosphorus, *Cladium* large patch growth and total phosphorus), delayed (landscape cover of *Phragmites* and *Cladium* and water level of the previous year), saturation (*Cladium* biomass and water level), threshold (small patch growth rate of *Cladium* and water level of the previous month) and non-linear (landscape cover of *Phragmites* and *Cladium* and total phosphorus in water) effects.

Keywords: *Cladium*; *Phragmites*; *Typha*; Water level; Flooding; Duration of flooding; Total phosphorus; Single plant; Patch; Landscape

1. Introduction

Ecological processes and environmental controls are thought to shift with the scale of observation and hence the domains of scale usually signify different underlying processes (Wu and Loucks, 1995). On the other hand, it has been assumed that controlling factors of plant performance are the same irrespective of the level of organization involved (Keddy, 2000), and some recent modeling exercises have reported invariance of population responses to scaling (Wootton, 2001). Thus, controlling factors at one level can be extrapolated to other levels of organization. The main controlling factors of emergent wetland vegetation dynamics appear to be water quantity and quality and sedimentary nutrients (Keddy, 2000). These have mostly been related to plant features in a straightforward, linear manner (Urban et al., 1993; Kohl et al., 1998; Miao et al., 2000). Other response forms to environmental factors, however, are also common in biological populations (Berryman, 1999; Hanski, 1999; Schulze et al., 2005), and hence may be present in emergent vegetation, but they have not been reported as yet.

Studies on controlling factors of emergent vegetation in wetlands have been performed at different levels of organization of plant species, from the single plant (Dykyjová and Kvet, 1978) to the landscape (Shay et al., 1999), covering short-term periods (Davis, 1991; Weisner and Miao, 2004) and long-term periods (Alvarez et al., 2005; Liu and Cameron, 2001) of observation. Patch studies in wetland vegetation, however, are rarely tackled (Bodensteiner and Gabriel, 2003, is a remarkable exception), despite the fact that helophytes are good model targets for patch studies. Since changes in flooding regime and nutrient availability affect the expansion of emergent taxa (Cronk and Fennessy, 2001), it is conceivable that these changes impinge on different organizational levels in different ways and with time lags, as it occurs in terrestrial ecosystems (Peters et al., 2006) and subtropical wetlands (Wu et al., 2006). Studies of multiple environmental drivers are now attempting to disentangle the complex behaviour of ecosystem properties, both in aquatic (Findlay et al., 2006) and terrestrial environments (Turner, 2005).

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This study has been carried out in Tablas de Daimiel National Park (Tablas hereafter). The organizational levels chosen are the single plant, the small- and the large patch and the wetland landscape. The size of small patches is considered here as that smaller than 1 ha. Preliminary data (Cirujano et al., 2003) have shown that most vegetation stands in the wetland attained these sizes, larger patches occurring in small numbers. Large patches have been reported to behave differently from small patches in terrestrial vegetation (Wu and Loucks, 1995), whereas the wetland level of organization is the key one for environmental management. In addition, quantitative ecology of emergent plants has been undertaken in cold temperate (Cizková et al., 2000) and tropical wetlands (Davis, 1994), but there are less studies in semiarid climates, although some emergent species, such as *Phragmites*, become increasingly widespread in Mediterranean areas (Cirujano, unpublished data).

Therefore, the goals of this study, carried out in a Mediterranean floodplain, have been: (1) to describe structural features (plant growth, biomass, patch cover- and wetland cover growth) of helophytes at different organizational levels, from the single plant to the wetland population, (2) to search for environmental controlling factors of emergent vegetation at these levels, and (3) to test if helophyte vegetation is invariant to scaling-up conditions in their responses to those environmental factors.

2. Material and methods

2.1. Study site

Tablas de Daimiel National Park (Fig. 1) is a floodplain wetland, located in Central Spain (39°08′N, 3°43′W). The wetland covers 20 km^2, with an average water depth of 0.90 m, and it is situated in a 13,000 km^2 catchment. The wetland is fed by a 5000 km^2 aquifer, but groundwater discharge to the wetland has been discontinued since 1986. The maximum flooded area is 16.75 km^2. Annual precipitation is *ca.* 400 mm, and mean temperatures are 0.5 °C in January and 33.8 °C in July (Álvarez-Cobelas and Verdugo, 1996). Originally, the wetland was the result of the overflowing of two rivers (the northeastern Gigüela river and the eastern Guadiana river) and upwelling waters from the aquifer. Additionally, 14 watermill dams contributed to the change from riverine to lacustrine conditions. Water quantity and quality in Tablas were impaired by man-made actions in the catchment, and hence abiotic factors impinging on helophytes, such as total phosphorus, flooding and water level, were partly the outcome of that anthropogenic forcing. Nowadays, the Gigüela river provides the only surface water inflow and determines all water quality, water levels and sedimentation patterns that occur along a NE–SW gradient (Sánchez-Carrillo and Álvarez-Cobelas, 2001). This gradient is 10.5 km long, from the main water inlet at the NE extreme to the main water outlet at the SW extreme (see Fig. 1). Roughly, NE sites show shorter water retention time and are shallower than SW sites.

Physiognomically, Tablas is a mixture of water tables, that can be colonized by submerged plants, and helophyte patches. In spite of species richness of emergent vegetation (21 species; Cirujano, 1996), two taxa (*Cladium mariscus* (L.) Pohl, cut-sedge; *Phragmites australis* (Cav.) Trin. ex Steudel, common reed) have dominated (>90% of overall helophyte cover) the wetland for many years. In addition to plant responses to anthropogenic changes affecting abiotic factors, such as decreasing water availability and impairing water quality,

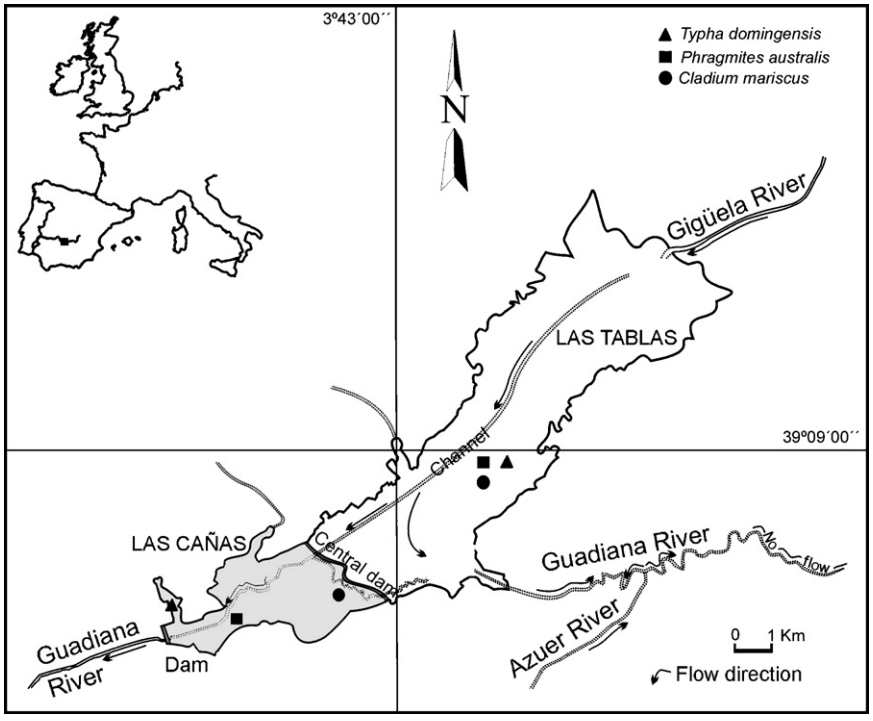

Fig. 1. Study site: Tablas de Daimiel National Park, Central Spain. Sites of shoot elongation measurements: circles, *Cladium*; squares, *Phragmites*; triangles, *Typha*.