THE EFFECTS OF DENSITY AND LIGHT AVAILABILITY ON THE STIPE MORPHOLOGY OF *Pterygophora californica*

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Previous research has suggested that the morphology of kelps varies with plant density and light intensity, obscuring possible relationships between morphology and age, but holding out the potential for using these plants as indicators of underwater climate. *In situ* transplant experiments were used to test the effects of light availability and density on the morphology of *Pterygophora californica* stipes. Variation in light had no significant effect on stipe growth. Variation in density significantly affected growth: stipes at high density grew slower in basal diameter and faster in stipe length than those at lower densities. This may lead to increased mortality via dislodgement. Plant density may affect tissue deposition rates along the axis of the stipe, resulting in ring size variations. Light and density measurements of this study are compared to those of another study at the same location. Appreciable variation (from 1-3% to 8%) in relative light intensity, but not in density is noted suggesting that the portion of light removed by a subsurface canopy of adult *P. californica* is a function of canopy size or cover as well as individual density.

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Introduction:

It is well documented that both density dependent and independent factors act to structure plant communities. The affects of these factors are ultimately the result of changes at the individual level, which are then translated through the population and the community (Harper, 1977; Antonovics & Levin, 1980; Schiel & Foster, in press). Density independent factors such as wave exposure, season, depth, temperature, and light have all been shown to affect algal growth (Sundene, 1964; Chapman, 1973; Gerard & Mann, 1979; Kain, 1979; Cousens, 1982; Dean & Jacobson, 1984). Density dependent effects are ultimately a result of variations in other factors such as water motion, nutrient distribution, and light availability. Density studies involving terrestrial and marine plant populations have focused on the relationship between density and the growth, recruitment, and survivorship of individuals (Black, 1974; Jupp & Drew, 1974; Harper, 1977; Schiel & Choat, 1980; Lonsdale & Watkins, 1982; Hutchings & Budd, 1981a,b; Cousens & Hutchings, 1983; Schiel, 1985a,b). Results of terrestrial plant studies suggest that high densities adversely affect the individual, but the few studies involving marine algal species have revealed mixed results (Schiel & Foster, in press).

The effects of density on algal growth are most often measured

through changes in biomass, or total length of the individual. However, measuring density dependent effects through changes in biomass alone can be misleading, since biomass is a cumulative result of pre-treatment and treatment conditions (Jupp, 1972). To properly assess density effects through changes in biomass, individuals must be recruited at the experimental densities. Using growth in one dimension as a measure of density effects can also be deceptive because algal growth in one direction may be at the expense of growth in other directions (Kain, 1976). Density effects on growth are better assessed with measurements in several dimensions.

My interest in density dependent effects stems from earlier research indicating that the rings present in the stipe of Pterygophora californica and some other members of the Laminariales can be used to indicate age (Mac Millan, 1902; Kain, 1979; John, 1969; Dayton et al., 1984; DeWreede, 1984; Hymanson et al., in prep.). The ability to age individuals is a powerful tool which permits the description and comparison of populations in terms of age specific events such as age at reproductive maturity, growth rate through time, and age at death. However, variations in ring morphology which affect the accuracy of ring counts are known to occur (Kain, 1979; Hymanson et al., in prep.). In P. californica, variations (often extreme) also occur in other morphometric characteristics such as stipe length and stipe diameter precluding their use as a primary source of age estimation, or as tools to corroborate age estimation by ring counts (Hymanson, et al., in

prep.). If the factors affecting stipe morphology can be understood, the accuracy of aging P. californica by stipe ring counts could be increased, and methods of interpreting the past ecology of a population could possibly be elucidated.

Thus, the experiments in this study were designed to answer two questions: (1) What effect does the density of monospecific stands of P. californica have on the stipe morphology of individuals? (2) Do variations in light quantity affect the stipe morphology of P. californica?

Organism & Study Site:

Pterygophora californica (Ruprecht, 1852) is a perennial brown alga in the order Laminariales. It ranges from British Columbia into Baja California (Abbott & Hollenberg, 1976). The conspicuous phase of this plant is the diploid sporophyte which is composed of a holdfast, erect woody stipe, a terminal vegetative blade, and lateral spore producing blades (Figure 1). The holdfast and stipe are perennial (Abbott, & Hollenberg, 1976) and in the main study area the abundance and size of blades varies seasonally (Canestro, in prep.; pers. obs.). Growth in length is initiated by an intercalary meristem located between the stipe and terminal blade. Sporophylls arise from lateral buds of meristomatic tissue. Growth in stipe diameter is initiated by a meristoderm lying just under the epidermis of the stipe.

Pterygophora californica requires a hard substrate for attachment. It is found most frequently in subtidal habitats, often associated with kelp forests of Macrocystis pyrifera and/or Nereocystis lutekeana. In these situations P. californica forms an understory canopy below the surface kelp canopy, but above virtually all other algae.

Quantitative experiments on P. californica were done in Stillwater Cove, Carmel Bay, California (36° 53.5'N 121° 56.5'W; Figure 2). This site has been described in detail by Foster (1982) and Reed and Foster (1984). The experimental area (i.e., that location within the cove to which plants were transplanted) was on the shoreward side of two small rock islands located in about the middle of the cove. Here, the bottom, roughly 8 m deep, was composed of large boulders situated in a sand and cobble matrix. The density of P. californica was relatively low, probably due to limited space for attachment of recruits. The plant collection area (i.e., that location within the cove from which plants were taken) was on the seaward side of the rock islands at about 10 m depth. This area consisted of several large rock reefs interspersed among stable boulder fields and patches of sand. Extensive stands of P. californica occurred on these rock reefs. During the late spring and summer, growth of M. pyrifera can turn the entire site into one large kelp forest (Reed & Foster, 1984).

Methods & Materials:

In March, 1985 150 P. californica were transplanted to experimental racks within Stillwater Cove (Figure 3). All plants used were haphazardly chosen from a stand of plants that recruited in 1983-1984 (Canestro, in prep.). Plants were pried loose from the substrate at the haptera using a putty knife. The haptera were then sewn through slits cut into strips of rubber inner-tubing. These plants were then re-attached to the experimental racks by tying the strips of tubing around the pipe leaving the haptera in direct contact with the pipe. Of the 150 plants transplanted, 120 were re-attached to racks in various treatments at the experimental area. The remaining 30 plants were re-attached to each of 2 transplant control racks placed at the collection area. Twelve plants were randomly chosen at the collection area to serve as non-transplanted controls. Twelve plants that naturally occurred at the experimental area served as non-transplanted controls there. No individual to be transplanted was kept from the subtidal for more than one hour, during which time plants were kept in the water, or moist and shaded. All transplanting was done within a 2 day period.

To determine the mean density of P. californica in Stillwater Cove just prior to transplantation, a random sample of the number of plants/m^2 $\pm$ s.e. (n = 30/stand) was obtained from 2 natural stands. The means of these samples (6.8 $\pm$ 0.8, and 8.0 $\pm$ 1.1) were not

significantly different from one another, and the data sets were pooled for an overall density of 7.4 ± 1.0 plants/m^2. The average area (in cm^2) that a plant at mean density would occupy assuming a uniform dispersion pattern could then be calculated.

Although plants in natural stands often exhibit a clumped pattern of dispersion, a uniform dispersion pattern was used in these experiments to standardize the affects of density treatments on the individual. All treatment and control plants were established using the uniform dispersion model to achieve 3 different densities: mean (equivalent to 7.4 plants/m^2, or 1 plant/1,369 cm^2); 4 times the mean (high density, equivalent to 29.7plants/m^2, or 1 plant/324 cm^2); and 1/4 the mean (low density, equivalent to 1.86 plants/m^2, or 1 plant/5,329 cm^2). In the low and mean density treatments experimental plants were attached to the 4 center bars of a rack. Buffer plants were attached around the perimeter of these racks to ensure that all experimental plants were at the same density. In the high density treatment 5 plants were attached to each of the 6 cross bars (30 plants total); experimental plants of this treatment were then randomly chosen from the sub-set of plants surrounded on all four sides by other plants. Each treatment was replicated twice, and experimental plants were chosen in each replicate. Experimental plants were tagged with a label identifying the treatment, the replicate number, and the plant number. Tags were made from dymo^{tm} labels, and attached loosely to the plant's stipe with nylon cable ties.

Two racks planted at mean density were fitted with shades to test for the effects of variations in light availability on plant morphology. Shades were made of 3 layers of neutral density fiberglass window screening mounted 1.3 m above the racks. This thickness of shade was closest to achieving the amount of light reduction caused by a subsurface canopy of adult P. californica growing at the collection area. Another 2 racks planted at mean density were fitted with covers of 0.061 cm thick clear vinyl. Covers were attached in the same manner as shades. These covers served as controls, duplicating the physical affects of shades without causing the large reduction in light. Light measurements were made at the collection and experimental areas on three separate occasions using a Li-Cor LI-188B integrating quantum/radiometer/photometer fitted with a LI-193SB spherical in situ quantum sensor, and a cosine deck cell. Only wavelengths within the photosynthetically active region (400 nm to 700 nm) were measured. Light measurements are reported in terms of the number of photons/m^2/s, and the percent of surface light.

During the course of the experiment plaster of paris spheres (chalk blocks) were attached to poles and placed in the center of racks with shades and covers in the experimental area, and in the center of open racks in both areas. The poles positioned the chalk blocks at a height equal to that of the plants. The dry weight of the chalk blocks was measured before attachment and 3 days after attachment, the

amount of weight lost being a reflection of water movement (Doty, 1971).

After all plants were moved and tagged, initial measurements of stipe length (the distance in cm between the top of the haptera and the intercalary meristem), basal and apical stipe diameter (widest diameter just above the haptera and just below the first set of lateral blades respectively), total number of blades, and the length and position (terminal or lateral) of the longest blade were made on 96 plants: 72 experimental plants, transplanted to the various treatments in the experimental area, 12 non-transplanted controls at the collection area, and 12 non-transplanted controls at the experimental area. All measurements were repeated monthly for five months.

For many statistical tests, data sets were broken into 2 major groups: treatments and controls of the shading experiment; and treatments and controls of the density experiment. The experimental design allowed some controls to serve for both groups. Cochran's C test was used in association with all ANOVAs to test for homogeneity of variance. Tukey's multiple comparison test, and proportions of variance (prop. σ^2) calculated from mean square estimates were done only for those ANOVAs yielding significant results.

Initial size frequency distributions of stipe length, and basal and apical diameter for all experimental and control plants were tested for normality using the Chi-Square goodness of fit test. One-way nested ANOVAs were used to determine if initial differences in stipe

length, and basal and apical diameter within and between treatments were significant. The degree of relationship between the total growth increment and the initial size of all experimental and control plants was tested for the 3 measures of stipe growth using linear regression, and a subsequent ANOVA to test the significance of the slope. These tests of the initial size data and their distributions were used to determine if parametric statistics could be utilized in the analysis of experimental data, and whether a correction factor needed to be applied to total growth increment data.

After the final set of field measurements, experimental plants were harvested and brought back to the laboratory where the weight of blade and stipe tissue was determined separately for each plant. A one-way nested ANOVA was used to test for significant differences in the weight of plant parts within and between treatments.

After weighing, the lower 10 cm of each stipe was removed and preserved in 10% formalin for microscopic analysis. Possible differences in stipe ring morphology were tested for by microscopic sampling. Cross sections (5-8 microns thick) of 60 stipes of plants from the density experiment were prepared, mounted, and stained using standard histological techniques (Luna, 1968; Preece, 1972). Each section was sampled three times at 100 power for the number of cells per 0.1 mm^2 at distances of 0.5 mm and 1.0 mm from the epidermis. The sampling distances chosen assured that only stipe material added during the course of the experiment was sampled, since

all plants had grown at least 2 mm in basal diameter by the end of the experiment. A t-test was used to determine if cell density varied significantly over the region of new growth. A two-way nested ANOVA and associated tests were used to determine if significant differences in cell density occurred within or between treatments.

Results:

Results of the Chi-Square goodness of fit test for normality showed that the initial size frequency distributions of all experimental and control plants did not differ significantly from a normal distribution (stipe length: $X^2 = 7.214$, $P > 0.25$; basal stipe diameter: $X^2 = 10.567$, $P > 0.10$; and apical stipe diameter: $X^2 = 11.859$, $P > 0.10$). ANOVAs of initial stipe length, and initial basal and apical diameter for all experimental and control treatments revealed no significant differences within or between treatments (Table 1). Regressions of initial size versus total growth increment, and associated ANOVAs of the slopes were not significant for any of the measurements of stipe growth (Table 2). The results of these tests of initial data indicate that the use of parametric statistics on uncorrected growth data is appropriate, and that any significant differences of growth data could be attributed to events occurring over the course of the experiment.

The light measurements of this experiment were used to quantify differences in light availability between areas and treatments.

Although light availability varies almost instantaneously and probably not linearly, consistent differences in measurements of short term light availability are probably indicative of longer term differences in light availability. Nearly 50% of the light available to juveniles at the collection area was removed by the presence of a subsurface canopy of adult P. californica (Table 3). This level of light reduction was exceeded under shades in the experimental area were individuals received 70% less light than those individuals not covered or shaded. However, the absolute quantity of light available to shaded individuals was nearly equal to the absolute quantity of light received by juveniles under an adult canopy at the collection area. Shades served to reduce the availability of light without an increase in plant density, but whether the amount of reduction is physiologically equivalent to that of the adult canopy at the collection area is unknown. Individuals under clear covers at the experimental area received only 20% less light than those individuals not covered or shaded. These results indicate that the clear covers served to mimic the physical effects of shades without causing the same degree of light reduction.

A qualitative comparison of the mean weight loss from chalk blocks indicated that the presence of shades or covers did not reduce water motion through plants at the experimental area, but that water motion was less vigorous in the experimental area than in the collection area (Table 4).

No significant differences among replicates or between

treatments in the shading experiment were found in stipe length, or apical stipe diameter (Table 5). Significant differences between treatments for basal stipe diameter were found, but Tukey's multiple comparison test revealed that the non-transplanted controls at the collection area were the sole source of variation, their growth being significantly faster in basal stipe diameter than all transplanted individuals.

Density results were much more variable (Table 6). Significant differences among replicates were found for apical stipe diameter, obviating tests for treatment effects. Replicate differences may have been due to experimenter error, since it was virtually impossible to measure apical stipe diameter at the same point each time because of the natural attrition and addition of blades. No significant differences among replicates were found for stipe length or basal stipe diameter, but in both cases significant treatment effects were found. Tukey's multiple comparison test showed that for stipe length, the high density treatment was the only source of treatment variation, with plants at high density growing faster in stipe length than their lower density counterparts. Tukey's multiple comparison test showed that both transplanting and high density were responsible for treatment variation in basal stipe diameter, with plants at high density growing slower in basal stipe diameter than their lower density counterparts, and non-transplanted controls at the collection area growing faster in basal stipe diameter than all other plants.

Weight of perennial tissue did not differ significantly between treatments (Table 7). This result was expected since the weight of this portion of the alga is a function of both pretreatment and treatment effects.

Determination of the average proportional increase or decrease in blade number revealed large differences between density treatments: low density plants lost an average of 15% of their blades; high density plants lost an average of 0.01% of their blades; and mean density plants gained an average of 45% more blades. These results suggest that differences in blade weight should exist between treatments, although an ANOVA was unable to detect these differences because of significant variation between replicates (Table 7). The discrepancy here is probably due to inherent variation in the data. The addition of a single blade can greatly affect the average proportional change in blade number, although this same blade would add very little to the weight of the entire blade mass.

Microscopic analysis of cell density (number of cells/0.1 mm^2) was used to assess differences in stipe ring morphology between density treatments and controls. Cell density measurements were quite consistent between stipe sampling depths, with a two-way t-test showing no significant difference ($t = 0.820$; $P > 0.25$). A two-way ANOVA testing for cell density differences between density treatments and controls was significant (table 8). Tukey's multiple comparison test indicated that the variation was due to differences

between the low density treatment, and non-transplanted controls at the collection site. Thus, cell density differences could not be attributed to experimental effects.

Graphs of the basal stipe diameter growth increment through time for the density treatments (Figure 4) show that growth rates of the experimental plants diverged in the final months of the experiment, with low density > mean density > high density. Similar graphs (Figure 4) compare the growth increment of control and mean density experimental plants through time. The total growth increment of the non-transplanted controls at both areas was similar to that of the transplanted treatment and control plants, suggesting that the effects of transplantation on stipe diameter were minimal.

Discussion:

Results of the density experiment show that stipe growth of P. californica in Stillwater Cove is density dependent, with high density plants growing faster in stipe length and slower in basal stipe diameter than their lower density counterparts. Results of the shading experiment suggest that extended periods of light reduction, at the levels used, do not significantly affect the stipe growth of established P. californica in Stillwater Cove.

Besides changes in external morphology, variation in basal stipe diameter growth has other consequences. It is known that the stipe

rings of P. californica in Stillwater Cove are annual (Hymanson, et al., in prep.). If plant density affects growth in basal stipe diameter, then it must also affect ring morphology, since the cells which form the rings makeup the stipe diameter.

The mechanism(s) causing variations in basal stipe diameter is (are) unclear. Histologic study of stipe cross sections showed that differences in basal stipe diameter were not due to differences in cell density. MacMillan (1902) found that the size of cells in the light rings of P. californica was greater than the size of cells in the dark rings, and histologic work done on control plants in this study supports this. However, cell size differences did not appear to occur in tissue laid down during the course of this experiment. Variations in basal stipe diameter growth may instead be caused by variatioons in stipe growth rates. During the final months of the density experiment basal stipe diameter growth rates began to diverge (Figure 4). Plant density could be affecting the rate at which tissue is deposited along the diameter resulting in smaller or larger rings --an analogous situation occurs in trees (Fritts, 1976).

The constraints of this study undoubtedly affected the outcome of the field experiments. Field experiments were conducted at a more sheltered area and were terminated after five months because it was not known if the experimental racks could survive winter storms. Because the experiments ran only thorough the spring and summer, seasonal changes such as winter storms that are known to affect

density and light availability did not influence the results (Rosenthal, et al., 1974; Dayton, et al., 1984). These constraints probably reduced the magnitude of change in stipe morphology, suggesting that the results are a conservative expression of the effects of density and light on the stipe morphology of P. californica.

The proportion of variance in basal stipe diameter, and stipe length (Table 6) explained by density treatment variations shows that a significant amount of the total variation is accounted for by the experimental model; however, the majority still rests with the residuals. Undoubtedly other factors, both density dependent and independent exert control over the growth of P. californica.

Water motion may be another factor affecting plant growth. Qualitative analysis of the results of the chalk block experiment shows that water motion at the experimental area was much less vigorous than water motion at the collection area. Epiphytic growth on plants at the experimental area was much more extensive than on plants at the collection area. Further, within the experimental area, epiphytic growth was greatest on plants in the low density treatment, and least on plants in the high density treatment. Differences in the degree of epiphytic cover may be one manifestation of the noted difference in water motion. These epiphytes may affect the growth of plants by filtering out light of vital wavelengths, and by inhibiting the absorption of nutrients.

There is no evidence that P. californica at higher densities "do

better" than their low density counterparts because of their increased stipe length. Schiel (1985b) found that high densities of monospecific stands of Sargassum sinclairii and Carpophyllum maschalocarpum resulted in greater stipe lengths, greater biomass, and greater reproductive output, but also greater mortality rates. He suggested that rapid increases in length may be detrimental to survival, leading to increased risks of storm dislodgement. However, P. californica may have a different ecological response to increased growth than these Fucalian algae. Yet, in P. californica haptera number appears to increase with stipe diameter (pers. obs.), as found by Kain (1979) in Laminaria hyperborea, and suggested by Novaczek (1981) in Ecklonia radiata. The chance for premature dislodgement of P. californica could be enhanced if the increase in haptera number is reduced relative to the increase in stipe length.

There is no clear reason why algae at higher densities grow greater in stipe length than their lower density counterparts, although the fact that they do is a consistent result (Fang, et al., 1962; Schiel & Choat, 1980; Coyer & Zaugg-Haglund, 1982; Schiel, 1985b). Some studies have suggested that increased stipe length is in response to the reduced light associated with crowding at higher densities (Fang, et al., 1962; Coyer & Zaugg-Haglund, 1982) although other studies suggest that light reduction has a negative affect on certain aspects of growth (Kain, 1979; Chapman & Lindley, 1980; Hutchings & Budd, 1981b). These differences may be due to the multitude of ways the

effects of light have been measured and interpreted, or site specific environmental effects. (Evans, et al., 1976; Luning, 1980).

The reduced light levels measured in this study had no significant effect on stipe growth. However, Dayton et al. (1984) and Reed and Foster (1984) did find that light significantly affected growth and recruitment. These differences may be explained by comparing the results of this study to those of Reed and Foster (1984) both of which took place in Stillwater Cove. Over the course of the 2 studies the density of P. californica changed very little (7.4 plants/m^2 for this study; and 7.3 plants/m^2 for Reed and Foster's study). However, light measurements taken at the same time of year, and during the period of maximum surface canopy cover did differ. Reed and Foster (1984) found that between 1% and 3% of the surface light passed through both the surface (Macrocystis pyrifera) and subsurface (P. californica) canopies. Measurements made in this study showed that about 8% of the surface light passed through the surface and subsurface canopies. This comparison shows some variation in the amount of light reaching a similar depth which cannot be explained by a concurrent variation in density. It is apparent that the amount of light removed by a subsurface canopy is a function of the canopy size or cover as well as individual density, suggesting that density dependent effects are not due to shear numbers alone.

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Table 1
Results Of ANOVA Testing Inital Size
Differences Among & Between All Treatments

Stipe Length

Source Of Variation	DF	SS	MS	F	P
Treatments	6	872.4	145.4	0.84	>0.25
Quadrates Within A Treatment	7	1,215.1	173.6	1.22	>0.25
Residual	70	9,931.4	141.9		
Total	83	12,018.9			

Basal Stipe Diameter

Source Of Variation	DF	SS	MS	F	P
Treatments	6	64.5	10.8	1.60	>0.25
Quadrates Within A Treatment	7	43.9	6.7	0.15	>0.25
Residual	70	286.5	4.09		
Total	83	394.9			

Apical Stipe Diameter

Source Of Variation	DF	SS	MS	F	P
Treatments	6	45.8	7.64	1.77	>0.20
Qadrates Within A Treatment	7	30.3	4.32	0.70	>0.25
Residual	70	434.8	6.21		
Total	83	510.9			

Table 2

Results of Regression Analyses & Associated ANOVA Testing
The Relationship Between Initial Size & Growth Increment
For All Treatments

Measurement	n	r^2	F	P(B = 0)
Stipe Length	90	.02	2.10	>0.15
Basal Stipe Diameter	90	.004	0.32	>0.25
Apical Stipe Diameter	90	.01	0.76	>0.25

Table 3

Light Measurements

Location Of Measurement	Depth (m)	*Mean ± s.d. ($\mu E/s/m^2$) x 10^2	Percent Of Surface Light
Collection Area:			
At Top Of Adult *P. californica* Canopy	8	2.13 ± 0.08	15.8
**At Top Of Juvenile *P. californica* Canopy	9	1.08 ± 0.46	8.0
Experimental Area:			
At Top Of Plants Open Treatment	7	3.97 ± 1.26	22.7
At Top Of Plants Cover Treatment	7	3.14 ± 0.64	17.9
At Top Of Plants Shade Treatment	7	1.16 ± 0.05	6.6

*n = 3 in all cases.
**measurements taken beneath adult canopy.

Table 4

Results of Chalk Block Experiments

	Open Rack *Area 1	Shaded Rack *Area 2	Covered Rack Area 2	Open Rack Area 2
Mean Weight Loss ± s.d. (gm/Day)	45.7±19.2	20.9± 4.5	19.8±3.1	20.6 ± 4.4

*Area 1 = Collection area; Area 2 = Experimental area. n = 3 in all cases.

Table 5
Results Of ANOVA Testing Growth Differences
Between Treatments Of The Shading Experiment

Stipe Length

Source Of Variation	DF	SS	MS	F	P
Treatments	4	14.2	3.5	0.64	>0.25
Quadrates Within A Treatment	5	27.6	5.5	1.29	>0.25
Residual	50	213.6	4.3		
Total	59	255.3			

Basal Stipe Diameter

Source Of Variation	DF	SS	MS	F	P	Prop. Of σ^2
Treatments	4	11.2	2.8	15.61	<0.01	0.21
Quadrates Within A Treatment	5	0.9	0.18	2.40	>0.25	0.00
Residual	50	32.8	0.66			0.79
Total	59	44.9				

Apical Stipe Diameter

Source Of Variation	DF	SS	MS	F	P
Treatments	4	10.4	2.6	0.61	>0.25
Qadrates Within A Treatment	5	21.5	4.3	1.87	>0.10
Residual	50	115.0	2.3		
Total	59	146.9			

Table 6
Results Of ANOVA Testing Growth Differences
Between Treatments Of The Density Experiment

Stipe Length

Source Of Variation	DF	SS	MS	F	P	Prop. Of σ^2
Treatments	4	34.6	8.6	72.0	<0.001	0.30
Quadrates Within A Treatment	5	0.6	0.1	0.09	>0.25	0.00
Residual	50	69.8	1.4			0.70
Total	59	104.9				

Basal Stipe Diameter

Source Of Variation	DF	SS	MS	F	P	Prop. Of σ^2
Treatments	4	16.4	4.11	137.0	<0.001	0.20
Quadrates Within A Treatment	5	0.2	0.03	0.03	>0.25	0.00
Residual	50	50.3	1.01			0.80
Total	59	66.9				

Apical Stipe Diameter

Source Of Variation	DF	SS	MS	F	P
Treatments	4	3.8	0.9	----	
Qadrates Within A Treatment	5	41.3	8.3	3.01	<0.05
Residual	50	137.2	2.7		
Total	59	182.3			

Table 7

Results of ANOVA Testing Biomass Differences
Between Density Treatments

Blade Weight

Source Of Variation	DF	SS	MS	F	P
Treatments	4	624,232	156,058	----	
Quadrates Within A Treatment	5	348,216	69,643	5.78	>0.001
Residual	50	602,474	12,049		
Total	59	1,574,922			

Perennial Tissue Weight

Source of Variation	DF	SS	MS	F	P
Treatments	4	19,096	4,774	2.52	>0.10
Quadrates Within A Treatment	5	9,484	1,897	1.84	>0.10
Residual	50	51,635	1,033		
Total	59	80,215			

Table 8

Results of ANOVA Testing Cell Density Differences Between Density Treatments

Source Of Variation	DF	SS	MS	F	P	Prop. of σ^2
Treatments	4	647	161.7	6.79	<0.001	0.33
Residual	439	10,452	23.8			0.67
Total	443	11,098				

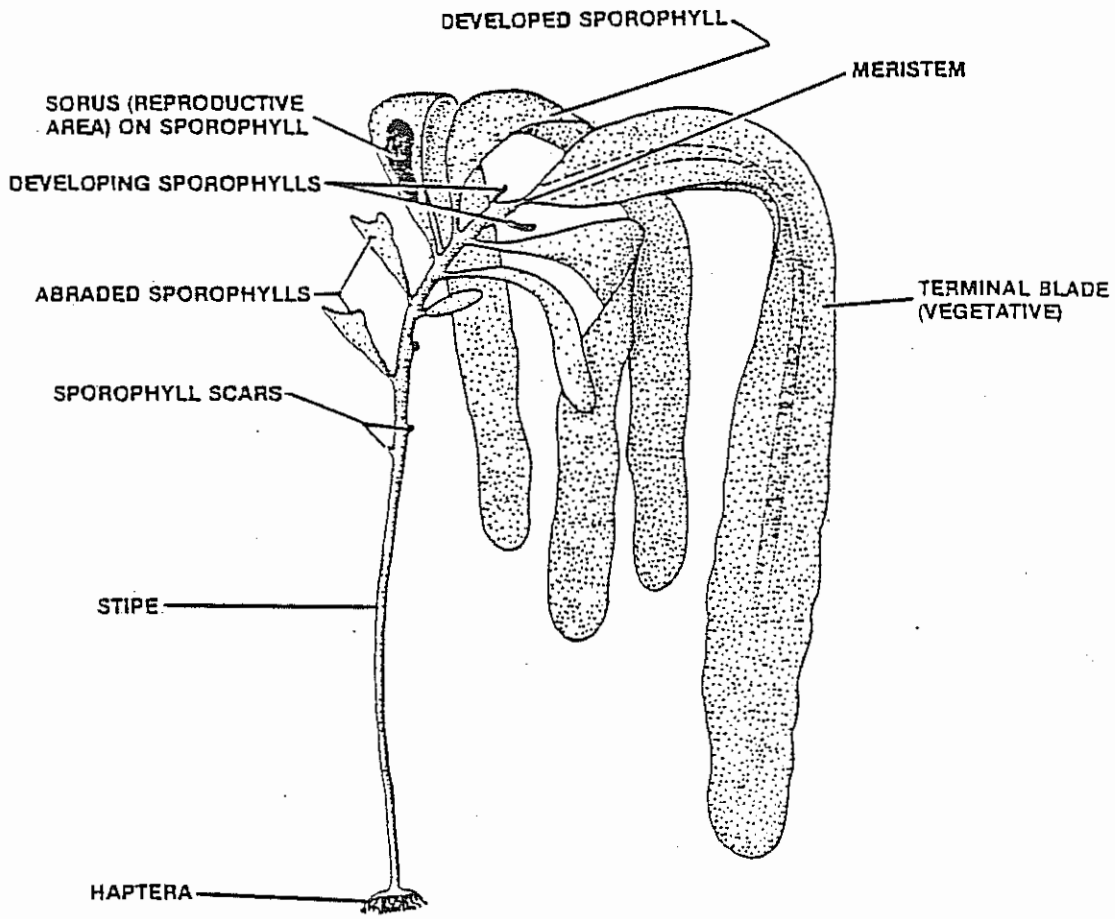

Figure 1. The morphology of Pterygophora californica (from Dawson & Foster, 1982).

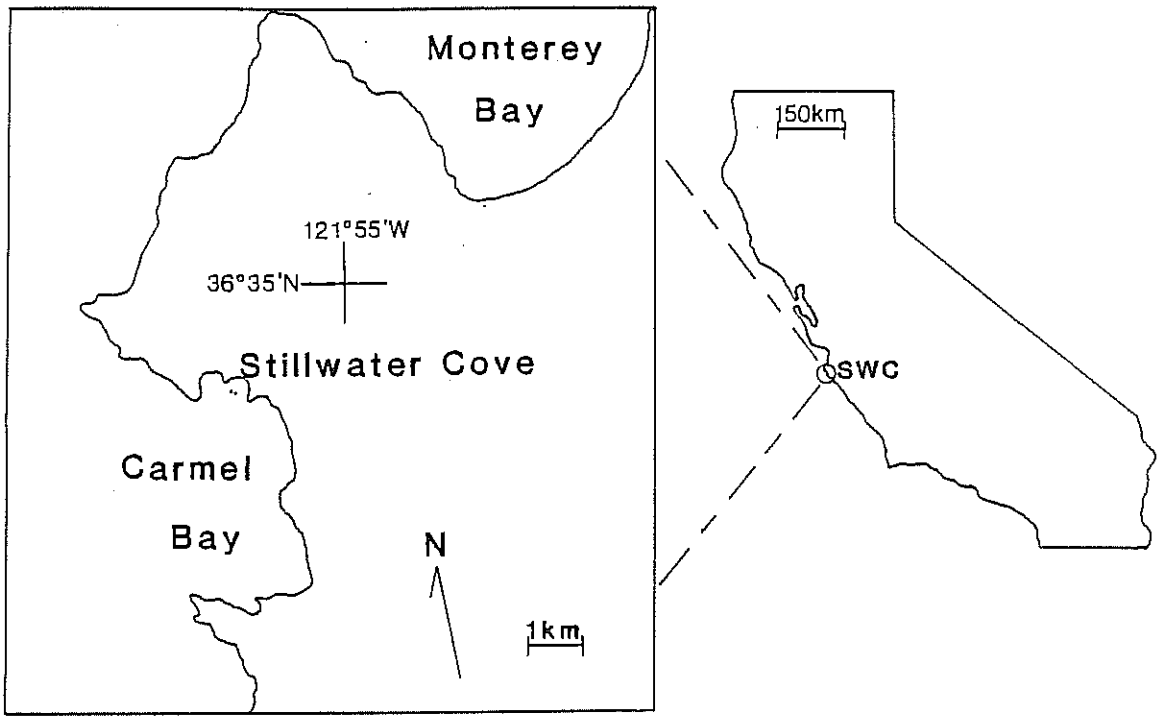

Figure 2. Map of study site. (Taken in part from Schiel, 1985a.)

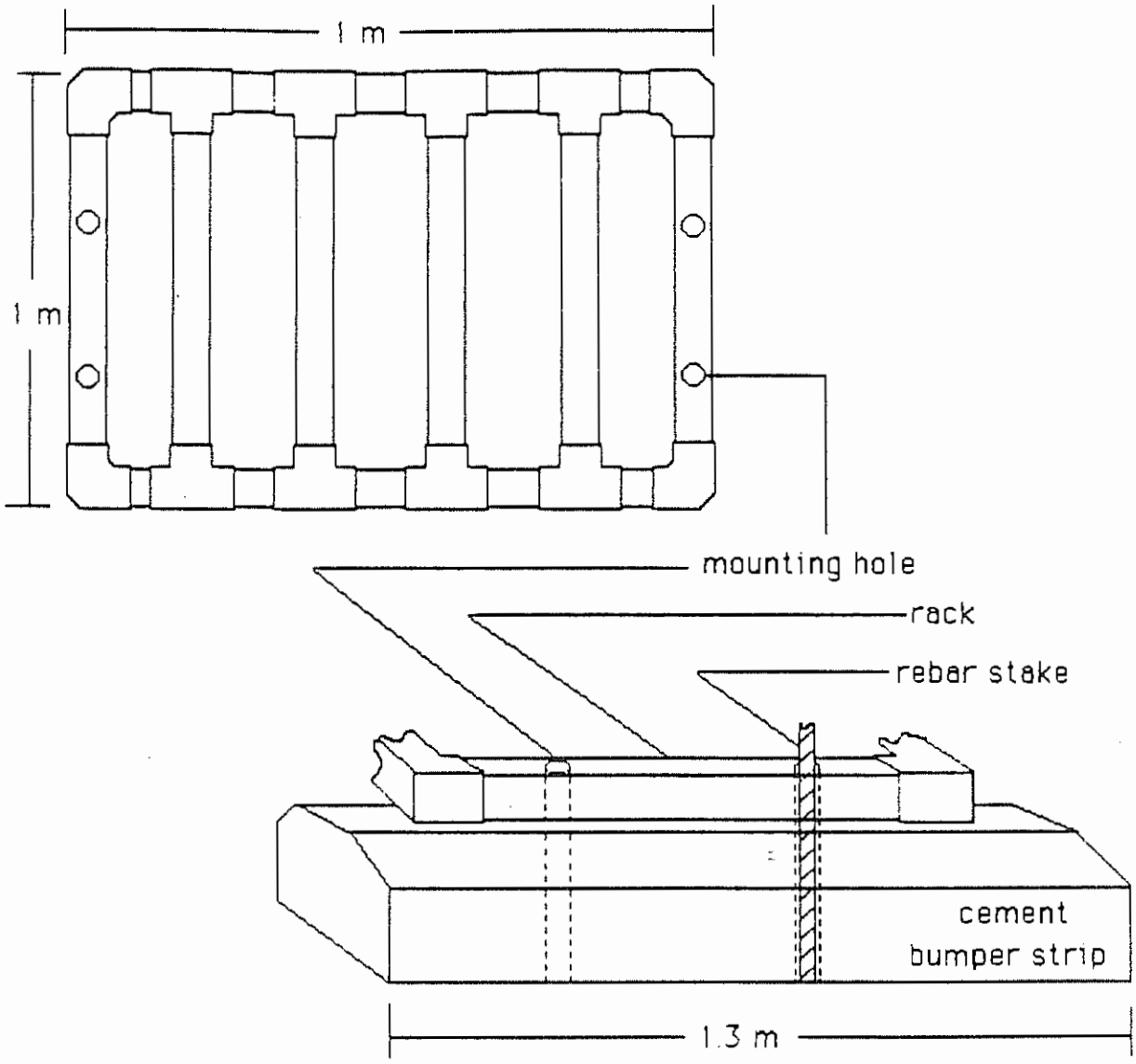

Figure 3. The transplant rack. Racks were constructed of class 100 PVC pipe measuring 3.8 cm (1 1/2 in) in diameter. Racks were mounted on cement bumper strips to elevate and anchor them. Rebar stakes were driven through holes in the racks and bumper strips, and into the substrate below to prevent the racks from floating or moving laterially.

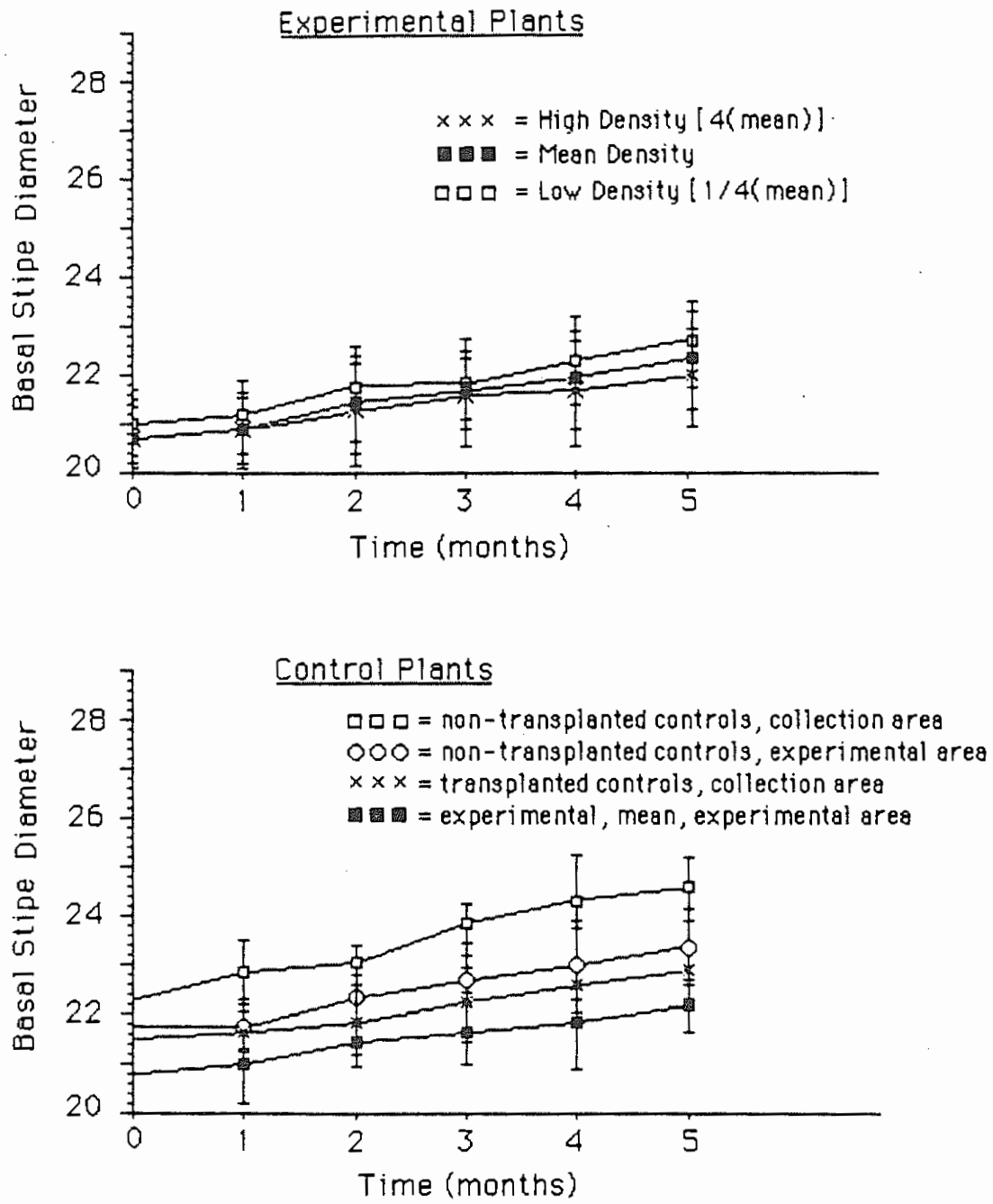

Figure 4. Growth of basal stipe diameter in experimental and control plants through time. Points = means ± s.d.; n = 2.