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Effect of Prolonged Flooding on the Invader *Spartina densiflora* Brong.

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INTRODUCTION

Spartina densiflora Brong. (Poaceae) is a species native to South America that is aggressively invading estuarine environments in SW Europe, NW Africa and SW North America. This invader shows a strong adaptability to different environmental conditions, and its populations are found from low to high topographic elevations (Bortolus 2006). *S. densiflora* has become the most important invasive plant in many estuaries of SW Iberian Peninsula (Gulf of Cádiz), altering the composition of plant communities and interfering in restoration projects. Research needs to be conducted on management methods that will control or eradicate this species, as has been suggested previously for other species of spartina (Hedge et al. 2003). Hellings and Gallager (1992) proposed managed flooding to control the expansion of *Phragmites australis* in tidal wetlands. Controlled flooding might be used to reduce the faster ramet turnover that *S. densiflora* shows in exposed low and middle marsh areas (Bortolus 2006), and to provide the open habitat necessary for germination and growth of other native species.

The aim of this study was to investigate the effects of continuous flooding, on the growth and photosynthetic apparatus (PSII photochemistry) of *S. densiflora* in order to assess the feasibility of using controlled flooding to eliminate or reduce the competitive nature of this invasive cordgrass.

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MATERIALS AND METHODS

Plant Material and Stress Treatments

In December 2005, clumps of *Spartina densiflora* Brong. were obtained from Guadiana marshes (37°11'N, 7°19'W; SW Spain) and planted in individual plastic pots of 25 cm of length and 20 cm of diameter, filled with local sediment. Pots were kept outdoors under natural environmental conditions with minimum and maximum mean temperatures of 11 ± 1 and 17 ± 2°C, respectively; and 40-60% relative humidity. Five replicates were allocated to each of two treatments: (1) no flooding, where the pots were maintained with water at field capacity so that the aerial portion of plants was not immersed and (2) continuous flooding, where the water level was maintained at plant height. In both cases, water from Ria Formosa coastal lagoon (37°1'N, 7°49'W; Portugal) was used, and the water in the flooded treatments was oxygenated using a diffuser (by bubbling air into the treatments via a compressor of 2 atm of pressure to avoid anoxia).

Growth Parameters

Above- and below-ground biomass (dry wt.) were determined after drying at 80°C for 48 h. The percentage of live and dead tillers and of new tillers were recorded at the end of the experiment, after two months.

Measurement of Chlorophyll Fluorescence

Chlorophyll fluorescence was measured using a portable modulated fluorometer (FMS-2, Hansatech Instruments Ltd., England) after 1, 2, 3, 4, 5, 6, 7 and 56 days of treatment. Measurements were made on 10 tillers per treatment. Light and dark-adapted fluorescence parameters were measured at dawn (stable 50 µmol m^{-2} s^{-1} ambient light) and at mid-day (1600 µmol m^{-2} s^{-1}) to investigate whether flooding affected the sensitivity of plants to photoinhibition (Qiu et al. 2003). Plants were removed from the water to take these readings.

Plants were dark-adapted for 30 minutes, using opaque covers (leaf-clips) designed for this purpose. The minimal fluorescence level in the dark-adapted state (F_0) was measured using a modulated pulse (<0.05 µmol m^{-2} s^{-1} for 1.8 µs) too small to induce significant physiological changes in the plant (Schreiber et al. 1986). An average reading over a 1.6 sec was recorded. Maximal fluorescence in this state (F_m) was measured after applying a saturating actinic light pulse of 15000 µmol m^{-2} s^{-1} for 0.7 s (Bolhàr-Nordenkampf and Öquist 1993). The value of F_m was recorded as the highest average of two consecutive points. Values of the variable fluorescence ($F_v = F_m - F_0$) and maximum quantum efficiency of PSII photochemistry (F_v/F_m) were calculated from F_0 and F_m. This ratio of variable to maximal fluorescence correlates with the number of functional PSII reaction centers and dark-adapted values of F_v/F_m can be used to quantify photoinhibition (Maxwell and Johnson 2000).

The same leaf section of each plant was used to measure light-adapted parameters. Steady state fluorescence yield (F_s) was recorded after adapting plants to ambient light conditions for 30 minutes. A saturating actinic light pulse of 15000 µmol m^{-2} s^{-1} for 0.7 s was then used to produce the maximum fluorescence yield (F_m') by temporarily inhibiting PSII photochemistry.

Using fluorescence parameters determined in both light- and dark-adapted states, the following were calculated: quantum efficiency of PSII ($\Phi_{PSII} = (F_m' - F_s)/F_m'$) (Genty et al. 1989); photochemical quenching ($qP = (F_m' - F_s)/(F_m' - F_0')$, where F_0' corresponds to open reaction center traps in the light-acclimated state), and non-photochemical quenching ($NPQ = (F_m - F_m')/F_m'$; Schreiber et al. 1986).

Statistical Analysis

Statistical analysis was carried out using Statistica v. 6.0 (Statsoft Inc.). Data were analyzed using one-way analysis of variance (*F*-test). Data were first tested for normality with the Kolmogorov-Smirnov test and for homogeneity of variance with the Brown-Forsythe test. Significant test results ($P \leq 0.05$) were followed by Tukey test for identification of important contrasts.

RESULTS AND DISCUSSION

Photosystem II photochemistry of *Spartina densiflora* demonstrated remarkable short-term tolerance of flooding, since no differences on Fv/Fm (maximum quantum efficiency of PSII photochemistry) and Φ_{PSII} (quantum efficiency of PSII) between 0 and 24 h under continuous flooding conditions during the first week of the study ($P > 0.05$; Figure 1) were found.

After two months of treatment, at both, dawn and midday, Fv/Fm was affected by flooding (ANOVA, $P < 0.01$). Fv/Fm and Φ_{PSII} values were significantly lower ($P < 0.01$ and $P < 0.001$, respectively) under 24 h (Fv/Fm = 0.77, $\Phi_{PSII} = 0.55$) than 0 h of flood (Fv/Fm = 0.82, $\Phi_{PSII} = 0.78$) at dawn (Figure 1). It is well known that a sustained decrease in F_v/F_m indicate the occurrence of photoinhibitory damage, in response to many environmental stresses (Maxwell and Johnson 2000). Photoinhibition is caused by damage to photosynthetic components, and this effect can be of short term and reversible (dynamic photoinhibition) or long term and irreversible (chronic photoinhibition; Werner et al. 2002). The flood-induced reduction of Fv/Fm represents chronic photoinhibition since the decrease at midday was irreversible, i.e. did not recover completely to the optimal values observed in undisturbed plants at dawn (Björkman and Demming 1987). Chronic submersion has been reported to induce photoinhibition in *Pouteria orniocoensis* (Osmond 1994). In our study, photoinhibition is caused by a lower proportion of open reaction centers (lower values of photochemical quenching, qP) resulting from a saturation of photosynthesis by light. This was a long-term and irreversible effect. The flood induced decrease of Φ_{PSII} at dawn was a consequence of both the decrease in qP and the increase in non-photochemical quenching (NPQ), which indicates that the plants dissipated light as heat to protect the photosynthetic reaction centers from light-induced damage (Maxwell and Johnson 2000). Reginfo et al. (2001) also found that NPQ increased with flooding in adult trees of *Eschweilera tenuifolia*.

The growth of *S. densiflora* was affected by flooding after two months of treatment. The living above-ground biomass was higher under 0 h than 24 h of flood (25.3 ± 3.6 g and 7.9 ± 2.2 g, respectively, $P < 0.01$), while there were no differences between treatments for the living below-ground biomass

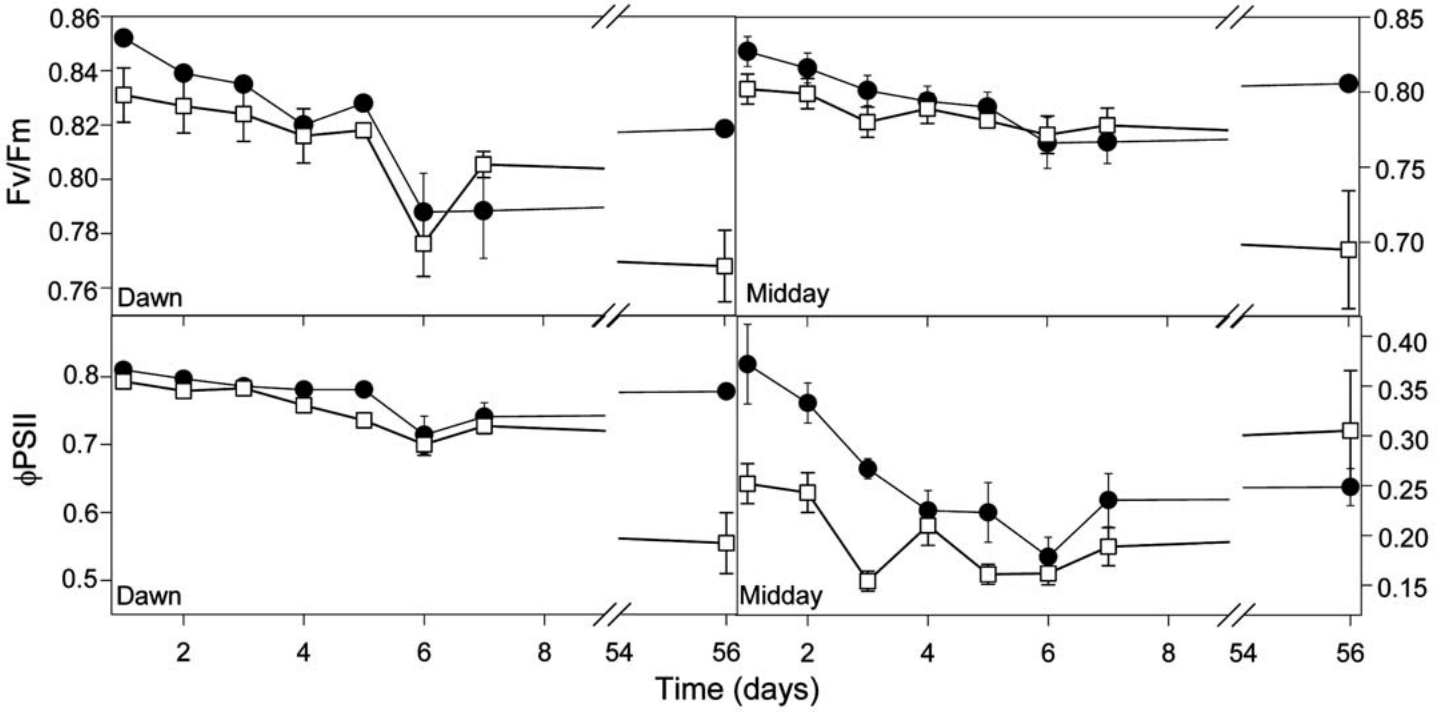

Figure 1. Maximum quantum efficiency of PSII photochemistry (F_v/F_m) and quantum efficiency of PSII (Φ_{PSII}), at midday and dawn, in *Spartina densiflora* in response to 0 (•) and 24 h (□) of flooding for two months. Values represent mean ±SE of ten replicates.

(c. 35 g, P > 0.05). In addition, a lower percentage of dead tillers (30.7 ± 0.9%) was recorded under 0 h, than under 24 h of flood (64.3 ± 2.5%). On the other hand, 22.2 ± 3.7 of new tillers were recorded under no immersion, while only 3.6 ± 1.6 were observed under continuous immersion. Pezeshki (2001) found that long periods of flooding reduced whole plant biomass and promoted plant senescence and mortality. *Paspalum distichum* exhibited marked reductions in the leaf and shoot numbers in flooded plants, compared to the plants in water-saturated soil conditions (Manuel et al. 1979). Similarly, flooding at 7, 14, 21 and 28 days significantly reduced the leaf number of *Fimbristylis miliacea* (Begum et al. 2006).

Our results showed that continuous flooding conditions for a two month period reduced the growth of *Spartina densiflora* and the efficiency of Photosystem II photochemistry. Extended periods of flooding could thus be used as a control technique of *Spartina densiflora*. However, it is necessary to perform long-term experiments and determine optimal flooding periods and which other species, in the low and middle marsh, are flood sensitive before management by flooding can be effective.

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