Morphological determinants of self-thinning in plant monocultures and a proposal concerning the role of self-thinning in plant evolution

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Understanding density-dependent dynamics in plant populations has been limited by the lack of a clear mechanism responsible for self-thinning in plant monocultures. Although many plant populations exhibit predictable thinning dynamics based on the self-thinning rule, experimental support for possible mechanisms generating the self-thinning rule is lacking. Here. I review the formulation of the self-thinning rule based on plant geometry, and describe an experimental test of the geometrical hypothesis of self-thinning. Geometric theory predicts that plants of disparate morphologies should thin along lines with slopes different from −3/2. I examined the thinning dynamics of three species in the family Chenopodiaceae. *Salicornia europaea. Suaeda maritima*, and *Atriplex triangularis*, whose morphologies range from leafless, sparsely-branched and short (*Salicornia*) to bushy (*Atriplex*). As predicted by the geometric theory of self-thinning. *Salicornia* did not self-thin. *Atriplex* thinned along a line with slope −1.82, and *Suaeda* thinned along a line of intermediate slope, −2.50. These results strongly support a geometric basis for self-thinning.

Morphologically. *Salicornia* is similar to the earliest vascular land plants, and by analogy I propose that self-thinning was not a selective force in early land plant evolution. Competition for light among plants would result in selection for increased height and canopy spread, and the widespread occurrence of the self-thinning rule in contemporary natural plant populations is hypothesized to be a result of these morphological changes.

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Introduction

The study of self-thinning. the selective density-dependent mortality of individuals in overcrowded plant stands. has received much attention since Yoda et al. (1963) framed the −3/2 power, or self-thinning rule. It has been proposed that this single quantitative rule would describe completely the dynamics of any overcrowded plant stand (e.g. White 1980). Although several reviews of published data have attested to the generality of the self-thinning rule (White and Harper 1970. Gorham 1979. White 1980. Westoby 1984) this general-

ity recently has been called into question (Ellison 1987a. Weller 1987a,b. Zeide 1987).

Yoda et al. (1963) derived the self-thinning rule from geometric principles. If plant biomass (w) is proportional to the cube of some linear dimension, 1. [$w \alpha\ 1^3$] and the surface area of the ground covered by the plant, s, is proportional to the square of the *same* linear dimension [$s \alpha\ 1^2$] and inversely proportional to plant density [$s \alpha\ p^{-1}$], then by substitution. $w \alpha\ p^{-3/2}$. This derivation of the self-thinning rule rests on three assumptions (White 1981): (1) plant weight is a direct power function of the cube of some particular linear dimension. (2)

plants retain their geometric similarity during growth, and (3) self-thinning occurs only when the total coverage of a stand is greater than or equal to 100% of the total ground area.

Miyanishi et al. (1979) extended Yoda et al.'s (1963) allometric derivation to encompass variation in plant form, and following the method and assumptions of Yoda et al.'s model, they predicted the mean plant biomass-density relationships of five distinct, *idealized* plant morphologies: plants that grow only in one horizontal dimension (Type I: $w = Kp^{-1}$); plants that grow horizontally and vertically, but not in spread (Type II: $w = Kp^{-2}$); plants that grow in length and spread, but not height (Type III: $w = Kp^{-1}$); plants that grow in all three dimensions (Type IV: $w = Kp^{-3/2}$) and plants that grow only in height (Type V: $w = Kp^{-\infty}$). For the last (Type V), Miyanishi et al.'s (1979) model predicted that self-thinning will not occur. Miyanishi et al.'s (1979) model has been criticized strongly for three reasons (White 1981): (1) two-dimensional plants do not occur in nature; (2) the vague generality of the model robs the rule of its predictive power; (3) although Miyanishi et al. (1979) theoretically predicted the self-thinning exponent in the thinning equation to be proportional to some power of density, dependent on the proportionality of plant weight to ground area covered, the empirical data show that this exponent *is* $-3/2$ (but see Ellison 1987a, Weller 1987a, Zeide 1987). White (1980) considered thinning slopes between -1.3 and -1.8 to support the self-thinning rule while Weller (1987a) supported the use of rigorous statistical tests to determine whether observed thinning slopes differ significantly from $-3/2$. White (1981) concluded that in the "face of conflict between allometric theory and empirical generality, the biological imperative must be acknowledged". Nonetheless, White (1981) also finds that in the cases where biomass-morphology allometry is well-documented (i.e. for trees), that the self-thinning exponent is correctly predicted by allometric theory, and White (1984) has urged that students of plant demography pay closer attention to plant morphology in order to understand more clearly factors affecting plant population dynamics.

In three investigations to date that have examined the relationship between plant morphology and self thinning, Ellison (1987a) demonstrated that density-dependent dynamics were determined by plant shape in *Salicornia europaea* populations, Westoby (1976) found that thinning dynamics were not dependent on cultivar shape in *Trifolium subterraneum* L., and Lonsdale and Watkinson (1983) found that plant geometry could affect the slope and intercept of the self-thinning boundary for various herbaceous species.

The allometric derivation describes only the thinning boundary, and says nothing about the time-trajectory of the thinning process. Aikman and Watkinson (1980) modelled the course of thinning over time, along with the thinning boundary, by assuming logistic growth of

individual plants and competition as the mechanism for plant mortality. Their model assumed the self-thinning equation ($w = Ks^{3/2}$) where s is the area occupied by the plant (their assumptions 1 and 2), and so their formulation is essentially a restatement of Yoda et al.'s (Weller 1987a). However, they assumed that the exponent of the thinning equation ought to be 3/2 for *simplicity* [my emphasis], and stated, as Miyanishi et al. (1979) did, that the exponent ought to be expressed generally as an empirical parameter of plant growth and form to be evaluated from observed data. Holsinger and Roughgarden (1985) modelled the population dynamics of annual plants based on plant-plant interactions, and they showed that a thinning line with slope $-3/2$ is but a special case of a large set of possible outcomes.

In summary, then, when allometric relationships between plant dimensions and biomass are known, $w = Kp^{-3/2}$ is often found to be a good description of the self-thinning rule (White 1981, Westoby 1984), and models of plant population dynamics based on plant-plant competitive interactions can yield the time-course observed for thinning stands (Aikman and Watkinson 1980, Holsinger and Roughgarden 1985). These formulations, however, do not prove that plant allometry is responsible for the thinning boundary, or that plant-plant competition causes the characteristic self-thinning time-course. Miyanishi et al.'s model provides the basis for a critical test of the allometric theory, however. If a plant could be found to satisfy one of their ideal morphologies (other than Type IV, the "normal" morphology), and to have the biomass-density relationship predicted by their model, then the allometric model would be supported. In particular, a plant that grew only in height and did not self-thin would be the "exception that proves the rule". White (1981) rejected such plants from consideration in the thinning rule as non-sequiturs because they would not thin. Plants that grew only in height and did not self-thin at densities where similarly-sized but differently-shaped plants did, however, would increase our understanding of a potential mechanism for self-thinning in the same way that the study of genetic deletion has increased our understanding of gene function. Based on Miyanishi et al.'s (1979) model, one can test the hypothesis that populations of plants that lack leaves, and are sparsely branched (approximating Miyanishi et al.'s [1979] Type V morphology) do not self-thin, and that increased branching and height in plants results in the populations' thinning lines approaching a slope of $-3/2$.

Materials and methods

To test the hypothesis that populations of plants that are herbaceous, leafless, and sparsely-branched do not thin, and that populations of plants with successively larger leaves and canopies exhibit thinning slopes approaching $-3/2$, I examined experimentally the density-dependent dynamics of three species in the family Chenopodia-
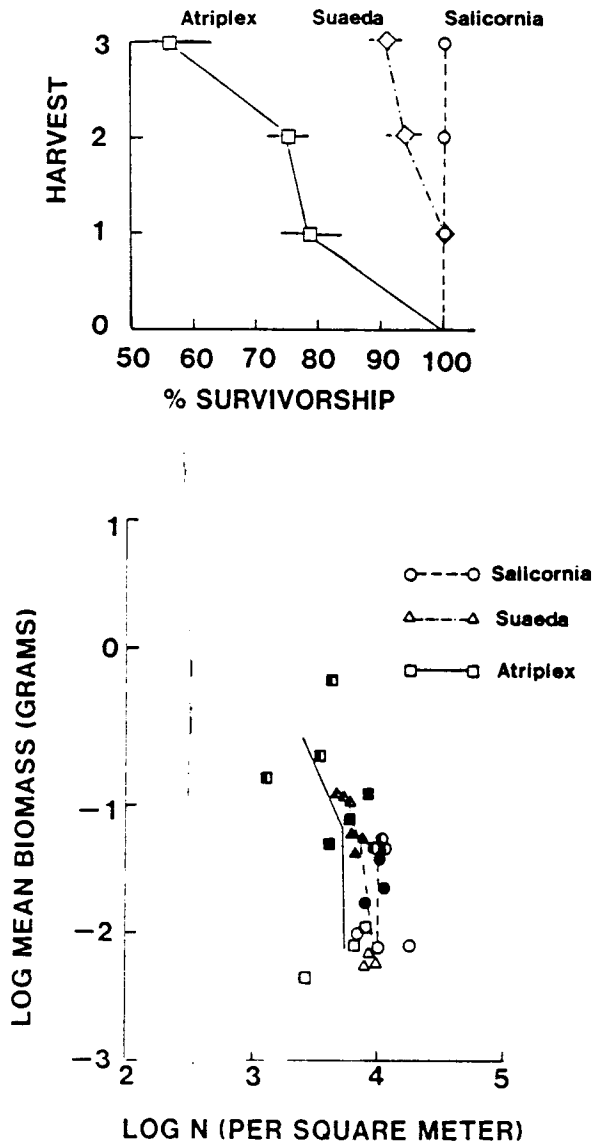
Fig. 1. Upper: Mean % survivorship (±1 SE) of the populations at each harvest date. Lower: Biomass-density relationships of the three species. Open symbols – 1st harvest; solid symbols – 2nd harvest; half-filled symbols – 3rd harvest. Thinning lines calculated using principal components analysis. Graph A is rotated 90° relative to its normal presentation to be comparable to graph B.

ceae: Salicornia europaea, Suaeda maritima (L.) Dum., and Atriplex triangularis Willd. These three herbaceous annual plants are morphologically distinct. All three species have regular branching, but Salicornia lacks leaves and, when growing at high densities, rarely branches (Ellison 1987a). The leaves of Suaeda are reduced, and Atriplex has broad leaves. All three of these plants are common to sea coasts and marshes of eastern North America, and are often found in populations exceeding 1,000 individuals per m^2 (Watkinson and Davy 1985, Ellison 1987a,b).

Nine replicate 12×12 cm quadrats of Suaeda and nine similar quadrats of Atriplex were established using 144 seeds/quadrat sown in regular square arrays. This density corresponds to 10,000 plants m^{-2}, a density at which small annual plants of other species self-thin (Harper 1977, Gorham 1979, White 1980). Experimental populations of Suaeda and Atriplex were established in plastic flats (50 × 30 × 6 cm) containing a 50–50 sterile mixture of coarse sand and potting soil in a greenhouse at Brown University. Three quadrats were arranged in each flat. Seeds were gathered from randomly chosen plants growing at Rumstick Cove, a nearby salt marsh (Bertness and Ellison 1987), and the number of replicates, although small, was determined by the available seeds. Greenhouse populations were watered as needed, and were not fertilized. Salicornia populations of similar density were studied in the field, and detailed results of investigations of density on survivorship and morphology of Salicornia are presented elsewhere (Ellison 1987a). Although I was unable to grow Salicornia from seed in the greenhouse, Salicornia seedlings transplanted into the greenhouse were identical in all respects to field populations (unpubl. data), and in order to account for population dynamics early in ontogeny, I use Salicornia data from field populations grown from seed.

Every six weeks, the aboveground biomass of three randomly-selected quadrats of each species was harvested. The total duration of the experiment, 18 wk, spanned the entire life-span of these plants, from germination through flowering. These annual species, therefore, would not have grown further if the experiment had run for a longer period of time. To avoid edge effects, only the center 10×10 cm of each quadrat was harvested. The total number of plants in each quadrat was counted, and the height of each plant was measured (± 0.1 cm), the number of branches (including secondary, tertiary, etc. branches) was counted, and each plant then was dried (95°C for 48 h) and weighed (± 0.001 g).

Thinning slopes were calculated for each species using principal components analysis using the PRINCOMP procedure of the Statistical Analysis System (SAS version 82.3, SAS Institute, Cary, NC, U.S.A.), because the data may not conform to the assumptions of regression analysis (Mohler et al. 1978, Riggs et al. 1978, Lonsdale and Watkinson 1983, Weller 1987a). Only data from the second and third harvests were used to compute thinning slopes because significant thinning was not observed until after the first harvest. I use the mean biomass-density relationship rather than the total biomass-density relationship in presenting my result. Weller (1987a) has argued that using the total biomass-density relationship is necessary to insure independence between the two variables. Because I weighed each plant separately then calculated the mean of these individual values, rather than simply dividing the total biomass by the number of plants to obtain mean mass, using the mean mass-density relationship is mathemat-

Tab. 1. Variation in height and number of branches (mean ± 1 SE) among the three plant species at successive harvests. Within a harvest, values with different superscripted letters are significantly different among species (P < 0.05, Scheffé for multiple comparisons among means). For a given character across harvests, values with different superscripted number are significantly different (P < 0.05, Scheffé test).

Harvest		Species		
		Salicornia	Suaeda	Atriplex
1	Height (cm)	4.3±0.07[a,1]	4.2±0.10[a,1]	4.4±0.14[a,1]
	Branches	0.2±0.03[a,1]	0	0.2±0.06[a,1]
2	Height	9.6±0.23[a,2]	15.8±0.44[c,2]	12.9±0.75[b,2]
	Branches	2.2±0.16[a,2]	3.7±0.19[b,2]	4.9±0.75[c,2]
3	Height	12.9±0.24[a,3]	21.6±0.73[b,3]	29.3±1.28[c,3]
	Branches	3.0±0.19[a,2]	7.2±0.14[b,3]	18.5±1.32[c,3]

ically appropriate. Homogeneity of slopes was examined using analysis of covariance (Freund and Littell 1981).

Results

No density-dependent mortality was observed in the *Salicornia* populations over the entire course of the experiment (Fig. 1). Ten percent of the *Suaeda* populations, and >40% of the *Atriplex* populations died as a result of density-dependent interactions (Fig. 1). Mean *Salicornia* biomass increased without attendant mortality (Fig. 1), but in the *Suaeda* and *Atriplex* populations, mean plant biomass increased while plant density concomitantly decreased (Fig. 1), as predicted by self-thinning theory. Because *Salicornia* populations did not thin, the inferred self-thinning "slope" is $-\infty$. *Suaeda* populations thinned along a line of slope -2.50. (r = 0.84) with intercept 8.00. (Fig. 1) and *Atriplex* populations thinned along a line of slope -1.82 (r = 0.47) with intercept 5.85 (Fig. 1). The three slopes are significantly different from each other (P = 0.044, analysis of covariance and test for homogeneity of slopes; Freund and Littell [1981]). *Suaeda* populations thinned along a line whose slope was significantly (P <0.05) steeper than -1.5 while the thinning slope of *Atriplex* populations was not significantly different from -1.5 (P>0.05), in accordance with the self-thinning rule.

Morphologically, the three species varied in plant height and number of branches. *Atriplex* was broad-leaved, and the tallest and most extensively branched of the three species. *Salicornia* was leafless, and the shortest and least branched. *Suaeda* was linear-leaved, and intermediate in height and branching (Tab. 1). In terms of Miyanishi et al.'s (1979) model, *Atriplex* has a Type III morphology, *Salicornia* a Type V morphology, and *Suaeda* an intermediate form closer to Type III than to Type V (Tab. 1).

Discussion

Morphological determinants of self-thinning.

The results presented here support Miyanishi et al.'s (1979) model of self-thinning based on plant geometry. Individual *Atriplex* increased in height, branching, and biomass over the course of the experiment (Fig. 1, Tab. 1), and nearly half of the plants in the populations died (Fig. 1), and the *Atriplex* populations thinned along a line (on a log-log) plot with a slope of -1.82 (Fig. 1). *Suaeda* individuals also increased in height, branching, and biomass over the course of the experiment, but had far fewer branches than *Atriplex* individuals (Fig. 1, Tab. 1). The overall morphology of *Suaeda* is more vertically-oriented than that of *Atriplex*, and in agreement with Miyanishi et al.'s (1979) generalization, the slope of the line that *Suaeda* populations follow during thinning, -2.50, is much steeper than -1.5 (Fig. 1). *Salicornia* increased only in height over its growing season, and did not self-thin (Fig. 1, Tab. 1).

Alternatives to the geometric model that explain the absence of self-thinning in high density *Salicornia* populations are few. Either the densities used were not high enough for self-thinning to occur or self-thinning is precluded by environmental factors. Although other populations of small annual plants whose thinning dynamics have been studied self-thin when densities exceed 5,000 plants m^{-2} (reviewed by Harper 1977, Gorham 1979, White 1980, 1981, Westoby 1984), the *Salicornia* populations studied here exceeded 10,000 plants m^{-2}. The population dynamics of *Salicornia* in Great Britain, the Netherlands, Canada, and the United States have been studied by several investigators, and density-dependent mortality has never been found in any of the studied populations (Joenje 1978, Ungar et al. 1979, Jefferies et al. 1981, Hartman and Engler 1982, Riehl and Ungar 1982, Watkinson and Davy 1985, Ellison 1987a, Ungar 1987). These studies have been conducted under a wide range of environmental conditions, and it seems unlikely that a specific environmental factor would preclude self-thinning in *Salicornia* populations worldwide. The absence of density-dependent mortality in
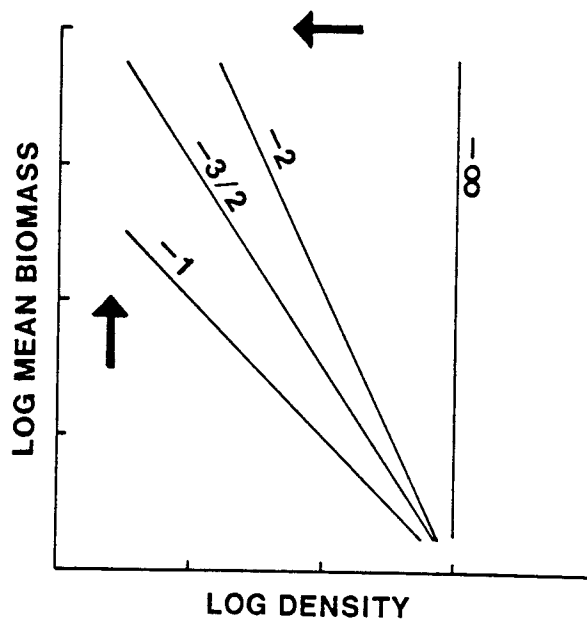
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Fig. 2. Evolutionary change in the slope of the thinning boundary predicted to occur concomitantly with the evolution of plant form. The thinning slope would have become less steep with increasing canopy spread and would have steepened with increasing plant height.

Self-thinning: an evolutionary interpretation

Support for the geometric model of self-thinning also sheds light on how plant morphology and density-dependent dynamics may have interacted over the course of terrestrial vascular plant evolution. Plant morphology has changed dramatically since the first vascular plants colonized land roughly 400 Myr ago (Stewart 1983). If natural selection has preserved plants that grow allometrically in three dimensions, then plants exhibiting the biomass-density relationship $w = Kp^{-3/2}$ should predominate in natural communities. The earliest vascular land plants (e.g. *Cooksonia*) appeared at the end of the Silurian period, and were leafless and sparsely branched (e.g. Kidston and Lang 1921, Stewart 1983, Tiffney and Niklas 1985, Niklas 1986). According to Miyanishi et al.'s (1979) model, such plants (like *Salicornia*) would not have self-thinned. By the end of the Devonian, 50 Myr later, leaves, wood, and elaborately branched morphologies were common (e.g. Knoll et al. 1984), and plants with such morphologies (like *Atriplex*) that would thin along lines with slopes near to −3/2 now dominate terrestrial vegetation.

Salicornia, *Suaeda*, and *Atriplex* can be viewed as morphological analogues of the earliest terrestrial vascular plants. If the branching and leaf structures only are considered, *Salicornia*, *Suaeda*, and *Atriplex* exhibit a spectrum of morphologies that range from the "primitive" to the "derived". Knoll et al. (1984) constructed a system to score morphological and anatomical advancement in early vascular plants. For each character measured, the scale ranges from 0 upwards, with an increased score implying increased derivation of the character. Using Knoll et al.'s (1984) scale, scoring branching order (range 0–4), branching pattern (range 0–2), regularity of branching (range 0–2), stelar type (range 0–3), xylem maturation (range 0–2), cambial activity (range 0–1), axial emergences (range 0–5), and photosynthetic surfaces (range 0–3), *Salicornia* scores a 6, *Suaeda* scores a 12, and *Atriplex* an 18.

This result does *not* imply phylogenetic relationships among the three species studied. Rather, this result illustrates that in external morphology, *Salicornia* resembles primitive land plants, and *Suaeda* and *Atriplex* resemble more derived ones. The thinning dynamics of *Salicornia*, *Suaeda*, and *Atriplex* (Fig. 1) may parallel the thinning dynamics of early land plants, and present a useful conceptual model with which to investigate the evolutionary importance of plant morphology and density-dependent dynamics (Fig. 2).

Historically, as leaf size and canopy size increased (as in the continuum of morphologies from *Salicornia* to *Atriplex*), plant-plant competition for light is thought to have resulted in selection for still further increases in size and canopy spread (Niklas and Kerchner 1984, Niklas 1986). King (1981) and Niklas and Kerchner (1984) have shown theoretically that increases in leaf size and canopy spread require concomitant increases in

Salicornia population appears to be a general result, and is explained most simply by *Salicornia*'s phenotypically plastic morphology (see also Ellison 1987a).

The differences between the thinning slopes of *Atriplex* and *Suaeda* (Fig. 1) can reflect only differences intrinsic to the plants. These two species were grown under identical conditions, and the observed differences in thinning dynamics, like those of *Salicornia*, are explained most easily by differences in plant geometry. Lonsdale and Watkinson's (1983) data on two species with disparate morphologies are in qualitative agreement with this interpretation. Populations of *Festuca pratensis*, a grass with erect leaves, had a thinning slope of −1.78, and that of populations of *Agrostemma githago*, a dicotyledonous plant with opposite leaves, had a thinning slope of −1.68 (Lonsdale and Watkinson 1983). Lonsdale and Watkinson's (1983) results based on plant density and plant biomass are similar to those presented here in that increased canopy cover (branching) resulted in an increase in the slope of the thinning line.

The results presented here illustrate that the slope of the line relating mean plant biomass to surviving plant density that thinning populations follow over time can be predicted by plant morphology. These results support strongly Miyanishi et al.'s (1979) generalization of the self-thinning rule, and argue for more in-depth examinations of the interactions between plant morphology and plant population dynamics.

plant height and supportive tissue (e.g. wood) and that the latter morphological changes could impel further increases in canopy spread and leaf size or area available for photosynthesis (Niklas and Kerchner 1984, Niklas 1986). I propose that the widespread adherence to the self-thinning rule among diverse plant species in the modern flora is a direct result of these morphological changes in early land plant evolution. The transition from plant species that do not thin to those that do is mirrored by the absence of thinning in *Salicornia* populations and the strict adherence of *Atriplex* populations to the self-thinning rule.

Changes in extant plant morphology also could affect seed dispersal patterns which in turn could further affect density-dependent interactions in monocultures. Sparsely-branched small plants might disperse seeds nearer the parent plant than larger, more eleborately-branched plants would. A consequence of localized seed dispersal would be dense monocultures of related (at least half-sib) individuals. It is plausible that natural selection could have favored small stature and minimal branching at high densities in plants with localized dispersal to minimize competition among relatives as a way of maximizing inclusive fitness. Among plants with longer dispersal distances, increased growth and branching would be advantageous as neighbors more likely would be unrelated. Seed dispersal in *Salicornia* under natural conditions is highly localized, with approximately 50% of the seeds falling within 10 cm of the parent plant (Ellison 1987c). However, the remainder of *Salicornia's* seeds travel long distances in water, and morphology as the determinant of thinning dynamics in *Salicornia* populations appears to be more parsimonious than a mechanism dependent on vagaries of ocean currents. Seed dispersal curves of *Suaeda* and *Atriplex* are undocumented and merit further study.

The results of this comparative study of the thinning dynamics of *Salicornia*, *Suaeda*, and *Atriplex* show that increased plant branching and plant height leads to increased density-dependent mortality and closer adherence to the self-thinning rule in dense monocultures. Experiments investigating the rapidity with which more elaborately-branched plants could invade populations of sparsely-branched plants are now underway. The results from these studies may enhance our understanding of how intraspecific competition and the evolution of plant form have interacted to determine patterns of plant population dynamics in modern plant communities.

References

Aikman, D. P. and Watkinson, A. R. 1980. A model for growth and self-thinning in even-aged monocultures of plants. – Ann. Bot. 45: 419–427.

Bertness, M. D. and Ellison, A. M. 1987. Determinants of pattern in a New England salt marsh plant community. – Ecol. Monogr. 57: 129–147.

Ellison, A. M. 1987a. Density-dependent dynamics of *Salicornia europaea* monocultures. – Ecology 68: 737–741.

– 1987b. Effects of seed dimorphism on the density-dependent dynamics of experimental populations of *Atriplex triangularis*. – Am. J. Bot. 74: 1280–1288.

– 1987c. Effects of competition, disturbance, and herbivory on *Salicornia europaea* populations. – Ecology 68: 576–586.

Freund, R. L. and Littell, R. C. 1981. SAS for linear models: a guide to the ANOVA and GLM procedures. – SAS Institute, Cary, NC.

Gorham, E. 1979. Shoot height, weight, and standing crop in relation to density of monospecific plans stands. – Nature. Lond. 279: 148–150.

Harper, J. L. 1977. Population biology of plants. – Academic Press, London.

Hartman, J. M. and Engler, M. 1982. Density effects on growth and survival of *Salicornia bigelovii* and *S. europaea*. – Biol. Bull. 162: 365–266.

Holsinger, K. E. and Roughgarden, J. 1985. A model for the dynamics of an annual plant population. – Theor. Pop. Biol. 28: 288–313.

Jefferies, R. L., Davy, A. J., and Rudmik, T. 1981. Population biology of the salt marsh annual *Salicornia europaea* agg. – J. Ecol. 69: 17–32.

Joenje, W. 1978. Plant colonization and succession on embanked sandflats. – Ph.D. diss., Univ. of Groningen, The Netherlands.

Kidston, R. and Lang, W. H. 1921. On old red sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. IV. Restorations of the vascular cryptogams and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organisation of land-plants. – Trans. R. Soc. Edinburgh 52: 831–854.

King, D. 1981. Tree dimensions: maximizing the rate of height growth in dense stands. – Oecologia (Berl.) 51: 351–356.

Knoll, A. H., Niklas, K. J., Gensel, P. G., and Tiffney, B. H. 1984. Character diversification and patterns of evolution in early vascular plants. – Paleobiology 10: 34–47.

Lonsdale, W. M. and Watkinson, A. R. 1983. Plant geometry and self-thinning. – J. Ecol. 71: 285–297.

Miyanishi, K., Hoy, A. R. and Cavers, P. B. 1979. A generalized law of self-thinning in plant populations. – J. Theor. Biol. 78: 439–442.

Mohler, C. L., Marks, P. L., and Sprugel, D. G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. – J. Ecol. 66: 599–614.

Niklas, K. J. 1986. Computer-simulated plant evolution. – Sci. Am. 254(3): 76–86.

– and Kerchner, V. 1984. Mechanical and photosynthetic constraints on the evolution of plant shape. – Paleobiology 10: 79–101.

Riehl, T. E. and Ungar, I. A. 1982. Growth and ion accumulation in *Salicornia europaea* under saline field conditions. – Oecologia (Berl.) 54: 193–199.

Riggs, D. S., Guarniere, J. A., and Addelman, S. 1978. Fitting straight lines when both variables are subject to error. – Life Sci. 22: 1305–1360.

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Stewart, W. N. 1983. Paleobotany and the evolution of plants. – Cambridge Univ. Press. London.

Tiffney, B. H. and Niklas, K. J. 1985. The history of clonal growth in land plants: a paleobotanical perspective. – In: Jackson, J. B. C., Buss, L. W., and Cook, R. (eds), Population biology and the evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 35–66.

Ungar, I. A. 1987. Population characteristics, growth and survival of the halophyte *Salicornia europaea*. – Ecology 68: 569–575.

– , Benner, D. K. and McGraw, D. C. 1979. The distribution and growth of *Salicornia europaea* on an inland salt pan. – Ecology 60: 329–331.

Watkinson, A. R. and Davy, A. J. 1985. Population biology of salt marsh and dune annuals. – Vegetatio 62: 487–497.

Weller, D. E. 1987a. A reevaluation of the −3/2 power rule of plant self-thinning. – Ecol. Monogr. 57: 23–43.

– 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. – Ecology 68: 813–821.

Westoby, M. 1976. Self-thinning in *Trifolium subterraneum* not affected by cultivar shape. – Aust. J. Ecol. 1: 245–247.

– 1984. The self-thinning rule. – Adv. Ecol. Res. 14: 167–227.

White, J. 1980. Demographic factors in populations of plants. – In: Solbrig, O. T. (ed.), Demography and dynamics of plant populations. Blackwell, Oxford, pp. 21–48.

– 1981. The allometric interpretation of the self-thinning rule. – J. Theor. Biol. 89: 475–500.

– 1984. Plant metamerism. – In: Dirzo, R. and Sarukhán, J. (eds), Perspective on plant population ecology. Sinauer Assoc., Sunderland, MA, pp. 15–47.

– and Harper, J. L. 1970. Correlated changes in plant size and number in plant populations. – J. Ecol. 58: 467–485.

Yoda, K., Kira, T., Ogawa, H., and Hozumi, K. 1963. Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. – J. Biol. Osaka Cy. Univ. 14: 107–129.

Zeide, B. 1987. Analysis of the 3/2 power law of self-thinning. – Forest Sci. 33: 517–537.