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LIGHT ADAPTATIONS OF PLANTS: A MODEL BASED
ON THE SEAGRASS ZOSTERA MARINA L.

UNIVERSITY OF ALASKA, M.S., 1979

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LIGHT ADAPTATIONS OF PLANTS: A MODEL BASED ON THE SEAGRASS
ZOSTERA MARINA L.

A
THESIS

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University of Alaska in partial Fulfillment
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By
William Dennison, B.A.
Fairbanks, Alaska
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LIGHT ADAPTATIONS OF PLANTS: A MODEL BASED ON THE SEAGRASS

ZOSTERA MARINA L.

RECOMMENDED:

Keith Van Cline

John J. Goering

Joseph M. Colwell

Van Almond

D. E. McRoy

Chairman, Advisory Committee

P. Bunnell

Program Head

APPROVED:

Van Almond

Director, Institute of Marine Science

December 28, 1979^{VA}

Date

Van Almond

Dean of the College of Environmental Sciences

December 11, 1979

Date

Keith B. Mather /pk

Vice Chancellor for Research and Advanced Study

26 December 1979

Date

ABSTRACT

Adaptations to light by a temperate seagrass, *Zostera marina* L. (eelgrass), were investigated along a depth transect representing a gradient of plant development. Various light adaptive strategies are proposed in a conceptual model and tested along the natural gradient and under *in situ* light manipulation experiments.

The major light capturing strategy which *Zostera* employs is that of changing leaf area. Chlorophyll *a* to *b* ratios and amounts, measures of adaptation to light quality and quantity, demonstrated little or no adaptive trends when integrative samples were used. The altered light experiments did not affect chlorophyll content but did affect leaf production rates. Although the relative vertical distribution of leaf area is constant along the transect, the absolute leaf area varies, as measured by leaf area index (LAI = area of leaves/area of bottom). A measured maximum LAI of 17 is higher than other aquatic and most terrestrial ecosystems.

PREFACE

This study investigates the adaptations of plants to light gradients. The adaptation to gradients of light quality and quantity is both a physiological and biological plant response. The different scale of response mechanisms has led to the broad approach of this study, from molecular pigment ratios to total light absorbing surface area. The various parameters analyzed are approximations with varying degrees of relevance to the adaptation that they address. For example, the measure of leaf area corresponds to the proposed leaf area adaptation differently, and perhaps more closely, than the measure of chlorophyll *a* to chlorophyll *b* ratio corresponds to the proposed chromatic adaptation. As the choice of parameters reflects the relevance to the adaptation, the choice of sampling schemes reflects the scale of the problem being addressed. The assessment of the plant community and the assessment of single shoots require a different approach. This is saliently demonstrated by a comparison of the distribution of chlorophyll in single shoots and in integrated canopy samples. This study is on an ecosystem level, and the sampling scheme must necessarily be one of appropriate scale. Methods of aquatic and marine plant biology are largely oriented toward microscopic organisms, an inappropriate scale for the macroscopic seagrasses. Consequently, methods of terrestrial biology were applied to this particular marine ecosystem. The vertical sectioning of the leaf canopy into horizontal strata (stratified clip technique) used in this study is an adaptation of terrestrial methodology. The integrated sampling of old, young, large and small leaves and shoots serves to group the plants and

plant parts into strata: the strata are what the quanta or light particles encounter as they enter the ecosystem. The distribution of life in horizontal layers, or strata, combined with vertical gradients of environmental factors, especially light, serve as selective pressures for physiological and genetic adaptations to conditions the organism encounters. This research delves into the manner that plants go about reconciling themselves with their environment.

This restless world
Is full of chances, which by habit's power
To learn to bear is easier than to shun.
Armstrong. Act of Preserving
Health, Book 2

ACKNOWLEDGEMENTS

I am grateful for the many unique learning opportunities provided by my graduate advisor, Dr. C. Peter McRoy. In addition to learning how to swim underwater through an eelgrass jungle, walk over mud flats with snowshoes and live in WWII quonset huts, I have gained some perspectives on what it is to be a scientist. He has provided insights on how to address a particular question; additionally how to find the question to address.

My graduate committee, Drs. V. Alexander, J. M. Colonell, J. J. Goering and K. van Cleve, helped guide me through the academic maze and gave me their time and support. I was fortunate to have access to Dr. M. J. Klug on sabbatical leave from Michigan State University.

Participation in a team research effort, the Seagrass Ecosystem Study (SES), has provided me with the opportunity to meet and exchange ideas with other seagrass researchers, and more importantly, provided the framework for this particular investigation. SES technicians, principal investigators and graduate students assisted in the collection and processing of samples.

Discussions of ideas and problems with Drs. R. J. Barsdate, E. J. Brown, F. S. Chapin III and T. C. Royer provided fresh perspectives. Fred Short assisted with the sampling design and made helpful suggestions.

The formidable task of maintaining a field camp at Izembek Lagoon was made simpler by the Izembek National Wildlife Refuge staff. The U.S. Department of the Air Force 714th Aircraft Control and Warning

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INTRODUCTION

The acquisition of radiant energy and subsequent conversion to chemical energy is the major concern of primary producers. Radiant energy, or more specifically, light energy between the wavelengths ca. 400-700 nm, is not uniformly distributed on the earth's surface. Variations of light intensity and changes of the light spectrum occur and plants correspondingly adapt to these nonuniformities. In this study various light adaptive mechanisms available to plants are proposed in a conceptual model. The model groups the adaptations into four categories and predicts the plant responses under various light regimes. The proportional amounts of the different light adaptations are assessed in a seagrass ecosystem in order to test plant responses to shifts in light quality and quantity. From the prediction and testing of light adaptations an understanding of the plant's interaction with the environment can be gained.

Seagrasses are a functional grouping of approximately 50 species of marine flowering plants. Shoots, or leaf turions, are bundles of leaves that arise from a horizontal stem, the rhizome. Roots serve to anchor the plants and absorb and transport nutrients from the sediments. There is little structural material; seagrasses are largely supported by the water itself. Reproduction is both sexual (hydrophilous pollen) and vegetative (lateral branching of the rhizome). Seagrasses are distributed along the coastlines of the world's oceans except for the most polar seas (den Hartog, 1970).

Nearshore marine ecosystems that are dominated by marine flowering plants are regions of high biological productivity (McRoy and McMillan, 1977). Seagrass carbon is largely channeled into a detritus food web with little direct grazing (McConnaughey and McRoy, 1979): large exports of carbon from seagrass ecosystems contribute to the food webs of coastal waters (Barsdate *et al.*, 1974). Seagrasses affect silt and sand deposition, organic matter accumulation, nutrient cycling and water movement. These marine vascular plants contribute to the surface area available for colonization, serve as a nursery for fishes and invertebrates, effectively pump nutrients from the sediments into the water column and stabilize sediments (McRoy and Helfferich, 1977; Phillips and McRoy, 1979).

Seagrass ecosystems, though recognized for many years, have only recently been intensively investigated. The proliferation of research efforts has in part led to the Seagrass Ecosystem Study (International Decade of Ocean Exploration/National Science Foundation). The major theme of this study has been the investigation of various components of the seagrass ecosystems along a gradient of successional maturity. The testing of the hypothesis of the succession of ecosystem processes (process succession) has been employed in various tropical and temperate seagrass ecosystems. This research investigates the responses of a temperate seagrass ecosystem to changes in light quality and quantity.

Seagrass ecosystems of temperate and high latitudes of the Northern Hemisphere are typically dominated by *Zostera marina* L. (eelgrass). The ecological role that *Zostera* plays in the ecosystem is variable, in

classical ecology terminology, ranging from a colonizer to a climax species (den Hartog, 1970).

CONCEPTUAL MODEL

The light adaptive mechanisms available to plants are conceptualized as being components of the total plant response (Figure 1). The model includes predictions of plant responses under different light regimes. Each of the adaptive mechanisms will be considered in detail.

Chromatic adaptation refers to the change in relative amounts of various photosynthetic pigments as a response to the changes in light quality. Chromatic adaptation has been long recognized (Engelmann, 1883; Gaudokov, 1903), usually as a factor in depth zonation of various algal types (Steemann-Nielsen, 1975). The alternative explanation for algal depth zonation (Oltmanns, 1892) emphasizes the effect of light quantity (Dutton and Juday, 1944). The effects of light quality and quantity are distinguished in this conceptual model as chromatic and quantum capture adaptation, respectively. The selective filtering of the light passing through water (Jerlov, 1976) or leaf canopies (Federer and Tanner, 1976) leads to a spectral shift in the light available for photosynthesis. The absorbance peaks for accessory pigments (pigments other than chlorophyll *a*) are at shorter wavelengths than that of chlorophyll *a* (chl *a*) (cf. Smith and French, 1963). Accessory pigments act as light harvestors, transferring the light energy with varying efficiencies to specialized chl *a* molecules to be ultimately converted to chemical energy. The relative amounts of chl *a* molecules and the various

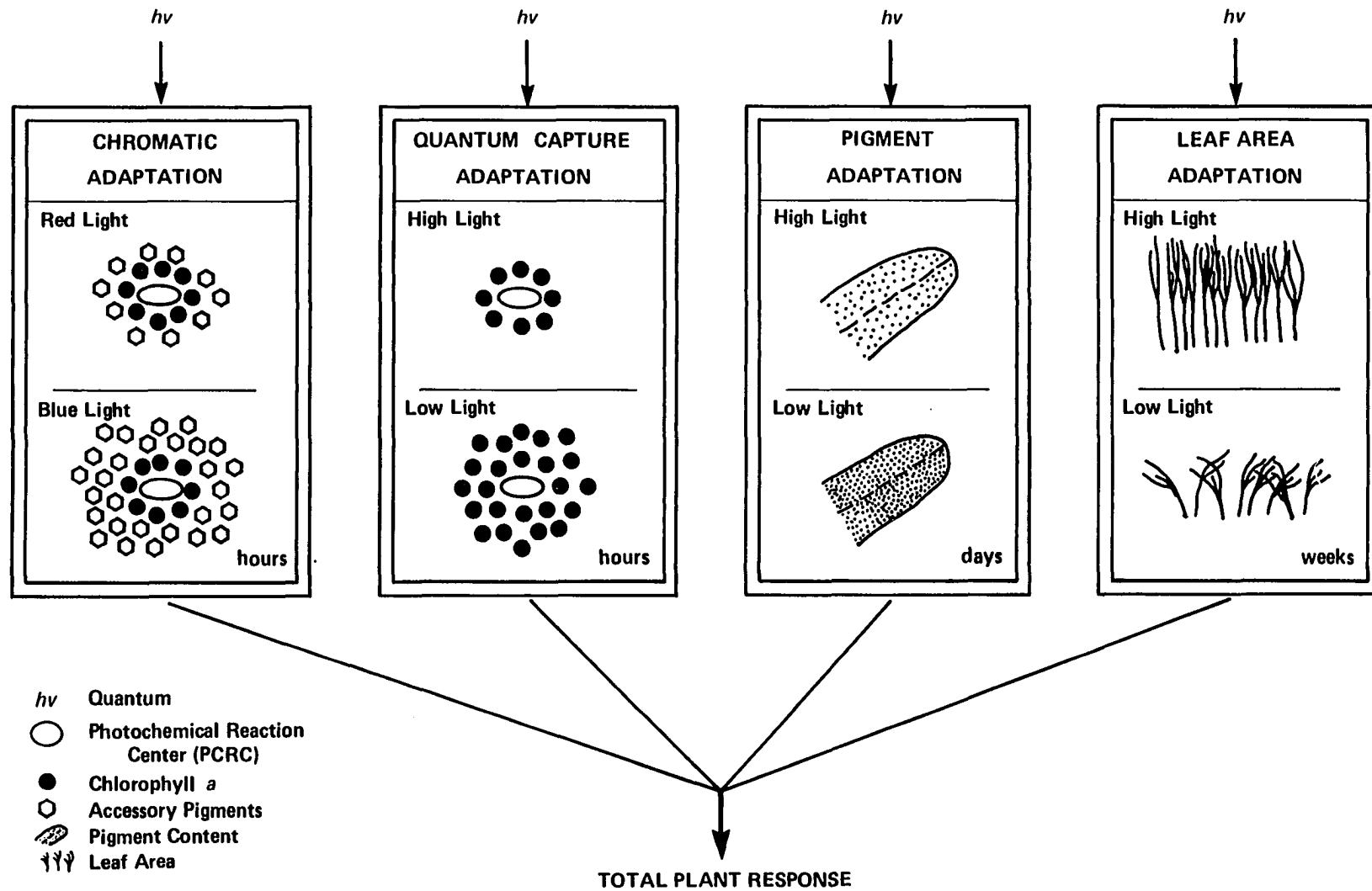


Figure 1. A conceptual model of light adaptations by plants represented by a four way adaptive scheme with predicted plant responses under different light regimes and time scale for adaptive response.

accessory pigments determine the relationship between photosynthetic efficiency and radiant energy wavelength, often expressed as an action spectrum (Haxo and Blinks, 1950).

This model proposes that plants can most efficiently absorb light relatively enriched in the red wavelengths (unfiltered light) with a pigment complement rich in chl *a* (high ratio of chl *a* to accessory pigments). Light relatively enriched in the blue and green wavelengths (light filtered by water or leaf canopies) is most efficiently absorbed by plants with relatively more accessory pigments (low ratio of chl *a* to accessory pigments). The chl *a* to chl *b* ratio is used in this study as an estimate of the chl *a* to accessory pigment ratio. This measure of the chromatic adaptation ignores the carotenoid accessory pigments in *Zostera* but does include the major accessory pigment, chlorophyll *b*.

The quantum capture adaptation is related to the functional state of the photosynthetic pigments. This model recognizes the pigment functional state as a major adaptive mechanism although few studies have explored the ecological implications of this recently recognized adaptation (Clough *et al.*, 1979). The capability of determining the amounts of photochemical reaction centers (PCRC = chl *a* molecules capable of exciting electrons) and light harvesting pigments (LHP = molecules that transfer light energy to the PCRC) has provided a measure of the efficiency of quantum capture by pigments (cf. Sestak and Demeter, 1976).

This model predicts relatively lesser amounts of LHP (lower LHP/PCRC) in high light intensities and relatively greater amounts of LHP (higher LHP/PCRC) in reduced light intensities. Terrestrial data from

Berry (1978) supports this hypothesis; a "shade" plant had a higher LHP/PCRC (approximated by chl $\alpha + b$ /photosystem 1 PCRC) than a "sun" plant and the "sun" plant increased the LHP/PCRC ratio with reduction of light. Kawamura *et al.* (1979) measured the entire pigment complements of both photosystems (I and II) in several species of algae and found higher LPH/PCRC values in reduced light and lower LPH/PCRC values in higher light. In this study the ratio of chl α to chl b is used as a crude indicator of the LHP/PCRC inverse. The chl α molecules are the only pigment containing PCRCs while chl b molecules are entirely LHPs. Using the chl α to chl b ratio as an estimator of quantum capture adaptation assumes the chl α molecules contain a constant proportion of PCRCs.

Pigment adaptation refers to the change in the amount of photosynthetic pigments as a response to the changes in light quantity. The concept of changes in pigment amount in relation to the amount of light has been recognized for some time (Boysen-Jensen, 1933). A more refined approach expresses this adaptive mechanism in terms of leaf chlorophyll concentration as a function of light intensity (Gabrielsen, 1940, 1948). In the aquatic realm, changes in pigment content of phytoplankton as function of irradiance have been noted (cf. Steemann-Nielsen and Jørgensen, 1968).

This model predicts increasing amounts of chlorophyll per leaf area with decreasing light intensity. The two major pigments in *Zostera*, chlorophylls α and b , are analyzed as a function of leaf area to assess pigment adaptation.

Leaf area adaptation is the relationship between the plant's light absorbing surface and light intensity. The leaf area distribution of plant canopies has a large influence on the interception of photosynthetically active radiation (PAR = 400-700 nm light energy) (cf. Monsi *et al.*, 1973). In an early study, Monsi and Saeki (1953) related the leaf inclination of plant canopies to the interception of light. Since then, vertical and horizontal leaf distribution, leaf arrangement and inclination, and light regimes within plant canopies have been investigated (Monsi *et al.*, 1973). The various leaf canopy structure adaptations to light have been simplified for this conceptualization. Erect leaf canopies (vertical leaf orientation) generally absorb and utilize light more efficiently than more planar leaf canopies (horizontal leaf orientation) (Tanaka, 1972). Also, higher irradiances can support higher leaf areas than can low irradiances (Mooney, 1972).

The scale of the leaf area adaptation as expressed in this study is on the plant community level, while the preceding adaptations are physiological adaptations within a single plant. The model predicts a dense, erect leaf canopy at high light intensities and a sparse, non-erect leaf canopy at low light intensities. This adaptation is assessed by determining the leaf area distribution within the leaf canopy and by integrating the leaf area of the canopy over a unit of ground surface (LAI = one-sided leaf area index). LAIs are useful for comparison of light absorbing surface within and between ecosystems.

The objective of this research was to assess the light adaptations of a seagrass ecosystem as conceptualized in the four way adaptive

scheme. Gradients of light quality and quantity are found within leaf canopies and with varying water depth. Consequently, this study investigates light adaptations within vertical profiles of the leaf canopy and on a transect of variable water depths. *In situ* light perturbation experiments were used in conjunction with the study of the natural system. The *Zostera* plants were analyzed for chl *a*/chl *b* (chromatic and quantum capture adaptations), chl *a+b*/leaf area (pigment adaptation) and leaf area distribution and production (leaf area adaptation).

MATERIALS AND METHODS

Study Site

One of the largest stands ($\approx 115 \text{ km}^2$) of *Zostera marina* in the world is in Izembek Lagoon, Alaska ($55^{\circ}15'N$, $163^{\circ}05'W$). This large lagoon ($\approx 218 \text{ km}^2$) is a shallow embayment of the Bering Sea located on the distal end of the Alaska peninsula (Figure 2). Izembek Lagoon has a mean tide range of 1 meter; 67 percent of the lagoon water exchanges daily with the Bering Sea (Barsdate *et al.*, 1974). Little fresh water dilution occurs, however there are significant temperature changes in the lagoon (Biebl and McRoy, 1971). Sediment accumulation and binding by eelgrass plants form raised benches or mud flats. In Izembek Lagoon the raised benches cover most of the lagoon (78%) with a network of tidal channels accounting for the remaining 22 percent (McRoy, 1966).

A 0.7 km transect from intertidal to subtidal was used as a representation of areas throughout the lagoon (Figure 3). Six sampling sites were selected along the transect (A-F). The transect is located in a

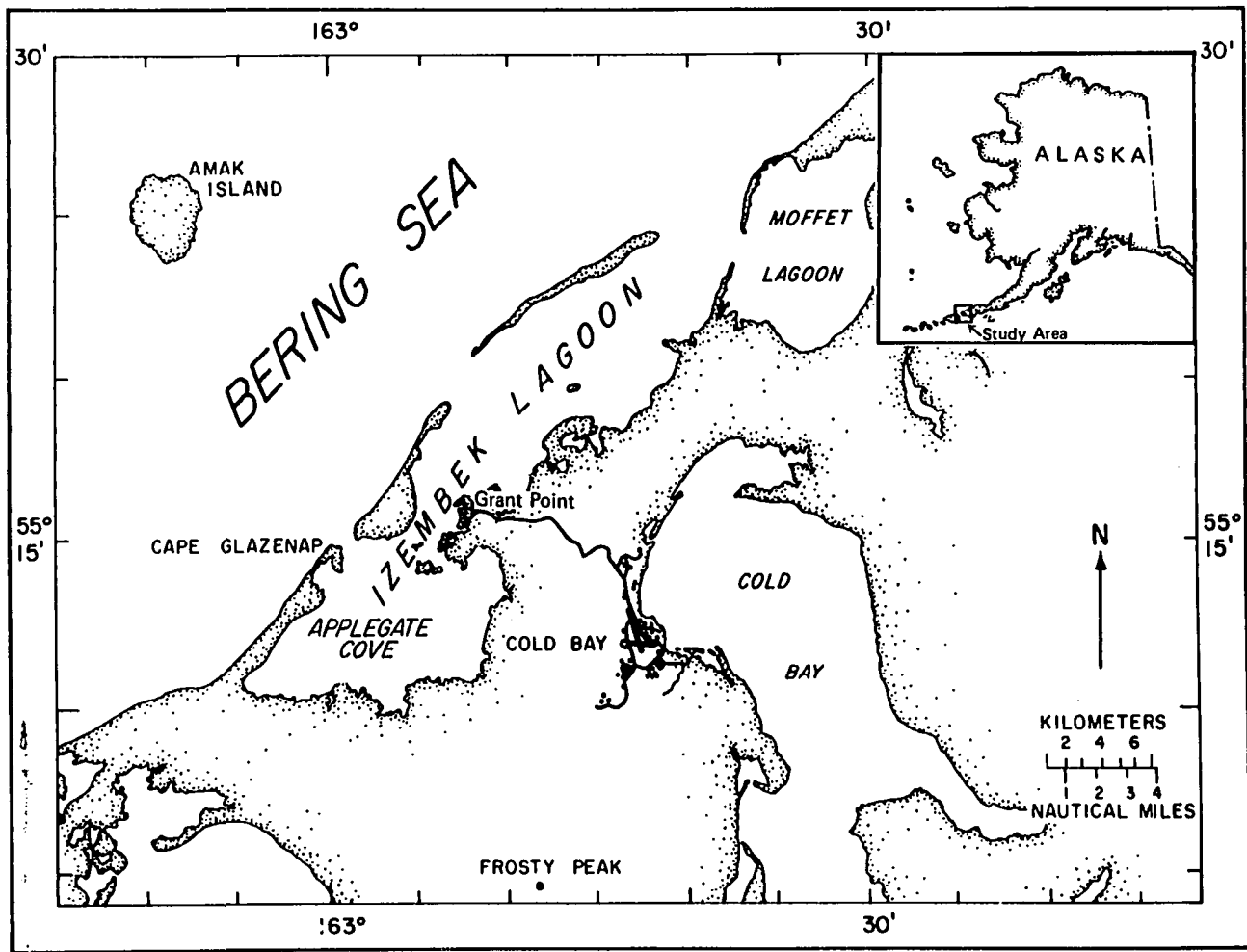


Figure 2. Location of Izembek Lagoon, Alaska.

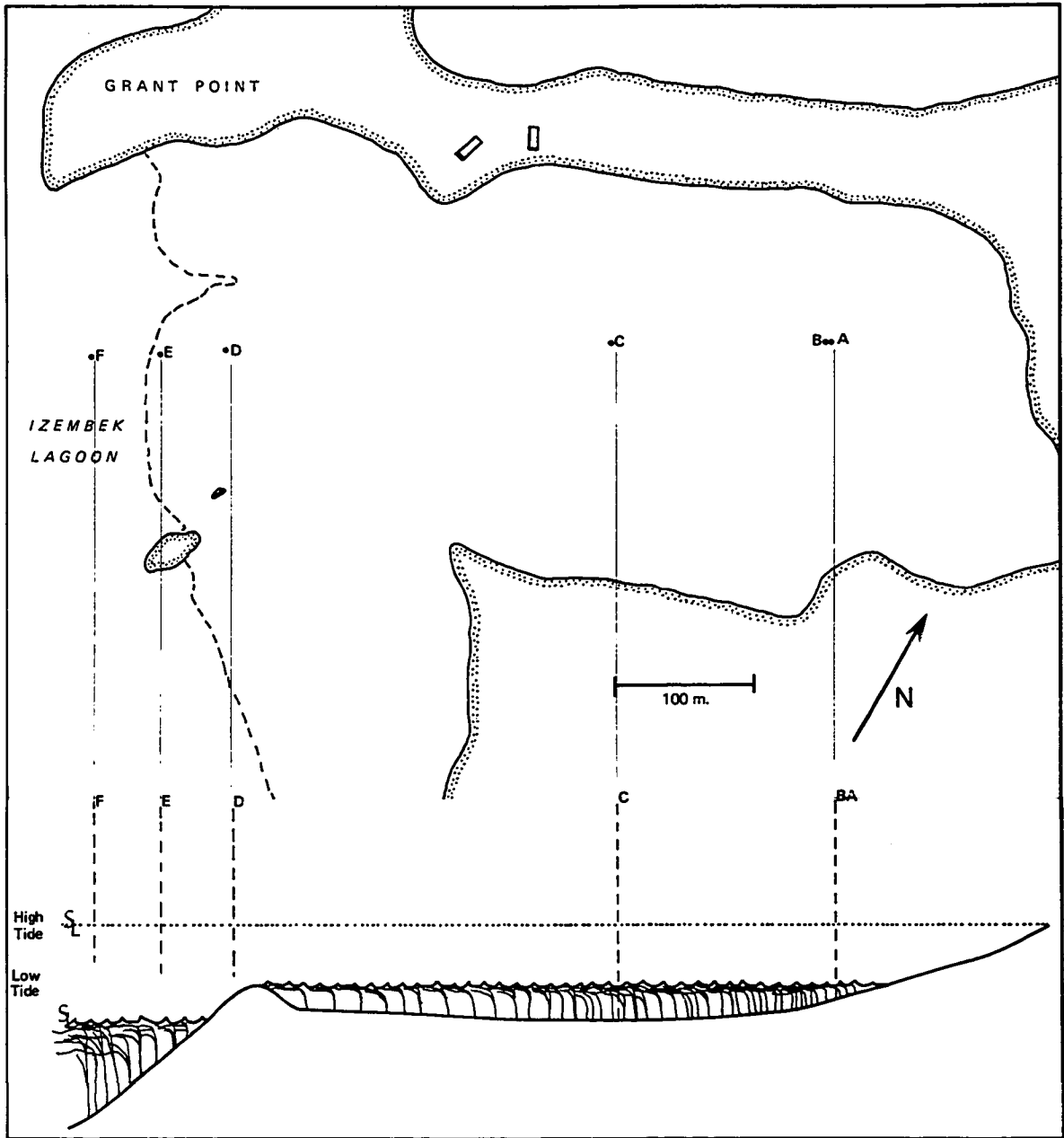


Figure 3. Grant Point transect map showing locations of the six sampling stations (above). Diagrammatic cross section of the transect at low tide with a projected high tide (below).

small inlet in the lagoon; the configuration of the basin and the tide range produce extended ebb tides and rapid flood tides in the inlet. The basin has the characteristics of a tide pool (Biebl and McRoy, 1971); the shallow water stations (A-C) remain submerged at the lowest neap tides. The stations with deeper water at high tide (D-F) are actually relatively more exposed at low tide.

More than a spatial sampling scheme, the transect represents an annually reoccurring gradient of eelgrass system development that is reflected in several plant community parameters (McRoy, unpublished data). The trends exhibited in plant growth form, stratification, reproductive strategies, life cycles, and production/biomass relationships reflect a gradient of ecosystem development as delineated by Odum (1969).

Plant Pigment Analysis

Leaf samples were collected weekly for a three month period (June-August) at low tide from the six sampling sites, stations A-F (Appendix). Vegetative (non-reproductive) shoots were clipped at the sediment-water interface and placed in water tight bags out of direct sunlight. Prior to analysis, the *Zostera* shoots were stored overnight in a seawater tub in reduced light. Three to six shoots with undamaged leaves roughly equal to the average leaf canopy height were selected for pigment analysis. Leaf epiphytes were removed by scraping the leaf surface with tissue paper and a razor blade. Four samples were taken at 5-10 cm intervals from the base of the shoot; two samples for leaf area ($\pm 0.01 \text{ cm}^2$)/dry weight ($\pm 0.001 \text{ g}$) determinations and two samples for chlorophyll extraction.

A manually operated tissue grinder or mortar and pestle was used in reduced light to macerate the leaf segments until the plant tissue was visibly destroyed. Pigment extraction was performed with 90 percent acetone and a small amount of $MgCO_3$. Extraction was carried out in a dark refrigerator for 20-24 hours. Natural settling of the plant tissue during extraction resulted in blank corrections less than 0.010 absorbance units. Absorbance values were read at 665 and 645 nm with a 750 nm turbidity correction on a Baush & Lomb Spectrophotometer 70 with 1 cm disposable cuvetts. The chlorophyll extraction procedure was largely that of Vollenweider (1969) while calculations were made with SCOR/UNESCO (1966) trichromatic equations modified for just chlorophylls α and b :

$$\text{mg chl } \alpha/\text{dm}^2 \text{ or g} = (11.64 \times \text{OD}_{665} + -2.16 \times \text{OD}_{645}) \times \text{CF}$$

$$\text{mg chl } b/\text{dm}^2 \text{ or g} = (-3.94 \times \text{OD}_{665} + 20.97 \times \text{OD}_{645}) \times \text{CF}$$

OD₆₆₅ = Corrected optical density at 665 nm

OD₆₄₅ = Corrected optical density at 645 nm

$$\text{CF} = \frac{\text{vol acetone (ml)} \times \text{leaf area (dm}^2\text{)} \text{ or dry wt (g)}}{\text{cell length (cm)} \times 1000}$$

Leaf Canopy Structure

Vegetative shoots were collected weekly throughout the three month sampling period. Of the shoots collected at each of the six stations (A-F), 20 intact shoots of full canopy height were chosen for leaf area and leaf dry weight determinations. The leaf canopy was sectioned into 5 or 10 cm segments by the stratified clip technique (Monsi and Saeki, 1953). Leaf area was determined with a Lambda LI-3100 area meter

($\pm 0.01 \text{ cm}^2$), samples were then dried at 90°C for 24 hours, cooled to room temperature and weighed ($\pm 0.001 \text{ g}$).

Estimates of shoot density and plant biomass were made by first clipping shoots at the sediment-water interface, and then counting and weighing the shoots within the sampling area ($0.02\text{--}0.25 \text{ m}^2$). Twenty shoot density/plant biomass samples were taken at each station throughout the three month period. Leaf area index was calculated by the product of the vegetative shoot density and the average one-sided leaf area/shoot. A correction term was used to adjust the LAI values to the corresponding leaf biomass values.

Light Manipulation Experiments

A sun reflector was placed in the eelgrass bed at two locations; Station A (high shoot density) and Station D (high LAI). The reflectors were $1.2 \times 2.4 \text{ m}$ pieces of plywood with several coats of high gloss white paint (Figure 4). Supported by fence posts and guylines, the reflectors were oriented vertically facing south. Incident PAR was measured by a hand held quantum sensor (LI-185A) placed 1 cm below the water surface. The maximum PAR increase was ≈ 50 percent 20 cm in front (south) of the reflectors at low tide, with decreasing additions of light at increasing distances away from the reflectors.

Light shading screens were also placed in the eelgrass bed at Stations B and D (Figure 4). The 2.8 m^2 hexagon screens were made of three layers of fine mesh fiberglass screening supported by a plastic pipe frame. They were buoyed by styrofoam floats and remained $\approx 10 \text{ cm}$ above

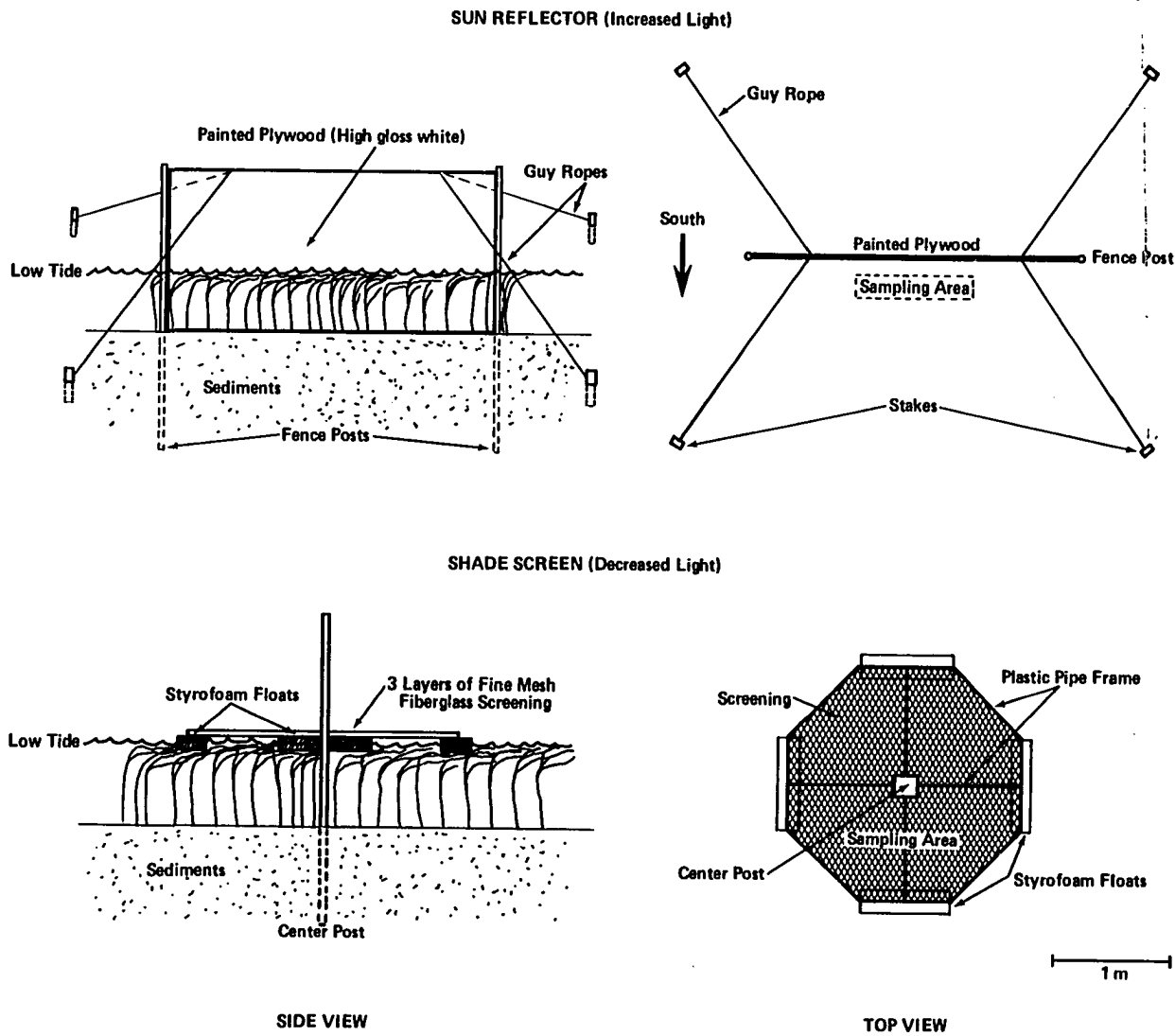


Figure 4. Top and side view of sketches of sun reflector (above) and light shading screen (below) used in the light manipulation experiments.

the water surface as they moved up and down the tides, affixed from lateral movement by a central rod. PAR under the shading screen was \approx 20 percent of incident PAR.

Leaf Production

Leaves were marked by punching small holes in ca. 30 shoots at each treatment, a variation of the staple technique of Zieman (1968). The holes were punched with a syringe needle a few millimeters above the bundle sheath. The shoots were harvested 14 days after the holes were punched and the scars located. Leaves on a shoot were sectioned into two categories: "new leaf growth" and "initial leaf." "New leaf growth" was that which had been produced since the holes were punched, between the sheath and scars. "Initial leaf" was that which had been present at the time of marking; the stem portion of the plant and between the scars and the leaf tips. The "new leaf growth" and "initial leaf" were measured for leaf area. A ratio of leaf production was calculated; new leaf area/initial leaf area. This was divided by the number of days (14) and the inverse taken as the standing stock turnover time (in days).

RESULTS

Plant Community Parameters

Several spatial trends are evident in the plant community parameters (Figure 5). The total shoot density generally increases toward tide pool stations. The anomaly of the general tendency of density, Station A, is likely due to an edge effect. The inshore areas of

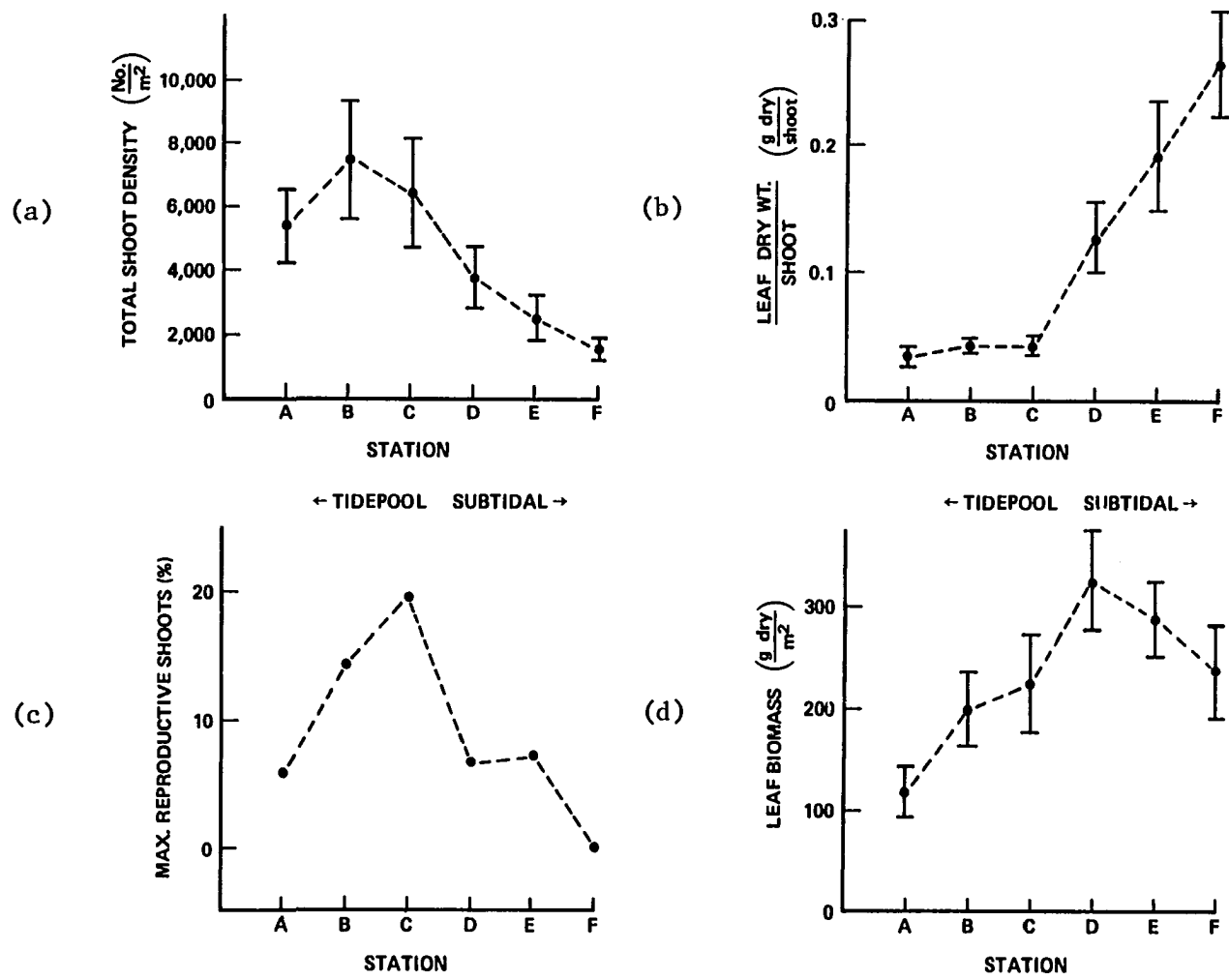


Figure 5. Plant community parameters along the transect (June-August, 1978). (a) Total shoot density ($\bar{X} \pm 95\%$ C.I.); (b) leaf dry weight per shoot ($\bar{X} \pm 95\%$ C.I.); (c) leaf biomass ($\bar{X} \pm 95\%$ C.I.); and (d) maximum percent of reproductive shoots (% of total shoots).

Izembek Lagoon are periodically scoured by winter ice. These localized perturbations lead to reduced plant growth; the plants are maintained in a colonizing state. While the tide pool plants are very dense, they also are relatively small as indicated by lower leaf dry weight per shoot values. The small, dense plants of the tide pool are contrasted with the large, sparse plants of the subtidal. The leaf biomass (per m^2) has a maximum at Station D, decreasing both inshore and offshore. The reproductive strategy of the *Zostera* plants is variable. In general, the subtidal plants largely or entirely produce new shoots by lateral branching of the rhizome, a form of vegetative reproduction. The small tide pool plants produce sexually reproductive shoots; up to 20 percent of the shoots bear pollen and flowers.

Pigment Ratio

The ratio of chl *a* to chl *b* was found to be significantly higher ($\alpha = 0.05$) with increasing distance above the base of the shoots (Figure 6). Chl *a*/chl *b* also showed significant variation ($\alpha = 0.05$) between stations, with the higher ratios found in the more subtidal stations, D-F (Figure 6). The overall trend is one of increasing chl *a*/chl *b* in the upper portions of the leaf canopy and in the more subtidal stations. The statistical determination of confidence intervals and comparison of means was done with the assumption that the ratio was normally distributed. This assumption was endorsed by a frequency histogram distribution of chl *a*/chl *b* (Figure 7).

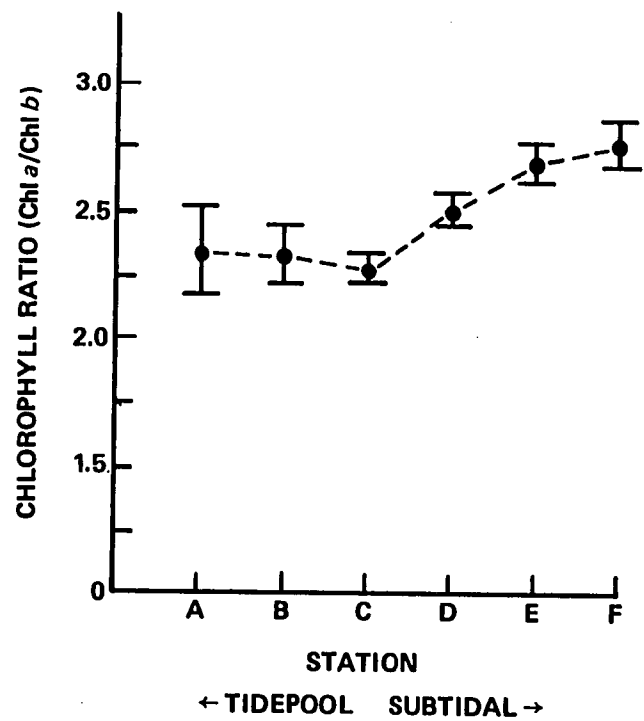
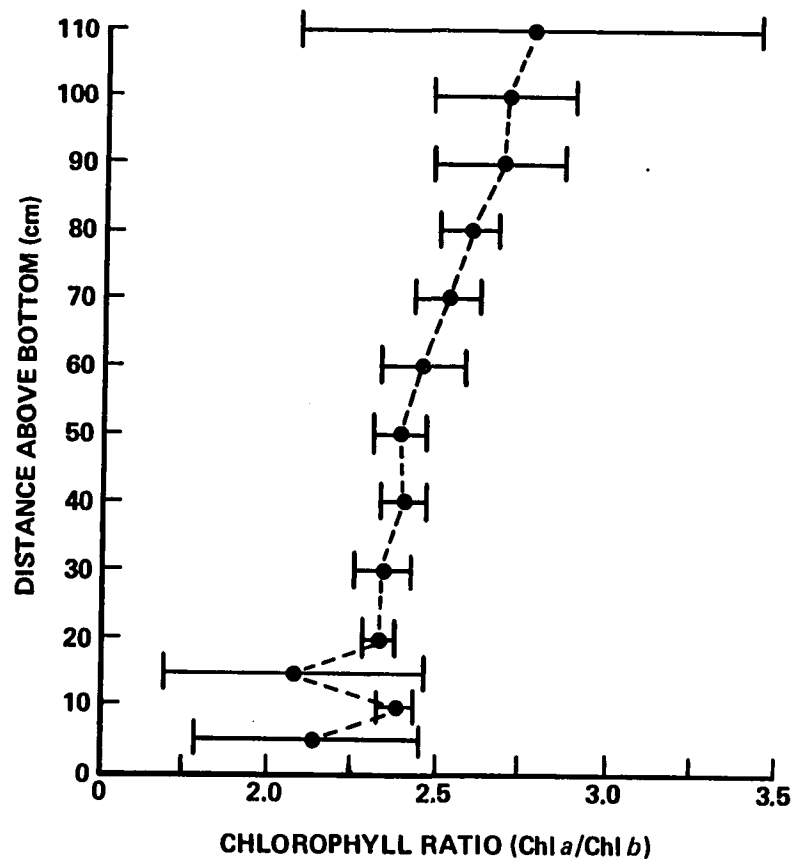


Figure 6. Ratio of chlorophyll *a* to chlorophyll *b* of *Zostera marina* leaves (June-August, 1978). Chl *a*/Chl *b* ($\bar{X} \pm 95\%$ C.I.) relative to distance above the bottom at all stations (left). Chl *a*/Chl *b* ($\bar{X} \pm 95\%$ C.I.) relative to station (right).

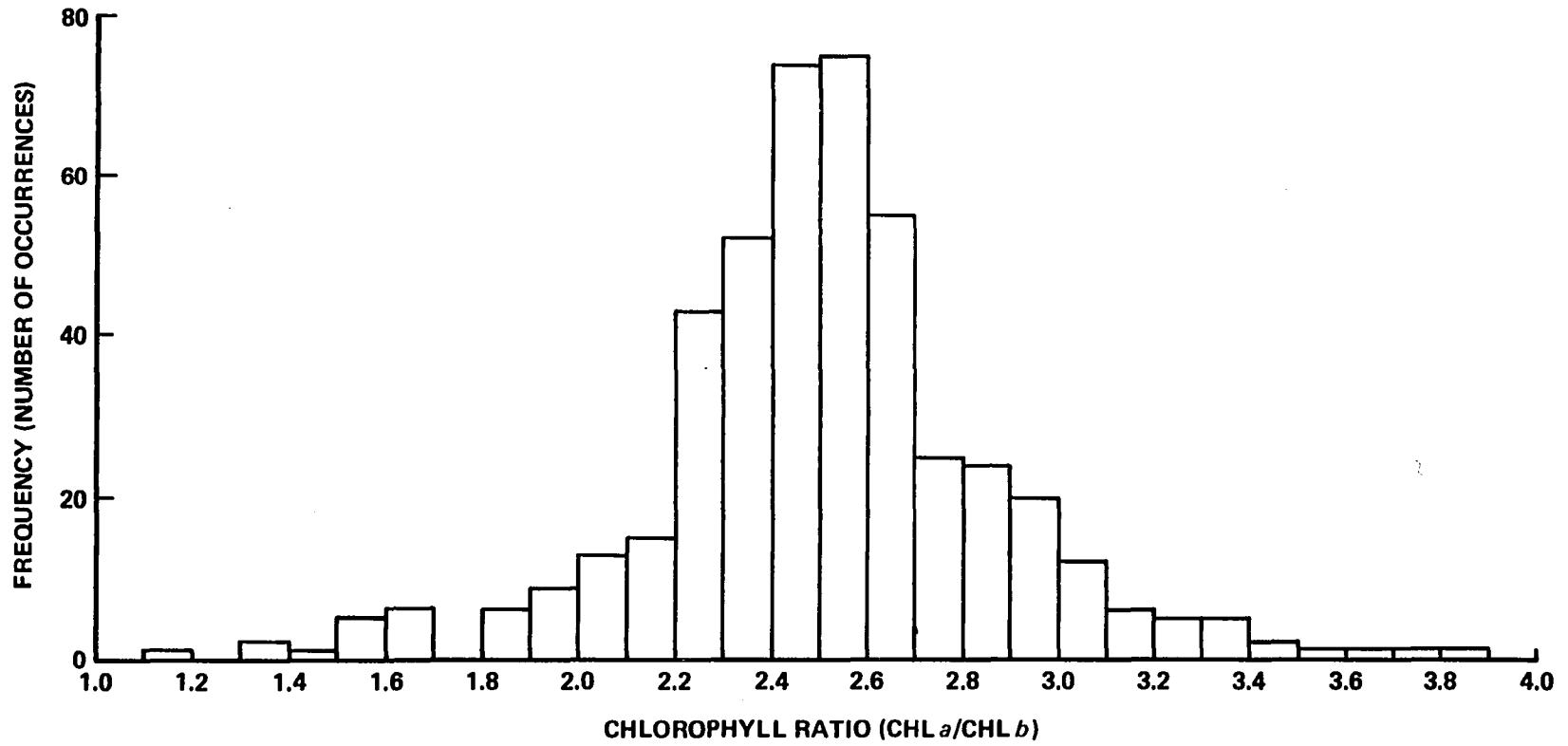


Figure 7. Frequency histogram of chlorophyll *a* to chlorophyll *b* ratios.

Pigment Concentration

The concentration of chl *a* varied within individual shoots (Figure 8). The distribution of plant pigments appears to be related to the growth characteristics of *Zostera*. The youngest leaves on a shoot grow from the basal meristem between the next youngest leaves. The oldest leaf on a shoot (furthest from the center) contained the greatest concentration of pigments with lesser concentrations evident in the younger leaves. The variation of chlorophyll content within single shoots leads to variation between shoots. The variable number of leaves per shoot (mode = three leaves/shoot) results in shoots with younger leaves (fewer leaves/shoot) and shoots with older leaves (more leaves/shoot). The shoots with younger leaves have relatively less chlorophyll than shoots with older leaves.

A large sample containing both young and old leaves, and small and large shoots integrates the variations within and between shoots in one measurement. Employing this sampling scheme, the chl *a+b* concentration per unit leaf area did not vary significantly ($\alpha = 0.05$) throughout the leaf canopy (Figure 9). Significant changes ($\alpha = 0.05$) in the mean chl *a+b* content per leaf area did occur between all six stations (Figure 9), largely due to high chl $a+b/dm^2$ values at Station C. No significant differences were evident when comparing the mean chl $a+b/dm^2$ values without Station C. The significance of the high chl $a+b/dm^2$ values at Station C is questionable; the arbitrary fractioning of the leaf canopy can lead to a relative sample weighting of the stem versus leafy portions of the plants. For example, a small sampling of the leaf canopy would not likely contain any of the stem portion of the plant (less chlorophyll), while more intense sampling probably would contain stem portions.

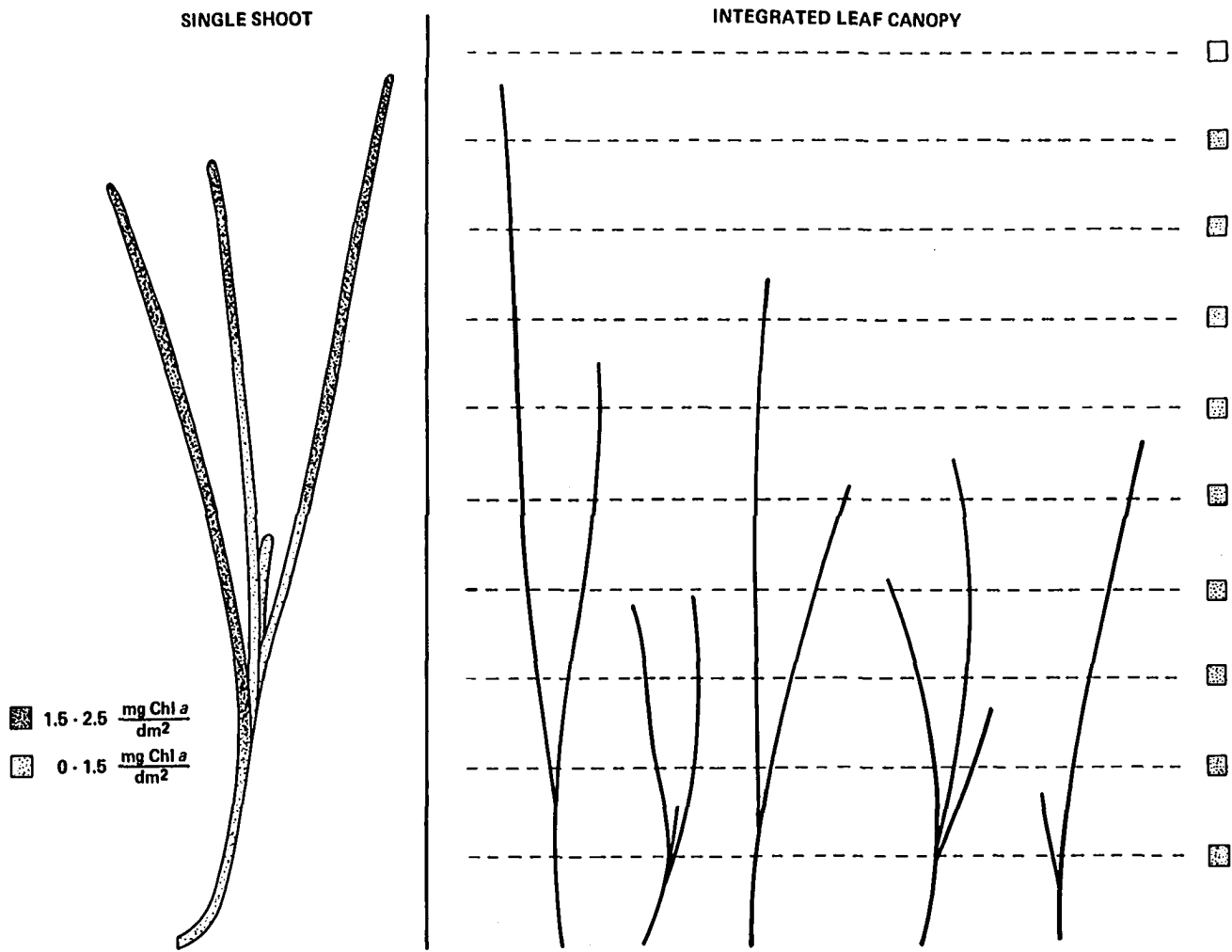
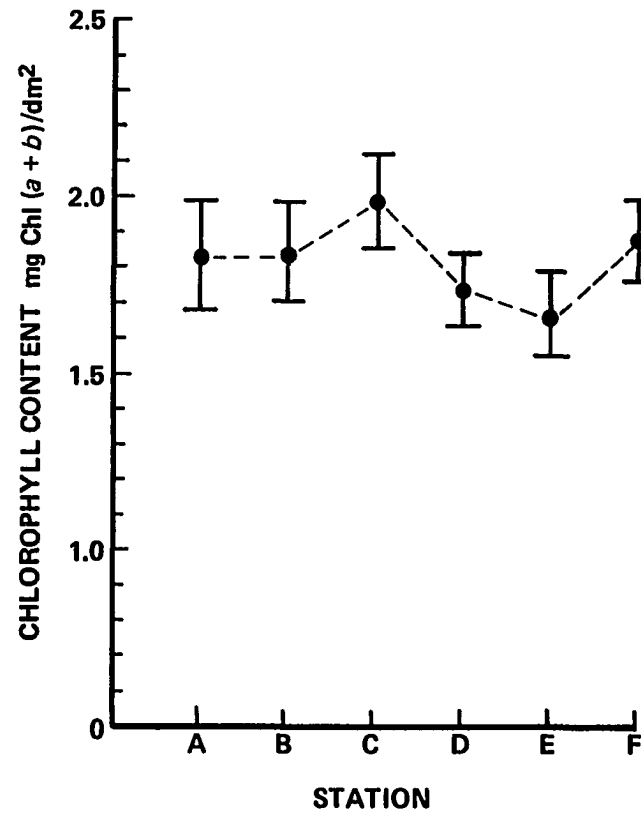
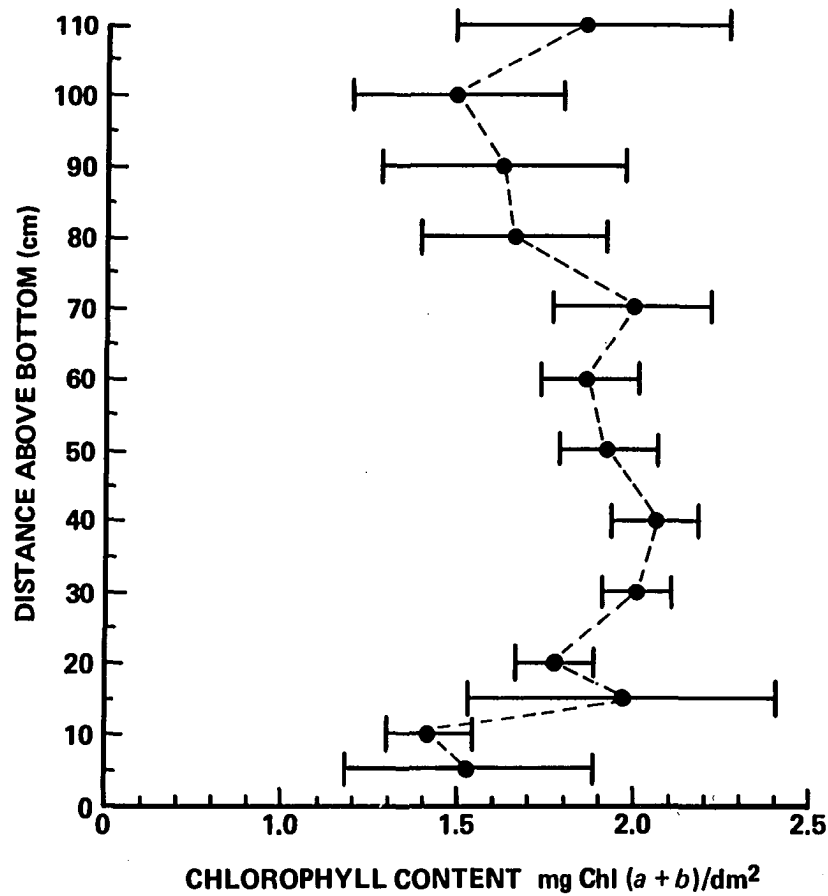


Figure 8. Chlorophyll *a* content within a single shoot of *Zostera marina* (left) compared to chlorophyll *a* of integrated leaf canopy samples (right).



← TIDEPOOL SUBTIDAL →

Figure 9. Total chlorophyll content of *Zostera marina* leaves (June-August, 1978). Chl *a+b* per leaf area ($\bar{X} \pm 95\%$ C.I.) relative to distance above the bottom at all stations (left). Chl *a+b* per leaf area ($\bar{X} \pm 95\%$ C.I.) relative to station (right).

Leaf Area

The distribution of leaf surface area represents a measure of the light absorbing area. Unlike chlorophyll ratio or concentration, the leaf area and leaf biomass are not uniformly distributed throughout the leaf canopy (Figure 10). The highest leaf area is found at roughly one fifth of the total canopy height, with a gradual diminution of leaf area above and below this point. Leaf biomass, on the other hand, is greatest near the bottom, decreasing toward the top of the leaf canopy (Figure 10). The ratio of leaf area to leaf biomass (specific leaf area) or the inverse ratio (specific leaf weight) is constant throughout the leaf canopy except for the stem region. The overall mean specific leaf area is $2.5 \pm 0.1 \text{ dm}^2/\text{dry g}$ ($\bar{X} \pm 95\% \text{ C.I.}$) and the corresponding specific leaf weight is $0.39 \pm 0.02 \text{ dry g/dm}^2$ ($\bar{X} \pm 95\% \text{ C.I.}$).

The vertical distribution of leaf area follows the same general pattern at the six stations. This is evident when the canopy heights and leaf area maximums of the different stations are normalized. The plots of relative canopy height and relative leaf area of the six stations are markedly similar (Figure 11). These normalized graphs reveal that the small, dense leaf canopies of the tide pool have the same relative distribution of leaf area as the large, well developed canopies of the subtidal stations.

While the relative distribution of leaf area in the plant canopy was essentially the same at all stations, the absolute leaf areas changed. The LAI, a measure of the absolute leaf area, does vary between stations (Figure 12). The mean LAIs are significantly different

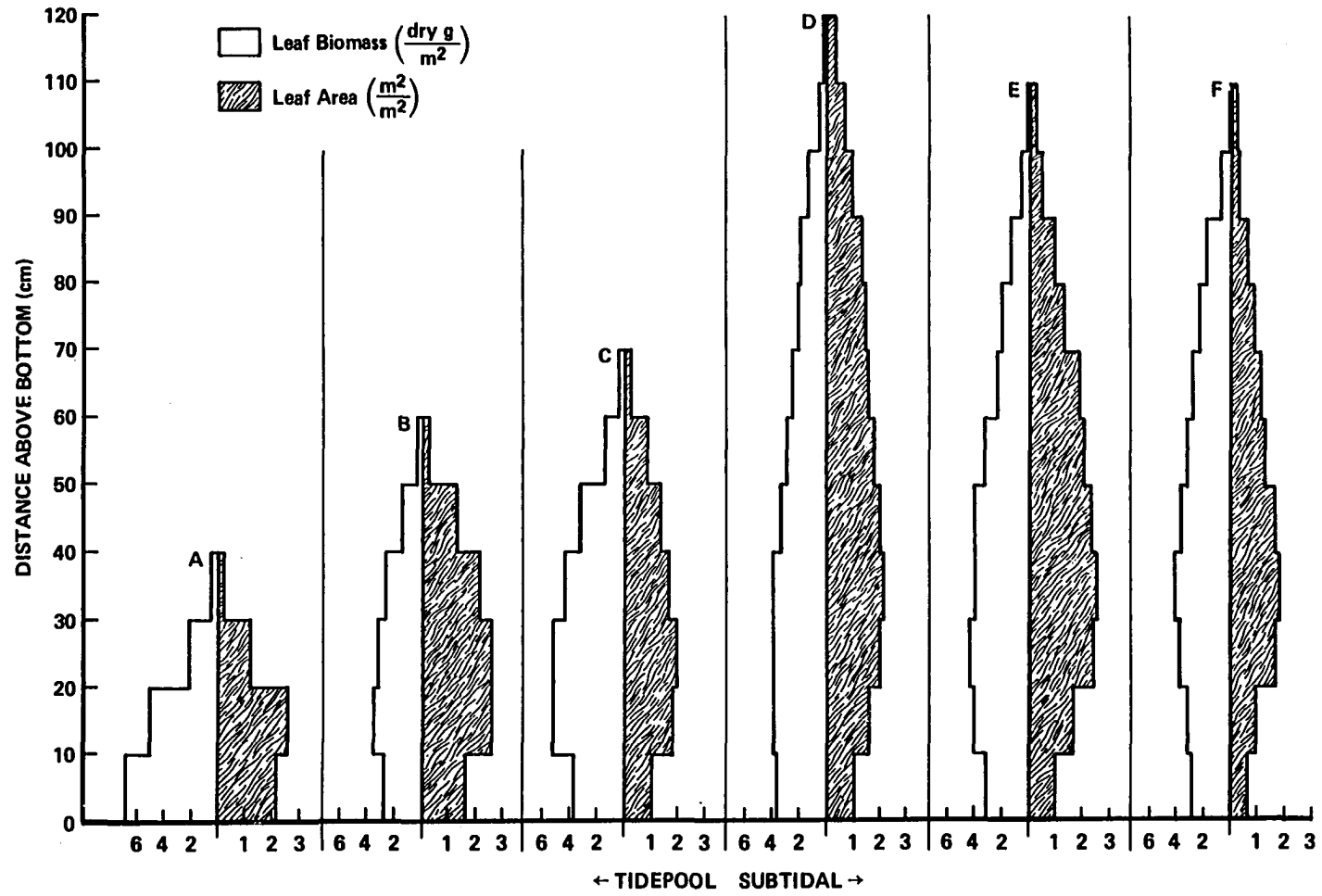


Figure 10. Leaf canopy structure of *Zostera marina*. Vertical distribution of leaf area and leaf biomass along the transect (Stations A-F) at the seasonal maximum biomass (20 July 1978).

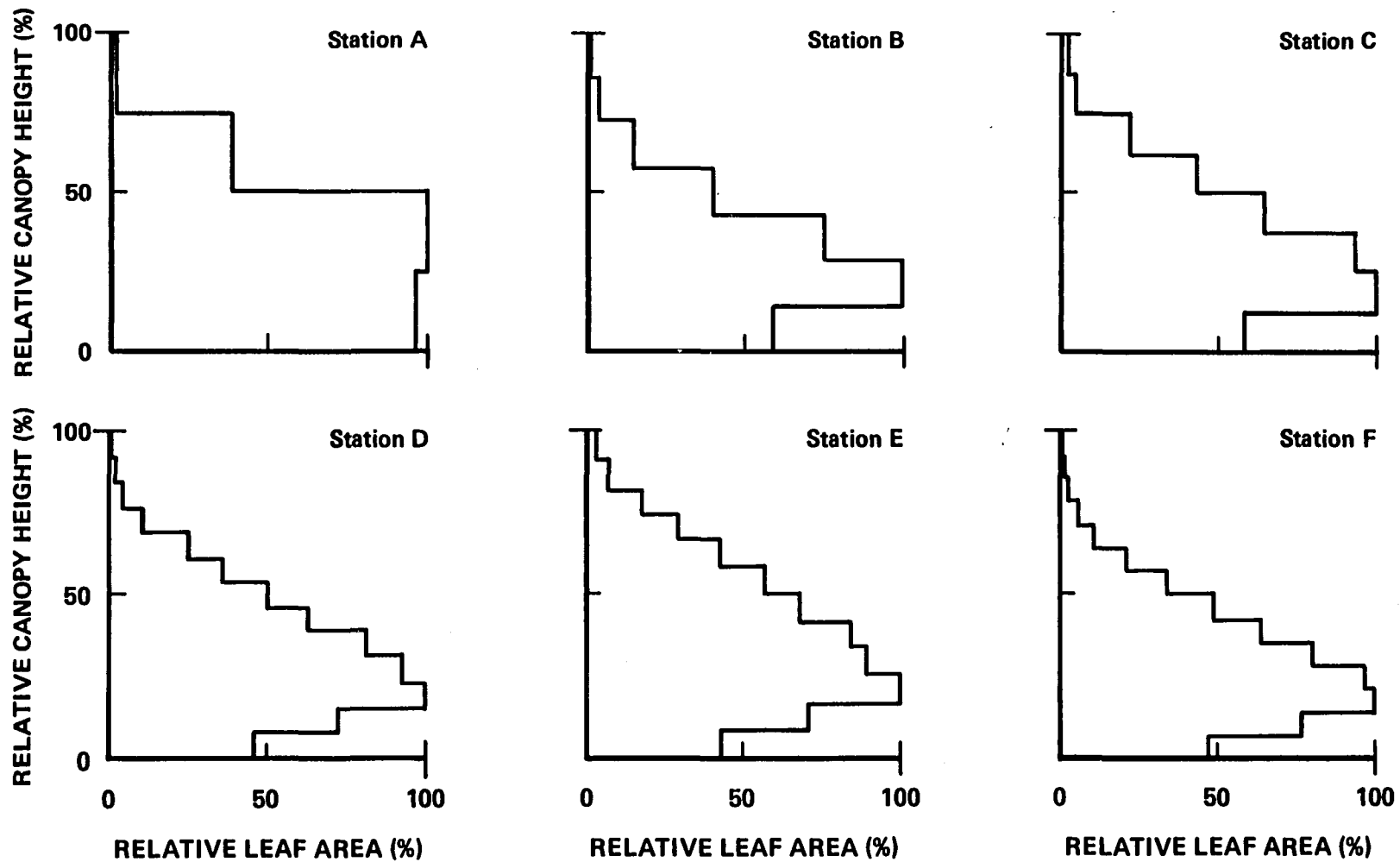


Figure 11. Relative leaf area (% of maximum) and relative canopy height (% of total) distributions for the six sampling stations (June-August, 1978).

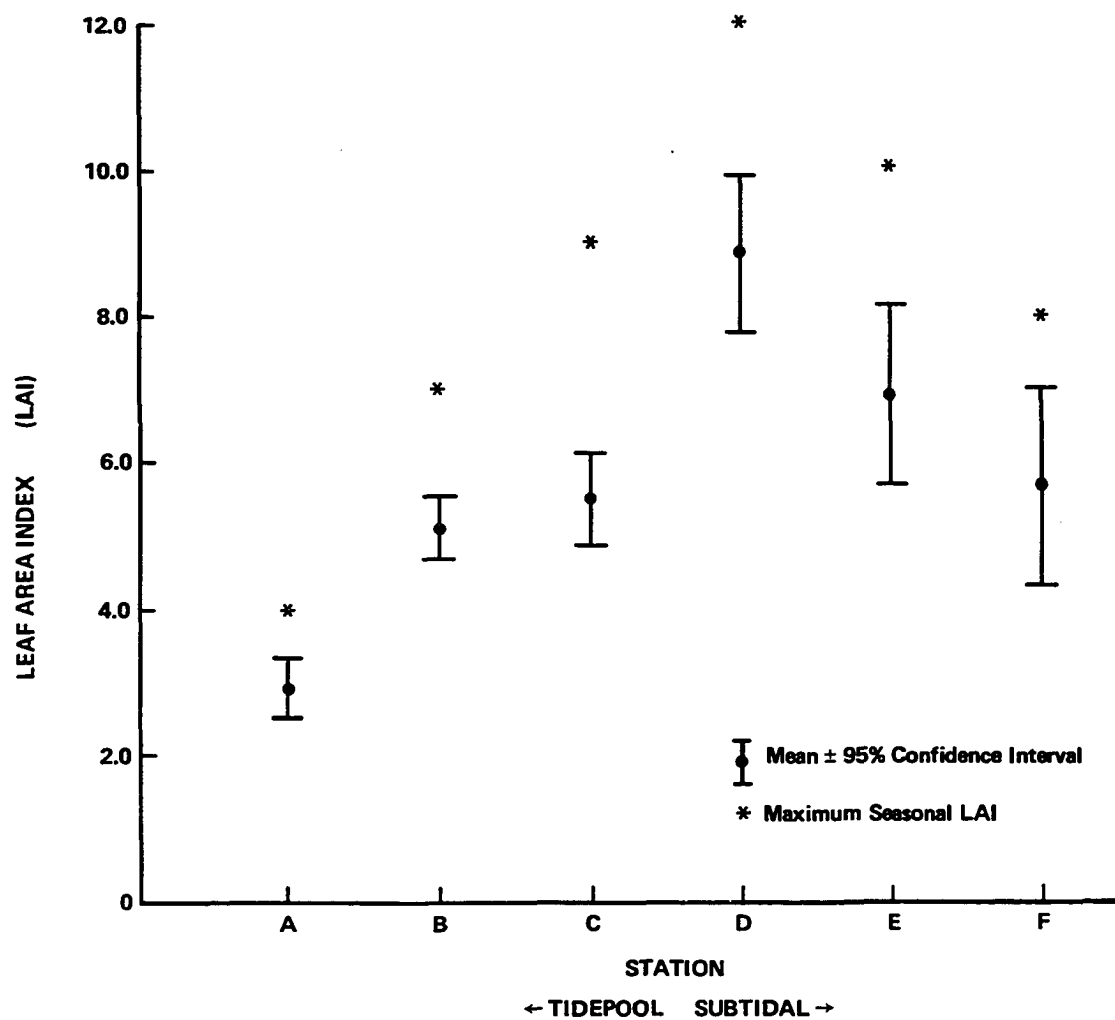


Figure 12. Mean and seasonal maximum LAI along the transect (June-August, 1978).

from each other ($\alpha = 0.05$) with a mid-transect maximum (Station D). The 1978 maximum LAI was 12, in 1979 the highest observed LAI was 17.

Light Manipulation Experiments

The different *in situ* experimental light regimes were analyzed for plant response to the altered light conditions. At both stations, B and D, the chlorophyll ratios and concentrations were not significantly altered ($\alpha = 0.05$) during the 14 day experiments (Table 1). On the other hand, the standing stock turnover times, determined from the leaf production measurements, were substantially different at the two stations. The turnover times at Station B were relatively short, with longer turnover times at Station D. At Station B there was little variation in turnover time under the different light regimes. However, at Station D a faster turnover was indicated for the increased light condition.

DISCUSSION

Testing the Conceptual Model

Changes in light quality in nature are inevitably accompanied by changes in light quantity. Consequently, the separation of the light quality and light quantity adaptations in plants is generally difficult. Björn (1976) predicts a 12 nm absorbance peak decrease with every ten-fold decrease in light quantity. The accessory pigments, especially chl *b* with 100 percent conversion efficiency of light energy to chl *a*, act entirely as light harvesting pigments. The accessory pigments also

Table 1. Chlorophyll ratios and amounts ($\bar{X} \pm 95\%$ C.I.) and standing stock turnover times in the light manipulation experiments.

Station	Light Regime	Chlorophyll Ratio (chl <i>a</i> /chl <i>b</i>)	Chlorophyll Amount (chl <i>a</i> + <i>b</i> /dm ²)	Turnover Time (days)
B	Decreased	2.3 ±0.0	2.4 ±0.4	44
B	Control	2.4 ±0.1	2.4 ±0.1	37
B	Increased	2.3 ±0.2	2.4 ±0.8	34
D	Decreased	2.4 ±0.0	2.2 ±0.1	172
D	Control	2.4 ±0.2	2.4 ±0.3	160*
D	Increased	2.4 ±0.0	2.2 ±0.1	65

*Estimation

absorb light at shorter wavelengths than chl *a*. Thus a plant could adapt to both a spectral shift and concomitant decrease in irradiance simply by increasing the relative amounts of accessory pigments. The ratio of chl *a* to accessory pigments can, therefore, be a response to light quality and/or light quantity. This study uses the chl *a* to chl *b* ratio as an approximation of the chl *a* to accessory pigment ratio. Chl *a*/chl *b* is used to assess both chromatic and quantum capture adaptations.

The conceptual model predicts a decrease in the chl *a*/chl *b* ratio in the lower portions of the leaf canopy with relatively more accessory pigments to absorb the shorter wavelength light and act as light harvesting pigments. Light becomes enriched in blue and green wavelengths and the intensity is diminished as it passes through the leaf canopy. A decrease of chl *a*/chl *b* in the lower canopy does occur in the *Zostera* leaves (Figure 6). The trend is similar in form but not in magnitude to that found in single eelgrass shoots by Stirban (1968). The range of chl *a*/chl *b* for single shoots of *Zostera marina* was 0.8-2.8 (base to tip), and in this study the range of integrated sample means is 2.1-3.0 (bottom to top).

Not only does the chl *a*/chl *b* decrease at the bottom of the leaf canopy (relatively more chl *b*), the relative carotenoid pigment concentration probably increases. Stirban (1968) has shown a decrease in the chl *a* to carotenoid pigment ratio toward the base of single *Zostera* shoots. The photosynthetic contribution of these pigments is not well defined; however, they have been found to absorb shorter wavelength light than chl *a* (Steemann-Nielsen, 1975).

The conceptual model predicts a decrease of chl *a*/chl *b* with an increase in water depth resulting in more light harvesting pigments absorbing diminished light at shorter wavelengths. The trend observed in *Zostera* indicates the reverse; an increase of chl *a*/chl *b* with increasing high tide water depth. This may not be non-light adaptive as it first appears. The long shoots and shallow low tide water depths at Stations D-F produce a temporary floating mat of eelgrass leaves in the top few centimeters of water. The ratios could be adaptive to only the low tide condition (possibly higher rates of photosynthesis). It also may be simply a morphological trait of *Zostera* to increase the chl *a*/chl *b* with time. The longer leaf turnover times, and consequently older leaves of Stations D-F and older leaf portions in the top of the leaf canopy, may account for the trends observed in chl *a*/chl *b*.

The effect of light quality on seagrass photosynthesis has been reported (Buesa, 1975). However, the changes in light quantity appear to be the overriding controlling factor in the depth distribution of tropical seagrasses (Buesa, 1975; Wiginton and McMillan, 1979). This suggests the chl *a*/chl *b* ratio of seagrasses can be regarded as a measure of the quantum capture adaptation rather than chromatic adaptation. A chl *a*/chl *b* trend with water depth was observed with some tropical seagrasses (Wiginton and McMillan, 1979); however, other temperate seagrasses did not demonstrate a depth gradient of chl *a*/chl *b* (Drew, 1978). Seaweeds on the other hand appear to adapt to both light quality and light quantity with changes in the chl *a* to accessory pigment ratio (Ramus *et al.*, 1976).

The physiological responses to light quality and quantity, both appraised by chl *a*/chl *b*, seem to be quite limited. The chl *a*/chl *b* of a plant is likely a characteristic of functional plant groupings (Keast and Grant, 1976). A general trend of increasing ratio with altitude is found in plants with chlorophylls *a* and *b* (Figure 13). The overall average chl *a*/chl *b* ratio of *Zostera* (2.5) falls on the lower end of the observed range (Table 2 and Figure 13).

A hereditary or genetic adaptation reflected in the plant genotype occurs on a different time scale than the aforementioned physiological type of adaptations. Chromatic adaptation is expressed as a phylogenetic trait; the pigment complement of algal types and higher plants is fixed (Steemann-Nielsen, 1975). The relative amounts of various accessory pigments can vary only between the major plant groupings. The successful invasion of the marine environment by land plants was probably delayed until the evolution of certain flowering plants (monocotyledons) (den Hartog, 1970). Higher plants have a complex leaf structure with only chlorophylls *a* and *b* plus an assortment of the ubiquitous carotenoids. As a result, they generally do not utilize blue light (common in seawater) very efficiently (Gabrielsen, 1940). The monocotyledonous plants have a relatively simple leaf structure leading to less light scattering (Inada, 1976). The graminoid growth form results in less light absorption by structural material (Mooney, 1972). The monocots also have the plasticity to develop structural modifications for life in the aquatic environment, e.g. epidermal chloroplasts (Hutchinson, 1975, p. 139). These morphological characteristics of monocots were

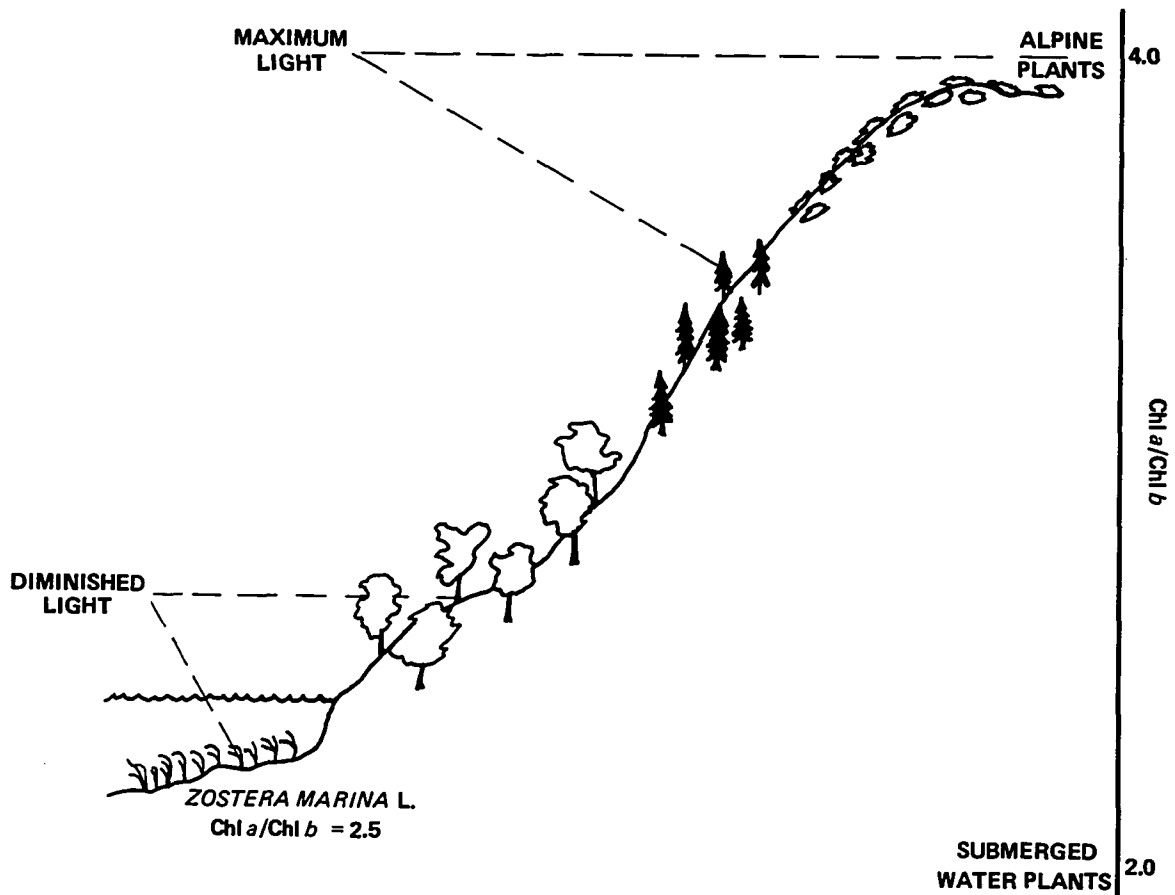


Figure 13. Range of chlorophyll *a* to chlorophyll *b* ratios found in plants (from Björn, 1976) with the *Zostera* chlorophyll ratio ($\bar{X} = 2.5$) from this study.

Table 2. Comparison of plant chlorophyll ratios and amounts.

Plant	mg chl <i>a</i> / g wet	mg chl <i>a</i> / g dry	mg chl <i>a+b</i> / g wet	mg chl <i>a+b</i> / dm ²	chl <i>a</i> / chl <i>b</i>	Reference
<i>Zostera</i>	0.48	1.8	0.68	1.81	2.48	This study
"	0.38	2.0				McRoy, 1966
"	0.30-1.20					McRoy, 1970
"					0.81-2.81	Stirban, 1968
<i>Halophila</i>			0.97		1.64	Wiginton and McMillan, 1979
<i>Syringodium</i>			0.84		1.95	"
<i>Halodule</i>			1.95		2.15	"
<i>Thalassia</i>			1.03		2.41	"
"		1.7				Pomeroy, 1960
"		1.6				Buesa, 1974
"		2.1-3.0				Burkholder and Burkholder, 1959
"		1.4				Margalef, 1961
<i>Posidonia</i>				2.4-5.0	1.6-3.2	Drew, 1978
<i>Cymodocea</i>				2.2-3.9	2.2-4.0	"
Terrestrial					2.0-4.0	Björn, 1976
"				0.2-8.7		Gabrielsen, 1948
"				2.5-7.5		Björkman, 1978

possibly necessary to overcome the lack of various accessory pigments and have at least in part made life in the sea possible. In this respect, the pigment complement or chromatic adaptation of seagrasses has probably affected their evolution from land to the sea.

Other than measurements of the chl *a*/chl *b* ratio, the amount of quantum capture adaptation has not been assessed in seagrasses. The increase of the relative amount of light harvesting pigments with plant age has been reported (Sestak and Demeter, 1976). If this relationship holds true for *Zostera*, a possible light adaptative mechanism exists due to variable leaf turnover rates.

There is little evidence of light adaptation in this *Zostera* ecosystem by pigment concentration. The lack of variation of the chlorophyll content of leaves as a function of depth in the leaf canopy indicates that the *Zostera* leaf canopy does not respond to light variations by changing chlorophyll amounts. The profile of chlorophyll is basically a reflection of the profile of leaf area. The small variations of chlorophyll along the transect also indicate uniformity of pigment content. The lack of measurable chlorophyll response in the experimental light conditions lend support to this. Although the experiment was of relatively short duration (14 days), the rapid turnover of chlorophyll molecules (Riper *et al.*, 1979) and rapid response of chlorophyll content of tropical seagrasses in reduced light experiments (Wiginton and McMillan, 1979) lend support to the conclusion that the pigment content does not vary.

The physiological capability of pigment adaptation does not seem to be reflected in the ecological distribution of pigments in this study.

The one month aquaria experiments of Wiginton and McMillan (1979) used irradiances generally less than those found in natural conditions, but the experiments demonstrated the ability of the tropical seagrasses to alter their chlorophyll content. The seasonal chlorophyll content varies in *Zostera* (McRoy, 1966) indicating a similar capability of pigment adjustments.

The seagrasses adapted to more pronounced depth gradients (1 to 42 m) do demonstrate higher chlorophyll contents in the plants living in light conditions approaching the compensation point (Drew, 1978; Wiginton and McMillan, 1979). Ramus *et al.* (1976) found higher chlorophyll contents of marine red and green algae in reduced light. However, the large brown algae do not appear to vary the chlorophyll content of the fronds (McFarland and Prescott, 1959).

The studies of Drew (1978) and Wiginton and McMillan (1979) demonstrate the effect of a pronounced light gradient on the degree of pigment adaptation. While large light gradients do occur within the leaf canopy of *Zostera*, they are compacted to within the few meters of water depth in Izembek Lagoon. The gradients of light quality and quantity in this seagrass ecosystem can therefore be spanned by single shoots. To successfully adapt to light by change in pigment ratio, the pigment functional state or the pigment amount, the adaptation would necessarily be within a single leaf. This appears less likely an occurrence than if a leaf were able to adapt to a constant light regime throughout its development. This provides a partial explanation for the lack of appreciable adaptive response by pigment ratio, functional state, or amount.

For the remaining adaptive mechanism, the conceptual model indicates an erect leaf canopy under high light, a more planar one under low light. The leaf canopy of seagrasses in general is largely supported by the water column, and changes in the water level or the buoyancy of the shoots affect the leaf inclination. The bulk of the eelgrass leaf canopy is made up of long strap-like leaves. The leaves are gas filled sacs, up to 50-60 percent by volume (McRoy and McMillan, 1977). The amount of gas in the lacunal system varies, it appears to increase during periods of intense photosynthesis (O_2). *Zostera* shoots were observed to approach a vertical inclination during high light and a more horizontal inclination during low light. Hence the leaf canopy has an active response mechanism to variable light. This is rather unique, in that most plants have fixed leaf inclinations.

The above general response mechanism is important in subtidal eelgrass meadows but other factors largely control leaf inclinations in Izembek Lagoon. Izembek Lagoon and other Alaskan eelgrass beds contain high subtidal and even intertidal eelgrass growth (McRoy, 1970). This leads to the dominating factor in leaf inclination, the tidal state. In Izembek Lagoon the water currents generated by the tides and the height of the tide largely control the leaf inclination (Figure 14). At high tide the leaves are inclined more vertically than at low tide. The more erect leaves at high tide indicate more efficient light absorption and higher canopy photosynthesis (Duncan, 1971; Sheeny and Peacock, 1977); however, there are other factors which favor photosynthesis at low tide. There is less water absorption of light at low tide and self-shading is

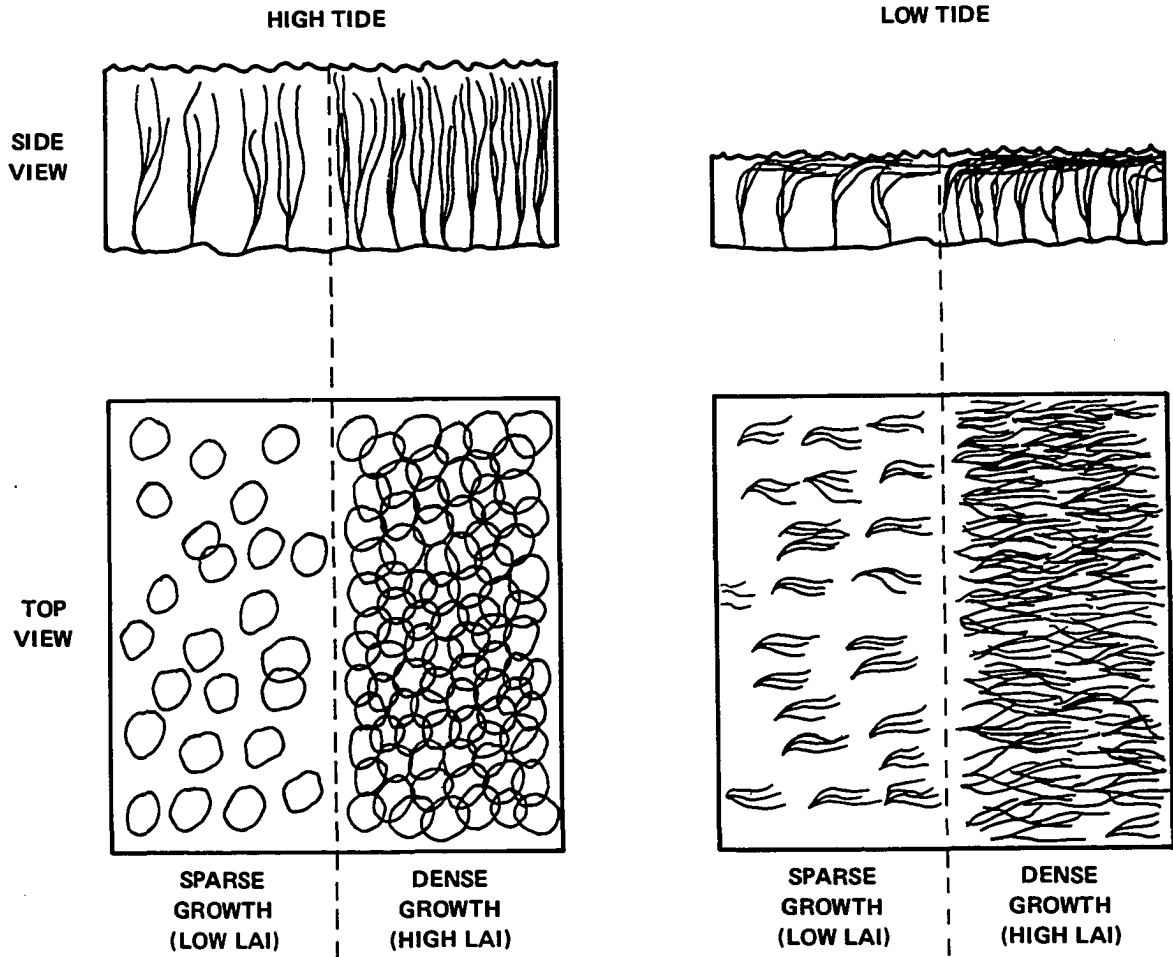


Figure 14. Diagram of tidal influence on leaf canopy structure of *Zostera* plants. At high tide (left) the circles represent space occupied by a shoot with overlap indicating self-shading; at low tide (right) the lines represent leaves floating at the water surface.

probably not as prevalent as with most higher plants. The thin *Zostera* leaves with their simple structure allow light to reach the lower canopy and the currents and waves change the leaf positions allowing a more equitable light distribution. Also the summer water temperatures at low tide are generally higher, more closely approaching the optimum for eelgrass photosynthesis (Biebl and McRoy, 1971). These factors preclude an understanding of the influence of tide level on light absorption and canopy photosynthesis.

The conceptual model predicts an increase of light absorbing surface at high light intensities. The leaf area has been used as an indicator of light absorbing surface. While there are other ways of changing the light absorbing surface, e.g. chromatophore position (Nultsch and Pfau, 1979) or size (Zurzycki and Metzner, 1977), the leaf area is the major mechanism for changing the photosynthetic light surface.

The integrated leaf areas, LAIs, are substantially different from each other along the transect. There is no simple relationship between LAI and light regime, the mid-transect LAI maximum at Station D suggests a combination of factors affecting LAI.

The light manipulation experiments indicate that the effect of light on leaf production in the tide pool (Station B) was not substantial. This is contrasted to the results obtained at Station D, where increased leaf production was indicated at the increased light experiment. The decreased light experiment did not appear to affect the leaf production at Station D, however Backman and Barilotti (1976) did observe a significant decrease of *Zostera* shoot density under *in situ* decreased light intensities.

The results of the experiments along with the study of the natural system serve to delineate the major light adaptive mechanism. Of the various adaptations conceptualized in this study, the change in leaf area is the major mechanism which the *Zostera* ecosystem utilizes to efficiently capture light.

Leaf Canopy Structure

The components of the leaf canopy structure; the stem region, reproductive shoots, and the leafy portion will be discussed in relation to light absorption. This will be followed with a comparison of the *Zostera* leaf canopy structure with that of other ecosystems.

The stem region of *Zostera* appears to be functionally different from the leafy portion. The shoot is thicker in the stem; it is essentially a bundle of all the leaves. The chlorophyll amount is reduced in the stem, and in addition Stirban (1968) reported a drastically reduced chl *a*/chl *b*. From carbon uptake profiles of *Zostera americana* (Harrison, 1978) and freshwater plants (Ikusima, 1965) it appears that the stem is not a site of appreciable photosynthesis. This portion of the plant is probably a net respiratory loss for *Zostera marina* especially in the well developed canopies with little light reaching the lower levels. Consequently, the remaining leafy portion of the canopy is the major photosynthesizing leaf material.

The reproductive shoots of *Zostera* are longer than the more abundant vegetative shoots (den Hartog, 1970). These shoots are very buoyant and they extend above the rest of the leaf canopy. This probably

aids in pollen and seed dispersal. Like the stem region of the plant, the reproductive shoots are not likely sites of appreciable photosynthesis (Harrison, 1978), especially considering the short term phenology of reproduction.

The average chlorophyll content of the leaves is $1.8 \text{ mg chl } a+b/\text{dm}^2$, slightly less than the $2.0 \text{ mg chl } a+b/\text{dm}^2$ that Gabrielsen (1948) indicates as the upper limit for a first order relationship between chlorophyll content and energy yield (Figure 15). He defines energy yield as the percent of incident radiation that is converted to chemical energy. His study demonstrates that leaf chlorophyll content above 2.0 increases energy yield at proportionally smaller increments to a maximum at 4-5 $\text{mg chl } a+b/\text{dm}^2$, beyond which point additional chlorophyll does not affect the rate of photosynthesis. It is apparent from Gabrielsen's classic study that *Zostera* has a leaf chlorophyll content that very efficiently utilizes light energy. A plant that can respond to light with varying leaf areas can most efficiently utilize its chlorophyll if low pigment concentrations are maintained. Most terrestrial plants probably cannot maintain high leaf areas due to water loss and nutrient limitation. The higher leaf chlorophyll contents of land plants account for a loss of efficiency of light capture probably in order to provide sufficient quantity of capture.

The high tide vertical distribution of *Zostera* leaf area demonstrates a maximum in the lower portion of the canopy. The leaf area distributions of terrestrial plants fall into two major categories; the grass-type with a mid canopy maximum of leaf area and the forb- or herb-type with an upper canopy maximum (Monsi *et al.*, 1973). The eelgrass

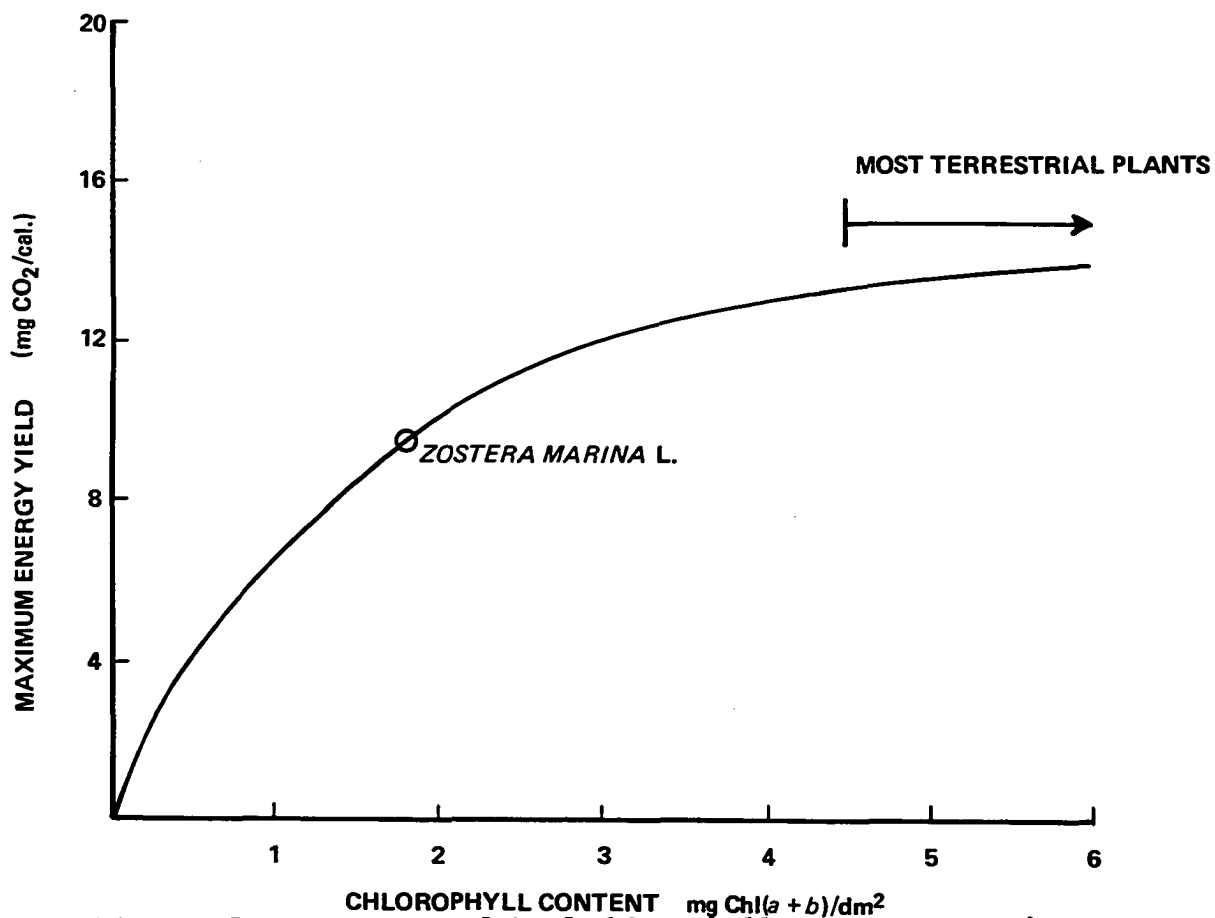


Figure 15. Influence of leaf chlorophyll content on maximum energy yield for terrestrial plants (from Gabrielsen, 1948) with the *Zostera* chlorophyll content ($\bar{X} = 1.8$) from this study.

leaf canopy with a maximum leaf area in the lower canopy appears to fall into a separate grouping (Figure 16). The general scheme of *Zostera* leaf canopy structure is complicated by the influence of tides in Izembek Lagoon. The leaf area distribution of *Zostera* is dynamic, going from an upper canopy maximum (herb-type) at low tide to a lower canopy maximum at high tide. Lower canopy maxima plants probably include other seagrass species (unpublished data) but not freshwater plants (Ikusima, 1965).

The stratification of leaf area insures optimal rates of canopy photosynthesis under variable light conditions (Odum *et al.*, 1958). Light saturation of eelgrass occurs at an irradiance ca. 40 percent of surface irradiance (McRoy, 1974; Williams, 1977). The depth of the light saturation in the leaf canopy will be dependent on the total irradiance such that relatively high light will force the light saturation zone to a lower level in the canopy. At high light intensities, the leaf canopy is light saturated in the upper portions which reduces the photosynthetic efficiency. However, the greater amounts of light reaching the greater leaf areas in the lower canopy compensates for the upper canopy light saturation, yielding a larger net amount of total canopy photosynthesis. At low light, the leaf canopy receives quanta at rates less than that of light saturation. The high tide leaf canopy distribution for *Zostera* and perhaps seagrasses in general, leads to efficient net canopy photosynthesis under the variable light conditions prevalent in the submerged habitat.

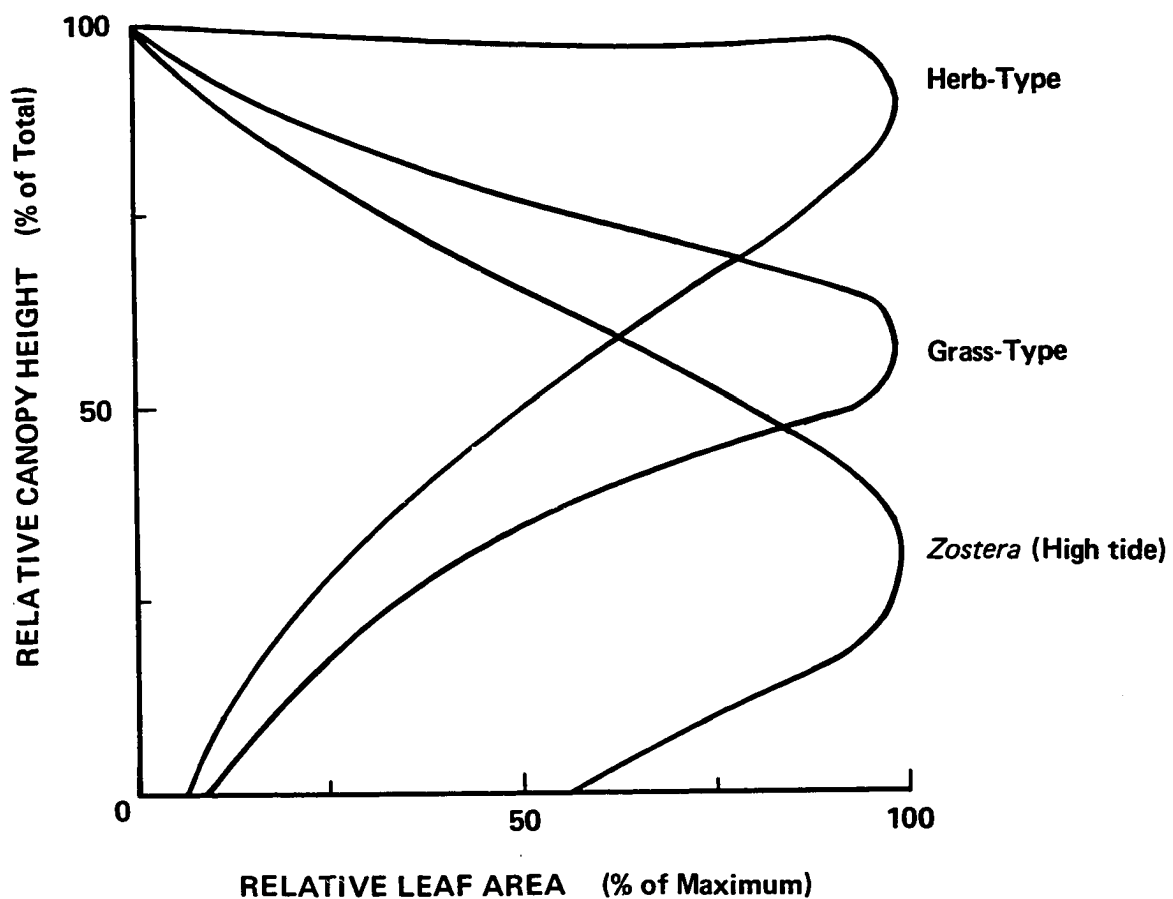


Figure 16. Leaf canopy structure of *Zostera* compared with the two major terrestrial and aquatic plant groupings (from Monsi *et al.*, 1973; Ikusima, 1965).

Leaf Area Index

The maximum leaf area index (LAI) observed in this *Zostera* stand is higher than that of other aquatic and most terrestrial ecosystems (Table 3). The maximum LAI of this seagrass ecosystem is most similar to the terrestrial forest ecosystems. The production of the high LAI is certainly an important feature of this ecosystem, but why such a high LAI?

A high LAI combined with a relatively low leaf chlorophyll content can still absorb a large portion of the available light. The production of leaf area in seagrasses is not restrained by water budgets or to a large degree by nutrient limitation as is leaf production of terrestrial plants (Grier and Running, 1977). Also, the seagrasses are periodically flushed with waves and tides, cleaning leaf blades of particulate matter and expunging concentration gradients. Life in the shallow sea eliminates the problem of water loss and allows the exploitation of nutrient-laden sediments (McRoy *et al.*, 1972), which reduces the limitation of leaf area production. A high surface area can be advantageous, providing a large exchange surface for absorption of the essential compounds and elements.

The growth form of seagrasses is suited to the production of high LAIs. Submerged aquatic plants, in general, have little or no aboveground structural material with the possible exception of the stem region and aboveground rhizome sections. This provides for the absorption of light largely or entirely by photosynthetic tissue. Presumably the translocation of carbon within and between shoots dampens inequities in the light

Table 3. Comparison of the maximum LAI of aquatic and terrestrial ecosystems.

Ecosystem	Maximum LAI	Reference
Seagrass:		
<i>Zostera</i>	16.8	This study
"	10.6*	Brown, 1962
<i>Posidonia</i>	14.2	Bay, 1978
"	8.3	Drew, 1971
"	7.0	Drew, 1978
<i>Thalassia</i>	9.3*	Gessner, 1971
<i>Thalassia/Syringodium</i>	2.3	McRoy, unpublished
<i>Cymodocea/Caulerpa</i>	5.5*	Gessner and Hamner, 1960
<i>Cymodocea</i>	1.4	Drew, 1978
Temperate Evergreen Forest	20	Waring and Franklin, 1979
Temperate Deciduous Forest	13.7	Arunga and Monsi, 1963
Tropical Rain Forest	12	Mooney, 1972
Grasses and Herbs	11.1	Arunga and Monsi, 1963
Agriculture	10	Marzola and Bartholomew, 1979
Marine Algae	9.3	McFarland and Prescott, 1959
Freshwater Plants	8.1	van der Valk and Bliss, 1971
Alpine Tundra	3.6	Caldwell <i>et al.</i> , 1974
Arctic Tundra	1.4	Dennis <i>et al.</i> , 1979
Desert	0.7	Arunga and Monsi, 1963
Prairie	0.6	Conner <i>et al.</i> , 1974

*indicates reported LAI was divided by 2 to obtain one-sided LAI

profile. The lateral branching of the rhizome with new shoot production allows for rapid response to increasing seasonal or annual irradiances. Correspondingly, the sloughing of shoots can rapidly adjust for decreasing light. The rapid response to changing light regimes leads to more efficient adaptation.

There are few naturally maintained monocultures: most ecosystems have many plant species. Yet the temperate and some tropical seagrasses form single species stands of the major plants (den Hartog, 1970). Fields of plants dominated by a single species typically have LAI values greater than corresponding mixed species plant stands (Arunga and Monsi, 1963; Dennis *et al.*, 1979).

In addition to these possible factors contributing to the high LAI observed in this study, the temperate seagrasses have unique characteristics that may account for the LAIs that are higher than other aquatic angiosperms. The high latitude seagrass stands tend to be in shallower water than low latitude seagrasses. The shallow water accounts for less light filtering by water especially at low tide. Also the epiphytes, a major component of tropical seagrass ecosystems (McRoy and McMillan, 1977) and of aquatic macrophyte stands (Hutchinson, 1975, p. 515), do not appear to be a major component of the *Zostera* stand at Izembek Lagoon. The relatively low epiphyte standing stock is likely due to factors other than those contributing to the eelgrass standing stock. Some investigators feel that epiphytes operate independently of the macrophyte; they suggest different controlling factors (Capone *et al.*, 1979).

The high LAI that the eelgrass meadow produces has important effects on the ecosystem. The high LAI provides and intensifies feedback to the physical environment.

An effect of the leaf area is to dramatically increase the habitat complexity. An eelgrass bed with a high LAI can effectively increase the sea floor by 30 times (one-sided LAI x 2). An obvious effect is the increased substrate for attachment by epiphytic organisms (McRoy and McMillan, 1977). Other than epiphytes, an associated microfauna and other animals utilize the eelgrass leaves in various ways (Kikuchi and Pérès, 1977). The functioning of this seagrass ecosystem as a nursery area for juvenile fishes and invertebrates (Kikuchi and Pérès, 1977) is extremely enhanced with high LAIs.

During an ebbing tide at Izembek Lagoon, water flows from the raised benches that contain eelgrass into the tide channels. The leaf blades serve as baffles reducing the water flow (Ginsburg and Lowenstam, 1958; Burrell and Schubel, 1977). Some water is usually retained until the flood tide, protecting both the eelgrass and benthic fauna from dessication. The baffling effect of a high LAI also leads to extraction and entrapment of fine waterborne particles. The binding and stabilization of the sediments by the root system along with the increased production of sedimentary material can bring about dramatic alteration of the sedimentation processes (Burrell and Schubel, 1977).

SUMMARY AND CONCLUSIONS

The variety of physiological and biological plant responses to gradients of light quality and quantity can be grouped into four categories that make up a predictive model of light adaptation in plants. Testing this model was done in a temperate seagrass ecosystem dominated by *Zostera marina*. The light adaptations were investigated along a depth transect in Izembek Lagoon. The transect ran across a natural gradient of plant development which reflected a gradient of ecosystem processes. Changes in the light regime were induced *in situ* at two points along the transect, with an increased and decreased light experiment at both points. The eelgrass canopy was sampled by collecting vertical sections of leaves (stratified clip technique) for measurements of chlorophyll *a* to *b* ratios (chromatic and quantum capture adaptations), chlorophyll amounts (pigment adaptation) and leaf area distribution (leaf area adaptation). Chlorophyll ratios and amounts and leaf production measurements were made at the different light treatments.

The chlorophyll ratios and amounts did vary substantially within and between shoots. However, when large integrative samples were measured, there was little evidence of major adaptive trends. The chlorophyll ratios and amounts did not vary substantially along the natural gradient of seagrass development or under the *in situ* increased and decreased light regimes. The relative vertical distribution of leaf area was constant throughout the eelgrass meadow. However, the absolute distribution of leaf area, LAI, changes significantly along the gradient of plant development. Leaf production was affected by the changes in

light. The results of the light manipulation experiments and the distribution of LAI along the transect indicate a light limiting situation in the subtidal stations. Combining this with transect sediment nutrient pools (McRoy, unpublished data) which indicate a nutrient limiting situation in the tide pool stations yields a hypothesized gradient of limiting factors (Figure 17).

In conclusion, the change of leaf area is the major adaptive mechanism to changing light regimes of the *Zostera marina* stand in Izembek Lagoon. The other physiological adaptive mechanisms, photosynthetic pigments ratios, functional state or amounts, are less important. The chlorophyll *a* to *b* ratio is relatively low (2.5), but within the range of other submerged aquatic plants. The chlorophyll concentrations of the leaves (1.8 mg chl *a+b*/dm²) is also relatively low compared to other plants. The maximum LAI (17) is one of the highest reported for any aquatic or terrestrial ecosystem. The low leaf chlorophyll content, shallow water habitat, tidal flushing, growth form, and single species stand are factors contributing to the high LAI. The LAI interacts in the seagrass ecosystem to increase habitat complexity, provide attachment substrate, increase water retention, and stimulate sedimentation.

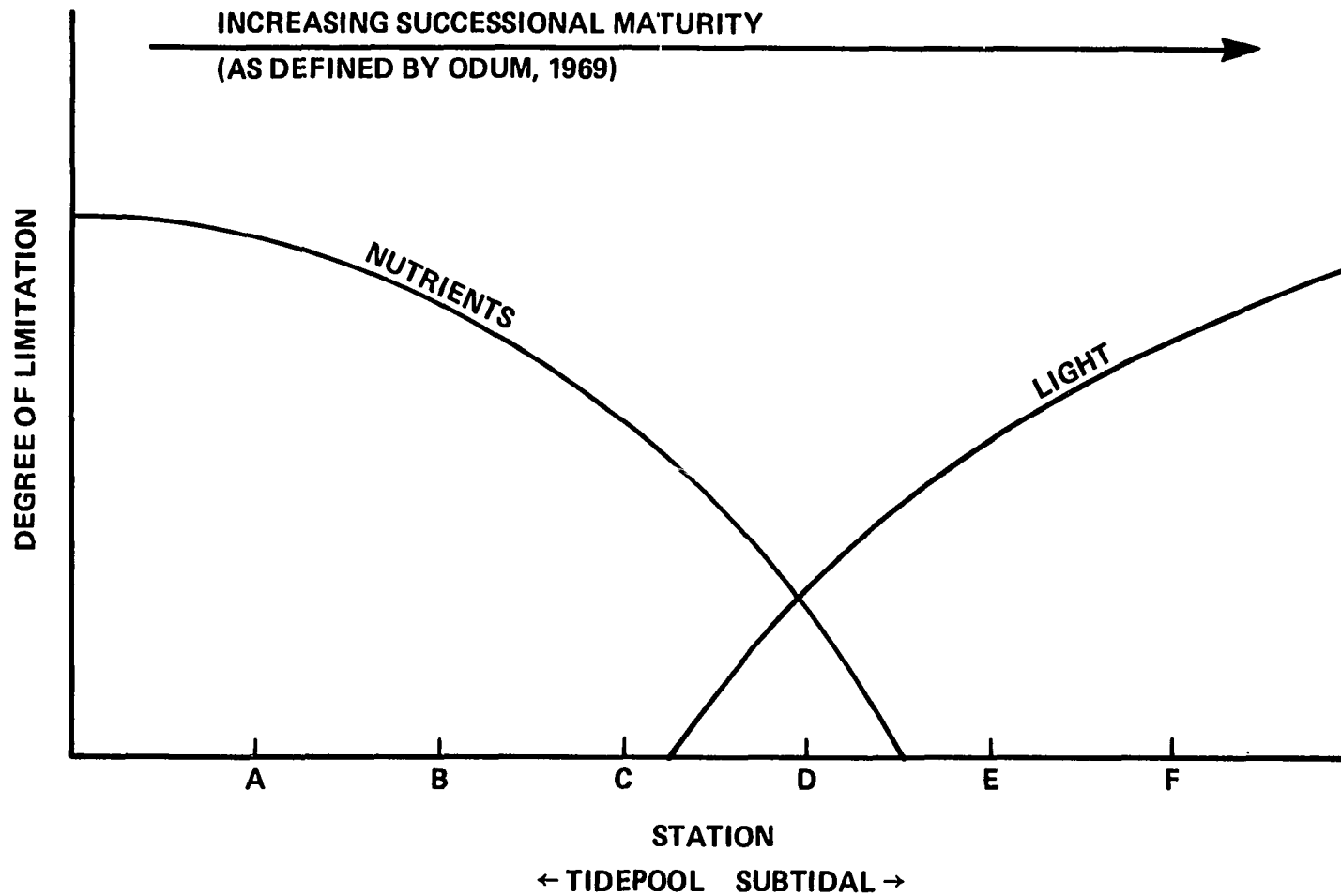


Figure 17. Hypothesized major limiting factors along the transect.

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APPENDIX

LEAF AREA/DRY WEIGHT AND CHLOROPHYLL DATA FROM
IZEMBEK LAGOON, 1978

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg ch1 a/dm ²	mg ch1 b/dm ²	mg ch1 a/g dry	mg ch1 b/g dry
01June78-A	6090		0-5	0.99	0.007	0.60	5	1.08	0.48	2.2	1.0
"	"		5-10	1.58	0.007	0.96	10	0.90	0.44	2.5	1.2
"	"		10-15	0.82	0.003	0.51	15	1.56	0.98	-	-
"	"		15-20	0.17	0.000	0.10	-	-	-	-	-
01June78-B	8742		0-10	0.82	0.016	1.91	10	1.70	0.77	-	-
"	"		10-20	3.61	0.016	3.46	-	-	-	-	-
"	"		20-30	1.63	0.006	1.42	-	-	-	-	-
01June78-C	7901		0-10	2.43	0.012	1.92	10	1.36	0.62	2.8	1.3
"	"		10-20	2.76	0.010	2.18	20	1.17	0.49	3.5	1.5
"	"		20-30	0.91	0.004	0.72	-	-	-	-	-
"	"		30-40	0.07	0.000	0.06	-	-	-	-	-
01June78-D	4716		0-10	2.61	0.015	1.23	10	1.45	0.65	3.2	1.4
"	"		10-20	4.82	0.017	2.27	20	1.52	0.67	4.1	1.8
"	"		20-30	3.77	0.012	1.78	30	1.21	0.53	3.7	1.6
"	"		30-40	1.75	0.005	0.83	40	1.50	0.70	4.4	2.0
"	"		40-50	0.30	0.001	0.14	-	-	-	-	-
01June78-E	2740		0-10	2.63	0.021	0.72	10	1.48	0.62	2.1	0.9
"	"		10-20	5.51	0.027	1.51	20	1.58	0.63	4.2	1.7
"	"		20-30	6.37	0.022	1.75	30	1.67	0.68	4.5	1.8
"	"		30-40	4.03	0.015	1.10	40	2.20	0.96	-	-
"	"		40-50	1.41	0.005	0.39	50	1.92	0.94	4.5	2.2
"	"		50-60	0.29	0.001	0.08	-	-	-	-	-
01June78-F	1669		0-10	4.92	0.049	0.82	10	0.44	0.22	0.6	0.3
"	"		10-20	8.38	0.048	1.40	20	1.38	0.58	2.0	0.9
"	"		20-30	9.68	0.038	1.62	30	1.68	0.68	4.2	1.7
"	"		30-40	6.59	0.027	1.10	40	1.67	0.67	-	-
"	"		40-50	3.86	0.016	0.64	-	-	-	-	-
"	"		50-60	1.16	0.005	0.19	-	-	-	-	-
07June78-A	5930		0-5	0.85	0.007	0.50	5	1.31	0.58	2.4	1.0
"	"		5-10	2.00	0.008	1.19	10	1.14	0.50	2.2	1.0
"	"		10-15	1.50	0.005	0.89	15	1.21	0.65	2.2	1.2
"	"		15-20	1.46	0.004	0.87	-	-	-	-	-
"	"		20-25	0.42	0.001	0.25	-	-	-	-	-
"	"		25-30	0.09	0.000	0.05	-	-	-	-	-
07June78-B	8367		0-10	1.88	0.010	1.44	5	0.96	0.60	1.9	1.2
"	"		10-20	2.77	0.010	2.32	10	1.06	0.54	2.8	1.4
"	"		20-30	1.34	0.004	1.12	15	1.19	0.61	3.1	1.6
"	"		30-40	0.18	0.001	0.15	20	1.58	0.97	3.1	1.9
07June78-C	7424		0-10	1.53	0.009	1.14	10	1.58	0.71	5.3	2.4
"	"		10-20	3.61	0.014	2.22	20	1.49	0.67	4.3	2.0
"	"		20-30	2.28	0.007	1.40	30	1.14	0.60	3.7	1.9

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl a/dm ²	mg chl b/dm ²	mg chl a/g dry	mg chl b/g dry
07June78	C	7424	30-40	0.52	0.002	0.33	40	2.19	2.63	-	-
07June78	D	4518	0-10	2.33	0.017	1.05	10	1.24	0.56	2.3	1.1
"	"	"	10-20	4.89	0.029	2.21	20	1.02	0.44	3.3	1.4
"	"	"	20-30	6.83	0.026	3.09	30	1.26	0.57	3.9	1.7
"	"	"	30-40	5.24	0.020	2.37	40	1.60	0.73	3.5	1.6
"	"	"	40-50	3.64	0.016	1.64	50	1.51	0.77	3.2	1.7
"	"	"	50-60	1.98	0.008	0.89	-	-	-	-	-
"	"	"	60-70	0.95	0.004	0.43	-	-	-	-	-
"	"	"	70-80	0.29	0.000	0.13	-	-	-	-	-
07June78	E	2657	0-10	3.30	0.024	0.90	10	1.45	0.60	3.0	1.2
"	"	"	10-20	6.24	0.027	1.66	20	1.64	0.79	5.0	2.4
"	"	"	20-30	7.14	0.024	1.90	30	1.67	0.72	5.0	2.1
"	"	"	30-40	4.73	0.017	1.26	40	1.80	0.87	5.6	2.7
"	"	"	40-50	3.27	0.011	0.87	50	1.74	1.06	4.6	2.8
"	"	"	50-60	1.32	0.005	0.35	-	-	-	-	-
07June78	F	1641	0-10	5.28	0.052	0.86	10	1.47	0.59	1.9	0.8
"	"	"	10-20	10.59	0.055	1.74	20	1.45	0.56	2.9	1.1
"	"	"	20-30	10.93	0.042	1.79	30	1.49	0.54	2.9	1.0
"	"	"	30-40	7.06	0.031	1.16	40	1.65	0.64	3.1	1.2
"	"	"	40-50	3.63	0.017	0.60	50	1.80	0.80	3.9	1.8
"	"	"	50-60	1.62	0.008	0.27	-	-	-	-	-
14June78	A	5743	0-5	0.78	0.006	0.45	5	1.06	0.49	2.8	1.3
"	"	"	5-10	1.93	0.007	1.11	10	1.10	0.38	5.2	1.8
"	"	"	10-15	1.66	0.006	0.95	15	1.43	0.60	3.9	1.6
"	"	"	15-20	0.86	0.003	0.49	20	1.73	0.59	9.3	3.2
"	"	"	20-25	0.30	0.001	0.17	-	-	-	-	-
14June78	B	7930	0-10	2.54	0.014	2.01	10	1.21	0.36	5.7	1.7
"	"	"	10-20	4.37	0.016	3.47	20	1.13	0.44	9.0	3.5
"	"	"	20-30	2.16	0.008	1.71	30	1.29	0.50	5.7	2.2
"	"	"	30-40	0.38	0.001	0.30	-	-	-	-	-
14June78	C	6868	0-10	1.35	0.007	0.93	10	1.51	0.64	7.1	3.0
"	"	"	10-20	3.02	0.011	2.07	20	1.76	0.76	8.4	3.6
"	"	"	20-30	3.15	0.010	2.16	30	1.92	0.83	9.8	4.2
"	"	"	30-40	1.23	0.004	0.84	-	-	-	-	-
"	"	"	40-50	0.27	0.000	0.19	-	-	-	-	-
14June78	D	4286	0-10	2.53	0.017	1.08	10	1.52	0.59	4.8	1.9
"	"	"	10-20	4.60	0.024	1.97	20	1.50	0.61	5.5	2.2
"	"	"	20-30	6.47	0.025	2.77	30	1.61	0.74	5.5	2.5
"	"	"	30-40	5.11	0.019	2.19	40	1.42	0.53	7.1	2.7
"	"	"	40-50	3.07	0.010	1.32	50	1.35	0.50	5.9	2.2
"	"	"	50-60	1.63	0.006	0.70	-	-	-	-	-

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg ch1 a/dm ²	mg ch1 b/dm ²	mg ch1 a/g dry	mg ch1 b/g dry
14 June 78	D	4286	0-70	0.44	0.001	0.19	-	-	-	-	-
14 June 78	E	2561	0-10	3.38	0.027	0.87	10	0.74	0.26	2.0	0.7
"	"	"	10-20	6.26	0.036	1.60	20	1.37	0.54	3.0	1.2
"	"	"	20-30	8.59	0.032	2.20	30	1.38	0.52	6.4	2.4
"	"	"	30-40	7.62	0.029	1.95	40	1.42	0.53	7.1	2.7
"	"	"	40-50	5.55	0.022	1.42	50	1.35	0.50	5.9	2.2
"	"	"	50-60	3.65	0.015	0.93	60	2.17	0.50	8.1	1.9
"	"	"	60-70	2.38	0.009	0.61	70	2.91	0.98	9.9	3.3
"	"	"	70-80	0.97	0.004	0.25	-	-	-	-	-
14 June 78	F	1608	0-10	4.17	0.040	0.67	10	0.09	0.55	0.2	1.0
"	"	"	10-20	7.09	0.043	1.14	20	1.08	0.39	3.8	1.4
"	"	"	20-30	8.41	0.038	1.35	30	1.27	0.45	4.8	1.7
"	"	"	30-40	7.44	0.031	1.20	40	1.37	0.47	5.1	1.7
"	"	"	40-50	4.83	0.022	0.78	50	1.55	0.53	6.1	2.1
"	"	"	50-60	3.40	0.015	0.55	60	1.71	0.59	5.4	1.9
"	"	"	60-70	2.36	0.010	0.38	70	1.88	0.70	2.0	0.8
"	"	"	70-80	1.04	0.005	0.17	-	-	-	-	-
22 June 78	A	5530	0-5	1.17	0.008	0.65	5	0.79	0.31	1.2	0.5
"	"	"	5-10	2.31	0.010	1.28	10	1.14	0.44	2.2	0.8
"	"	"	10-15	2.47	0.010	1.37	15	1.16	0.45	2.0	0.8
"	"	"	15-20	2.13	0.008	1.18	20	1.28	0.47	2.3	0.9
"	"	"	20-25	1.25	0.004	0.69	25	1.41	0.56	3.4	1.3
"	"	"	25-30	0.49	0.002	0.25	-	-	-	-	-
22 June 78	B	7430	0-10	2.44	0.013	1.81	10	1.06	0.44	2.7	1.1
"	"	"	10-20	4.56	0.015	3.39	20	1.28	0.50	3.2	1.3
"	"	"	20-30	2.87	0.009	2.13	30	1.37	0.55	6.0	2.4
"	"	"	30-40	1.12	0.003	0.83	-	-	-	-	-
"	"	"	40-50	0.12	0.000	0.09	-	-	-	-	-
22 June 78	C	6232	0-10	1.45	0.007	0.90	10	0.84	0.34	2.2	0.9
"	"	"	10-20	2.86	0.009	1.78	20	1.24	0.50	3.9	1.6
"	"	"	20-30	2.84	0.009	1.77	30	1.54	0.71	4.4	2.0
"	"	"	30-40	1.25	0.004	0.78	40	1.89	0.81	5.3	2.3
"	"	"	40-50	0.20	0.001	0.12	50	1.48	1.26	4.6	3.9
22 June 78	D	4021	0-10	2.31	0.012	0.93	10	1.02	0.36	1.6	0.6
"	"	"	10-20	3.88	0.018	1.56	20	1.67	0.63	6.9	2.6
"	"	"	20-30	5.87	0.020	2.36	30	1.51	0.78	4.4	2.3
"	"	"	30-40	5.54	0.019	2.23	40	1.69	0.65	4.7	1.8
"	"	"	40-50	3.90	0.011	1.57	50	1.82	0.73	4.0	1.6
"	"	"	50-60	2.50	0.007	1.01	60	1.80	0.97	4.3	2.3
"	"	"	60-70	1.14	0.003	0.46	70	1.61	1.03	3.3	2.1
22 June 78	E	2451	0-10	3.33	0.019	0.82	10	0.82	0.31	1.3	0.5

29June78-A	5343	0-10	2.90	0.016	1.55	10	1.43	0.57	-	-
"	"	10-20	4.13	0.016	2.21	20	1.30	0.47	1.2	0.4
"	"	20-30	2.21	0.009	1.18	-	-	-	-	-
"	"	30-40	0.27	0.001	0.14	-	-	-	-	-
29June78-B	6992	0-10	2.70	0.013	1.89	10	0.73	0.25	2.1	0.7
"	"	10-20	4.87	0.016	3.41	20	1.92	0.25	5.6	0.7
"	"	20-30	2.84	0.008	1.99	30	0.97	0.40	2.9	1.2
"	"	30-40	1.01	0.003	0.71	-	-	-	-	-
"	"	40-50	0.31	0.001	0.22	-	-	-	-	-
"	"	50-60	0.18	0.001	0.13	-	-	-	-	-
29June78-C	5675	0-10	1.35	0.006	0.77	10	0.86	0.35	1.8	0.8
"	"	10-20	2.82	0.008	1.60	20	1.38	0.60	4.4	1.9
"	"	20-30	3.00	0.009	1.70	30	1.46	0.63	4.4	1.9
"	"	30-40	1.95	0.006	1.11	40	1.73	0.73	6.1	2.6
"	"	40-50	0.83	0.003	0.47	50	1.64	0.66	6.5	2.6
"	"	50-60	0.17	0.000	1.10	-	-	-	-	-
29June78-D	3790	0-10	2.66	0.011	1.01	10	0.58	0.21	0.9	0.3
"	"	10-20	3.87	0.013	1.47	20	1.16	0.45	2.9	1.1
"	"	20-30	5.08	0.014	1.93	30	1.70	0.44	4.8	1.2
"	"	30-40	4.85	0.013	1.84	40	1.60	0.61	4.5	1.7
"	"	40-50	3.81	0.011	1.44	50	1.48	0.58	4.6	1.8
"	"	50-60	2.38	0.006	0.90	60	1.58	0.64	3.9	1.6
"	"	60-70	1.48	0.005	0.56	70	1.18	1.47	3.0	1.2
"	"	70-80	0.61	0.002	0.23	80	1.36	0.51	6.0	2.3
"	"	80-90	0.52	0.002	0.20	90	1.13	0.43	5.3	2.0
29June78-E	2355	0-10	3.57	0.019	0.84	10	0.63	0.25	0.9	0.4

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
22 June 78	F	2451	10-20	5.96	0.021	1.46	20	1.46	0.55	3.2	1.2
"	"	"	20-30	6.50	0.021	1.59	30	1.63	0.64	4.0	1.6
"	"	"	30-40	6.30	0.021	1.54	40	2.31	0.87	6.7	2.5
"	"	"	40-50	4.85	0.016	1.19	50	1.37	0.49	3.5	1.3
"	"	"	50-60	3.46	0.011	0.85	60	1.66	0.63	3.4	1.3
"	"	"	60-70	1.61	0.005	0.39	70	1.83	0.78	2.7	1.1
"	"	"	70-80	0.41	0.002	0.10	-	-	-	-	-
22 June 78	F	1571	0-10	4.60	0.034	0.72	10	0.90	0.34	1.2	0.5
"	"	"	10-20	8.35	0.038	1.31	20	1.27	0.46	2.2	0.8
"	"	"	20-30	9.87	0.036	1.55	30	1.59	0.58	3.6	1.3
"	"	"	30-40	8.04	0.030	1.26	40	1.36	0.47	3.0	1.0
"	"	"	40-50	6.04	0.022	0.95	50	1.58	0.52	3.5	1.2
"	"	"	50-60	3.73	0.013	0.59	60	1.54	0.50	3.4	1.1
"	"	"	60-70	2.72	0.011	0.43	70	2.11	0.72	3.5	1.2
"	"	"	70-80	0.53	0.002	0.08	-	-	-	-	-

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl a/dm ²	mg chl b/dm ²	mg chl a/g dry	mg chl b/g dry
29 June 78	F	255	10-20	6.24	0.024	1.47	20	1.21	0.48	3.0	1.2
"	"	"	20-30	8.55	0.027	2.01	30	1.21	0.47	3.9	1.5
"	"	"	30-40	7.12	0.024	1.68	40	1.39	0.53	3.7	1.4
"	"	"	40-50	5.60	0.018	1.32	50	1.30	0.48	6.9	2.5
"	"	"	50-60	3.70	0.014	0.87	60	1.22	0.47	4.9	1.9
"	"	"	60-70	2.74	0.011	0.65	70	1.04	0.42	2.5	1.0
"	"	"	70-80	1.69	0.006	0.40	-	-	-	-	-
"	"	"	80-90	0.61	0.002	0.14	-	-	-	-	-
29 June 78	F	1539	0-10	5.60	0.030	0.86	10	0.79	0.32	1.2	0.5
"	"	"	10-20	9.62	0.043	1.48	20	1.04	0.40	2.5	1.0
"	"	"	20-30	13.41	0.046	2.06	30	1.35	0.54	3.6	1.4
"	"	"	30-40	12.06	0.044	1.86	40	1.34	0.52	3.5	1.4
"	"	"	40-50	9.35	0.036	1.44	50	1.47	0.53	3.5	1.3
"	"	"	50-60	6.76	0.028	1.04	60	1.28	0.82	2.6	1.7
"	"	"	60-70	4.80	0.023	0.74	70	1.47	0.50	3.1	1.0
"	"	"	70-80	2.99	0.014	0.46	80	1.56	0.52	3.2	1.1
"	"	"	80-90	1.10	0.006	0.17	90	1.94	0.60	5.7	1.8
06 July 78	A	5156	0-10	3.57	0.020	1.84	10	1.32	0.53	3.2	1.3
"	"	"	10-20	4.38	0.015	2.26	20	1.34	0.54	3.3	1.3
"	"	"	20-30	1.98	0.007	1.02	30	1.55	0.85	4.3	2.4
"	"	"	30-40	0.49	0.001	0.25	-	-	-	-	-
06 July 78	B	6555	0-10	1.99	0.008	1.30	10	1.33	0.52	3.8	1.5
"	"	"	10-20	3.56	0.010	2.33	20	1.33	0.54	4.0	1.6
"	"	"	20-30	3.23	0.009	2.12	30	1.36	0.56	5.8	2.4
"	"	"	30-40	2.25	0.006	1.47	40	1.05	0.43	4.0	1.6
"	"	"	40-50	0.99	0.003	0.65	50	1.16	0.55	5.2	2.5
"	"	"	50-60	0.30	0.001	0.20	-	-	-	-	-
06 July 78	C	5119	0-10	1.66	0.006	0.85	10	1.38	0.53	3.6	1.4
"	"	"	10-20	2.76	0.008	1.41	20	1.89	0.78	5.7	2.3
"	"	"	20-30	2.40	0.006	1.23	30	1.87	0.76	5.5	2.3
"	"	"	30-40	1.72	0.004	0.88	40	2.19	0.95	4.3	1.9
"	"	"	40-50	1.04	0.003	0.53	50	1.74	0.72	4.1	1.7
"	"	"	50-60	0.36	0.001	0.18	60	1.74	0.73	2.4	1.0
06 July 78	D	3558	0-10	2.54	0.011	0.90	10	1.03	0.37	1.6	0.6
"	"	"	10-20	3.95	0.019	1.41	20	0.94	0.36	2.8	1.1
"	"	"	20-30	6.75	0.022	2.40	30	1.33	0.51	3.6	1.4
"	"	"	30-40	6.33	0.020	2.25	40	1.05	0.42	3.3	1.3
"	"	"	40-50	5.37	0.017	1.91	50	1.51	0.59	4.0	1.5
"	"	"	50-60	4.45	0.014	1.58	60	1.52	0.58	3.7	1.4
"	"	"	60-70	3.02	0.011	1.07	70	1.54	0.58	4.0	1.5
"	"	"	70-80	2.09	0.008	0.74	80	1.76	0.75	2.8	1.2

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
06 July 78	D	3558	80-90	0.98	0.003	0.35	-	-	-	-	-
06 July 78	E	2259	0-10	2.89	0.014	0.65	10	0.65	0.22	1.0	0.3
"	"	"	10-20	4.42	0.020	1.00	20	1.00	0.38	2.3	0.9
"	"	"	20-30	6.83	0.022	1.54	30	1.15	0.55	3.0	1.4
"	"	"	30-40	7.04	0.023	1.59	40	1.12	0.41	2.6	0.9
"	"	"	40-50	6.03	0.021	1.36	50	1.25	0.46	2.9	1.1
"	"	"	50-60	4.85	0.017	1.10	60	1.50	0.54	2.9	1.0
"	"	"	60-70	3.83	0.014	0.87	70	1.24	0.45	2.3	0.8
"	"	"	70-80	2.56	0.011	0.58	80	1.37	0.49	2.3	0.8
"	"	"	80-90	1.76	0.005	0.40	90	1.05	0.45	1.4	0.6
"	"	"	90-100	0.61	0.002	0.14	-	-	-	-	-
06 July 78	F	1506	0-10	4.69	0.026	0.71	10	0.87	0.33	1.3	0.5
"	"	"	10-20	9.00	0.038	1.36	20	1.27	0.48	2.9	1.1
"	"	"	20-30	11.55	0.044	1.74	30	1.42	0.54	3.8	1.5
"	"	"	30-40	9.95	0.039	1.50	40	1.65	0.60	4.1	1.5
"	"	"	40-50	7.74	0.032	1.17	50	1.28	0.45	3.2	1.1
"	"	"	50-60	5.58	0.024	0.84	60	1.43	0.48	3.5	1.2
"	"	"	60-70	3.25	0.014	0.49	70	1.67	0.55	3.9	1.3
"	"	"	70-80	1.31	0.006	0.20	-	-	-	-	-
13 July 78	A	4969	0-10	3.21	0.016	1.60	10	1.02	0.46	2.9	1.3
"	"	"	10-20	4.05	0.016	2.01	20	0.77	0.35	2.3	1.0
"	"	"	20-30	2.30	0.008	1.14	30	1.51	1.72	-	-
"	"	"	30-40	0.29	0.001	0.14	-	-	-	-	-
13 July 78	B	6117	0-10	2.34	0.011	1.43	10	1.39	0.60	3.5	1.5
"	"	"	10-20	3.98	0.013	2.43	20	1.57	0.70	3.3	1.5
"	"	"	20-30	3.50	0.011	2.14	30	1.27	0.60	3.1	1.5
"	"	"	30-40	2.04	0.006	1.25	-	-	-	-	-
"	"	"	40-50	0.17	0.001	0.10	-	-	-	-	-
13 July 78	C	4562	0-10	2.26	0.010	1.03	10	0.84	0.40	1.7	0.8
"	"	"	10-20	3.80	0.012	1.73	20	1.85	0.84	3.3	1.5
"	"	"	20-30	3.93	0.012	2.14	30	1.37	0.61	3.4	1.5
"	"	"	30-40	3.23	0.010	1.25	40	1.61	0.69	2.9	1.2
"	"	"	40-50	2.04	0.007	0.10	50	1.84	0.89	4.7	2.3
"	"	"	50-60	0.98	0.003	0.45	60	1.69	0.66	1.9	0.8
"	"	"	60-70	0.31	0.001	0.14	-	-	-	-	-
13 July 78	D	3326	0-10	3.09	0.015	1.03	10	0.40	0.15	1.1	0.4
"	"	"	10-20	4.44	0.017	1.48	20	0.70	0.28	1.4	0.6
"	"	"	20-30	6.27	0.020	2.09	30	1.10	0.46	3.9	1.6
"	"	"	30-40	6.49	0.020	2.16	40	1.19	0.50	4.5	1.9
"	"	"	40-50	5.93	0.019	1.97	50	1.19	0.49	3.8	1.5
"	"	"	50-60	4.50	0.015	1.50	60	1.19	0.49	3.4	1.4

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
13 July 78	D	3326	60-70	3.57	0.012	1.19	70	1.23	0.49	4.0	1.6
"	"	"	70-80	2.64	0.010	0.88	80	1.31	0.55	4.5	1.9
"	"	"	90-100	0.70	0.003	0.23	90	1.09	0.46	4.0	1.7
"	"	"	100-110	0.49	0.002	0.16	100	1.00	0.42	3.7	1.5
13 July 78	E	2163	0-10	3.75	0.022	0.81	10	0.83	0.30	1.2	0.4
"	"	"	10-20	5.93	0.026	1.28	20	0.94	0.37	2.1	0.8
"	"	"	20-30	9.15	0.032	1.98	30	1.23	0.49	3.4	1.4
"	"	"	30-40	9.62	0.032	2.08	40	1.60	0.63	4.3	1.7
"	"	"	40-50	8.96	0.030	1.94	50	1.46	0.57	4.1	1.6
"	"	"	50-60	7.93	0.027	1.72	60	1.34	0.51	4.7	1.8
"	"	"	60-70	6.47	0.022	1.40	70	1.38	0.53	4.5	1.7
"	"	"	70-80	4.80	0.015	1.04	80	1.29	0.46	3.7	1.3
"	"	"	80-90	3.28	0.011	0.71	90	1.33	0.47	4.2	1.5
"	"	"	90-100	1.89	0.006	0.41	100	1.40	0.50	4.0	1.4
"	"	"	100-110	0.68	0.002	0.15	-	-	-	-	-
13 July 78	F	1474	0-10	4.96	0.035	0.73	10	0.79	0.34	1.7	0.7
"	"	"	10-20	7.68	0.038	1.13	20	1.19	0.49	2.4	1.0
"	"	"	20-30	12.14	0.043	1.79	30	1.49	0.61	3.5	1.4
"	"	"	30-40	11.52	0.043	1.70	40	1.44	0.58	4.2	1.7
"	"	"	40-50	10.34	0.040	1.52	50	2.12	0.84	3.8	1.5
"	"	"	50-60	9.29	0.036	1.37	60	2.24	0.89	5.2	2.1
"	"	"	60-70	7.30	0.029	1.08	70	2.51	0.97	8.4	3.2
"	"	"	70-80	5.49	0.022	0.81	80	2.17	0.87	5.9	2.4
"	"	"	80-90	2.97	0.011	0.44	-	-	-	-	-
"	"	"	90-100	1.68	0.006	0.25	-	-	-	-	-
20 July 78	A	4782	0-10	4.15	0.019	1.98	10	1.02	0.45	2.3	1.0
"	"	"	10-20	5.07	0.014	2.42	20	0.81	0.42	1.8	1.0
"	"	"	20-30	2.36	0.006	1.13	-	-	-	-	-
20 July 78	B	5680	0-10	2.50	0.008	1.42	10	1.12	0.47	2.4	1.0
"	"	"	10-20	4.14	0.010	2.35	20	1.20	0.52	3.7	1.6
"	"	"	20-30	4.16	0.010	2.36	30	1.55	0.68	4.8	2.1
"	"	"	30-40	3.28	0.008	1.86	40	1.21	0.56	2.8	1.3
"	"	"	40-50	1.92	0.005	1.09	50	1.31	0.57	-	-
"	"	"	50-60	0.32	0.001	0.18	-	-	-	-	-
20 July 78	C	4006	0-10	2.05	0.008	0.82	10	1.01	0.41	1.4	0.6
"	"	"	10-20	3.66	0.011	1.47	20	1.19	0.51	4.5	1.9
"	"	"	20-30	3.95	0.011	1.58	30	1.12	0.48	3.8	1.7
"	"	"	30-40	3.39	0.009	1.36	40	0.90	1.40	2.9	1.3
"	"	"	40-50	2.83	0.007	1.13	50	1.04	0.46	2.5	1.1
"	"	"	50-60	1.39	0.003	0.56	60	1.28	0.63	2.4	1.2
"	"	"	60-70	0.42	0.001	0.17	-	-	-	-	-

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl a/dm ²	mg chl b/dm ²	mg chl a/g dry	mg chl b/g dry
20 July 78-D	3095		0-10	3.37	0.018	1.04	10	0.48	0.20	0.8	0.3
"	"	"	10-20	4.73	0.018	1.46	20	0.82	0.32	1.8	0.7
"	"	"	20-30	6.10	0.018	1.89	30	1.18	0.48	3.4	1.4
"	"	"	30-40	6.47	0.018	2.00	40	1.77	0.71	5.8	2.3
"	"	"	40-50	6.06	0.017	1.88	50	1.39	0.55	3.9	1.5
"	"	"	50-60	5.36	0.015	1.66	60	1.28	0.51	3.2	1.3
"	"	"	60-70	4.63	0.012	1.43	70	1.61	0.62	3.9	1.5
"	"	"	70-80	4.19	0.011	1.30	80	1.01	0.38	3.2	1.2
"	"	"	80-90	3.82	0.010	1.18	90	1.07	0.38	3.4	1.2
"	"	"	90-100	2.92	0.008	0.90	100	1.44	0.48	4.7	1.6
"	"	"	100-110	1.58	0.004	0.49	110	1.73	0.82	2.3	1.1
"	"	"	110-120	0.62	0.002	0.19	-	-	-	-	-
20 July 78-E	2067		0-10	4.64	0.026	0.96	10	0.48	0.20	0.8	0.3
"	"	"	10-20	7.56	0.033	1.56	20	0.79	0.31	1.5	0.6
"	"	"	20-30	11.43	0.037	2.36	30	0.98	0.38	2.6	1.0
"	"	"	30-40	11.55	0.034	2.39	40	1.00	0.38	3.2	1.2
"	"	"	40-50	10.85	0.033	2.24	50	1.39	0.53	3.5	1.3
"	"	"	50-60	9.61	0.030	1.99	60	1.04	0.37	2.8	1.0
"	"	"	60-70	8.38	0.021	1.73	70	1.22	0.43	3.6	1.3
"	"	"	70-80	5.99	0.019	1.24	80	1.25	0.39	3.4	1.1
"	"	"	80-90	4.32	0.013	0.89	90	1.08	0.36	2.6	0.9
"	"	"	90-100	2.15	0.007	0.44	100	0.93	0.30	2.3	0.7
20 July 78-F	1441		0-10	4.43	0.030	0.64	10	0.66	0.24	1.4	0.5
"	"	"	10-20	6.49	0.032	0.94	20	0.58	0.39	1.3	0.9
"	"	"	20-30	11.16	0.038	1.61	30	1.32	0.49	3.5	1.3
"	"	"	30-40	12.27	0.041	1.77	40	1.28	0.45	3.8	1.4
"	"	"	40-50	11.01	0.036	1.59	50	1.33	0.45	3.6	1.2
"	"	"	50-60	9.15	0.034	1.32	60	1.67	0.53	4.0	1.3
"	"	"	60-70	7.98	0.029	1.15	70	1.34	0.42	3.7	1.2
"	"	"	70-80	6.13	0.024	0.88	80	1.61	0.54	3.7	1.3
"	"	"	80-90	4.64	0.019	0.67	90	1.72	0.53	3.3	1.0
"	"	"	90-100	2.43	0.009	0.35	100	1.69	0.60	2.9	1.0
"	"	"	100-110	1.13	0.004	0.16	-	-	-	-	-
27 July 78-A	4595		0-10	3.68	0.017	1.69	10	1.05	0.49	2.1	1.0
"	"	"	10-20	3.88	0.013	1.78	20	0.93	0.42	2.0	0.9
"	"	"	20-30	1.41	0.005	0.65	-	-	-	-	-
27 July 78-B	5242		0-10	2.78	0.012	1.46	10	0.88	0.39	2.0	0.9
"	"	"	10-20	5.26	0.016	2.76	20	1.24	0.55	3.0	1.4
"	"	"	20-30	4.53	0.013	2.37	30	0.91	0.41	2.6	1.2
"	"	"	30-40	2.94	0.008	1.54	40	1.52	0.71	4.8	2.2
"	"	"	40-50	0.62	0.002	0.33	-	-	-	-	-

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
27July78-C	3449		0-10	2.29	0.009	0.79	10	0.76	0.31	1.8	0.7
"	"	"	10-20	3.33	0.011	1.15	20	1.56	0.69	3.7	1.6
"	"	"	20-30	3.56	0.011	1.23	30	1.30	0.59	4.0	1.8
"	"	"	30-40	3.14	0.010	1.08	40	1.21	0.55	3.5	1.6
"	"	"	40-50	2.54	0.008	0.88	50	0.69	0.34	2.6	1.3
"	"	"	50-60	1.42	0.004	0.49	-	-	-	-	-
"	"	"	60-70	0.24	0.001	0.08	-	-	-	-	-
27July78-D	2863		0-10	3.58	0.017	1.02	10	0.51	0.23	0.9	0.4
"	"	"	10-20	4.81	0.019	1.38	20	0.99	0.41	2.3	1.0
"	"	"	20-30	6.96	0.023	1.99	30	1.42	0.59	3.9	1.6
"	"	"	30-40	7.45	0.024	2.13	40	1.30	0.52	3.3	1.3
"	"	"	40-50	7.18	0.024	2.06	50	1.32	0.53	3.6	1.5
"	"	"	50-60	6.44	0.022	1.84	60	1.30	0.52	3.5	1.4
"	"	"	60-70	5.47	0.020	1.57	70	1.41	0.58	4.2	1.7
"	"	"	70-80	4.62	0.015	1.32	80	1.03	0.42	3.5	1.4
"	"	"	80-90	3.35	0.012	0.96	90	1.19	0.50	4.7	2.0
"	"	"	90-100	2.27	0.008	0.65	100	0.97	0.41	3.4	1.5
"	"	"	100-110	0.82	0.003	0.23	-	-	-	-	-
27July78-E	1971		0-10	4.15	0.025	0.82	10	0.40	0.18	0.8	0.4
"	"	"	10-20	6.25	0.028	1.23	20	0.63	0.24	1.7	0.6
"	"	"	20-30	9.58	0.033	1.89	30	0.72	0.29	2.0	0.8
"	"	"	30-40	10.08	0.032	1.99	40	1.18	0.46	2.8	1.1
"	"	"	40-50	9.21	0.032	1.82	50	1.21	0.46	2.4	0.9
"	"	"	50-60	8.03	0.028	1.58	60	1.30	0.48	2.5	0.9
"	"	"	60-70	6.68	0.022	1.32	70	1.15	0.43	2.6	1.0
"	"	"	70-80	5.02	0.014	0.99	80	1.07	0.35	4.5	1.5
"	"	"	80-90	3.74	0.012	0.74	-	-	-	-	-
"	"	"	90-100	2.05	0.008	0.40	-	-	-	-	-
27July78-F	1409		0-10	5.39	0.033	0.76	10	0.75	0.32	1.1	0.5
"	"	"	10-20	7.37	0.037	1.04	20	1.14	0.47	2.5	1.0
"	"	"	20-30	10.16	0.039	1.43	30	1.35	0.53	3.5	1.4
"	"	"	30-40	12.15	0.040	1.71	40	1.36	0.52	3.6	1.4
"	"	"	40-50	11.76	0.041	1.66	50	1.27	0.50	3.7	1.5
"	"	"	50-60	10.95	0.040	1.54	60	1.38	0.52	4.0	1.5
"	"	"	60-70	9.32	0.035	1.31	70	0.98	0.36	3.1	1.2
"	"	"	70-80	7.40	0.027	1.04	80	1.01	0.36	2.4	0.9
"	"	"	80-90	5.92	0.022	0.83	-	-	-	-	-
"	"	"	90-100	3.53	0.013	0.50	-	-	-	-	-
"	"	"	100-110	2.47	0.010	0.35	-	-	-	-	-
"	"	"	110-120	1.25	0.005	0.18	-	-	-	-	-
03Aug78-A	4408		0-10	4.12	0.016	1.82	10	1.53	0.64	2.9	1.2

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
03Aug78-A	4408		10-20	3.77	0.013	1.66	20	1.16	0.47	2.2	0.9
"	"	"	20-30	0.87	0.003	0.38	30	1.72	0.43	1.2	0.3
03Aug78-B	4804		0-10	2.92	0.011	1.40	10	1.27	0.57	2.5	1.1
"	"	"	10-20	5.14	0.015	2.47	20	1.27	0.58	3.6	1.6
"	"	"	20-30	4.45	0.014	2.14	30	1.31	0.57	2.9	1.3
"	"	"	30-40	2.78	0.009	1.34	40	0.53	0.12	1.0	0.2
"	"	"	40-50	0.68	0.002	0.33	-	-	-	-	-
03Aug78-C	2893		0-10	2.36	0.009	0.68	10	1.21	0.50	2.2	0.9
"	"	"	10-20	3.51	0.010	1.02	20	1.34	0.59	4.2	1.9
"	"	"	20-30	3.52	0.010	1.02	30	1.76	0.78	4.3	1.9
"	"	"	30-40	2.73	0.008	0.79	40	1.32	0.58	3.1	1.4
"	"	"	40-50	2.06	0.006	0.60	50	1.10	0.50	2.9	1.3
"	"	"	50-60	0.92	0.003	0.27	60	1.41	0.60	2.3	1.0
03Aug78-D	2631		0-10	3.35	0.014	0.88	10	0.61	0.24	1.0	0.4
"	"	"	10-20	4.60	0.017	1.21	20	0.99	0.41	2.1	0.9
"	"	"	20-30	6.69	0.021	1.76	30	1.46	0.60	3.8	1.5
"	"	"	30-40	6.45	0.020	1.70	40	1.96	0.80	4.7	1.9
"	"	"	40-50	6.27	0.018	1.65	50	1.07	0.45	2.4	1.0
"	"	"	50-60	5.70	0.017	1.50	60	0.84	0.34	1.7	0.7
"	"	"	60-70	5.39	0.016	1.42	70	0.76	0.32	1.6	0.7
"	"	"	70-80	3.47	0.011	0.91	80	0.46	0.16	1.3	0.5
"	"	"	80-90	2.26	0.008	0.59	90	4.06	1.40	5.8	2.0
"	"	"	90-100	0.80	0.002	0.21	-	-	-	-	-
03Aug78-E	1875		0-10	4.33	0.024	0.81	10	0.98	0.39	1.5	0.6
"	"	"	10-20	6.82	0.028	1.28	20	1.39	0.56	2.7	1.1
"	"	"	20-30	9.90	0.032	1.86	30	1.14	0.45	2.7	1.1
"	"	"	30-40	11.44	0.034	2.14	40	1.07	0.42	2.3	0.9
"	"	"	40-50	11.02	0.033	2.07	50	0.98	0.38	2.4	0.9
"	"	"	50-60	10.07	0.028	1.89	60	0.98	0.36	2.5	0.9
"	"	"	60-70	9.28	0.026	1.74	70	0.82	0.23	1.9	0.5
"	"	"	70-80	7.49	0.022	1.40	80	0.51	0.17	1.2	0.4
"	"	"	80-90	5.95	0.019	1.11	90	0.48	0.13	1.4	0.4
"	"	"	90-100	4.12	0.013	0.77	100	1.36	0.55	2.5	1.0
"	"	"	100-110	2.17	0.007	0.41	-	-	-	-	-
03Aug78-F	1376		0-10	5.03	0.034	0.69	10	1.28	0.38	1.8	0.5
"	"	"	10-20	6.99	0.039	0.96	20	1.74	0.71	3.3	1.3
"	"	"	20-30	10.24	0.045	1.41	30	1.60	0.60	4.4	1.7
"	"	"	30-40	12.45	0.042	1.71	40	1.02	0.36	3.1	1.1
"	"	"	40-50	11.61	0.044	1.60	50	1.40	0.46	2.9	0.9
"	"	"	50-60	11.23	0.044	1.55	60	1.11	0.34	2.5	0.8
"	"	"	60-70	10.80	0.041	1.49	70	1.41	0.45	3.1	1.0
"	"	"	70-80	9.01	0.036	1.24	80	1.13	0.35	2.4	0.8

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl a/dm ²	mg chl b/dm ²	mg chl a/g dry	mg chl b/g dry
03Aug78	F	1376	80-90	7.04	0.029	0.97	90	0.82	0.24	1.9	0.6
"	"	"	90-100	4.91	0.020	0.68	100	0.60	0.21	1.7	0.6
"	"	"	100-110	2.82	0.011	0.39	110	1.10	0.39	3.3	1.2
"	"	"	110-120	1.23	0.006	0.17	120	1.24	0.61	2.9	1.4
10Aug78	A	4221	0-10	4.14	0.013	1.75	10	1.57	0.64	4.5	1.8
"	"	"	10-20	3.55	0.013	1.50	20	1.42	0.59	4.9	2.0
"	"	"	20-30	1.49	0.005	0.63	30	3.51	1.19	6.0	2.0
10Aug78	B	4367	0-10	3.85	0.015	1.68	10	2.10	0.90	4.3	1.8
"	"	"	10-20	5.44	0.015	2.38	20	1.74	0.75	3.8	1.7
"	"	"	20-30	4.08	0.013	1.78	30	1.46	0.46	3.8	1.2
"	"	"	30-40	1.32	0.004	0.58	40	0.86	0.15	1.4	0.3
"	"	"	40-50	0.24	0.001	0.10	50	0.70	0.29	1.6	0.7
10Aug78	C	2336	0-10	2.52	0.010	0.59	10	1.42	0.58	2.1	0.9
"	"	"	10-20	4.47	0.013	1.04	20	1.69	0.73	3.3	1.4
"	"	"	20-30	4.28	0.012	1.00	30	1.51	0.64	4.3	1.8
"	"	"	30-40	3.53	0.010	0.82	40	1.55	0.64	4.3	1.8
"	"	"	40-50	2.94	0.008	0.69	50	0.80	0.38	2.6	1.2
"	"	"	50-60	1.75	0.005	0.41	60	0.55	0.36	2.6	1.7
"	"	"	60-70	0.31	0.001	0.07	-	-	-	-	-
10Aug78	D	2400	0-10	3.19	0.016	0.77	10	0.53	0.21	1.0	0.4
"	"	"	10-20	4.71	0.016	1.13	20	1.00	0.40	2.4	1.0
"	"	"	20-30	7.41	0.020	1.78	30	1.59	0.63	4.0	1.6
"	"	"	30-40	7.37	0.020	1.77	40	1.60	0.64	4.2	1.7
"	"	"	40-50	7.24	0.019	1.74	50	1.45	0.57	4.3	1.7
"	"	"	50-60	6.92	0.018	1.66	60	1.13	0.46	3.7	1.5
"	"	"	60-70	6.05	0.017	1.45	70	0.79	0.32	2.4	1.0
"	"	"	70-80	4.94	0.014	1.19	80	0.56	0.22	1.7	0.7
"	"	"	80-90	2.85	0.008	0.68	90	0.55	0.24	2.6	1.2
"	"	"	90-100	0.81	0.002	0.19	100	0.47	0.17	1.5	0.5
10Aug78	E	1779	0-10	4.18	0.026	0.74	10	0.49	0.18	0.7	0.3
"	"	"	10-20	6.22	0.027	1.11	20	0.69	0.26	1.4	0.5
"	"	"	20-30	9.58	0.032	1.70	30	1.04	0.42	2.7	1.1
"	"	"	30-40	10.53	0.033	1.87	40	1.03	0.40	2.7	1.0
"	"	"	40-50	10.37	0.032	1.84	50	0.97	0.38	2.1	0.8
"	"	"	50-60	9.34	0.029	1.66	60	1.14	0.44	2.8	1.1
"	"	"	60-70	8.70	0.026	1.55	70	1.10	0.40	2.6	0.9
"	"	"	70-80	7.58	0.024	1.35	80	1.21	0.43	2.5	0.9
"	"	"	80-90	6.20	0.019	1.10	90	2.36	0.84	2.9	1.0
"	"	"	90-100	3.53	0.012	0.63	100	1.01	0.35	2.9	1.0
"	"	"	100-110	1.92	0.007	0.34	110	1.27	0.31	2.0	0.5
10Aug78	F	1344	0-10	4.44	0.027	0.60	10	0.79	0.31	1.4	0.6

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg chl <i>a</i> /dm ²	mg chl <i>b</i> /dm ²	mg chl <i>a</i> /g dry	mg chl <i>b</i> /g dry
10Aug78	F	1344	10-20	6.83	0.036	0.92	20	1.20	0.48	3.7	1.5
"	"	"	20-30	11.65	0.042	1.57	30	1.50	0.58	4.7	1.8
"	"	"	30-40	10.95	0.041	1.47	40	1.61	0.59	4.6	1.7
"	"	"	40-50	9.91	0.039	1.33	50	1.60	0.58	4.6	1.7
"	"	"	50-60	7.78	0.030	1.05	60	1.48	0.52	4.9	1.7
"	"	"	60-70	5.59	0.021	0.75	70	1.77	0.68	4.3	1.6
"	"	"	70-80	3.17	0.012	0.43	80	1.88	0.71	4.9	1.8
"	"	"	80-90	0.61	0.002	0.08	-	-	-	-	-
17Aug78	A	4034	0-10	3.61	0.013	1.46	10	1.28	0.55	3.9	1.7
"	"	"	10-20	4.16	0.014	1.68	20	1.36	0.57	3.3	1.4
"	"	"	20-30	1.47	0.005	0.59	30	1.63	0.56	3.3	1.1
17Aug78	B	3929	0-10	2.39	0.009	0.94	10	0.84	0.32	2.3	0.9
"	"	"	10-20	4.66	0.013	1.83	20	1.83	0.77	4.6	2.0
"	"	"	20-30	4.54	0.013	1.78	30	1.92	0.81	4.8	2.0
"	"	"	30-40	3.62	0.012	1.42	40	1.76	0.73	3.6	1.5
"	"	"	40-50	2.13	0.007	0.84	50	1.31	0.54	2.5	1.0
"	"	"	50-60	0.73	0.003	0.29	60	0.95	0.83	2.4	1.0
"	"	"	60-70	0.30	0.001	0.12	70	0.65	0.22	2.4	0.8
17Aug78	C	1780	0-10	2.19	0.009	0.39	10	0.66	0.28	1.3	0.5
"	"	"	10-20	4.09	0.012	0.73	20	1.33	0.59	3.3	1.5
"	"	"	20-30	3.92	0.011	0.70	30	1.72	0.74	4.2	1.8
"	"	"	30-40	3.37	0.011	0.60	40	1.12	0.48	2.9	1.2
"	"	"	40-50	2.88	0.009	0.51	50	1.01	0.41	2.5	1.0
"	"	"	50-60	1.57	0.005	0.28	60	1.33	0.60	2.6	1.2
"	"	"	60-70	0.30	0.001	0.05	70	1.55	0.73	4.5	2.1
17Aug78	D	2168	0-10	4.31	0.023	0.93	10	0.85	0.25	1.6	0.5
"	"	"	10-20	5.75	0.023	1.25	20	1.23	0.47	3.1	1.2
"	"	"	20-30	8.74	0.025	1.89	30	1.56	0.62	4.0	1.6
"	"	"	30-40	8.30	0.024	1.82	40	1.60	0.63	4.3	1.7
"	"	"	40-50	8.39	0.024	1.80	50	1.84	0.71	4.4	1.7
"	"	"	50-60	7.43	0.022	1.61	60	1.63	0.62	3.5	1.4
"	"	"	60-70	6.26	0.019	1.36	70	1.36	0.53	3.5	1.4
"	"	"	70-80	4.88	0.015	1.06	80	1.09	0.42	3.1	1.2
"	"	"	80-90	3.04	0.009	0.66	90	1.14	0.46	3.1	1.2
"	"	"	90-100	1.12	0.004	0.24	100	0.55	0.22	1.2	0.5
17Aug78	E	1683	0-10	4.51	0.025	0.76	10	0.75	0.29	1.4	0.6
"	"	"	10-20	6.73	0.030	1.13	20	0.83	0.31	1.5	0.6
"	"	"	20-30	10.01	0.034	1.68	30	1.06	0.39	2.9	1.1
"	"	"	30-40	10.71	0.034	1.80	40	1.37	0.38	3.8	1.1
"	"	"	40-50	9.89	0.031	1.66	50	1.02	0.37	3.1	1.1
"	"	"	50-60	8.83	0.028	1.49	60	0.95	0.35	3.0	1.1

Date	Station	Total Shoot Density (No./m ²)	Canopy Segment (cm)	Leaf Area (cm ² /shoot)	Dry Weight (g dry/shoot)	LAI	Distance Above Bottom (cm)	mg ch1 a/dm ²	mg ch1 b/dm ²	mg ch1 a/g dry	mg ch1 b/g dry
17Aug78	E	1683	60-70	8.60	0.026	1.45	70	0.95	0.34	3.0	1.1
"	"	"	70-80	7.92	0.025	1.33	80	0.95	0.33	2.9	1.0
"	"	"	80-90	6.00	0.021	1.03	90	0.74	0.23	2.3	0.7
"	"	"	90-100	3.34	0.011	0.56	100	0.94	0.30	3.7	1.2
"	"	"	100-110	1.14	0.004	0.20	110	1.24	0.37	4.5	1.3
17Aug78	F	1331	0-10	5.31	0.030	0.70	10	0.87	0.37	1.2	0.5
"	"	"	10-20	8.25	0.037	1.08	20	0.69	0.28	1.4	0.6
"	"	"	20-30	11.25	0.041	1.47	30	1.25	0.48	2.8	1.1
"	"	"	30-40	11.48	0.042	1.51	40	1.35	0.50	2.8	1.0
"	"	"	40-50	10.92	0.042	1.43	50	1.24	0.42	2.7	0.9
"	"	"	50-60	9.52	0.040	1.25	60	1.43	0.47	3.0	1.0
"	"	"	60-70	7.20	0.031	0.94	70	1.79	0.60	3.1	1.0
"	"	"	70-80	5.23	0.023	0.69	80	1.02	0.31	2.8	0.8
"	"	"	80-90	3.43	0.016	0.45	90	1.46	0.40	3.4	0.9
"	"	"	90-100	1.53	0.007	0.20	100	1.46	0.36	2.6	0.6