Survivorship and Spatial Development of *Spartina alterniflora* Loisel. (Gramineae) Seedlings in a New England Salt Marsh

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ABSTRACT

Patterns of survival and spatial arrangement of tillers of *Spartina alterniflora* were examined in natural and in artificially produced bare areas, and in pure stands of adult *S. alterniflora* in a New England salt marsh. Seedling growth and survival were high in naturally occurring bare patches and in artificial patches, whether created by continual clipping of adult plants to ground level throughout the growing season or by providing bare substrate after removal of adult plants. Seedling growth and survivorship increased with increasing size of bare area. *S. alterniflora* seedlings were also common in areas dominated by adult plants, but no seedlings survived a whole first growing season under the mature canopy, probably because of competition from adult plants.

In large bare areas, *S. alterniflora* seedlings grew non-directionally, reaching heights of 0·5 m, and producing as many as 36 tillers in one growing season. Examination of leaf area ratios suggested that the production of tillers increased photosynthetic capacity in seedlings with several tillers in contrast to seedlings without tillers. Thus, seedlings can apparently tiller and colonize free space radially without a loss of photosynthetic capacity.

These results suggest that while seedling success is generally limited by adult plants in monocultures of *S. alterniflora*, in disturbed spaces seedling success is high and results in a rapid non-directional proliferation of sexually generated clones that ultimately preclude the successful invasion of future seedlings.

Key words: Clones, directional growth, leaf area ratio, salt marsh cordgrass, seedling survivorship, *Spartina alterniflora* Loisel.

INTRODUCTION

The rhizomatous perennial grass *Spartina alterniflora* Loisel. is a dominant species in coastal salt marsh communities of eastern North America, usually occurring in dense monospecific stands along the seaward edge of marshes. *S. alterniflora* regenerates both vegetatively and by seed. Investigators, however, have not agreed on that relative importance of vegetative growth and sexual reproduction in maintaining natural populations. Chapman (1974) reported that seeds have low viability, and the colonization is accomplished primarily by a vegetative spread of rhizomes rather than by a dissemination of seeds. In contrast, Mooring, Cooper and Seneca (1971) reported 52 per cent germination success of *S. alterniflora* seeds in the laboratory, and Broome, Woodhouse and Seneca (1974) stated that seedlings are the primary means of natural colonization of *S. alterniflora* on freshly deposited sediments in North Carolina. Broome *et al.* also reported success in establishing new stands by artificial seeding. In Great Britain, the role of seedlings of *Spartina anglica* C. E. Hubbard in marsh establishment has been investigated (Ranwell, 1964; Hubbard, 1965, 1970; Taylor and Burrows, 1968),

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but there is no general consensus about the relative importance of seeding in the establishment and maintenance of British marshes. Data on the distribution, survivorship and development of naturally occurring seedlings, however, are sparse.

In New England marshes, *S. alterniflora* germinates from April to the end of June. Seedlings begin to tiller soon after germination, and the spatial location of tillers may be important in determining seedling success (Bell and Tomlinson, 1980). Sessile clones, whether of rhizomatous plants like *S. alterniflora* or of colonial marine invertebrates, develop in a variety of spatial patterns. These may be divided into two basic types (Harper, 1981). Clones may grow by proliferating ramets along runner-like axes growing in a fixed direction, or they may grow non-directionally by filling all available space. Directional and non-directional morphologies represent the extremes of a continuum (Harper, 1981) and some clones may be able to switch from one growth form to the other. Winston (1976) described a colonial bryozoan which can grow in a variety of forms, from runner-like to sheet-like, depending on food availability.

Spatial morphology has been frequently interpreted as an ecological strategy. Directional and non-directional ontogenies have been compared in terms of competitive ability, habitat selection, and/or resource gathering efficiency (e.g. Bell and Tomlinson, 1980). Harper (1981) distinguished two colonizing strategies of vegetative rhizomatous plants. 'Phalanx' colonizers advance slowly (often non-directionally) on a broad, dense front which is highly resistant to invasion by rhizomes of other species, whereas 'guerilla' colonizers send out single, directional rhizomes, and colonize bare areas very rapidly. Buss (1979) argued that colonial marine invertebrates employ directional growth as a means of locating spatial refuges, thereby escaping unfavorable conditions at the original site of settlement. Similarly, Salzman (1985) interpreted the non-random placement of ramets by *Ambrosia psilostachya* as a means of adaptive habitat choice. Bell (1974, 1979) characterized rhizome branching angles in *Medeola virginiana* L. and *Alpinia speciosa* L. as optimally suited to achieve maximal exploitation of space without interference between ramets. Cook and Cain (1985), on the other hand, found no evidence for selection for ideal rules of growth or geometrical occupation of space in different populations of *M. virginiana*.

In this paper, three aspects of *S. alterniflora* seedling biology are examined: (1) the natural conditions of conspecific crowding in which seedlings survive and tiller, (2) patterns of tillering and clonal expansion of seedlings, and (3) the effects of these developmental patterns on the seedling's leaf area ratio.

STUDY SITE

Field work was carried out during the summer of 1984 in the salt marsh at Rumstick Cove, a small protected embayment of Smith Cove in Barrington, Bristol County, Rhode Island, USA (for a complete description of Rumstick Cove, see Bertness, 1984). *S. alterniflora* occurs along the seaward edge of the marsh in a pure stand 2–8 m wide, extending from approximately +0·1 m mean tidal height up to the mean high water line (+1·2 m), where it is replaced by a mixture of *Spartina patens* Muhl. and *Distichlis spicata* (L.) Greene. Along the gradient from the leading edge of the marsh to the *S. patens/D. spicata* zone, the height of *S. alterniflora* declines from a maximum of 1·5–2 m to a minimum of 200–300 mm, with a fairly abrupt transition from tall to short plants occurring at about 1·0 m mean tidal height. In this paper, tall form *S. alterniflora* refers to plants about 1·5 m in height by the end of the growing season; the tall form zone is the area where such plants occur, from +0·1 to +1·0 m mean tidal height. Short form *S. alterniflora* refers to plants < 1 m tall; the short form zone is the area from +1·0 to +1·2 m mean tidal height.

SEEDLING SURVIVORSHIP

Methods

The density of *S. alterniflora* seed germination was quantified in the spring of 1984 in three marsh zones (the tall form *S. alterniflora* zone, the short form *S. alterniflora* zone, and the *S. patens/D. spicata* zone). Thirty artificially created bare patches with an area of 0·25 m² (*small patches*) were examined in each zone. These patches were created in March 1983 by excavating the substratum to a depth of 300–400 mm and replacing it with bare substratum (Bertness and Miller, 1984). Survival of seedlings in these small patches was monitored in all three zones and in natural bare patches > 1 m² (*large patches*) in tall and short form *S. alterniflora* zones. All *S. alterniflora* seedlings in both the large and the small patches were tagged with plastic-coated coloured wire ties in April 1984, and were inspected every two weeks for mortality. Seedlings in 0·25 m² control quadrats with intact adult canopies were also monitored in each of the three marsh zones described above.

Five 1·5 × 1 m quadrats were established in April 1984 in the tall and short form *S. alterniflora* zones to assess the effects of adult plants on seedling survivorship. All above-ground vegetation in one half of each quadrat was clipped weekly and removed, and the other half was undisturbed. No regrowth of above-ground vegetation occurred after six weeks. In both the clipped and control halves, all naturally occurring *S. alterniflora* seedlings were marked. Survivorship was monitored every two weeks until the end of September 1984.

At the end of August 1984, the heights of the initial (parent) tillers and all daughter tillers were measured, and the number of daughter tillers of each marked seedling was counted. To assess survivorship of first-year seedlings over winter, 12 first-year clones in each height form zone of varying size (5–28 tillers) were monitored from November 1984 until April 1985.

Results

Initial seedling density was the highest in the tall form *S. alterniflora* zone, one-third as great in the short form *S. alterniflora* zone, and negligible in the *S. patens/D. spicata* zone (Table 1), a reflection of the different amount of seeds set in each marsh zone (M. D. Bertness, *unpublished data*). In the large patches, seedling survivorship was relatively high (Table 1). Sixty-three per cent of seedlings survived in the tall form zone, and 87 per cent survived in the short form zone. Seedling survivorship was much lower in the small artificial patches (Table 1), where only 14 per cent survived in the tall form zone, 11 per cent in the short form zone, and 8 per cent in the *S. patens/D. spicata* zone. Beneath the intact adult canopy no seedlings survived in either the tall form zone or the *S. patens/D. spicata* zone, and only 8 per cent survived in the short form zone.

TABLE 1. *Initial density and per cent survivorship of seedlings over the entire summer* (l_x) *in the three marsh zones*

Zone	Initial density/0·25 m²	l_x (%)		
		Under canopy	Small patches	Large patches
Tall *S. alterniflora*	14·0 ± 2·57 (40)	0 (0/119)	14 (58/402)	63 (39/62)
Short *S. alterniflora*	3·6 ± 0·66 (40)	8 (2/26)	11 (13/117)	87 (35/40)
S. patens/D. spicata	0·3 ± 0·09 (40)	0 (0/2)	8 (1/13)	—

Values are means ± s.e. Sample size is in parentheses.

TABLE 2. *Tiller height and number for seedlings in small and large patches*

Patch size	Zone	Parent tiller height (m)	Daughter tiller height (m)	No. of daughter tillers
Small	Tall form	0.47 ± 0.03 (50) *	0.10 ± 0.01 (52)	1.0 ± 0.20 (52)
	Short form	0.33 ± 0.03 (25) *	0.07 ± 0.02 (17)	0.7 ± 0.21 (25)
Large	Tall form	0.47 ± 0.02 (51)	0.16 ± 0.08 (414) *	8.1 ± 0.95 (51) *
	Short form	0.49 ± 0.02 (48)	0.19 ± 0.06 (598) *	12.5 ± 0.85 (48) *

Means ± s.e., with sample size in parentheses.
* Pairs of values (tall *vs* short form *S. alterniflora* zones) are significantly different at $P < 0.05$ (Scheffé test).

TABLE 3. *Percentage survivorship* (l_x) *of seedlings, seedling height, and number of tillers of seedlings in clipped areas*

Zone	l_x (%)	Parent tiller height (m)	Daughter tiller height (m)	No. of daughter tillers
Small form	12 (131/1078)	0.35 ± 0.01 (131)	0.08 ± 0.01 (165)	1.3 ± 0.15 (131)
Short form	20 (33/169)	0.35 ± 0.02 (33)	0.08 ± 0.01 (77)	2.3 ± 0.51 (33) *

Means ± s.e., sample size in parentheses.
* Pairs of values are significantly different at $P < 0.05$ (Scheffé test). No seedlings survived in control areas in either zone ($n = 693$ seedlings in tall form zone, $n = 83$ seedlings in short form zone).

In the small patches, seedlings in the tall form zone were approx. 50 per cent taller than seedlings in the short form zone ($P < 0.05$), but none of the seedlings in any of the small patches produced more than one or two small daughter tillers (Table 2). All these seedlings appeared unhealthy and etiolated. In contrast, seedling heights in the large patches in the tall and short form zones did not differ significantly (Table 2). Seedlings in the short form zone, however, produced significantly more and larger tillers than seedlings in the tall form zone ($P < 0.05$, Table 2).

In the clipping experiment, only seedlings in the clipped areas survived (Table 3) and, as in the large patches, seedling height did not differ between zones. But seedlings in the short form zone produced significantly more daughter tillers ($P < 0.02$, Table 3). Daughter tillers in the clipped areas were small, about half the size of those in large bare patches (cf. Tables 2 and 3), suggesting that the live roots and rhizomes in the clipped areas inhibited seedling growth in comparison with the completely bare substrate.

All of the 24 first-year clones tagged in November 1984 survived until the following April.

SPATIAL DEVELOPMENT

Methods

Seedlings in large bare patches were tagged in early May 1984, and were monitored on three dates during the summer of 1984 (6 July, 25 July, and 13 August) to quantify the spatial development of *S. alterniflora* clones growing in the absence of adults of the same species. At each monitoring date, the distance (± 5 mm) from parent tiller to each

TABLE 4. *Numbers of seedlings with significant and non-significant directionality of growth*

Date	Zone	Significant directionality	No significant directionality
6 July 1984	Tall form	1	15
	Short form	1	25
25 July 1984	Tall form	0	27
	Short form	3	39
13 August 1984	Tall form	5	32
	Short form	7	40

Significant directionality indicates $P < 0.05$, Rayleigh's test and Hotelling's one-sample test (Batschelet, 1981). See text for statistical details.

daughter tiller, the angle ($\pm 5°$) between a line drawn from the parent to each daughter tiller and an arbitrarily selected axis, and the height (± 5 mm) of all tillers were measured. Because of seedling mortality and loss of tags, the number of clones monitored varied from 48–54 clones in the tall form zone, and from 49 to 50 in the short form zone.

Two statistical tests were used to examine whether clones grew directionally or non-directionally. Rayleigh's test (Batschelet, 1981) was used to determine whether the placement of daughter tillers was random with respect to direction. Hotelling's one-sample test (Batschelet, 1981) was used to account for both direction and distance of daughter tillers from the parent tiller. Hotelling's one-sample test determines if the 'centre of mass' of a clone has shifted away from the parent tiller. Such a shift would occur if, for example, the parent tiller produced a single daughter tiller some distance away and the daughter tiller subsequently became surrounded by new tillers. To conform to the requirements of the statistical tests, only seedlings with more than five tillers were examined statistically (Batschelet, 1981). Statistical calculations were performed using a FORTRAN program available on request from the second author.

Results

The results of both Rayleigh's test and Hotelling's test agreed in all respects. Virtually all of the clones (91 per cent) showed no significant directionality of development (Table 4). Most seedlings grew as expanding circles centred about the parent tiller (Fig. 1). Eighteen-week old seedlings in the short form zone had spread radially nearly twice as far as those in the tall form zone ($P < 0.001$). Seedlings in the short form zone attained a mean maximum parent-to-daughter tiller distance of 62 ± 5 mm (range 10–130, $n = 49$), while those in the tall form zone averaged 36 ± 4 mm (range 10–100, $n = 47$).

PHOTOSYNTHETIC CAPACITY

Methods

The growth of a plant is frequently described as relative growth rate (RGR) or the relative change in plant weight over time, dW/Wdt (Blackman, 1919; Fitter and Hay, 1981). RGR may be subdivided into two variables, the net assimilation rate (NAR) (the change in plant weight relative to the surface area of assimilatory tissue, dW/Adt), and the leaf area ratio (LAR) (the ratio of assimilatory surface to plant weight, A/W) (Blackman, 1968; Fitter and Hay, 1981). NAR and LAR may be regarded as normally reflecting photosynthetic efficiency and photosynthetic capacity, respectively (Fitter and
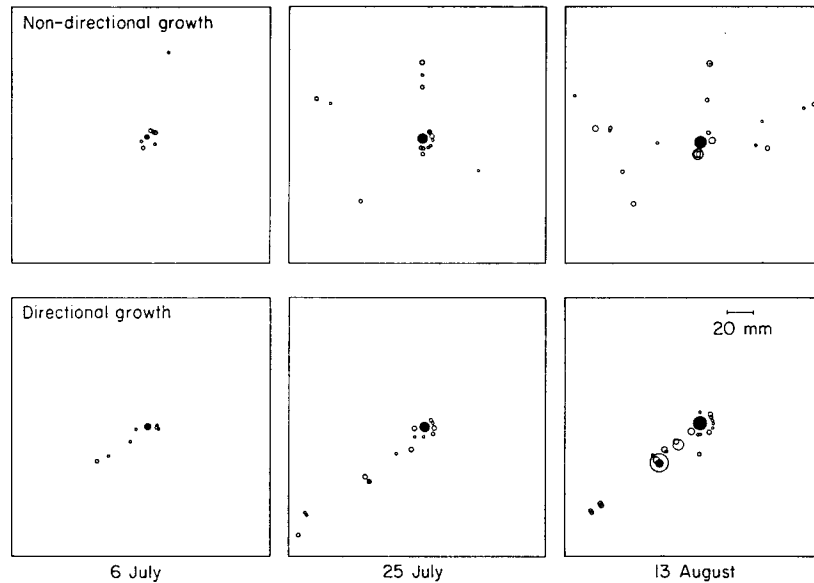
FIG. 1. Spatial morphology and ontogeny of two representative *Spartina alterniflora* seedlings. Each circle represents one tiller. Solid circle is the parent tiller. Circle diameter is proportional to tiller height. Top: a seedling growing without any directionality. 72 of 84 cases showed no significant directionality on the last sample date (Table 4). Bottom: a seedling exhibiting directional growth.

Hay, 1981). It has been shown that in the C_4 grass, *Spartina townsendii* H. and J. Groves, a natural hybrid of *S. alterniflora* and *S. maritima* (Curt.) Fernald, photosynthetic rate increases without bound with increasing temperature and/or light availability (Long, Incoll and Woolhouse, 1975; Long and Incoll, 1979). It has been suggested that *S. alterniflora* is also C_4 (e.g. Long *et al.*, 1975), and it would be expected that *S. alterniflora* would also show similar increases in photosynthetic rate with either increasing light availability or temperature. An increase in LAR in this C_4 grass leads to an overall increase in available photosynthetic area, and would be expected to lead to an increase in the plant's relative growth rate.

A clonal plant can increase the surface area of its assimilatory tissue either by growing new leaves on a pre-existing shoot, or by developing new shoots. One consequence of the second method might be a change in the photosynthetic capacity of the entire clone. For *S. alterniflora* and other grasses, the photosynthetic capacity of the clone would change if tillering yielded a different amount of assimilatory surface area per unit plant weight than did the growth of pre-existing shoots, effecting a change in leaf area ratio (LAR).

Is there an advantage for *S. alterniflora* in terms of increased photosynthetic capacity to having many daughters in a clone? This question could be addressed by comparing the LAR of a solitary plant with the LAR of a large clone under equivalent conditions. Since no conditions exist at Rumstick Cove in which solitary *S. alterniflora* seedlings grow together with large clones, and since LAR values might vary among genotypes, an artificial comparison that obviated both these difficulties was constructed. The parent tiller of a large clone, taken by itself, was used as a reasonable approximation to a solitary tiller of similar age and size. The LAR of the parent tiller was compared with the total LAR of the entire clone. This comparison accounts for genotypic and environmental variation. LARs for partial clones were also calculated by taking into

account the parent plus the oldest daughter tiller, parent plus two oldest, parent plus three oldest, and so on until all daughter tillers were included. If the cumulative LAR were to increase as tillers were added sequentially from oldest to youngest, the inference would be that clones had a net advantage in photosynthetic capacity over solitary plants, whereas if cumulative LAR decreased, the inference would be that clones incur a net reduction in photosynthetic capacity when producing daughters.

To examine this effect, 15 seedlings from large bare patches in each height form zone were sampled on 6 July and 1 August 1984. The shoot height (± 0.5 mm) of each tiller was measured. Tillers were sorted by descending height within each clone. Shoot height is a reliable indicator of tiller age in these seedlings (W. S. Metcalfe, personal observation). Each tiller's leaves were cut off at the base of the lamina and the following morphological variables were measured (± 0.5 mm): stem length from ground level to the point of attachment of the youngest leaf, stem diameter at the midpoint of its length, leaf lamina length, and leaf width at the base of the lamina. These values were then used to calculate area of photosynthetic tissue. Stems of *S. alterniflora* are photosynthetic and were also included in the calculations. Stems with leaves removed approximate to a cylinder in shape, and their surface area was calculated as π (stem diameter x stem height). Leaves, which are green on both sides, approximate to isosceles triangles, and their area was calculated as $2(\frac{1}{2} \times$ leaf length $\times$ leaf width). After the linear measurements were taken, tillers were dried for 48 h at 75 °C and weighed (± 0.5 mg). Leaf area ratios were calculated for each seedling for the tallest tiller in a clone taken by itself, then the two tallest, and so forth, as described above.

Results

Figure 2 presents leaf area ratios calculated for partial and for whole clones. The curves are strikingly flat, but the LAR for whole clones tended to be higher than the
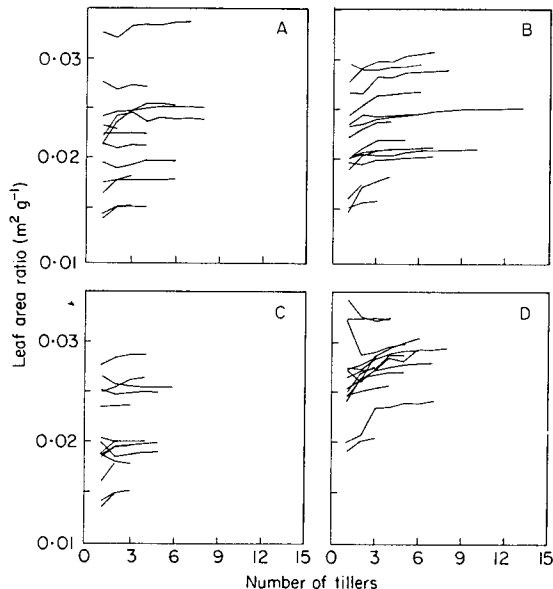

FIG. 2. LAR curves for partial and whole clones. A, Seedlings from the tall form *Spartina alterniflora* zone, July sample; B, Tall form zone, August sample; C, Short form zone, July sample; D, Short form zone, August sample. Each curve represents one clone. Tillers were added sequentially from tallest to shortest. Thus, the value for one tiller is the LAR of the tallest (= parent) tiller taken alone, and the rightmost value is the LAR of the whole clone (see text for further details).

TABLE 5. *Mean per cent differences* (± 1 *s.e.*) *between parent and whole clone LAR, and per cent differences between greatest and smallest LAR*

Date	Zone	Parent *vs* whole clone	Greatest *vs* smallest
` 6 July 1984	Tall form	4·4±1·55 (13)	123·1
	Short form	1·2±2·62 (14)	93·2
1 August 1984	Tall form	8·3±1·43 (15)	93·2
	Short form	7·4±2·13 (15)	58·8

Sample sizes in parentheses.

LAR of the tallest (= parent) tiller taken alone. Whole clone LARs were significantly higher than that of the parent tiller alone in the July tall form zone sample ($P < 0.05$, sign test; Fig. 2A), the August tall form zone sample ($P < 0.01$, sign test; Fig. 2B), and the August short form zone sample ($P < 0.05$, sign test; Fig. 2D), but not the July short form zone sample ($P > 0.05$, sign test; Fig. 2C). Over all, the difference between single tiller LAR and whole clone LAR was $\leqslant 9$ per cent (Fig 2, Table 5). Compared to the flatness of LAR curves for individual seedlings, the dramatic two-fold variation among clones indicates substantial genotypic and/or environmental effects on individual photosynthetic capacity (Fig. 2; Table 5).

DISCUSSION

At Rumstick Cove, *S. alterniflora* seedlings were unable to compete successfully with adults of the same species. Seedlings did not survive under the adult canopy and seedling success increased with increasing bare patch size (Tables 1 and 3). In large patches, seedlings attained heights as great as 0·5 m and produced up to 36 daughters in one summer (Table 2). Such clones had excellent survivorship: all 24 first-year clones tagged in November 1984 overwintered successfully. Thus, while sexual reproduction apparently contributed little to the maintenance of established stands of *S. alterniflora*, it may be important in the invasion of large, disturbance-generated patches which are created throughout the marsh when dead stems of *S. alterniflora* are deposited onto the marsh by spring tides (Reidenbaugh and Banta, 1980; Hartman, Caswell and Valiela, 1983). The vegetation beneath the debris is killed and when it decomposes, a patch of bare ground remains (Hartman *et al.* 1983).

In the absence of competition, *S. alterniflora* seedlings tiller rapidly and develop into large clones. The results presented here suggest that the production of tillers slightly increased the photosynthetic capacity (as inferred from estimates of LAR) of clones relative to that of a solitary shoot (Fig. 2, Table 5). The effect observed was small ($\leqslant 9$ per cent), but increases occurred in a majority (71 per cent) of seedlings. Although derived from an artificial comparison, these data suggest at least that *S. alterniflora* seedlings suffer no net reduction of photosynthetic capacity as a result of clonal growth. Genotypic and/or environmentally-induced phenotypic differences in LAR, on the other hand, were as great as two-fold (Table 5, Fig. 2).

S. alterniflora clones exhibited non-directional growth (Table 4, Fig. 1). The exceptions found to non-directional growth in these data are most simply explained as random artefacts of the architecture of *S. alterniflora* rhizome systems. *S. alterniflora* shoots grow in tussocks consisting of a parent tiller plus daughter tillers developed from axillary buds at the base of the parent shoot. Tussocks are connected to each other by rhizomes which loop underground. If only one rhizome is produced during the summer, the plant

appears to grow directionally away from the parent shoot. Most seedlings, however, produce several rhizomes and expand without directionality. Caldwell (1957) showed that in clones of *S. townsendii*, non-directional growth continued indefinitely in the absence of competition, resulting in large circular clones. It seems likely that this would also occur in clones of *S. alterniflora*.

These results suggest that while seedling establishment in *S. alterniflora* is limited by adult *S. alterniflora* plants, seedling success is high in areas without surrounding vegetation. Seedlings in areas lacking vegetation grow non-directionally, as rapidly expanding clones, and most likely preclude the establishment of future sexual propagules. Thus, while seedling success appears to be of little importance in the maintenance of undisturbed natural stands of *S. alterniflora*, seedling recruitment appears to be important in the recolonization of disturbed bare areas and in the formation of new marshes.

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