

Physiological Integration among Clonal Ramets during Invasion of Disturbance Patches in a New England Salt Marsh

SCOTT W. SHUMWAY*

Graduate Program in Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

Received: 14 June 1994 Accepted: 25 March 1995

Resource sharing between ramets growing across environmental resource gradients may have important consequences for clonal plant populations and community dynamics. As the clonal salt marsh grasses, *Spartina patens* and *Distichlis spicata*, vegetatively colonize disturbance-generated bare patches, they span steep gradients in soil salinity and available sunlight. Examination of water relations and carbon translocation in the field and greenhouse revealed that connected ramets of these marsh grasses share water and carbon in response to gradients in resource availability. Ramets colonizing disturbance patches rely upon physiological integration with connected parent ramets to overcome water stress associated with hypersaline patch environments. In addition, upon establishment inside a bare patch, daughter ramets may translocate carbon back to shaded parent ramets in the surrounding vegetation outside of patches.

Physiological integration of ramets colonizing disturbance-generated bare patches and parent ramets outside of patches may explain the predominance of vegetative invasion over sexual recruitment in marsh succession. Hypersaline soil conditions, which inhibit seedling recruitment into patches, have little effect on the success of clonal colonizers that can import water from parent ramets. This success appears to be due to the ability of clonal marsh grasses to translocate water and carbon products between ramets growing across opposing gradients in resource availability.

© 1995 Annals of Botany Company

Key words: Clonal integration, *Distichlis spicata*, halophytes, salt marsh ecology, secondary succession, *Spartina patens*.

INTRODUCTION

Many higher plants exhibit clonal growth morphologies characterized by a horizontal rhizome connecting reiterated shoots or ramets. Physiological integration of connected ramets enables individual plants (genets) to experience and respond to microenvironments that may differ dramatically in quality (for review see Pitelka and Ashmun, 1985). In some cases clonal plants may be able to survive in seemingly unfavourable habitats because of the ability to translocate resources from ramets growing in favourable microhabitats to ramets located in less favourable areas. Sharing of water (Salzman and Parker, 1985; Alpert and Mooney, 1986; Lau and Young, 1988; Alpert, 1990), carbon (Ashmun, Thomas and Pitelka, 1982; Newell, 1982; Hartnett and Bazzaz, 1983; Callaghan, 1984; Alpert and Mooney, 1986), and nitrogen (Evans, 1988; Alpert, 1991) across environmental resource gradients has been demonstrated for several taxa of clonal plants. Physiological integration of connected ramets may also enable clonal plants to select preferentially one extreme of a habitat gradient for increased growth (Salzman, 1985) and to exploit patchy resource-rich microsites while simultaneously expanding across environments characterized by low resource availability (Slade and Hutchings, 1987). Physiological integration of ramets should

give clonal plants an advantage over non-clonal species in colonizing disturbed habitats, especially those characterized by high physical stress or resource deficiencies.

Clonal salt marsh plants colonizing disturbance-generated bare patches are ideal for addressing questions about clonal integration during secondary succession. New England high salt marshes are characterized by distinct vegetation zones composed of nearly monospecific stands of a few dominant perennial species. *Spartina patens* (Ait.) Muhl., salt hay, and *Juncus gerardi* Loisel., black rush, respectively, occupy the seaward and terrestrial edges of the high marsh. *Distichlis spicata* (L.) Greene, spike grass, is sparsely scattered throughout the high marsh. High marsh species will be referred to by their generic names throughout the remainder of the paper. These species experience steep gradients in salinity and sunlight as they colonize disturbance-generated bare patches. Bare patches are created when extensive mats of dead plant stems (wrack) from the previous season are rafted onto the high marsh by spring tides and winter storms (Hartman, Caswell and Valiela, 1983) and smother the underlying vegetation. Such patches quickly become hypersaline relative to surrounding vegetation due to solar evaporation of poorly draining tidal water (Bertness, Gough and Shumway, 1992). Bare patches are colonized almost exclusively by vegetative expansion of surrounding plants, and patch succession follows a predictable sequence. *Distichlis* is the first species to invade patches vegetatively and is followed by *Spartina* and later *Juncus* (Bertness,

* Current address: Department of Biology, Wheaton College, Norton, MA 02766, USA.

1991). This pattern of invasion is presumably the result of interspecific differences in physiology and growth morphology (Bertness *et al.*, 1992). *Distichlis* has a runner morphology (guerilla morphology *sensu* Lovett-Doust, 1981) with widely spaced ramets (spacing of 20 cm is not uncommon) composed of a few tillers. *Spartina* has a turf morphology (phalanx *sensu* Lovett-Doust, 1981) with more closely spaced ramets (≤ 5 cm) and many tillers per ramet. *Juncus* forms a yet more tightly compressed turf with very little space between ramets (< 2 cm). *Distichlis* and *Spartina* are highly salt tolerant, possessing specialized salt removal glands (Anderson, 1974; Hansen *et al.*, 1976). *Juncus*, which lacks salt glands, is relatively intolerant of high salinities and is unable to survive inside most bare patches (Bertness *et al.*, 1992).

In this study I investigate the role of physiological integration among ramets in the invasion of bare patches. *Spartina* and *Distichlis* runners (defined here as rhizomes and their connected ramets) growing into disturbance patches experience gradients in sunlight and salinity as they extend from dense surrounding vegetation into bare substrate. Plants colonizing bare patches may experience an initial cost of growing in a physically stressful environment, which is presumably offset by some benefit to the entire plant. I hypothesized that ramets growing into hypersaline patches may import water from parent ramets located in the surrounding vegetation to overcome the stress of growing in a high salinity environment. I hypothesized that ramets in bare patches translocate carbon back to parent ramets that experience intense shading in the undisturbed vegetation. I tested the ability of *Spartina* and *Distichlis* to translocate water and carbon between ramets growing across gradients in salinity and sunlight in the field and in the greenhouse. The results suggest that clonal grasses are able to translocate resources across patch borders during secondary succession. The observed patterns are interpreted within the larger context of salt marsh community dynamics (Bertness, 1991; Shumway and Bertness, 1992; Bertness and Shumway, 1993).

METHODS

Field work was conducted at Rumstick Cove in Barrington, RI, USA. Rumstick Cove is a typical small New England salt marsh (Nixon, 1982) which has been studied extensively (Bertness and Ellison, 1987; Bertness, 1991; Shumway and Bertness, 1992).

Field water potentials

Xylem water potentials were measured on *Spartina* and *Distichlis* ramets with and without rhizome connections to parent ramets to test for physiological integration between ramets colonizing bare patches and parent ramets in the surrounding vegetation. Differences in water potential may be used to infer the direction of water movement in the xylem. Low water potential may also be used as an indicator of high water stress (Kramer, 1983). Natural high marsh bare patches chosen for this experiment were categorized as low salinity [< 22 parts per thousand (ppt) NaCl] or high

salinity (> 25 ppt NaCl) on the basis of monthly soil salinity measurements. Pore-water was collected from a soil depth of 5 cm using 1.25 cm PVC sampling tubes (see Bertness, 1991 for details) at the centres of patches ($n = 5$ per patch) and 1 m away in dense vegetation. Water was removed from the tubes monthly (Jun.–Aug.) and salinity was measured using a hand-held NaCl refractometer.

In each patch 16 ramets of similar size were selected along different invading runners inside the patch and in the ambient vegetation 1 m away from the patch border. Only ramets located at the proximal end of a runner that could be visually identified as extending from dense vegetation into a bare patch were used for measurements on colonizing ramets. Half of the marked ramets were randomly designated as controls and the other half were selected to have their connecting rhizomes severed. This was repeated for *Distichlis* and *Spartina* in as many natural bare patches as could be found in 1987 and 1988 (For *Distichlis* $n = 2$ low and 6 high salinity; *Spartina* $n = 3$ low and 3 high salinity) along the interface between the *Spartina* and *Juncus* vegetation zones. Xylem water potentials were measured for individual leaves from a set of ramets ($n = 16$ inside and 16 outside of each patch) between 1300 and 1600 h on a sunny day using a Scholander-type pressure chamber (PMS Instruments Model 1000). A single leaf was selected from each ramet and measurements were made in the field immediately after cutting the leaf from the plant. Mid-day water potentials were chosen as the time of day when plants would be experiencing the greatest water stress. The rhizomes of experimental ramets were then severed by running a sharp knife 5 cm from the ramets to a depth of 15 cm (excavation has shown rhizomes to be located within 10 cm of the surface and roots to be concentrated directly below ramets). Water potentials were remeasured on the same plants 24 h later. The interaction terms of separate two-way ANOVAs (treatment \times measurement time) were used to test for differences between experimental and control treatments inside and outside of each patch type before and after severing of rhizomes (measurement time). In cases where the interaction was significant ($P < 0.05$) *a posteriori* paired *t*-tests were used to test for significant changes in water potential before and after rhizome severing for each treatment. Standard Bonferroni corrections were used to reduce type I error associated with multiple *a priori* tests (Rice, 1989). Adjusted *P*-values are reported with the results. Any parallel changes (non-significant interaction term) in water potential exhibited by experimental and control treatments were attributed to temporal environmental changes.

Integration across an imposed salinity gradient in the greenhouse

To corroborate the field experiments, I examined the ability of runners to translocate water across salinity gradients under controlled greenhouse conditions. In Aug. 1988 *Spartina* and *Distichlis* runners from Rumstick Cove were planted in the Brown University greenhouse. Plants were collected > 5 m apart to ensure that they were distinct genotypes ($n = 12$ per species). Plants were grown in the

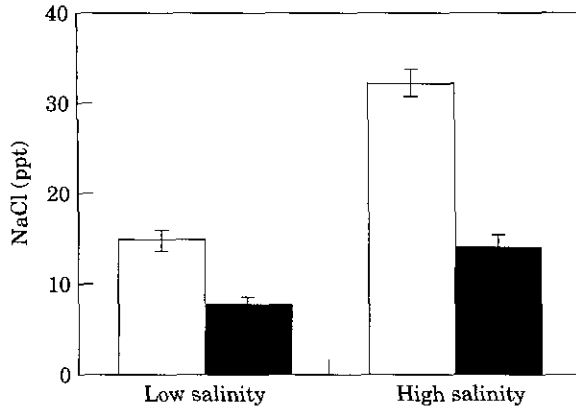


FIG. 1. Soil salinities ($\bar{x} \pm s.e.$) of low and high salinity bare patches, □, and the surrounding vegetated areas, ■, used for the water potential experiment conducted in the field.

greenhouse for 2 years in a soil mixture consisting of equal parts perlite, vermiculite, and artificial potting soil. Prior to the experiment, three runners consisting of four ramets connected by a common rhizome (roughly 15 cm long) were cloned from each genotype for use in each of three watering treatments. Runners were planted in plastic bins (25 × 38 × 13 cm) with plastic dividers extending widthwise across the middle of each bin. Dividers were waterproofed at the edges using silicone caulking. Rhizomes were fitted through a slit in the divider that was then sealed with duct tape. Runners were planted with half of their ramets on one side of the divider and the rest on the other side. Subdivisions were randomly assigned to receive fresh or salt water (30 ppt NaCl) so that bins belonged to one of three watering treatments: both sides receiving fresh water (fresh–fresh), both sides receiving salt water (salt–salt), or one side receiving fresh water and the other receiving salt water (fresh–salt). Plants were allowed to acclimate to the new pots for 2 weeks before experimental watering was initiated.

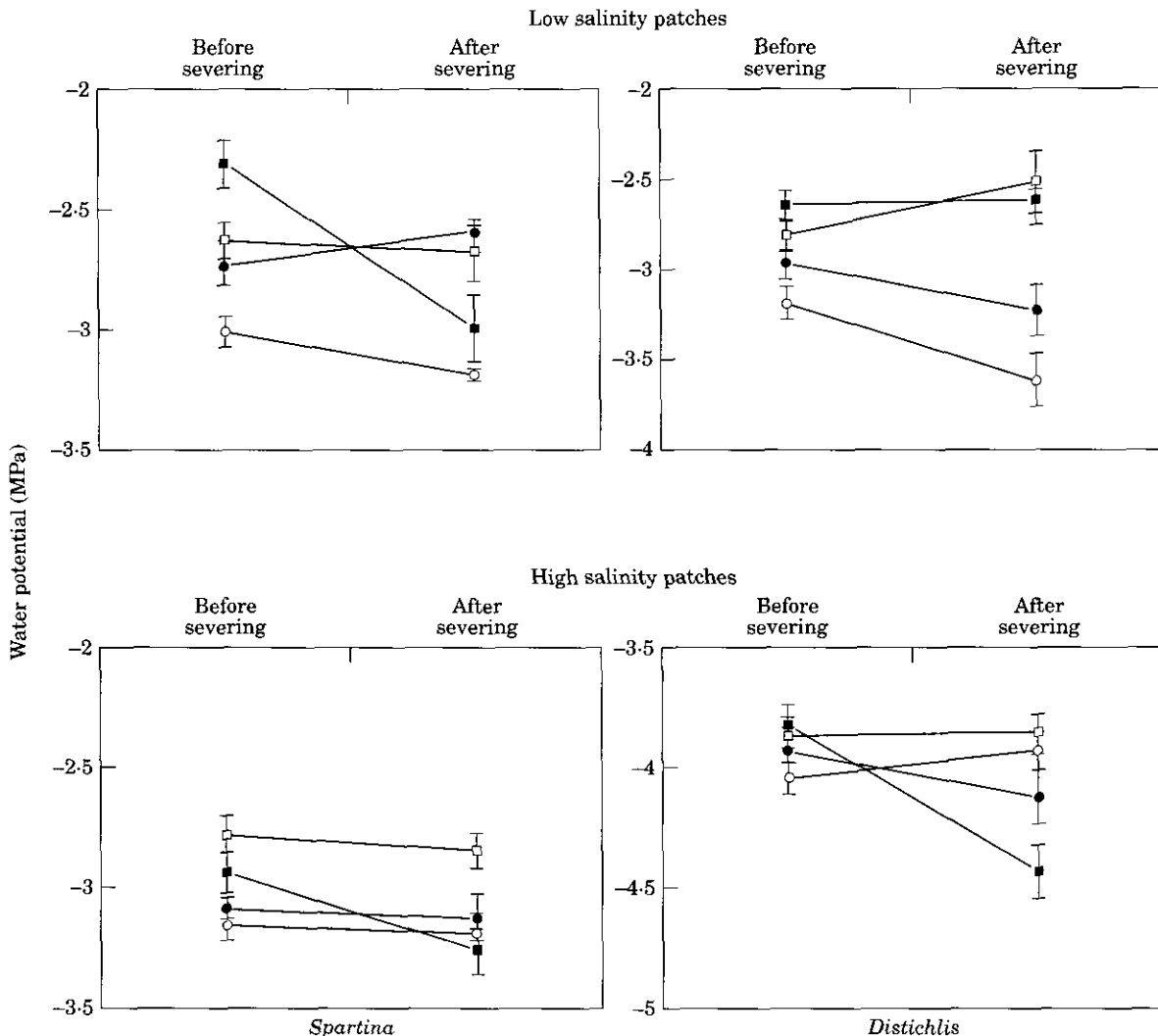


FIG. 2. Mid-day xylem water potentials ($\bar{x} \pm s.e.$) of *Spartina* and *Distichlis* ramets growing inside bare patches with rhizomes severed (■) and intact (□) and ramets growing outside of patches in dense vegetation with severed (●) and intact (○) rhizomes.

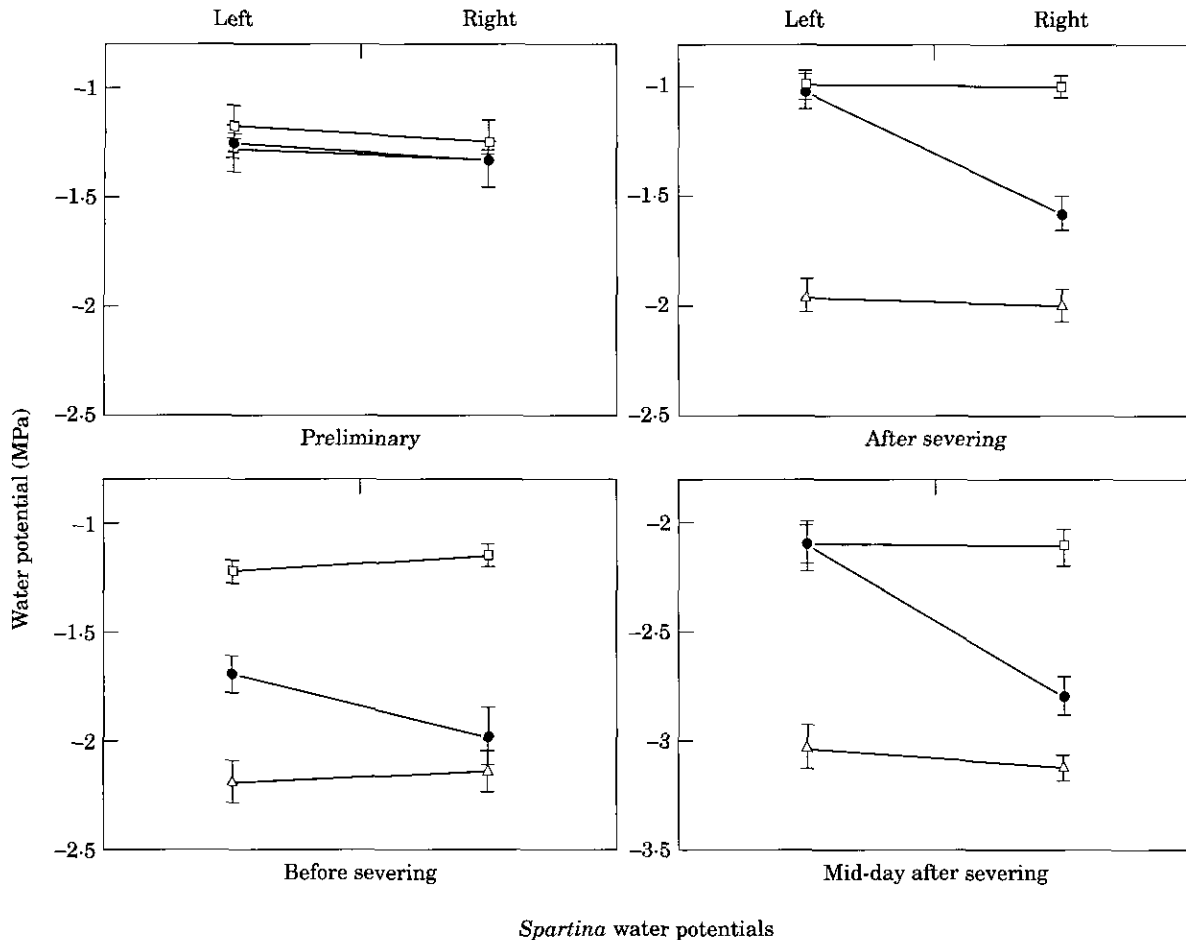


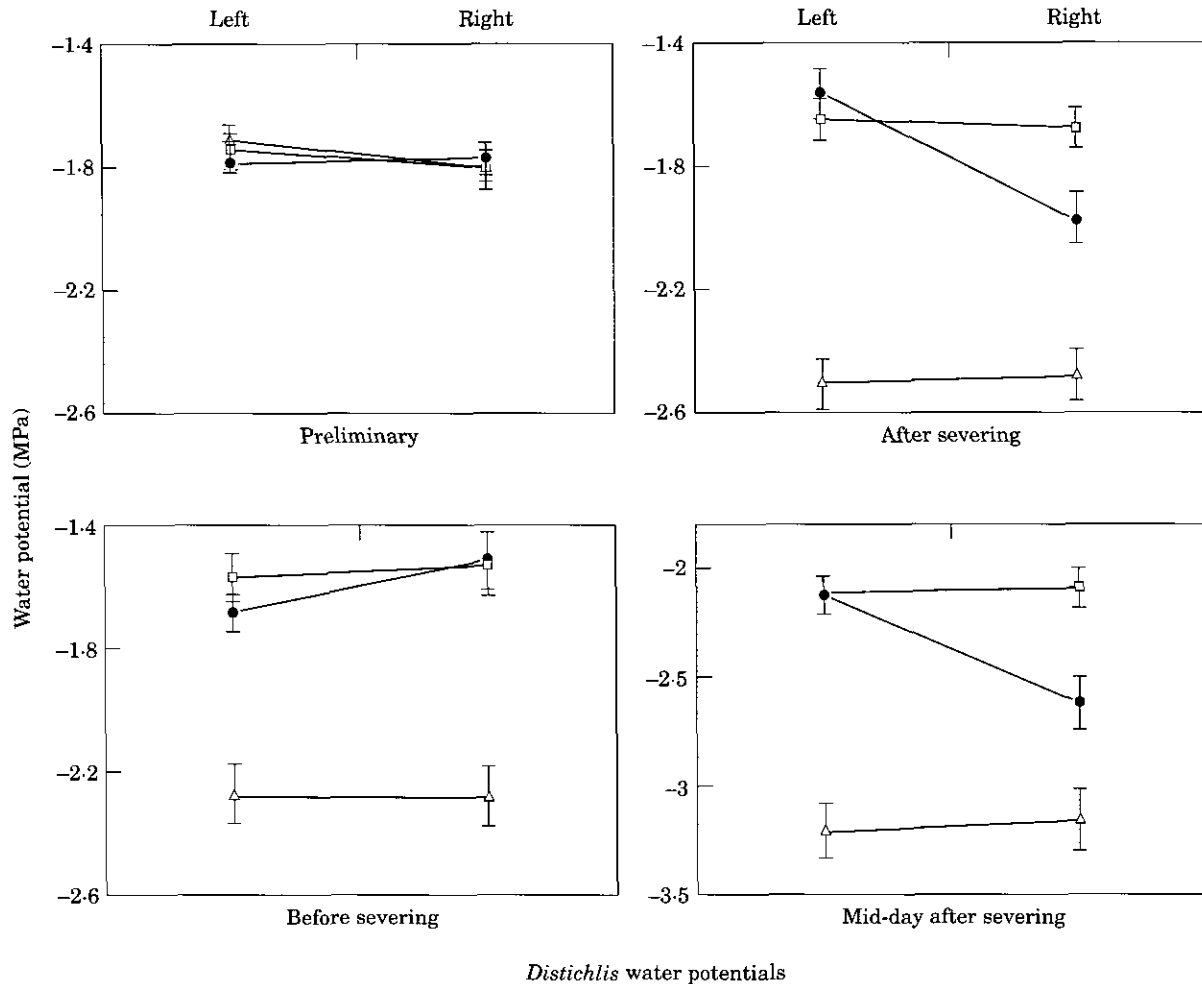
FIG. 3 For legend see facing page.

The experiment ran for 2 months (15 Jul.–15 Sep.). All plants were fertilized once a week with a 20:20:20 N:P:K fertilizer. When all replicates were still receiving fresh water, initial physiological measurements were made and numbers of tillers counted. Early morning (0500–0900 h) xylem water potentials were measured using a pressure chamber. Photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was measured at mid-day (1000–1600 h) using a portable infrared gas analysis system (LCA-2, Analytical Development Corporation). Natural light was used for these measurements with an irradiance of $1000\text{--}1300 \mu\text{E m}^{-2} \text{ s}^{-1}$. After 2 months of experimental watering, these measurements were repeated and then rhizomes were cut adjacent to either side of the dividers. The following day water potentials were measured in the early morning and again during mid-day (1300–1400 h). Photosynthesis was also measured after severing of rhizomes. The water potentials and the photosynthetic rates of ramets on opposite sides of the divider in each treatment were compared using one-way ANOVAs.

Carbon sharing

The ability to transport carbon products between ramets was examined with autoradiographs of ^{14}C -labelled

Distichlis and *Spartina* runners colonizing bare patches. Two patches located at the upper reaches of the *Spartina* vegetation zone were selected for this experiment. For each patch and each species, equal-sized mature ramets ($n = 3\text{--}4$ per treatment) were labelled inside bare patches and just outside patches. Labelled ramets were part of a runner growing into a bare patch from the surrounding vegetation. A metal wire stand with a syringe of $100 \mu\text{l}$ acetic acid positioned over a flip-top micro-centrifuge tube containing $10 \mu\text{Ci NaH}^{14}\text{CO}_3$ in $100 \mu\text{l H}_2\text{O}$ at pH 8 was placed next to the ramet to be labelled. The stand and ramet were sealed in a clear plastic bag that formed an airtight seal with the ground. The micro-centrifuge tube was opened and acid added to volatilize the ^{14}C as $^{14}\text{CO}_2$. Ramets sealed in bags were allowed to take up $^{14}\text{CO}_2$ for 2 h during mid-morning on a cloudless sunny day (0900–1100 h, 25 Jul. 1987). After 2 weeks the labelled ramets along with connecting rhizomes, ramets, and roots were excavated, dried, and taped intact to herbarium paper. Autoradiographs were made by pressing the mounted runners against X-ray film (Kodak X-OMAT AR-5) at -10°C for 2 weeks. Developed autoradiographs were scored visually for presence *vs.* absence of photosynthate movement to acropetal (proximal, to younger daughter ramets) and basipetal (distal, back to parents) ramets and to developing shoot tips.



FIGS 3 and 4. Xylem water potentials (MPa) of *Spartina* and *Distichlis* growing in the greenhouse under fresh-fresh (□), fresh-salt (●) and salt-salt (△) watering treatments. Note the different y-axis scale for mid-day measurements. Each data point represents the mean (\pm s.e.) of 12 replicates. The only treatments to differ significantly from one side of the divider to the other were the fresh-salt treatments with rhizomes severed ($P = 0.0001$ ANOVA, each species).

Light availability inside bare patches and the surrounding vegetation was quantified in Jun. and Aug. of 1987 using a Li-Cor Solar Monitor (Model 1776). Light attenuation was determined by measuring solar radiation 5 cm from ground level inside patches and in surrounding vegetation, as well as above the vegetation canopy.

RESULTS

Field water potentials

Runners invading disturbance patches spanned a two-fold increase in salinity from vegetation to bare substrate (Fig. 1). Pore-water salinities inside low salinity patches ranged from 5–22 ppt NaCl ($\bar{x} \pm$ s.e. = 14 ± 1) while high salinity patches ranged from 25–50 ppt ($\bar{x} \pm$ s.e. = 32 ± 2) at the time water potentials were measured.

Distichlis and *Spartina* ramets colonizing disturbance patches relied on rhizome connections with parent ramets to relieve water stress in the hypersaline patches. Xylem water

potential generally decreased for ramets inside patches after severing of their rhizomes, but not in uncut controls or ramets outside of patches (Fig. 2). After severing of rhizome connections *Spartina* ramets colonizing bare patches experienced significant drops in xylem water potential in both low and high salinity patches ($P < 0.004$ paired *t*-tests) while unsevered controls did not ($P < 0.001$ ANOVA, treatment \times measurement time interaction for each patch type). Ramets outside of low salinity patches experienced a slight increase in water potential after severing while water potential of controls dropped between measurements ($P < 0.0001$ ANOVA, treatment \times measurement time). Ramets outside of high salinity patches did not display a significant change in water potential between measurements for either treatment ($P > 0.75$ ANOVA, treatment \times measurement time). Xylem water potentials of severed ramets were roughly 0.5 MPa lower (more negative) in high salinity relative to low salinity patches ($P < 0.0001$ ANOVA).

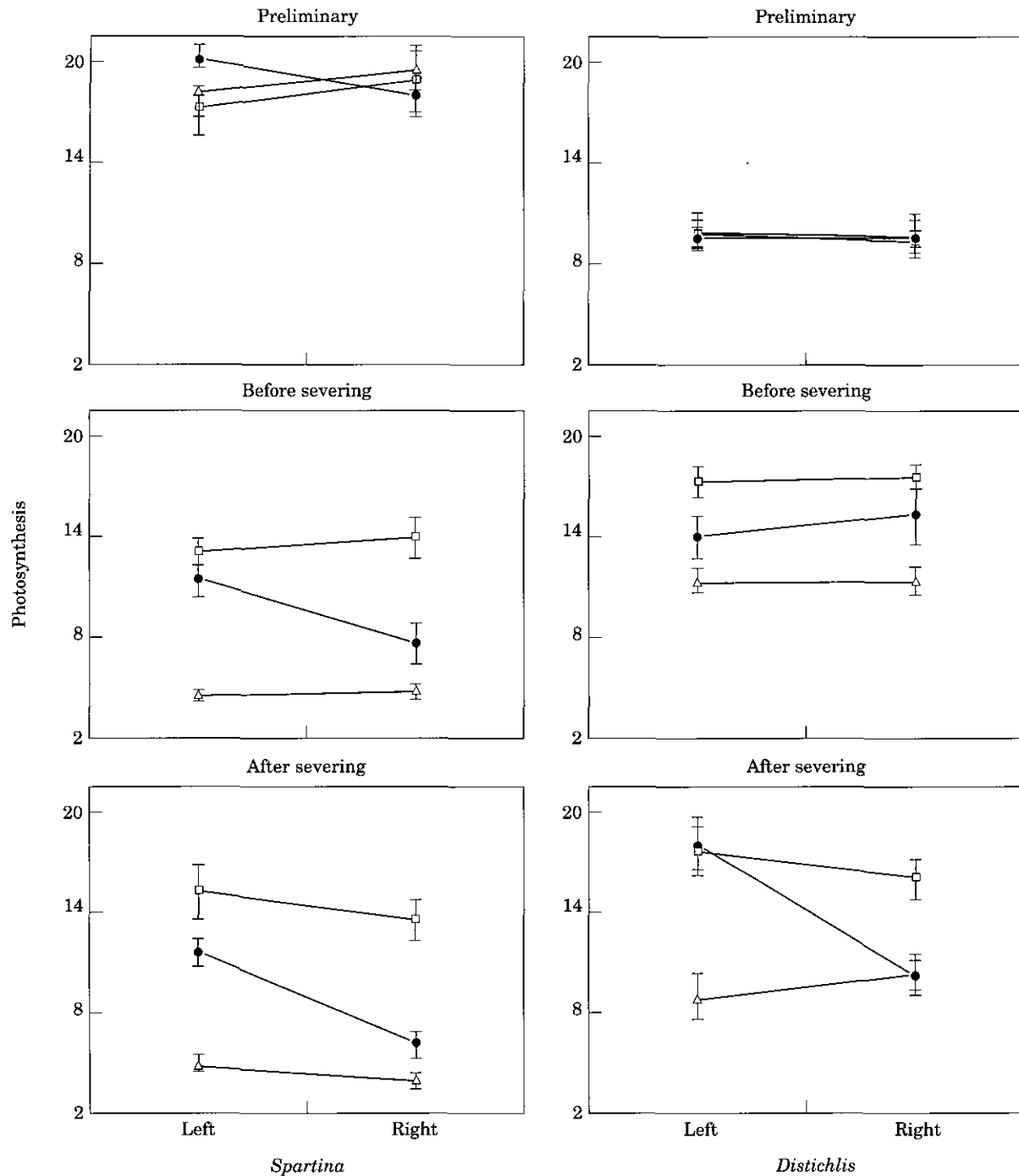


FIG. 5. Photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of *Spartina* and *Distichlis* grown in fresh-fresh (\square), fresh-salt (\bullet) and salt-salt (\triangle) watering treatments in the greenhouse. The only replicates to differ significantly from one side of the divided pots to the other were fresh-salt treatments with severed rhizomes for both species ($P < 0.0005$) and the *Spartina* fresh-salt treatment before severing ($P < 0.05$ ANOVA).

Distichlis ramets inside low salinity bare patches did not show any change in water potential in response to severing ($P > 0.40$ ANOVA, treatment \times measurement time), however, control ramets located outside of patches experienced an unexplained decrease in water potential between measurements ($P < 0.005$ ANOVA, treatment \times measurement time interaction). As with *Spartina*, *Distichlis* ramets inside high salinity bare patches experienced a significant decrease in

water potential from -3.82 to -4.42 MPa following rhizome severing ($P < 0.0004$ paired *t*-test) while intact controls did not experience a change in water potential between measurements ($P < 0.0001$ ANOVA, treatment \times measurement time interaction). Severed and intact control replicates located outside patches did not show differential changes in water potential between measurements ($P > 0.30$ ANOVA, treatment \times measurement time). Water potentials

were approximately 1 MPa lower (more negative) for plants associated with high salinity patches for all treatments ($P < 0.0001$ ANOVA).

Integration across an imposed salinity gradient in the greenhouse

In the greenhouse, runners of *Spartina* and *Distichlis* showed physiological integration of connected ramets exposed to high and low salinities (Figs 3–4). Prior to experimental watering, measurements of xylem water potential, photosynthetic rate, and tiller number failed to detect any differences between ramets at separate ends of the divided pots for either *Distichlis* or *Spartina* ($P > 0.10$ in all cases, one-way ANOVA). After 2 months of experimental watering, however, water potentials of the fresh–fresh treatment averaged 1 MPa higher (less negative) than plants in the salt–salt treatment (Fig. 3). Water potentials of *Spartina* runners in the fresh–salt treatment were slightly, but not significantly, lower for salt ramets relative to fresh watered ramets ($P = 0.09$ one-way ANOVA) while *Distichlis* did not show any difference in water potential between fresh and salt watered ramets with rhizomes intact ($P > 0.15$). After severing of rhizome connections the fresh–fresh and salt–salt treatments still failed to show any difference in water potential between ramets on opposite sides of the divider. In sharp contrast, the fresh–salt runners showed striking differences in water potential on opposite sides of the divider. After severing, ramets receiving salt water averaged early morning and mid-day water potentials that were 0.6 and 0.5 MPa lower for *Spartina* and *Distichlis*, respectively, than their previously connected counterparts on the freshwater side of the bin ($P < 0.0001$ for each species, ANOVA).

Patterns of photosynthesis were similar to the responses observed for xylem water potential (Fig. 5). Runners receiving only fresh water had higher photosynthetic rates than runners receiving only salt water and showed no differences between ramets at opposite sides of the dividers. The mean photosynthetic rate of *Spartina* ramets in the fresh–salt treatment was 34% lower for salt water ramets than fresh water ramets (Fig. 5, $P < 0.05$ one-way ANOVA). Prior to rhizome severing fresh–salt *Distichlis* runners showed no difference in photosynthesis between ramets. After severing rhizomes, photosynthetic rates of *Spartina* and *Distichlis* ramets receiving salt water dropped 45% relative to formerly connected ramets receiving fresh water ($P < 0.0005$ ANOVA).

Carbon sharing

Plants colonizing bare patches spanned a five-fold gradient in total available sunlight as they extended from the surrounding vegetation. Bare patches received 98.7 ± 0.5 ($\bar{x} \pm \text{s.e.}$)% of ambient sunlight in Jun. and 77.8 ± 8.2 ($\bar{x} \pm \text{s.e.}$)% of ambient sunlight in Aug. Vegetated areas surrounding patches received 82% less sunlight than patches in Jun. and 88% less sunlight in Aug.

TABLE 1. Carbon movement in ^{14}C -labelled runners

Location of labelled ramets	Number labelled	% with acropetal movement to ramets inside patch	% with basipetal movement to parent ramets	% with movement to developing shoot tips
<i>Spartina patens</i>				
Inside patch	6	0	67	100
Outside patch	6	17	83	100
<i>Distichlis spicata</i>				
Inside patch	8	75	63	75
Outside patch	6	50	33	83

Autoradiographs of *Spartina* and *Distichlis* invading patches showed carbon sharing with labelled photosynthate moving between ramets in almost every replicate (12 out of 12 *Spartina*, 13 out of 14 *Distichlis*, Table 1). There were no apparent differences in photosynthate movement between plants growing in different patches. Sixty-seven per cent of the *Spartina* and 63% of the *Distichlis* ramets labelled inside of bare patches translocated carbon basipetally to leaves of parent ramets growing outside of patches. Seventy-five per cent of the colonizing *Distichlis* ramets also translocated carbon in the acropetal direction to sister colonizers. Seventeen per cent of *Spartina* and 50% of *Distichlis* ramets labelled just outside of bare patches translocated photosynthate acropetally to daughter ramets colonizing patches. These ramets also translocated carbon basipetally to other ramets growing in the shaded vegetation in 83% of the *Spartina* and 33% of the *Distichlis* replicates. Nearly all replicates of both species translocated carbon to newly developing shoot tips. The shoot tips which had yet to produce leaves were usually non-photosynthetic, located in the acropetal direction and actively colonizing open space in bare patches.

DISCUSSION

Runners of *Spartina* and *Distichlis* colonizing bare patches exhibit physiological integration of intracolonial ramets growing across the steep gradients in salinity and available sunlight between disturbance-generated bare patches and surrounding vegetation. Experiments conducted on runners growing across salinity gradients in the field and in the greenhouse suggest that ramets in saline soils ameliorate stress by importing water from intracolonial ramets growing in relatively freshwater conditions. In addition to inferring patterns of integration, the results from the field severing experiments may reflect the physiological response of ramets to natural fragmentation. The drops in water potential exhibited by severed colonizing ramets, but not for severed ramets outside of patches, suggests that fragmentation of clones would increase water stress on colonizers but not for ramets outside of patches. Runners colonizing patches exhibited acropetal and basipetal translocation of carbon between ramets across a gradient in light availability. In accordance with traditional source–sink models, newly developing, often non-photosynthetic, shoot tips were

heavily supported by parent ramets. Colonizing ramets inside bare patches were observed to translocate carbon basipetally to parent ramets located in the surrounding vegetation.

Reciprocal sharing of resources across multiple environmental gradients

Spartina and *Distichlis* runners invading bare patches reciprocally translocate water and carbon between colonizing ramets growing inside patches and parent ramets located in the surrounding vegetation. Simultaneous reciprocal sharing of resources between clonal ramets was demonstrated in a greenhouse study of water and carbon movement in the beach strawberry (Rosaceae), *Fragaria chiloensis* (Alpert and Mooney, 1986). In the beach strawberry, carbon and water were translocated between ramets in response to opposing gradients in soil moisture and available sunlight. In another study, Evans (1988, 1991) demonstrated acropetal and basipetal translocation of resources in *Hydrocotyle bonariensis* growing across environmental gradients. The paucity of such studies is surprising as clonal plants frequently grow along multiple gradients in light, nutrients, and water as a result of environmental heterogeneity. Therefore, reciprocal sharing of resources between ramets is probably a common phenomenon in clonal plants and deserves further study.

Clonal integration and the dominance of vegetative processes in marsh succession

New England high marshes are densely populated plant communities characterized by intense interspecific competition (Bertness and Ellison, 1987). Growth into new areas is restricted to disturbance patches where competitive interactions are relaxed, but environmental stress in the form of salinity is intensified (Bertness and Shumway, 1993). The ability of *Distichlis* and *Spartina* to share water and carbon across environmental gradients may explain the predominance of clonal invasion over seedling recruitment in bare patch succession (Shumway and Bertness, 1992; Bertness and Shumway, 1993).

Secondary succession of marsh bare patches occurs primarily by clonal growth as opposed to sexual recruitment (Bertness *et al.*, 1992; Shumway and Bertness, 1992). Seedling recruitment in salt marsh bare patches is severely constrained by depressed seed germination and seedling survival under saline soil conditions (Shumway and Bertness, 1992). Lovett-Doust (1981) has pointed out that physiological integration of ramets may enable vegetative recruitment into areas unsuitable for seedling establishment. This appears to be true in salt marsh succession where patches are invaded primarily by clonal grasses with physiologically integrated ramets rather than by emerging seedlings (Shumway and Bertness, 1992). The ability of *Spartina* and *Distichlis* tiller transplants to survive in small low salinity patches, but not inside larger hypersaline patches (Bertness, 1991) provides further evidence that

clonal connections to parent ramets outside patches are necessary for successful recruitment to hypersaline patches.

ACKNOWLEDGEMENTS

I thank Mark Bertness for his constant support and guidance, Dave Hirata, Lisa Shumway, and all the others who assisted me in the field and greenhouse, Lynn Rothschild for helping develop the ¹⁴C protocol, Peter Alpert for providing inspiration to begin the project, and the residents of Rumstick Cove for access to the field site. Comments by Annie Schmitt, Steve Gaines, Doug Morse, and Janis Antonovics greatly improved the manuscript. This work was supported by grants to S. Shumway from Sigma Xi and the New England Botanical Club and to M. Bertness from the Ecology Program of the National Science Foundation.

LITERATURE CITED

- Alpert P. 1990. Water sharing among ramets in a desert population of *Distichlis spicata* (Poaceae). *American Journal of Botany* 77: 1648–1651.
- Alpert P. 1991. Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis*. *Ecology* 72: 69–80.
- Alpert P, Mooney HA. 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. *Oecologia* 70: 227–233.
- Anderson CE. 1974. A review of structure in several North Carolina salt marsh plants. In: Reimold RJ, Queen WH, eds. *Ecology of halophytes*. New York: Academic Press, 307–344.
- Ashmun JW, Thomas RJ, Pitelka LF. 1982. Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. *Annals of Botany* 49: 403–415.
- Bertness MD. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72: 125–137.
- Bertness MD, Ellison AM. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57: 129–147.
- Bertness MD, Shumway SW. 1993. Mediation of secondary succession mechanisms by physical stress in a New England salt marsh. *American Naturalist* 142: 718–724.
- Bertness MD, Gough L, Shumway SW. 1992. Salt tolerances and the distribution of vascular plants in a New England salt marsh. *Ecology* 73: 1842–1851.
- Callaghan TV. 1984. Growth and translocation in a southern hemisphere sedge, *Uncinia meridensis*. *Journal of Ecology* 72: 529–546.
- Evans JP. 1988. Nitrogen translocation in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia* 77: 64–68.
- Evans JP. 1991. The effect of resource integration on fitness related traits in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia* 86: 268–275.
- Hansen DL, Dayanandan P, Kaufman PB, Brotherson JD. 1976. Ecological adaptations of salt marsh grass, *Distichlis spicata* (Gramineae), and environmental factors affecting its growth and distribution. *American Journal of Botany* 63: 635–650.
- Hartman J, Caswell H, Valiela I. 1983. Effects of wrack accumulation on salt marsh vegetation. In: *Proceedings of the 17th European Marine Biology Symposium*, Brest, France, 99–102.
- Hartnett DC, Bazzaz FA. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology* 64: 779–788.
- Kramer PJ. 1983. *Water relations of plants*. New York: Academic Press.
- Lau R, Young D. 1988. Influence of physiological integration on survivorship and water relations in a clonal herb. *Ecology* 69: 215–219.
- Lovett-Doust L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *Journal of Ecology* 69: 743–755.
- Newell SJ. 1982. Translocation of ¹⁴C-photoassimilate in two sto-

- loniferous *Viola* species. *Bulletin of the Torrey Botanical Club* **109**: 306–317.
- Nixon SW. 1982.** *The ecology of New England high salt marshes: a community profile.* Washington, DC: U.S. Fish and Wildlife Service.
- Pitelka LF, Ashmun JW. 1985.** Physiology and integration of ramets in clonal plants. In: Jackson JBC, Buss LW, Cook RE, eds. *Population biology and evolution of clonal organisms.* New Haven: Yale University Press, 399–435.
- Rice WR. 1989.** Analyzing tables of statistical tests. *Evolution* **43**: 223–225.
- Salzman A. 1985.** Habitat selection in a clonal plant. *Science* **228**: 603–604.
- Salzman AG, Parker MA. 1985.** Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. *Oecologia* **65**: 273–277.
- Shumway SW, Bertness MD. 1992.** Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia* **92**: 490–497.
- Slade AJ, Hutchings MJ. 1987.** Clonal integration and plasticity in foraging behaviour in *Glechoma hederacea*. *Journal of Ecology* **75**: 1023–1036.