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Intertidal “trees”: consequences of aggregation on the mechanical and photosynthetic properties of sea-palms *Postelsia palmaeformis* Ruprecht

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Abstract: Sea-palms *Postelsia palmaeformis* Ruprecht are annual brown algae that grow on wave-swept rocky shores, often forming dense stands. Unlike most macroalgae, *Postelsia* stands upright in air – like trees. The stipe flexibility that permits *Postelsia* to withstand waves is provided by the low elastic modulus (5–10 MPa) of stipe tissue; in spite of the weakness (low breaking stress, ≈ 1 MPa) of this tissue, a large amount of energy (≈ 100 kJ/m³) is required to break a stipe because they can be extended by 20–25% before breaking. Although made of such easily deformed tissue, *Postelsia* can stand upright in air due to the width (high second moment of area) and resilience of their stipes, but the brittleness (low work of fracture, 400–900 J/m²) that accompanies this resilience renders them susceptible to breakage if they sustain deep scratches. Although wave-induced stresses experienced by individuals in aggregations are not lower than those experienced by isolated sea-palms, photon flux densities of photosynthetically active radiation within these dense groves are less than 10% of those above *Postelsia* canopies. A number of morphological features differ between canopy, understory, and isolated individuals. Canopy plants in dense aggregations are taller than isolated individuals and may exceed limiting proportions for elastic stability. *Postelsia* shows photosynthetic characteristics of “shade-adapted” plants, understory individuals being especially effective at using low light. Despite this, blade growth rates of understory plants are lower than those of either canopy or isolated individuals.

Key words: Aggregation; Allometry; Biomechanics; Intertidal ecology; Macroalga; *Postelsia palmaeformis*

INTRODUCTION

Intertidal organisms are subject to the physical consequences of living both in water and in air. The mechanical support system of an intertidal alga must withstand hydrodynamic forces when submerged and must bear the plant’s weight when surrounded by air. On wave-swept shores, macroalgae withstand wave action primarily by deforming when exposed to moving water; their flexibility and extensibility permit them to move with the flow, to take on streamlined shapes, and to absorb safely the strain energy imparted by the water’s impact (for reviews see Koehl, 1986; Denny et al., 1989). Most

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large intertidal macroalgae are flexible to the extent that they cannot support their own weight in air; at low tide they bend over and lie on the substratum. A few species of intertidal macroalgae, however, maintain an erect stature throughout the tidal cycle. *Postelsia palmaeformis* Ruprecht (hereafter *Postelsia*) is a striking example of the latter. This kelp bears a superficial resemblance to a palm tree, hence its common name, the “sea-palm”.

Postelsia sporophytes, which can attain heights of 50–75 cm (Paine, 1986, 1988), consist of a crown of blades supported atop a tapered stipe that is attached to the substratum by a holdfast (Fig. 1A). The stipe is hollow along much of its length and is capable of growth in diameter due to the presence of a meristoderm beneath the cortex. No conducting elements for the transport of materials from the substratum to the blades exist within the stipe, which thus serves primarily to support the crown. Sieve elements for the transport of photoassimilates from crown to stipe are not reported in *Postelsia*, although they occur in many species in the Laminariales (Lobban et al., 1985). The blades grow continuously from a basal meristematic region and function both in photosynthesis and spore production (Abbott & Hollenberg, 1976). Although rarely submerged for any length of time (Paine, 1986), *Postelsia* sporophytes are bent over by every incoming wave they encounter. Watching a stand of *Postelsia* in the face of a large wave is similar to watching a field of tall grass subjected to a strong gust of wind: the plants bend almost prostrate as the wave hits, only to spring back to their original posture once it has passed. We were intrigued by *Postelsia* because of its peculiar tree-like morphology and the seemingly contradictory demands of standing upright in a low density medium (air) while withstanding dynamic forces in a higher density one (water).

Due to its abundance in certain intertidal communities, the life history and ecology of *Postelsia* have been well studied. An annual kelp of the family Laminariales, *Postelsia* occurs along exposed rocky coastlines from Morro Bay, California, to Vancouver Island, British Columbia (Abbot & Hollenberg, 1976). Sea-palms are found only in the mid-intertidal zone, the region typically dominated by the mussel *Mytilus californianus* L., and only in areas subjected to extreme wave action (Paine, 1979, 1988; Leigh et al., 1987). Within this region, sea-palms typically form dense stands (ranging from one to > 100 m²; Dayton, 1973; Paine, 1979), although isolated individuals are occasionally observed. The reasons for the aggregated distribution and the limitation to exposed habitats appear to be two-fold. (1) Meiospores produced in the longitudinal grooves on the blades are dripped onto the substratum at low tide and settle close to the parent plant, typically within 1–2 m (Dayton, 1973; Paine, 1979, 1988). (2) *Postelsia* seems to require the presence of mussels, which competitively exclude the turf-like algae in whose presence *Postelsia* does not persist (Paine, 1988). *Mytilus californianus* also outcompetes *Postelsia* for space, making the local persistence of sea-palms dependent on the removal of mussels by wave action and wave-borne logs (Dayton, 1973; Paine, 1979, 1988). The requisite rate of predictable annual disturbance is available only on very exposed shores (Paine, 1979).

The morphology of *Postelsia* plants growing in aggregations appears to be different from that of isolated individuals. The holdfast area per plant is lower for aggregated plants than for isolated ones (Paine, 1979). We have also noticed that aggregated *Postelsia* are appreciably taller and appear to have narrower crowns than isolated individuals, raising questions about environmental effects on growth form. Perhaps crowding within stands of this kelp leads to a morphological response analogous to that observed in trees: plants in dense stands grow long and slender in response to reduced light levels and decreased wind-induced sway within the stand (e.g., Holbrook & Putz, 1989).

The purpose of our study was to explore the relationship between the demands of the environment and growth form of *Postelsia*. We focused on two questions: (1) What are the structural features (spatial arrangement of plants, as well as thallus shape and stipe tissue mechanical properties) that enable *Postelsia* to stand upright in air while being flexible enough to withstand wave action? and (2) What are the mechanical and photosynthetic consequences of living in dense aggregations? In attempting to answer these questions we have measured certain aspects of the gross morphology, tissue mechanical properties, and photosynthetic capacity of both isolated and aggregated *Postelsia*, as well as aspects of the wave-induced tensile stresses and irradiance encountered by each in their natural habitats.

MATERIALS AND METHODS

STUDY SITES

The primary study population was located at Garrapata Beach State Park (121°56' W, 56°27' N), about 10 km south of Point Lobos, CA. Plants were collected from this site for measurements of thallus dimensions, mechanical properties, and photosynthetic capacity. Photon flux densities were also measured at Garrapata Beach. A second study population was located on Tatoosh Island, WA (124°44' W, 48°24' N), at the same site as that used in several ecological studies of *Postelsia* (Dayton, 1971, 1973; Paine, 1979, 1986, 1988). Measurements of morphology, tissue mechanical properties, and blade growth rates were made on plants collected at Tatoosh.

MORPHOMETRICS

Morphological measurements (diagrammed in Fig. 1A) were made on clumped and isolated *Postelsia* plants. *Postelsia* clumps vary in size from only a few meters across to stands that cover large (tens of meters) areas of rocky shore. We considered a plant as isolated if it was at least 30 cm from the nearest neighbor; clumped plants were those located at least two crown diameters (approx. 30 cm) inward from the edge of a dense stand. Within a dense stand, individuals <25 cm tall were classified as understory plants because the top of their crowns were beneath the lowermost extent of the blades of those individuals that had access to the top of the stand; individuals > 25 cm tall were

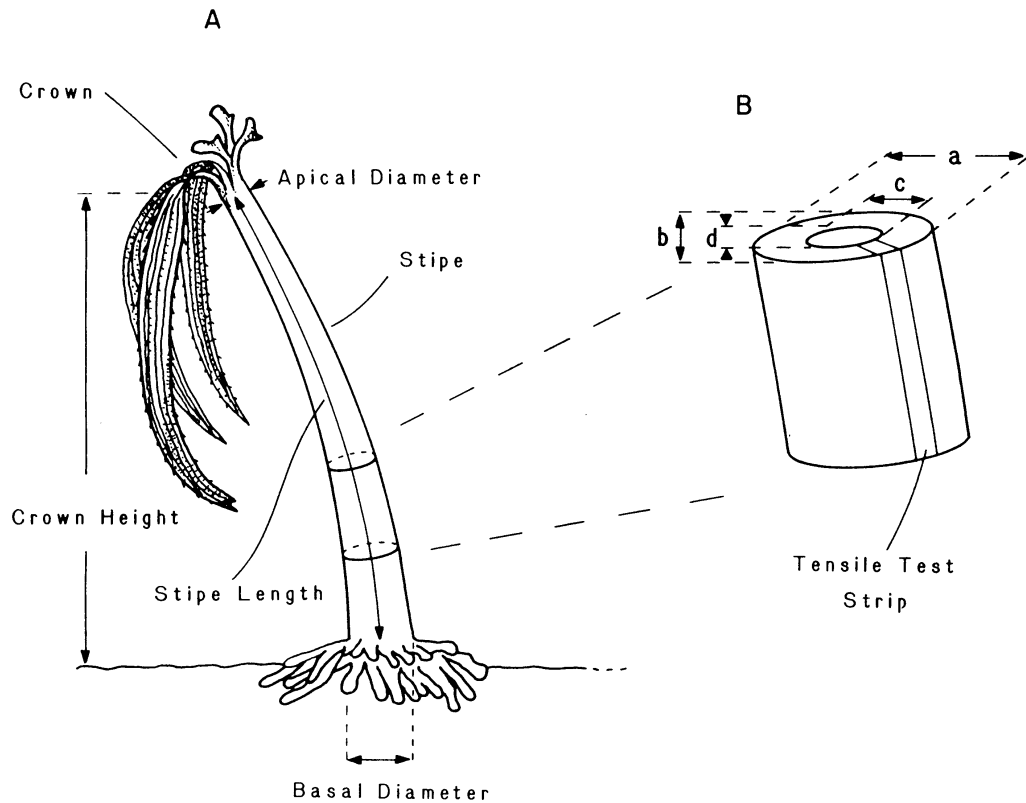


Fig. 1. (A). Diagram of a mature *Postelsia* sporophyte, indicating the morphological parameters measured. Most of blades have been removed to provide a view of the stipe's apex. (B). Expanded view of one section of stipe showing the orientation of the strip used in tensile tests, and the dimensions used in the calculation of the second moment of area.

considered to be canopy plants. At Garrapata Beach 113 individuals growing within dense stands and 60 nearby isolated plants were chosen for measurement. Plants were sampled by reaching to the substratum of each stand, selecting the first stipe contacted, and removing the individual just above the holdfast with a razor blade. This sampling method minimizes bias because we could not see to the base of the stand when individual stipes were contacted. Plants were collected during August of 1985 and 1987 and from > 15 separate stands scattered along approximately 0.5 km of coastline. At Tatoosh plants were sampled by tossing a quadrat into a dense stand and sampling all individuals within this marked area. In August 1987 an 0.08 m^2 quadrat was used and 15 plants were collected; the closest 15 isolated plants to a haphazardly selected point outside the dense stand were also measured. As isolated individuals are often quite scattered, this entailed sampling more than 300 m^2 . In August 1989 a larger quadrat (0.21 m^2) was tossed into a large stand of *Postelsia* and all canopy ($n = 28$) and understory ($n = 10$) plants within it were measured; all isolated plants ($n = 11$) in the vicinity of that stand were also sampled.

Stipe length and the actual height from the substratum to the top of the stipe (while

in air) were measured in the field before each plant was cut off at the base. Crown widths were measured by holding the plant upright and measuring the maximum diameter of the crown and its perpendicular as viewed from above with a ruler. The stipe was weighed and then cut at right angles to its long axis at a minimum of six positions along its length, and orthogonal external and internal stipe diameters were measured (to 0.1 mm) using vernier calipers. The blades were weighed and counted; then five blades per plant were randomly selected for measurement of length and width. Blades were divided into two parts – the flattened and grooved distal portions and the cylindrical proximal portions – and the total biomass of each part was measured.

While the California plants were sampled from a number of dense stands, plants collected at Tatoosh (Washington) each year were all growing in close proximity. In order to assess whether morphological differences between isolated and clumped plants at Tatoosh might be due to sampling from only one stand, we compared the variance of measurements of clumped plants in Washington and California. If interstand variation significantly exceeds intrastand variability, then we expect the variance of the California plants to exceed that of the Washington individuals. Tests of homogeneity of variance (F-test) of height : diameter ratio, stipe taper, and % crown mass (defined below), however, do not indicate significant differences in variability between the two sites ($p < 0.05$). No significant deviations from normality were observed in any of these parameters as determined by visual examination of normal probability plots.

Morphometric data from the two study sites were compared (using either a *t*-test or a Kruskal–Wallis test (for ratio data) to compare means, ANCOVA to compare regression relations) and, if there were no significant differences within a group (i.e. canopy, understory, or isolated), the data were pooled. Mean values of the three morphological groups (isolated, canopy, and understory) were analyzed using either a one-way ANOVA followed by multiple comparisons according to the Scheffe test or a Kruskal–Wallis test for ratio data. ANCOVA was used to compare slopes and intercepts of regressions.

MECHANICAL PROPERTIES OF STIPE TISSUE

Laboratory measurements were made of a number of mechanical properties of *Postelsia* stipe tissue: elastic modulus, tensile breaking strength and extension, energy required to break a sample of the tissue, and work of fracture. All measurements were made at room temperature on fresh stipe tissue kept wet with sea water.

Elastic modulus

The elastic modulus of stipe tissue, a measure of the stiffness or resistance of a material to deformation, was determined by two methods. One method involved short lengths (approx. 0.10 m) of stipe of nearly uniform diameter that were tested in cantilever bending by placing the specimen horizontally at the edge of a table, firmly clamping one end (maximum stipe diameter parallel to the table), applying known

weights (F) to the free end, and measuring the resulting downward deflection (D) with vernier calipers. In all cases the deflection was less than 10% of the cantilever length (L). The minimum second moment of area of the stipe cross section ($I = \pi/4 (ab^3 - cd^3)$, Fig. 1B), a measure of the contribution of the stipe's cross-sectional shape to bending stiffness, was calculated assuming that the neutral surface passed through the section's center of area (Roark & Young, 1975). From these data the apparent elastic modulus of bending (E_{bending} , (Pa)) was determined from the formula:

$$E_{\text{bending}} = FL^3/(3DI) \quad [1]$$

L , F , D , I , E_{bending} have the units m, N, m, m^4 , and Pa, respectively. The product ($E_{\text{bending}} I$) is the flexural stiffness (units: $\text{N} \cdot \text{m}^2$) of a stipe section, a measure of its resistance to bending.

Elastic moduli were also measured directly on straight-sided strips of excised stipe (Fig. 1A). Specimens were prepared and tensile tests were conducted using standard techniques on a Monsanto tensometer (Koehl & Wainwright, 1985), and compression tests were conducted on a specially constructed tensometer (Denny, 1984). If the stress (σ , force per cross-sectional area of the specimen) in a tissue that is being deformed in tension or compression is plotted as a function of the tissue's extension (extension ratio, $\lambda = l/l_0$, where l is the extended specimen length and l_0 is its initial length), the slope of this curve is the elastic modulus (E). *Postelsia* tensile σ - λ curves show a steep slope, which we call the initial modulus ($E_{\text{tension(initial)}}$) at low λ 's (generally $\lambda < 1.1$), and then rather abruptly shift to a shallower slope, which we call the final modulus ($E_{\text{tension(final)}}$) at higher λ 's.

Breakability

We measured several aspects of the breaking performance of *Postelsia* stipe tissue. Samples pulled in the Monsanto tensometer were extended until they broke and the tensile strength (σ_{brk} , breaking stress, units: Pa) and extensibility (λ_{brk} , extension ratio of the tissue at the time of breakage) were measured for all samples. Data were discarded if the sample fractured in the vicinity of the tensometer grips. The area under the stress-extension curves is a measure of the energy per volume of tissue that is required to break the specimen (B , units: J/m^3). This energy is an indication of the work that must be done by moving water to break an unflawed plant of a given stipe volume, and thus provides a measure of the breakability of a structure rather than a measure of the resistance of a material to crack propagation.

In contrast, the work of fracture of a tissue, the work required to create new surfaces in a material as a crack propagates (W , units: J/m^2), is a measure of the toughness of the tissue itself (Wainwright et al., 1976). Although resilient structures can be difficult to break because they are highly extensible (e.g., rubberbands, *Postelsia* stipes), they can undergo sudden, brittle fracture when loaded if they have been flawed.

We measured the work of fracture of *Postelsia* stipe tissue by taking advantage of the

fact that it is often much easier to break a material if a sample contains a sharp-ended flaw or crack; in such a case, when a crack is present, the ability to resist breakage is a measure of the material's work of fracture. We bent a stipe to a known radius of curvature, and hence to a known distribution of stresses within the stipe (see Timoshenko & Gere, 1980). We then slowly inserted a razor blade into the tensile side of the stipe. When the razor cut reached a critical depth (L_{crit}), the stipe spontaneously and rapidly fractured. L_{crit} was determined by examining the fracture surfaces of the broken stipe; the position where the razor cut stopped and the glassy fracture surface began was readily identified. The local stress at the end of the razor cut (σ_L) at the time of fracture can be calculated (Wainwright et al., 1976):

$$\sigma_L = E y/R \quad [2]$$

where E is the tensile elastic modulus (Pa), y is the radial distance from the neutral surface of the stipe to the innermost tip of the razor cut (m), and R is the radius of curvature of the central axis of the stipe (m). The local stress (σ_L) can be used to calculate the work of fracture (W) (Wainwright et al., 1976; Gordon, 1978):

$$W = \pi L_{\text{crit}} \sigma_L^2 / (2E). \quad [3]$$

STRUCTURAL STABILITY

When a column, such as a *Postelsia* stipe plus crown, becomes too tall, it bows under the load of its own weight. This Euler (elastic) buckling occurs when failure is not permanent; if the load is reduced sufficiently, the column can elastically regain its original posture. The maximum height (H_{crit}) that a vertical column can reach before buckling under its own weight was determined by Greenhill (1881) as:

$$H_{\text{crit}} = C (E/(\rho g))^{1/3} (r)^{2/3} \quad [4]$$

where C is a constant that depends on the taper of the column, E is the elastic modulus (Pa), ρ the mass per volume of the column material (kg/m^3), g is the acceleration due to gravity (9.81 m/s^2), and r is the basal radius (m). King & Loucks (1978) modified this form of the Euler equation for the elastic stability of a column to include a point load at the top of the structure (i.e. the crown). Solving for the critical dimensions for which the energy stored within the column due to its curvature equals the loss in potential energy due to bending over, King & Loucks (1978) determined the constant of proportionality (C) to be a function of the ratio of crown to trunk weight (k):

$$C(k) = [(0.007601 + 0.08655 k + 0.334 k^2) / (0.001427 + 0.02907 k + 0.1695 k^2 + 0.6125 k^3)]^{1/3} \quad [5]$$

We assessed the potential for this type of structural instability in *Postelsia* by assuming that the load on the structure consisted of a point load at the top of the stipe due to the weight of the blades, plus a distributed load due to the stipe's weight. Because

Postelsia stipes are hollow, we calculated the second moment of area for each measured stipe cross-section and then determined the radius of a circular cross-section of equivalent I. This dimension, which we refer to as the equivalent radius (r_{eq}), was used in determining H_{crit} .

WAVE-INDUCED STRESSES

Because *Postelsia* are flexible, they move with the water and bend as waves hit them. The maximum forces that must be withstood by the stipes and holdfasts occur after the plants are maximally bent and no longer able to move with the flow. It appears that *Postelsia* subjected to waves at Tatoosh are moving with the flow when the accelerations are highest, but must bear the drag forces occurring when velocities are highest (Koehl, 1986).

Wave-induced tensile stresses imposed on *Postelsia* stipes were estimated as follows. A typical clumped plant was chosen and a string was attached to the end of its stipe just below the crown. The string was pulled parallel to the substratum (in the approximate direction of wave-induced drag) using a spring scale. The bending induced by this applied force approximated the deformations that occurred as waves crashed through a *Postelsia* stand. At a series of forces, photographs of the stipe and an adjacent rule were taken. For each photograph, the curvature, ξ , of the stipe was measured at a series of points spaced approximately 1 cm apart along the stipe. The bending-induced tensile stress at each point was then calculated as:

$$\text{bending-induced tensile stress} = E_{\text{bending}} (\xi - \xi_0)y \quad [6]$$

where E_{bending} is the average apparent modulus in bending for *Postelsia* (measured as described above), ξ_0 is the curvature of the stipe at that point when no force is applied, and y is the radius of the stipe at that point (Timoshenko & Gere, 1972). In addition to bending the stipe, drag also applies a component of force along the stipe's axis. The maximum direct tensile stress thus imposed was determined at each point by dividing the axial component of force (i.e., the force tangential to the stipe axis) by the cross-sectional area at that point.

LIGHT ATTENUATION

Photosynthetic photon flux density (PPFD) was measured along a vertical transect through several (5) dense stands of *Postelsia* at the Garrapata site. At low tide, readings were made using a hand-held quantum sensor (LiCor LI-192SB) that records the instantaneous light flux ($\mu E \cdot m^{-2} \cdot s^{-1}$, 400–700 nm). During periods of moderate wave activity (i.e., sufficient wave action to bend the plants back and forth, but not enough to prevent access to the stand) and integrating quantum scalar irradiance meter (Biospherical Instruments QSL-140) was used. This instrument measures the accumulated light flux (400–700 nm) striking a 2 cm Teflon sphere. Due to the precarious position of the researcher, short (2 min) time intervals were used. The distribution of

light within *Postelsia* stands was measured during 2 days in both 1985 and 1986 for a variety of ambient PPF_D's and times of day. "Leaf" area index (L.A.I., m² blades/m² substratum) of one of these stands was determined by measuring the heights of all individuals within a 1 m² quadrat and estimating the total blade surface area from allometrical relations between stipe length and blade mass. Blade area/mass relations determined for photosynthetic measurements (see below) were used to calculate blade area per area substratum.

PHOTOSYNTHESIS

Photosynthetic rates of *Postelsia* blade tissue at different PPF_D's were determined in the laboratory in August of 1985 and 1987 by measuring oxygen evolution. Canopy, understory, and isolated (defined above) plants were collected at the Garrapata Beach site and one healthy blade per plant was chosen haphazardly. A sample (approx. 4 cm²) was cut from the midsection of each such blade and was placed in running seawater overnight to minimize "wound response" in tissue respiratory behavior. Each sample was then placed in an insulated, stirred chamber containing 5 ml of ultrafiltered (0.2 μm), buffered (pH = 8.5) sea water. Ten μl of 1 M sodium bicarbonate was added to the seawater so that carbon limitations would not affect photosynthetic rates. The exterior of the chamber was connected to a water bath and kept at a constant temperature of 15 ± 1 °C. Prior to beginning the readings, the partial pressure of oxygen in the seawater was reduced to approximately 20% of its saturated value by bubbling a mixture of N₂ and CO₂ through the chamber. Light was supplied by a Kodak projector lamp (500 W) outfitted with a series of neutral density filters: PPF_D was measured using the integrating quantum sensor described above. At each light level oxygen evolution was measured using a Clark-type oxygen electrode (Rank Brothers), for 3 min, beginning when a steady rate was reached. Dark respiration rates were also determined at both the beginning and end of the light measurements by covering the chamber and allowing O₂ consumption to reach a constant value. Photosynthetic rate was plotted as a function of PPF_D and the photon flux density at which photosynthesis saturated was determined to be that at the intersection of the regression lines of the initial (low light) readings and the maximum photosynthetic rate (P_{\max}). Further details of this technique are described in Dennison & Alberte (1985).

Photosynthetic performance of blades was determined for a total of seven understory, six canopy, and six isolated plants. In addition, the photosynthetic rate of one piece of stipe tissue was measured at various PPF_D's. In this case, the tissue sample consisted of a quarter of a disk of stipe (shaped like a piece of pie; 1.5 cm height, 2.0 cm radius) oriented with its exterior towards the light source.

Enhanced photosynthetic capacity at low irradiance levels can result either from an intrinsically high capacity for light capture and carbon fixation (high P_{\max} /g pigment) or from a greater concentration of light-capturing molecules within the tissue itself (high g pigment/g biomass). In 1987, light-capturing pigment concentrations of *Postelsia* blade

tissues were determined. Following measurement of photosynthetic performance, the tissue sample was measured, weighed, and placed first in DMSO for 15 min, and then in absolute acetone for 2 h in total darkness. Absorption at 665, 631, 582, and 480 nm of the DMSO extracts were determined using a Beckman DU-7 spectrophotometer; the acetone extracts were diluted with methanol and water and read at 664, 631, 581, 470 nm. Concentrations of chlorophylls *a* and *c* and fucoxanthins were calculated from these readings as described by Jeffrey & Humphrey (1975).

In order to model the effects of the photosynthesis : light relationships measured in the laboratory on the potential for photosynthesis under field conditions, it was necessary to have information on the distribution of light both in space (i.e., at microsites (canopy or understory) within *Postelsia* stands) and in time. Cumulative hours of total solar radiation (W/m^2 , data tabulated in intervals of $50 \text{ W}/\text{m}^2$) at the Monterey Bay Aquarium, located approximately 20 km north of the Garrapata Beach site, were used as an estimate of the radiation environment of the study area. Five-minute averages of total solar irradiance were measured using a Weather Measure model 3020 star pyranometer. We considered the photon flux density of PAR to be half of the total incoming radiation (Monteith, 1973). An estimate of the potential photosynthetic capacity was calculated using laboratory photosynthetic rates of isolated, canopy, and understory individuals and radiation data collected during August 1987 (the same time that the photosynthetic measurements were made). Photosynthetic capacity for the month of August 1987 was calculated according to:

$$\sum_{i=0}^{i_{\max}} [\text{hours}(\text{PPFD}_i) * \text{photosynthesis}(K_{\text{att}} * \text{PPFD}_i)] \quad [7]$$

where the subscript *i* indexes ranges of PPFD in increments of $50 \text{ W}/\text{m}^2$, $\text{hours}(\text{PPFD}_i)$ = the cumulative number of hours of above-canopy PPFD within range *i*, K_{att} = a light attenuation factor specific for each microsite (fraction of ambient), $K_{\text{att}} * \text{PPFD}_i$ = the median effective light level at each microsite, and $\text{photosynthesis}(K_{\text{att}} * \text{PPFD}_i)$ = the mean laboratory measured photosynthetic rate of understory, canopy, or isolated plants at a particular effective irradiance ($\mu\text{M O}_2 \cdot (\text{g fresh blade mass})^{-1} \cdot (\text{h})^{-1}$). Light attenuation curves were used to estimate the average light environment experienced by canopy and understory plants. As there was no difference in substratum light readings at low tide (when the plants were still) and when they were experiencing moderate wave activity, we considered the contribution of direct sunlight reaching into the understory (light-flecks) to be small. Based on measurements of light attenuation within *Postelsia* stands, we assumed that blades within the crowns of isolated plants received 100% of incident PPFD, understory plants 5%, and canopy plants 80%.

BLADE GROWTH RATES

Blade growth rates were measured at the Tatoosh site in August 1989 prior to the plants being sampled for morphological measurements. A small hole was made at the upper (proximal) end of the flattened portion of two to four blades per individual (Mann, 1973). Growth rates were determined by measuring the distance this hole was displaced towards the distal end of the blade after 29 days. Blade dimensions (width and mass per length) were measured and growth rates expressed on both an area (cm^2/day) and mass (g/day) basis. In addition, at the end of the measurement period the total mass of each marked blade was determined allowing calculation of relative growth rate ((new mass per day)/(total blade mass), units: day^{-1}).

“Leaf” area index (L.A.I.) was determined by photographing the patch of substratum over which they had stood. The photograph was projected onto a Jandel digitizing tablet interfaced with an IBM-PC computer and the area of the patch was measured. Blade area per plant was estimated by multiplying the weight of all the blades by the area/weight measured for blades of that plant.

RESULTS

ALLOMETRIC STUDIES

Stem allocation patterns differed between *Postelsia* plants growing in dense stands and those growing as isolated individuals. Both understory (stipe length < 25 cm) and

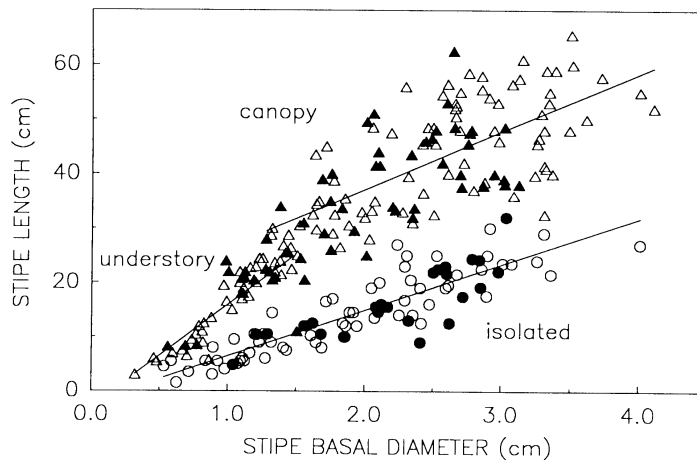


Fig. 2. Stipe length (cm) as a function of basal equivalent diameter (cm) for isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. Clumped plants < 25 cm tall were considered understory plants, while taller plants were treated as canopy individuals. The slopes of the regression equations (isolated: $y = -1.98 + 8.43x$, $r^2 = 0.77$, d.f. = 83; canopy: $y = 15.92 + 10.60x$, $r^2 = 0.47$, d.f. = 119; understory: $y = -2.88 + 18.79x$, $r^2 = 0.71$, d.f. = 49) were significantly different ($F = 7.59$, $p < 0.001$, d.f. = 2), with the increase in height per increase in diameter being significantly greater for the understory plants compared with isolated and canopy individuals (which did not differ).

canopy plants growing in dense clumps had longer stipes than isolated individuals of the same basal diameter (Fig. 2). The steeper slope of the stipe length vs. basal diameter relationship for the understory plants indicates a greater increment in stipe length relative to diameter growth as compared to either canopy or isolated plants. For plants with stipe mass > 10 g (corresponding to isolated plants of > 8 cm and clumped plants > 17 cm tall), the height : diameter ratio of individuals growing in dense stands (understory $X = 16.5$, $SE = 0.46$, $n = 45$; canopy $X = 17.5$, $SE = 0.32$, $n = 120$) was more than twice that of isolated individuals ($X = 7.7$, $SE = 0.20$, $n = 66$; Kruskal–Wallis $T = 139.44$, d.f. = 2, $p < 0.001$).

Within an individual plant the equivalent stipe radius decreased linearly along the stipe. Taper (ta) is defined here as

$$ta = 1 - r_{eq,a}/r_{eq,b} \quad [8]$$

where $r_{eq,a}$ and $r_{eq,b}$ represent the equivalent radius at the stipe apex and base, respectively. By this definition, a perfectly columnar plant would have a taper of zero, while a plant whose stipe narrowed to a point would have a taper of one. The taper of canopy plants ($X = 0.50$, $SE = 0.005$, $n = 121$) was significantly greater than that of either isolated ($X = 0.39$, $SE = 0.012$, $n = 84$) or understory individuals ($X = 0.42$, $SE = 0.017$, $n = 52$; Kruskal–Wallis $T = 66.70$, d.f. = 2, $p < 0.001$).

Isolated plants supported more blade biomass than clumped plants (either canopy or understory) of the same stipe length (Fig. 3). The steeper slope of the regression for the canopy plants indicates a relatively greater increase in blade mass per increase in stipe length compared to both understory and isolated plants. Greater blade biomass

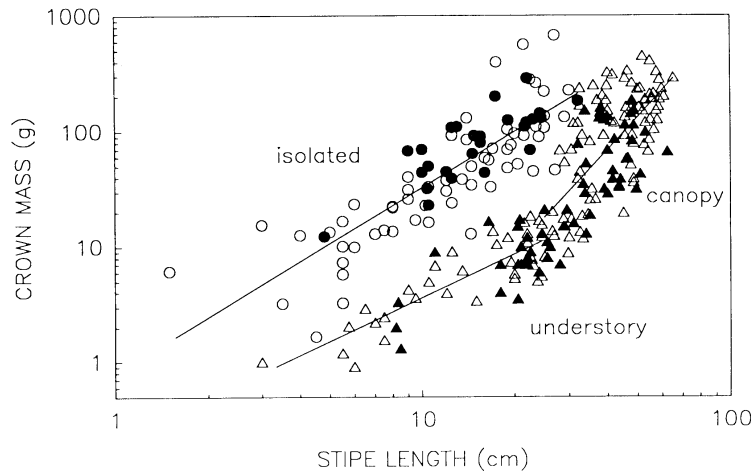


Fig. 3. Crown biomass (g; log scale) as a function of stipe length (cm; log scale) for isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. The slopes of the regression equations (isolated: $y = -0.09 + 1.61x$, $r^2 = 0.69$, d.f. = 58; canopy: $y = -2.78 + 2.88x$, $r^2 = 0.45$, d.f. = 84; understory: $y = -0.70 + 1.26x$, $r^2 = 0.67$, d.f. = 50) differed significantly ($F = 12.77$, $p < 0.002$, d.f. = 2) with the increase in blade biomass per increase in stipe length of canopy plants being greater than for either isolated or understory plants (which did not differ).

(for a given stipe length) in isolated plants was due to having both longer and more numerous blades. Mean blade length (Fig. 4A) and number of blades (Fig. 4B) was significantly correlated with stipe length. Mean blade width (Fig. 4C) was significantly smaller in understory plants; blade width was significantly correlated with stipe length

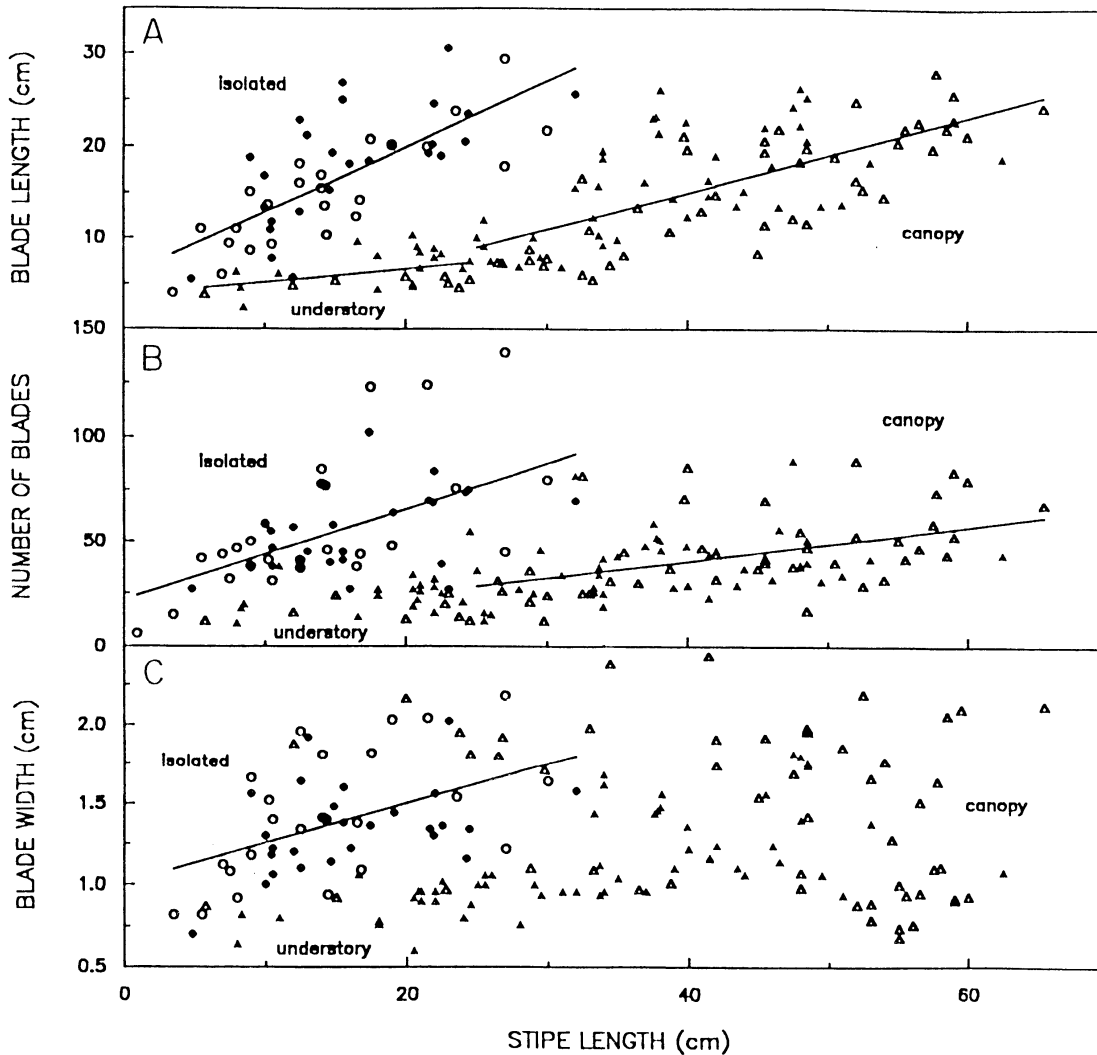


Fig. 4. (A). Mean blade length (cm) as a function of stipe length (cm) for isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. Each point represents the mean length of five blades per plant. Mean blade length was significantly correlated with stipe length for isolated ($y = 5.71 + 0.71x$, $r^2 = 0.56$, d.f. = 49), canopy ($y = -1.21 + 0.40x$, $r^2 = 0.46$, d.f. = 82), and understory individuals ($y = 3.78 + 0.14x$, $r^2 = 0.17$, d.f. = 25). (B). Mean number of blades as a function of stipe length (cm). Number of blades was significantly correlated with stipe length for both isolated ($y = 22.05 + 2.19x$, $r^2 = 0.32$, d.f. = 50) and canopy ($y = 7.71 + 0.83x$, $r^2 = 0.21$, d.f. = 82) plants, but not for understory individuals ($p = 0.14$, d.f. = 26). (C). Mean blade width (cm) as a function of stipe length (cm). Blade width was significantly correlated with stipe length only in isolated plants ($y = 1.01 + 0.02x$, $r^2 = 0.23$, d.f. = 49). Mean blade width did not differ between isolated and canopy individuals; understory plants were significantly smaller ($F = 7.31$, $p < 0.001$, d.f. = 159).

only in isolated individuals. Percent of total crown biomass made up of the flat blade tissue (as opposed to the cylindrical proximal region) differed among the three groups (Kruskal–Wallis $T = 105.98$, d.f. = 2, $p < 0.001$). Crowns of isolated plants had the highest percent allocation to blade tissue ($X = 91.1\%$, $SE = 0.54$, $n = 86$), followed by the understory plants ($X = 87.3\%$, $SE = 0.94$, $n = 52$), and canopy individuals ($X = 81.2\%$, $SE = 0.48$, $n = 106$). Despite differences in crown mass and structure between isolated and clumped plants, the relationship between crown mass and apical stipe radius was similar in all groups (Fig. 5). Percent total biomass allocated to crown tissue (plants with stipe mass > 10 g) was significantly greater in isolated plants ($X = 63.9\%$, $SE = 1.22$, $n = 67$) than in either canopy ($X = 39.8\%$, $SE = 1.17$, $n = 106$) or understory plants ($X = 38.0\%$, $SE = 1.85$, $n = 41$; Kruskal–Wallis $T = 103.73$, d.f. = 2, $p < 0.001$).

MECHANICAL PROPERTIES OF STIPE TISSUE

The tensile and compressive moduli, strength, breaking extension, and breaking energy of stipe tissue from isolated and clumped plants did not differ significantly (Table I) and are similar to values reported for other species of marine algae (e.g., Koehl, 1984; Biedka et al., 1987). There were no differences in E measured at different places along the stipe (Koehl, unpubl. data). The work of fracture (W) for the stipe material of isolated plants is similar to that reported for another kelp (Vincent & Gravell, 1986), but significantly higher than stipe tissue of clumped plants ($t = 5.647$, $p < 0.001$, d.f. = 41). The structural basis for this difference is not known. When compared with wood (Table I), *Postelsia* stipe tissue is deformable (low elastic modulus) and weak (low breaking

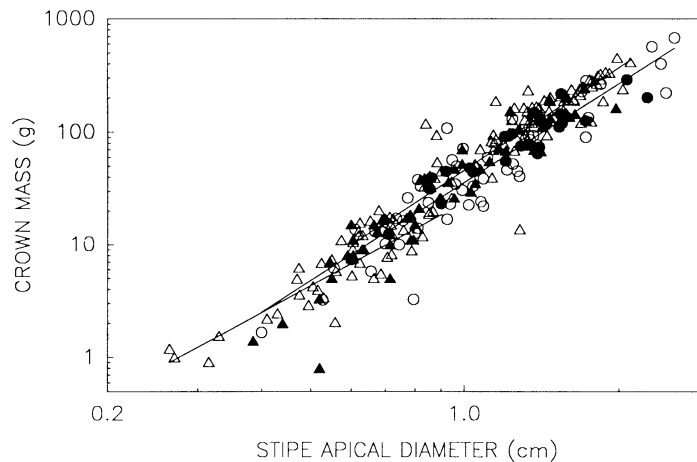


Fig. 5. Crown mass (g; log scale) as a function of apical stipe diameter (cm; log scale) for isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. There were no significant differences among the slopes of the regression equations for isolated ($y = 1.55 + 2.90 x$, $r^2 = 0.86$, d.f. = 84), understory ($y = 1.37 + 2.45 x$, $r^2 = 0.65$, d.f. = 51), or canopy ($y = 1.66 + 3.00 x$, $r^2 = 0.86$, d.f. = 118) individuals ($p > 0.05$). The y -intercept of the canopy plant regression, however, was significantly higher ($p < 0.05$).

TABLE I

Mechanical properties (defined in text) of *Postelsia* stipe tissue. Means (SE, n) between isolated and clumped plants did not differ significantly unless indicated ($***p < 0.001$). Values for wood (taken from Wainwright et al., 1976; Gorden, 1978) are shown for comparison. The breaking energy for wood (W) is estimated from the breaking strength and breaking strain by assuming a linear stress-strain curve.

		Clumped	Isolated	Wood
<i>Elastic modulus</i>				
E_{bending}	(MPa)	11.3 (2.56,5)	14.5 (4.66,3)	
E_{tension} (initial)	(MPa)	9.55 (0.527,39)	6.41 (0.465,26)	12,000
(final)		5.17 (0.455,29)	4.42 (0.361,15)	
$E_{\text{compression}}$	(MPa)	3.22 (0.361,12)		
<i>Breaking stress</i>				
σ_b	(MPa)	1.27 (0.064,39)	1.16 (0.074,29)	115
<i>Breaking extension ratio</i>				
λ		1.18 (0.061,39)	1.21 (0.055,28)	1.01
<i>Breaking energy</i>				
B	(kJ/m ³ · 10 ²)	1.37 (0.128,39)	1.88 (0.140,50)	6
<i>Work of fracture</i>				
W	(J/m ²)	398 (36.0,30)	*** 886 (102.9,13)	10,000

strength), has a breaking energy of the same order as wood (due primarily to being highly extensible), but is brittle (low work of fracture) and hence susceptible to failure should a defect or crack appear in the material. The brittle nature of *Postelsia* stipe material is typical of algal materials in general (see Denny et al., 1989). Note that the stiffness of *Postelsia* stipe material in compression is substantially lower than the stiffness in tension. As a result, the neutral surface of a *Postelsia* stipe in bending does not pass through the center of area in a cross-section (it is displaced toward the side of the stipe in tension (Timoshenko & Gere, 1972)), a factor that has not been taken into account when calculating the apparent elastic modulus from bending tests, but which has been considered in the calculation of the work of fracture.

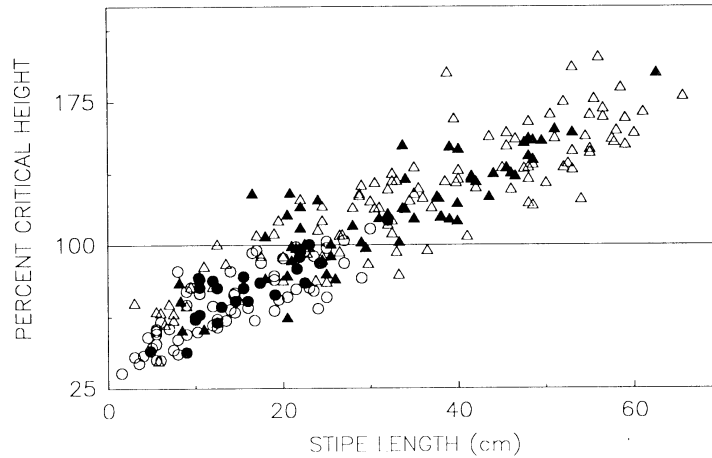


Fig. 6. Percent critical height ($100 \times \text{stipe length}/\text{critical height}$) as a function of stipe length (cm) calculated for isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. The horizontal line marks 100% critical height; any symbol above this line denotes an individual that is predicted to undergo Euler buckling.

ELASTIC STABILITY

The combination of a large crown mass and a slender stipe made of flexible material makes *Postelsia* susceptible to Euler buckling. The critical height (H_{crit} , equation 5) was calculated for each plant and the length of each stipe was expressed as a percentage of H_{crit} . If this percentage is greater than 100%, the plant is predicted to undergo Euler buckling and to have a crown elevation above the substratum that is less than its stipe length. Few of the isolated plants exceeded the 100% value, whereas many of the clumped plants did (Fig. 6). While plants below their H_{crit} had no difference between

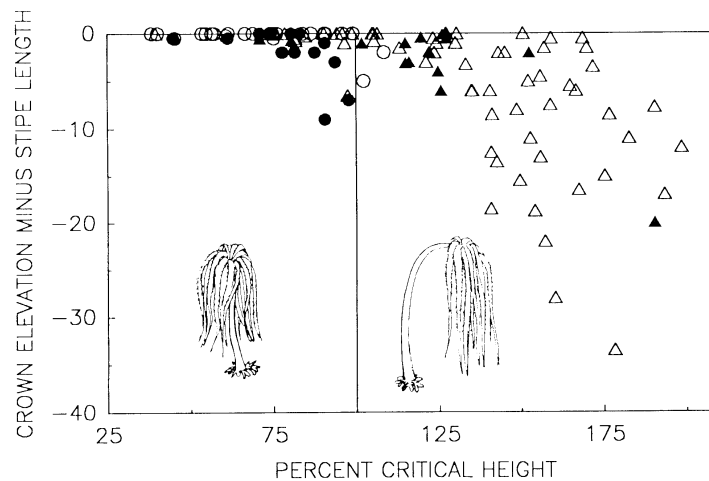


Fig. 7. The difference between stipe length and crown elevation (cm) in relation to percent critical height ($100 \times \text{stipe length}/\text{critical height}$) for both isolated (California (○) and Washington (●)) and clumped (California (△) and Washington (▲)) individuals. The solid vertical line marks stipes whose lengths equal H_{crit} .

stipe length and crown elevation (and thus were erect), plants above their H_{crit} had stipes that were longer than the elevations of their crowns (Fig. 7). Thus, tall canopy individuals in dense stands drooped over, while both the short understory plants in clumps and the isolated individuals stood erect.

Within dense stands the crowns of canopy plants touched one another, allowing tall plants to gain some support from their neighbors. The significance of this mutual support was illustrated by pulling neighboring plants away from canopy individuals: with no neighbors these plants bent over further, their blades coming to rest on the substratum in some cases. If the crowns were cut off of these buckled plants (thereby reducing the bending moment), the stipes regained a more upright posture. This indicates that the “drooping” of plants is due to elastic instability rather than to a permanent curvature of the stipe acquired during growth. Plants growing along the edges of clumps cannot be supported in all directions by neighboring plants. These individuals were either shorter (Koehl, unpubl. data), were appreciably bent over, or had smaller crowns.

After being bent toward the substratum by a wave, *Postelsia* returned to their pre-wave postures. This indicated that the potential (strain) energy stored in a deformed stipe exceeded the decrease in potential (gravitational) energy caused by being bent toward the substratum. This was true even for the drooped-over plants (i.e. those that had undergone Euler buckling), despite their departure from elastic stability as a vertical column.

WAVE-INDUCED STRESSES

As the load on a *Postelsia* stipe is increased, the stipe bends, thereby reducing the distance between the crown and the holdfast, and hence decreasing the applied bending moment (Fig. 8A). As a result, each increment in applied force produces a smaller increment in the maximum bending-induced tensile stress in the stipe (Fig. 8B). By the point at which the bulk of the crown is lying on the substratum (20 N and above in Fig. 8A), any increase in applied force (drag) results in very little increase in tensile stress. In other words, *Postelsia* stipes that are fully bent over by drag experience close to the maximum tensile stress that can be imposed by flowing water. Note that the tensile stress imposed by drag pulling along the axis of the stipe is an order of magnitude smaller than that resulting from the applied bending moment (Fig. 8B). It is common to see plants in the middle of large clumps fully bent over by breaking waves. We thus conclude that aggregation does not effectively shelter clumped plants from wave-induced drag.

LIGHT ATTENUATION

Photosynthetically active radiation (PAR), expressed as the percent of ambient light reaching the top of the canopy, was rapidly attenuated with increasing distance below the top of the canopy of dense *Postelsia* stands (Fig. 9). Light levels below approximately 55% of the canopy height (approximately the lower limit of the blades of canopy individuals), were less than 10% of the above-canopy value. Variation in substratum

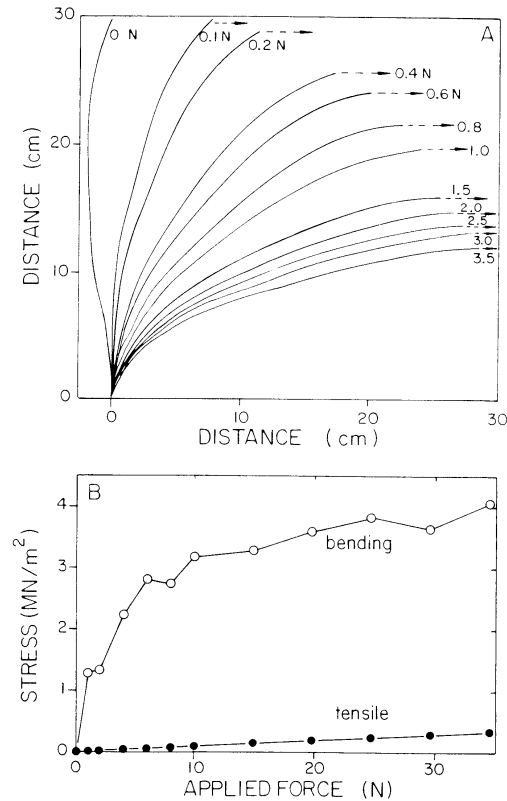


Fig. 8. (A). Position of a 30 cm *Postelsia* stipe when horizontal forces of various magnitudes (indicated by the numbers next to each line) were applied at the stipe apex to simulate hydrodynamic forces on the crown of the plant. Horizontal arrows indicate the direction of the applied force. Note that with each increase in force, the crown is brought nearer to the substratum, reducing the increase in bending moment. (B). Calculated maximum tensile stresses of the same stipe as in (A) as a function of applied load. The maximum bending-induced stress occurs near the base of the stipe (diameter = 2.31 cm). The maximum stress induced by direct tension on the stipe occurs just below the crown (diameter = 1.12 cm).

light levels may be due to the fact that the stipes had to be slightly pushed to the side in order to position the light sensor at this level. The “leaf” area index (L.A.I., m² blades/m² substratum) of an extensively sampled stand at the Garrapata Beach site was 14.1, which falls within the range of values (8–34) reported by Leigh et al. (1987) for *Postelsia* stands at Tatoosh. Light extinction curves for the Garrapata Beach stand allowed calculation of the extinction coefficient (κ) of the Beer–Lambert relation:

$$I = I_0 e^{-\kappa F} \quad [9]$$

where I = photon flux density ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) below F layers of leaves (in this case, $F = \text{L.A.I.}$), I_0 = photon flux density at the top of the canopy, and κ is an empirically-determined extinction coefficient that measures the efficiency of the leaves or blades at absorbing or reflecting light (Monsi & Saeki, 1953). The calculated extinction coefficient (assuming $F = 14.1$ for *Postelsia*) of 0.31 is similar to values found in grasslands (0.3 to 0.5) where leaves are vertical, but is lower than typical values for canopies composed

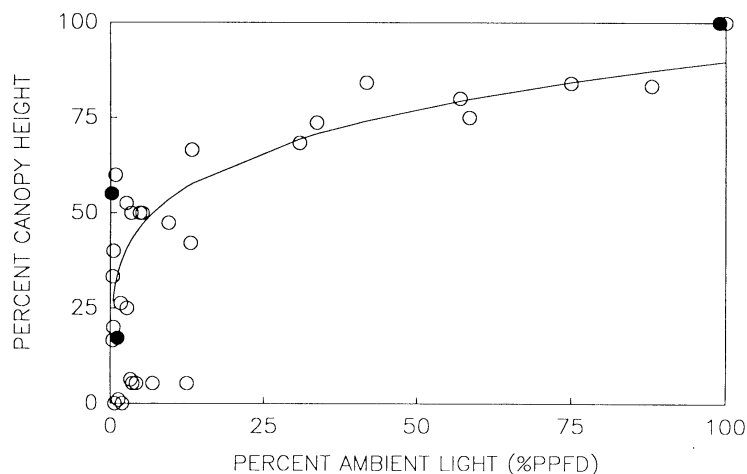


Fig. 9. Vertical attenuation of photon flux density of photosynthetically active radiation (PPFD), expressed as percent of PPFD above the canopy, measured during three different days. Vertical position within the canopy is expressed as percent of canopy height. Open symbols represent instantaneous PPFD readings made at low tide while plants were in air. Closed symbols represent PPFD measurements integrated over 2 min while plants were being moved back and forth by waves (see text). Maximum PPFD values ranged from $206 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for a cloudy morning to $2267 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for a sunny noon.

primarily of horizontally held leaves (0.7 to 1.5; Nobel, 1983). The nearly complete attenuation of light in dense *Postelsia* stands is thus due primarily to the extremely high blade coverage (high L.A.I.) rather than to a high efficiency of individual blades at absorbing or reflecting incident radiation.

Instantaneous measurements of photosynthetic photon flux density (PPFD) taken at low tide (when the plants were in air) agreed with integrated measurements made during periods when the plants were subjected to moderate wave activity (Fig. 9), indicating that light flecks created as canopy plants are moved by waves do not make a measurable contribution to irradiance levels in the understory. Since tall *Postelsia* plants growing in clumps lean upon each other, the resultant canopy is virtually continuous, which may explain why light flecks seldom penetrate dense stands. Furthermore, since plants on the edges of dense clumps tend to be both shorter and somewhat bent over, direct sunlight does not penetrate far into the stand from the side.

PHOTOSYNTHESIS

Blade tissue concentrations of chlorophylls *a* and *c* and the accessory pigment fucoxanthin (mg pigment/g fresh tissue weight) were similar in canopy and understory plants, while isolated individuals had significantly lower concentrations (Table II). Understory blade tissue, however, exhibited greater variance in the concentrations of all three pigments. P_{max} values calculated per mg chlorophyll *a* did not differ significantly between the isolated and understory plants; canopy individuals, however, had values significantly lower than isolated plants (Table II).

Maximum rates of oxygen evolution by blades of understory plants (per g fresh

TABLE II

Pigment concentrations (mg pigment/g fresh weight) and P_{\max} ($\mu\text{M O}_2 \cdot (\text{mg chlorophyll})^{-1} \cdot \text{min}^{-1}$) of *Postelsia* blade tissue collected during August 1987. Means (SE) accompanied by the same superscript do not differ significantly (Scheffe test, $p < 0.05$); $n = 3$ in all cases.

	chl <i>a</i>	chl <i>c</i>	Fucoxanthin	P_{\max}
Understory	0.466 ^a (0.0612)	0.073 ^c (0.0121)	0.218 ^c (0.0237)	1.24 ^{g,h} (0.253)
Canopy	0.353 ^a (0.0156)	0.050 ^{c,d} (0.0035)	0.191 ^c (0.0069)	0.71 ^b (0.117)
Isolated	0.140 ^b (0.0156)	0.023 ^d (0.0011)	0.079 ^f (0.0063)	1.99 ^{g,h} (0.215)

weight) were nearly twice those of both canopy and of isolated individuals (Fig. 10). However, the PPFD at which photosynthesis balances respiration (the light compensation point) and the irradiance level beyond which increased PPFD results in no further increase of photosynthetic rate (the photosaturation point) were similar for all three types of plants. Light compensation and photosaturation were reached at photon flux densities of PAR of 5–10 and 400–500 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$, respectively.

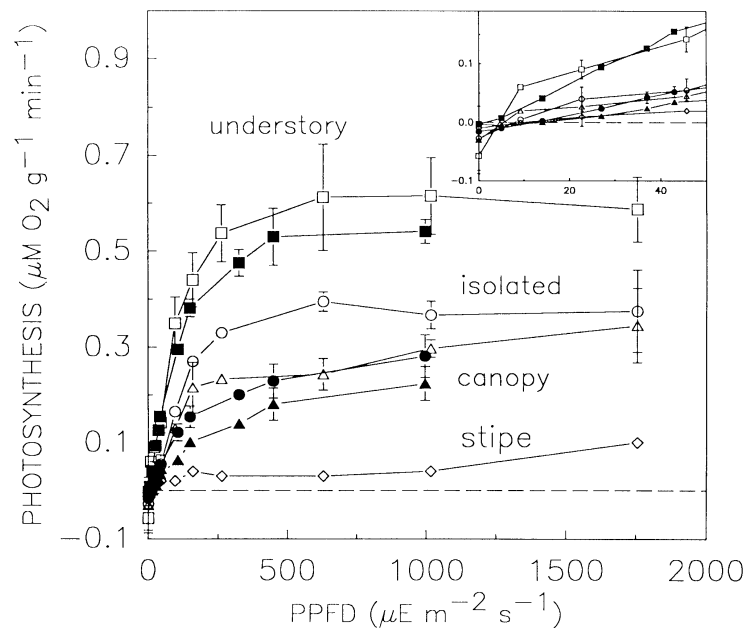


Fig. 10. Net oxygen production per tissue mass as a function of PPFD determined in the laboratory in August, 1985 (open symbols) and 1987 (closed symbols) for stipe (\diamond) and for blades from canopy (Δ), isolated (\circ), and understory (\square) individuals. Error bars represent the standard error of the mean of three individuals, except for the stipe tissue, in which case a single individual was used. Inset shows an expanded scale of the low irradiance measurements.

TABLE III

Mean (SE) blade growth rate of understory ($n = 10$), canopy ($n = 28$), and isolated ($n = 11$) *Postelsia* plants. Relative growth rate (RGR) is in units of $g_{(\text{growth})} \cdot g_{(\text{initial blade mass})}^{-1} \cdot \text{day}^{-1}$. There was no overlap in the range of values of isolated individuals as opposed to clumped (canopy or understory) plants.

	cm ² /day	g/day	RGR
Understory	0.023 (0.0031)	0.003 (0.0004)	0.0032 (0.00029)
Canopy	0.104 (0.0092)	0.013 (0.0013)	0.0052 (0.00288)
Isolated	0.553 (0.0422)	0.060 (0.0056)	0.0165 (0.00167)

Although the blades of understory *Postelsia* plants have the highest photosynthetic capacity on a fresh weight basis, they live in the least favorable light environment. Using the cumulative hours of total solar radiation measured at the Monterey Bay Aquarium as an estimate of the radiation environment of the study area, and assuming that all blades within the crowns of isolated plants receive 100% of incident PPFD, understory plants 5%, and canopy plants 80%, we estimated the photosynthetic potential of plants growing in each microhabitat. Despite higher maximum photosynthetic rates, the estimated photosynthetic capacity (per g fresh blade mass) of understory plants for the month of August was only 48% of the estimated capacity of isolated individuals, and 66% of that of canopy plants.

BLADE GROWTH RATES

Blade growth rates were approximately five times greater for isolated individuals than for either canopy or understory plants (L.A.I. = 6.3, Table III). This was true whether growth rates were expressed on an area, mass, or relative ($g \cdot (g \text{ blade})^{-1} \cdot \text{day}^{-1}$) basis. When expressed on either an area or a mass basis, blade growth rates of canopy individuals were larger than those of understory individuals. Relative growth rates of canopy and understory plants, however, were similar. Interpretation of relative growth rates are complicated by (1) the blades are simultaneously both the photosynthetic and reproductive organs and, thus, allocation to growth and reproduction may differ according to size and microsite; and (2) uncertainties regarding the degree of translocation of photoassimilate in this species.

DISCUSSION

MECHANICS OF UPRIGHT STRUCTURES DESIGNED TO WITHSTAND WAVES

Deformability versus stiffness

Postelsia survives the mechanical rigors of crashing waves primarily by being deformable. Like many other macroalgae, *Postelsia* is flexible enough that it is bent over by

moving water; such flexibility can reduce the hydrodynamic forces on a plant by various mechanisms, as described by Koehl (1986). In addition, because *Postelsia* stipe tissue is highly extensible, stretching by about 20–25% before fracturing, the stipes of these algae are difficult to break. *Postelsia* stipes have high breaking energies (high B), even though their tissues are relatively weak (i.e. have low breaking stresses (σ_{brk} values), compared with other biological materials, Koehl, 1986). Certain other large algae in mechanically rigorous habitats have also been found to be weak but extensible (e.g., *Nereocystis luetkeana*, *Durvillea antarctica*, Koehl & Wainwright, 1977; Koehl, 1984, 1986). Like *Postelsia*, these kelp tend to be washed away each year. This contrasts with the long-lived macroalgae (e.g., *Laminaria setchelli* and *Lessonia nigrescens*, Koehl, 1984, 1986, unpubl. data) on wave-swept shores whose stipes are made of relatively strong but inextensible tissue.

Postelsia meets the seemingly contradictory mechanical demands of withstanding crashing waves by being deformable and of standing upright in air. To perform both functions, a *Postelsia* stipe must have a flexural stiffness ($E \cdot I$) sufficiently high to permit it to support the weight of the crown in air, but sufficiently low to permit it to undergo large-amplitude bending when subjected to the additional load of a wave force. Furthermore, if a *Postelsia* is to stand up in air, the tissue of its stipe must be resilient enough to bounce back to its original shape after each wave hits.

Both upright and buckled *Postelsia* store sufficient strain energy in their stipes to return them to their pre-wave postures after a wave has pushed them over. The price of such resilience, however, is often brittleness since resilient materials are effective at delivering released strain energy to the tip of a crack (Gordon, 1978; Atkins & Mai, 1985). Structures made of brittle materials can undergo sudden, catastrophic failure when loaded if they have cracks or flaws that are sufficiently sharp and deep. This is true even of very extensible resilient structures, as illustrated by the unfortunate consequences of stretching a rubberband with a razor nick in it. A survey of *Postelsia* on Tatoosh in late August revealed that 11% of the plants had broken off mid-stipe ($n = 66$); scratches were obvious on some of the stumps that matched the sharp edges of neighboring barnacles and mussels. Nonetheless, most broken *Postelsia* that washed ashore on Tatoosh did not have fractured stipes, but rather had failed because their holdfasts or the organisms under them had been detached from the substratum (Koehl, unpubl. data). This suggests that the depth and sharpness of most naturally occurring scratches in *Postelsia* stipes are not great enough to lead to brittle fracture when the plants are hit by waves. Hence, the brittleness that goes hand-in-hand with the resilience of *Postelsia* stipe tissue does not appear to be an important liability for these algae.

Postelsia compared with terrestrial trees

In spite of the superficial similarity between *Postelsia* and terrestrial trees, there are important differences in their mechanical design. Because drag, lift, and acceleration reaction are proportional to the density (mass/volume) of the fluid (e.g., Denny et al.,

1985), the hydrodynamic force on a marine organism hit by a wave is about 850 times greater than the aerodynamic force on a terrestrial creature of the same dimensions hit by a gust of wind moving at the same velocity and acceleration. Because *Postelsia* withstand these mechanical rigors of wave-swept habitats by being flexible and extensible, they must build their stipes of tissue that is easily deformed (i.e. has a low elastic modulus, E). Therefore, the flexural stiffness ($E \cdot I$) of the stipes is imparted largely by their wide shape (high second moment of area, I). In contrast, the trunks of terrestrial trees are built of wood, a material that is both much stiffer (E) and much stronger (σ_{brk}) than *Postelsia* stipe tissue (e.g. Garratt, 1931; Markwardt & Wilson, 1935; Vincent, 1982). Therefore, a very slim, light woody stem can have the same $E \cdot I$ as a wide, heavy *Postelsia* stipe. Hence, the high modulus (E) of wood permits trees to achieve much greater heights than are possible for *Postelsia*. Wood, however, has a very low breaking extension (λ_{brk}) compared with stipe tissue, and woody plants often break or suffer severe structural damage when they are bent over by strong winds.

Structural instability

Since *Postelsia* stipes do not break when they are bent by waves, loss of canopy position when emersed rather than catastrophic tissue damage when immersed is the primary danger of structural instability. Isolated *Postelsia* plants grow to approximately 100% of their calculated critical heights, while the tallest clumped plants actually exceed these values by nearly a factor of two. Plants that exceeded their critical heights were visibly “buckled”, although their crowns remained supported above the substratum due to the close proximity of neighboring plants. In contrast, terrestrial trees generally retain a margin of safety between their actual and critical dimensions (i.e., are overbuilt by 20–60%; McMahan, 1975; King, 1981, 1986, 1987; Rich, 1986; Rich et al., 1986; Holbrook & Putz, 1989). Under conditions of intense competition terrestrial plants may reduce their margin of mechanical safety, but are unable to reach or exceed their critical height unless some form of external support, such as guy-wires or neighboring plants, are present.

If a margin of safety in elastic buckling is not required in *Postelsia* (since aggregated plants can lean on their neighbors and since stems do not break when they fall over), why do any individuals have less crown biomass than they can in theory support (i.e. why do any individuals fall below the “critical height” line in Fig. 6)? The fact that crown biomass as a function of stipe apical radius was similar for clumped and isolated plants (Fig. 5) suggests that there may be a constraint on crown development in small plants. The constraint might be either a mechanical one (hydrodynamic drag force on the crown versus its strength of attachment to the top of the stipe) or a developmental one (number of blades that can grow from a given apical area). We made some simple calculations to explore the idea that small *Postelsia* individuals are shorter than their predicted buckling height (i.e. they have less crown biomass than their stipes could support) due to insufficient apical area for crown attachment. We calculated the crown mass that

each plant could support at its buckling height (H_{crit}) and then predicted the stipe apical radius (using the empirical relation between crown mass and apical radius) to which a crown of that mass could be attached. Small individuals of both isolated and clumped plants had to be nearly columnar, or in some cases obconical (wider at the top than at the bottom), to provide sufficient attachment area for the calculated buckling load. While not conclusive, these calculations indicate that developmental constraints may place limits on the morphology of small *Postelsia* plants.

CONSEQUENCES OF LIVING IN AGGREGATIONS

Flow environment

One consequence of aggregation for many terrestrial (e.g., Monteith, 1973) and aquatic (e.g., Jackson & Winant, 1983; Koehl & Alberte, 1988) plants is reduction of the velocity of the air or water flow encountered by individuals within the aggregation, such that clumped individuals encounter lower mechanical loads and slower transport of fluid-borne materials than do isolated plants. Although we do not have measurements of water velocities within dense *Postelsia* stands, we have indirect evidence that plants within these aggregations are not mechanically sheltered from wave forces. Direct measurement of flow velocities within *Postelsia* stands are complicated by the physical impact of moving stipes and blades on the flow sensor. Reports of water velocities up to 8 m/s at 15 cm above the substratum in a sparse aggregation (dense *Postelsia* all around, but none actually within reach of the sensor), however, suggests that water movement in the vicinity of *Postelsia* groves is not substantially diminished compared to those that would occur in the absence of the stands (Koehl, 1986; Denny, 1988). Furthermore, the fact that *Postelsia* is typically restricted to the surf zone of exposed sites makes the likelihood of local depletion of dissolved gases and nutrients within these stands unlikely.

Local plant density, however, may affect desiccation rates. Due to both their position in the intertidal zone and the fact that they are restricted to very exposed coasts, *Postelsia* plants are wetted by virtually every incoming wave except when extremely low tides and calm weather co-occur. Under such conditions, plants growing in dense aggregations would be expected to desiccate less rapidly (Hay, 1981). Both high temperatures and tissue desiccation were reported to reduce photosynthetic rates of *Postelsia* plants growing in San Luis Obispo County, California (Young, 1971). These measurements were made by drying the blade tissue in air and then measuring O_2 evolution in water. Other studies of the photosynthesis of other marine macrophytes have reported both increases and decreases in photosynthetic rates in air with slight desiccation (10–20% of initial water content; Johnson et al., 1974; Quadir et al., 1979; Hay, 1981; but see Foster, 1982).

Population persistence

Postelsia is an annual alga. Although it is possible for a solitary sporophyte surrounded by suitable substratum to “seed” the next year’s population, the probability of a local population continuing in subsequent years is directly related to its density (Paine, 1979, 1988). Living in an aggregation therefore may aid this annual kelp in maintaining its position in the rocky intertidal against the competitive encroachment of other species.

Light

An important consequence of aggregation to plants is shading. Although the basic physiognomy of a dense *Postelsia* stand is reminiscent of a forest, these two types of canopies differ in a number of ways. The standing crop (dry matter per unit substratum) of short *Postelsia* aggregations is about an order of magnitude lower than that of tall terrestrial forests, although the leaf area index (area of blades or leaves per substratum) of *Postelsia* is comparable to or greater than that of forests (Leigh et al., 1987). Photon flux densities in the understory of tropical rain forests are generally less than 5% of canopy values, but include a significant input due to sunflecks filtering in between the crowns of canopy trees (e.g., Chazdon & Fetcher, 1984; Oberbauer et al., 1988). Similarly, light is much reduced in the understory of *Postelsia* stands (Fig. 9), but we did not observe any flecks of direct light penetrating the canopy. The spaces that generally separate the crowns of trees are thought to be maintained by mechanical action as the relatively stiff branches are battered back and forth in the wind (Putz et al., 1984). In contrast, such “crown-shyness” gaps are completely lacking in a *Postelsia* grove. Not only do rubbery *Postelsia* fail to abrade their neighbors, but also canopy plants exceed their critical heights and thus depend on neighboring plants for mechanical stability; their crowns converge, preventing any direct sunlight from reaching the understory.

The productivity ($\text{kg} \cdot \text{yr}^{-1} \cdot (\text{substratum area})^{-1}$) of *Postelsia* aggregations can be as much as an order of magnitude greater than that of forests (Leigh et al., 1987). These authors argue that the “stirring” of blades by waves may enhance algal productivity. Surprisingly, the photon flux density under a canopy of *Postelsia* being bent back and forth by waves is as low as that within a grove standing still in air. (Because of the hazards of making such measurements, we do not know if this is also true under conditions of extremely heavy wave action.) This is in contrast to the increased photon flux density measured under ruffled *Nereocystis* blades when they are subjected to water flow that makes them flutter and flail about (Koehl & Alberte, 1988). Although *Postelsia* crowns remain tightly clumped when an aggregation is pushed over by a wave, the blades move around: they are blown out parallel to the direction of the flowing water, and then are flipped about as the plants return to their pre-wave postures. Hence, even though the overall photon flux density under a *Postelsia* canopy does not increase when the plants are subjected to wave action, reshuffling of blades by waves may permit different blades to emerge from the canopy at different instants. Such reshuffling should lead to more even access to light by the many blades in a *Postelsia* canopy.

Morphology and physiology

Aggregated *Postelsia* differ morphologically from isolated individuals in a number of ways, the most striking of which is the greater height of their stipes. We do not yet know whether these variations are due to genetic differences between aggregated and isolated plants, or to plastic growth responses of individuals to their microhabitats. Several factors suggest that morphological differences between clumped and solitary *Postelsia* may well be due to plastic responses: (1) a number of other species of brown algae show great morphological plasticity (e.g., reviewed in Koehl, 1986); and (2) neighboring *Postelsia* are likely to be closely related since dispersal distances are small (Dayton, 1973; Paine, 1979) and since one sporophyte plant is sufficient to found a population (Paine, 1988). If *Postelsia* are morphologically plastic, which environmental cues are likely to trigger the structural differences between plants in different microhabitats?

Both light intensity and mechanical perturbation are known to influence stem allometry in woody plants (Larson, 1963; Wilson & Archer, 1977, 1979; King, 1981). Trees growing in dense stands, and hence subject to lateral shade and protection from wind-induced sway, tend to be taller, more slender, and less tapered than open-grown conspecifics (Telewski & Jaffe, 1986; Holbrook & Putz, 1989). As maximum water velocities appear to be undiminished in dense *Postelsia* groves, refuge from wave forces in aggregations may not be an important factor in influencing the morphological differences between isolated and clumped plants. In contrast, photon flux densities are significantly reduced in aggregations, suggesting that light may influence the morphology of *Postelsia*.

Photosynthetic data for *Postelsia* blade tissue also suggest physiological responses to light limitation. The fact that the light saturation point is approximately the same for understory, canopy, and isolated individuals ($400\text{--}500 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) indicates that *Postelsia* operates primarily within the range expected for shade-adapted individuals (Dring, 1982). Although understory plants probably never experience light levels sufficient to realize their maximum photosynthetic rates, they have a higher photosynthetic capacity at low light levels than do canopy or isolated individuals, allowing them a greater net carbon gain than could be attained by canopy or isolated plant experiencing those light levels.

Increased access to light is generally considered to be the primary factor in the evolution of vertical stature in terrestrial plants (cf. Givnish, 1982; Niklas & Kerchner, 1984). Furthermore, experimental studies designed to separate the effects of shading and mechanical agitation on terrestrial tree form suggest that, while both factors influence stem allometry, access to light is of greater importance (Holbrook & Putz, 1989). While in the absence of experimental manipulations it is not possible to assign a causal relationship between light availability and stipe allometry in *Postelsia*, our studies suggest that the development of an erect or "tree-like" growth form in *Postelsia* is related to increased access to light by taller individuals. In turn, the extent to which these plants can extend their height is limited by their elastic stability. Thus the flexibility

that allows *Postelsia* to survive wave-induced hydrodynamic forces places limits on the allometry and size of plants. It thus appears that the interaction between light and water motion plays an important role in determining the morphology of the sea-palm.

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