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Effects of intraspecific competition on growth and photosynthesis of *Atriplex prostrata*

Li-Wen Wang^{a,b}, Allan M. Showalter^{a,b}, Irwin A. Ungar^{a,*}

^a Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA

^b Molecular and Cellular Biology Program, Ohio University, Athens, OH 45701, USA

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Abstract

We investigated the effect of intraspecific competition on growth parameters and photosynthesis of the salt marsh species *Atriplex prostrata* Boucher in order to distinguish the effects of density-dependent growth inhibition from salt stress. High plant density caused a reduction of 30% in height, 82% in stem dry mass, 80% in leaf dry mass, and 95% in root dry mass. High density also induced a pronounced 72% reduction in leaf area, 29% decrease in length of mature internodes and 50% decline in net photosynthetic rate. The alteration of net photosynthesis paralleled growth inhibition, decreasing from $7.6 \pm 0.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at low density to $3.5 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at high density, indicating growth inhibition caused by intraspecific competition is mainly due to a decline in net photosynthesis rate. Plants grown at high density also exhibited a reduction in stomatal conductance from $0.7 \pm 0.1 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at low density to $0.3 \pm 0.1 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at high density and a reduction in transpiration rate from $6.0 \pm 0.3 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at low density to $4.3 \pm 0.3 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at high density. Biomass production was inhibited by an increase in plant density, which reduced the rate of photosynthesis, stomatal conductance and leaf area of plants. © 2005 Elsevier B.V. All rights reserved.

Keywords: *Atriplex prostrata*; Density; Growth inhibition; Halophytes; Intraspecific competition; Photosynthesis

* Corresponding author. Present address: 44 Walker Street, Athens, OH 45701, USA. Tel.: +1 740 593 3015; fax: +1 740 593 1130.

E-mail address: ungar@ohio.edu (I.A. Ungar).

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1. Introduction

Growth and development of plants occurring in salt marsh habitats may be determined by a combination of abiotic and biotic factors (Pennings and Callaway, 1992). Both salt stress and competition affect biomass production of halophytes in salt marshes (Adam, 1990; Ungar, 1991). Increases in plant density may lead to an asymmetric frequency distribution of plants in which there are a few large individuals and numerous small plants (Weiner, 1986; Drake and Ungar, 1989) or to a symmetrical competitive response in which all individuals have an equal decline in biomass production (Ellison, 1989). In the case of asymmetric distribution, size variation among plants generally increases when there is competition for light because larger individuals may reduce light available to smaller individuals and thus suppress their growth (Weiner, 1990). Smaller individuals might be lost due to high density-dependent mortality, because halophytes have relatively high light requirements (Ungar, 1991).

Intraspecific competition is reported to reduce biomass production in halophytes in both field and laboratory investigations (Ellison, 1987; Pennings and Callaway, 1992; Bertness and Yeh, 1994; Rahman and Ungar, 1994; van Kleunen et al., 2001). Specifically, biomass production of *Atriplex prostrata* Boucher, a facultative halophyte, is negatively affected by intraspecific competition within a natural population (Riehl and Ungar, 1983; Drake and Ungar, 1989). Although much is known about the whole plant response to intraspecific competition, little is known about the mechanisms responsible for density dependent growth inhibition in salt marsh species.

To better understand the dynamics and consequences of intraspecific competition of *A. prostrata*, we used controlled laboratory conditions to address the following questions: (1) Which growth parameters of *A. prostrata* are density-dependent? (2) Does self-thinning happen when *A. prostrata* is growing at high density? (3) Are photosynthesis, stomatal conductance, and transpiration affected by plant density?

2. Materials and methods

Seeds were collected from *A. prostrata* (syn. *Atriplex triangularis* Willd.) plants growing in a salt marsh at Rittman, Ohio in October 1994. The marsh is located at a site where salt mining is taking place on the property of the Morton salt company. Seeds were sown in 100 cm² white-sand-filled pots in plastic trays filled with water and germinated in an incubator under a 25 °C/5 °C, 12-h day:12-h night regime (20 μmol m⁻² s⁻¹, 400–700 nm). Plastic wrap was used to cover the tray to prevent evaporation. Two weeks after germination, seedlings were thinned to desired densities (2, 4, 8, or 16 seedlings per pot). Riehl and Ungar (1983) reported plant densities of from 1 to 23 plants 100 cm⁻² from June to October under field conditions in the Rittman, Ohio salt marsh. These field observations were used to determine plant densities used in this experiment. A total of 40 pots (10 pots per density treatment) were placed in plastic trays. Trays were filled with half-strength Hoagland and Arnon No. 2 solution and maintained in an environmental growth chamber under a 25 °C/15 °C, 14-h day:10-h night regime (400–700 nm, 400 μmol m⁻² s⁻¹).

Distilled water was added daily to each tray to replace water lost because of evaporation and transpiration. Nutrient solutions were replaced weekly.

After 4 weeks, five plants from each density treatment were randomly chosen from different pots to measure photosynthetic rate (A) at ambient light levels, transpiration rate (E), and stomatal conductance with an ADC Infrared Gas Analyzer (Model: LCA-3), and water use efficiency (WUE) was calculated as A/E. Leaves from the second node were used for these measurements. After photosynthesis was measured, 10 plants from each treatment were randomly chosen from different pots to measure plant height and length of the first, second, third, and fourth internodes. Area of leaves from the first, second, and third nodes was measured using a Licor portable area meter (Model: LI-3000) with three replicate readings for each leaf. Each of these 10 plants was dried in a forced draft oven at 60 °C for 3 days to obtain the dry mass of leaves, stems and roots.

The results for growth and photosynthesis were analyzed with a one-way ANOVA using NCSS (version 2000) and/or SigmaStat (version 2.03) statistical package. A \log_{10} transformation was used to normalize data of dry mass, which were not normally distributed. If a significant difference was determined among means, a Bonferroni post hoc test was used to determine significant differences between pairwise comparisons among individual treatments.

3. Results

A one-way ANOVA indicated that *A. prostrata* plants grown at lower densities (2 and 4 plants per pot) were significantly taller than those grown at higher densities (8 and 16 plants per pot; $F = 16.99$, $P < 0.001$; Table 1). There was no significant difference in the length of the first and second internodes from the top of the plants at the time of harvest ($F = 1.30$ and 0.61 ; $P = 0.2892$ and 0.6138 , respectively). Third and fourth internodes of plants grown at 2 and 4 plants per pot were significantly longer than those of plants grown at the higher densities (8 and 16 plants per pot; $F = 7.68$ and 10.35 , respectively; $P < 0.001$ for both; Table 1).

A. prostrata grown at lower densities produced more leaf ($F = 26.42$, $P < 0.001$), and stem ($F = 16.89$, $P < 0.001$) dry biomass than those grown at higher densities (Table 2). *A. prostrata* grown at a density of 2 plants per pot accumulated significantly greater root dry

Table 1
Effect of plant density on height and length of internodes (cm \pm S.E.) of *A. prostrata*

	2 plants pot ⁻¹	4 plants pot ⁻¹	8 plants pot ⁻¹	16 plants pot ⁻¹
Height	34.3 \pm 1.7 ^{a*}	39.3 \pm 1.0 ^a	26.0 \pm 2.1 ^b	24.2 \pm 1.4 ^b
First internode	1.4 \pm 0.2 ^a	1.0 \pm 0.1 ^a	1.6 \pm 0.3 ^a	1.1 \pm 0.3 ^a
Second internode	5.3 \pm 0.5 ^a	4.3 \pm 0.5 ^a	5.3 \pm 0.8 ^a	5.2 \pm 0.7 ^a
Third internode	8.1 \pm 0.5 ^a	9.2 \pm 0.4 ^a	6.2 \pm 0.7 ^b	6.6 \pm 0.4 ^b
Fourth internode	6.6 \pm 0.8 ^a	8.7 \pm 0.4 ^a	5.1 \pm 0.6 ^b	4.7 \pm 0.4 ^b

* Different superscript letters (a and b) in a row indicate that the two means are statistically different as determined by a Bonferroni post hoc test.

Table 2

Effect of plant density on mean dry mass production (g ± S.E.) of *A. prostrata*

	2 plants pot ⁻¹	4 plants pot ⁻¹	8 plants pot ⁻¹	16 plants pot ⁻¹
Stem	0.5 ± 0.1 ^{a*}	0.4 ± 0.1 ^a	0.2 ± 0.0 ^b	0.1 ± 0.0 ^b
Leaf	0.5 ± 0.1 ^a	0.4 ± 0.1 ^a	0.2 ± 0.0 ^b	0.1 ± 0.0 ^c
Root	0.7 ± 0.3 ^a	0.3 ± 0.1 ^{a,b}	0.1 ± 0.0 ^b	0.1 ± 0.0 ^b

* Different superscript letters (a–c) within a row indicate that the two means are statistically different as determined by a Bonferroni post hoc test.

mass than those at densities of 8 and 16 plants per pot ($F = 16.86$, $P < 0.001$; Table 2). Density did not affect water content of stems and roots ($F = 1.292$, $P = 0.292$ and $F = 1.894$, $P = 0.148$, respectively). However, leaves from plants grown at densities of 4, 8 and 16 plants per pot had significantly lower water content than leaves of plants from a density of 2 plants per pot ($F = 10.748$, $P < 0.001$).

When leaves from a particular node, either first, second, or third were sampled, the leaf area from low densities (2 and 4 plants per pot) was significantly larger than that from higher densities (8 and 16 plants per pot; $F = 16.044$, $P < 0.001$ for first node; $F = 12.558$, $P < 0.001$ for second node; $F = 8.677$, $P < 0.001$ for third node; Table 3).

Overall, net photosynthetic rate differed significantly among different density groups ($F = 11.002$, $P < 0.001$), and plants from lower densities (two and four plants per pot) had a higher net photosynthetic rate than plants from higher densities (8 and 16 plants per pot; Table 4). Transpiration rates of plants grown at various densities were significantly different ($F = 10.405$, $P < 0.001$; Table 4), with plants grown at 2 and 4 plants per pot having significantly higher transpiration rates than plants grown at a density of 16 plants per pot. Plants grown at four per pot also had significantly higher transpiration rates than

Table 3

Effect of plant density on mean leaf area (cm² ± S.E.) from the first, second, and third node of *A. prostrata*

	2 plants pot ⁻¹	4 plants pot ⁻¹	8 plants pot ⁻¹	16 plants pot ⁻¹
First internode	13.4 ± 1.5 ^{a*}	11.3 ± 0.9 ^a	6.5 ± 1.0 ^b	4.0 ± 0.4 ^b
Second internode	11.5 ± 1.5 ^a	10.1 ± 1.3 ^a	5.5 ± 0.7 ^b	4.0 ± 0.4 ^b
Third internode	10.6 ± 1.8 ^a	9.5 ± 1.5 ^a	4.9 ± 0.8 ^b	2.9 ± 0.3 ^b

* Different superscript letters (a and b) in a row indicate that the two means are statistically different as determined by a Bonferroni post hoc test.

Table 4

Effect of density on photosynthesis rate, transpiration rate, stomatal conductance and water use efficiency (mean ± S.E.) of *A. prostrata*

	2 plants pot ⁻¹	4 plants pot ⁻¹	8 plants pot ⁻¹	16 plants pot ⁻¹
Net photosynthetic rate (μmol CO ₂ m ⁻² s ⁻¹)	7.6 ± 0.9 ^{a*}	6.2 ± 0.4 ^{a,b}	4.5 ± 0.4 ^{b,c}	3.5 ± 0.4 ^c
Transpiration rate (mmol H ₂ O m ⁻² s ⁻¹)	6.0 ± 0.3 ^{a,c}	6.5 ± 0.3 ^a	5.1 ± 0.5 ^{b,c}	4.3 ± 0.3 ^b
Water use efficiency (μmol CO ₂ /mmol H ₂ O)	1.3 ± 0.2 ^a	1.0 ± 0.1 ^b	0.9 ± 0.1 ^b	0.8 ± 0.1 ^b
Stomatal conductance (mol H ₂ O m ⁻² s ⁻¹)	0.7 ± 0.1 ^a	0.8 ± 0.1 ^a	0.5 ± 0.1 ^{a,b}	0.3 ± 0.1 ^b

* Different superscript letters (a–c) within a row indicate that the two means are statistically different as determined by a Bonferroni post hoc test.

plants grown at a density of eight plants per pot. In terms of the calculated water use efficiency, there was an overall significant difference among density treatments ($F = 16.437$, $P < 0.001$; Table 4). Plants grown at a density of 2 plants per pot had significantly higher ($P < 0.05$) water use efficiency than plants grown at other densities examined. Stomatal conductance differed significantly among plants grown at various densities ($F = 6.941$, $P = 0.003$; Table 4), with plants grown at 2 and 4 plants per pot having significantly higher ($P < 0.05$) transpiration rates than plants grown at a density of 16 plants per pot.

4. Discussion

Dry mass production of *A. prostrata* decreased significantly in the higher density treatments. Although self-thinning has been observed for other species in plant monoculture (Gorham, 1979; Westoby, 1984), none of the plants grown at highest densities died during this experiment. This may be because the densities examined were not high enough for self-thinning to occur. Instead, high density caused growth inhibition as indicated by declines in height, leaf area, and biomass of stems, leaves, and roots. However, *Salicornia europaea* growing at high densities under field conditions also did not self-thin and exhibited a symmetrical decrease in biomass (Ellison, 1987). In a plant monoculture that does not self-thin, many investigators have shown that a biomass distribution consisting of a few large plants and many small plants may develop when individuals compete for resources (Harper, 1977; Turner and Rabinowitz, 1983; Weiner, 1986). Drake and Ungar (1989) found that when densities were 10 plants 100 cm^{-2} or greater competition was asymmetrical in field experimental populations of *A. prostrata*, producing a large number of small individuals and few large individuals.

The number of nodes that plants produced at various densities was not significantly different, but the length of mature internodes (third and fourth from the top) was reduced in plants grown at high densities. *A. prostrata* grown at high densities had significantly smaller leaf areas than those at low densities. None of the leaves exhibited symptoms of nutrient disorders, confirming that nutrient deficiency was not a significant factor in this system. None of the plants were wilted at any point, indicating that water stress was not a problem. We believe that reduced leaf area and lower rates of photosynthesis for plants grown at high densities were the primary physiological factors responsible for reductions in biomass production in *A. prostrata*. Indeed, the net photosynthetic rate of plants grown at low densities was double that for plants grown at high density, which is correlated with density dependent reductions in biomass observed for stems and leaves.

Plants grown at the highest density had significantly lower root mass than plants grown at lower densities. Moreover, the relative allocation of biomass to roots when compared to stem and leaf biomass was greater in plants grown at two plants per pot (45% of total dry mass) than for those grown at 16 plants per pot (23% of total dry mass). According to the model of Vargas-Mendoza and Fowler (1998) as well as that of “size symmetrical competition”, which represents a proportional division of resources (Weiner, 1990), water use is proportional to the relative size of plants. A reduction in stomatal conductance may also contribute to the reduction in net photosynthesis by decreasing CO_2 diffusion (Cornic et al., 1992). As Weiner (1990) indicated, at increased plant density, light becomes a

limiting factor, causing a reduction in plant biomass. Because water and nutrients were provided regularly and were not limiting in our experiment, reduced light levels due to crowding could be the main reason for reduction in growth parameters and photosynthetic rates at high densities. Further investigations into the interaction between light level and crowding need to be carried out to determine the precise effects of these factors on growth of marsh plants.

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