SALTMARSHES ON PEAT SUBSTRATE ON THE SOUTHWEST COAST OF IRELAND: EDAPHIC PARAMETERS AND PLANT SPECIES DISTRIBUTION

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Abstract. Saltmarshes on peat substrate are common along the western Atlantic coast of Ireland. The peat which underlies these marshes was formed under freshwater conditions in post glacial times, after which these systems were subjected to a marine transgression. The aim of this study was to determine the relationship between edaphic factors, substrate type and saltmarsh vegetation, specifically investigating the role of edaphic factors in determining the distribution of saltmarsh species *Atriplex portulacoides* in Ireland. Edaphic parameters measured for each substrate included pH, moisture content, ammonium and nitrate. The peat was found to differ markedly from other substrates. Using canonical correspondence analysis it was found that pH and ammonium were the major drivers in influencing saltmarsh vegetation on peat substrate. Under both *in situ* and *ex situ* conditions *Atriplex portulacoides* showed an affinity for drier substrate and its absence from fringe marshes in Ireland is likely due to a combination of both biotic and abiotic factors, including intolerance to high soil moisture levels.

Key words: saltmarsh vegetation, peat, edaphic properties, *Atriplex portulacoides*

1. INTRODUCTION

Saltmarshes develop on low energy coasts and have been defined as areas arising from the accretion of sediments or the accumulation of organic matter *in situ* under the influence of the tide (Chapman, 1960; Beeftink, 1977). This definition, however, does not account for all types of saltmarsh. In particular, this definition is not suitable to define those saltmarshes that have formed on non-marine substrates such as peat. Such saltmarshes are common along the Irish western seaboard. A complete inventory of all saltmarshes in Ireland was carried out, which classified them according to their morphology and nature of the substrate (Curtis and Sheehy Skeffington, 1998). Out of the 250 saltmarshes surveyed, 57 were found to have an underlying peat substrate. The term 'fringe saltmarshes' was proposed to describe saltmarshes on peat substrate.

Fringe saltmarshes occur in sheltered rocky bays or in narrow bands between the sea and heath dominated hinterland. The peat which underlies these marshes was formed under freshwater conditions in post glacial times (10,000 B.P.) when climatic conditions resulted in the formation of ombrogenic blanket bogs and the accumulation of thick layers of peat (Sheehy Skeffington and Curtis, 2000). These blanket bogs developed to the greatest extent in regions with a pronounced oceanic climate, giving rise to a high density of these marshes along the western Atlantic seaboard (Mitchell, 1986). The blanket bogs are predominantly made up of *Sphagnum-Molinia* type peat in the upper horizons and some contain wood peat, incorporating birch and alder remains, in the lower horizons (Jessen, 1948). A subsequent marine transgression resulted in a shift from freshwater conditions to saline conditions for some of the blanket bogs. This transgression is estimated to have occurred between 4000 and 2000 B.P. (O'Connell, 1988).

Marshes on peat substrate can also be found in Scotland and other parts of North Atlantic Europe (Adam, 1990). However, in these marshes, peat was formed under the influence of the sea (Sheenan, 1995; Allen, 2000). Thus, the ontogeny of Irish peat (fringe) marshes is essentially different, consisting of a clearly distinct freshwater phase of peat formation, followed by a marine dominated period.

The peat saltmarshes of Ireland are unique in their ontogeny, as well as their vegetation. To date, these systems have not been studied in any detail, nor have they been compared with non-fringe systems. Three other types of substrate are predominant in Irish saltmarshes. These are sand, associated with sand flats and sand dunes systems; mud, associated with estuarine saltmarshes; and a mixture of sand/mud, which can be associated with bay, estuarine and dune systems (Curtis and Sheehy Skeffington, 1998). Invariably these substrates have different edaphic properties compared with peat, but the degree to which they differ and the consequences thereof, are unknown. It has long been recognised that the vegetative community at a particular site is determined by environmental controls, comprising both biotic and abiotic influences, resulting in a community that is capable of stable co-existence under such conditions. Abiotic factors that distinguish saltmarshes from many other terrestrial and aquatic systems include waterlogging, acidity or alkalinity, salinity, and the availability of nutrients.

It has been observed that the common saltmarsh shrub *Atriplex portulacoides* (L.) Aellen (previously known as *Halimione portulacoides*) is largely absent from the fringe marshes on the west coast of Ireland, while being locally abundant on the east coast (Sheehy Skeffington & Curtis, 2000) (Figure 1). It had been hypothesised by Sheehy Skeffington & Curtis (2000) that relatively intensive grazing on the west compared with the east coast was the limiting factor for the distribution of *A. portulacoides* in Ireland. Grazing can seriously inhibit growth and prevents *A. portulacoides* becoming dominant (Dormann *et al.*, 2000; Van Wijnen *et al.*, 1999), but species are rarely completely excluded as a result of grazing practices.

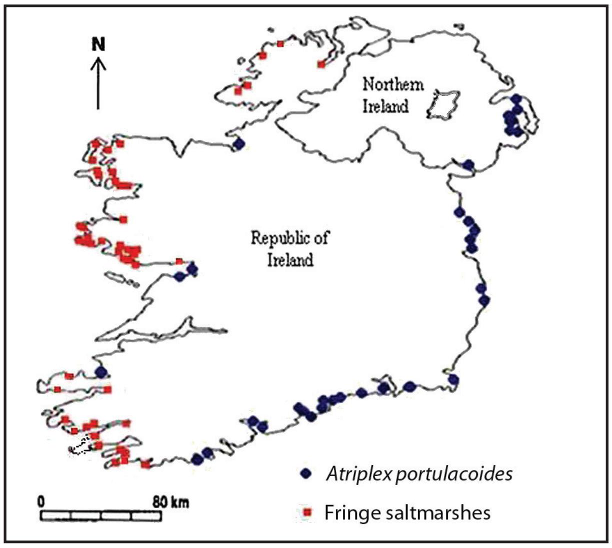

Fig. 1 Map of Ireland showing the location of fringe saltmarshes and *Atriplex portulacoides*. (Adapted from Sheehy Skeffington and Curtis, 2000)

Evidence exists to support the theory that the distribution of *A. portulacoides* is limited by waterlogging, aeration and tidal inundation. Based on their ontogeny, it has been suggested that fringe marshes may be poorly drained and water logged, as is the typical nature of reed swamps and peat substrates (Montemayor *et al.,* 2008). Consequently, it can be hypothesized that the distribution of *A. portulacoides* on salt marshes is limited by soil waterlogging, and that *A. portulacoides* is excluded from the west coast of Ireland due to the predominance of poorly drained fringe systems on peat substrate.

The aim of this study was to determine relationships between edaphic factors, substrate type and saltmarsh vegetation in fringe marshes on the west coast of Ireland. Specifically the role of edaphic factors in determining the distribution of the saltmarsh species *A. portulacoides*, under *in situ* and *ex situ* conditions, was investigated.

2. MATERIALS AND METHODS

2.1. Field sampling

Study sites were selected on the basis of their classification in Curtis and Sheehy Skeffington (1998). One saltmarsh on each of four substrates: peat, sand, mud and sand/mud, was chosen for this study. These sites were located at Ahakista (51°35′56″N, 09°36′6.2″W), Ballyheigue (52°21′31″N, 09°50′13″W), Timoleague (51°38′29″N, 08°45′37″W) and Kilbrittain (Harbour View) (51°39′10″N, 08°40′23″W) respectively.

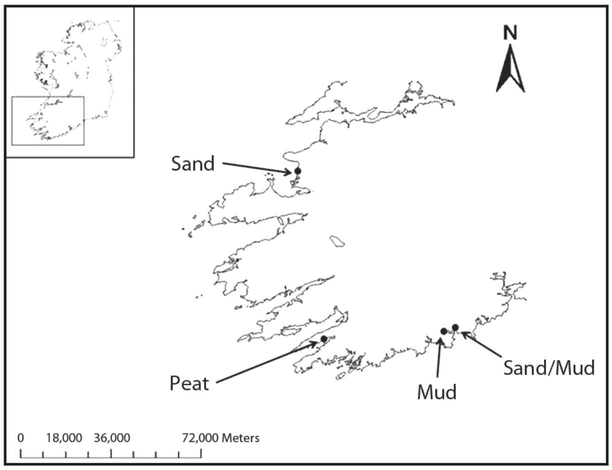

Fig. 2 Map of four selected saltmarsh sites on different substrates in southwest Ireland: sand located at Ballyheigue, Co. Kerry, peat (fringe marsh) at Ahakista Co. Cork, mud at Timoleague, Co. Cork and sand/mud at Kilbrittain (Harbour View), Co. Cork.

At each site nine quadrats were sampled: three in the upper, middle, and lower shores, during April and June 2009. The size of the quadrat for vegetation analysis was 2 × 2m based on the concept of minimal area study (Kent and Coker, 1992). Species were identified and percentage cover recorded for each quadrat. Soil cores were taken at each quadrat using a 5cm diameter soil auger. The cores were taken to a depth of 15cm. Soil samples for available nitrogen analysis were homogenised and frozen as soon as possible as recommended by ISO/TS 142560-1 (2003). Soils were extracted with 1M KCl (ISO/TS 142560-1, 2003). Subsequent analyses of nitrate and ammonium were carried using automated Flow Injection Analysis (Lachat Quikchem IC+FIA 8000) by the accredited Aquatic Services Unit laboratory at UCC. pH was determined in aqueous suspension 1:2 soil:water ratio (Allen, 1989) using an Orion 3 soil pH meter (Thermo Electron Cooperation, Singapore). Moisture content was measured gravimetrically and the soil was oven dried at 40°C to a constant weight (Allen, 1989). Both the soil sampling and vegetation analyses were carried out at each site over consecutive days in order to minimise the effect of environmental variables, such as weather, and also to sample at similar times of the tidal cycle. Sampling began at low tide each day so that results were comparable between sites.

2.2. Ex situ growth experiment

In order to examine the influence of substrate and/or waterlogging on the growth of *A. portulacoides* an *ex situ* experiment was carried out. Cuttings of approximately 3 to 5cm length were taken from Kilbrittain saltmarsh, Co. Cork. These were planted in prepared seed trays containing a rooting medium of potting compost, washed sand, and perlite. Cuttings were watered with freshwater to aid establishment. After five weeks healthy root systems had developed sufficient to conduct the growth experiments. One week prior to the experiment seedlings were watered with varying concentrations of seawater gradually increasing to 35ppt.

Peat substrate for the experiment was extracted from a fringe marsh at Schull, Co. Cork (51º30'46"N, 09º35'7"W) and sand substrate was also taken from Kilbrittain saltmarsh. The peat and sand were then transferred to flower pots of 8cm diameter. In each pot a single rooted cutting was planted and all pots were kept in a glass house with a photo period of 16 hours light (18ºC) and 8 hours dark (10ºC). Four submergence treatments using seawater were carried out on both peat and sand substrate. These comprised constant submergence, submergence for 24 hours twice a week, submergence for 1 hour twice a week and a control which was watered when required. The experiment was conducted for 5 weeks before plants were harvested, after which changes in root and shoot length, biomass and leaf number were measured as growth responses.

2.3. Statistical analysis

To improve homogeneity of variance, moisture data, ammonium and nitrate data were transformed (arcsine and natural log respectively) prior to analysis. A oneway ANOVA was carried out using SPSS (PASW® Statistics 17) software. Differences in means ($p<0.001$) were assessed by Bonferonni *ad hoc* comparisons.

To establish the relationships between plant species and spatial–temporal changes in edaphic variables, canonical correspondence analysis (CCA) (ter Braak, 1987) was performed using the Multi-Variate Statistical Package (MVSP) program Version 3.1 (Kovach Computing Services). Species data were square root transformed prior to analysis.

For the growth experiment two Interaction ANOVAs were conducted for each growth response for plants grown in sand and peat substrates. Both were compared to identify the influence substrate and submergence would have. A Tukey test was used to identify where any significant relative difference in shoot length, root length, overall biomass or leaf number lay. This allowed differences between treatments to be identified, but also identified the significance of substrate and submergence regime on these results.

3. RESULTS

3.1. Edaphic parameters

Peat has the lowest pH of the four substrates that were tested, averaging at 6.55. The highest pH value was obtained for the sand substrate, averaging at 8.52 (Figure 3(a)). One way ANOVA revealed that there were significant differences in pH between the four substrates $F(_{3,67})=112.28$, $p<0.001$. Bonferroni comparisons showed that the pH of peat was significantly lower ($p<0.001$) compared with that of sand, mud and sand/mud. The pH of the mud substrate was also significantly lower compared with that of sand and sand/mud substrates. The pH of sand substrate was not significantly different to that of sand/mud.

The peat substrate was found to have the highest moisture content followed by mud, and then sand/mud. Sand substrate had the lowest moisture content (Figure 3(b)). Oneway ANOVA showed that there were significant differences in moisture content between the four substrates $F(_{3,69})=148.68$, $p<0.001$. Bonferroni comparisons showed that peat substrate has a significantly higher moisture content than sand or sand/mud. There was no significant difference in moisture content between peat and mud substrate. Sand has a significantly lower moisture content than mud but not sand/mud substrate.

Ammonium content also differed significantly between the four substrates $F(_{3,67})=46.46$, $p<0.001$ (Figure 3(c)). Peat substrate contains up to three times more NH_4 than the other substrates. Bonferroni comparisons revealed that NH_4 content in peat is significantly higher ($p<0.001$) compared with sand, mud and sand/mud substrates.

Significant differences in nitrate levels were also detected between the four substrates $F(_{3,57})=49.23$, $p<0.001$. Nitrate levels were found to be significantly higher in peat compared with mud and sand/mud substrates (Figure 3(d)). Although peat substrate contained substantially more nitrate than sand substrate, this difference was not significant.

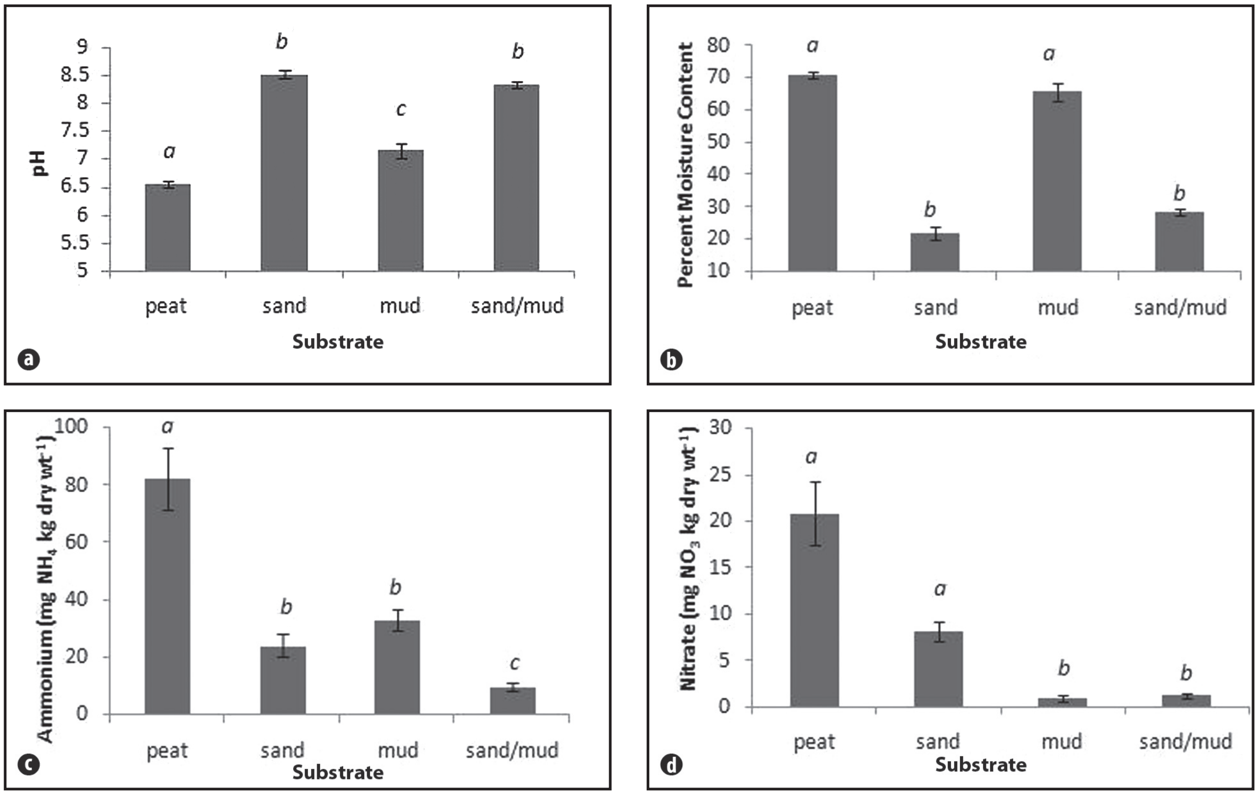

Fig. 3 (**a**) pH, (**b**) moisture content, (**c**) ammonium (NH_4) and (**d**) nitrate (NO_3) content of saltmarsh substrates, peat, sand, mud and sand/mud. Each value is mean ± SE (*n*=18). Bars with same letter are not significantly different by Bonferroni at 0.001 level.

3.2. VEGETATION ANALYSIS

Species abundance for each substrate is presented using the Domin scale (Dahl and Hadăc, 1941) in Table 1. The relationship between the distribution of salt marsh vegetation and edaphic variables was analysed using canonical correspondence ordination. The most important variables which explained variations in the vegetation data set were pH, ammonium and nitrate content (Figure 4). Both are strongly correlated with axis two. At the extreme end of the positive side of axis 2, appear species which can tolerate high ammonium in soils, *Juncus maritimus, Juncus gerardii* and *Triglochin maritima*.

Table 1. Plant species cover at each of the four saltmarsh sites in southwest Ireland (see Figure 2). Cover scale (Domin Scale) 1, <2% cover; 2, 2%cover; 3, 3% cover; 4, 4-10% cover; 5, 11-25% cover; 6, 26-33%; 7, 34-50% cover; 8, 51-75%; 9, 76-90%; 10, 91-100% cover.

Number	Species	Peat	Sand	Sand/Mud	Mud
1	*Juncus maritimus*	6	-	-	-
2	*Puccinellia maritima*	5	7	7	5
3	*Juncus gerardii*	5	-	-	3
4	*Armeria maritima*	4	-	4	-
5	*Plantago maritima*	7	3	4	5
6	*Spergularia media*	4	1	1	1
7	*Glaux maritima*	3	4	1	-
8	*Triglochin maritima*	4	-	-	1
9	*Aster tripolium*	4	5	4	5
10	*Limonium humile*	-	-	1	1
11	*Cochlearia officinalis*	3	5	1	5
12	*Spartina sp.*	-	4	4	5
13	*Atriplex portulacoides*	-	-	5	4

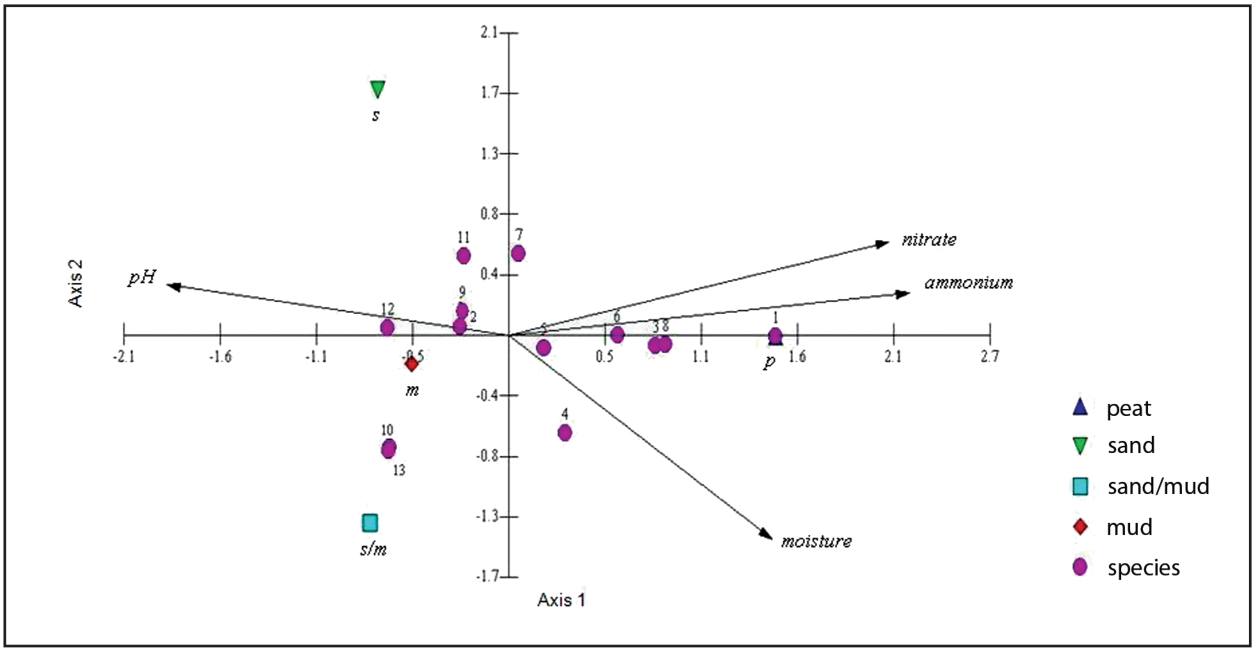

Fig. 4 Canonical correspondence ordination of salt marsh vegetation in Southwest Ireland showing correlation between principal plant species and edaphic variables. Species numbered according to Table 1. P, peat; s, sand; s/m, sand/mud; m, mud. Eigenvalues: axis 1, 0.301; axis 2, 0.123. Species-environment correlation: axis 1, 1.00; axis 2, 1.00. Percentage cumulative variance of species–environment relation accounted for the two first axes: 87.4%.

On the extreme of the negative side of axis 2, and correlating with increases in pH, appear *Spartina sp*. Near the origin of the coordinates the most significant species are *Plantago maritima, Puccinellia maritima* and *Aster tripolium*. Nitrate is highly correlated with ammonium. Both *A. portulacoides* and *Limonium humile* have the most negative scores. The peat substrate is located on the positive axis, i.e. removed from both *A. portulacoides* and *Limonium humile*.

3.3. GROWTH EXPERIMENT

To investigate further the negative relationships between peat substrate, soil moisture content and *A. portulacoides* distribution (Figure 4), the performance of *A. portulacoides* plants under a range of inundation regimes were investigated. Plants grown in sandy or peat substrate and constantly submerged in salt water were found to suffer a decrease in root length, with an average loss of 13% and 22%, respectively. Root loss was not significantly different between the two substrates (Figure 5(a)). The greatest percentage increase in root length (121%) was found for plants grown in peat, submerged for 1 hour twice weekly, although this was not significantly greater than plants in peat watered only occasionally (control). Nevertheless, the increase in root length when submerged for 1 hour twice weekly was significantly greater than plants grown in peat that were submerged for 24hrs twice weekly (p<0.05) or constantly submerged (p<0.001). When plants were grown in sand substrate, those that were watered occasionally exhibited the greatest increase in relative root length. This increase in root length in occasionally watered plants was significantly greater than in plants on sand that were constantly submerged (p<0.01), and substantially (but not significantly) greater than observed in plants submerged for 24hrs or 1hr twice weekly.

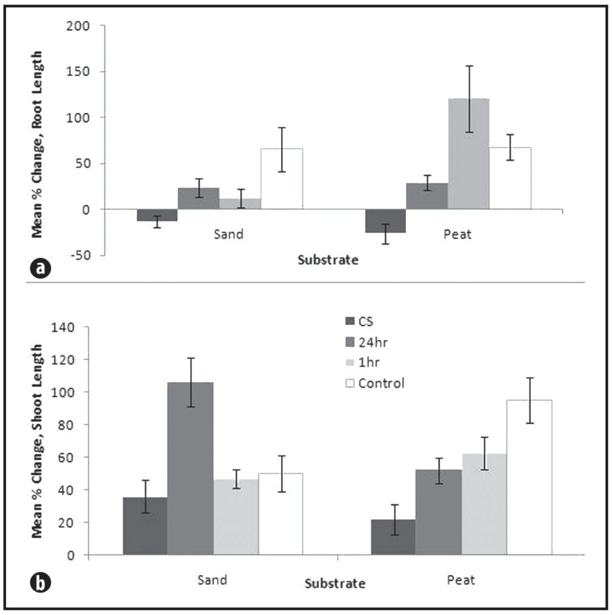

Fig. 5 Mean percentage change in (**a**) root length and (**b**) shoot length of *Atriplex portulacoides* grown on sand and peat substrates for 5 weeks using seawater in treatments CS – Constant submergence, 24hr- submergence for 24 hours twice weekly, 1hr- submergence for 1 hour twice weekly and Control - watered occasionally. Each value is mean ± SE (*n*=10).

On average, shoot length increased in all plants (Figure 5b). Interaction ANOVA found no significant influence of substrate type on relative shoot growth. However, the interaction between substrate and submergence regime had a significant influence on shoot length (p<0.05). Submergence alone was also found to have a significant influence on relative shoot growth (p<0.001).

Plants grown in peat substrates, constantly submerged in salt water exhibited the lowest percentage increase in shoot length (23%). Percentage shoot growth increased as the time spent submerged was reduced, such that plants on peat that were occasionally watered with salt water exhibited the largest percentage increase in shoot length (95%). An interaction ANOVA identified a significant difference (p<0.001) between constantly submerged plants and the occasionally watered controls. Plants that were submerged for only 24hrs or 1hr, twice weekly, also displayed a significant increase (p<0.05) in relative shoot length compared to those constantly submerged. Thus there was a strong tendency for relative shoot growth to increase with a reduction in submergence. Plants grown on sand submerged for 24hrs, twice weekly, displayed a significant increase in shoot length (p<0.05) compared to the other submergence regimes. Those submerged for 1hr, twice weekly, or watered occasionally exhibited no significant difference in percentage growth to those constantly submerged. The general trend was that shoot length for plants on sand did increase, but not significantly, when submergence time was reduced.

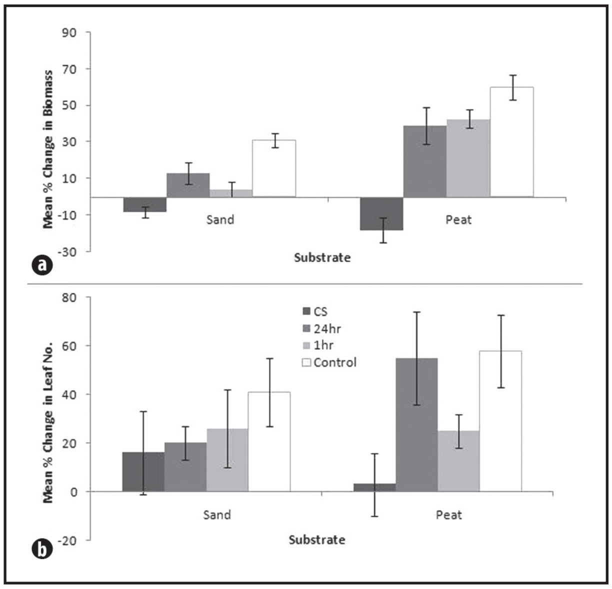

Fig 6 Mean percentage change in (**a**) biomass and (**b**) leaf number of *Atriplex portulacoides* grown on sand and peat substrates for 5 weeks using seawater in treatments CS – Constant submergence, 24hr- submergence for 24 hours twice weekly, 1hr- submergence for 1 hour twice weekly and Control- watered occasionally. Each value is mean ± SE (*n*=10).

Total biomass was measured to quantify both above and below ground productivity as a response to different submergence regimes and substrates. Interaction ANOVA found that substrate had a highly significant influence on relative change in biomass (p<0.01). Likewise submergence was found to have a highly significant influence on relative change in plant biomass (p<0.001). A significant interaction between substrate and submergence was also found (p<0.05). A loss in plant biomass was observed in plants constantly submerged grown in both sand and peat. Plants that were grown in sand and occasionally treated with salt water displayed a significant increase in biomass (p<0.05) compared with those constantly submerged. Smaller increases in biomass were observed in plants that were periodically submerged. Overall, the general trend for plants raised on sand substrate was for biomass to increase as submergence was reduced. In contrast, when plants were raised on peat substrate, the 24hr, 1hr and control treatments resulted in a highly significant increase in biomass compared with the constantly submerged sample (p<0.001). The trend was for biomass to increase as submergence was reduced but no significant differences were found between 24hr or 1hr, twice weekly, submergence or those watered occasionally.

Substrate type did not have an effect on the relative change in leaf number of treated plants (interaction ANOVA). Moreover, no significant interaction was found between substrate and submergence. In plants grown in sand and treated with salt water an increase in leaf number was observed as submergence was reduced. However, leaf numbers were not statistically different across treatments.

4. DISCUSSION

Substrate-linked edaphic factors were measured for four types of saltmarsh substrate. Out of the four substrates studied it was clear that the peat substrate was the most distinct with respect to edaphic factors. The edaphic properties which distinguished the peat substrate from the other three substrates were low pH and high ammonium content. Typically, the pH of terrestrial peat bogs is approximately 4.0 (Clymo *et al.*, 1984), whereas the pH of the peat substrate in the fringe marsh was found to be 6.55. The pH difference may be due to tidal inundation. Seawater can raise the pH of peat; bivalent magnesium is the third most abundant ion in seawater, and can be adsorbed by peat, resulting in a rise in pH (Sjörs and Gunnarsson, 2002). Similarly, the higher pH of coastal blanket bogs in Ireland compared with inland raised bogs has been attributed to the effect of sea spray (Gorham, 1953; Sjörs and Gunnarsson, 2002).

The biogeochemical cycling of nitrogen in wetland systems is complex. In anaerobic soils, ammonium-nitrogen is the dominant form of available nitrogen (Huang and Pant, 2009). Ammonium-nitrogen is also the dominant form of nitrogen in all substrates in this study. The significantly higher levels of ammonium that are found in the peat substrate may be due to the higher amount of organic nitrogen matter associated with peat. Low levels of ammonium-nitrogen are characteristic of aerobic, coarser textured soils such as sand (Hazeldon and Boorman, 1999). Indeed, this study found that the sand has significantly lower ammonium content than the peat substrate. Nitrification is dependent on the aeration and pH of the soil. Nitrification has a pH optimum of 7 to 8 and is an oxygen dependant process (Sprent, 1987). Fringe marshes that are characterized by low pH as well as low soil oxygen due to water saturation are therefore expected to be low in nitrate- nitrogen. The pH of the peat substrate in this study however may not be low enough to inhibit nitrification because the nitrate content of the peat is in fact higher than in the other substrates.

Due to a high water holding capacity, which influences drainage dynamics, peat substrate can be saturated or semi-saturated most of the time (Boelter, 1968). The high moisture content observed in this study reflects this. The mud substrate also had high moisture content because the mud in this study was composed of clay and silt particles (Sheehy Skeffington and Curtis, 2000). Clay also has a high water holding capacity (Mitchell and Soga, 1976). The course texture of sand permits water circulation and drainage to take place and therefore the soil moisture content was low for this substrate.

It is clear from the analysis of substrate-linked edaphic parameters that peat substrate fringe systems differ significantly from saltmarsh systems on other substrates and it is therefore concluded that fringe systems are distinct systems based on these parameters.

Canonical correspondence ordination showed that several edaphic factors were highly influential in determining the relationship between substrate type and saltmarsh vegetation (Figure 4). Ammonium, nitrate and pH are highly correlated with axis one. The peat substrate is located on the positive side of axis one with increasing ammonium levels and decreasing pH. On the negative side of axis one the sand, mud and sand/mud substrates are located. This again demonstrates that the peat substrate is markedly different from the other substrates. Species near the origin include *Plantago maritima, Puccinellia maritima* and *Aster tripolium*. These species occur in all sites, tolerating all four substrates, whilst not being found on substrates with more extreme pH, nitrate or ammonium levels or moisture content.

Plant species located at the positive side of axis one, namely, *Juncus maritimus, Juncus gerardii* (Juncaceae) and *Triglochin maritima* (Juncaginaceae) are most likely to be found on soils with high ammonium content. Species from these families are currently widely used in constructed wetlands for the removal of excess nutrients such as ammonium (Greenway, 2007). Both *A. portulacoides* and *Limonium humile* have the most negative scores and therefore are least likely to grow in soils high in ammonium and moisture. *A. portulacoides* is a member of the Chenopodiaceae family, which are known to be ammonium sensitive (Britto and Kronzucker, 2002). The position of this species in Figure 4 reflects this.

The high moisture content of peat observed in Figure 3(a) also influenced the relationship between substrate type and vegetation. Species such as *Juncus maritimus*, associated with the peat substrate in Figure 4 are capable of tolerating high moisture content and prolonged periods of flooding. In terms of species distribution *Spartina sp*. are also capable of tolerating high moisture levels. However, its location in Figure 4 suggests that pH is a more influencing factor in its distribution than moisture content. It is concluded, therefore, from this analysis that pH and ammonium are major drivers of vegetation in fringe systems, thus resulting in a distinct community of plant species capable of co-existing in these marshes.

Armstrong *et al.* (1985) noted that the distribution of *A. portulacoides* in the field was along creek banks, which were exceptional in their high degree of aeration. Sanchez *et al.* (1998) showed that, of all the vegetation communities on a specific marsh, the water table was lowest (–16cm) within the *Atriplex* stands. Water-table depth was also negatively correlated with redox potential, but they did not find that tidal inundation discriminated against *A. portulacoides.* It would thus appear that *A. portulacoides* is incapable of surviving in continuously waterlogged or excessively wet soils, but that occasional, short-lived inundation by the tide does not negatively affect these plants (Sanchez *et al.,* 1998). *A. portulacoides* and other *Atriplex* or *Atriplex* species do not develop extensive aerenchyma systems (Justin and Armstrong, 1987; Asad, 2001), showing that they are likely to be intolerant of waterlogged conditions.

The results of the *ex situ* growth experiments conducted in this study largely agree with this. Roots of plants raised in anaerobic, waterlogged, conditions showed a significant decrease in root length over the five week period during which they were submerged, and visible damage to the roots could be seen. Root stress was evident in the form of blackened, brittle roots. Roots of plants watered only occasionally exhibited the greatest increase in length, again suggesting an affinity for drier conditions.

Biomass is perhaps the most widely used indicator of plant productivity in salt marsh ecosystems (Jensen, 1985; Groenendijk and Vink-Lievart, 1987). Biomass accumulation comprises all above ground and below ground tissue and does not discriminate against lateral shoots and lateral roots, unlike the measurement of the longest shoot or longest root. The overall trend in this study was that growth was highest on the driest soils. Plants constantly submerged were found to suffer a loss of biomass; even though there was an increase in shoot length. The loss of biomass correlated with a loss in root length. Despite an increase in leaf number many of the original, larger leaves had been lost and replaced by more, new, but smaller leaves. Leaf number was found to increase across all submergence regimes indicating that *A. portulacoides* is capable of generating new growth despite being stressed.

This study has shown that in *ex situ* conditions *A. portulacoides* shows an affinity for well drained, aerated soils, and that the duration of submergence has a significant influence on the growth responses of both its above ground and below ground tissues. However, the results also showed that the peat substrate had a significantly positive effect on plant biomass when watered only occasionally. This establishes the fact that *A. portulacoides* is capable of primary production on peat substrate under *ex situ* conditions in the absence of competitor species. Generally, plants developed better under drier conditions, suggesting that this may determine distribution in saltmarshes. Thus, a combination of intolerance to high soil moisture content, combined perhaps with a decrease in competitive strength may control *A. portulacoides* distribution. Indeed, to become established on a fringe marsh *A. portulacoides* would have to compete with species that can tolerate high levels of ammonium and moisture and low pH i.e. *Juncus maritimus*. The relatively high moisture content of peat substrates may therefore comprise a competitive disadvantage. Additionally, our data indicate that other abiotic and biotic factors such as sensitivity to ammonium may also play a role in controlling *A. portulacoides* distribution along the west coast of Ireland. Previously, Sheehy Skeffington and Curtis (2000) linked the distribution of *A. portulacoides* to the intensive grazing of saltmarshes on the west coast by cattle and sheep. This study indicates that a combination of multiple abiotic and biotic factors, including intolerance to high soil moisture levels, is most likely to be responsible for determining *A. portulacoides* distribution in Ireland

5. CONCLUSIONS

The analysis of edaphic parameters shows that peat substrate from fringe systems differs significantly from other saltmarsh substrates. Canonical correspondence ordination showed that pH and ammonium were major drivers of vegetation in fringe systems, resulting in a distinct community of plant species capable of co-existing under fringe marsh conditions. *A. portulacoides* clearly showed an affinity for drier conditions under both *in situ* and *ex situ* conditions and it is concluded that its absence from fringe marshes in Ireland is likely due to a combination of both biotic and abiotic factors, including intolerance to high soil moisture levels.

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