Pak. J. Bot., 19(2): 123–130, 1987.

SALINITY AND DENSITY EFFECTS ON DEMOGRAPHY OF *ATRIPLEX TRIANGULARIS* WILLD.

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Abstract

The effect of density-dependent and density-independent factors in regulating the resource allocation, reproductive effort, and fecundity of *Atriplex triangularis* populations were studied in field and laboratory conditions. Total biomass production and reporductive output of *A. triangularis* varied with changes in soil salinity and plant density. At low soil salinity, where plants produced greater biomass and had higher reproductive output, increased density resulted in a substantial decline in biomass production and a 500 fold lower reproductive output. At higher soil salinities, density-independent factors caused lower biomass production and reproductive output. Small plants were produced under these conditions, containing 57 seeds per plant. Increased density caused a five fold reduction in biomass production and reduced fecundity to only 17 seeds per plant. Increase in density resulted in significant decreases in plant size but the proportion of the resources allocated to reproduction was not affected by changes in density.

Introduction

The effect of density-dependent or density-independent factors on populations has been the subject of much controversy over the past several years. In part, the basis of this discussiom may lie in different temporal and spatial scales of reference, as well as differing expectations concerning the presence of equilibrium vs nonequilibrium states in natural populations (Connell, 1978). Much of this controversy stems from a lack of adequate information about density-dependent regulation, particularly with regards to its frequency of occurrence, intensity, spatial pattern, and interactions with density-independent factors (Antonovics & Levin, 1980). In plant populations density stress usually results in either a phenotypically plastic responses or in an increase in mortality (Harper, 1977; Keddy, 1981). A considerable variation was noted among species regarding the importance of environmental factors and of density in determining the reproductive output of plants (Keddy, 1981). Moreover, the degree of density-dependent response varies with environmental conditions such as nutrient status. Interspecific crowding, salinity and drought (Keddy, 1981; Ungar *et al.*, 1979; Ungar, 1983). In salt marsh environments mortality of plants is primarily related to abiotic factors (Ungar *et al.*, 1979; Jefferies *et al.*, 1981). However, a few studies have reported that *Salicornia europaea* and *Atriplex triangularis* also respond to increased density with a plastic response in

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both the growth and reproductive capacity of individuals (Jefferies *et al.,* 1981; Ungar, 1983). These findings indicate that density-dependent factors effect plant responses in saline environments. Information is, therefore, needed not only on comparative density stress but also how this response pattern varies under different salinity regimes.

Atriplex triangularis Willd., an annual halophyte of the family Chenopodiaceae, is found in coastal and inland salt marshes of North America. Two populations of *A. triangularis* present in the salt marsh at Rittman, Ohio, USA show a noticeable physiological and phenotypic variability (Ungar, 1983; Khan & Ungar, 1984ab, 1985; 1986). The present study investigates the effects of density-dependent and density-independent factors in regulating the survival, resource allocation, reproductive effort and fecundity of *A. triangularis* populations under both field and laboratory conditions.

Materials and Methods

Field Studies: A series of quadrats were established to determine the effect of competition on survival and resource allocation in low and high saline environment. Ten plots (10 cm x 10 cm) each having 1, 10 and original field population size of plants (mean = 25) were established in the high salt zone in 1981 and in both high (2% NaCl) and low (0.5% NaCl) salt zones during the 1982 season. Density of 1 and 10 plants per plot was obtained by thinning the quadrats. Plants were harvested at the end of the growing season, and dry weight of roots, stems, leaves and fruits were determined. Reproductive effort and fecundity was also estimated.

Labortatory Studies: To study the interaspecific competition under saline conditions, cores (5.5 cm in diam.) of soil samples from low and high salt populations of *Atriplex* were brought to the laboratory in April 1981. Soil cores with *Atriplex* seedlings in 7.5 cm diam., plastic pots with a hole in the bottom were placed in a plastic tray in which a constant level of water was maintained throughout the experimental period. Seedlings were thinned to 1 and 10 plants per pot and one set was left undisturbed at the original density (mean = 25) as a control. Each treatment had ten replicates. Plants were harvested at the mature fruiting stage after 16 weeks. Dry weight of roots, stems, leaves, and fruits was determined.

Simultaneously similar experiments were designed for the area of lower salinity with *A. triangularis* populations where 1% and 3% NaCl solutions were used for watering. At the end of 16 week growth period the dry weight of roots, stems, leaves, and fruits was determined.

Statistical analysis of all data was done using the computer programs of "Statistical Analysis System" such as GLM, MEAN, and LSD on IBM 370 computer.

Results

Field Studies: The effect of thinning in low salt populations in field experiments were more marked as compared to the populations growing in high salt areas (Table 1). Dry weight of plants that were grown singly was about 40 times higher than for plants growing at field densities. Reproductive effort was also higher in plots containing single plant as compared to plots with 25 plants. In high density plots more resources were allocated to leaves and stems than to roots and fruits. Fecundity of plants grown singly averaged 1175.5 seeds as compared to 52 seeds per 10 cm x 10 cm area at field densities.

The plants growing in the high salt zone had a lower biomass production than those present in the low salt zone (Table 1). The effect of density on biomass production, fecundity, and reproductive effort was significant ($P < 0.0001$) in high salt populations, but differences were not as great as in the low salt populations.

Laboratory Experiment: A. triangularis plants grown to maturity showed that at low salinity intraspecific competition played a prominent role in biomass production (Fig. 1).

Table 1. Effect of salinity and density of plants on the growth and fecundity of *Atripiex triangularis* under field conditions.

Variable	Number of plants quadrat^{-1} 10 cm x 10 cm						LSD ($P < 0.05$)	
	1		10		25			
	Low Salt	High Salt	Low Salt	High Salt	Low Salt	High Salt	Densiy	Salinity
Root (%)	5.69 ±0.95	18.25 ±6.94	13.32 ±3.94	7.42 ±0.87	8.38 ±0.81	11.48 ±0.76	6.29	5.13
Stem (%)	32.12 ±2.63	24.14 ±1.91	33.16 ±3.98	34.33 ±5.20	34.91 ±1.17	32.92 ±2.17	6.38	5.21
Leaf (%)	34.95 ±3.14	29.50 ±4.07	32.70 ±3.01	35.98 ±4.28	43.37 ±2.69	33.43 ±3.50	7.16	5.85
Fruit (%)	27.14 ±4.58	28.11 ±4.51	20.81 ±4.04	22.26 ±3.73	12.88 ±1.88	22.17 ±2.61	7.18	5.85
Total weight (g)	7.82 ±1.36	0.59 ±0.15	1.77 ±0.42	0.27 ±0.05	0.20 ±0.02	0.12 ±0.03	1.59	1.30
Small seed mean no. plant^{-1}	732.10 ±237.49	33.40 ±9.50	92.82 ±28.12	23.97 ±4.44	7.84 ±1.54	11.20 ±2.91	228.98	186.82
Medium seed mean no. plant^{-1}	363.30 ±140.49	17.33 ±5.23	64.46 ±36.89	6.59 ±1.16	43.33 ±40.50	4.54 ±1.75	135.22	110.32
Large seed mean no. plant^{-1}	79.10 ±31.54	5.89 ±1.92	18.67 ±8.70	2.50 ±0.53	0.61 ±0.18	1.25 ±0.67	29.47	24.04
Total seed mean no. plant^{-1}	1175.50 ±341.54	56.62 ±14.61	175.95 ±67.80	33.06 ±5.30	51.78 ±40.84	16.99 ±5.09	338.43	276.11

Seed size ranges = Small = 1.0 – 1.45 mm; Medium = 1.46 – 1.95 mm and Large = 1.96 – 2.80 mm.

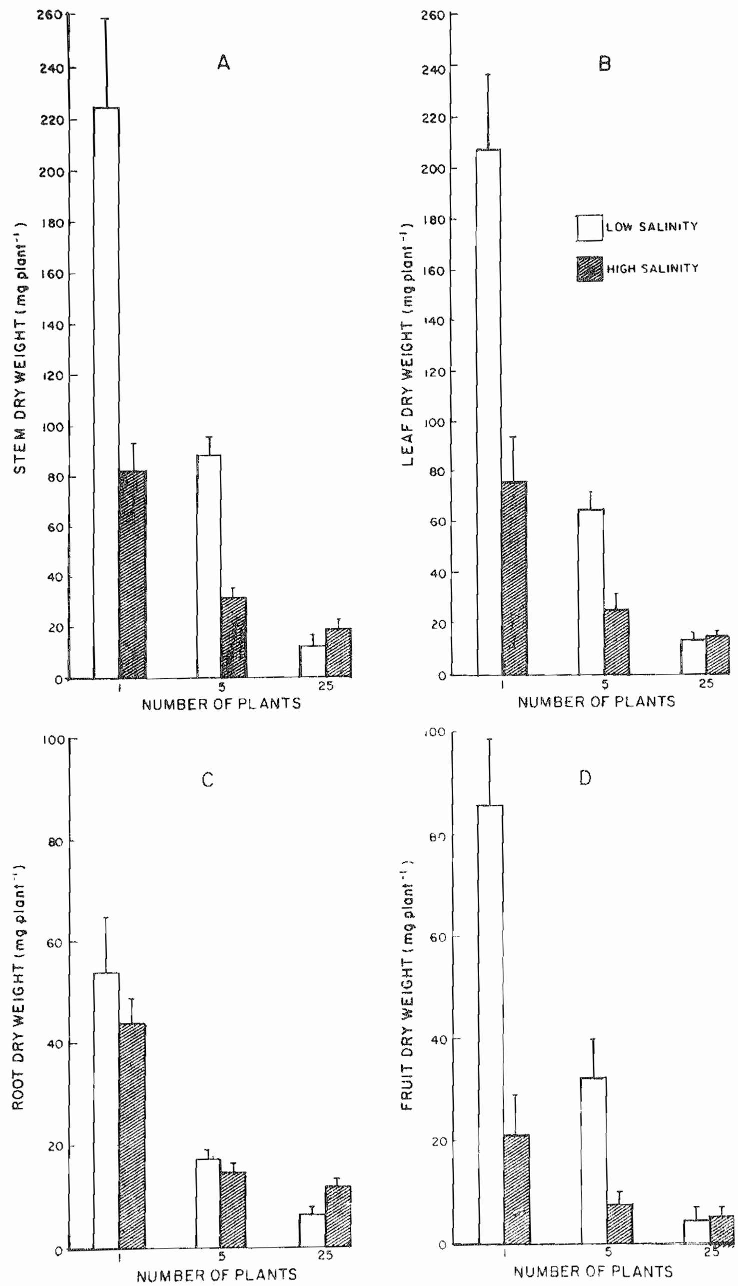

Fig. 1. Effect of salinity and density on the growth and reproduction of *Atriplex triangularis* plants grown under saline conditions.

Dry weight of stems, leaves, roots, and fruits were significantly lower in treatments with 5 and 10 plants per plot. At high salinity, the effect of competition was not as substantial as at low salinity. Biomass of the plants in treatments having one plant per pot was significantly ($P < 0.0001$) higher than for other treatments. The pattern was the same in case of reproductive effort and fecundity of plants (Figs. 1 & 2). The total plant biomass was higher at 1% NaCl than for the plants grown in 3% NaCl (Table 2). Biomass decreased with an increase in density and this reduction was more pronounced in low salt, treatment than in high salt treatments. Resource allocation was similar at all densities and salinities tested. However, reproductive effort of the plants grown singly was much higher than for plants grown at higher densities. This difference was more obvious for low salt conditions than for the high salt treatment. Fecundity also showed similar pattern.

Discussion

The competitive ability of plants may vary because environmental stress may influence the extent to which the competitive potential of plants can be realized (Grime, 1977). Competition is not restricted to productive habitats, but its significance in unproductive habitats is reduced by the effects of density-independent factors (Szwarcbaum & Waisel, 1973). Plants respond to increased density, either through increased mortality, a plastic response in growth and reproductive capacity or by a combination of above (Sharitz & McMormick, 1972; Watkinson & Harper, 1978; Keddy, 1981; Jefferies *et al.*, 1981; Ungar, 1983).

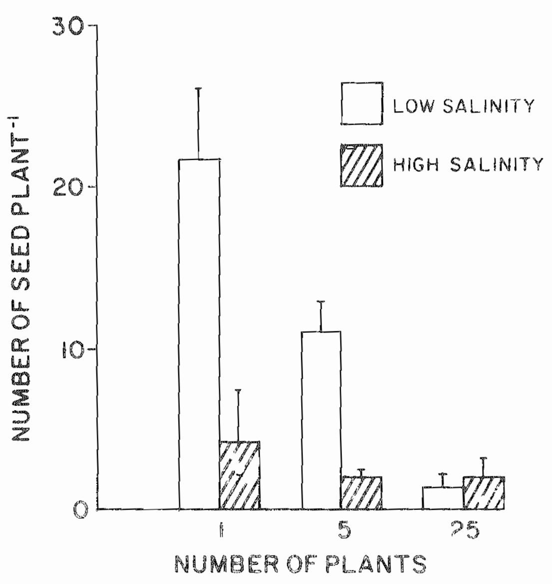

Fig. 2. Effect of salinity and density on the fecundity of *Atriplex triangularis* grown under laboratory conditions.

Table 2. Salinity and density on the growth and fecundity of *Atriplex triangularis* under laboratory conditions.

Variable	NaCl-1%			NaCl-3%			LSD ($P < 0.05$)	
	1 Plant	10 Plants	25 Plants	1 Plant	10 Plants	25 Plants	Density	Salinity
Leaf (%)	34.57	34.96	28.76	32.30	35.53	36.49	5.41	4.42
	±1.78	±2.80	±2.69	±4.03	±2.34	±2.03		
Stem (%)	42.54	43.17	55.45	54.59	53.14	50.79	5.61	4.59
	±1.49	±2.52	±3.13	±2.84	±2.57	±2.48		
Root (%)	8.18	12.75	10.46	6.74	9.06	9.07	2.64	2.16
	±0.93	±1.17	±1.33	±1.99	±1.15	±1.47		
Fruit (%)	14.72	9.12	5.29	6.36	2.27	3.65	3.15	2.58
	±2.30	±1.82	±1.12	±1.26	±0.93	±0.71		
Total weight (mg)	437.70	97.14	42.38	256.38	63.23	31.26	42.30	34.59
	±18.35	±8.34	±6.41	±40.98	±6.33	±3.10		
Small seed	11.20	0.94	0.16	3.75	0.48	0.23	4.21	3.63
mean no. plant^{-1}	±3.28	±0.25	±0.04	±1.25	±0.08	±0.05		
Medium seed	15.70	2.24	0.57	6.28	0.27	0.39	3.28	2.74
mean no. plant^{-1}	±2.42	±0.40	±0.16	±2.57	±0.11	±0.11		
Large seed	4.30	0.60	0.21	3.00	0.18	0.19	0.97	0.85
mean no. plant^{-1}	±0.72	±0.13	±0.05	±2.00	±0.02	±0.10		
Total seed	31.20	4.04	1.11	13.03	0.93	0.91	9.93	10.73
mean no. plant^{-1}	±5.23	±0.79	±0.27	±3.50	±0.21	±0.27		

Seed size ranges = Small = 1.0 – 1.45 mm; Medium = 1.46 – 1.95 mm and Large = 1.96 – 2.80 mm.

Growth and reproduction of *A. triangularis* varied in response to changes in salinity and density. At low salinity, where plant produce more biomass and had a high density-independent reproductive output increased density resulted in a substantial decline in biomass production and a corresponding reduction in reproductive output. In the high salt zone, density-independent effects reduced both total biomass production and reproductive output of plants. Small plants were produced under these conditions containing few seeds. The absence of intraspecific effects in high salt stress zone, increased density reduced plant biomass production five fold and fecundity to only 17 seeds per plant. Increased density resulted in a signficant decrease in plant size but the proportion of resource allocated to reproduction was not affected by change in density.

Keddy (1981) found that *Cakile edentula* plants growing near sand dune beaches of North America were larger and had higher reproductive output, but increased density caused a reduction in both size and reproductive output. At the land-ward end, density-independent effects reduced size and reproductive output, and plants produced only one or two fruits each in the absence of intraspecific effects. At this more stressful site increased density inhibited reproduction entirely. Keddy (1981) stressed the need to identify the physical factors affecting survivorship and reproductive output, and whether or not they acted in a density-independent or density-dependent manner.

Jefferies *et al.*, (1981) found that high mortality of *Salicornia europaea* occurred between the stages of production of ripe seeds and seedling establishment. He referred to this mortality as being density-independent and attributed it to effects of drought, hypersaline conditions or wave action. Fecundity of *S. europaea* plants was density-dependent. The number of seeds produced per plant depended both upon plant density in both the upper and lower marsh, although this dependence was more marked in low marsh populations. Biomass production in the lower marsh was higher than for the upper marsh in the absence of density-dependent effects. An increase in density resulted in a marked decrease in number of branches per plant and plant height (Jefferies *et al.*, 1981). Density-dependent reduction in plant size and reproductive output has also been reported (Watkinson & Harper, 1978; Keddy 1980; Liddle *et al.*, 1982).

In *A. triangularis* populations salinity stress which is related to change in soil moisture content was a major density-independent factor in regulating plant weight. Presence of density-dependent effects caused a further reduction in plant weight and reproduction. No evidence of mortality in relation to density effects was observed (Khan, 1985). This indicates that both density-dependent and density-independent factors were involved in regulating *A. triangularis* populations, with density-independent factors playing a dominating role.

Time of germination and salinity also determined the size of plants and their reproductive output (Khan & Ungar, 1986) and the data reported here suggests that addition of density-dependent effects increased the reduction in size of *A. triangularis* plants and their reproductive output. Density-dependent effects are marked in the low salt habitats, whereas high salt stress reduced the effect of density-dependent factors.

Acknowledgement

I am thankfull to Prof. Dr. Irwin A. Ungar, Ohio University, Athens, Ohio, USA, for his help and encouragement throughout this work.

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(Received for publication 27 December 1986)