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.

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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 (Dykyjova 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).
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 (Cizkova´ 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 km², with an average water depth of 0.90 m, and it is situated in a 13,000 km² catchment. The wetland is fed by a 5000 km² aquifer, but groundwater discharge to the wetland has been discontinued since 1986. The maximum flooded area is 16.75 km². 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,
ploughing and man-made fire have decreased cut-sedge cover in the 1970s and 1980s (Cirujano et al., 2003). Cattail (Typha domingensis (Pers.) Steudel) cover has always been negligible, except in 2001 when it has shown a remarkable cover increase.

Further information on the wetland can be found in Alvarez-Cobelas and Cirujano (1996) and Alvarez-Cobelas et al. (2001).

2.2. The abiotic environment

Monthly overall flooded area was provided by the Tablas staff in 2000–2002. In each sampling station, water level was measured on each sampling date in these years. Annual duration of flooding was calculated for each sampling station following the Kadlec and Knight (1996) method. Total nitrogen and total phosphorus concentrations in the water column were also measured on each sampling date after Bachmann and Canfield (1996) and APHA (1992) procedures, respectively. Sediment samples for elementary nitrogen and phosphorus analysis were taken with a grab in the same places where helophyte biomass was measured in 2001. Sedimentary nitrogen was measured with a Perkin-Elmer 2400 II elemental analyzer, whereas sedimentary phosphorus was quantified after the Instrumental method of the Soil Science Society of America (1971).

On a long-term basis, there were very few data for these variables that could be used to relate with vegetation maps drawn from aerial photographs. Therefore, they had to be estimated from indirect sources. Flooding was measured monthly by the Tablas staff since 1983, but flooding data also had to be reconstructed for earlier years. Monthly discharge data of the streams entering the wetland since 1945 enabled us to know overall flooding, taking the maximum storage of the wetland (15 hm$^3$) and an average water balance (Sánchez-Carrillo, 2001) into account. Nutrient data for the incoming streams have been recorded since 1973. Water pollution increased from the late 1970s (Alvarez-Cobelas et al., 2001) and so we assumed that earlier data (until 1945) could be similar to the lowest ones recorded in that decade. Total phosphorus was used as a surrogate of water quality because it is most often used as eutrophication index in freshwaters (Vollenweider, 1968). Few total phosphorus data for the wetland were available until 1992, and these have been reconstructed by multiple regression, using annual discharge input ($D$, hm$^3$ year$^{-1}$), yearly averaged total phosphorus in discharge water ($TP_{input}$, mg L$^{-1}$) and annual-averaged wetland flooding ($F$, ha year$^{-1}$) as independent variables. Yearly data used for this regression were those of 1975, 1989, 1990 and 1992–2001. A stepwise regression demonstrated that these independent variables were all statistically significant ($P < 0.05$) to explain annual total phosphorus ($TP_{wetland}$) variability, yielding the following equation:

\[
TP_{wetland} = 0.243TP_{input} + 0.001F - 0.024D - 0.348,
\]

$\lambda^2 = 0.70$, $n = 13$

2.3. The single plant level: growth rate and their controlling factors

Since we wanted to compare the ecological performance of three helophyte species and the highly fluctuating abiotic factors might enhance much the growth of one species over the growth of others, we decided to select those areas where we assumed that abiotic factors were less detrimental for the growth of each species. Our criterion was to select sites where plant growth was as optimal as possible. Since two environmentally different areas occurred in this wetland concerning flooding and water level, the shallower NE and the deeper SW (see above), two sites were selected for each species, one at the NE half and another at the SW half of the wetland. For individual growth, 10 plants of each species were tagged in each stand and their main leaf (Cladium and Typha) or stem (Phragmites) growth were recorded monthly. Growth rates of these elongating shoots were calculated assuming an exponential growth mode for all plant species, applying the commonly used RGR equation (e.g. Hutchings, 1997).

Despite the fact that the RGR is usually employed with biomass data, we have decided to use shoot length on account of its easier measurement. A strong relationship was present between the length of the main stem or leaf and the plant aboveground biomass of the single plant has been found in preliminary tests with 50 plants of each species ($r^2 = 0.81, 0.88$ and $0.78$ for cut-sedge, reed and cattail, respectively, $P < 0.00001$). This biometric approach has been followed often with emergent plants (e.g. Ostendorp et al., 2001; Romero et al., 1999; Vretare et al., 2001). Studies in previous years suggested that exponential growth was the best fitting model. Alvarez-Cobelas et al. (unpublished) observed only little spatial competition.

Water level and sedimentary and water-column nitrogen and phosphorus were related with instantaneous growth rates of each species, whereas duration of flooding was with yearly averaged growth rates of each species, using non-parametric Spearman correlation (Conover, 1999) and type-II regression. The statistical package STATISTICA6.0 (Statsoft Inc., Tulsa, OK, USA) was used for most tests; type-II regression was undertaken with the free software created by Pierre Legendre (www.bio.umontreal.ca/casgrain/fr/lab).  

2.4. The small patch level: biomass, cover growth and their controlling factors

Biomass and plant cover were recorded in patches smaller than 1 ha. Our preliminary tests indicated that biomass and plant cover were statistically uncorrelated ($P > 0.05$). Sub-optimal growth (see below) and self-thinning, when plant stands were overcrowded, could be responsible for this lack of correlation. Since plant cover was the variable that could be measured more easily at the levels above the single plant level, we undertook cover measurements at the small patch-, the large patch- and the landscape level.

Late summer, maximum aboveground biomass was cut in $1 \text{m}^2$ plots distributed throughout the wetland in 2000, 2001 and
most patches of Typha developed, 10 small patches of Cladium were measured only in 2002; using a retrodigger, square plots of 1 m² were excavated down to the deeper layer of roots (usually 1.0–1.5 m deep). All roots, rhizomes and stems were gathered, sorted, sent to the laboratory, dried and weighted separately for each species. Drawings of underground organs reported elsewhere (Conway, 1936; Fiala, 1978; Rodewald-Rudescu, 1974) enabled us to separate rhizomes from roots of each species prior to belowground biomass quantification.

Cladium and Typha small patches were usually well defined, grew in all horizontal directions and could be studied easily, but most patches of Cladium were small and numerous, whereas those of Typha were large and scarce in this wetland (Cirujano et al., 2003). Therefore, in sites where stands were well developed, 10 small patches of Cladium and two large patches of Typha were tagged and its perimeter growth was followed monthly for more than a year. Reed growth, however, took place as advancing fronts from marginal- to water table areas. The reed study was then carried out as follows: in the border place as advancing fronts from marginal- to water table areas. This was undertaken on 2001 data when enough data were available for meaningful statistical tests. We also compared the slopes of biological traits (i.e., biomass, patch cover rate and shoot elongation rate) versus cover slopes using a MANCOVA approach to determine whether differences in cover-scaled biological traits might arise from different wetland site locations; a Pillai's test was also carried out to get significance levels for MANCOVA because it is more advisable when sample sizes are small as it was the case. All data were \( \log_{10} \) transformed prior to ANCOVA and MANCOVA analyses to meet normality assumptions.

2.5. The large patch level: cover growth and its controlling factors

Only few helophyte patches observed were very large (Cirujano et al., 2003): 20 were larger than 5 ha. Georeferenced maps were built from aerial photographs taken in 1945, 1956, 1977, 1984, 1993, 1997 and 2001, and the large patches were located in the wetland, being 8 for reed and 10 for cut-sedge. Since cattail patches were very small until 2001, when a substantial expansion was observed, these were neglected in this analysis. ArcView 3.2 (ESRI, 1996) enabled us to estimate cover of each single large patch, calculating their expansion (ha year\(^{-1}\)) in the same way of small patches. This expansion rate was again related to yearly averaged water level, duration of flooding and total phosphorus. Despite the fact that sedimentary phosphorus could be more meaningfully related to helophyte growth than water-column phosphorus (Cronk and Fennessy, 2001), the lack of long-term data for that factor prompted us to use water-column data, which was significantly related to sedimentary data (see below). Since patch growth in the long-term might arise from annual changes in water level and phosphorus, we calculated long-term averages of both variables for each patch. We then performed Spearman correlations between these abiotic variables and growth rate of patch cover for each species. We also tested for annual differences between NE and SW sites in patch cover rate in relation to cover for cut-sedge and reed, also using an ANCOVA approach.

2.6. The landscape: abiotic factors and long-term cover changes

Long-term dynamics of helophyte cover was ascertained from aerial photographs (see above), which enabled us to draw vegetation maps for each year. An aerial georeferenced survey, carried out in 2001, was the basis for this task. Detailed field work by Cirujano from 1993 was useful to discern between cut-sedge and reed patches in aerial photographs. The difficult task of discriminating reed and cattail cover in photographs (Maheu-Giroux and de Blois, 2005) was unimportant for most years because cattail only significantly grew in 2001, when we could not discriminate it. We estimated 2001 cattail cover as 18% out of overall reed cover, spreading over 6% of the whole wetland area. Cover growth (or decay, ha year\(^{-1}\)) was assumed to occur linearly, and hence it was calculated in the same way as patch growth.

Spearman correlations and type-II regressions among yearly averaged abiotic variables (total phosphorus concentration in...
3. Results

3.1. Abiotic factors

Flooding took place seasonally in 2000–2002 with peaks in springtime, but in-site water level and duration of flooding were very variable. NE sites were more fluctuating than SW sites on the average, the former attaining 0–100 cm and 0–100% for water level and duration of flooding, respectively. SW sites experienced 60–140 cm and 40–100% for these variables. In Cladium and Typha sites water level ranged between 10–40 and 0–140 cm, respectively, whereas in Phragmites sites these attained 0–60 cm. Total nitrogen in the water-column ranged 0.1–0.7 mg P kg\(^{-1}\), whereas total phosphorus ranged 0.02–0.18 mg P L\(^{-1}\). Sedimentary nitrogen was in the range of 2–8 mg N kg\(^{-1}\) (DW), whereas sedimentary phosphorus attained 0.1–0.7 mg P kg\(^{-1}\) (DW). Sedimentary nutrients appeared to be related with water-column total phosphorus \((r^2 = 0.71, P < 0.05)\), but sedimentary nitrogen was not related with water-column total nitrogen \((P > 0.05)\). On a long-term basis, flooding fluctuated greatly, with strong seasonality until 1975 and then much higher variabilities until present, often experiencing no flooding at all for years in most places of the wetland. Nutrient fluxes into the wetland were also very variable \((0–388 \text{ g N m}^{-2} \text{ year}^{-1})\) and \(0–80 \text{ g P m}^{-2} \text{ year}^{-1}\). Annual averages of phosphorus concentrations ranged from 0.08 to 0.75 mg P L\(^{-1}\) since 1974. More abiotic data can be found in Alvarez-Cobelas et al. (2001) and Ribeiro (2005).

3.2. The plant level: growth rate and its controlling factors

Growth rates of cut-sedge were higher at NE sites \((P < 0.05, U\text{-test} ; \text{Fig. 2, left panel})\), but overall, growth rates were low ranging from 0.001 to 0.022 day\(^{-1}\). Reed growth was similar in the 2 years of study at both sites \((P > 0.05, U\text{-test})\). The overall range of growth rates was 0.001–0.045 day\(^{-1}\) (Fig. 2, middle panel). In 2001 cattail growth rates were markedly higher at SW sites than at NE sites \((P > 0.05, U\text{-test}; \text{Fig. 2, right panel})\), its range being 0–0.040 day\(^{-1}\).

Sedimentary nutrients displayed significant relationships with plant growth rates. Cladium rate was positively related with nitrogen \((r^2 = 0.53, P < 0.05)\), Phragmites rate was negatively related with the N:P ratio \((r^2 = 0.76, P < 0.05)\), with the critical value around 4, whereas Typha was negatively related with sedimentary nitrogen and phosphorus \((r^2 = 0.72\) for both, \(P < 0.05)\). The relationships between water-column nutrients and helophyte growth rates were weak, only phosphorus being positively related with growth rates \((r^2 = 0.31, 0.23\) and 0.20 for cut-sedge, reed and cattail, respectively, \(P < 0.05)\). Water level was weakly but positively related with growth rates of Cladium and Typha \((r^2 = 0.36\) and 0.19, respectively, \(P < 0.05)\).

3.3. The small patch level: biomass, cover growth and their controlling factors

Cut-sedge biomass attained the highest values at NE sites, where its populations always grew better. In 2001 and 2002 more biomass was recorded than in 2000 \((2.16 \pm 0.68, 4.78 \pm 1.67, 4.69 \pm 2.19 \text{ kg DW m}^{-2} \text{ in 2000, 2001 and 2002, respectively})\). Belowground biomass, only measured in 2002, was lower than aboveground biomass \((2.26 \pm 2.26 \text{ kg DW m}^{-2} \text{ versus} 4.69 \pm 2.19 \text{ kg DW m}^{-2} \text{ for belowground- and aboveground biomass})\), thus showing a 1:2 ratio. Average water level appeared to control Cladium biomass up to 20–40 cm, above which water level increase did not enhance biomass increase \((\text{Fig. 3, left panel})\). We also observed a negative statistically significant relationship between sedimentary phosphorus and cut-sedge biomass \((\text{Fig. 3, middle panel})\) and a 1-year delayed, unimodal response of biomass to average water level \((\text{Fig. 3, right panel})\), suggesting biomass inhibition at deeper water depths.

Reed biomass also appeared to be higher at the NE entrance (the shallower sites of the wetland and where river discharge took place), and it was higher in 2000 than in next years, attaining 4.02 \(\pm 1.76, 2.74 \pm 1.18\) and 3.26 \(\pm 1.50 \text{ kg DW m}^{-2}\).
in 2000, 2001 and 2002, respectively. Belowground biomass was higher than aboveground biomass in 2002 (4.03 ± 1.00 kg DW m⁻² versus 3.26 ± 1.50 kg DW m⁻²; \( P < 0.05, t \)-test). Reed biomass could be controlled by water level variability (positive relationship; Fig. 4, left panel) and by averaged water level of the preceding year as well (negative relationship; Fig. 4, right panel).

*Typha* biomass was similar over time showing low spatial variability in the wetland (2.63 ± 1.48, 2.14 ± 0.84 and 4.03 ± 2.41 kg DW m⁻² in 2000, 2001 and 2002, respectively). Belowground biomass was similar to aboveground biomass in 2002 (3.97 ± 1.82 kg DW m⁻² versus 4.03 ± 2.41 kg DW m⁻²; \( P > 0.05, t \)-test). Cattail biomass appeared to be related with sedimentary phosphorus, also showing a positive and non-linear relationship with average duration of flooding in the preceding year (Fig. 5).

Cut-sedge small patches grew steadily, albeit with a winter standstill (Fig. 6, upper left panel), ranging from 0.1 to 2 cm day⁻¹. Its growth rate was related with water level of the previous month (Fig. 6, lower right panel; \( r^2 = 0.31, P < 0.05 \), but such a relationship was better above the threshold value of 17 cm, values deeper than that being more frequent in 2001.
3.4. The large patch level: cover growth and its controlling factors

Cut-sedge large patches suffered strong shrinkages over time (Fig. 7, left panel), having ranges from −71 to 57 ha year\(^{-1}\), whereas reed patches showed alternate expanses and declines over time, ranging from −29 to 20 ha year\(^{-1}\) (Fig. 7, right panel). Rate variabilities were very high (CVs 100–1500 and 70–222\% for cut-sedge and reed, respectively). Time-averaged water level and duration of flooding were not related with growth rates of large patches of any species (\(P > 0.05\)), but a negative relationship between averaged total phosphorus and growth rates of cut-sedge patches was found\(^{3}\) (\(r^2 = 0.35\), \(P < 0.05\)).

Under constant plant cover, large patch growth rates of *Cladium* did not differ between NE or SW sites for any year tested. The only year when this difference occurred for *Phragmites* was 1977 (Table 3).

### 3.5. The landscape: abiotic factors and long-term cover changes

Long-term cover growth rates ranged from −23 to 25 and from −70 to 90 ha year\(^{-1}\) for cut-sedge and reed, respectively (Fig. 8). Water-column phosphorus concentration was not related with helophyte cover (\(P > 0.05\)), but cut-sedge and reed cover were related with average flooding in the preceding year, albeit in an opposite way: *Cladium* increased and *Phragmites* decreased as flooding increased (Fig. 9, upper panels). No statistically significant relationship was found between helophyte cover and duration of flooding (\(P > 0.05\)). Furthermore, water phosphorus content in a representative site of the wetland could be related with helophyte cover, again negatively, i.e., reed cover increased and cut-sedge cover decreased as phosphorus content rose (Fig. 9, lower panels). Stepwise regressions, however, related cut-sedge cover and water level, on one hand, and reed cover and total phosphorus, on the other. When environmental relationships were attempted with growth rates of cover, no statistically significant relationship was found with average (either delayed or not) flooding or duration of flooding (\(P > 0.05\)); only yearly averages of water-column total phosphorus were negatively related with growth rates of cut-sedge and reed cover (\(F = 7.28\), \(P > 0.05\)).

![Fig. 7. Average growth rates of *Cladium* (left panel) and *Phragmites* (right panel) large patches and their variability.](image-url)

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**Table 1**

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Covariate</th>
<th>Pillai test</th>
<th>Treatment</th>
<th>Pillai test</th>
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</thead>
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<td><em>Cladium</em></td>
<td>Biomass</td>
<td>(F_{1,14} = 0.01)</td>
<td>(F_{1,14} = 10.49^{**})</td>
<td>(F_{1,14} = 0.95)</td>
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<td>Patch expansion rate</td>
<td>(F_{1,14} = 0.16)</td>
<td>(F_{1,14} = 0.32)</td>
<td>(F_{1,14} = 0.14)</td>
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<td></td>
<td>Shoot elongation rate</td>
<td>(F_{1,14} = 0.27)</td>
<td>(F_{1,14} = 7.24^{**})</td>
<td>(F_{1,14} = 0.22)</td>
</tr>
<tr>
<td><em>Phragmites</em></td>
<td>Biomass</td>
<td>(F_{1,9} = 3.70)</td>
<td>(F_{1,9} = 2.25)</td>
<td>(F_{1,9} = 4.06)</td>
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<td></td>
<td>Patch expansion rate</td>
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<td>(F_{1,9} = 0.04)</td>
<td>(F_{1,9} = 0.08)</td>
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<td>Shoot elongation rate</td>
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<td>(F_{1,9} = 0.00)</td>
<td>(F_{1,9} = 0.05)</td>
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<td><em>Typha</em></td>
<td>Biomass</td>
<td>(F_{1,10} = 2.21)</td>
<td>(F_{1,10} = 0.20)</td>
<td>(F_{1,10} = 0.87)</td>
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<td>Patch expansion rate</td>
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<td>(F_{1,10} = 0.56)</td>
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<td>Shoot elongation rate</td>
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<td>(F_{1,10} = 0.02)</td>
<td>(F_{1,10} = 0.56)</td>
</tr>
</tbody>
</table>

Data of the small patch organization level in 2001. All raw data have been log-transformed before analyses. The interaction term (treatment × covariate) is not reported because it is never statistically significant at \(P < 0.05\).

\(^{1}\) \(P < 0.05\).

\(^{**}\) \(P < 0.01\).

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Reed fronts advanced faster in summertime (Fig. 6, upper right panel), ranging from 1 to 30 cm day\(^{-1}\), but stopped in late October, and this rate of advance was positively related with average water level (\(r^2 = 0.80\), \(P < 0.05\)). Cattail patches also depicted the highest growth rates in summertime, ranging 1–30 cm day\(^{-1}\) (Fig. 6, lower left panel), its growth rate being positively related with water level of the previous month (\(r^2 = 0.33\), \(P < 0.05\)).

Biomass and shoot elongation rate differed very significantly between NE or SW wetland sites when *Cladium* plant cover was kept constant, but no *Phragmites* continuous variable changed significantly under constant plant cover (Table 1). Concerning *Typha*, patch growth rate was only higher in SW sites when plant cover was kept constant (Table 1), the other variables not being statistically significant (\(P > 0.05\)).

MANCOVA tests showed that biological traits of *Phragmites* and *Typha* were statistically different along with constant plant cover between wetland sites, but no such difference was found for *Cladium* (Table 2).
related with cover growth rates of Cladium ($r^2 = 0.33$, $P < 0.05$).

4. Discussion

4.1. The single plant level

Only leaf elongation rates of Typha came (Fig. 2, right panel) close to the highest reported rates (Dykyjová and Kvet, 1978). Cladium and Phragmites never reached the highest reported rates (Fig. 2, upper and middle panels; Conway, 1938; Dykyjová and Kvet, 1978; Lorenzen et al., 2001). Furthermore, these species show strong inter-site variability (Fig. 2). Therefore, helophyte growth in our studied wetland at the single plant level was suboptimal, as also judged by linear relationships between growth and environmental controls.

For shoot elongation, controlling factors were found to differ among species. For Cladium it was nitrogen, as in other studies (Urban et al., 1993; Miao and Sklar, 1998). For Phragmites the sedimentary N:P ratio was important, as also reported by Güsewell et al. (2003) for many wetland species, thus providing an explanation for conflicting evidence on abiotic controls of reed growth (Clevering, 1998; Kohl et al., 1998). In Typha, however, RGR was related negatively to water N and P in this study, despite positive relationships in other wetlands (Grace, 1988; Miao et al., 2000).

4.2. The small patch level

The aboveground biomass of three helophytes in Tablas is often higher than that previously reported (for instance, Dykyjová and Kvet, 1978; Miao and Sklar, 1998; Vymazal, 1995). Cut-sedge and reed densities have been higher than in other wetlands (data not shown; Miao and Sklar, 1998; Rolletschek et al., 1999), which may explain the apparent discrepancy between suboptimal growth of single plants (see above) and higher biomasses than in anywhere else. The aboveground:belowground biomass ratio of these helophytes, however, has been lower in Tablas than in most wetlands (Dykyjová and Kvet, 1978; Fiála, 1978; Lorenzen et al., 2001).

Controlling factors of small patch biomass also differ for the three species involved (Figs. 3–5). The significance of all relationships between abiotic factors and biomass revealed in this study has already been reported (Björk, 1967; Hürlimann, 1951; Lorenzen et al., 2001; Miao et al., 2000). What is new here is the non-linear relationships found (delays and inhibition processes), and all three species have shown some of them.
No previous studies exist on the \textit{C. mariscus} patch growth. For \textit{C. jamaicense}, Brewer (1996) compares some phenotypic features of patches, concluding that patches growing without other interspersed plants are larger and have more and longer rhizomatous structures. The low aboveground:belowground biomass ratio found for \textit{C. mariscus} in our study will support Brewer’s findings. In Tablas patch size dependence on flooding occurs when water depth is deeper than 17 cm (Fig. 6, lower right panel). That threshold effect suggests that patch growth responds to water level in a different manner than either \textit{Cladium} single plants or biomass. Bodensteiner and Gabriel (2003) suggest that patches of reed are related with deeper water depth; we have also found that reed patch expansion in Tablas was related with water level. No data are available in the literature on cattail small patch dynamics; our study suggests that it is related with the water level of the previous month.

4.3. The large patch level

Rates of growth were far more variable for \textit{Cladium} (Fig. 7, left panel) than for \textit{Phragmites} (Fig. 7, right panel). Expansion and shrinkage of large patches has been shown independently of water level for both species studied, which is contrary to the effects demonstrated by Bodensteiner and Gabriel (2003) in large reed patches. Averaged water-column phosphorus, however, was negatively related with growth of cut-sedge patches, but no such relationship is found for reed patches. This independency of patch growth from water level is remarkable because it points to endogenous factors (such as seed recruitment, growth by stolons, belowground competition among rhizomes of different species, etc.) to explain the response of large vegetation stands, which are probably impaired by eutrophication in the case of \textit{Cladium} (Davis, 1994).

4.4. The landscape level

There are increasing numbers of long-term studies in wetlands at the landscape level (Leendertse et al., 1997; Visser et al., 1999; Alvarez et al., 2005). Our 1945–2001 study shows a trend of reed cover increase and cut-sedge cover decrease over time (Fig. 8). In most studies water level increase and water pollution are the causes for the observed changes. In Tablas water pollution is certainly the most important cause for reed cover increase (Fig. 9, lower panels), but water level is the main factor responsible for long-term cover changes of cut-sedge (Fig. 9, upper panels). Notwithstanding this, when cover expansion rates are considered, no average flooding effects are observed, and only a weak water quality effect may be suggested for cut-sedge decline at the landscape level. A recent study (Saltmarsh et al., 2006) reports that the photosynthetic efficiency of reed is higher than that of cut-sedge as water stress increases. This mechanism may be important in natural habitats, but it only partly explain the patterns observed in Tablas because water quality impairment may also affect emergent species in this wetland.

4.5. Helophyte responses to abiotic factors across levels of organization

Multiple effects were apparent in the responses of helophyte populations to environmental factors in Tablas, as found elsewhere (e.g. Breitburg et al., 1998). Table 4 shows the main results observed in this study and suggests a wide array of responses. The significance of abiotic factors controlling plant growth does not appear to depend upon the level of observation involved, contrary to suggestions by hierarchy theory (O’Neill et al., 1986; Wu and Loucks, 1995); shifts in the relative importance of these factors (as shown by the coefficients of determination), however, take place when moving from one organizational level to another. Furthermore, helophyte vegetation showed responses to environmental variables that were positive (cattail biomass and sedimentary phosphorus), negative (cut-sedge biomass and sedimentary phosphorus, cut-sedge large patch growth and total phosphorus), delayed (landscape cover and water level of the previous year), saturated (cut-sedge biomass and water level), inhibiting (cut-sedge biomass and water level of the previous year), threshold (small patch growth rate of cut-sedge and water level of the previous month) and non-linear (landscape cover of both species and total phosphorus). Even the same factor may act differently across organizational levels for the same species, such as what occurs with water level and \textit{Cladium}.

In addition, some variables (for example, flooding), which operate at a higher level of plant organization (the metapopulations of helophytes at the landscape level) are partly responsible for the dynamics of other variables, such as water level, which is the outcome of flooding and local topography. These variables operate at lower levels of plant organization. Therefore, in Tablas there are not only multiple effects of abiotic factors on emergent vegetation, but it is likely that local and landscape factors interact to influence helophyte cover and its dynamics in the short- and the long-term. This factor interaction across scales of observation has been reported elsewhere for explaining the distribution of riparian vegetation (Dixon et al., 2002). Such a complex behaviour of driving factors may be the cause for the failure to explain helophyte dynamics at higher organizational levels by their dynamics at lower levels in this study.

Tablas helophytes appear to be an interesting example of metacommunity, displaying mass effects (Leibold et al., 2004). \textit{Cladium}, \textit{Phragmites} and \textit{Typha} local population dynamics (i.e., at the patch scale) are quantitatively affected by dispersal from nearby patches, most of which occurs by underground rhizome growth. It is clear that different patches experience different environmental conditions at a given time, as shown by the high variability of growth rates (Figs. 6 and 7), their local connections being guaranteed by rhizome spread, and – as a result – these patches can have potentially strong influences on the relationships between local conditions and community structure. A conceptual framework where interactions among drivers and processes across scales occur in terrestrial plant metacommunities has recently been proposed by Peters and Havstad (2006) for arid and semiarid systems. These authors
Table 4
Responses of emergent vegetation to environmental factors (variance explained as $r^2$, $P < 0.05$) at different levels of organization in Tablas de Daimiel National Park

<table>
<thead>
<tr>
<th>Environmental factor</th>
<th>Shoot elongation rate (day$^{-1}$)</th>
<th>Standing stock (g DW m$^{-2}$)</th>
<th>Small patch cover increase (cm day$^{-1}$)</th>
<th>Large patch cover increase (ha year$^{-1}$)</th>
<th>Wetland cover (ha)</th>
<th>Wetland cover increase (ha year$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Position in wetland (NE vs. SW)</td>
<td>Cladium: NE &gt; SW; Phragmites: NE = SW; Typha: NE &lt; SW</td>
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<tr>
<td>Water level in the preceding month (cm)</td>
<td></td>
<td></td>
<td></td>
<td>Cladium: TR 0.31, +; Phragmites: 0.80, +; Typha: 0.33, +</td>
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<tr>
<td>Yearly averaged water level (cm)</td>
<td>Cladium: 0.36, +; Typha: 0.19, +</td>
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<tr>
<td>Annual water level variability (cm)</td>
<td></td>
<td></td>
<td></td>
<td>Cladium: SR$, +; Phragmites: 0.48, +; Typha: 0.48, +;</td>
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<tr>
<td>Yearly averaged water level in the preceding year (cm)</td>
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<tr>
<td>Average flooding in the preceding year (ha)</td>
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<td></td>
<td></td>
<td>Cladium: UR$, +; Phragmites: 0.69, –; Typha: 0.66, +</td>
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<td>Flooding duration in the preceding year (% year)</td>
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<tr>
<td>Total P in water (mg P L$^{-1}$)</td>
<td>Cladium: 0.31, +; Phragmites: 0.23, +; Typha: 0.20, +</td>
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<tr>
<td>Sedimentary N (mg N kg$^{-1}$ DW)</td>
<td>Cladium: 0.53, +; Typha: 0.72, –</td>
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<tr>
<td>Sedimentary P (mg P kg$^{-1}$ DW)</td>
<td>Cladium: 0.72, –; Typha: 0.73, +</td>
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<td>N:P sedimentary ratio</td>
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</tbody>
</table>

The sign of the statistically significant interaction is also shown. A non-parametric $U$-test was also undertaken to discriminate the response of shoot elongation between the main environmental sites in the wetland: NL: non-linear response; SR: saturation response; TR: threshold response; UR: unimodal response, including inhibition.

$a$ No determination coefficient could be calculated.
have identified levels of organization much in the same way as we do, and those levels often experience non-linear dynamics across scales. Such a framework may be equally useful to understand the responses of helophytes to environmental factors.

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