

## THE GROWTH DYNAMICS OF *HALOPHILA HAWAIIANA*

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### ABSTRACT

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A functional growth model was developed for *Halophila hawaiiiana* Doty and Stone, based on its regular plastochrone interval, and the relationship between leaf area and plant biomass. The model allows estimates of biomass, productivity and turnover from easily collected field samples. From these samples, the number of actively growing apical buds, total leaf number and total leaf area for a unit area were determined. This model was applied to a meadow in Kaneohe Bay, Oahu. The mean biomass was 104.25 g dry wt. m<sup>-2</sup> and the productivity 7.11 g dry wt. m<sup>-2</sup> day<sup>-1</sup>. The turnover time was 14.7 days.

### INTRODUCTION

Understanding the growth dynamics of a species is important in assessing its role in the ecosystems in which it occurs. Among the seagrasses, a wealth of information dealing with stand biomass, productivity, turnover and growth patterns has been documented for the large-leaved species such as *Thalassia testudinum* Banks ex König and *Zostera marina* L. However, documentation of these aspects of growth dynamics is generally lacking for the smaller-leaved species.

The lack of attention to the small-leaved seagrasses is due, in part, to an absence of adequate methods for measuring their growth and productivity under field conditions. Leaf marking (Zieman, 1974, 1975) has been generally accepted as a good method for measuring growth in situ (Zieman and Wetzel, 1980). However, this method is impractical for plants that have small delicate leaves.

### GENERAL DESCRIPTION OF *HALOPHILA*

*Halophila*, being pantropical, is the most widely distributed seagrass genus and can be found in nearly every habitat capable of supporting seagrasses (den Hartog, 1970). Balfour (1878) and Tomlinson (1974, 1982) have

provided detailed information on the anatomy of the species, as well as some general information on growth patterns.

*Halophila hawaiiiana* Doly et Stone (Fig. 1) exhibits rhizomatous growth, and produces erect leaves that protrude a few cm above the substrate. Growth of this plant is dependent on its apical bud meristems. These periodically produce a pair of foliage leaves, 2 scale leaves, an unbranched root and a single lateral branch meristem at each node (Ancibor, 1979; Tomlinson, 1982). The branch meristem normally remains inactive, but in some cases may become active, producing a branch that takes on the characteristics of an axial rhizome.

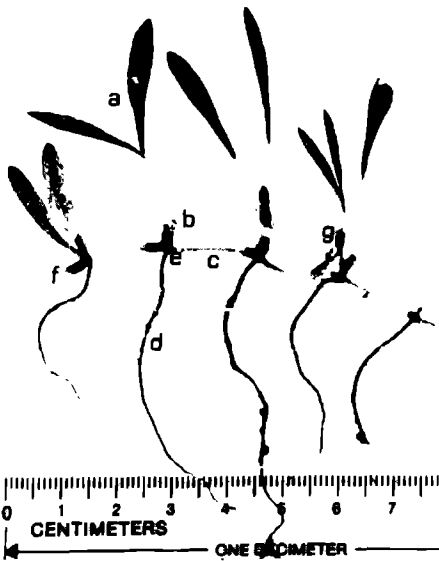


Fig. 1. *Halophila hawaiiiana*: (a) foliage leaves; (b) scale leaves; (c) rhizome; (d) unbranched root; (e) node; (f) apical bud; (g) short branch.

## MATERIALS AND METHODS

### *Dimensional analysis*

Samples were collected in April and May 1983 (spring) and January and February 1984 (winter) from Ahuolaka Island, Kaneohe Bay, Oahu (21° 28' N, 157° 48' E). A total of 69 samples was collected from 10 × 10-cm quadrats placed randomly throughout the monospecific *H. hawaiiiana* meadow.

The leaf area for each sample was determined by removing all blades and

petioles, placing these between sheets of thin plastic film and passing them through a Li-cor model 3100 area-meter. All plant parts were then thoroughly cleaned, decalcified in a 20%  $\text{H}_3\text{PO}_4$  solution and then dried for 24 h at 105°C. The dried biomass was weighed to the nearest 0.01 g.

### *Growth experiments*

Growth studies were conducted in order to test a hypothesis, based on observation, that *H. hawaiiiana* produces new foliage leaves at regular intervals. The production of 2 new foliage leaves is associated with the formation of 1 new node. In laboratory and field experiments, growth of *H. hawaiiiana* was measured as a function of the number of nodes produced in 14 days. Growth increments including the most recently produced internode and node were recorded as a fraction, based on an evaluation of the size of the leaves on that node relative to mature leaves on the axial rhizome. Production and growth of lateral branches were also recorded.

### *Growth-chamber experiments*

Thirty-four plants, each having a single apical bud, were measured for rhizome diameter, number of nodes and internode length. These were floated in 500-ml-deep petri dishes with filtered and sterilized natural seawater. Lighting was provided by 8 40 W fluorescent lamps and maintained at a 12:12 h. photoperiod. The instantaneous photon flux density at the level of the plants was  $320 \mu\text{mole m}^{-2} \text{s}^{-1}$ , providing an integrated daily photon flux density of  $13.8 \text{ mole m}^{-2}$ . The seawater was partially replaced every 3 days, and kept in continuous slow agitation. The temperature was maintained at 22–25°C. Growth increments were measured at 3, 6, 9 and 14 days.

### *Floating cage experiments*

The growth experiment was repeated with potted plants in Kaneohe Bay under conditions that were considered to be similar to those found in the meadow being examined. This experiment was used to estimate the overall growth rate, since measurements could only be made at the beginning and at the end. Eighty plants were measured for rhizome diameter and number of nodes present, then potted in coral sand and placed in the lagoon at the Hawaii Institute of Marine Biology. The pots were suspended in floating wire cages so that they remained 50–60 cm beneath the water surface. The instantaneous photon flux density at the level of the plants reached as high as  $390 \mu\text{mole m}^{-2} \text{s}^{-1}$  at noon; an estimated photon flux density of 12–14  $\text{mole m}^{-2}$  was available to the plants daily. Temperatures ranged between 22 and 26°C. All growth increment measurements were made after 14 days.

The experiment was also used to evaluate the production of lateral branches. After 14 days, the amount of growth exhibited by existing branches and the number and length of new lateral branches were recorded. An additional 39

plants with apical buds excised were potted and grown next to the intact plants. These were similarly measured after 14 days.

### *Meadow dynamics assessment*

Twenty new quadrat samples were taken in March 1984. All leaves from each sample were counted and total leaf area was estimated from a sub-sample of 50 leaves (petiole inclusive). The number of apical buds, frequency of branches and their lengths were recorded. These data were then used in conjunction with the information acquired from the earlier examinations of dimensional analysis, growth and branching to develop a general model of productivity of the meadow at Ahuolaka Island.

## RESULTS

### *Dimensional analysis*

The biomass/leaf area relationship was analyzed by fitting a linear regression with a forced zero intercept (Fig. 2). The high value for the coefficient of determination ( $r^2 = 0.96$ ) shows the close correlation of these 2 measurements. The possibility that seasonal growth variation between spring 1983 and winter 1984 samples might have an effect on this relationship was examined, and no significant difference was found. McRoy (1970) observed a similar relationship between the length and biomass of *Zostera marina* leaves.

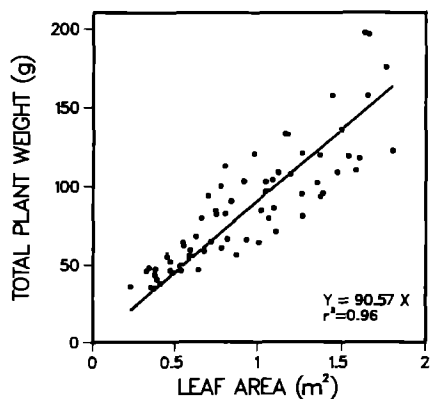


Fig. 2. Linear regression of leaf area and dry plant weight. There are 69 observations from field samples collected during April and May 1983 and January and February 1984. The regression has been forced to have a zero intercept. Data are expressed on a  $m^2$  basis.

## Growth rates

Growth-chamber studies were carried out on free-floating plants to determine if the more conspicuous anatomical components (nodes and corresponding leaves and roots) were produced at a constant rate. The overall mean growth rate was  $0.27 \text{ nodes day}^{-1}$ , with a standard deviation of 0.086, giving a coefficient of variation of 31.9%. A trend of initially slow growth followed by more regular growth rates was observed (Fig. 3). The rate of growth during each of the 4 measurement periods was compared using a Waller-Duncan test, and found to form 2 significant groups (at the 5% protection level), separating the growth rate during the first measurement period from that during the subsequent periods. It is reasonable to assume that the handling of the plants resulted in the initial decrease in their growth rates. Virnstein (1982) noted a similar 1–3-day lag in growth for *Halodule wrightii* Aschers. plants that had their leaves clipped. Therefore, the mean of the last 3 periods,  $0.29 \text{ nodes day}^{-1}$ , is considered to be a more reliable estimate of growth. As expected, the standard deviation, 0.084, and the coefficient of variation, 29.0%, are smaller for this period. This growth rate is equivalent to an average 3.5 days being required for the production of 1 node.

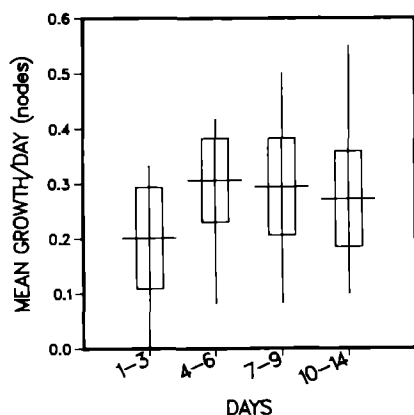


Fig. 3. Growth rates (based on the number of new nodes produced) calculated for plants during 4 measurement periods in laboratory culture. Each vertical bar represents the range of 34 observations. The mean and standard deviation are represented as a horizontal bar and a box.

The average growth rate of the potted plants grown in Kaneohe Bay was  $0.24 \text{ nodes day}^{-1}$ , with a standard deviation of 0.051 and a coefficient of variation of 21.3%. This rate is equivalent to 1 new node being produced every 4.2 days. While these results are considered to be closer to those expected under normal conditions in a *Halophila* meadow, the possible in-

fluence of transplantation shock similar to that observed in the growth-chamber experiment must be considered.

The results of the floating cage experiment were further analyzed for any influence of rhizome length and diameter at the start of the experiment on the rate of growth. The initial rhizome length (ranging from 4 to 6 nodes) showed no correlation ( $r^2 = 0.052$ ) with the number of nodes produced. Therefore, it is unlikely that the use of plant fragments biased the growth estimates in the experiments. The rhizome diameter was found to be weakly correlated ( $r^2 = 0.285$ ) with the number of nodes produced. However, when plants having a rhizome diameter of 1 mm or less were excluded, no correlation was found ( $r^2 = 0.042$ ). The smaller rhizome diameter might indicate slower-growing plants.

### *Apical bud excision experiment*

Lateral branches in *Halophila* spp. are infrequent and typically short, with 2–3-mm-long internodes. The apical bud excision experiment provided a measurement of the degree of lateral branch suppression.

After 14 days, plants having the apical bud excised produced new lateral branches at 69.7% of the available nodes (those nodes not having a branch present at the start of the 14-day period). A size of 2–4 nodes was reached on 58% of these new branches. In contrast, control plants produced new branches at only 10.3% of the available nodes. Only 12% of these reached a size of 2 nodes (Fig. 4). In order for a new branch to reach a size of 4 nodes within the 14-day period, a production rate of at least  $0.29 \text{ nodes day}^{-1}$  would be necessary. This compares with the average production rate of undamaged plants.

A similar trend was observed on branches present at the start of the 14-

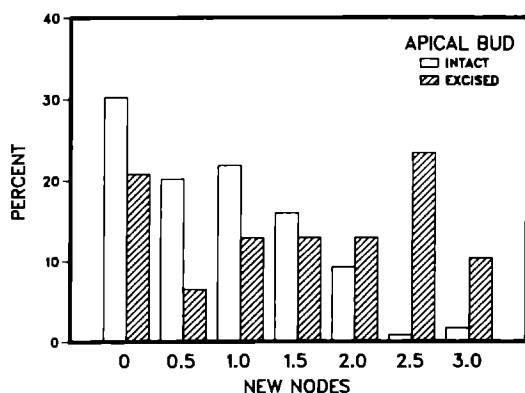


Fig. 4. The effect of apical bud removal on development of lateral branches. The number of nodes on lateral branches were measured after 14 days. Vertical bars show the distribution of branches with different node numbers (measurable growth increments) as a percentage of those measured.

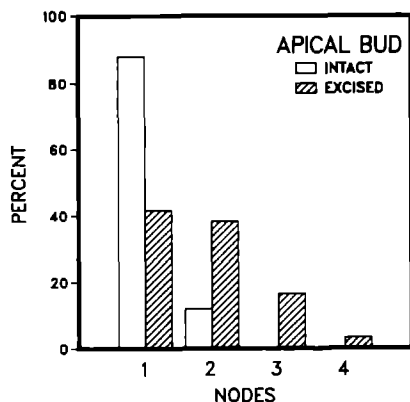


Fig. 5. The effect of apical bud removal on the growth of branches existing at the start of the 14-day growth period. Vertical bars represent the distribution of branches that produced different numbers of nodes, and are expressed as a percentage of those measured.

day period. A greater percentage of the branches on the experimental plants increased in size by 2 or more nodes (Fig. 5).

Lateral branch suppression on control plants was further indicated by the production of short internodes (2–3 mm). Internodes produced in new growth of branches on experimental plants reached a length of up to 20 mm.

#### *Meadow dynamics assessment*

A large *H. hawaiiiana* meadow was sampled to provide the basis for estimates of its biomass, production and turnover.

The leaf density was found to average 30 650 leaves  $\text{m}^{-2}$ , with a standard deviation of 7955 and a coefficient of variation of 26%. The average leaf area was 1.151  $\text{m}^2 \text{m}^{-2}$  (one sided), with a standard deviation of 0.332 and a coefficient of variation of 28.8%. There was an average of 4390 apical buds  $\text{m}^{-2}$ , with a standard deviation of 1121 and a coefficient of variation of 25.5%.

#### DISCUSSION

Earlier studies on seagrass growth dynamics (Patriquin, 1973; Sand-Jensen, 1975; Jacobs, 1979) have utilized the plastochrone interval (the amount of time between the initiation of sequential leaves) as an indicator of the growth rate (Tomlinson and Bailey, 1972; Tomlinson, 1974). For *H. hawaiiiana*, this is most easily measured as the time between the formation of 2 successive nodes. This node becomes a natural marker for the productivity of the plant because of the subsequent development of similar plant structures at each node.

The growth-chamber experiment was designed to test whether the plastochrone interval of *H. hawaiiiana* is sufficiently constant to predict the rate of growth. The low variation that was found among plants indicates that this measure can be used for such a prediction. Floating-cage experiments (close to natural conditions) provided values that could be applied to field situations.

One of the differences between the 2 experiments measuring the plastochrone interval was the amount of light provided to the plants. The growth chamber plants had a lower incident light level, but this level remained constant throughout the 12-h photoperiod. The result was that a greater amount of light was provided to the growth-chamber plants than to those in outdoor floating cages over the duration of the experiment, although the difference was not large. It may be that this factor accounts for the slight difference in the plastochrone interval observed between the 2 experiments. This should be kept in mind when the plastochrone interval is used for growth dynamics estimations that involve plants occurring over a range of depths.

### *Growth dynamics model*

The verification of a constant plastochrone interval, and the premise that a given leaf area will support a predictable biomass, now become useful in formulating a model that can be used in *Halophila* meadow assessments. Productivity and turnover for the entire plant can be estimated from a model that expresses the relationships between the values measured in field samples, the plastochrone interval (*P.I.*) and the biomass to leaf area relationship (*S*).

$$\frac{\text{Apical buds}}{P.I.} \times \frac{2 \text{ leaves}}{\text{Apical bud}} = \frac{\text{New leaves}}{\text{Day}} \quad (1)$$

$$\frac{\text{New leaves}}{\text{Day}} \times \frac{\text{Mean area}}{\text{Leaf}} = \frac{\text{New leaf area}}{\text{Day}} \quad (2)$$

$$\frac{\text{New leaf area}}{\text{Day}} \times S = \frac{\text{Total productivity}}{\text{Day}} \quad (3)$$

$$\frac{\text{Leaf area}}{\text{Productivity/day}} \times S = \text{Turnover time (days)} \quad (4)$$

In this model, all measurements refer to a unit area.

A particular value of this model is that the field measurements that it requires are simple to obtain, once the plastochrone interval and biomass to leaf area relationship are determined. The plastochrone interval for a given geographic location can be determined by temporarily placing a marker at the apex of individual plants in a *Halophila* meadow for a period of 1 or 2



weeks. Leaf area (generally on a sub-sample) and the density of the actively growing apical buds are easily collected data. The apical buds of branches having more than 2 nodes and without the characteristically short internodes of suppressed branches would qualify as being active. The relatively short period of time required to collect and process samples allows extensive sampling from within a meadow.

### *Meadow dynamics assessment*

Using the mean values for the data presented earlier for the Kaneohe Bay *Halophila* meadow and applying the determined *P.I.* and *S* values, the following assessment of biomass, productivity and turnover was made.

On the basis of leaf area samples, the dry weight plant biomass for the meadow is estimated to be  $104.25 \text{ g m}^{-2}$ . A *P.I.* of 4.2 days and apical bud density of  $4390 \text{ m}^{-2}$  produce an estimated  $2090 \text{ leaves m}^{-2} \text{ day}^{-1}$ . Calculating the average individual leaf area (one sided) to be  $3.755 \times 10^{-5} \text{ m}^2 \text{ leaf}^{-1}$  (from mean leaf density  $\text{m}^{-2}$  and mean leaf area  $\text{m}^{-2}$ ), it is estimated that  $7.85 \times 10^{-2} \text{ m}^2$  is produced daily for each square meter of meadow area. This translates to a productivity of  $7.11 \text{ g dry wt. m}^{-2} \text{ day}^{-1}$  if *S* = 90.57 (Fig. 2). Compared with productivity of larger-leaved seagrasses, these values for the small-leaved *Halophila hawaiiiana* are surprisingly high (Patriquin, 1973; Jacobs, 1979).

Turnover rate was determined by the following calculation:

$$\frac{104.25 \text{ g dry wt. m}^{-2}}{7.11 \text{ g dry wt. m}^{-2} \text{ day}^{-1}} = 14.7 \text{ days} \quad (5)$$

or  $6.8\% \text{ day}^{-1}$  turnover. This is extremely fast when compared with the large-leaved seagrasses (Patriquin, 1973, Jacobs, 1979); hence the high productivity. Virnstein (1982) found a similar high turnover for *Halodule wrightii*.

The overall implications of this study are that a complete analysis of seagrass meadow dynamics can include an evaluation of the small-leaved seagrasses. A method whereby such an evaluation can be made has been formulated specifically for *Halophila* and applied to a monospecific meadow of *H. hawaiiiana*. The results show that the productivity of this small plant may provide a large contribution to the overall productivity and ecological significance of a seagrass meadow in the tropics.

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