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PRIMARY RESEARCH PAPER

Responses of two invasive macrophyte species to salt

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Abstract Aquatic ecosystems are particularly sensitive to the introduction of species due to human activities. Increasing salinity in freshwaters due to sea intrusion or to human activities (road salt, industry, etc.) is known to have a negative impact on aquatic organisms and could play a role in the dynamics of invaders. This study compares salt tolerance levels of two introduced aquatic plants *Myriophyllum aquaticum* (Velloso) Verdcourt and *Ludwigia grandiflora* (Michaux) Greuter and Burdet. Plants were collected in spring, summer and autumn 2010, and were exposed to a range of salt concentrations (1, 3 and 6 g/L). Plant growth was determined by measuring seven morphological traits and their photosynthetic activity. Increased salt levels induced a decline in growth and photosynthetic activity in *L. grandiflora*, while photosynthetic activity in *M. aquaticum* remained constant at all salt concentrations. The response of both species to salt varied according to the season. *M. aquaticum* allocated its energy to growth in autumn, whereas the growth of *L. grandiflora* remained constant whatever the season. Our results suggested that *M. aquaticum* stimulated root and leaf production at the end of summer, which conferred resistance to salt stress and allowed this species to become invasive by overcompensating for this stress. Conversely, *L. grandiflora* induced premature senescence and lost its leaves. In the context of worldwide salinisation of freshwaters, *M. aquaticum* could colonize brackish water and other water bodies, whereas *L. grandiflora* invasion could be limited.

Keywords *Ludwigia grandiflora* · *Myriophyllum aquaticum* · Morphological traits · Photosynthetic activity

Introduction

Aquatic ecosystems are particularly sensitive to the introduction of species due to human activities (Ruiz & Carlton, 2003; Brunel, 2009). The characteristic conditions of inland waters, such as internal connectivity, high seasonal and spatial variability, and the

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degree of interaction that coastal ecosystems have with terrestrial ecosystems (shorelines), make them especially vulnerable to the invasion of exotic plants. It is estimated that non-native, invasive species cost the U.S. economy $120 billion annually in lost production, control costs and environmental damage (Pimentel et al., 2005). The invasion of natural communities by introduced plants represents a considerable challenge for conservationists and managers due to significant damage in freshwaters.

Invasive species can radically change the species composition through competition, predation and alteration of habitat. For example, Stiers et al. (2011) showed that taxonomic composition of aquatic invertebrate assemblages in ponds invaded by *Hydrocotyle ranunculoides*, *Ludwigia grandiflora* and *Myriophyllum aquaticum* differed from uninvaded ponds and alteration in the aquatic vegetation and the detritus community. In Florida, exotic aquatic plants, such as *Hydrilla verticillata*, *Eichhornia crassipes* and *Pistia stratiotes*, affect fish and other aquatic animal species, choking waterways, altering nutrient cycles and reducing recreational use of rivers and lakes (Pimentel et al., 2005).

The invasion of an environment by a new species is influenced by three additional factors: the number of propagules entering the new environment, the characteristics of the new species and the susceptibility of the environment to invasion (Lonsdale, 1999). A major objective of research on biological invasion is to understand invasive processes so as to provide prevention and management advice in order to reduce the ecological and socio-economic impacts of biological invasion. In this topic, there have been many attempts to predict outcomes by focusing on the traits of potential invaders and of the invaded community. Traits are used to predict species potential invasiveness into the introduced area (Herron et al., 2007; Moles et al., 2008). They are also used to identify the similarity among invasive species in a similar habitat (Kolar & Lodge, 2001; Lloret et al., 2005).

Fluctuation in resource availability has been identified as a key factor in controlling habitat invasibility (Davis et al., 2000). The causes of the invasion by species, as well as their persistence in the environment, could be explained simultaneously by the tolerance of these species to disturbances (Konstantinov et al., 2002), such as salinisation, and by the strategies which these species adopt in their new environment. Even if salinisation occurs as a result of natural processes (i.e. regulated marshes in estuarine conditions, Ghassemi et al., 1995), the rate of salinisation has increased significantly due to irrigation for agricultural production and practices (Williams, 1987), to demand for water (Estrela et al., 1996) and to use of salt for snow removal on roads (Löfgren, 2001). How salt conditions can limit or enhance the spread of invasive species is a new topic of research in the prediction and management of coastal areas that are prone to invasion. For example, in New Zealand, laboratory tests indicated that salt was the most suitable treatment in terms of elimination of *Ceratophyllum demersum* (Matheson et al., 2007).

Field surveys have shown that normally widespread freshwater macrophytes are no longer found at salinities of around 4 g/L (Brock, 1981). At salinities between 1 and 5 g/L, the plant niche changes and species richness and abundance of aquatic plants decreases (James & Hart, 1993; Brock et al., 2005; James et al., 2009; Smith et al., 2009). Various studies have focused on the impact of increased salinity on the growth of freshwater macrophytes (Haller et al., 1974; Twilley & Barko, 1990; Warwick & Bailey, 1997; Macek & Rejmankova, 2007), on their distribution (Bertness et al., 1992; Sim et al., 2006; Tripathi et al., 2007; Watt et al., 2007; Goodman et al., 2010) and on their physiological responses to this stress (Rout & Shaw, 2001; Abraham, 2010). Canadian waterweed (*Elodea canadensis*), for example, reduces its net photosynthesis production at such low levels of salt as 100 mg chloride per litre (Zimmermann-Timm, 2007). Furthermore, little knowledge exists about the strategy of invasive plants to resist salt and about the effects of increasing salinity on different life stages of species. We focused our research on two invasive aquatic plant species: *M. aquaticum* and *L. grandiflora*, which are considered as high-risk species (Brunel, 2009; Thiébaut & Dutartre, 2009) because of the cost of their management in Europe. According to Dutartre et al. (2007), the cost of treating 4 ha of *L. grandiflora* and *M. aquaticum* in France using mechanical extraction was 38 k€. Furthermore, the occupation of the riverbeds by the very dense monospecific stands of *L. grandiflora* or *M. aquaticum* increases the risks of flooding, caused by water level fluctuations and of water quality deterioration (i.e., oxygen depletion in dense beds, restricted water movement, trapped suspended solids and clogged sediment) and has an impact on aquatic fauna and native plants as a result of competition for resources and space.

In light of this, predicting outcomes by focusing on the traits and strategy of invaders, in response to salt stress according to the season, could lead to a better management of these species in coastal areas. The present study was carried out (1) to compare the changes in the activity of photosynthesis and the growth of two invasive aquatic macrophytes *M. aquaticum* and *L. grandiflora* in response to salt treatments and (2) to analyse the influence of seasonal patterns induced by salt stress.

Materials and methods

Biological materials

The Parrotfeather, *M. aquaticum*, is an aquatic (or semi-terrestrial) perennial plant that overwinters as rhizomes. It grows as a submerged plant with long shoots or as an emergent and floating growth form (Hussner, 2009). It is native to tropical and subtropical South America (Aiken, 1981). In 1890, the first plants reached North America and since then the species has spread to many areas like Europe (Les & Mehrhoff, 1999), New Zealand and Austria (Hussner, 2009). *M. aquaticum* thrives in well-lit ponds, ditches, canals and slow-running streams. Although it grows best when rooted in shallow waters, it has been known to occur as a floating plant in the deeper waters of nutrient-enriched lakes (Muller, 2004). It is most often found in eutrophic water bodies, but is capable of growing as a terrestrial plant when ponds dry out, so it is well adapted to moderate water level fluctuations (Fernandez et al., 1990).

The Water Primrose, *L. grandiflora*, is an amphibious plant. It is native to South America and was introduced voluntarily in 1820 in south-eastern France for its ornamental quality (Dandelot et al., 2008). It has also colonized many countries in Europe (Dutartre et al., 2006; Hussner, 2009). *L. grandiflora* inhabits marshes, swamps, ponds, lakes, ditches, channels and slow-running rivers as well as humid meadows (Dutartre et al., 2006). Its growth is enhanced by increasing nutrient availability but the plant is able to develop in oligotrophic waters (Hussner, 2010). It shows high tolerance to different water levels (Hussner, 2010).

Both species can form dense mats on the surface of the water which may restrict light and could thus alter the distribution of native plants (Gordon, 1998). They show a high-regeneration capacity and the ability to form new shoots from single nodes (with or without leaves) (Hussner, 2009) which enhance plant dispersal and its spread.

Experimental design

These experiments were set up to determine whether the salt tolerance/sensitivity of the two species collected in field differs according to the season. Plant samples were collected in the spring, summer and autumn from a pond called Apigné, in Brittany, France (48°05′31.3″N; 01°44′41.3″W). The experiment was carried out in April, July and October, 2010. For each season, green stems and apices of *M. aquaticum* and *L. grandiflora* with no trace of necrosis were selected and cut into 10 cm lengths. These apices had no roots, buds or lateral stems. After 1 week of acclimation, *M. aquaticum* and *L. grandiflora* were cleaned gently by hand to remove epiphytic algae and put in salt treatment. The plants were distributed randomly in each container. Nine independent replicates were assigned by species and by salt treatment. NaCl (99% of sodium chloride) was added to tap water. The tap water was slightly basic with a moderate nutrient concentration (mean annual value: conductivity = 379 μS cm^{-1}; pH = 8.87; $[NO_3^-] = 22.68$ mg/L; $[NO_2^-] = 0.18$ mg/L; $[NH_4^+] = 0.11$ mg/L; $[PO_4^{3-}] = 0.05$ mg/L). The four salt concentrations tested corresponded to concentrations found in coastal marshes: control (0 g/L), 1, 3 and 6 g/L. Each plant was placed in a separate container (dimensions ($L \times W \times H$): 8 cm × 8 cm × 15 cm) with 0.5 L salt solution and no sediment to avoid salt adsorption on the sediment. All containers were placed randomly in the growth chamber at a photon flux density of 23.6 μmol s^{-1} m^2 with a 12-h light/12-h dark cycle and at a temperature of 13°C. This temperature was the mean temperature observed in spring and autumn, and also avoided algal growth. The water level in each container was maintained by adding tap water, to avoid increasing salt concentrations, to offset losses from evaporation and to avoid plant desiccation. Seven morphological traits and the photosynthetic performance of each plant were measured after 28 days of exposure to saline solution.

Photosynthetic performance

Photosynthetic performance was monitored for 3 h after 3, 7, 15, 21 and 28 days to assess the salt stress responses. Photosynthetic yields of the four combinations of "species concentration" were measured using a pulse amplitude modulated fluorometer (Underwater fluorometer DIVING PAM, Walz GmbH, Effeltrich, Germany). The parameter measured was photosynthetic yield. Instant light response was obtained using the actinic irradiances to the leaf using the fibre optics and leaf Clip Holder 2030-B. Dark adaptation clips were used in all experiments to ensure that the distance between the fibre optic head and the leaf sample was constant. Photosynthetic yield was measured on intact apex leaves after dark acclimation for 30 min before measurements were made.

Plant morphological traits

The ability to characterize the growth of macrophytes is partially based on the relative growth rates (RGR) of the plants. This measurement of RGR was adapted from Hunt (1990): $\mathrm{RGR} = (\ln L2 - \ln L1)/(T2 - T1)$, where $L1$ and $L2$ refer to total length, at times 1 and 2 (Barrat-Segretain & Elger, 2004). Morphological measurements were the number of lateral shoots, the number and mean length of roots. The length and width of one leaf taken at 3 cm from each plant apex were measured using Scion Image software. The number of leaves on the stem was measured for *L. grandiflora*.

Statistical analyses

Statistical analyses were carried out using statistical R™ 2.13.0 software. A two-way ANOVA was used to test for significance ($P < 0.05$) between salinity (df = 3), between season (df = 2) and the interaction of the two factors (df = 6). ANOVA assumptions regarding normality were not met for all traits (using the Shapiro–Wilk W test; Zar, 1984). Therefore, transformations were used to meet ANOVA assumptions regarding homoscedasticity and normality and applying Tukey's HSD tests. However, untransformed means and standard errors are presented for ease of interpretation (Newman et al., 1996; Blumenthal et al., 2003). The number of lateral shoots, the number and the mean length of roots and the width of leaves were log-transformed, and data on the total number of leaves were square root transformed prior to analyses to achieve a normal distribution of residuals.

Results

Interactions between salinity and season

Significant interactions between salt treatment and season were observed (Table 1). The mean of RGR ($F = 3.92$; df = 6; $P = 0.0016$, Fig. 1a) of *M. aquaticum* was higher in autumn at all salt concentrations than in spring at 3 and 6 g/L of salt, whereas the number of lateral shoots ($F = 3.16$; df = 6; $P = 0.0073$) was higher in spring at 1 g/L than in summer at all concentrations and in autumn at control, 1 and 6 g/L (Fig. 1c). The number of roots ($F = 2.73$; df = 6; $P = 0.0177$) of *M. aquaticum* increased from spring to autumn, but decreased with increasing salinity (Fig. 1d). Leaf width ($F = 2.69$; df = 6; $P = 0.0192$) of *M. aquaticum* was higher in spring at all concentrations than in summer and autumn (Fig. 1g). Similarly, the number of roots of *L. grandiflora* ($F = 2.84$; df = 6; $P = 0.0138$) decreased with the salinity but was higher in autumn in comparison to spring and summer (Fig. 2d).

Salt treatment

At the 6 g/L salt concentration, photosynthetic activity of *L. grandiflora* was lower than at 1 g/L ($F = 4.77$; df = 3; $P = 0.0067$, Fig. 2b), while photosynthetic activity of *M. aquaticum* remained constant (Fig. 1b). At the 6 g/L salt concentration, the RGR of *M. aquaticum* ($F = 3.96$; df = 3; $P = 0.0105$, Fig. 1a) and *L. grandiflora* ($F = 4.16$; df = 3; $P = 0.0081$) decreased significantly (Fig. 2a). The number of roots produced by *M. aquaticum* (Fig. 1d) and *L. grandiflora* (Fig. 2d) was reduced significantly at a salinity of 6 g/L (*M. aquaticum*: $F = 8.50$; df = 3; $P < 0.0001$; *L. grandiflora*: $F = 9.35$; df = 3; $P < 0.0001$); their lengths were affected dramatically at 3 g/L for *L. grandiflora* ($F = 3.40$; df = 3; $P = 0.0471$, Fig. 2e) and at 3 and 6 g/L salinity for *M. aquaticum* ($F = 9.27$; df = 3; $P < 0.0001$; Fig. 1e). The number of leaves of *L. grandiflora* decreased significantly at the 6 g/L salt concentration ($F = 6.28$; df = 3; $P = 0.0006$; Fig. 2h).

Seasonal effect

The photosynthetic activity of *M. aquaticum* (Fig. 1b) tended to be lower in the summer than in autumn

Table 1 Summary of ANOVA on morphological traits and transformed traits of *M. aquaticum* and *L. grandiflora*, during a 28-day experiment

Traits	Effect	*M. aquaticum*		*L. grandiflora*	
		F	*P*	*F*	*P*
Photosynthetic activity	Salinity	0.21	ns	4.77	0.0067
	Season	2.71	0.08	2.27	ns
	Salinity × season	0.71	ns	1.89	ns
RGR	Salinity	3.96	0.0105	4.16	0.0081
	Season	58.17	<0.0001	0.91	ns
	Salinity × season	3.92	0.0016	1.68	ns
Number of lateral shoots	Salinity	4.15	<0.0001	0.19	ns
	Season	13.16	0.0084	4.32	0.0161
	Salinity × season	3.16	0.0073	0.99	ns
Number of roots	Salinity	8.50	<0.0001	9.35	<0.0001
	Season	22.99	<0.0001	24.54	<0.0001
	Salinity × season	2.73	0.0177	2.84	0.0138
Root length	Salinity	9.27	<0.0001	3.40	0.0471
	Season	2.11	ns	0.67	ns
	Salinity × season	0.93	ns	0.52	ns
Leaf number	Salinity			6.28	0.0006
	Season			5.39	0.0061
	Salinity × season			1.36	ns
Leaf length	Salinity	0.13	ns	1.46	ns
	Season	28.76	<0.0001	8.83	0.0004
	Salinity × season	1.37	ns	0.95	ns
Leaf width	Salinity	2.42	ns	0.56	ns
	Season	234.14	<0.0001	14.90	<0.0001
	Salinity × season	2.69	0.0192	1.55	ns

Effect of salinity: $n = 27$, df = 3; effect of season: $n = 36$, df = 2; effect of salinity × season interaction: $n = 9$, df = 6

ns not significant

($F = 2.71$; df = 2; $P = 0.08$), while photosynthetic activity of *L. grandiflora* was not affected by the season (Fig. 2b). The morphology of the plants was significantly affected by the season. RGR of *L. grandiflora* did not show a seasonal difference. Both species produced less lateral shoots in summer ($F = 13.16$; df = 2; $P = 0.0084$ for *M. aquaticum*, Fig. 1c and $F = 4.32$; df = 2; $P = 0.0161$ for *L. grandiflora*, Fig. 2c). *M. aquaticum* produced less roots in spring than in summer and autumn ($F = 22.99$; df = 2; $P < 0.0001$; Fig. 1d) and *L. grandiflora* produced more roots in autumn than in summer and spring ($F = 24.54$; df = 2; $P < 0.0001$; Fig. 2d). Leaf length of *M. aquaticum* was the highest in autumn ($F = 28.76$; df = 2; $P < 0.0001$; Fig. 1f) and leaf length of *L. grandiflora* was the smallest in summer ($F = 8.83$; df = 2; $P = 0.0004$, Fig. 2f), although leaf width was highest in spring for both species ($F = 234.14$; df = 2; $P < 0.0001$; Fig. 1g for *M. aquaticum* and $F = 14.90$; df = 2; $P < 0.0001$ for *L. grandiflora*, Fig. 2g). Defoliation of *L. grandiflora* occurred in summer ($F = 5.39$; df = 2; $P = 0.0061$; Fig. 2h).

Discussion

Salt impact on invasive aquatic plants

When exposed to salt, plant survival, RGR, productivity (Hart et al., 1991; McGregor et al., 2007; Munns & Tester, 2008), photosynthesis (Parida & Das, 2005)

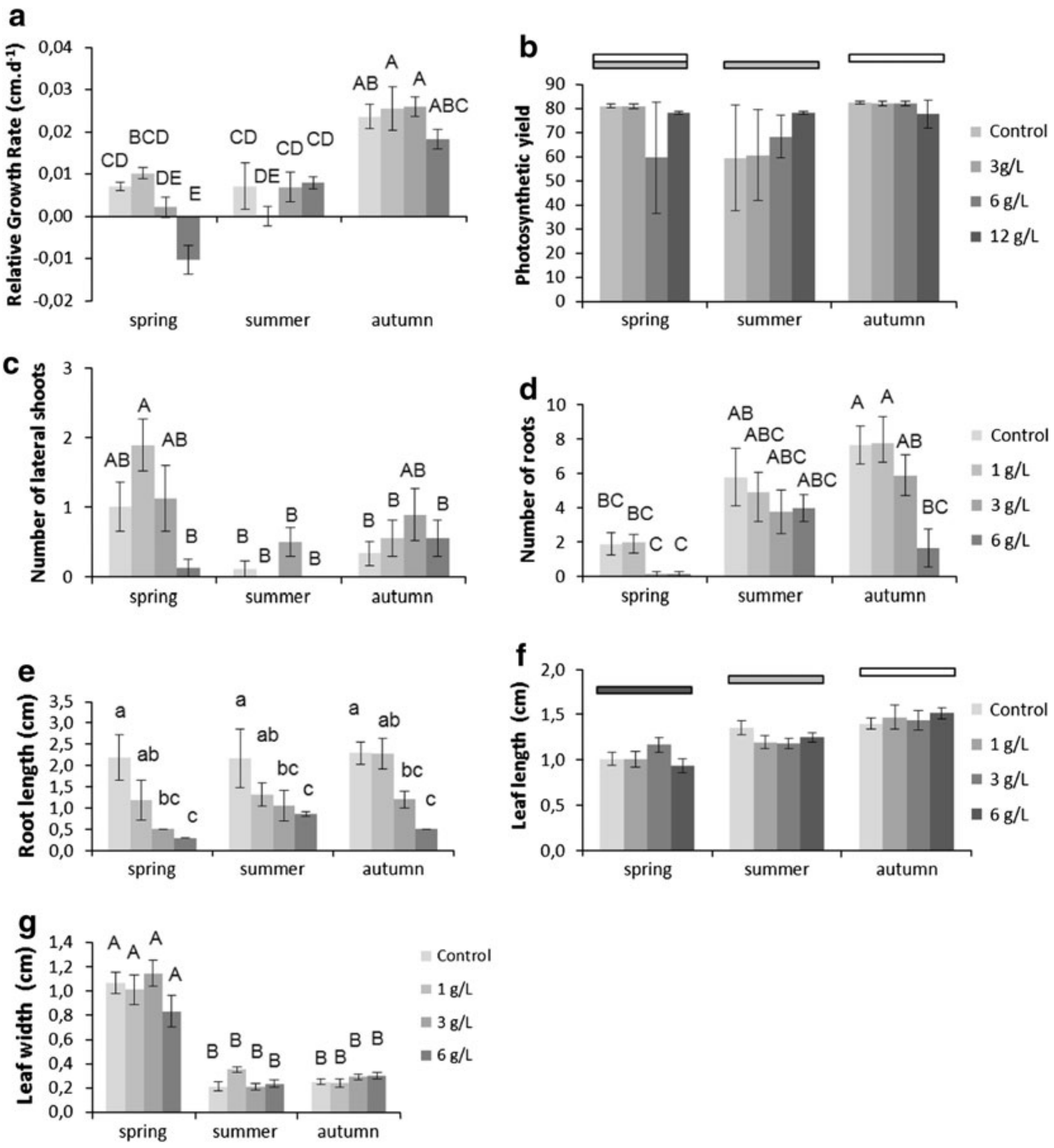

Fig. 1 Influence of salinity (mean ± SE, $n = 27$), season (mean ± SE, $n = 36$) and their interaction (mean ± SE, $n = 9$) on the growth and the morphology of *M. aquaticum* (**a** relative growth rate; **b** photosynthetic yield; **c** number of lateral shoots; **d** number of roots; **e** root length; **f** leaf length; **g** leaf width), after a 28-day experiment. Different *colours of horizontal bars* indicate significant differences between season effects. Different *small letters above columns* indicate significant differences between salt treatments. Different *capital letters above columns* indicate significant differences between interaction of salt treatments and season effects

and development are reduced. Lateral and apical growth of *M. aquaticum* were both affected by increasing salinity (6 g/L), while lateral growth was stimulated at 1 and 3 g/L. Stress can boost the tolerance of the plant through the induction of acclimation responses (Potters et al., 2007). Biomass allocation is one of the traits allowing the characterization of plant strategy. In plants, growth and resource uptake are intimately linked. Thus, ramification patterns can be interpreted as a result of previous resource availability and resultant growth (Stoll et al., 1998) or could be a mechanism to favour dispersal from areas with high salinity to a less stressful environment. Although we established salt

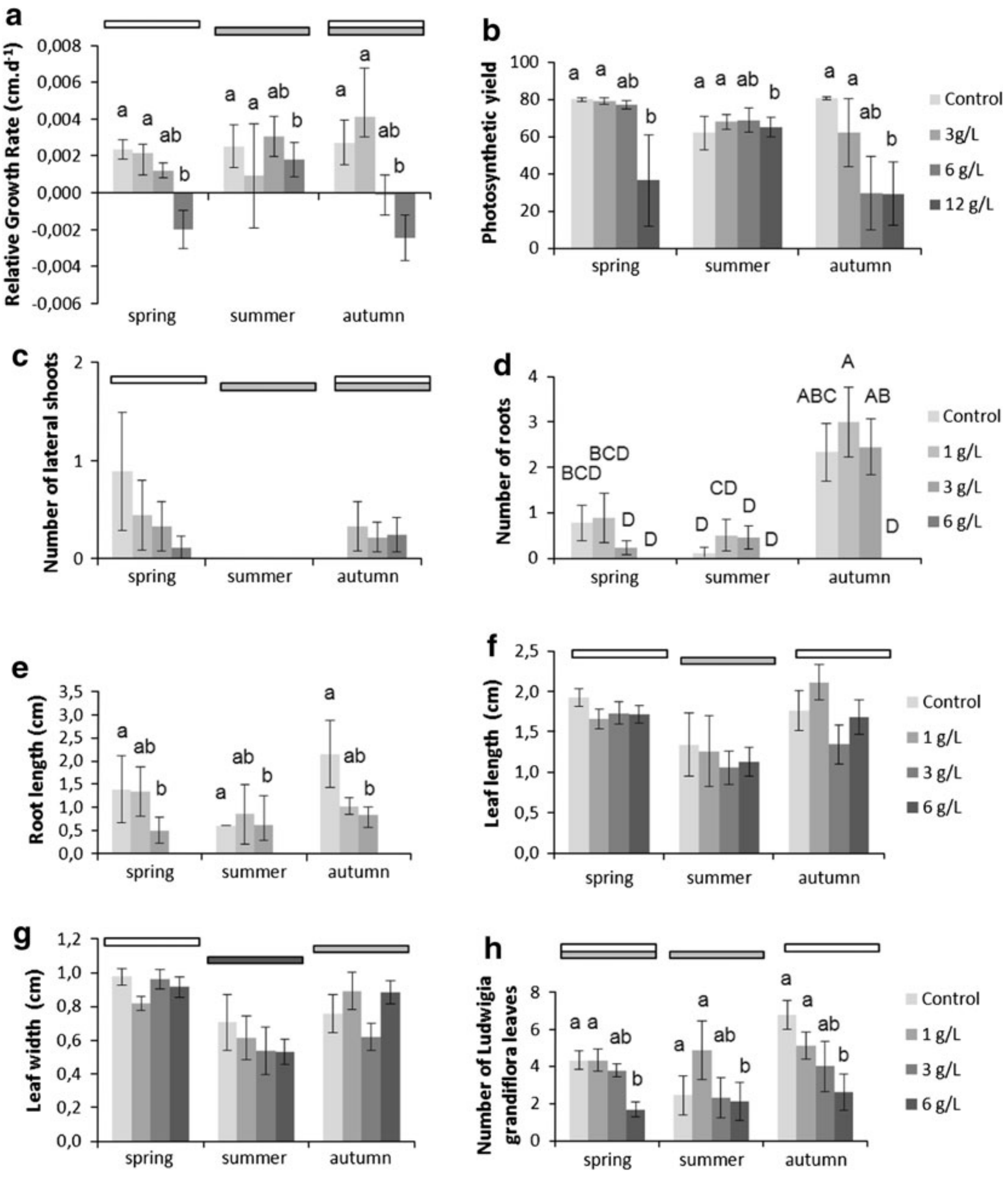

Fig. 2 Influence of salinity (mean ± SE, $n = 27$), season (mean ± SE, $n = 36$) and their interaction (mean ± SE, $n = 9$) on the growth and the morphology of *L. grandiflora* (**a** relative growth rate; **b** photosynthetic yield; **c** number of lateral shoots; **d** number of roots; **e** root length; **f** leaf length; **g** leaf width; **h** number of *L. grandiflora* leaves), after a 28-day experiment. Different *colours of horizontal bars* indicate significant differences between season effects. Different *small letters above columns* indicate significant differences between salt treatments. Different *capital letters above columns* indicate significant differences between interaction of salt treatments and season effects

sensitivity of Water Primrose at 6 g/L, Grillas et al. (1992) found that biomass production of *L. grandiflora* was affected by drought and salinity of 10 g/L. These results are partially corroborated in the literature. Jampeetong & Brix (2009) found that the RGR of *Salvinia natans* was affected by the concentrations of 3 and 6 g/L. Similarly, Haller et al. (1974) found that the toxic salt concentration for the growth of *M. aquaticum* was between 10 and 13.3 g/L. A salinity of 6 g/L seems to be toxic for both aquatic plants. The

RGR became positive for the Parrot Feather, whereas it was negative for the Water Primrose. However, plants also may respond to the environment simply by altering their growth rate without affecting the allocation of resources or plant morphology (Schlichting, 1986). More surprisingly, we established that both amphibious species differed in their level of sensitivity/salt tolerance and that the magnitude of salt stress varied between these two species. The two species responded to the treatments differently even though they belong to the same biological type.

Our results also showed an inhibition of *L. grandiflora* photosynthesis, which could be explained by salt accumulation in developing leaves and by a stomatal response induced by reducing water potential (Munns, 2002; Jampeetong & Brix, 2009). We found no significant difference in photosynthetic activity of *M. aquaticum.* This species was able to tolerate changes of salinity without significant photosynthetic stress symptoms. Defoliation appeared for *L. grandiflora* at high-salt concentrations, but not for *M. aquaticum.* Defoliation occurred by premature senescence of leaves: the older leaves first became yellow-green and then brown indicating marked injury of old leaves. Loss of leaf tissue entailed a loss of valuable resources, especially carbon and nitrogen (Lovett & Tobiessen, 1993), and induced the reduction of photosynthetic activity. Similar responses have been found for other aquatic macrophytes exposed to saline conditions (Haller et al., 1974; Rout & Shaw, 2001; Jampeetong & Brix, 2009). The reduction of the number and the length of roots for both species could be a mechanism to control the ion uptake in a stressful environment and was probably caused by the reduction in turgor pressure within the cells that restricted cell expansion (Jampeetong & Brix, 2009). According to Nielsen et al. (2003), at salinities of 1 g/L, freshwater macrophytes reduce root development. In contrast to Haller et al. (1974), we did not find an increase in root growth of *M. aquaticum* due to salt concentrations in an attempt to overcome an internal water deficit by increasing the root surface area. *M. aquaticum* was able to use root and leaf resources to respond to salt stress, whereas this was not the case for *L. grandiflora*. The reduction of root growth could be also a mechanism to limit anchorage to sediment and favour dispersal from areas with high salinity to a less stressful environment.

In conclusion, stress preferentially affects some species more than others, and plants differ in their stress response capacity (Lichtenthaler, 1996). Many plants redirect their growth when exposed to stress. Some plants fail to grow, some grow only slightly and others exhibit a large increase in growth. Several plants are able to alter their morphological characteristics under different environmental conditions (Schlichting, 1986). In our study, *M. aquaticum* seemed to have an overcompensation strategy to tolerate salt stress at the end of the growing season. The release of apical dominance is assumed to be one of the mechanisms causing overcompensation. According to the classification proposed by Kautsky (1988), *M. aquaticum* could be considered as a competitive species, with a high-photosynthetic rate and high-vegetative growth to respond to stress. Conversely, *L. grandiflora* seemed to avoid salt stress all the year round with a 'sit and wait' strategy. Grime (1989) says that 'sit and wait' mechanisms of foraging are common among animals of continuously hostile environments, but it is only relatively recently that similar phenomena have been detected in bryophytes and flowering plants of unproductive habitats.

Influence of season on the plant response to salt stress

A significant temporal effect was found for most of the traits, suggesting that the response to salt stress changed seasonally. Plants often exhibit different sensitivities to environmental stressors at different stages of growth (Zedler et al., 1990) and seasonality in salinity strongly conditions the plant growth cycle (Lillebo et al., 2003). Leaves, stems and roots vary between species in construction, lifespan and relative allocation (Westoby et al., 2002). We have established that the number of lateral shoots produced by both species was higher in spring than in summer and autumn. In autumn, *M. aquaticum* allocated its energy to apical growth which could improve its photosynthetic performance, in order to store energy for the winter. Moreover, we observed that the stem diameter of *M. aquaticum* was larger in autumn than in spring and summer. In most aquatic plants, peaks of carbohydrate storage occur in summer or autumn and they are depleted in spring when plant growth resumes (Madsen, 1991). Carbohydrate allocation patterns have not been identified for *M. aquaticum*, but starch allocation was greatest in stolons, with a centralized store (Wersal, 2010). According to Wersal (2010), insoluble starch is the long-term storage carbohydrate in the plant and can support plant growth. *M. aquaticum* may be able to store more starch in its stems which could confer a better resistance to stress in autumn. Conversely, the stem diameter of *L. grandiflora* did not increase during the year. We hypothesize that carbohydrates, starch and nitrogen were not stored in the stem, but in other organs, for instance, in leaves. Rejmánková (1992) has shown that *L. peploides* allocates more than 70% of nitrogen to leaves. The leaf size reduction for *L. grandiflora* and to a lesser extent for *M. aquaticum* in the summer could be attributed to a decrease in leaf gain and greater leaf loss, particularly at 6 g/L, suggesting that this could be related to a reduction in leaf cell expansion (Van den Brinke & van der Velde, 1993; Warwick & Bailey, 1997, 1998). The production of roots later in the year by both species enhances resource supply maintenance and guarantees consistency of supply to metabolism under a low-stress pressure. This could also be an overwintering mechanism in order to enhance their growth in the following spring.

Implications in the context of changing salinity

The economic value of wetlands and their ecological functions have increased managers' interest in restoring modified and invaded salt marshes sites (Luken & Walters, 2009). Wetlands are particularly vulnerable to invasion and to increased salinity levels through saline water management regimes. The potentials of both species to increase invasion in a context of increasing salinity differ. *M. aquaticum* could colonize brackish waters and could extend its distribution. Furthermore, the increase of its lateral growth and its regenerative ability could enhance the dispersal capacity to a less stressful environment. Conversely, our results suggested that the dispersal capacity of *L. grandiflora* would be limited, as no adaptation mechanism seems to have been established. The increased salinity in the environment could limit invasion by *L. grandiflora* and might reduce their invasion dynamics. In the wetlands bordering the Mediterranean Sea in southern France, management with salt water was used successfully to eradicate salt-sensitive *Ludwigia peploides* (Grillas, 2004).

However, our experiments constitute a simplification of natural ecosystems. It is difficult to determine the exact salinity level that is toxic to a plant, because preconditioning of the plant and possibly environmental and physiological factors alter the levels of toxicity to some degree (Haller et al., 1974). Many factors have not been taken in account in this study, for instance, the influence of sediment, weather and tidal range on plant growth. Consequently, these data offer a reference point and toxic levels are probably within limited ranges of the concentrations reported (Haller et al., 1974). In addition, salt tolerance is based on relative performance, recognizing that overall success is controlled by a number of processes including, but not limited to, photosynthesis and growth (Bertness et al., 1992).

Little data exist on the salt tolerance of invasive aquatic plants. The impact of salt increase on native communities in coastal wetlands should be studied. This information would be useful to develop quantitative salt impact models that predict the effects of increasing salinity on the biodiversity. The use of these models would have two major aims: to reduce the subjectivity in decision making and to provide a framework for incorporating estimates of uncertainty into assessments of the risks of salinisation on particular plants.

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