

PHYSIOLOGICAL SNAPSHOTS REFLECT ECOLOGICAL PERFORMANCE OF THE SEA PALM, *POSTELSIA PALMAEFORMIS* (PHAEOPHYCEAE) ACROSS INTERTIDAL ELEVATION AND EXPOSURE GRADIENTS¹

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Postelsia palmaeformis Ruprecht is an intertidal kelp found only on very wave-exposed rocky shores of the northeast Pacific. In areas dominated by mussels, *Postelsia* depends on wave-induced disturbances to complete its life-history cycle. *Postelsia* also recruits where mussels are absent, but not at less wave-exposed shores. Thus, physical conditions related to wave exposure limit its horizontal distribution. It is not clear what limits the vertical distribution of *Postelsia*. We investigated factors contributing to *Postelsia*'s limited distribution using transplant experiments, demographic monitoring, and field fluorometry to evaluate growth and performance across gradients of tidal elevation and wave exposure. Survivorship and growth were sharply reduced at upper and wave-protected edges relative to mid-level, wave-exposed sporophytes. Reproductive output was reduced at upper and lower levels, and growth but not survivorship was lower at the lower level. Effects were independent of population of origin and were a manifestation of the environment. Maximum electron transport rates (ETR_m), light saturation parameters (E_k), and maximum quantum yields ($\Delta F/F_m$) provided insight into physiological dynamics; all were lowest at the high edge, but increased when desiccation stress was alleviated by a mock sea-spray treatment. The ETR_m and E_k values of low sporophytes were not as high as the values for mid-sporophytes, despite higher or equivalent nitrogen content, chl *a*, and absorbance, suggesting a trade-off between light-capturing and carbon-fixation capacity. Physiological limitations at upper and lower levels and deleterious desiccation effects at wave-protected sites prevent establishment, thus constraining *Postelsia* to a mid-zone, wave-exposed distribution. Physical conditions related to wave exposure may limit the horizontal distribution of *Postelsia* because this kelp is also found

in areas where mussels are lacking but not on less wave-exposed shores.

Key index words: demography; desiccation; ecology; PAM fluorometry; physiology; *Postelsia palmaeformis*; rocky intertidal; wave exposure

Abbreviations: A, absorbance; α , initial slope of a photosynthesis–irradiance curve; $\Delta F/F_m$, maximum quantum yield of fluorescence; $\Delta F'/F'_m$, quantum yield of fluorescence; E , irradiance; ETR_a , area-specific photosynthetic electron transport rate; E_k , light saturation parameter; ETR_m , maximum area-specific photosynthetic electron transport rate; MHHW, mean higher high water; MLLW, mean lower low water; PAM, pulse-amplitude-modulation; RLCs, rapid light curves

The sea palm, *Postelsia palmaeformis* Ruprecht, is an endemic, intertidal kelp of the northeast Pacific. It has a disturbance-facilitated, annual life history that apparently restricts its distribution to wave-exposed habitats (Dayton 1973, Paine 1979). Algal spores are typically shed in the summer, and their survivorship through the microscopic gametophyte phase is enhanced on the moist and shaded rocky surfaces below intact mussel beds (Blanchette 1996). Juvenile sporophytes typically sprout up in early spring in wave-ripped patches formed in the mussel bed during winter storms (Dayton 1973, Paine 1979, 1988, Blanchette 1996). In the absence of disturbance, mussels preemptively exclude *Postelsia* from space on the shore (Dayton 1973). However, *Postelsia* can and does recruit to habitats where mussels are absent (Paine 1988). However, it is notable that *Postelsia* is absent from wave-protected shores where mussel beds are lacking. It is not clear what determines the vertical limits of *Postelsia* distribution.

A paradigm of intertidal ecology is that lower distributional limits of species are set by biological interactions, while upper limits are set by physical factors (Connell 1972). A parallel paradigm (or perhaps more

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aply put, a perpendicular paradigm) exists for limits along wave exposure gradients, with biological interactions prevailing at wave-protected locations and physical factors prevailing at wave-exposed locations (Menge and Sutherland 1976, 1987). Our observations suggest that *Postelsia* is limited by some combination of desiccation or temperature at the upper edges of its distribution as it is often bleached and eventually sloughs off at high tidal heights. We have also observed that *Postelsia* is smaller in size at three of the four edges of its intertidal distribution: the lower edge, the upper edge, and the wave-protected edge. These observations suggest that additional factors impacting growth and survivorship of *Postelsia* sporophytes work in concert with disturbance and limited spore dispersal to constrain *Postelsia*'s local distribution.

We hypothesized that the smaller stature of *Postelsia* at the three distributional edges (upper, lower, and more protected) was the result of physiological stress. Specifically, we postulated that this reduction in physiological performance likely contributes to its characteristic distribution pattern by reducing growth, survivorship, and reproductive output of individuals living at the edges of the species local distribution. Although it is commonly accepted that physiological stress can reduce the ecological performance of organisms at the edges of their distributions, few studies have documented ecological and physiological performance simultaneously in the field. We used a three-pronged approach to investigate *Postelsia*'s physiological tolerance to conditions encountered at the edges of its natural distribution: physiological measurements, ecological experiments, and demographic monitoring. We measured the physiological performance of *Postelsia* thalli in the high, mid, and low parts of its vertical distribution using a pulse-amplitude-modulation (PAM) fluorometer. We performed a common garden experiment, transplanting individual *Postelsia* from a mid-*Postelsia* zone, wave-exposed site to high-, mid-, and low-level habitats at each of three levels of wave exposure. We also monitored growth and survivorship of transplanted individuals and of naturally occurring individuals within each habitat, as well as the reproductive output in natural populations at each tidal height.

METHODS

Our fieldwork was carried out at two sites just north and south of Depoe Bay, Oregon: Fogarty Creek Point (FC) (44°51'N, 124°03'W) and Depoe Bay South Point (DB) (44°49'N, 124°04'W). Both sites are basaltic headlands fully exposed to ocean waves. *Postelsia* is typically found in multiple clusters of 50 to >100 individuals scattered throughout the mussel bed at these sites. The number of clusters and density within clusters varies markedly from year to year (Whitmer 2002). The transplant experiment was carried out at DB during 1993. Demographic monitoring was carried out at DB in 1993 concurrently with the transplantation experiment and subsequently at FC in 2002 in conjunction with the physiological measurements.

Transplant experiments. To determine if *Postelsia* are able to grow or survive in wave-protected habitats, or just above or

below its naturally occurring intertidal distribution, we transplanted juvenile *Postelsia* from a wave-exposed mid-zone habitat to these locations at DB. Holdfasts of juvenile sporophytes were chiseled from the rocky bench keeping enough rock intact and attached below the haptera to embed it in an epoxy-putty (Z-spar[®]) lined cavity chiseled into the substratum at the desired transplant location. Ninety individuals were transplanted in this manner: 30 each to low, mid, and high tidal heights, and then within each tidal height 10 of the 30 transplants were allocated to wave-exposed, intermediately exposed, or wave-protected locations. Individuals transplanted in the high and low levels or to the wave-protected locations were placed just beyond the distribution of naturally occurring *Postelsia*, while individuals transplanted to mid-tidal heights at exposed or intermediate wave exposures were within the distributional boundaries of extant populations at this site. Furthermore, individuals transplanted to mid-tidal height wave-exposed locations (location of origin) served as manipulation controls. Relative wave exposure was confirmed by measurements of maximum wave forces made using dynamometers (Bell and Denny 1994) for a 24 h period once each month between June and November (Blanchette 1994). Although we do not have any genetic data, it is likely that the transplanted individuals were closely related because *Postelsia* has very limited dispersal and the individuals were taken from one location within a single source population (Coyer et al. 1997).

Demographic monitoring. At DB in 1993 transplanted individuals were censused each month between April and November. Stipe length, basal stipe diameter, number of blades, and length and width of four haphazardly chosen blades were measured for each surviving individual. Thus, survivorship was also monitored monthly as part of each census. For comparative purposes, we also monitored haphazardly selected, naturally occurring individuals adjacent to high, mid, and low transplants during August. In the high and low levels, we selected the highest and lowest distributed individuals, respectively, closest to transplanted individuals.

In 2002 we performed monthly demographic monitoring of the *Postelsia* population at FC, where we also took our physiological measurements. On March 26, we mapped the location of 15 haphazardly selected individuals within the high, mid, and low levels by triangulation from two stainless steel marker bolts just above *Postelsia*'s upper limit and measured the stipe length of each mapped individual. Survivorship, stipe length, and number of blades were measured on April 30, June 10, July 9, July 24, and September 5; basal stipe diameter was measured on the same dates except for April 30. To maintain a robust sample size for growth measurements, we replaced dead individuals each month with the closest individual to the previously mapped individual.

We collected 24 *Postelsia* from the FC site encompassing a range of representative morphologies (e.g. tall and thin, short and stocky, short and thin, etc.) to establish a predictive relationship between morphological measurements and biomass. Stipe basal diameter (cm) is a strong predictor of both wet and dry weight (g) (wet weight^{1/2} = -2.08 + 6.81 × stipe diameter, $r^2 = 0.98$, $P < 0.0001$, $n = 24$; dry weight^{1/2} = 0.72 + 2.39 × stipe diameter, $r^2 = 0.97$, $P < 0.0001$, $n = 24$). Stipe length was not a good predictor of biomass (the maximum r^2 value we obtained in exploring predictive regression equations was 0.87). Variation in sporophyte morphology was such that individuals might vary in height yet have similar biomass and basal stipe diameters (i.e. they could be short and stocky or tall and skinny) especially above ~25 cm stipe length (unpublished data). Therefore, we used the wet mass equation regressed on basal stipe diameter to estimate biomass for each month where we had basal stipe diameter data.

We also estimated reproductive output at FC by measuring the area of the sporophyll tissue on each of three fronds haphazardly selected and collected fronds from each censused plant. *Postelsia* sporophylls appear as a dark stripe along the center of each frond. The presence or absence of unilocular sporangia in the darkened portion of the frond was confirmed by microscopic inspection. Each of the three fronds was placed on an illuminated light table sandwiched between two overhead transparencies. An outline of the dark sporophyll tissue was traced onto the upper sheet with a permanent marker. The acetate-kelp sandwich was then transferred to an optical scanner and the upper sheet slightly displaced so that each frond and its associated sporophyll tracing could be scanned. The area of the whole frond and its sporophyll tissue, if any, were estimated using digital image analysis software (SigmaScan ver. 4.0). We multiplied the average area of the three fronds by the number of fronds on each plant to calculate surface area and estimate reproductive output of each plant. We assumed that spore density and viability did not vary among individuals or levels within the *Postelsia* zone, and that reproductive output is directly proportional to sporophyll area.

Physiological measurements: PAM fluorometry. We used a diving PAM fluorometer (WALZ, Effeltrich, Germany) to assess the physiological state of *Postelsia* thalli across its vertical distribution. During photosynthesis, absorbed light energy may be used for photochemical reactions, dissipated as heat or reemitted as fluorescence. The quantum efficiencies of these three pathways sum to unity, but each one is strongly controlled by ambient irradiance (Falkowski and Raven 1997). Using the PAM fluorometer, we controlled the amount of light reaching the fronds and measured the light re-emitted as fluorescence to generate rapid light curves (RLCs) (Genty et al. 1989, Falkowski and Raven 1997, Kühl et al. 2001). The irradiance sensor of the PAM fluorometer was calibrated against a Li-190 quantum sensor (LiCor, Lincoln, NE, USA) and subsequently used to determine the amount of actinic irradiance reaching the surface of the fronds during RLC measurements. The RLCs were measured by applying a series of increasing actinic irradiances in nine discrete increments lasting 10 s and then determining the quantum yield of fluorescence ($\Delta F'/F_m'$). Thallus absorbance was measured using a leaf clip with the PAM quantum sensor in place below the algal thallus, and then measuring the light reaching the sensor in the presence and absence of the thallus. Thallus absorbance was calculated as the proportion of incident irradiance not passing through the thallus.

We estimated area-specific photosynthetic electron transport rate (ETR_a) (Gorbunov et al. 2001) as the product of the quantum yield of fluorescence and absorbed PAR,

$$ETR_a = \Delta F'/F_m' \times E \times A$$

where $\Delta F'/F_m'$ is the quantum yield of fluorescence, E is irradiance, and A is the absorbance of the frond (Genty et al. 1989, Gorbunov et al. 2001). We fit the data to a standard photosynthesis-irradiance (P-E) model (Webb et al. 1974, Falkowski and Raven 1997), using ETR_a as the response variable to estimate the maximum electron transport rate (ETR_m) and the light saturation parameter (E_k) (fitting method and model are specified below). Absorbance of each frond was measured rather than using the average absorbance because there was obvious variation in pigmentation among fronds from different individuals and tidal heights (K. J. Nielsen, C. A. Blanchette, B. A. Menge, and J. Lubchenco, personal observation). Fronds were haphazardly selected from the top of the crown and measurements were always made about midway along the length of a fully intact frond. Before each light curve, we also measured the maximum quantum yield of fluorescence ($\Delta F'/F_m'$) of each frond after it was dark adapted for 15 min.

We made the fluorescence measurements on emerged individuals over the course of sunny, morning low tides on July 21, 2001 and June 14, 2002. *Postelsia*'s intertidal range at FC is from 0.64 to 1.95 m above mean lower low water (MLLW) and the lower edge of its distribution may have been emerged for as long as ~5.5 h during these extreme low tides. We collected data approximately halfway through the emersion period and again just before the tide returned. On June 14, 2002 we made fluorescence measurements on nine individuals at low and high levels and eight individuals in the middle level of the same population at FC that we used for the demographic monitoring.

On July 21, 2001 we assessed the extent to which sea spray might ameliorate physiological stress in *Postelsia*. We made fluorescence measurements on individuals in the mid and high levels of the same wave-exposed *Postelsia* population described above. To mimic sea spray, we used a spray bottle filled with seawater to spray half the individuals in the high area of the sea palm zone every 10 min after the initial measurements were made. Sprayed individuals were a randomly selected subset of nine of the initial 19 high-level sporophytes. However, due to the speed with which the returning tide and waves threatened us and proceeded to wet the sporophytes, final measurements were only completed on a total of 11 individuals: seven non-sprayed and four sprayed ones.

Pigment, C, and N content. We measured chl *a*, C, and N content of *Postelsia* thalli across its vertical distribution at FC on September 5, 2002 at low, mid, and high intertidal zones. We sampled a single frond from 10 haphazardly selected individuals in each zone. We used a paper hole punch to collect tissue samples for pigment analyses. We sampled the center portion of the frond, which was dark and clearly reproductive, as well as vegetative tissue near the meristem region of the frond just above the stipe. Samples for pigment analyses were frozen in liquid nitrogen in the field, returned to the laboratory, and stored at -80°C until the high-performance liquid chromatography (HPLC) analysis was performed. We extracted pigments by homogenizing the samples on ice using ground glass tissue homogenizers in 1 mL of chilled 90% HPLC grade acetone. The homogenates were transferred to 15 mL centrifuge tubes. The homogenizer units were rinsed three times with 0.5 mL of chilled 90% acetone and the rinses were combined with the samples. The samples were brought to a final volume of 3 mL, extracted at -80°C for 24 h, and then hand delivered to the analytical lab at the College of Oceanic and Atmospheric Sciences, Oregon State University, where HPLC pigment analyses were performed. We expressed chl *a* content on an area-specific basis.

The remainder of each frond was stored in a cooler on ice for transport back to the lab and then stored at -20°C until being ground for C and N analyses. We separated vegetative and reproductive tissues, oven-dried the samples, and then ground them with a mortar and pestle in liquid nitrogen. C and N analyses were performed by the Marine Sciences Institute analytical lab (University of California, Santa Barbara, CA, USA).

We also retained some of the remaining tissue from each frond to calculate the wet and dry weights per unit area of frond, but we did not separate vegetative and reproductive tissues. We used a rectangular section from just below the middle of the frond that included reproductive and vegetative tissue. We measured the area of each tissue sample while wet with a ruler. Wet weights were obtained after damp drying fronds to remove surface moisture and dry weights were obtained after drying to constant weight at 60°C .

Statistical analyses: transplant experiments. We used one-way ANOVAs for each date to analyze variation in growth with respect to tidal height and wave exposure. Repeated measures analysis was not performed because mortality reduced

sample sizes over time. In all cases the distribution of residuals was checked by inspection of residual plots. Transformations were used if necessary to normalize the distribution of residuals.

Demographic monitoring. Survivorship data were analyzed using Kaplan–Meier univariate survival analysis (JMP[®] ver. 4). If an individual died between census dates, we assumed the date of demise was halfway between census dates. We compared the stipe lengths, total photosynthetic surface area, and biomass of transplanted and naturally occurring individuals at each tidal height using ANOVA on data from the August census, with the exception of the high zone where we used data from July as that was the last date for which there were surviving individuals from the transplant experiment. All three metrics were log transformed before analysis to control for heteroscedasticity. For the demographic monitoring performed in 2001–2002 at FC, stipe lengths, total photosynthetic surface area, and biomass and reproductive output were all analyzed by ANOVA for each time period separately. Repeated measures analysis was not carried out because mortality reduced sample sizes over time and we added new individuals into our sample at each sampling interval to keep samples sizes constant over time. In all cases the distribution of residuals was checked by inspection of residual plots. Transformations were used if necessary to normalize the distribution of residuals.

Physiological measurements. RLCs were modeled as P–E curves (Jassby and Platt 1976) (substituting ETR_a as a measure of photosynthetic rate) using the standard exponential function: $ETR_a = ETR_m[1 - (e^{-\alpha E/ETR_m})]$ (Webb et al. 1974, Falkowski and Raven 1997), where ETR_m is the maximum electron transport rate and $E_k = \alpha/ETR_m$. Curves were fit using Proc NLIN in SAS (ver. 8.02) and yielded our estimates of ETR_m and E_k with 95% confidence intervals. A term for photoinhibition was not included in the model because (1) raw data plots did not show evidence of downturn at high irradiances and (2) models failed to converge in most cases when this parameter was included. Hougaard’s measure of skewness was examined to assess the statistical properties of the parameter estimates (SAS 1989). Most estimates were close to linear; thus statistical inferences for these parameters are not biased (SAS 1989). A few parameters exhibited some skewness and are interpreted with caution. None were deemed excessively non-linear (e.g. skewness was $\ll 1.0$ in most cases and <0.28 in all cases) (SAS 1989).

Pigment, C, and N content data were analyzed by ANOVA (JMP[®] ver. 4). Tidal height and tissue type were treated as fixed factors. A full model with interaction terms was fit for each response variable, and the distribution of residuals was checked by inspection of residual plots and goodness of fit to a normal distribution. Transformation was not required to meet ANOVA assumptions for any of the response variables.

RESULTS

Transplant experiment and in situ monitoring at DB. Survivorship of transplanted *Postelsia* thalli was lowest at high and wave-protected sites (Fig. 1, A and B). By August all high and wave-protected transplants had died. Survivorship differed among tidal heights with middle-of-zone plants surviving the longest (median survival times are 14, 71, and 42 days in the high, mid, and low areas of the *Postelsia* zone, respectively; Wilcoxon test, $\chi^2 = 5.87$, $P = 0.0531$; log-rank test, $\chi^2 = 6.94$, $P = 0.0311$; Note. The log-rank test emphasizes differences over longer times, whereas the Wilcoxon test emphasizes

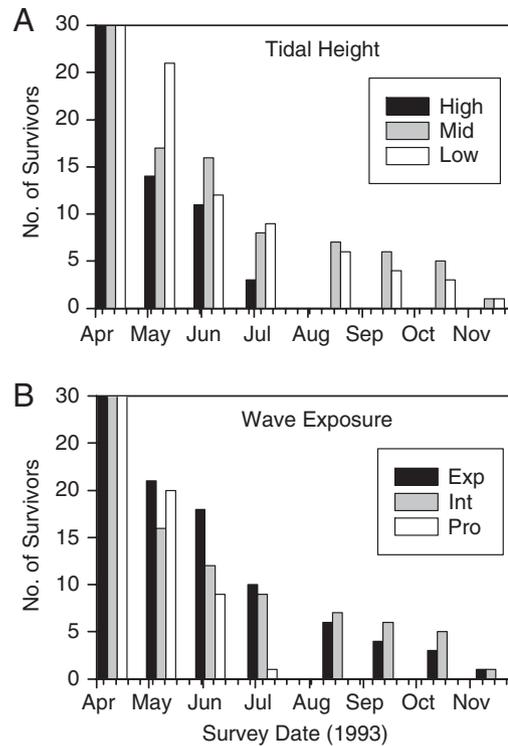


FIG. 1. *Postelsia* survivorship. Proportional survivorship of transplanted *Postelsia*. (A) High, mid, and low intertidal zones (pooled across wave exposure) and (B) wave-exposed, intermediate, and protected zones (pooled across tidal heights) at Depoe Bay South Point during 1993; 30 individuals were transplanted into each zone and wave exposure.

initial differences (JMP 2001)). Statistical analysis of the wave exposure data suggests that survivorship also varied among the three different wave exposures over the long term, with wave-protected individuals having the lowest survivorship (median survival times are 71, 42, and 42 days in the wave-exposed, intermediate, and protected areas, respectively; Wilcoxon test, $\chi^2 = 3.53$, $P = 0.1711$; log-rank test, $\chi^2 = 6.72$, $P = 0.0347$).

Growth. At the start of the experiment, transplanted individuals had stipe lengths of 3.8 ± 0.2 (95% CI) cm, a total photosynthetic surface area of 102.2 ± 6.5 (95% CI) cm^2 , and a biomass of 2.9 ± 0.2 (95% CI) g wet weight. There were no differences in these characteristics among the different transplant locations at the start of the experiment except for stipe length in the wave exposure comparisons (Tables 1 and 2). Sporophytes transplanted to the intermediate wave exposure location were slightly shorter (average stipe length = 3.4 ± 0.3 (95% CI) cm) than sporophytes transplanted to the wave-exposed and protected locations (Table 2, Fig. 3).

Tidal level in the *Postelsia* zone had a large effect on growth. *Postelsia* thalli transplanted to low and high levels did not grow as tall as those transplanted into the mid-zone (Fig. 2A, Table 1). Although high-level sporophytes grew slightly in the first 2 months, increasing

TABLE 1. ANOVA of growth by tidal height.

Date	df	SS	F	P-value
<i>Stipe length</i>				
April 10, 1993	2, 87	280.5	1.67	0.1944
May 8, 1993	2, 54	10,607	18.19	<0.0001
June 5, 1993	2, 38	17,044	11.25	0.0002
July 5, 1993	2, 17	28,280	7.28	0.0052
August 17, 1993	2, 11	68,956	38.37	<0.0001
September 15, 1993	1, 8	54,722	26.59	0.0009
October 16, 1993	1, 6	36,053	12.76	0.0118
<i>Photosynthetic surface area</i>				
April 10, 1993	2, 87	2854	1.49	0.2320
May 8, 1993	2, 46	120,122	5.66	0.0064
June 5, 1993	2, 32	4,032,380	7.56	0.0021
July 5, 1993	2, 16	5,584,414	6.07	0.0109
August 17, 1993	1, 11	577,219	1.20	0.2963
September 15, 1993	1, 8	1,413,256	2.54	0.1496
October 16, 1993	1, 6	226,515	0.45	0.5261
<i>Ln (biomass)</i>				
April 10, 1993	1, 87	2.37	1.25	0.2926
May 8, 1993	2, 54	10.35	8.32	0.0007
June 5, 1993	2, 36	6.49	4.24	0.0222
July 5, 1993	2, 17	5.80	4.49	0.0272
August 17, 1993	1, 11	0.10	0.27	0.6124
September 15, 1993	1, 8	0.14	2.31	0.1672
October 16, 1993	1, 6	0.15	1.66	0.2448

in length, photosynthetic surface area, and biomass, they remained smaller in photosynthetic surface area and biomass than either mid- or low-level sporophytes (Fig. 2, Table 1) until they all died sometime before August. Average stipe length and photosynthetic surface area of mid-zone sporophytes did not increase after August (Fig. 2, A and B). Photosynthetic surface area began to decline after August (Fig. 2B). Low-level sporophytes remained shorter than mid-level sporophytes through

TABLE 2. ANOVA of growth by wave exposure.

Date	df	SS	F	P-value
<i>Stipe length</i>				
April 10, 1993	2, 87	805	5.16	0.0076
May 8, 1993	2, 54	3120	3.63	0.0333
June 5, 1993	2, 36	3692	1.64	0.2088
July 5, 1993	2, 17	4702	0.71	0.5075
August 17, 1993	1, 11	3	0.00	0.9855
September 15, 1993	1, 8	749	0.09	0.7780
October 16, 1993	1, 6	3674	0.45	0.5287
<i>Photosynthetic surface area</i>				
April 10, 1993	2, 87	2220	1.15	0.3223
May 8, 1993	2, 46	14,083	0.54	0.5836
June 5, 1993	2, 32	3,194,397	5.45	0.0092
July 5, 1993	1, 17	1043	0.00	0.9709
August 17, 1993	1, 11	73,066	0.14	0.7164
September 15, 1993	1, 8	2,086,677	4.42	0.0686
October 16, 1993	1, 6	413,819	0.88	0.3839
<i>Ln (biomass)</i>				
April 10, 1993	2, 87	1.72	0.89	0.4111
May 8, 1993	2, 54	1.12	0.71	0.4986
June 5, 1993	2, 36	7.43	5.02	0.0119
July 5, 1993	2, 17	6.79	5.78	0.0122
August 17, 1993	1, 11	0.42	1.25	0.2875
September 15, 1993	1, 8	0.00	0.01	0.9363
October 16, 1993	1, 6	0.03	0.29	0.6099

TABLE 3. ANOVA comparing transplanted and naturally occurring *Postelsia*.

Source	df	SS	F	P-value
<i>Ln (stipe length)</i>				
Tidal height	2	15.76	102.9	<0.0001
Group	1	0.82	10.8	0.0022
Tidal height \times group	2	0.97	6.4	0.0042
Error	38	2.91		
$r^2 = 0.89$				
<i>Ln (photosynthetic surface area)</i>				
Tidal height	2	42.75	74.0	<0.0001
Group	1	0.02	0.1	0.7882
Tidal height \times group	2	0.36	0.6	0.5391
Error	38	10.98		
$r^2 = 0.83$				
<i>Ln (biomass)</i>				
Tidal height	2	42.94	75.9	<0.0001
Group	1	4.11	14.5	0.0005
Tidal height \times group	2	2.36	4.2	0.0231
Error	38	10.74		
$r^2 = 0.87$				

November (Fig. 2A), but had similar photosynthetic surface area and biomass (Fig. 2, B and C).

The most pronounced effect of wave exposure on transplanted sporophytes was the decline in all three metrics of growth for wave-protected transplants in June and July (Fig. 3, Table 2) just before they all died (Fig. 1B). Although the intermediate wave exposure sporophytes started out shorter than the others, all three groups converged in length by June. By August, stipe length, photosynthetic surface area, and biomass of the remaining sporophytes had either leveled off or began to decline at intermediate and exposed locations (Fig. 3).

The size of transplanted individuals was similar to the size of naturally occurring individuals within the same habitat in August when we censused both simultaneously. Growth was apparently maximized (based on the size measurements) in the mid level and lowest in the high level for all three metrics (stipe length, photosynthetic surface area, and biomass) (Fig. 4, Table 3). In the mid and high levels transplanted individuals were indistinguishable from naturally occurring individuals for all three metrics, but in the high level transplanted individuals had somewhat longer stipes and greater biomass than naturally occurring individuals (Fig. 4, A and C, Table 3).

In situ monitoring at FC. Survivorship decreased with increasing tidal height, matching the pattern of survivorship documented in the transplant experiments. Analysis of the survivorship data suggests that low tidal level *Postelsia* thalli survived longer than mid- or high-level thalli, but the results were only marginally significant (median survival time is 120 days in the low level vs. 55 days in mid and high levels; Wilcoxon test, $\chi^2 = 5.68$, $P = 0.059$; log-rank test, $\chi^2 = 2.29$, $P = 0.318$).

Growth. Stipe lengths increased between April and September, and differed among tidal heights at each

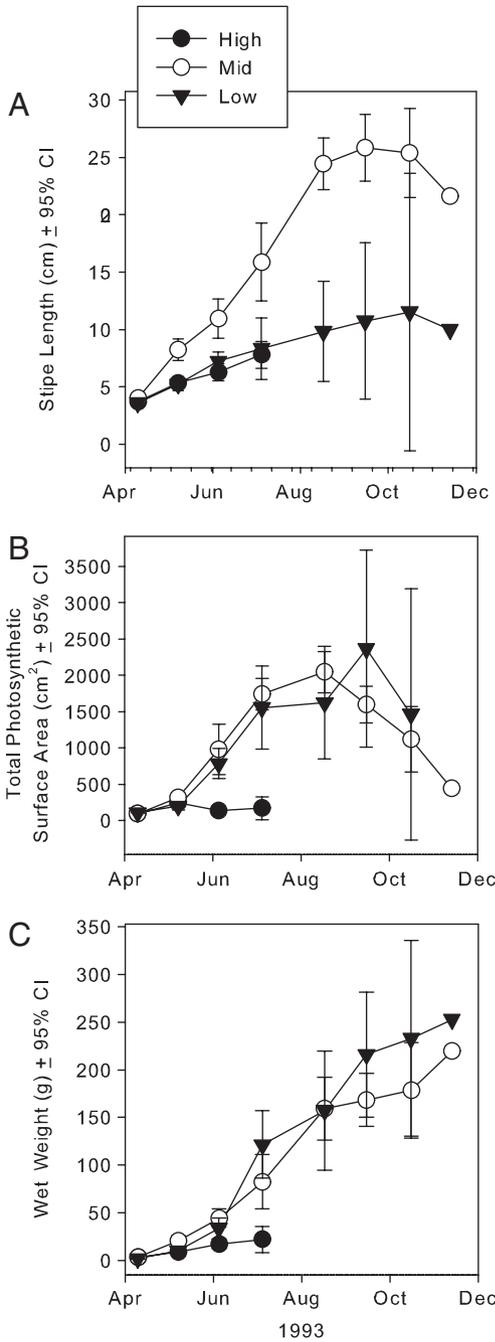


FIG. 2. Variation in growth of transplanted *Postelsia* at high, mid, and low tidal heights. (A) Stipe length, (B) total photosynthetic surface area of blades, and (C) biomass.

census date (Fig. 5A; $P < 0.0001$ for all dates). The average stipe length for mid-level sporophytes was always longest and for high-zone plants was always shortest (Fig. 4A). However, by June mid- and low-level sporophyte stipe lengths converged (Fig. 4A).

The total photosynthetic surface area varied with tidal height in June, July, and August, but not in September (Fig. 5A; June: $P = 0.0089$, $F = 5.78$, $df = 2, 24$; July: $P = 0.0047$, $F = 6.18$, $df = 2, 38$; August:

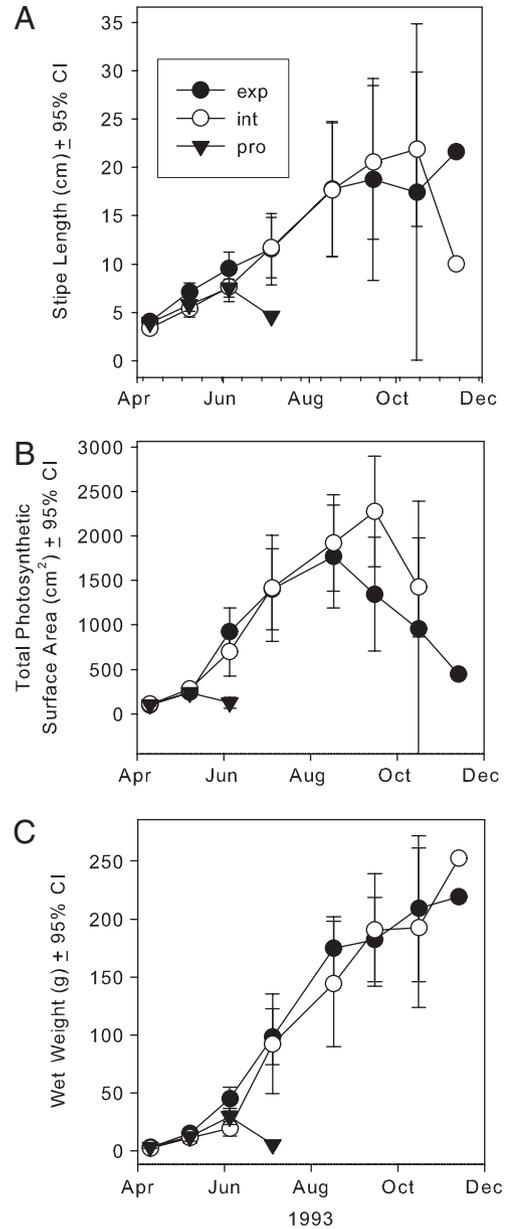


FIG. 3. Variation in growth of transplanted *Postelsia* at wave-exposed, intermediate, and protected sites. (A) Stipe length, (B) total photosynthetic surface area of blades, and (C) biomass.

$P = 0.0162$, $F = 4.61$, $df = 2, 38$; and September: $P = 0.3514$, $F = 1.10$, $df = 2, 20$). In all months mid-level plants had the highest average surface area, and were greater in area than high-level sporophytes except in September (Fig. 5A). Low- and mid-level sporophytes continued to increase in surface area through August, but then either declined or remained the same through September (Fig. 5B). Only high-zone sporophytes continued to increase in surface area through September (Fig. 5B).

The average biomass of sporophytes increased over the summer through July (Fig. 5C). Mean biomass differed among zones for each census date except for the

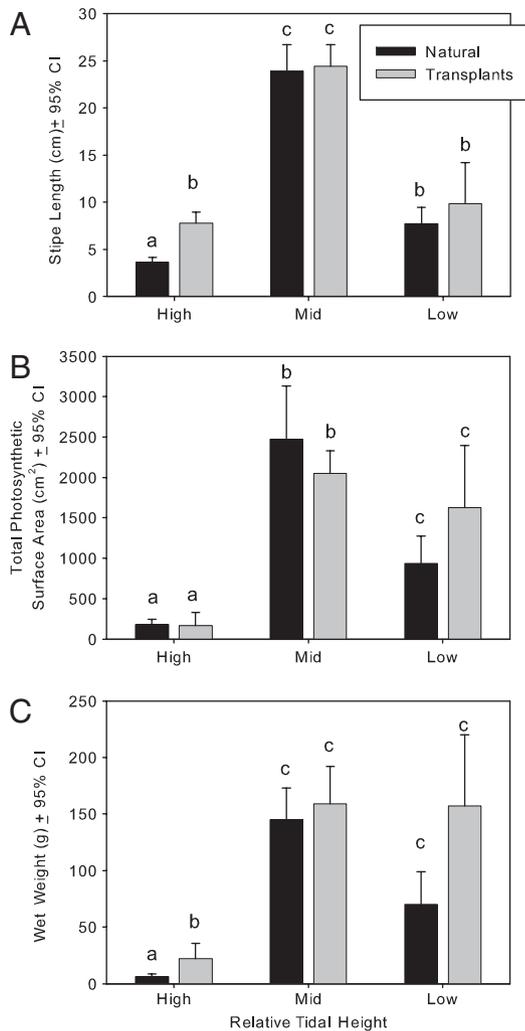


FIG. 4. Comparison of naturally occurring and transplanted *Postelsia* at Depoe Bay during August 1993 (except high-zone transplants which were last measured in July 1993 and did not survive to the August census date). (A) Stipe length, (B) total photosynthetic surface area, and (C) biomass. Lowercase letters that differ indicate statistically significant differences among groups.

final one in September (June: $P < 0.0001$, $F = 17.40$, $df = 2, 37$, $r^2 = 0.48$; July: $P < 0.0001$, $F = 12.51$, $df = 2, 39$, $r^2 = 0.39$; August: $P < 0.0001$, $F = 17.06$, $df = 2, 40$, $r^2 = 0.46$; and September: $P = 0.2414$, $F = 1.53$, $df = 2, 19$, $r^2 = 0.14$). In June and July, the average biomass of high tidal level plants was less than that of low- or mid-level plants (Fig. 5C). By August, mid-level plants had the highest average biomass and average biomasses in all three levels were different (Fig. 5C). By September, the average biomass of plants in each level had converged (Fig. 5C).

Reproductive output. None of the sporophytes from the FC population had any sporophyll tissue until early July, but all plants had some sporophyll tissue by September. Only $50\% \pm 27\%$ (mean and 95%CI) of the high-level sporophytes had developed sporo-

phylls by the end of July. The area of sporophyll per individual varied with tidal height in July, August, and September (Fig. 5D; July: $P = 0.0162$, $F = 4.61$, $df = 2, 38$; August: $P = 0.0001$, $F = 11.61$, $df = 2, 41$; September: $P = 0.0358$, $F = 3.95$, $df = 2, 20$). Sporophyll area continued to increase through September for mid-level sporophytes, but low-level sporophytes reached a plateau by the end of July (Fig. 5D). Mid-level sporophytes had higher sporophyll area than both high and low tidal level plants in August and September (Fig. 5D). High-level sporophytes had lower sporophyll area than low- or mid-level sporophytes in July and August (Fig. 5D).

Physiological measurements: fluorometry. During 2002, the maximum electron transport rate (ETR_m), the RLC parameter analogous to maximum photosynthetic rate, increased over time across all tidal heights (Fig. 6A). Light activation of the Calvin cycle enzyme RUBISCO, possibly in concert with increasing temperature, is the likely cause of the increase in ETR_m between early and later morning measurements. The ETR_m rates declined with increasing tidal height early during the day (Fig. 6A), but later on mid-level sporophytes had the highest ETR_m , followed by low-level sporophytes and then the high-level sporophytes (Fig. 6A). The initial negative association between ETR_m and tidal height may reflect decreased photosynthetic capacity due to longer emersion and desiccation experienced by sporophytes at higher tidal heights. The light saturation parameter, E_k , followed the same trend as ETR_m increasing over time (Fig. 6, A and B), but clear differences among levels were only apparent early during the low tide, when high level sporophytes had a lower E_k than either mid- or low-level sporophytes (Fig. 6B). Maximum quantum yields ($\Delta F/F_m$) declined over time, most notably in the high level (Fig. 6C; $P = 0.0259$, $F = 4.30$, $df = 2, 23$). Thal- lus absorbance also declined with increasing tidal height (Fig. 6D; $P = 0.0426$, $F = 3.63$, $df = 2, 23$). Physical stresses at high tidal elevations, including longer periods of exposure to desiccating and high light conditions, result in algal thalli with reduced pigmentation and capacity to absorb light, as well as reduced photosynthetic capacity (measured as the maximum quantum yield of fluorescence).

RLCs were only done in the mid and high tidal levels in 2001, but trends in the parameter values derived from the P-E models fit to the curves with respect to time and tidal height were the same as in 2002, except that differences were more pronounced overall and sporophytes appeared to be experiencing greater physiological stress during 2001 (Figs. 6 and 7). Maximum photosynthetic rate (ETR_m), the light saturation parameter (E_k), and maximum quantum yield of fluorescence ($\Delta F/F_m$) all increased over time during low tide, but decreased with increasing tidal height (Fig. 7, A–C). Being sprayed with seawater between the two sets of measurements ameliorated some of the physiological stress; high-level sporophytes sprayed with seawater had higher ETR_m , $\Delta F/F_m$, and E_k than those

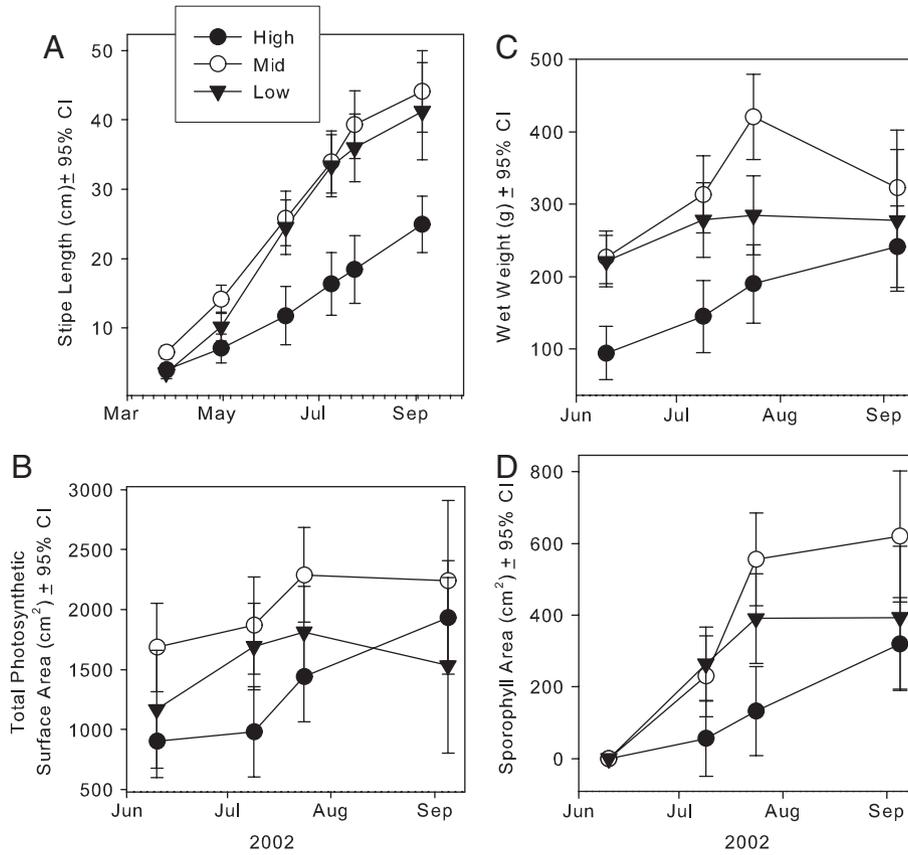


FIG. 5. Variation in growth and reproductive output of naturally occurring *Postelsia* at high, mid, and low tidal heights. (A) Stipe length, (B) total photosynthetic surface area of blades, (C) biomass, and (D) sporophyll area.

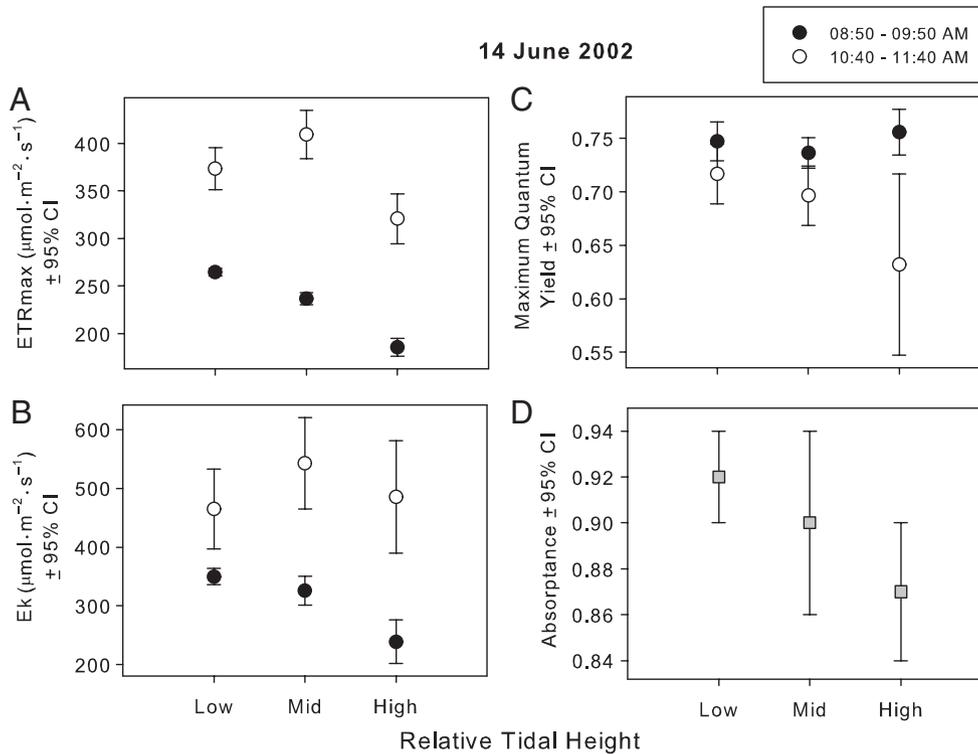


FIG. 6. Field fluorescence and absorbance measurements June 14, 2002 at Fogarty Creek Point. (A) Maximum area specific electron transport rate (ETR_m), (B) light saturation parameter (E_k), (C) maximum quantum yield ($\Delta F/F_m$) measured after 15 min of dark adaptation in a leaf clip, and (D) thallus absorbance. Parameter estimates in A and B are derived from fitted rapid light curves (see Methods for details).

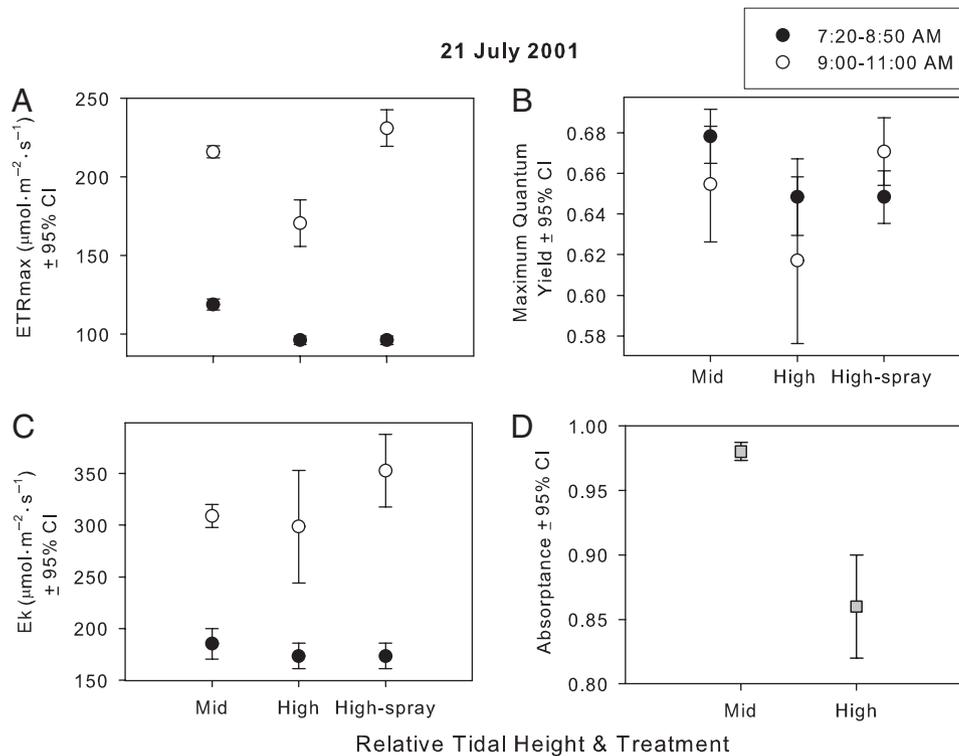


FIG. 7. Field fluorescence and absorbance measurements July 21, 2001 at Fogarty Creek. (A) Maximum area-specific electron transport rate (ETR_m), (B) light saturation parameter (E_k), (C) maximum quantum yield ($\Delta F/F_m$) measured after 15 min of dark adaptation in a leaf clip, and (D) thallus absorbance. Parameter estimates in A and B are derived from fitted rapid light curves (see Methods for details). After the first set of measurements, half of the high-zone individuals were randomly assigned to the salt-water spray treatment.

that were not sprayed (Fig. 7, A–C). In 2001 there was strong variation in thallus absorbance among levels (Fig. 7D; $P < 0.0001$, $F = 70.48$, $df = 1, 18$). This difference was more pronounced than what we observed in 2002 (Figs. 6D and 7D).

Chl *a*, *C*, and *N* content, specific weights. The amount of chl *a* in the fronds varied with both tidal height and tissue type (Fig. 8A; tidal height \times tissue type interaction: $P = 0.0076$, $F = 13.96$, $df = 2, 53$). The chl *a* content was much higher in sporophyll tissues across all tidal heights and lowest in the high level for both tissue types (Fig. 8A). Sporophyll tissue of mid-level sporophytes had the highest chl *a* content (Fig. 8A).

The C:N ratios varied with tidal height, but not with tissue type (Fig. 8B; $P < 0.0001$, $F = 19.25$, $df = 1, 54$). High-level plants had the highest ratios, while low-level plants had the lowest ratios (Fig. 8B). However, percent nitrogen by dry weight (%N) varied with both tidal height and tissue type ($P < 0.0001$ for both). We found higher nitrogen content in sporophyll than vegetative tissues (2.53% vs. 2.14% N). The area-specific weights of *Postelsia* fronds (including both sporophyll and vegetative tissues) were lower in the high level than in the mid or low levels (Fig. 8C).

DISCUSSION

Through a combination of approaches we have explored the factors that serve to constrain the local dis-

tributional limits of *Postelsia*. Using common garden transplant experiments, we were able to assess the effects of different environmental conditions on the ecological performance of sporophytes. We compared the ecological performance of transplanted individuals to those naturally occurring in or near these habitats at the edges of *Postelsia*'s local distribution to separate the role of environment from population of origin. We complemented these experimental and demographic measurements with a suite of physiological measurements during periods of emersion to investigate the role of physiological stress in mediating longer-term ecological performance. During the course of these experiments, we observed morphological variation between study sites that merits further investigation, but this variation is likely confounded by interannual differences making absolute comparisons difficult to interpret in this study. Below we discuss the environmental factors likely to constrain *Postelsia* along the three edges of its distribution.

High tidal level. Kelps are common members of low intertidal zone communities at temperate latitudes. *Postelsia* are unusual kelps in that they occur in and above the mussel bed at mid to high tidal heights (between 0.64 and 1.95 m above MLLW at Fogarty Creek) with their upper limit not far below MHHW (mean higher high water) (2.4 m). Thus, these sporophytes spend a considerable portion of the day emersed and subject to a combination of desiccation,

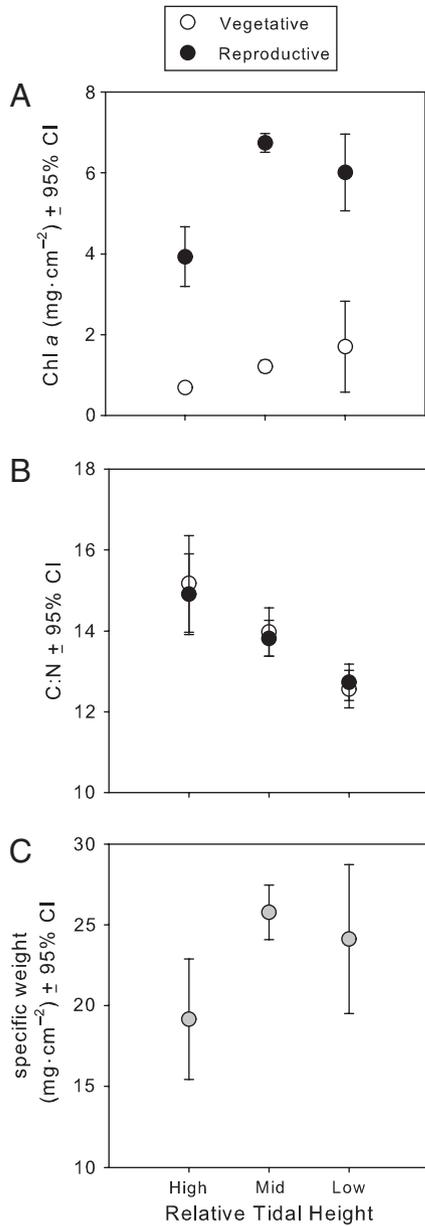


FIG. 8. Frond characteristics of *Postelsia* at high, mid, and low tidal heights. Vegetative and reproductive portions were sampled for each frond and analyzed to determine (A) chl *a* content and (B) C:N ratios. (C) Area-specific weights of whole fronds.

temperature, and insolation stresses. In our demographic monitoring of both the transplant experiment and naturally occurring high-level sporophytes, we observed consistently high mortality, with more than 50% of individuals perishing before reaching reproductive maturity. High-level sporophytes also grew more slowly, having shorter stipe lengths and less total photosynthetic surface area resulting in lower total biomass. For the sporophytes that survived, onset of reproduction was delayed and total reproductive output, as indexed by sporophyll area, was reduced. The combination of high mortality and reduced reproduc-

tive output suggests that there is a large decline in ecological performance for sporophytes in the high intertidal zone.

Physiological parameters estimated from the RLCs show that high tidal level sporophytes have lower maximum electron transport rates (ETR_m), and a tendency toward lower maximum quantum yields ($\Delta F/F_m$), and light saturation parameters (E_k) than either mid- or low-level sporophytes. Absorbance and chl *a* are also lower in the high zone, suggesting either acclimation to high light (i.e. a sun-adapted phenotype) or photodegradation of chl *a*. However N content is also low both as a percentage of dry weight and relative to C content. These lines of evidence suggest that high-level sporophytes cannot marshal sufficient resources to efficiently utilize the solar radiation they receive and absorb. If low chl *a* and absorbance represented a sun-acclimated phenotype, we would expect to also see higher ETR_m . Desiccation stress generally reduces the photosynthetic efficiency of all photosynthetic organisms and provides an opportunity for light dissipation mechanisms to become overwhelmed and consequently for photodamage to ensue. Low N content further compromises the ability of high-level sporophytes to repair or replace damaged biomolecules involved in essential photosynthetic pathways. Reduction in chl *a* is one way to reduce the amount of light absorbed and can be viewed as a protective or compensatory mechanism analogous to sun-acclimated leaves in higher plants (Lambers et al. 1998). However when coupled with low N, reduced photosynthetic efficiency, and reduction in long-term growth and reproduction, it suggests the compensatory capacity of this organism has been surpassed.

Protected zone. *Postelsia*'s restriction to wave-exposed habitats has been hypothesized to be due to its dependence on free space created by wave-mediated disturbances to the mussel bed. However, *Postelsia* does not occur in more wave-protected areas even when mussel beds are absent and free space is available. Our transplant experiment to more wave-protected habitats demonstrated that space is not the only requisite for survival and growth of *Postelsia* sporophytes; environmental conditions in wave-protected habitats apparently are not optimal either. All sporophytes transplanted to the wave-protected location died before August, with more than 50% perishing before the end of June. Although some sporophytes transplanted to an intermediate wave exposure managed to survive the summer, more than 50% had also died by the end of June. Surprisingly, growth of intermediate wave exposure transplants did not decline compared with sporophytes transplanted to more wave-exposed locations in April or May, but total photosynthetic surface area began to decline in June, and wet weight followed suit by July.

Although we did not make physiological measurements comparing performance at different wave exposures, we suggest that desiccation plays a role as wave splash is reduced in wave-protected locations.

The increases in physiological performance (as measured by the parameters $\Delta F/F_m$, ETR_m , E_k) from our intermittent spraying experiment on high tidal height individuals all support this line of reasoning if we can reasonably assume that sea spray is less prevalent at these locations. Wing and Patterson (1993) have demonstrated that optimal light utilization and highest photosynthetic rates occur when *Postelsia* fronds are shaken during turbulent flow creating light flecks at a frequency close to the periodicity of the wave frequency on wave-exposed benches. Because all sporophytes died at wave-protected locations (regardless of tidal height) by August and all high-level sporophytes also died (regardless of wave exposure) by August, we suspect that a combination of desiccation and light limitation (a limitation stress *sensu* Davison and Pearson 1996) contributes to the exclusion of *Postelsia* sporophytes from wave-protected habitats. However, in the absence of experimentation we cannot determine the relative importance of these putative limiting factors.

Low tidal level. Perhaps the most intriguing result of this study was the reduction in physiological and ecological performance of sporophytes at the lower edge of the *Postelsia* zone. Low-level sporophytes did not suffer a dramatic decrease in survivorship like high or protected zone sporophytes, but did experience declines in growth and reproductive output (relative to the mid level) that were also reflected in our physiological measurements. In the transplant experiment, low-level sporophytes were much shorter than mid-level sporophytes. Naturally occurring sporophytes also had lower photosynthetic surface area and biomass than mid-level sporophytes. In addition, the reproductive output of low tidal level sporophytes was lower than for mid-level sporophytes. Although these differences were not as striking as in the high tidal level, they are surprising given that N and chl *a* content is high and desiccation stress was presumably negligible relative to higher tidal height locations. Furthermore, it suggests that the lower limit of *Postelsia*'s distribution might be set by physiological stress rather than biological interaction.

Physiological evidence suggests that despite high absorptance, N content, and lower desiccation potential (proximity to wave splash and reduced emersion times) during low tide, maximum electron transport rates (ETR_m), and the light utilization capacity (E_k) of low tidal level thalli were not able to shift up over the low tide interval to the extent observed in mid-level sporophytes (Fig. 6, A and B). We would expect to see shift-ups in ETR_m and E_k over the course of the morning as some of the enzymes in the carbon reduction cycle are light activated. This inability to up-regulate ETR_m and E_k in combination with high N, chl *a*, and absorptance and no difference in maximum quantum yields suggests a resource trade-off between light-capturing and carbon-fixation capacity, a trade-off commonly observed between sun and shade acclimated leaves in higher plants (Lambers et al. 1998). Based on this evidence, we deduce that low tidal level sporo-

phytes experience lower average light levels while submerged than their higher level neighbors due to the attenuation of light through the water column yielding a "shade" phenotype. We speculate that because low-level *Postelsia* thalli are shade acclimated to maximize light capture while underwater, they are ill-equipped to cope with the relatively higher light environment upon emersion, resulting in lower total carbon fixation and consequently lower growth and reproductive output.

This is an intriguing result especially when considered in light of recent work on *Fucus gardneri* by Williams and Dethier (2005) showing that variation in carbon acquisition associated with putative intertidal stress gradients while emersed pales in comparison with the ~2 orders of magnitude greater photosynthetic rate when *Fucus* is immersed. Adopting a strategy that optimizes phenotype to typical submerged conditions rather than attempting to mitigate adverse water conditions makes sense in terms of energy allocation and is consistent with their results. However, finding evidence of a cost associated with that strategy that appears to be a response to emersion is at odds with their results. However, there are considerable differences in the life histories and habitat characteristics of these two species (e.g. annual vs. perennial, presence vs. absence of a free-living, microscopic gametophyte stage, wave-exposed vs. wave-protected, etc.); we speculate that different life history and environmental constraints may yield different physiological solutions to balancing an intertidal alga's carbon budget. At present we cannot say if taxon-specific differences in physiological strategies might explain this apparent contradiction, but we consider this an area ripe for future investigations.

CONCLUSIONS

Postelsia is thought to thrive on mid-zone, wave-exposed shorelines due in part to limited dispersal and a disturbance-dependent life history that depends on waves to remove its primary competitor, the California mussel, *Mytilus californianus* (Dayton 1973, Paine 1979). Here we document additional physiological and ecological limitations further contributing to *Postelsia*'s restricted local distribution in the absence of mussel competitors. Physiological stresses associated with emersion appear to limit *Postelsia*'s upper distribution through declines in growth, survivorship, and reproductive output. Interestingly, both physiological and ecological performance decline at the lower edges of *Postelsia*'s range also expressed as reductions in growth and reproductive output, but not survivorship. Because low tidal level sporophytes have high N and chl *a* content relative to high-zone sporophytes, we postulate that low-level sporophytes are limited by light. In wave-protected locations the lack of sea spray and reduced water motion combine to create physiological stress reducing survivorship. We predict that the combined effects of several of these factors along with re-

stricted spore dispersal and habitat availability are likely to limit *Postelsia*'s geographic distribution at the large scale.

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