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Life history and population dynamics of *Atriplex triangularis*

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Abstract

Life history and population dynamics were examined for an annual halophyte, *Atriplex triangularis* Willd., in an inland salt marsh at Rittman, Ohio. The effect of salinity and precipitation on survival, growth, and reproduction of *Atriplex triangularis* under field conditions was determined. Early germination enhanced the possibility of survival and reproduction of this species. No distinct ecotypes were found, but various populations demonstrated different degrees of phenotypic plasticity in response to salinity, indicating that genetic selection for plasticity in growth response is taking place along the salinity gradient. Most seeds fell directly below the parent plant, but a small number was found in traps up to 0.5 meter from fruiting individuals. High temperature, salinity, and darkness individually, and in combination, inhibited the germination of small seeds more than large seeds.

Introduction

Salinity tolerance probably played a primary role in the evolution of inland halophytes as only occasional submergence occurs in these habitats after heavy rainfall (Ungar, 1972, 1974a, 1974b). There are usually greater seasonal soil moisture variations in inland than in coastal saline soils. This is due to the absence of tidal activity and the unpredictability of precipitation, which is limited to particular seasons for some of the drier climates (Ungar, 1968). The physical complexity of salt marshes, as well as predictable temporal fluctuations in edaphic conditions, results in considerable environmental heterogeneity (Jefferies, 1977). Genetic differences along environmental gradients were described for salt marsh species by Jefferies *et al.* (1970), Gray & Scott (1980) and Jefferies & Gottlieb (1982, 1983).

Our research is concerned with the demography of a halophyte *Atriplex triangularis* Willd. (Syn. *Atriplex patula* var. *hastata* (L.) Gray, Chenopodiaceae). It is an herbaceous, weedy annual, of cosmopolitan distribution, commonly found in coastal and inland saline marshes (Osmond *et al.*, 1980; Ungar, 1983). Although *Atriplex triangularis* is capable of growing in highly saline environments, it reaches maximum growth in less saline conditions (McMahon & Ungar, 1978; Riehl & Ungar, 1983; Karimi, 1984). The life cycle of *A. triangularis* spans 9 months (from February to October) and plants are subjected to great variation in edaphic conditions. Its limitation to moderately saline habitats indicates that both biotic and abiotic factors control its distribution.

The life history patterns of halophytes are not yet well understood and only a few case studies are available (Beeftink *et al.*, 1978; Jefferies *et al.*, 1979,

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1981, 1983; Rozema, 1978; Philipupillai & Ungar, 1984; Ungar, 1983). This paper addresses a number of questions about the demography of *A. triangularis* growing in an inland salt marsh.

Materials and methods

Species and habitat

Life cycle stages of *Atriplex triangularis* were examined during the growing season in 1981 and 1982. Populations were studied from a salt marsh at Rittman, Ohio (81°47′39″E; 40°57′30″N) which is located adjacent to a salt mining operation of the Morton Salt Company. This salt marsh has four main vegetation zones occurring along a 50 m gradient of decreasing soil salinity (mean values, N = 10): Pan *Salicornia* (75 mS cm^{-1}), *Salicornia* (49 mS cm^{-1}), *Atriplex* (33 mS cm^{-1}), and *Hordeum* zones (<10 mS cm^{-1}). The *Atriplex triangularis* seedlings were distributed from the *Salicornia* to the *Hordeum* zones. Plants found growing near the *Salicornia* zone were smaller and less branched than those growing near the *Hordeum* zone.

Demography

Twenty 10 × 10 cm permanent quadrats were established randomly in low salinity (adjacent to *Hordeum*) and high salinity (adjacent to *Salicornia*) zones containing *Atriplex*. Five soil salinity sensors (Soil Moisture Equipment Corporation no. 5100A) were buried in the root zone at 10 cm depth and within 5 cm of the permanent quadrats. Monthly measurements of *in situ* soil solution conductivity were made using a Soil Moisture Equipment Corporation no. 5500 salinity bridge. The positions of quadrats were randomly assigned, using a table of random numbers, along a 10 meter line parallel to the length of the high salt (*Salicornia*) and low salt (*Hordeum*) zones. The number of plants surviving in each uncleared plot were counted biweekly throughout the growing season from April to October. In order to reduce disturbance in quadrats, ten seedlings were randomly collected from just outside of each quadrat every month of the growing season and their oven dry weights recorded (80 °C for 48 h). All plants growing in quadrats were harvested in October and the oven dry weight of the roots, stems, leaves and seeds was determined.

In April, May, and June 10 different 10 cm × 10 cm plots were cleared in the *Atriplex* zone in order to determine the number of seeds that germinated after a site was cleared. The survival of germinating seedlings was followed by counts made monthly from April to October. In October measurements of root, stem, leaf, and fruit dry weights were made. The fresh weight:dry weight ratio was used as an estimate of succulence.

Ecotypic differentiation

In May seedlings were transplanted in 10 soil cores (5.5 cm in diameter), containing 10 seedlings each, into the various zones to determine the phenotypic plasticity within populations: a. from the low salt *Atriplex* zone (adjacent to *Hordeum*) to the high salt *Atriplex* (adjacent to *Salicornia*) and the *Salicornia zone;* b. from the high salt *Atriplex* zone to the low salt *Atriplex* zone and the *Salicornia* pan zone; c. from the *Salicornia* zone to the low and high salt *Atriplex* zones. Seedling transplants were also made within sites to determine if transplants caused injury. Plants were harvested when they reached maturity; in October seedling height, dry weight, and seed production was measured.

Seed floatation experiment

Total floating time of small (1.0–1.5 mm), medium (1.5–2.0 mm), and large (>2.0 mm) seeds and fruits was estimated by placing them in a beaker containing 1% NaCl solution at room temperature (23 °C). Each treatment contained either 25 seeds or fruits, and these were replicated four times. Because floating seeds would normally be agitated in nature, after 6 days seeds and fruits were agitated for 1 minute every alternate day for 32 days and the number of seeds which remained floating was recorded.

Dispersal

To estimate the distance of seed dispersal, a method similar to that used by Rabinowitz & Rapp

(1980) was employed. The trap used was a petri dish containing a piece of Whatman no. 2 filter paper (9 cm diam.) coated with petroleum jelly. Traps were placed along a single radius at distances of 0, 50, 100, and 200 cm from 10 plants. The filter paper with petroleum jelly was replaced every two weeks from September to December, and exposed filter paper was taken to the laboratory and examined under a dissecting microscope. Seeds of *Atriplex triangularis* were counted and sorted into three size classes (small = <1.5 mm, medium = 1.5 to 2.0 mm, large = >2 mm).

Germination periodicity

To determine the effect of high summer salinities and temperatures on seed germination, 240 nylon packets of small, medium, and large seeds (containing 25 seeds each enclosed in plastic screen) were placed on the soil surface or buried at 4 cm soil depth in high salt (adjacent to *Salicornia*) and low salt (adjacent to *Hordeum*) habitats during May. In June and July 10 replicates of each treatment were brought to the laboratory and the number of germinated seeds were determined.

To estimate the effect of overwintering and salinity on the time of germination, nylon stocking packets (containing 25 small, medium, or large seeds each) were put both on the soil surface and buried 4 cm below the soil surface at 10 locations in the high salt and low salt environments, during November 1982. Ten replicates (10 replicate × 2 treatments × 2 sites × 25 seed/packet = 1000 seeds) were brought to the laboratory monthly from February through May and the number of germinated seeds of a total of 4000 were counted.

Results

Rainfall and soil salinity

A monthly rainfall estimate was obtained for the 1981 and the 1982 growing season for Akron, Ohio U.S.A. (Table 1), the nearest weather station (25 km NE) to Rittman (United States Environmental Data and Information Service). The rainfall changes correlate with that of soil solution electrical conductivity during the summer months (Fig. 1). Soil solution electrical conductivity measured with buried sensors, was higher than average in May 1981 and this correlated with average rainfall in April. In the high salt zone, electrical conductivity reached its maximum in August, while in the low salt zone the soil solution electrical conductivity peaked in October.

Table 1. Monthly precipitation (cm) during the 1981 and 1982 growing seasons and 25 yr mean precipitation at Akron, Ohio.

Month	1981	1982	Mean (25 yr)
January	2.13	10.50	6.58
February	9.90	5.58	5.53
March	5.13	9.60	7.60
April	13.78	3.18	9.08
May	8.40	11.05	10.33
June	15.95	11.20	9.93
July	7.63	7.50	10.45
August	7.28	7.53	7.05
September	9.88	7.83	6.90
October	4.58	2.90	6.18
November	4.38	18.23	7.18
December	8.45	10.28	6.00
Total	97.49	105.38	92.81

Demography

During the 1981 growing season the density of *Atriplex triangularis* reached a peak in May, but high mortality of seedlings occurred in June and July (Fig. 2). A progressive decrease in density oc-

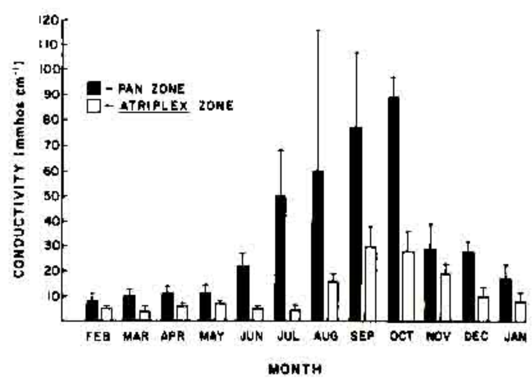

Fig. 1. Mean electrical conductivity (mmhos/cm = mS/cm) of soil solution in the low and high salt *Atriplex* zones during the 1982 growing season (N = 10 at each site). Bars = S.E. mean.

(Fig. 2). Density of plants in uncleared plots was noticeably higher than that of cleared plots (Fig. 2) and it decreased markedly with a delay in germination time. Few seedlings were recruited after the June clearing, and all died.

Seedling height gradually increased with time in the uncleared plots (Fig. 5). The pattern was the same for plots cleared in April, but seedling height was much reduced compared to uncleared plots. Seedlings emerging in plots that were cleared in May and June had a very short survival period. Final density of plants in uncleared plots was much higher than for plots cleared in April (Table 2). The plots which were cleared <11 April experienced a 75% reduction in germination, as well as a decrease in growth and seed production as compared to uncleared plots (Table 2). Plants in plots cleared >9 May experienced 100% mortality.

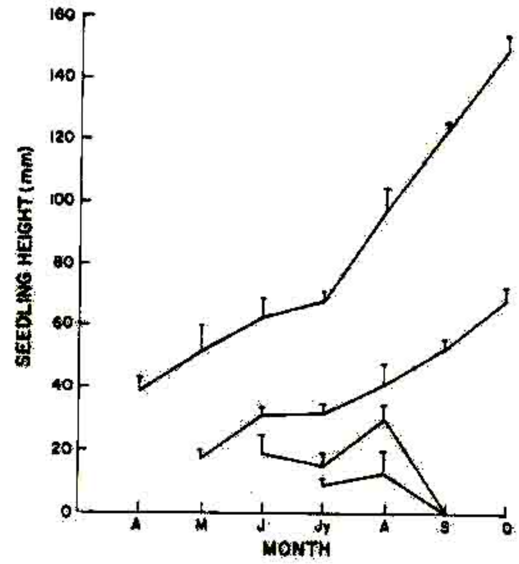

Fig. 5 Change in height of *Atriplex triangularis* individuals in uncleared and cleared 10 cm × 10 cm quadrats during 1981 growing season.

Ecotypic differentiation

Plants of *Atriplex triangularis* growing in different portions of the salinity gradient were different morphologically. The *Atriplex* population growing in the low salt zone adjacent to *Hordeum* were tall, much branched, and had the highest total weight and seed production (Table 3). Populations growing within the high salt *Atriplex* zone adjacent to *Salicornia* had 10% of the dry weight, and only 50% of the seed production of low salt populations. When *Atriplex* seedlings were transplanted from the *Atriplex* zone to the *Hordeum* zone, there was a four-fold increase in total dry weight. Seed production was also markedly increased and was similar to that of the plants growing in the same area. The ratio of small to large seed also increased significantly (Table 3).

Transfer of *Atriplex* seedlings from the *Atriplex* zone to the *Salicornia* zone resulted in a substantial decrease in total weight. These plants had a higher percentage of their resources allocated to roots and leaves but no seeds were produced in this treatment (Table 3). Transfer of seedlings from the *Hordeum* zone to the *Atriplex* zone resulted in a significant decrease in the total dry weight, but this was still higher than that for plants which were originally present in the *Atriplex* zone. Number of seeds, resource allocation to seeds, and seed size ratios were very similar to plants growing within the *Atriplex* zone. When cores from the *Salicornia* zone were transferred to the *Atriplex* zone, the *Atriplex* see-

Table 2. The effect of time of germination on the survival, growth, reproduction and fecundity of *Atriplex triangularis*.

Time of germination	Mean number of plants	Dry weight (mg plant^{-1})					Seed quadrat^{-1} (100 cm^2)			
		Leaf	Stem	Root	Fruit	Total	Small	Medium	Large	Total
<April 11	66.50	22.47	13.71	8.39	5.94	50.51	12.00	7.67	5.25	24.95
	±1.07	±0.98	±1.04	±0.42	±0.34	±6.69	±2.30	±1.37	±1.68	±3.20
April 11 to May 9	16.00	11.57	9.80	4.37	3.58	28.28	2.20	4.00	4.33	10.53
	±6.10	±0.35	±0.42	±0.34	±0.21	±5.28	±0.58	±2.80	±1.85	±0.69
>May 9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	±0.00	±0.00	±0.00	±0.00	±0.00	±0.00	±0.00	±0.00	±0.00	±0.00

> April 11 = cleared plots.

Table 3. Effect on growth and fecundity of transplanting of *Atriplex triangularis* from one zone into another.

Variable	AT→AT	AT→HORD	AT→SAL	HORD→HORD	HORD→AT	SAL→AT	LSD (P<0.05)
N	8.00	10.00	5.00	9.00	7.00	7.00	
Root (%)	10.44 ± 0.56	7.16 ± 1.00	16.31 ± 2.10	10.05 ± 1.05	13.79 ± 2.60	16.54 ± 3.35	5.37
Stem (%)	29.06 ± 1.07	32.60 ± 3.32	27.11 ± 3.70	31.78 ± 2.41	30.98 ± 4.11	27.17 ± 3.34	9.64
Leaf (%)	45.07 ± 2.74	33.22 ± 2.56	49.25 ± 3.80	34.48 ± 6.40	38.22 ± 4.04	36.88 ± 4.50	12.72
Fruit (%)	15.43 ± 2.70	20.92 ± 2.43	16.67 ± 0.00	23.68 ± 4.69	18.51 ± 3.05	21.31 ± 3.30	14.57
Total weight (mg)	111.27 ± 21.20	452.19 ± 90.68	16.15 ± 12.40	1325.56 ± 326.17	200.49 ± 54.98	106.38 ± 68.04	49.47
Small seed (No.)	66.00 ± 17.59	132.67 ± 24.40	0.00 ± 0.00	118.22 ± 46.36	63.00 ± 8.82	76.40 ± 57.65	6.69
Medium seed (No.)	14.43 ± 4.67	16.78 ± 3.41	0.00 ± 0.00	25.86 ± 11.91	19.60 ± 4.47	23.40 ± 16.72	25.58
Large seed (No.)	2.33 ± 1.20	1.62 ± 0.65	0.00 ± 0.00	6.67 ± 4.41	3.00 ± 1.14	7.60 ± 4.43	6.95
Total seed (No.)	80.36 ± 22.58	150.56 ± 25.29	0.00 ± 0.00	139.44 ± 56.37	85.60 ± 13.28	107.40 ± 78.51	6.69
Ratio S:M:L	28:6:1	82:10:1	0.00	18:4:1	21:7:1	10:3:1	

N = Number of quadrats with plants. AT = *Atriplex* zone, HORD = *Hordeum* zone, SAL = *Salicornia* zone.

dlings found in these cores showed the same total weight, resource allocation and fecundity as those naturally present in the *Atriplex* zone (Table 3).

Seed floatation

Seeds and fruits of *Atriplex triangularis* were tested for their capacity to float on the surface of a 1% NaCl solution. After a 6 day period almost 100% of the fruits remained floating. At this point the solution was agitated. Fruits began to sink on the 12th day (65%), but 35% remained floating for as long as 32 days at which point the experiment was terminated. Naked seeds floated for four days and then all sizes of seed began to sink, and after 12 days no seeds remained floating.

Dispersal

Populations growing in a low salt environment began to shed their seeds after September 23, and the rate of seed fall increased with time. The last measurement was taken on November 19 and at this time the number of seeds remaining attached to plants was estimated. From September 13 to november 19, 50% of the small seeds, 70% of medium seeds and 85% of the large seeds were shed from plants. Most seeds fell below the parent plants, but small numbers of seeds were dispersed a distance of 0.5 meters, with few disseminating beyond this limit (Table 4).

In the high salt environment no large seeds were found attached to the plant after November 19,

Table 4. Total seed rain m^{-2} of *Atriplex triangularis*.

Atriplex	Seed size	Distance from plant (m)				Attached seeds (m^2)	Total seeds (m^2)
		0.0	0.5	1.0	2.0		
Low salt	small	6798	1415	157	0	7310	15680
	medium	3526	1336	157	0	1210	6229
	large	2393	1100	0	643	419	4555
	total	12717	3851	314	643	8939	26464
High salt	small	5629	1572	2041	1239	3160	13641
	medium	3350	1258	1179	812	809	7408
	large	3417	2070	943	472	0	6902
	total	12396	4900	4163	2523	3969	27951

however 40% of the small and 23% of the medium seeds still remained attached. Seeds in this population were dispersed as far as 2 m from parent plants (Table 4).

Germination periodicity

In the first experiment packets of seeds from three size classes, small = <1.5 mm, medium = 1.5 to 2.0 mm, large = >2.0 mm, were placed in the field in April 1982 and were collected in June and July 1982 (Table 5). Percent of seed germination was found to be lower for all seed sizes at this time and germination of seeds was lower in subsurface samples than in surface samples. In the second experiment, seed packets were placed on the surface and buried in low and high salt environments in November. Germination was higher for small seeds during March in low salt environments, while, in high salt environments the rate of germination was similar for all months that seeds were collected (Table 5). Subsurface small seed samples had lower germination percentages than did surface samples, and large seeds germinated very early in the growing season. Germination percentages for large seeds were usually similar in surface and subsurface samples.

Discussion and conclusions

Mortality of halophytic plants in saline environments is attributed primarily to abiotic factors (Weaver, 1918, Ungar *et al.*, 1979; McGraw & Ungar, 1981; Jefferies *et al.*, 1981; Riehl & Ungar, 1982). Osmond *et al.* (1980) found that *A. vesicaria* and *A. stipitata* establishment was related to the quantity and periodicity of precipitation. Our data indicate that time of germination is important in determining the survivorship and fecundity of plants. Large seeds of *A. triangularis* which germinated earlier in the growing season had a better chance of survival than small seeds which germinated later.

The establishment and mortality of *Atriplex triangularis* seedlings appears to be dependent upon the precipitation pattern which affects soil salinity concentrations. During the 1981 growing season, precipitation in April was higher than normal, and correlated with an increase in the establishment of *A. triangularis* seedlings. Rainfall was normal in subsequent months and this resulted in high seedling mortality. In April 1982, precipitation was below normal and this was reflected in a decrease in seed germination and an increase in mortality. In both years, the risk of mortality was smaller for

Table 5. Germination responses of *Atriplex triangularis* seed taken from surface and subsurface samples of an experimental seed bank at different times during the growing season.

Seed size	Salinity	Depth	Experiment I April 1982 initiation		Experiment II November 1982 initiation			
			Month (1982)		Month (1983)			
			June	July	February	March	April	May
Small	Low	Surface	12.00 ± 3.1	26.80 ± 3.9	29.78 ± 7.8	71.60 ± 4.2	47.60 ± 6.5	48.00 ± 4.9
		Subsurface	9.14 ± 1.7	12.00 ± 1.3	28.44 ± 5.1	17.20 ± 2.5	8.80 ± 1.5	24.40 ± 3.1
	High	Surface	0.00 ± 0.0	8.00 ± 2.8	30.40 ± 4.4	34.20 ± 5.5	32.20 ± 5.3	29.55 ± 3.1
		Subsurface	6.50 ± 1.1	6.67 ± 1.3	13.25 ± 5.2	8.44 ± 1.4	6.86 ± 1.1	12.00 ± 1.9
Medium	Low	Surface	41.60 ± 6.2	66.40 ± 6.6	40.80 ± 6.2	75.20 ± 2.3	53.60 ± 6.5	65.00 ± 4.9
		Subsurface	9.14 ± 1.7	12.00 ± 1.3	57.78 ± 6.4	65.20 ± 4.9	31.20 ± 6.8	42.00 ± 2.3
	High	Surface	8.67 ± 1.6	16.50 ± 3.4	52.80 ± 8.6	56.00 ± 4.8	56.40 ± 7.6	48.80 ± 6.6
		Subsurface	6.50 ± 1.1	6.67 ± 1.3	26.00 ± 3.5	20.00 ± 2.8	25.33 ± 4.6	28.80 ± 4.3
Large	Low	Surface	41.60 ± 6.2	66.40 ± 6.6	35.20 ± 5.1	80.80 ± 3.8	79.60 ± 3.3	78.80 ± 4.9
		Subsurface	39.20 ± 6.0	20.40 ± 3.5	86.80 ± 1.8	80.80 ± 4.6	54.90 ± 7.6	61.90 ± 3.3
	High	Surface	8.67 ± 1.6	16.50 ± 3.4	60.60 ± 7.5	64.40 ± 8.0	68.00 ± 4.9	69.20 ± 5.5
		Subsurface	11.20 ± 3.9	9.70 ± 1.5	51.80 ± 6.2	59.60 ± 8.5	50.00 ± 8.4	53.60 ± 7.7

seedlings established earlier than for those developing later in the growing season. Individuals that were established before July had a better chance of surviving to the reproductive stage. Plants growing in low salt environments had a two-phase growth response in May and August, and the latter correlated with the reproductive phase. A gradual increase in growth was observed from May to August in the high salt zone.

Seedlings developing from large seeds have a larger root system which penetrates deeper into the soil. Later in the growing season when the upper layer of soil becomes more saline, larger plants which were established earlier survive, while later germinating shallow rooted small seedlings did not survive the increased soil salinity.

Ungar (1983) reported that large seeds of *A. triangularis* germinated early in the growing season and were not part of the persistent seed bank and therefore should be classified as a Type II transient seed bank in the sense of Thompson & Grime (1974). The small seeds of *A. triangularis* comprise a Type IV persistent seed bank in which seeds produced in the fall ordinarily do not germinate until the following spring and persist in the soil after the normal (February to June) germination period (Ungar, 1983; Khan & Ungar, 1984). The presence of a large number of small seeds in the soil insures the continuation of a population and protects against the threat of local extinction of populations. Cook (1979) suggested that the single most important characteristic of juvenile plants influencing their fitness is their size at the time of imposed environmental hazards. In *Atriplex hastata* and *A. patula* the large seeds germinated rapidly in comparison to small seeds which have a high capacity of survival (Chepil, 1946; Hulme, 1957). Both *A. hastata* and *A. patula* seeds were found to remain viable in the soil after five years burial (Roberts & Neilson, 1980).

Field experiments were established to determine whether or not there was an environmental effect on germination. We found that large seeds germinated more rapidly and were less inhibited by burial than small seeds, indicating that a persistent seed pool would only contain small seeds and that these seeds may be responsible for long term survival of *A. triangularis* populations. Light, salinity, seed size, and temperature appear to be the most important factors in controlling the germination of *Atriplex triangularis* seeds under field conditions.

The salt marsh at Rittman, Ohio has two populations of *A. triangularis* occupying habitats which can be distinguished on the basis of soil salinity concentrations. However, ecological isolation between these two populations is not complete, since during late fall and winter seeds can be transported from the one zone to the other because of flooding on the marsh. Selection may take place along various parts of the gradient for specific genotypes, and this may explain why individual plants show various degrees of phenotypic plasticity in both size and survival ability in various salinity zones. Genotypic selection in the *Atriplex* zone appears to be for greater salt tolerance and less morphological plasticity. Populations growing in the low salt zone had no survivors when they were transplanted to the *Salicornia* zone, while survivors from the *Atriplex* zone transplant had 1/6 the dry weight of those in the low salt zone. Plants from the *Atriplex* high salt zone transferred to the *Hordeum* zone accumulated twice the biomass of those left in the high salt zone, and some of the plants even survived when transplanted to the *Salicornia* zone. These data suggest that genotypes in the high salt habitats are either more salt tolerant or better adapted to the increased stress of transplant shock. Identification of allozyme patterns should be made to determine if genetic selection is taking place.

Total dry weight increased in transplants from high- to low-salt areas, but this increase was usually not equivalent to that of plants growing naturally in the low salt area. Gallagher *et al.* (1980) found that annual net productivity of tall *Spartina alterniflora* on creek banks reached 4 800 $gm^{-2} yr^{-1}$ as compared to short *S. alterniflora* on the high marsh that produced only 33% as much biomass. Production differences have been ascribed to high soil salinity stress, scarcity of ions, or scarcity of available nitrogen (Mendelssohn & Seneca, 1980; Pomeroy & Imberger, 1981; Wiegert *et al.*, 1983).

The significance of dispersal in the life cycle of a plant depends on the spatial and temporal heterogeneity of its environment (Harper, 1977). Our data indicate that most of the seeds produced by *Atriplex triangularis* remained in the vicinity of the parent plants. Seed reached maturity after mid-October and eventually fell below the dead or dying parent plants. However, a small number of seeds were dispersed for greater distances and this is related to seed transport because of flooding of the salt marsh.

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