

BRANCHING PATTERNS OF SALICORNIA EUROPAEA (CHENOPODIACEAE) AT DIFFERENT SUCCESSIONAL STAGES: A COMPARISON OF THEORETICAL AND REAL PLANTS¹

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ABSTRACT

Salicornia europaea L. (Chenopodiaceae) is an annual succulent halophyte that lacks leaves, is photosynthetically active over its entire surface, and branches in a predictable manner. A computer model based on that of Niklas and Kerchner (1984) was used to generate *S. europaea*-like branching patterns. The model was used to predict the morphology of *S. europaea* that could maximize light interception and minimize the total bending moment. The optimal branching pattern generated by the computer corresponded very closely to the form of *S. europaea* found in late-successional populations. The progression of model forms from the least efficient (lowest total projected surface area and highest bending moment) to the most efficient (highest projected surface area and lowest bending moment) parallels the observed phenotypic changes in morphology of *S. europaea* over the course of succession in New England salt marshes. Based on computer simulations, we conclude that morphological changes in the branching patterns of *S. europaea* during succession correspond to alterations of shape capable of coincidentally maximizing the interception of light and minimizing the total bending moment.

MANY THEORETICAL models of tree-like branching systems have been constructed by investigators interested in problems of light-gathering (Honda, 1971; Fisher and Honda, 1977, 1979a, b; Honda and Fisher, 1978; Borchert and Honda, 1984; Borchert and Tomlinson, 1984; Niklas and Kerchner, 1984), hydraulics (Murray, 1927; Zimmermann, 1978; Honda, Tomlinson, and Fisher, 1981; Niklas, 1986), physical load (McMahon and Kronauer, 1976; Niklas and O'Rourke, 1982; Niklas and Kerchner, 1984), succession (Horn, 1971), and evolutionary patterns of plant form (Hallé, Oldeman, and Tomlinson, 1978; Givnish, 1982; Niklas, 1982, 1986; Niklas and Kerchner, 1984). Although these models produce "trees" in the sense of a branched structure, few of them have been examined for their concordance with real trees. Those few that have been used to model real trees (e.g., the *Ter-*

minalia model of Fisher and Honda [1979a, b] and the *Tabebuia* model of Borchert [Borchert and Honda, 1984; Borchert and Tomlinson, 1984]) were constructed to model trees of a specific morphology and their general applicability has not yet been investigated. In contrast, Niklas and Kerchner (1984) and Niklas (1986) have developed a general model which predicts the forms of trees subject solely to constraints on the interception of light (i.e., the total projected photosynthetic surface area of the plant) and on the total bending moment imposed by the display of branches.

An assumption of many theoretical and empirical studies is that light can be a limiting resource, and plant shape and size have been predicted or shown to change as a function of the light environment (e.g., Gates, 1962; Parkhurst and Loucks, 1972; Givnish and Vermeij, 1976; Mooney and Gulmon, 1979). It is generally accepted that plants will reorient their light gathering surfaces as the solar angle changes, and it has been demonstrated that plants will grow in orientations that project large surface areas in the direction(s) of ambient light (e.g., Shackel and Hall, 1979; Ehleringer and Forseth, 1980; Forseth and Ehleringer, 1980; Nobel, 1981, 1982a, b; Werk and Ehleringer, 1984). Both the direction and intensity of direct radiation influences the temperature of plant tissues intercepting sunlight

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(e.g., Billings and Morris, 1951; Raschke, 1956; Gates, 1962; Forseth and Ehleringer, 1983; Werk et al., 1983; Ehleringer and Werk, 1986), and tissue temperature either directly or indirectly influences net assimilation rate (e.g., Gates, 1962; Ehleringer and Werk, 1986). Niklas and Kerchner (1984) and Niklas (1986) have shown that if a) a plant's entire surface is photosynthetically active, and b) light is the primary factor limiting growth, then the plant's optimal form would be a cylinder. However, if plants are subject to neighborhood competition (*sensu* Weiner, 1982), the optimal strategy would be to increase plant ht to overtop successfully nearby competitors. In particular, this model predicts that a plant that is entirely photosynthetic would, all else being equal, assume a cylindrical form to maximize light interception; with increasing branching, the amount of light which the plant could intercept would decline due to self-shading (Niklas and Kerchner, 1984).

Although the model of Niklas and Kerchner has been used to generate tree-like patterns which mimic trends observed in the evolution of vascular plants, this model has not yet been applied to extant plants. The predictive power of this model can be examined by investigating the branching patterns and other relevant morphological characteristics of plants whose morphologies satisfy the assumptions of the Niklas and Kerchner model.

Many gymnosperms and angiosperms have green photosynthetic stems and lack leaves. As such, these species fulfill the basic assumptions of Niklas and Kerchner's (1984) model. Among these species is *Salicornia europaea*, a succulent annual halophyte common to coastal areas of the United States. Because *S. europaea* lacks leaves, and its component parts are cylindrical in shape and completely photosynthetically active, *S. europaea* is a plant that satisfies the simplest case of Niklas and Kerchner's (1984) model. Niklas and Kerchner's (1984) model makes specific predictions concerning the morphologies of plants that have photosynthetic axes and no leaves. To examine the utility of the model, we ask, does a plant with photosynthetic axes and no leaves under conditions where light is the primary limiting factor have the morphology predicted by the model? We do *not* assume that other morphologies (e.g., flattened, solar-tracking leaves) would not function as well or better under similar conditions; rather we seek to examine specific predictions of Niklas and Kerchner's (1984) model. This model was used to generate all conceivable model "plants" with *S. europaea*-like branching structures.

Although model plants were generated according to the parameters of Niklas and Kerchner (1984), the ranges of values for these parameters were determined directly from field measurements of plants growing at different successional stages (Ellison, 1987a, b; see below). Adaptive landscapes, in which morphology and light interception define the three dimensional axes, were constructed. Forms that maximize light interception and minimize the total bending moment were determined from these landscapes. Comparisons between the predicted model plants with the various forms of *S. europaea* growing at different successional stages indicated a high conformity between theory and empirical data.

Although the ranges of growth and branching parameters used for the simulations were determined from field observations of *S. europaea*, the simulations do *not* simply recreate plants observed in the field. Rather, we examined model plants generated from a set of growth parameters of which those observed in the field form a subset. We ask, does the simulated plant that maximizes light interception and minimizes the total bending moment occur in nature, and if so, when in succession does it occur?

MATERIALS AND METHODS—Study site and study species—*Salicornia europaea* L. (Chenopodiaceae) is a succulent, annual halophyte common to salt marshes and tidal flats in North America and Europe (Ball, 1964; Brereton, 1971; Jefferies, Davy, and Rudmik, 1981; Jefferies, Jensen, and Bazely, 1983). *Salicornia europaea* grows as a series of leafless, cylindrical internodes (Anderson, 1974) with regular branching (Jefferies et al., 1981; Ellison, 1987b). The internodes consist of a photosynthetic outer cortex surrounding a central pith. At the end of the growing season, each internode produces six flowers, that each produce a single, ovoid seed. Dispersal occurs primarily by wind and water (Ellison, 1987a).

Field data were gathered from *S. europaea* populations found between +1.2 and +1.4 m mean tidal ht at Rumstick Cove, a protected 2 ha embayment of Smith Cove in Barrington, Rhode Island (a complete description of the site is given in Ellison [1987a]). At Rumstick Cove, as in other New England salt marshes, *S. europaea* is found commonly in disturbance-generated patches lacking other vegetation (Steiner, 1935; Chapman, 1940; Hartman, Caswell, and Valiela, 1983; Ellison, 1987a). These patches are created when debris, consisting of dead stems of the marsh cordgrass *Spartina alterniflora*, is rafted up onto the marsh

during storm tides. This debris kills the underlying vegetation, and when the debris decomposes a patch of bare ground remains (Hartman et al., 1983, Bertness and Ellison, 1987). *Salicornia europaea* is the first colonizer of these patches, but over time it is overgrown and competitively excluded from the patches by the perennial plants *Spartina patens*, *Distichlis spicata* and *Juncus gerardi*, which dominate New England marshes (Steiner, 1935; Chapman, 1940; Hartman et al., 1983; Ellison, 1987a). *Salicornia europaea* colonizes new patches at low density, but the seeds of a single plant land primarily within 20 cm of the parent plant (Ellison, 1987a). This local seedfall results in a dense population in the year following colonization. Within 3–5 years, however, a population of moderate size (<50 m²) is eliminated by the dominant grasses (Bertness and Ellison, 1987).

The model—The model of Niklas and Kerchner (1984) was used to simulate the three-dimensional geometry of *S. europaea* from field-determined morphological parameters (Ellison, 1987a; see below). This model is similar in many respects to that developed by Nobel and colleagues to study various cacti and succulents (Nobel, 1980, 1982a, b, c, 1986; de Cortazar, Aceredo, and Nobel, 1985). The morphology of a plant is generated by computer (IBM PC-XT) and displayed in a Cartesian coordinate system referenced to the diurnal pathway of the sun. The projected surface area of each model plant is computed as the solar angle varies. Unlike the Nobel model, which quantifies direct PAR, our modelling procedure determines how a dimensionless ratio (projected surface area/total surface area, or A_p/A) varies as a function of the solar angle (θ). The relative abilities of different morphologies to intercept PAR are determined by computing the differences among the areas under the A_p/A versus θ curves for different plant shapes, i.e., photosynthetic capability (I) is given by the equation

$$I = \int_{\theta=0^\circ}^{\theta=90^\circ} A_p(\theta)/A \cdot d\theta \quad (\text{Eq. 1})$$

Values for I are dimensionless and provide only a heuristic basis for comparisons among different plant shapes. It is possible, therefore, to make comparative predictions about the abilities of different morphologies to intercept sunlight and hence assimilate carbon under the assumption that the plants examined by this procedure have similar or identical photosynthetic properties. Since A_p/A is a dimen-

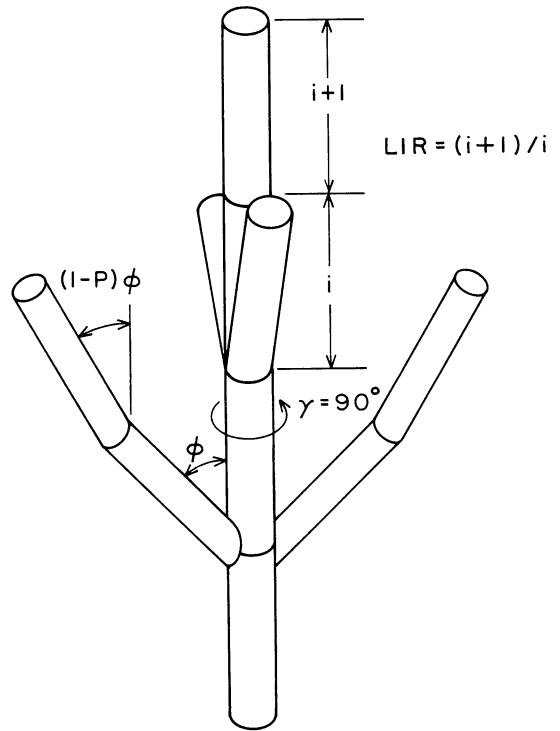


Fig. 1. Notation used for describing the morphological parameters used to generate the *Salicornia europaea*-like model plants. The branching angle (ϕ) is specified with respect to the main (vertical) axis. The rotation angle (γ) is fixed at 90° . The leader internode ratio (LIR) is the length of the $(i + 1)$ st internode divided by the length of the i th internode. When a branch continued to grow, positive phototropism was incorporated by setting the branch angle of the $(i + 1)$ st internode equal to 0.7 times the branch angle of the i th internode.

sionless ratio, absolute changes in plant or model-plant sizes are irrelevant to comparisons made on the basis of I . This has the advantage of providing a quantitative method for comparing among different plants solely on the basis of their morphologies.

The model also is capable of quantifying the total bending moment of the plant under static loading conditions of self-weight. According to engineering theory, bending moment, M , is proportional to local curvature, K , times flexural rigidity, C ; hence $M = KC$. In an homogeneous beam, flexural rigidity is equal to the product of Young's modulus and the second moment of inertia around the neutral axis (which for a solid cross section equals $\pi d^4/64$, where d is diameter) (Timoshenko and Gere, 1961). In the case of the simulated *Salicornia* plants, K is a function of the rotation angle γ and the bifurcation angle ϕ (Fig. 1), as well as total axis length l . Flexural rigidity is a function

TABLE 1. Morphological parameters (means \pm 1 SD; $N = 100$) of *S. europaea* from field populations at different successional stages. For each parameter, values with different superscripted letters are significantly different among the three successional stages ($P < 0.05$, Scheffé test for multiple comparisons among means)

Successional stage	Branch angle (°)	Internode ratio	Probability of		Phototropism
			Leader branching	Branch continuation	
Early	33.0 \pm 0.0004 ^a	0.77 \pm 0.221 ^a	0.74 \pm 0.057 ^a	0.92 \pm 0.158 ^a	0.31 \pm 0.024 ^a
Middle	45.0 \pm 0.0004 ^b	0.85 \pm 0.282 ^b	0.11 \pm 0.006 ^b	0.10 \pm 0.019 ^b	0.29 \pm 0.038 ^a
Late	43.8 \pm 0.0002 ^b	0.84 \pm 0.311 ^b	0.13 \pm 0.012 ^b	0.09 \pm 0.023 ^b	0.35 \pm 0.087 ^a

of l , d , and the mass weight of tissues, p . Thus, bending moment, M , can be restated by the equation

$$M = (\pi/\gamma)d^2l^2pg \sin(\phi/2) \quad (\text{Eq. 2a})$$

(g is the gravitational constant). Assuming that mass weight of tissues is constant throughout the plant,

$$M = k(d^2l^2/\gamma)\sin(\phi/2) \quad (\text{Eq. 2b}),$$

where k is the proportionality constant subsuming π , g , and p .

We modified Niklas and Kerchner's (1984) model in two ways. First, in the original model, when a branching event occurred, the leader axis bifurcated. In the *S. europaea* model, branching occurs laterally, behind the leader (Fig. 1). The branch angle, ϕ , is the angle that a branch makes with the main axis (Fig. 1) rather than the bifurcation angle as in the original model. The branch rotation angle, γ , which was variable in the original model, was fixed at 90° (Fig. 1) because the branch rotation angle of *S. europaea* is 90°. The second modification to the model was the incorporation of positive phototropism of the branches. Phototropism (P) of the branches was defined such that when a branch continued to elongate, the branch angle ϕ of the ($i + 1$)st internode with respect to the main axis was $(1 - P)$ times ϕ of the i th internode (Fig. 1). In all simulations, P was set at 0.3, the mean field measurement of *S. europaea* branch phototropism (see below). We did not vary the phototropism (P), as this is remarkably stable among plants from all three successional stages (Table 1). Increasing P decreases the total bending moment because it decreases ϕ . Increasing P also reduces I because branches become increasingly appressed to one another. In addition, it was possible to vary the size ratio of successive internodes to simulate the fact that older internodes are longer than younger ones. The leader internode ratio (LIR) is simply the length of the ($i + 1$)st internode divided by the length of the i th internode.

We varied the following four parameters in our simulations over ranges which encom-

passed those found in natural plants (see below): 1) $\phi = [30^\circ, 45^\circ, 60^\circ]$; 2) LIR = [0.5, 0.75, 1.0]; 3) the probability of branching (from 0.0–1.0 at intervals of 0.2); and 4) the probability that a branch, once formed, would continue to grow (from 0.0–1.0 at intervals of 0.2). Once a branch was two internodes long, it was considered a leader, and the probability of a leader continuing to grow was fixed at 1.0 in all simulations. By co-varying these four parameters, 324 possible trees were generated. A representative sample of these is given in Fig. 2 for $\phi = 45^\circ$, LIR = 1.0. For each model tree, we calculated the total bending moment and the total projected surface area of the plant (Niklas and Kerchner, 1984). The total projected surface area equals I (Eq. 1) minus the surface area of the plant not exposed to light due to self-shading. This quantity is a numerical solution obtained by computer simulation, not the result of an analytical solution. Niklas and Kerchner (1984) argued that physical load and projected surface area are competing constraints on plant form and that total projected surface area of the plant is a good approximation for its photosynthetic efficiency. The computer simulations integrate the total projected surface area of the plant from sunrise until noon (one-half that of the total day). In the discussion of our results, we use this integrated value of the total photosynthetic surface area, the *light interception efficiency* (E), which Givnish (1982) has argued may be the most important factor related to plant growth.

Each simulated tree grew for 10 ontogenetic iterations, the maximum allowed by computer memory limitations. At each iteration, each node of the previous iteration was able to branch or elongate (add another internode) according to the probability functions, but each terminal node was only able to elongate. Terminal internodes could only elongate, not branch, because *S. europaea* does not bifurcate terminally (except uncommonly as a result of traumatic reiteration [sensu Hallé et al., 1978]). The growth or branching of all nodes constituted one iteration. All model trees and calculations were generated using an IBM-XT microcom-

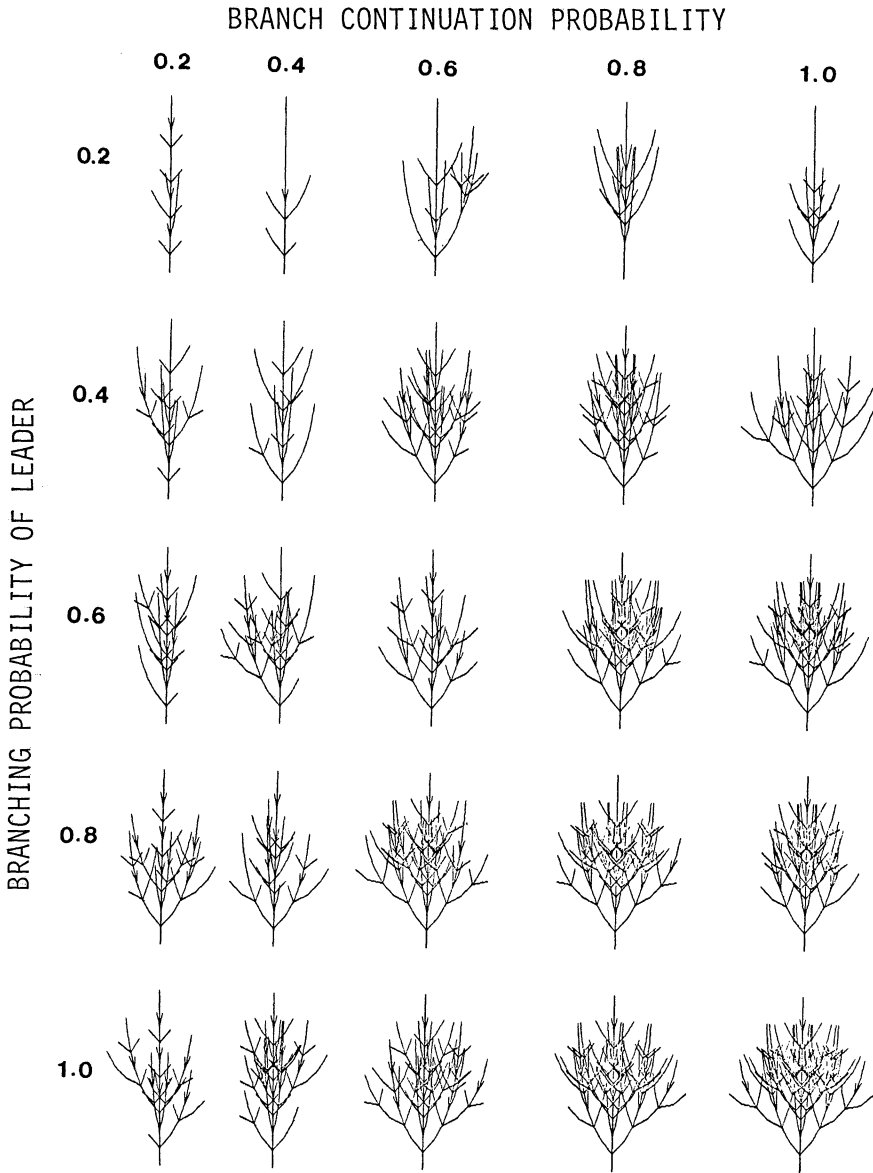


Fig. 2. Sample plants generated by the computer program when $\phi = 45^\circ$ and LIR = 1.0.

puter using a FORTRAN version of the program TREE BAS (Niklas and Kerchner, 1984).

Field data—Detailed methods of *S. europaea* data collection are described in Ellison (1987a, b) and are briefly summarized here.

One hundred plants, each growing in early- (low-density monocultures), middle- (high-density monocultures), and late-successional (beneath perennial canopies) *S. europaea* populations were examined to determine their branching angles, internode ratios, probability of branching, probability of branch contin-

uation, and phototropism. The probability of branching was calculated by dividing the observed number of branches by the potential number of branches (two per internode), and the probability of branch continuation was calculated by dividing the number of branches with two or more internodes by the total number of branches. Branching angles, internode ratios, and phototropism were measured as in Fig. 1.

RESULTS—*Results from the simulations*—Total bending moment was highest for high

BRANCHING PROBABILITY OF LEADER

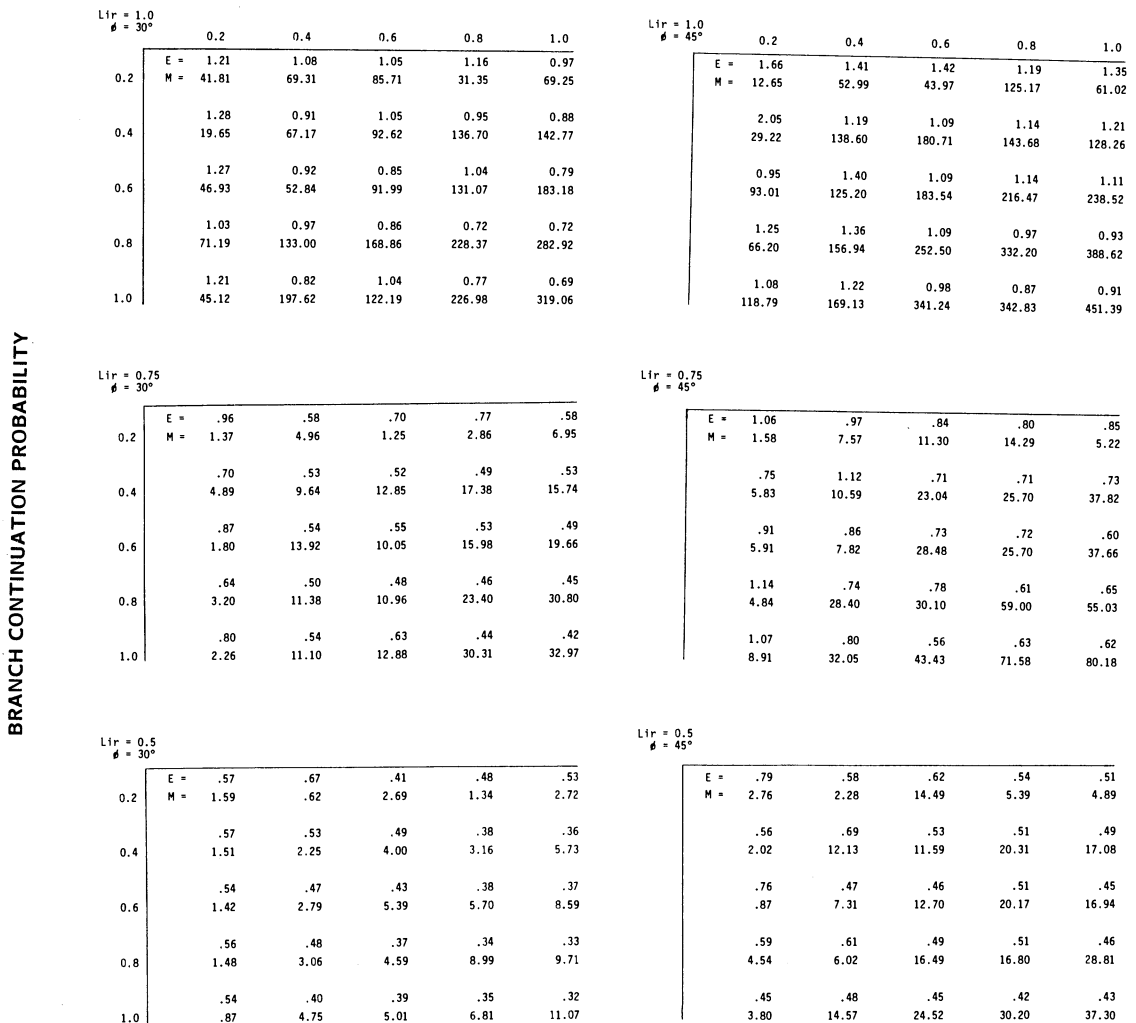


Fig. 3. Light interception efficiency (E) and total bending moment (M) calculated for each computer-generated plant when the branching angle $\phi = 30^\circ$ (left); 45° (right), and the leader internode ratio (LIR) = 0.5 (bottom); 0.75 (middle); 1.0 (top). Only the biologically nontrivial cases (see text) are shown.

probabilities of branching and branch continuation (Fig. 3). Real *S. europaea* plants are not observed to topple as a result of branch overloading in the field, however (A. M. Ellison, personal observation), and the small size of *S. europaea* and secondary thickening of its basal internodes may be developmental responses to the mechanical constraints imposed by physical loading of the branches.

The changes in total projected surface area of the model plants as a function of branching probability, branch continuation probability, leader internode ratio (LIR) and branching angle are presented graphically as adaptive landscapes (Fig. 4). Each landscape represents a

tensor-matrix composed of the probability of branching, the probability of branch continuation, and the light interception efficiency. A single adaptive landscape is presented for each of the six possible pairings of two values of the branching angle ϕ [30° , 45°], and the three values of the internode ratio LIR [0.5, 0.75, 1.0]. Results for $\phi = 60^\circ$ (a situation not found naturally [see *Field data* below]) are qualitatively identical to the $\phi = 30^\circ$ and 45° cases and are not presented graphically. In the discussion of the results, we omit the biologically trivial cases of no branches and/or no branch continuation.

For low branching angle ($\phi = 30^\circ$) and low internode ratio (LIR = 0.5), the model plants

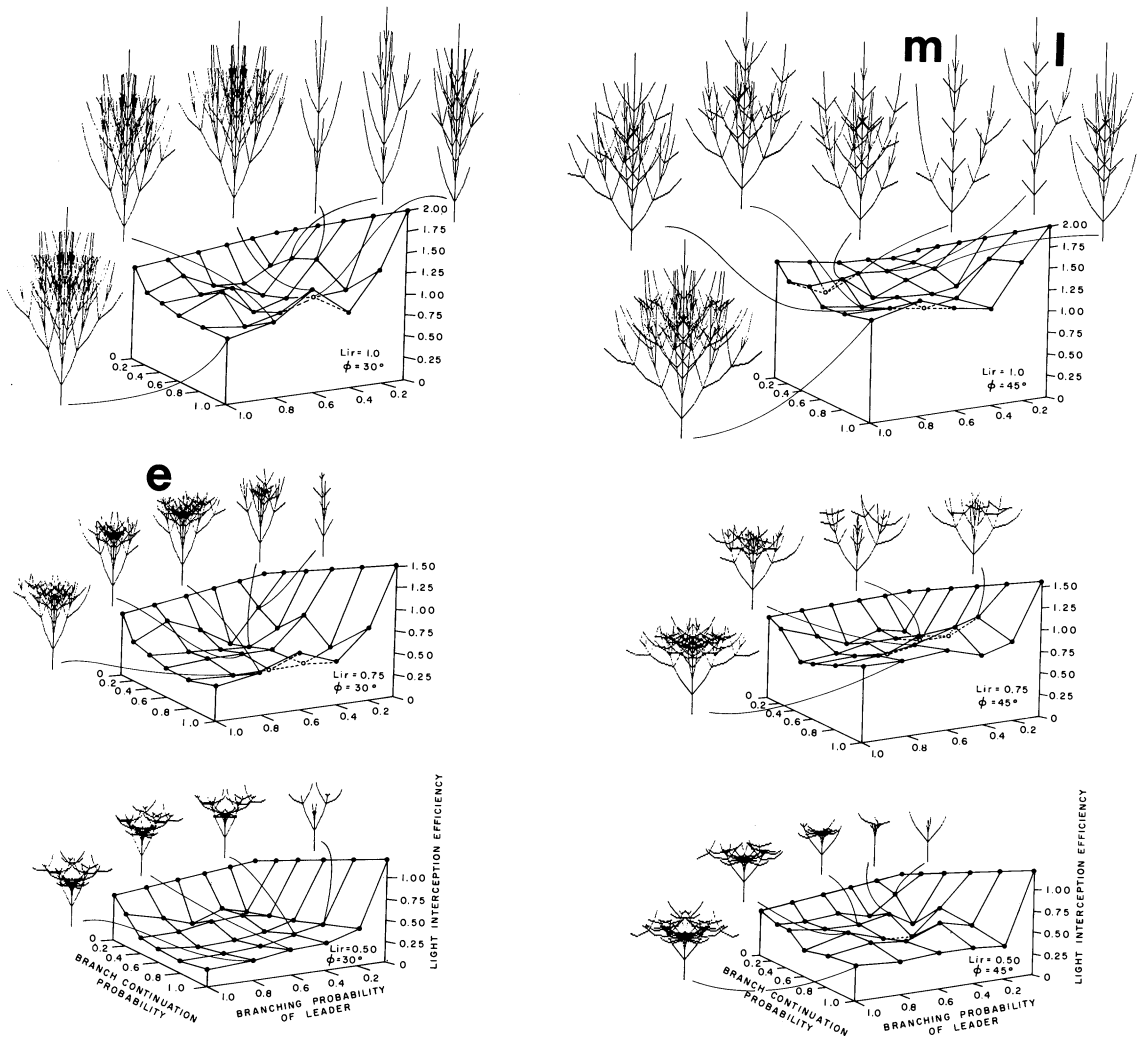


Fig. 4. Adaptive landscapes when $\phi = 30^\circ$ (right); 45° (left), and LIR = 0.5 (bottom); 0.75 (middle); 1.0 (top). Each landscape represents a tensor-matrix composed of the branch continuation probability, the branching probability of the leader and the light interception efficiency. Selected plants are shown which fall along the shortest path from least efficient to most efficient on each landscape. Model plants with forms akin to that found at different successional stages (see Table 1 and text) are marked. e = early successional type; m = middle successional type; l = late successional type.

with the lowest light interception efficiency are the ones with high probabilities of branching and branch continuation (Fig. 3, 4 bottom). The model predicts that increases in light interception efficiency will occur with decreasing probabilities of branching and branch continuation. As the internode ratio increases (i.e., the plants increase in ht relative to bushiness), the light interception efficiency for a plant constructed from a given pair of branching and branch continuation probabilities also increases (Fig. 3, 4). As plants increase in ht (LIR increases from 0.5 to 1.0), the model predicts that the plants will move up the landscape onto

its peaks and/or ridges. For $\phi = 30^\circ$, therefore, light interception efficiency increases with simultaneous decreases in branching and branch continuation probabilities and increases in LIR (ht).

For $\phi = 45^\circ$, the pattern is similar. Although the maximum ht of the landscape does not increase with increases in ϕ for a fixed LIR, the minimum ht of the landscape does increase (Fig. 4). For example, when $\phi = 45^\circ$ (Fig. 3, 4) the least efficient plant (when LIR = 0.5) has light interception efficiency = 0.42, while for $\phi = 30^\circ$, the least efficient plant has light interception efficiency = 0.32 (Fig. 3). When $\phi =$

45°, as when $\phi = 30^\circ$, increases in LIR result in increasing ht of the landscape, implying increased light interception efficiency, but no corresponding change in the steepness of the landscape. That is, with increasing LIR, all points of the landscape increase roughly equally in ht (Fig. 4).

When $\phi = 60^\circ$ the pattern is similar to the 30 and 45° cases. An increase in light interception efficiency relative to plants with smaller branching angles is only achieved in the bushiest plants; plants with few branches and/or low branch continuation probability are not much more efficient than similar plants with lower branching angles.

In summary, we find that for any pair of values for ϕ and LIR, plant forms that minimize the total bending moment, and maximize light interception efficiency are ones with few branches and low probability of branch continuation (Fig. 3, 4). We do not claim that the plants are *optimizing* the bending moment and the light interception functions simultaneously. Rather, plants with high light interception efficiencies coincidentally have low static loading, and vice versa. Holding both the probability of branching and the probability of branch continuation constant, an increase in LIR results in an increase in light interception efficiency for each value of ϕ . For any fixed value of ϕ , the steepness of the adaptive landscape does not change with changes in the LIR, but the overall ht of the landscapes does change. As LIR increases, both the lower end of the adaptive landscape (branching probability and branch continuation probability both equal 1.0) and the higher end of the adaptive landscape increase in ht (Fig. 4). For constant values of LIR, increasing ϕ does not change the maximum possible light interception efficiency, but does increase the minimum light interception efficiency. That is, for fixed LIR, increasing ϕ results in decreased steepness of the adaptive landscape, but does not change the final ht of the adaptive landscape.

Qualitatively, these results indicate that the least efficient model plants (lowest light interception efficiency and highest bending moment) are those with numerous branches, high probabilities of branch continuation, low branch angle, and distally shortened internodes. The most efficient model plants are those with few branches, low probabilities of branch continuation, high branching angle, and internodes of more or less equal size. We examined field populations of *Salicornia europaea* at different successional stages to determine in which stage of succession plants with high light interception efficiency and low static loading occurred.

Field data—Over the course of secondary succession, the morphology of an individual *S. europaea* plant changes (Table 1; Fig. 5–8). The leader internode ratio (LIR) of early-successional plants is 8% less than the LIR of middle- and late-successional plants ($P < 0.05$, Scheffé test of multiple comparisons among means; Table 1). The branching angle of early-successional plants is close to 30°, the minimum examined in the simulations, but in later-successional individuals, the branching angle increases to near 45° (Table 1). Branch phototropism, increases slightly but not significantly through succession ($P > 0.05$, Scheffé test) and is approximately 0.3 among all individuals (Table 1). Early in succession, virtually all of the internodes branch, but by middle succession, only 10% of the internodes branch (Table 1; Fig. 5–8). Branches of early-successional plants are also more likely to continue to grow, whereas branches of middle- and late-successional individuals are rarely more than one internode long (Table 1; Fig. 5–8). A decrease in branching concomitantly decreases the number of internodes, and hence affects plant fecundity directly. Plant fecundity is directly correlated with the number of branches ($r^2 = 0.87$, $F_{1,470} = 3266.7$, $P < 0.0001$ ANOVA), and early-successional plants produce more than 1,000 times as many seeds as do middle- and late-successional plants (Ellison, 1987a). More detailed data on the field ecology of *S. europaea* can be found in Ellison (1987a, b).

Qualitatively, plants growing early in succession are bushy. They are profusely branched and younger internodes are much smaller than older ones (Table 1; Fig. 5–8). Growth is rapid and new internodes often develop before the preceding ones reach their maximum size (personal observation). Conversely, plants growing later in succession are unbranched and etiolated, with elongated, equal-sized internodes (Fig. 5–8). That the successive internodes of late-successional plants are not much smaller than preceding ones (LIR ≈ 1) may result from lower rates of growth.

DISCUSSION—Our treatment of *S. europaea* has emphasized the capacity of different branching patterns to intercept direct solar radiation and changes in these patterns observed over a successional sequence. We have not dwelt extensively on the relative mechanical stabilities of different branching patterns as *S. europaea* rarely, if ever, has been observed to topple over in the field even under conditions of dynamic loading due to wind (A. M. Ellison, personal observation). Even bushy morphologies predicted to have the maximum bending

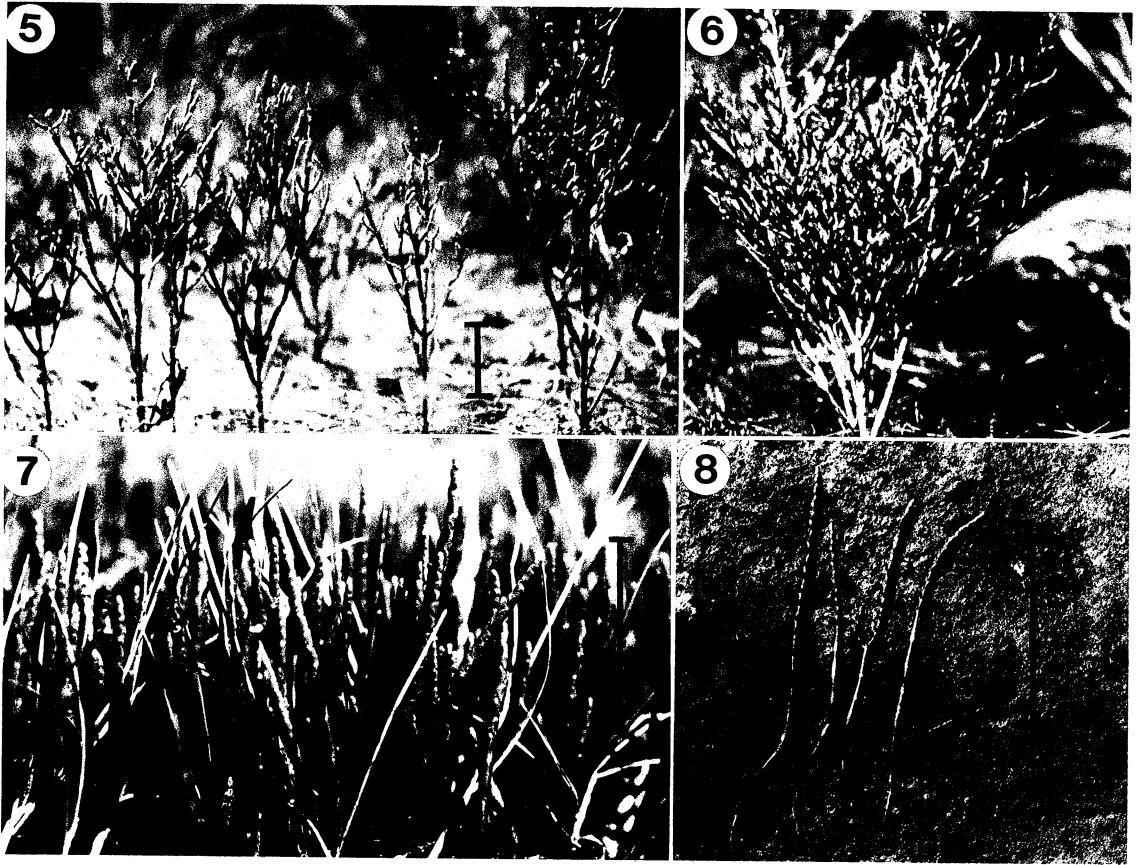


Fig. 5-8. Photographs of *S. europaea* from different successional stages. 5. Early-successional stand. 6. Early-successional individual. 7. Late-successional stand. 8. Late-successional individuals. Scale bar in Fig. 5-8 = 10 cm.

moment are observed to maintain their vertical posture. Because changes in morphology that increase light interception efficiency also reduce total static loading, both mechanical stability and light-gathering are coincidentally increased by morphological trends observed through succession. We say coincidentally; however, there is a mathematical connection between bending moment and light-interception capabilities. The branching angle ϕ and rotation angle γ (which influence the projected surface area of a plant as a function of the solar angle θ) are components of both the bending moment and light interception efficiency formulae. Similarly, the phototropism parameter P is defined partly in terms of ϕ . Consequently, mathematical optimization procedures can be applied to the trade-off between M and I .

There are no inherent assumptions about optimization of light gathering ability in the model used here. The model simply calculates the amount of light intercepted as a function of plant geometry. We have used the model to predict morphological changes that would optimize light interception. The distinction be-

tween the assumptions of the modelling procedure and the use to which the model was put is important. Although many theoretical and empirical studies have assumed that light can be a limiting resource, and plant size and shape can change as a function of available light (e.g., Gates, 1962; Parkhurst and Loucks, 1972; Givnish and Vermeij, 1976; Mooney and Gulmon, 1979), we make no claim that light per se is a limiting resource in the ecology of *S. europaea*. We do, however, argue that the amount of light available is a factor in determining *S. europaea* growth and form, and that light becomes an increasingly limited resource as the number of conspecific or heterospecific neighbors increases (see also Ellison 1987a). Indeed, successional changes in the number of individuals per area may involve a transition from self-shading (light-limited within a plant due to profuse branching) to mutual shading by increasing numbers of neighboring plants. The consequences of these two phenomena on the light-gathering ability of any given individual plant may be indistinguishable.

Niklas and Kerchner's (1984) model suc-

cessfully generated model plants with *S. europaea*-like branching patterns. The model plant form that was most efficient at gathering light and had the lowest total bending moment was cylindrical or sparsely-branched, had a high branching angle, and more or less equally-sized internodes (Fig. 3, 4). *Salicornia europaea* plants in late-successional field populations also were found to be cylindrical or sparsely branched, and had equal-sized internodes (Fig. 5–8; Table 1). Ellison (1987a) has shown that these morphological changes are in direct response to a reduction in light availability. Both *S. europaea* under the perennial canopy and artificially shaded early-successional plants show identical reduction in branching and increased internode ratio and etiolation (Ellison, 1987a). *Salicornia europaea* in light-limiting situations, therefore, is morphologically akin to the computer-generated plants that maximized light interception efficiency and minimized total bending moment (cf. Fig. 3–8; Table 1).

Changes in plant form in response to competition for light are often observed in high-density monocultures and late successional populations (see Harper, 1977, for a review). In high-density monocultures, a few large plants often dominate the stand and disproportionately contribute seeds to the next generation. In late-successional populations, a tall and unbranched plant may be able to grow up through the perennial canopy to reach available light. Both of these events depend on the plant obtaining enough light to grow, and a first step towards obtaining light is maximizing the surface area available for intercepting light.

In middle- and late-successional natural populations of *S. europaea*, where competition for light is intense, the morphology of individual plants is that predicted by the simulations to maximize light interception efficiency and to minimize static loading (cf. Table 1; Fig. 3–8). In light-limiting situations later in succession, the observed higher branch angle (approximately 45°) increases the available surface area projected to sunlight. The higher branch angle also decreases self-shading and increases shading of neighboring plants.

Branching influences light-gathering ability and is correlated with *S. europaea* fecundity; the number of flowers (and hence, seeds) produced is a function of the number of internodes. Computer-simulated plants that maximize light-gathering are sparsely branched and have few internodes (Fig. 4) and the analogous real plants would produce few flowers and seeds. In natural populations, unbranched *S. europaea* often have fewer than 20 internodes and

produce less than 120 seeds (Ellison, 1987a). Although maximization of light-gathering ability in a competitive situation enables these plants to survive, their reproductive capacity appears to be compromised.

The least efficient plant form derived from the model simulations was extremely bushy and squat. *Salicornia europaea* growing at low densities are extremely bushy, but are also very tall (Fig. 5, 6). Unlike the model plants that were constructed using 10 iterations (due to computer memory limitations), real plants growing early in succession often attain the equivalent of >30 ontogenetic generations with six orders of branching and over 6,000 internodes (Ellison, 1987a). A profusely branched, individual produces 3 orders of magnitude more seeds than an unbranched individual. Although there is a significant amount of self-shading in a branched individual, light is not a limiting resource in early-successional populations and there is no decreased probability of survival with increasing branching (Ellison 1987a). There is, however, an enormous payoff to the plant in terms of seed production.

We do not contend that both early- and late-successional *S. europaea* populations have adaptive morphologies based on the model's predictions. Late-successional *S. europaea* plants appear to have morphologies that maximize light interception and minimize static loading. Light has been shown experimentally to be the primary factor limiting *S. europaea* growth and reproduction late in succession (Ellison, 1987a), and the phenotypic change in the morphology of *S. europaea* observed over the course of succession is best viewed as an adaptive response to changes in light availability. Early successional individuals possess "maladaptive" morphologies with respect to the model's results. That is, the morphologies of early successional plants have low light interception efficiency and high static loading. Although some experimental evidence indicates that light is not a limiting resource for *S. europaea* growth early in succession (Ellison, 1987a), detailed studies of the photosynthetic biology of *S. europaea* are needed to elucidate further the limitations on its growth and form.

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