

Flood tolerance and the distribution of *Iva frutescens* across New England salt marshes

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Summary. Tidal flooding is widely believed to be an important determinant of marsh plant distributions but has rarely been tested in the field. In New England the marsh elder *Iva frutescens* often dominates the terrestrial border of salt marshes and we examined its flood tolerance and distribution patterns. Marsh elders only occur at elevations where their roots are not subject to prolonged water table flooding. Consequently they are found on the terrestrial border of marshes and at lower elevations associated with drainage ditches and locally elevated surfaces. Marsh elders transplanted to elevations lower than they normally occur died within a year with or without neighbors and greenhouse tests revealed that *I. frutescens* is much less tolerant of flooded soil conditions than plants found at lower marsh elevations. We also manipulated the water table level of field plots and found that increasing or decreasing water table drainage led to enhanced and diminished *I. frutescens* performance, respectively. Our results demonstrate the importance of water table dynamics in generating spatial patterns in marsh plant communities and provide further evidence that supports the hypothesis that the seaward distributional limits of marsh plant populations are generally dictated by physical processes.

Key words: Salt marsh ecology – Halophytic plants – Flooding – Wetland plant communities – *Iva frutescens*

Vascular plant zonation is one of the most striking features of salt marsh plant communities. Salt marsh landscapes are dominated by pronounced bands of vegetation paralleling the shoreline that correspond to distinct tidal elevations (Miller and Egler 1950; Chapman 1974; Nixon 1982; Zedler 1982). As is the case for the equally pronounced zonation of sessile invertebrates on intertidal rocky shores (Connell 1972), the zonation of marsh plants is thought to be the product of both physical and

biotic processes. In general, physical stresses have been found to set the seaward borders of marsh plant populations while biotic factors, particularly competitive processes have been found to limit the terrestrial borders of marsh plant populations (Snow and Vince 1984; Bertness and Ellison 1987; Bertness 1991a, b; Pennings and Callaway 1992).

The most conspicuous physical process limiting plant success in lower marsh habitats is tidal flooding. Flooded soils are generally anoxic (Armstrong 1975) and plants that live in waterlogged soils must have architectural and/or biochemical mechanisms to cope with periods of prolonged anaerobiosis. Architecturally marsh plants that live in flooded soils often have aerenchyma tissue or conductive tissue that diffuses gases from above to belowground plant parts (Teal and Kanwisher 1966; Armstrong 1970). Biochemically marsh plants found in flooded soils often have specialized metabolic machinery to cope with low oxygen levels (Mendelssohn et al. 1981; King et al. 1982). While considerable attention has been paid to understanding the mechanisms that marsh plants use to cope with waterlogged soil conditions, however, little work has been directed at understanding the role that tidal flooding plays in generating plant distribution and abundance patterns in nature (but see Gleason 1980, Bertness 1991a). In this paper we examine the distribution of the common New England perennial shrub *Iva frutescens*, or the marsh elder. We are unaware of any previous work on the flood tolerance or population ecology of *I. frutescens*.

The marsh elder is a conspicuous component of New England marsh plant communities, often forming a distinct band or zone at the terrestrial border of marshes and bordering tidal creek banks (Miller and Egler 1950; Nixon 1982). In this paper we examine the distribution of *Iva frutescens* in relation to tidal flooding. In particular, we: 1) quantify the distribution of adult *Iva* plants in relation to marsh elevation and tidal water table fluctuations, 2) experimentally examine the role of physical and biotic factors in limiting *Iva frutescens* to the terrestrial border of marshes, 3) quantify the flood

tolerance of marsh elders in relation to other plants in the high marsh, and 4) examine the response of marsh elders to artificially increased and decreased flooding conditions in the field. Together our results provide one of the only experimental demonstrations of the role played by tidal flooding in limiting vascular plant distributions in marsh habitats.

Methods

We studied *Iva frutescens* at Rumstick Cove in Barrington, Rhode Island USA. The marsh at the site has plant zonation typical of southern New England salt marshes and has been studied extensively (Bertness and Ellison 1987, Bertness 1991a, b). The low marsh, or marsh area below the mean high water tidal line (Nixon 1982), is exclusively dominated by a monoculture of the smooth cordgrass *Spartina alterniflora* (the *Spartina alterniflora* zone). The high marsh habitat is dominated by a monoculture of the salt hay *Spartina patens* on the seaward border (*Spartina patens* zone) and a monoculture of the black rush, *Juncus gerardi* on the terrestrial border (*Juncus* zone). Spikegrass, *Distichlis spicata*, occurs at low densities in both the *Spartina patens* and *Juncus* zones (Bertness and Ellison 1987). The marsh elder *Iva frutescens* occurs at the site in a discrete band on the terrestrial border of the marsh (the *Iva* zone). It also commonly borders creek banks in the *Juncus* zone and isolated individuals are sometimes found in the *Juncus* zone on locally elevated mounds.

We quantified the elevation of marsh elders at the study site with surveying equipment (Lietz B20 autolevel and stadia rod, ± 5 mm accuracy). From a standard reference point of known elevation we measured the elevation of the: 1) high/low marsh border, 2) *S. patens*/*J. gerardi* zone border, 3) *J. gerardi*/*I. frutescens* zone border, 4) *I. frutescens* plants bordering creek banks in the *Juncus* zone, 5) isolated *I. frutescens* in the *Juncus* zone but greater than 10 m from a creek bank, and 6) areas of stunted *I. frutescens* plants. Stunted plant areas were defined as areas supporting plants less than 0.5 m tall that had not been disturbed for at least 6 years (personal observation, see Bertness and Ellison 1987). At zonal borders we quantified elevations every 3–5 m along undisturbed borders. For *I. frutescens* plants we recorded the elevation at the base and at 3 approximately evenly spaced intervals 25 cm from the base. We quantified elevations surrounding *I. frutescens* plants to detect and measure their potential association with local topographic features.

Variation in *I. frutescens* morphology across the marsh was quantified by harvesting representative plants in the *I. frutescens* areas surveyed for elevation. Ten randomly selected representative *I. frutescens*, were harvested totally intact from each area. In the laboratory we measured the total height, number of primary branches, number of leaves, the width and length of 10 random leaves, root penetration depth and lateral spread, and the above and belowground dry weight of each plant.

Water table levels

To examine the potential exposure of plant roots to waterlogged soil conditions across the high marsh, we quantified the level of the water table every other day from May–August 1991. Water table levels were monitored in 20 × 20 cm (length × width) holes 20–25 cm deep by measuring the depth of water in the holes at low tide. We followed 16–20 permanent but randomly located water table holes in the: 1) *Juncus* Zone, 2) *Iva* Zone, 3) *Juncus*/*Iva* Zone border, 4) 1 m from creek banks in the *Juncus* Zone, and 5) in three areas of stunted *Iva* bushes.

Field transplants across zonal borders

To assess the relative importance of physical factors and competitive interactions in maintaining the zonation of adult *Iva*, bush-

es were transplanted into the *Juncus* and *Iva* zones with and without neighboring vegetation in both 1990 and 1991. Transplants were made in early May by excavating 20 × 20 × 20 cm (Length × Width × Depth) blocks of peat including all roots of the transplant replicate and transplanting them into holes in target areas. All plants used as transplant material consisted of plants with 2–3 (35–40 cm tall) branches from the previous growing season collected randomly from throughout the study area.

For competition-free treatments, 8 replicate transplants each year were moved into large 3 × 5 m areas cleared of all aboveground vegetation in each zone. These areas were maintained free of surrounding vegetation for the duration of the experiment. For treatments with neighbors, 8 replicates/zone/year were transplanted into random locations in *Juncus* and *Iva* zone vegetation.

Transplants were monitored by monthly measuring the photosynthetic rates and annually (August) counting the number of leaves produced by each replicate, and measuring the sizes (length and width) of 10 randomly collected leaves from each plant. Photosynthetic rate was measured on undamaged terminal leaves on cloudless days with a portable infrared gas analyzer (ADC 20, Morgan Instruments).

Greenhouse flood tolerance experiment

We examined the relative flood tolerances of *I. frutescens*, *Distichlis spicata* and *J. gerardi* in a greenhouse experiment. We grew *I. frutescens* seedlings and *J. gerardi* and *D. spicata* tillers under dry, waterlogged, and partially waterlogged conditions in a greenhouse for 5 months. Freshwater was used in these experiments to isolate waterlogging from salinity effects. *Iva frutescens* seedlings (5–10 cm tall, 3 months old) and *J. gerardi* and *D. spicata* tillers (2 live tillers connected to a 2–4 cm rhizome) were randomly collected at the field site in August 1990 and planted in 15 cm flower pots in commercial potting soil in a greenhouse. After six weeks 48 of the plants of each species were randomly divided into 3 equal groups ($n = 16$ plants/species/group) and assigned to full flooding, half flooding, or no flooding treatments. For the full flooding treatment, pots were placed in 1.5 m diameter wading pools with the water level flush with soil level (~ 10 cm). For the half flooding treatment pots were placed in similar wading pools in 5 cm of water. Nonflooded control replicates were placed in pools without water. Water in the pools was changed weekly and the positions of all pots and pools were randomly rotated weekly. All plants were watered daily and every other week were fertilized.

After 5 months the photosynthetic rate of each replicate was measured under full sunlight at midday under cloudless conditions, and each replicate plant was measured (height, number of leaves), dried and weighed.

Field water table manipulations

To experimentally examine the role of water table levels on the success of *I. frutescens* in the field we manipulated the water table in two separate experiments. The first experiment was designed to assess the effect of increased drainage in the *Juncus* zone on *Iva* success. We transplanted standard-sized *I. frutescens* as described above into four 4 × 5 m plots in the *Juncus* zone 1 m from creek banks. The areas used were just below the elevation where *I. frutescens* occurs in the *Juncus* zone bordering creek banks. We transplanted 8 *I. frutescens* bushes into each plot and then in two of the plots we dug 4 parallel drainage ditches 20 cm wide, 25 cm deep, 1 m apart and at right angles to the natural creek bank. In each undrained plot we also transplanted 8 *I. frutescens* bushes (as described above) elevated 15 cm above the substrate as a second method of partially alleviating root zone flooding. Peat blocks with elevated transplants were placed on the marsh surface stabilized with metal stakes. To assess the effect of the drainage treatments on water table levels four water table holes were dug in each of the four plots (2 drained and 2 control) and monitored every other day for

3 months. Plants in the drainage experiment were monitored monthly. Full sunlight photosynthetic rates, and leaf counts were made on each replicate monthly from June–August 1991.

In a second experiment we examined the effect of decreasing water table drainage on established *I. frutescens* by diking creek bank areas supporting dense *I. frutescens* stands. We selected four 5-m stretches of creek banks separated from one another by at least 4 m and supporting similar *I. frutescens* stands. Two of the areas were randomly assigned as controls and the remaining two areas were designated as drainage reduction areas. In April 1991 we blocked the drainage in the experimental areas with dikes. Each dike consisted of pilings (4×10 cm) driven into the creek bed 30 cm from the creek bank. Pilings were placed every 75 cm along each bank and heavy gauge plastic mesh (1×1 cm Vexar®) was stapled to the inside of the pilings. The resulting plastic mesh fence was then lined with heavy plastic sheeting and the gap between the creek bank and dike was filled with creek bank mud. Plants in the diked areas were not touched during construction. To assess the effect of decreased drainage on diked plants we measured the full sunlight photosynthetic rate of 30 randomly selected terminal leaves from at least 5–6 plants in each area monthly (June–August 1991). In August we also measured the length of 40 random new growth branches in each area, counted the leaves on each branch, and measured 8 randomly chosen leaves (length and width) on each branch.

Results

The distribution of Iva frutescens with marsh elevation

The major vegetation zones at the study site correspond to specific tidal elevations. The *S. alterniflora*/*S. patens* border occurred at an elevation of 123 cm above sea level, whereas the *S. patens*/*J. gerardi* and *J. gerardi*/*I. frutescens* borders occurred 15 and 32 cm higher, respectively. Variation in the elevation of these borders was strikingly small (Fig. 1).

Robust *I. frutescens* in the center of the *Iva* zone were at an elevation nearly 10 cm higher than the seaward border of the *Iva* zone, and marsh areas dominated by stunted marsh elders were at elevations slightly (5 cm) lower than the seaward border of the *Iva* zone. *Iva frutes-*

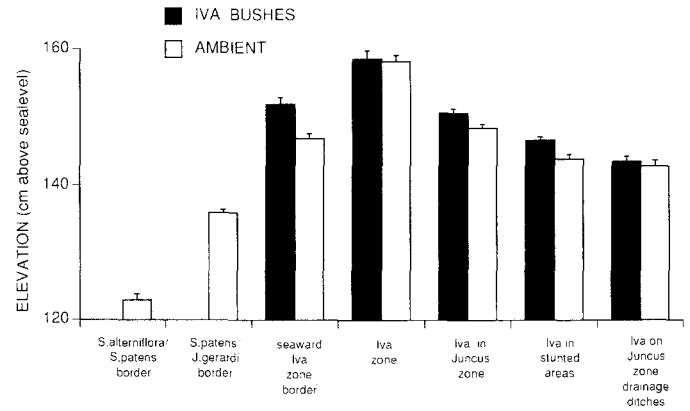


Fig. 1. Results of the elevational survey of vegetation features at the study site in Barrington, Rhode Island. Each bar represents the mean of 10–30 readings (\pm SE). For each *I. frutescens* bush surveyed an elevation was taken at the base and at 3 random points 25 cm from the plant (= ambient) to determine whether plants were associated with locally elevated substrate

cens on creek banks in the *Juncus* zone were also at lower (~ 5 cm) elevations than plants on the seaward border of the *Iva* zone (Fig. 1).

Established marsh elders at lower elevations were often associated with elevated substrate ($p < 0.01$ ANOVA, zone microhabitat interaction). Individuals in the *Juncus* zone, on the seaward border of the *Iva* zone, and in areas supporting stunted plants were frequently ($p < 0.05$, Scheffe tests) found on mounds (Fig. 1). In some cases mounds associated with adult *I. frutescens* were very distinct, up to 10 cm in height, and appeared to be the product of *I. frutescens* root development.

The size and distribution of established marsh elders varied dramatically across the marsh (Table 1). Individuals from the *Iva* zone or creek banks in the *Juncus* zone were much more robust than individuals on the *Iva*/*Juncus* zone border or in stunted plant areas. The biomass of established individuals in the middle of the *Iva* zone was three times higher than plants on the sea-

Table 1. *Iva frutescens* morphology variation across the study site. Data are from 10 haphazardly collected adult plants from each area (\pm SE)

	Area			
	<i>Iva</i> Zone	<i>Iva</i> / <i>Juncus</i> Zone border	Creek Banks	Stunted Plant Areas
Number of live branches	6.1 \pm 0.9	3.2 \pm 1.2	5.3 \pm 0.7	4.2 \pm 0.6
Branch heights (cm)	127 \pm 3.5	87 \pm 4	84 \pm 5	48 \pm 3
Number of leaves	586 \pm 69	202 \pm 23	519 \pm 5.8	165 \pm 36
Leaf lengths (cm)	7.8 \pm 0.1	7.6 \pm 0.1	7.5 \pm 0.1	6.1 \pm 0.1
Relative Leaf Size (Length \times Width in mm)	19.1 \pm 0.5	17.7 \pm 0.6	17.6 \pm 0.6	10.7 \pm 0.3
Root depth (cm)	25.4 \pm 1.3	17.5 \pm 2.8	12.3 \pm 2.0	13.1 \pm 2.0
Root expanse (cm)	49.6 \pm 5.1	37.2 \pm 6.1	46.5 \pm 9	41.4 \pm 5
Total dry weight (gms)	290 \pm 27	94 \pm 11	218 \pm 44	62 \pm 9

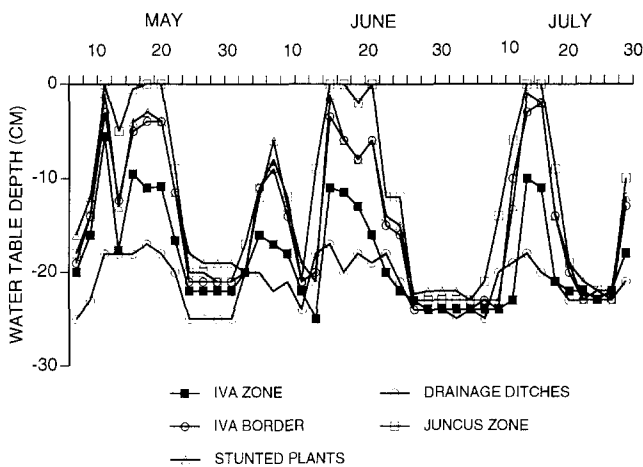


Fig. 2. Water table levels across the high marsh habitat of the study site. In each situation (zone) the data are mean water table depths from 10–20 randomly placed 25 cm deep water table holes. Data were taken every other day for 10 weeks. Standard errors are generally smaller than the symbols and are not shown

ward border of the *Iva* zone, whereas individuals in stunted plant areas were a third smaller than plants on the seaward border. Morphological data on *I. frutescens* also reveals that its root system is relatively shallow, particularly at lower marsh elevations (stunted plant areas, creek banks, Table 1).

Water table variation across the marsh

Water table levels varied markedly both temporally and spatially across the marsh (Fig. 2). During slack tides when the high marsh was not flooding during daily high tides, water table levels dropped below 20 cm and were similar at all locations across the high marsh. In contrast, however, differences in water table levels across the marsh were striking during spring tides (monthly maximum tides) when the high marsh was tidal flooded every day. During monthly spring tides the *Juncus* zone never drained and remained saturated with tidal water for 5–10 days at a time. Moreover, it usually took 2–3 days after flood tides covered the *Juncus* zone for the water table in the *Juncus* zone to drain. In sharp contrast to the *Juncus* zone, in the *Iva* zone and on creek banks in the *Juncus* zone the water table always drained substantially (below 10 cm) even during spring flood tides (Fig. 2). On the seaward border of the *Iva* zone and in areas of stunted *I. frutescens*, water table levels were intermediate. In both of these transitional areas the water table remained within 5–10 cm of the surface for 5–10 days during monthly spring tides. Since most *Iva* roots are located in the top 5–10 cm in all areas (unpublished data), these data suggest that the *Iva*/*Juncus* zone border corresponds to a major breaking point in root zone flooding. Above this border root zones are not flooded for periods longer than a day whereas below the border prolonged root zone flooding occurs monthly with spring tides.

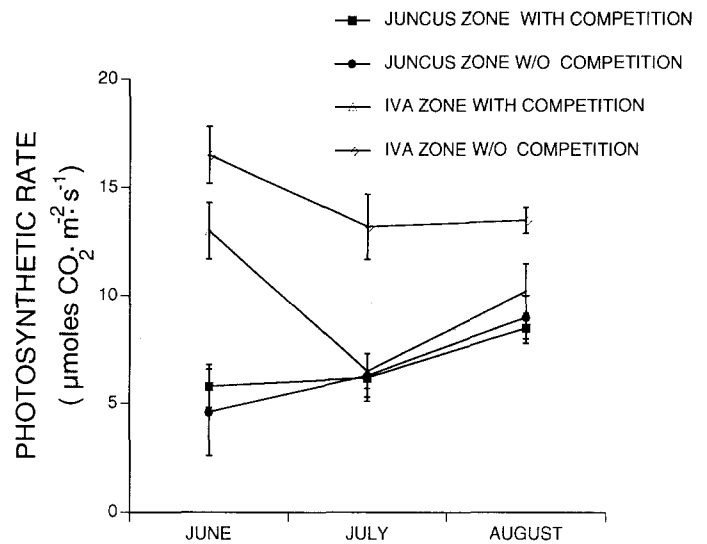


Fig. 3. Monthly photosynthetic rates of adult *I. frutescens* transplanted across the high marsh with and without competitors (surrounding vegetation). Each data point represents the mean (\pm SE) of 10 measurements taken under full sunlight

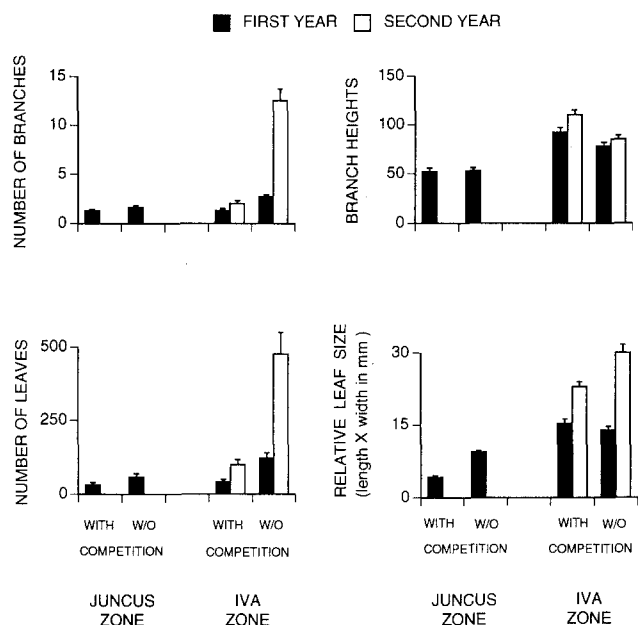


Fig. 4. Performance of adult *Iva frutescens* transplanted into the *Iva* and *Juncus* zones with and without competition (surrounding vegetation). Each bar represents the mean (\pm SE) of 8–10 transplants. None of the plants transplanted into the *Juncus* zone survived through a second growing season. Leaf size was simply calculated as leaf length \times maximum width for randomly selected leaves

Field transplants across the *Iva*/*Juncus* zone border

I. frutescens transplanted into the *Juncus* zone with and without *Juncus* present had sharply reduced photosynthetic rates in comparison to individuals transplanted into the *Iva* zone without neighbors (Fig. 3, $p < 0.01$, ANOVA). This suggests that *I. frutescens* is depressed in the *Juncus* zone by physical processes rather than by the presence of potential competitors. In contrast, in the *Iva*

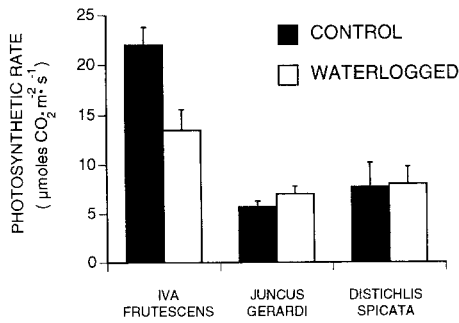


Fig. 5. Photosynthetic rates ($\bar{x} \pm \text{SE}$) of plants grown in the greenhouse under drained and waterlogged soil conditions for 4 months. For each case $n = 10$

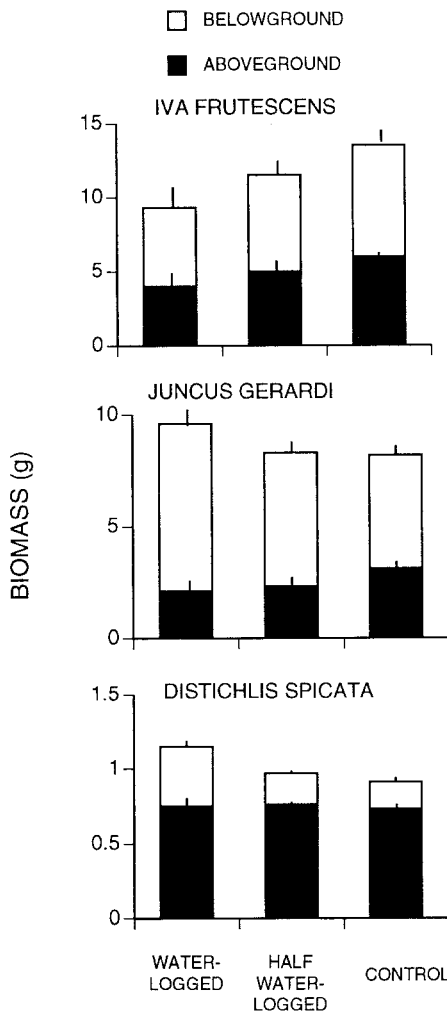


Fig. 6. Biomass ($\bar{x} \pm \text{SE}$) of plants grown in the greenhouse under drained and waterlogged soil conditions for 4 months ($n = 16$ each case). In the half waterlogged treatments plants were grown in pots with waterlogged soil at a depth of 5 cm below the soil surface

zone transplants without neighbors had higher photosynthetic rates than plants with competitors present ($p < 0.01$, zone \times treatment interaction, ANOVA), suggesting that intraspecific competition limits *Iva* growth in the *Iva* zone.

After a single growing season *I. frutescens* transplanted into the *Juncus* zone were severely stunted (by 60%)

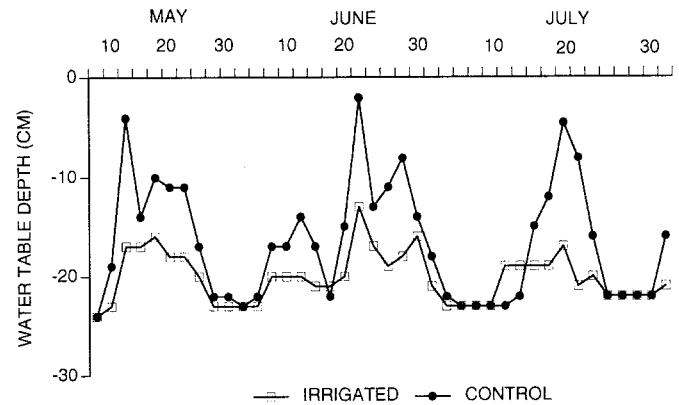


Fig. 7. Water table levels (from water table holes) in artificially irrigated plots and adjacent unmanipulated controls ($n = 8$ each case). Standard errors are generally smaller than the symbols

in comparison to transplants into the *Iva* zone without neighbors and none of the *I. frutescens* transplanted into the *Juncus* zone with or without neighbors survived a second growing season (Fig. 4). For *Iva* transplanted into the *Iva* zone, individuals transplanted to locations without potential competitors showed striking competitive release (Fig. 4). After one growing season competitor-free transplants produced over twice as many leaves as transplants with competitors, and after two seasons competition-free plants were nearly five times larger than plants with competitors (Fig. 4). While having fewer leaves and branches, however, *I. frutescens* transplants into the *Iva* zone with competitors were taller than transplants without competitors (Fig. 4).

Greenhouse flood tolerances

Greenhouse tests revealed marked differences in the flood tolerances of *I. frutescens* and the perennial turfs that dominate lower marsh elevations. After five months, the photosynthetic rates of waterlogged *I. frutescens* (Fig. 5) were reduced by nearly a third in comparison to controls ($p < 0.01$, ANOVA). In contrast, the photosynthesis of *J. gerardi* and *D. spicata* was not significantly influenced by waterlogging ($p > 0.50$, ANOVA; both cases).

After five months in waterlogged soil *I. frutescens* seedlings were 40% smaller (Fig. 6) than their counterparts reared in control conditions ($p < 0.01$, ANOVA), while *J. gerardi* and *D. spicata* tended ($p < 0.10$, ANOVA) to grow better under waterlogged than control conditions. Moreover, in contrast to *I. frutescens* both *J. gerardi* and *D. spicata* allocated more biomass to belowground than aboveground structures under waterlogged conditions, than under control conditions ($p < 0.01$, ANOVA)

In addition to stunted growth, *I. frutescens* seedlings reared under waterlogged conditions developed morphological features generally associated with plants found on waterlogged, anaerobic soils. Hypertrophied lenticels and aboveground (aerial) roots were found on *I. frutescens* reared in waterlogged soils, but not on seedlings grown under control conditions.

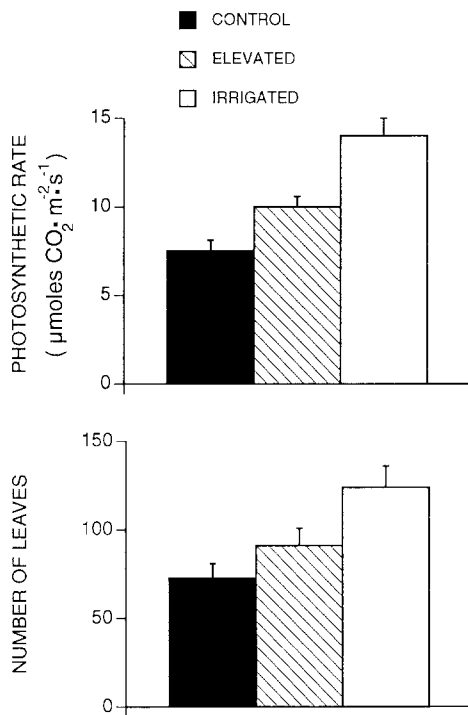


Fig. 8. Performance of *Iva frutescens* adults transplanted into the *Juncus* zone in control plots, experimentally irrigated plots and elevated above the surface. Each base represents the mean \pm SE of 8–10 replicates 12 weeks after transplantation

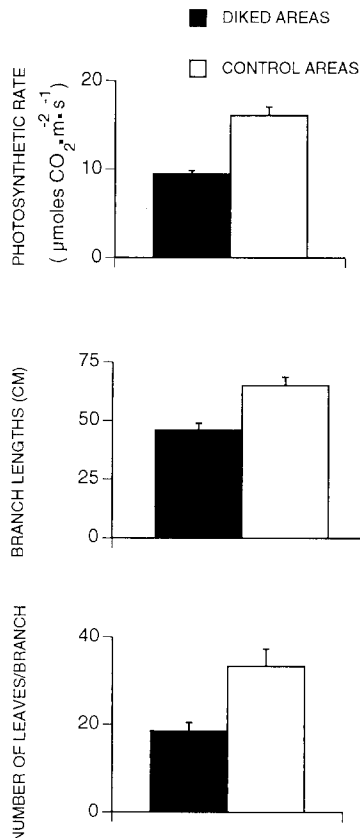


Fig. 9. Performance of established *Iva frutescens* adults bordering creek banks in the *Juncus* zone in control areas and areas that had been diked to limit water table drainage ($\bar{x} \pm$ SE) $n=24$ for each situation

Field water table manipulations

Ditching plots in the *Juncus* zone to lower the water table effectively ($p < 0.01$, ANOVA) drained experimental plots relative to adjacent unmanipulated control plots (Fig. 7). In the ditched plots even during monthly spring tides the water table generally fell below 15 cm every day, whereas in control plots the water table frequently remained above 15 cm during spring tides.

Iva frutescens transplanted to ditched plots or elevated above the surface had higher photosynthetic rates and produced more leaves than controls (Fig. 8, $p < 0.01$, ANOVA; both cases). Ditching and elevating plants above the substrate did not influence *I. frutescens* stem heights or leaf sizes ($p > 0.50$, ANOVA; both cases). Ditching did not effect the biomass or tiller densities of either *J. gerardi* or *D. spicata* ($p > 0.80$, ANOVA, all cases).

Diking *Juncus* zone creek banks supporting established *I. frutescens* stunted marsh elder performance (Fig. 9). By August the photosynthetic rate of plants in diked areas was nearly half that of adjacent undiked plants ($p < 0.01$, ANOVA) and the growth of plants in diked areas was strongly suppressed. Plants in diked areas produced shorter branches and only half as many leaves as plants in undiked control areas ($p < 0.01$, ANOVA; both cases).

Discussion

Our results suggest that frequent tidal flooding limits marsh elders to high marsh habitats that are not subject to extended periods of flooding and that water table dynamics are an important determinant of spatial patterns in marsh plant communities.

Spatial patterns in water table drainage and marsh plant distributions

Marsh plant communities are characterized by striking tidal zonation where the breaking points between plant vegetation zones correspond to major breaking points in tidal flooding (Johnson and York 1915; Miller and Egler 1950; Nixon 1982). This tight correspondence between flooding and vascular plant zonation has long suggested to ecologists that tidal flooding and water table levels are important determinants of marsh zonation patterns.

Experimental evidence that flood tolerances dictate marsh plant zonation patterns, however, has been lacking. Changes in marsh vegetation patterns associated with disturbances that alter water table levels (Lesser 1975) and abrupt elevational shifts in substrate oxygen levels that correspond to vegetation shifts (Gleason 1980; Mendelssohn et al. 1981) have been cited as support for the role of flooding patterns in generating marsh plant zonation. Our work has not only shown that the zonation of marsh elders corresponds to field flooding pat-

terns and tolerances, but that experimentally manipulating water table levels in the field leads to predictable effects on marsh elder success.

Flooding effects on marsh plants

The major problem created for plants by tidal flooding is anoxic soils (Armstrong 1975) and plants living in flooded soils must have mechanisms to oxygenate their roots. *Spartina alterniflora* which dominates frequently flooded low marsh habitats in New England has well-developed aerenchyma tissue that diffuses oxygen to their roots (Teal and Kanwisher 1966; Gleason 1980) as well as metabolic mechanisms to deal with prolonged periods of anaerobiosis (Mendelssohn et al. 1981). Experimentally increasing the drainage of low marsh habitats increases cordgrass growth and production (Wiegert et al. 1983; King et al. 1982) demonstrating that flooding can limit cordgrass growth in low marsh habitats.

The low marsh/high marsh border represents an abrupt transition from daily flooded low marsh habitats to regularly drained habitats. In New England marshes *Spartina alterniflora* and *Spartina patens* monocultures abut one another at the major tidal breaking point. *Spartina patens* lacks effective aerenchyma tissue and is unlikely to oxygenate low marsh soils (Gleason 1980). Consequently, when transplanted into the low marsh, *S. patens* dies with or without *Spartina alterniflora* present revealing that it is precluded from the low marsh by physical rather than biotic processes (Bertness and Ellison 1987; Bertness 1991a). In contrast *S. alterniflora* is excluded from persisting in the high marsh by the competitive displacement of high marsh turfs (Bertness 1991a).

Our work has shown that plant zonation on the terrestrial border of New England marshes is also dictated by tidal flooding and marsh water table dynamics. At elevations in the *Juncus* zone immediately below the *Iva* zone, spring tides saturate the substrate for 5–10 day periods, whereas in the *Iva* zone periods of prolonged flooding are uncommon (Fig. 2). We have shown that: 1) *I. frutescens* dies when transplanted to lower tidal heights in the *Juncus* zone where it is exposed to prolonged root zone flooding (Fig. 4), 2) that *I. frutescens* is relatively intolerant of flooding conditions in comparison to plants found at lower marsh elevations (Figs. 5 and 6), and 3) that artificially manipulating the water table on the terrestrial border of the marsh strongly affected marsh elder performance (Figs. 8 and 9). Together these data provide strong experimental evidence that tidal flooding limits the distribution of *I. frutescens* across New England marshes.

Our laboratory flooding experiment and elevation survey of *I. frutescens* habitats also suggest that *I. frutescens* may play an active role in generating marsh elevation patterns through hummock formation (*sensu* Kozlowski 1984). At our study site adult *I. frutescens* are often found associated with elevated mounds at lower but not higher marsh elevations (Fig. 1). These mounds

or hummocks can be conspicuous and appear to be the product of *I. frutescens* root growth and sediment binding. Hummock formation is not unusual in woody wetland plants and has generally been interpreted as a plant response to elevate roots above waterlogged anaerobic substrate (Kozlowski 1984).

Physical processes and marsh plant zonation

While tidal flooding clearly plays a major role in dictating marsh plant zonation patterns, flood tolerances are obviously only responsible for determining the lower elevation limits of marsh plants (Gleason 1980; Bertness and Ellison 1987). In general, marsh plants have been found to be capable of thriving above their natural elevation limits in marsh habitats in the absence of interspecific competitors (Snow and Vince 1984; Bertness and Ellison 1987; Bertness 1991a, b; Pennings and Callaway 1992).

To date all available evidence strongly suggests that the conspicuous tidal zonation of marsh plant communities is simply the product of the lower borders of marsh plant populations being set by harsh physical conditions while the upper borders are generally limited by interspecific competitive processes. Further elucidation of the establishment and maintenance of marsh plant zonation patterns will require a clearer mechanistic understanding of how marsh plants deal with physical stresses and the determinants of competitive dominance.

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