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## DENSITY-DEPENDENT DYNAMICS OF *SALICORNIA EUROPAEA* MONOCULTURES<sup>1</sup>

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Investigators have studied in great detail the responses of individual plants to competition in monocultures (reviewed by Westoby 1984), and these studies have resulted in the self-thinning rule, the one “law” of plant ecology (Hutchings 1983; but see Weller 1987). Although many plant populations self-thin (Gorham 1979, White 1980), the mechanism(s) of self-thinning is (are) poorly understood (Miyanishi et al. 1979, White 1981, Charles-Edwards 1984, 1985, Westoby 1984, Lonsdale 1985). Investigators have also observed that hierarchical distributions occur in dense stands (e.g., Ford 1975, Harper 1977, Turner and Rabinowitz 1983, Weiner 1985), and conflicting hypotheses exist to explain this pattern (Turner and Rabinowitz 1983).

Here, I report results from a study of density-dependent phenomena in *Salicornia europaea* L. (Chenopodiaceae) monocultures. *Salicornia* occurs commonly in coastal salt marshes and inland salt pans where often it is found in stands exceeding 10 000 plants/m<sup>2</sup> (Riehl and Ungar 1982, Ellison 1987). *Salicornia* lacks leaves entirely, and photosynthesis is carried out by the succulent green stems (de Fraine 1912, Fahn and Arzee 1959). This study was conducted at Rumstick Cove, a protected 2-ha salt marsh in Barrington, Bristol County, Rhode Island, USA. Complete descriptions of Rumstick Cove and *Salicornia* are given in Ellison (1987).

### Methods

To document morphological variation among individuals and to examine the role of density in deter-

mining plant morphology and survival, in April 1984 I selected a large (6 × 9 m), dense (>10 000 plants/m<sup>2</sup>) monospecific stand of *Salicornia* for experimentation. This population was located 1.2 m above sea level in an area of the salt marsh otherwise dominated by salt-meadow grass (*Spartina patens*). Within this natural stand, I randomly placed 99 quadrats (10 × 10 cm) and divided them into four density treatments: 1 plant per quadrat (45 replicates), 10 plants per quadrat (30 replicates), 50 plants per quadrat (15 replicates), and natural high-density controls (9 replicates). The treatments corresponded to 100, 1000, 5000, and >10 000 plants/m<sup>2</sup> respectively. I assigned treatments randomly and thinned quadrats (by uprooting and removing seedlings) to the assigned densities on 1 April 1984 using a random dot sheet. High-density control quadrats were not thinned. I examined the quadrats every other day and removed all late germinating seedlings from the thinned quadrats. All other plant species that recruited into the study area were also removed. On 15 June, 1 August, and 15 September 1984, I harvested a randomly chosen one-third of the quadrats from each treatment along with 15 low-density control plants from a nearby patch where *Salicornia* density was 10 plants/m<sup>2</sup>. At each harvest date, the height and stem diameter of each plant were recorded. The numbers of branches of each branch order (where the trunk was assigned order 0, branches off the trunk were assigned order 1, and so on) were also counted. After measurement, plants were individually dried (95°C for 48 h) and weighed (±0.001 g). At this site *Salicornia* growth normally does not continue beyond the end of September (A. M. Ellison, *personal observation*).

To examine plant density effects on plant size distributions, the Gini coefficient (*G*) of size inequality (Sen 1973, Weiner and Solbrig 1984) was calculated for each quadrat. *G* ranges from zero to one with zero being the value obtained if all the plants were exactly the same size, and 1 being the value obtained in an infinite population consisting of one large plant and infinitely many plants of no mass. 95% confidence intervals for *G* were calculated using a “bootstrapping”

TABLE 1. Effects of density on *Salicornia* survivorship and morphology. Quadrats were 10 × 10 cm. For each date, values are means ± 1 standard error.

Density (plants/m <sup>2</sup> )*		15 June	1 Aug	15 Sep
10 (control)	Biomass (mg)	290 ± 142 <sup>a</sup>	620 ± 95 <sup>b</sup>	3560 ± 231 <sup>c</sup>
	Height (mm)	134 ± 1.1 <sup>a</sup>	258 ± 12.7 <sup>b</sup>	464 ± 16.7 <sup>c</sup>
	Stem diameter (mm)	0.2 ± 0.01 <sup>a</sup>	0.3 ± 0.02 <sup>a</sup>	0.4 ± 0.02 <sup>a</sup>
	Highest order branch	0.4 ± 0.10 <sup>a</sup>	2.1 ± 0.15 <sup>b</sup>	2.9 ± 0.18 <sup>c</sup>
	No. plants harvested (% dead)	15 (0)	15 (0)	15 (0)
100	Biomass (mg)	20 ± 31 <sup>a</sup>	370 ± 50 <sup>b</sup>	790 ± 122 <sup>c</sup>
	Height (mm)	66 ± 5.9 <sup>a</sup>	209 ± 17.8 <sup>b</sup>	247 ± 23.3 <sup>b</sup>
	Stem diameter (mm)	0.1 ± 0.01 <sup>a</sup>	0.2 ± 0.02 <sup>a</sup>	0.2 ± 0.18 <sup>a</sup>
	Highest order branch	0.5 ± 0.13 <sup>a</sup>	2.0 ± 0.10 <sup>b</sup>	2.3 ± 0.17 <sup>b</sup>
	No. plants harvested (% dead)	15 (0)	15 (0)	9 (13)
1000	Biomass (mg)	20 ± 3 <sup>a</sup>	100 ± 9 <sup>b</sup>	250 ± 210 <sup>c</sup>
	Height (mm)	55 ± 3.5 <sup>a</sup>	142 ± 5.9 <sup>b</sup>	186 ± 5.2 <sup>c</sup>
	Stem diameter (mm)	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>
	Highest order branch	0.4 ± 0.05 <sup>a</sup>	1.5 ± 0.06 <sup>b</sup>	1.9 ± 0.08 <sup>c</sup>
	No. plants harvested (% dead)	100 (0)	96 (4)	90† (0)
5000	Biomass (mg)	10 ± 1 <sup>a</sup>	70 ± 4 <sup>b</sup>	160 ± 9 <sup>c</sup>
	Height (mm)	58 ± 1.3 <sup>a</sup>	145 ± 3.2 <sup>b</sup>	177 ± 4.8 <sup>c</sup>
	Stem diameter (mm)	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>
	Highest order branch	0.1 ± 0.02 <sup>a</sup>	1.2 ± 0.05 <sup>b</sup>	1.4 ± 0.05 <sup>c</sup>
	No. plants harvested (% dead)	250 (0)	228 (9)	190† (5)
> 10 000	Biomass (mg)	10 ± 1 <sup>a</sup>	30 ± 2 <sup>b</sup>	50 ± 2 <sup>c</sup>
	Height (mm)	43 ± 0.7 <sup>a</sup>	95 ± 2.3 <sup>b</sup>	128 ± 2.4 <sup>c</sup>
	Stem diameter (mm)	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>	0.1 ± 0.01 <sup>a</sup>
	Highest order branch	0.1 ± 0.01 <sup>a</sup>	0.7 ± 0.03 <sup>b</sup>	0.9 ± 0.04 <sup>b</sup>
	No. plants harvested (% dead)	681 (0)	313 (7)	300 (9)

\* Within each density, characters with different superscript letters differ significantly among harvest dates (Scheffé test for multiple comparisons among means). Density affected significantly all morphological parameters ( $P > .001$ , ANOVA), but not mortality ( $P > .10$ , ANOVA).

† One quadrat each from the 10 and 50 plants per quadrat treatments was lost at the final harvest.

procedure (Efron 1982, Weiner 1985). Gini coefficients and associated confidence intervals were calculated using a FORTRAN program.

### Results

Mortality was low in the *Salicornia* monocultures, exceeding 10% in only one of the experimental quadrats (Table 1). Most of the plants that died were severely damaged by the beetle *Erynephala maritima* Lac. (Chrysomelidae) and herbivory was not restricted to quadrats of any particular density. Plants in both low-density and high-density quadrats suffered damage, and percent mortality did not differ among density treatments ( $P > .10$ , ANOVA; Table 1).

The morphological differences among high- and low-density plants were striking. At all harvest dates, low-density plants were taller, heavier, larger in stem diameter, and more profusely branched than their high-density counterparts ( $P < .001$ , ANOVA, all characters; Table 1). Although all plants were not the same size, the degree of size inequality within experimental quadrats did not change throughout the summer and did not differ among density treatments. Gini coeffi-

cients neither increased or decreased over the growing season for any given density, and  $G$  did not differ significantly among different density treatments on any given harvest date ( $P > .05$ , Fig. 1). The value of  $G$  in these experimental quadrats did not differ from that of a normal distribution throughout the summer.

### Discussion

Although intraspecific competition is clearly important in determining plant biomass and morphology, these high-density *Salicornia* monocultures did not self-thin (Table 1). Two alternative hypotheses may explain the absence of self-thinning in these dense stands. Either the densities were not high enough for self-thinning to occur, or self-thinning was precluded by intrinsic or environmental factors. Monocultures of other small annual plants self-thin when their densities approach 10 000 plants/m<sup>2</sup> (Harper 1977, Gorham 1979, White 1980, 1981, Westoby 1984), but no investigator who has studied dense *Salicornia* populations in the field has observed self-thinning (Joenje 1978, Ungar et al. 1979, Jefferies et al. 1981, Hartman and Engler 1982, Riehl and Ungar 1982, Watkinson and Davy 1985),

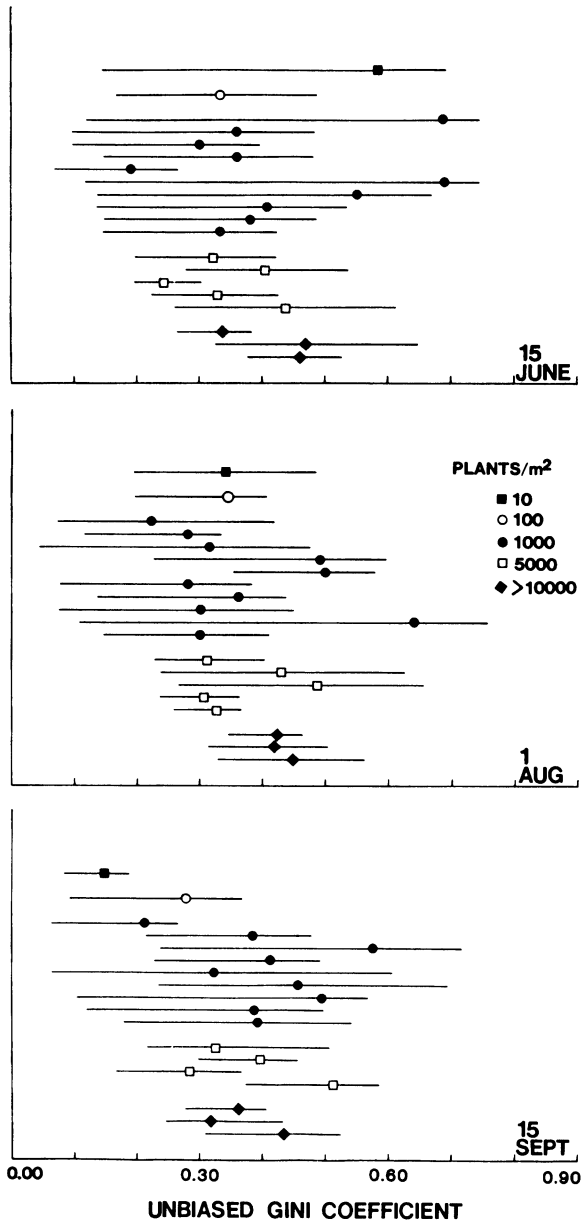


FIG. 1. Gini coefficients, with bootstrapped 95% confidence intervals, for biomass distributions of each experimental quadrat. Quadrats with  $>1$  plant per quadrat were not pooled for analysis because plants in one quadrat did not interact with plants in distant quadrats. To compare variation in biomass among individuals growing in dense plots with that of plants growing in isolation, the biomass values of low-density plants were pooled to create a single distribution as a measure of natural variation (Turner and Rabinowitz 1983). Because all quadrats have overlapping confidence intervals, the points are "spread" over the  $y$  axis to facilitate interpretation.

even though all these investigators examined populations denser than 10 000 plants/m<sup>2</sup>. The experiments described here were all conducted in a single large monoculture at a fixed tidal height, and the common garden design used here together with the absence of self-thinning in *Salicornia* populations studied worldwide, argue strongly against external factors precluding self-thinning in *Salicornia* populations.

The mechanism of self-thinning is poorly understood (White 1981, Charles-Edwards 1984, 1985, Westoby 1984, Lonsdale 1985). The geometry of *Salicornia* and the change in *Salicornia* morphology as density increases provide clues as to why these populations do not self-thin and support a general geometric mechanism for self-thinning. The distinctive morphology of *Salicornia* permits a relatively simple investigation into the allometry between various morphological parameters and plant biomass. Biomass is well predicted by the equation.

$$\text{Biomass} = b[(\text{height})(\text{basal diameter})^2 \cdot (\text{maximal branch order})]$$

( $F_{1,2384} = 15428.36$ ,  $P < .0001$ ,  $r^2 = 0.89$ ). Biomass, therefore, can be represented as an exponential function of the measured linear morphological parameters, and satisfies one of the necessary criteria for self-thinning: that biomass be a cubic function of linear measurements of plant size (White 1981). When growing at low densities, *Salicornia* increases exponentially in size; its volume increases as a function of plant height, stem diameter, and branching, while the area of ground it covers increases as a function of diameter and spread. Algebraically, the relationship of biomass to density derived from low-density stands is the familiar self-thinning equation  $w = Kp^{-3/2}$  (Yoda et al. 1963, Miyanishi et al. 1979, White 1981), where  $w$  is plant biomass,  $p$  is density, and  $K$  is a scaling constant. If high-density *Salicornia* plants grew in the same way that low-density ones did, then dense *Salicornia* monocultures would self-thin. However, at high densities, *Salicornia* increases in size in only one dimension, height (Table 1), and its volume increases as a linear function of height, thus violating the exponential growth requirement of the self-thinning rule (White 1981). The area of ground covered by a single plant remains constant throughout the growing season because its stem diameter is constant, and because virtually no branching occurs at high densities (Table 1). These morphological changes are directly a result of reduced light availability in dense stands (Ellison 1987).

Miyanishi et al. (1979) predicted that a plant that increases in size in height only would have a biomass-density relationship modelled by the equation  $w = Kp^{-\infty}$ , i.e., that self-thinning would not occur, and that

biomass would continue to increase as long as growth in height continued. *Salicornia* individuals growing at high densities do increase in biomass without attendant mortality (Table 1) as predicted by this model. These results lend credence to a geometric model of self-thinning (White 1981, Lonsdale and Watkinson 1983, Slatkin and Anderson 1984), and support strongly Miyanishi et al.'s (1979) generalization of this model.

In plant monocultures that do not self-thin, but whose individuals compete for resources, many investigators have shown that biomass distributions consisting of a few large plants and many small plants develop (e.g., Ford 1975, Waller 1985, Weiner 1985). Such biomass distributions can result from the suppression of the smaller plants' growth by the larger ones (the "dominance and suppression" hypothesis: Harper 1977), or by exponential growth of plants whose biomass distribution is initially normal (the "growth rate" hypothesis: Turner and Rabinowitz 1983). If dominance and suppression occur, the degree of size inequality should be smaller in low-density populations than in dense stands, while if the growth rate hypothesis is correct, there should be no difference in size inequality among low- and high-density stands. In both cases, the amount of variation is expected to increase with increasing mean plant mass (Turner and Rabinowitz 1983). Both high- and low-density monocultures of *Salicornia* exhibited size inequality, but there were no differences in the degree of size inequality among experimental monocultures of different densities (Fig. 1); consequently, dominance and suppression did not determine size inequality in these field populations of *Salicornia*. The degree of size inequality also did not increase with increasing mean mass (Table 1, Fig. 1), however, and this result is not predicted by the growth rate hypothesis (Turner and Rabinowitz 1983). The previous observation that high-density *Salicornia* grow in height only and do not self-thin also explains the lack of increase in size inequality with time in the high-density experimental populations. High-density plants approximate cylinders, and a cylinder that increases in height at a constant rate (as *Salicornia* does; Table 1) will add biomass at an arithmetic rate. Regardless of the shape of the initial biomass distribution, if all the plants grow at an arithmetic rate, only the mean of the distribution will change, not its variance. The results from this study illustrate the importance of plant morphology in determining plant population dynamics (White 1984) and highlight the need for further investigations of the interactions between them.

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## RELATIONSHIP OF LEAF LITTER DECOMPOSITION RATES TO RAINFALL IN THE MOJAVE DESERT<sup>1</sup>

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Santos et al. (1984) measured mass loss of creosotebush (*Larrea tridentata*) leaves at a site near Boulder City, Nevada, and at other sites in southern Arizona, southeastern California, and southwestern New Mexico. On the basis of these experiments they concluded that “. . . litter disappearance was better correlated with long-term average precipitation [ $r^2 = 0.82$ ] than with actual precipitation [ $r^2 = 0.46$ ] for the periods the litter bags were in the field.” These authors stated that their findings demonstrated “. . . the independence of both surface litter and buried litter decomposition from

rainfall,” and asserted that “. . . long-term climatic patterns are obviously more important as selective forces shaping the structure of desert soil communities than are the short-term yearly fluctuations.”

We report here the results of a leaf litter decomposition experiment conducted in Rock Valley, Nye County, Nevada. The results of this experiment differ from those of Santos et al. (1984) and lead us to question whether the process of decomposition in arid environments is independent of rainfall.

### Methods

Rock Valley (elevation 1020 m) lies in the Mojave Desert  $\approx$  18 km west of Mercury, Nevada, at the United States Department of Energy's Nevada Test Site. The area has a history of past research and experimentation, including 6 yr of work (1971–1976) during the United States International Biological Program (Analysis of Ecosystems). General descriptions of Rock Valley may be found in earlier reports and articles (e.g., Turner 1973, French et al. 1974, El-Ghonyem et al. 1980).

We used 12  $\times$  12 cm bags made from fiber glass screen in the Rock Valley experiment. Leaves of *Larrea tridentata* and *Lycium pallidum* were collected in litter