ESTIMATION OF GROWTH RATE, PRODUCTION AND AGE OF THE MARINE ANGIOSPERM *THALASSIA TESTUDINUM* KÖNIG

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ABSTRACT: There is a linear relation between average growth rate and the average maximum leaf length of *Thalassia* stands. The ratio production-to-standing crop (wet weight including epiphytes) tends to be constant. New foliage leaves are developed at intervals of about 15 days, and by counting of leaf scars, the age, growth rate and production of underground parts can be estimated.

INTRODUCTION

THALASSIA testudinum König is the dominant marine angiosperm of the Caribbean. Growths of this plant stabilize shifting bottom sediments (Ginsburg and Lowenstam, 1958) and create habitats for a large number of plant and animal species (Stephens, 1966). According to Odum (1959) and Westlake (1963), production rates of *Thalassia* rank amongst those of the most highly productive plants known. Detrital food chains are probably the major link between production of *Thalassia* and that of higher trophic levels (Fenchel, 1970). Studies by Patriquin (1971) indicate that *Thalassia* obtains its nitrogen exclusively

from N_2 fixed by heterotrophic bacteria in the rhizosphere, and it is probable that *Thalassia* plays a major role in the nitrogen cycle in coastal waters.

Methods of estimating production based on seasonal increases in biomas are not applicable to plants such as *Thalassia* because rates of production and losses of leaf tissue are approximately constant throughout the year. The validity of applying techniques of estimating production based on measurements of oxygen production to aquatic plants has been questioned because of the retention of metabolic gases within the lacunal system (Hartman and Brown, 1967). The ^{14}C technique as applied to aquatic plants (Wetzel, 1964), while useful in experimental studies, is obviously limited in application to routine studies in the field. Zieman (1968) measured growth of *Thalassia* leaves by the elegantly simple technique of marking the leaves with metal staples.

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Very little is known concerning the age, growth rate and production of underground parts of aquatic angiosperms (Westlake, 1965). The present paper reports relationships which allow estimation of growth rate, production and age of *Thalassia* from easily obtained plant statistics. These studies were carried out in connection with studies on the nutrition and general ecology of *Thalassia* in the Barbados-Grenadine Islands region.

The vegetative morphology of *Thalassia* has been described in detail by Tomlinson and Vargo (1966). A creeping rhizome or "long shoot" branches at regular intervals giving rise to erect "short shoots" which bear strag-shaped foliage leaves (Fig. 1). These
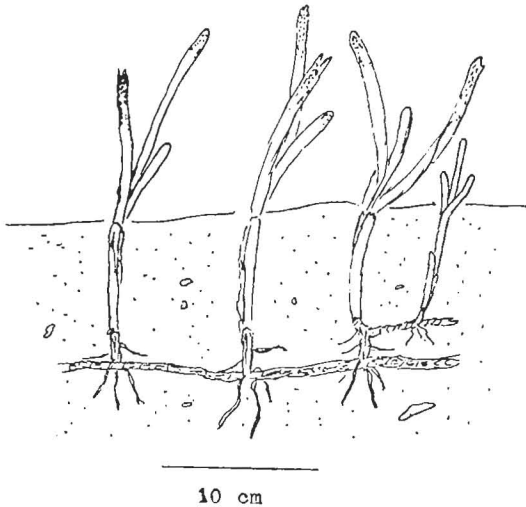

FIG. 1. Habit sketch of *Thalassia*. Old parts of leaves are encrusted with calcareous algae.

two axes are referred to here simply as rhizome and shoot. Leaves are produced apically on shoots and are borne in alternate positions. Normally only the leaves are observed above the substrate. Colorless scale-leaves occur on the rhizome. Branching of shoots, which occurs infrequently, gives rise to rhizome. Old distal parts of *Thalassia* leaves are typically covered by calcareous algal epiphytes

(Humm, 1964). At Barbados, growths of these epiphytes result in breaking off of the leaf tips of *Thalassia* (Figs. 1, 2) and the original rounded leaf tip is usually observed on only the youngest one or two leaves on a shoot. It was postulated that in the absence of heavy grazing, the maximum length reached by
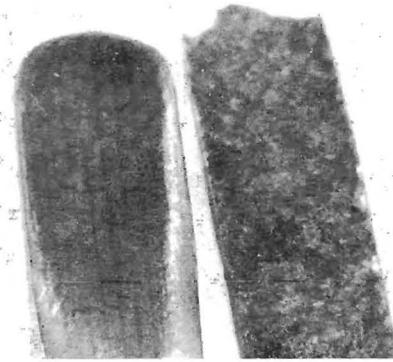

FIG. 2. (left) Distal end of young leaf, tip intact; (right) distal end of old leaf, encrusted with calcareous algae, and tip broken off. X 2.

a leaf is determined mainly by (1) the growth rate of the leaf, (2) the rate of encrustation by calcareous epiphytes, and (3) factors such as wave action which mechanically aid the actual breaking off process. Examination of leaves indicated little variation in the degree of encrustation by calcareous epiphytes between various stands at Barbados. This, and observations of marked differences in maximum leaf length between adjacent stands (i.e. stands subject to the same level of wave action), suggested that variations in leaf length are due mainly to variations in growth rate. Growth rate measurements utilizing Zieman's (1968) technique of stapling leaves were made on stands of differing leaf lengths to determine the relation between maximum leaf length and average growth rate. At the same time, the relation of production to standing crop was examined, and a study of underground parts suggested a means of estimating age, growth rate and production of underground parts.

METHODS AND MATERIALS

Observations were carried out on *Thalassia* stands at St. Lawrence and Bath, Barbados, in the summer of 1969. Data obtained in connection with other studies of a *Thalassia* stand at St. Katherine's Point, Bermuda, in August 1970, are also reported. All of these stands were in depths of less than 2 m below mean low water. The stands were subject to various degrees of wave action. On the basis of observations of wave height and water depth, and considerations of the solitary wave theory (King, 1959), wave action is referred to as gentle, moderate or strong (estimated maximum bottom velocities of orders of 20, 85 and 120 cm/sec).

Growth rates of individual leaves were determined by placing a metal staple on each leaf at a fixed height above the substrate, and determining the staple height after five days for the Barbados stands, and after 43 hours for the Bermuda stand. Staples, oriented vertically, were placed at 3 cm height in stands of generally short leaves, and at 5 cm height in stands of generally long leaves. Posts were inserted into the substrate to check for changes in the substrate (reference) level. On each of ten leaves in a stand of long leaves, a second staple was placed 3 cm above the first staple and the interval measured after 5 days. The average interval for the eight recovered leaves was 3.2 cm, indicating little or no elongation above the level of the first staple (Zieman, 1968 reported that 18% of the elongation of the leaves he studied took place above staples placed at 3 cm height above the substrate).

Two procedures were followed in the selection of leaves for marking. At each of 13 stands (Series 1), 50 leaves of greater than 3 or 5 cm length within an approximately 1 m² area were selected simply by closing the eyes and reaching for a leaf. An average of 60% of those marked were recovered (found) for growth measurements after 5 days. Average growth rates at these stands were estimated by dividing the total of the individual growth increments by the number of observations. A sample of leaves at each of the stands was taken from a 3/16 m² area (three separate 1/16th m² areas combined) by cutting leaves at substrate level. For each sample, the leaves were counted, and lengths of the 20 to 30 longest leaves and widths of 50 leaves measured. The weight of each leaf sample was determined after shaking the leaves and blotting them briefly with newspaper to remove excess water. For two other stands at Barbados (Series 2), one at Bath and one at St. Lawrence, all leaves on each of a number (25 at Bath, 12 at St. Lawrence) of shoots were marked. Those too short to be marked at the 5 cm level were marked by horizontally oriented staples, and the length of each such leaf and its particular shoot were noted. Staple position, width, length, presence or absence of original leaf tip, and the particular shoot were determined for each leaf at the end of 5 days. All leaves at each stand were combined for determination of wet weight. Average growth rates of the Series 2 stands were calculated by adding all growth increments including the total lengths to leaves which emerged subsequent to marking. Leaves on 13 shoots were marked at the Bermuda stand as for the Barbados stands. Leaf statistics at the Bermuda stand are based on a sample of leaves from 20 shoots in the same stand.

AVERAGE GROWTH RATE AND MAXIMUM LEAF LENGTH

$L_{5\%}$, the average length of the longest 5% of the leaves in the leaf samples is used as a measure of the 'average maximum leaf length' of the *Thalassia* stands. A plot of average growth rate (G) versus $L_{5\%}$ for the Series 1 stands is given in Figure 3. There is a highly significant correlation between G and $L_{5\%}$ (Spearman's rank correlation coefficient r = 0.90, P < 0.001). The relation between these statistics is linear; the least squares regression of Fig. 3 is given by

$$G = 0.318 \, L_{5\%} - 1.40$$

While these data indicate that the differences in maximum leaf length between the various stand were associated mainly with differences in growth rate, the
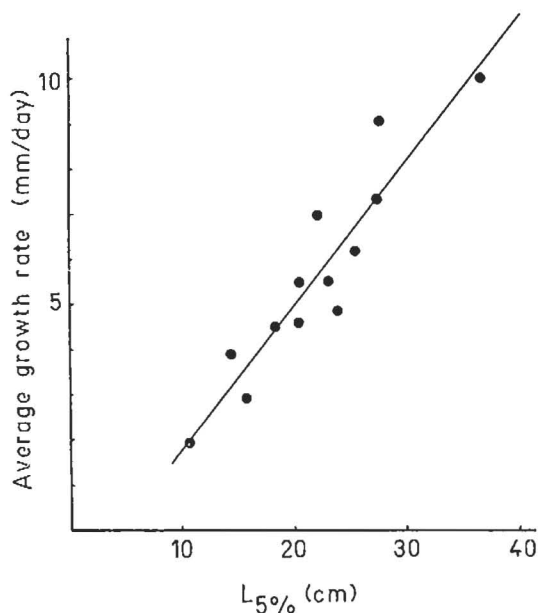
FIG. 3. Relation of leaf growth rate to the maximum length of leaves ($L_{5\%}$) in *Thalassia* stands

$$G = 0.210\ L_{5\%} - 0.92$$

In stands of leaf densities of 75 leaves and greater per 3/16 m², there is little difference between $L_{5\%}$ and an unweighted (by leaf density) measure of the average maximum leaf length, L_{10} -the average length of the 10 longest leaves in a 3/16 m² sample. For the Series 1 stands, which varied in leaf density from 73 to 413 leaves per 3/16 m², the ratio L_{10} -to-$L_{5\%}$ varied from 0.94 to 1.06. For another sample of 807 leaves, the L_{10} -to-$L_{5\%}$ ratio was 1.06. Use of an unweighted measure is convenient when large numbers of samples are being processed, or when it is wished to carry out measurements without removal of leaves from the substrate. At very low leaf densities it is obviously necessary to use a weighted measure. However, weighting can be somewhat arbitrary, perhaps 3 leaves in samples of low leaf density, 10 leaves in samples of intermediate leaf density, and 20 leaves in samples of high leaf density.

PRODUCTION AND STANDING CROP

Production of leaf tissue at the Series 1 stands was estimated as

$$P_m = n\ x\ G_c \times w\ x\ c$$

where P_m is production (g dry wt leaf tissue/m² per day), n is the number of leaves per m², G_c is the observed average growth rate multiplied by 0.66 (cm/day), w is the average leaf width (cm), and c is the dry weight of epiphyte-free leaf tissue (g/cm²), c varies with the average width of the leaves (Fig. 4):

$$c = 3.38 + 1.43\ \textcolor{magenta}{w}$$

where c is in mg/cm², and w is in cm. Production values were compared with standing crop values (wet weight including epiphytes) by calculation of the production-to-standing crop (P/SC) ratio. The mean of these ratios for the Series 1 stands is 0.0037 (SD = 0.00057). The P/SC ratios of the Series 2 stands were calculated by adding all increments of growth, multiplying by c and dividing by the wet weight of all

estimates are in error because leaves of various ages were not marked in proportion to their occurrence. Selection of leaves for marking in the Series 2 stands was not subject to this bias, and thus the average growth rate estimates of these stands can be expected to be more accurate. The observed average growth rates were 7.1 and 5.3 mm/day for the Bath and St. Lawrence Series 2 stands respectively, and the growth rates predicted from their $L_{5\%}$ measures (Table I) were 10.0 and 8.6 mm/day. Examination of the original data indicates that the older, slower growing leaves were greatly undersampled in the Series 1 stands; 15% of the leaves in the Series 2 stands exhibited no growth over the 5 day period, whereas only 7% of all leaves in the Series 1 stands exhibited no growth. A correction is applied to the above regression by multiplying the intercept and slope by 0.66, the average of the observed growth rate-to-estimated growth rate ratios of the Series 2 stands. The corrected regression is thus
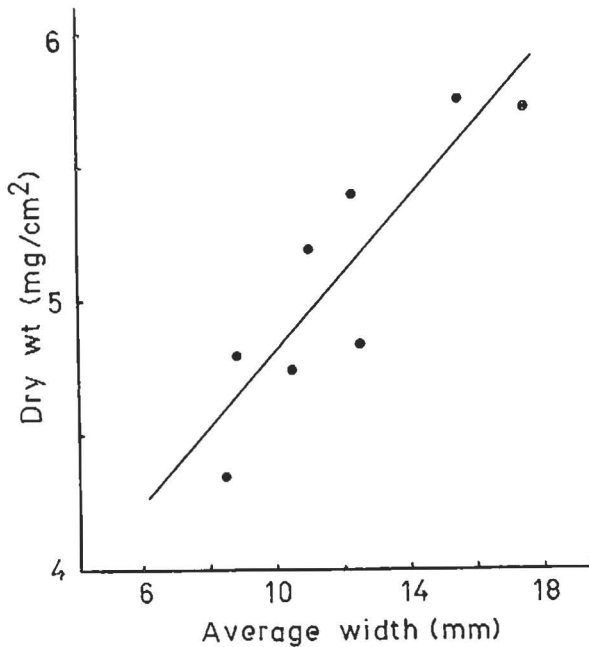
FIG. 4. Dry weight of epiphyte-free leaf tissue as a function of average leaf width

leaves; the ratios are 0.00375 and 0.00360 for the Bath and St. Lawrence stands respectively. The agreement of these ratios suggests that the P/SC ratio is reasonably constant. At least as a first approximation, production of the Barbados *Thalassia* stands can be estimated by multiplying standing crop (wet wt including epiphytes) by 0.0037.

Fourteen samples of Barbados *Thalassia*+ epiphytes had an average dry weight-to-wet weight ratio of 0.190 (SD = 0.020). For one of these samples the amount of calcareous material, estimated as the loss fo dry weight following treatment with hydrochloric acid, was 45% of the dry weight. The amount of calcareous material of Bermuda *Thalassia* was not measured, but it was noticeably less than at Barbados. This is reflected in the lower dry weight-to-wet weight ratio of the Bermuda *Thalassia*, 0.144. Removal of calcareous material from large samples of *Thalassia* is a tedious procedure. Unless epiphytes are removed, there seems to be little advantage in using dry weight over wet weight as a measure of standing crop. Because wet weight is

proportionally less influenced by variations in the amount of calcareous material than is dry weight, variations in wet weight probably more closely reflect variations in the amount of *Thalassia* tissue than do variations in the dry weight.

GROWTH OF INDIVIDUAL LEAVES

In studies of growth and production of *Thalassia* in Florida, Zieman (1968) observed the appearance of 6 new leaves on 6 shoots over a 14 day period, 11 new leaves on 10 shoots over a 16 day period and 8 new leaves on 4 shoots over a 32 day period. He concluded that "under normal conditions a branch produces a new blade every 14 to 16 days." From observations of new leaf appearance (Table I) the frequency of new leaf development was estimated as 15.6 days for the Bath stand, 12.0 days for the St. Lawrence stand and 11.7 days for the Bermuda stand. The 95% confidence intervals for these estimates (from the binomial distribution: 9.4-33 days for the Bath stand, 7.4-32 days for St. Lawrence and 4.2-92 days for Bermuda) are large, and the observations are considered consistent with those of Zieman (1968).

Periodicity in leaf development was also estimated from data of the Series 2 stands as follows. It is assumed: (1) all leaves on a given shoot follow a similar pattern of growth from time of initial emergence from the substrate to maturity and cessation of growth; thus if two leaves with their original tips present occur on the same shoot, the length of the older of the two is the length the younger would reach after growing for an interval (T) equal to the difference in their ages; (2) the growth rate decreases linearly with age of a leaf; (3) the observed growth rates of individual leaves were the instantaneous growth rates at time 2.5 days after they were marked. Based on these assumptions, T was estimated as

$$T = (A + 2.5 D)/(G_y - 0.5 D)$$

where A is is the difference in length of two leaves with original tips on a shoot (mm), D is the difference in their average

growth rates over the 5 day period (mm/ day), and G_y is the average growth rate of the younger of the two leaves over the 5 day period. Leaf data from 6 shoots were suitable for making this estimate (Table II). The estimates of T have a mean of 15.1 days.

The longest unmarked leaf (leaf which emerged after marking) of the Series 2 stands was 11.0 cm in length. Assuming that this leaf emerged from the substrate immediately after marking, then its average growth rate over the 5 day period was 22 mm/day. The growth rates of the other leaves on this shoot were 10.4, 1.4 and 0 mm/day. Assuming, as above, that all leaves on a shoot have a similar growth pattern, and that the observed growth rates represent instantaneous rates at times 2.5, 17.5, 32.5 and 47.5 days, then the growth of an individual leaf on this shoot may be represented as in Fig. 5. This figure suggests that the growth rate of a leaf decreases more or less regularly with age, and cessation of growth occurs sometime between 35 and 45 days.

PRODUCTION PER SHOOT

The concept of an 'average growth rate' may be somewhat misleading when used in the sense of 'the average growth rate of all leaves in a stand' because (1) it includes leaves at all stages of maturity growing at very different rates, and (2) its magnitude is in part determined by the length of time dead leaves remain attached to the shoot. Comparison of data on the number of dead leaves and the average number of leaves per shoot (Table I) indicates that the length of time dead leaves remain attached to the shoot is influenced by wave action. The high number of dead leaves at the Bermuda stand may also have been associated with a low degree of epiphyte infestation at that stand. These data show that the average growth rate of the leaves in a stand is meaningful only as a parameter relating production per unit area to the number of leaves present. A suggested statistic for the purpose of comparing growth rates, in the physiological sense, between different stands is I_s, the
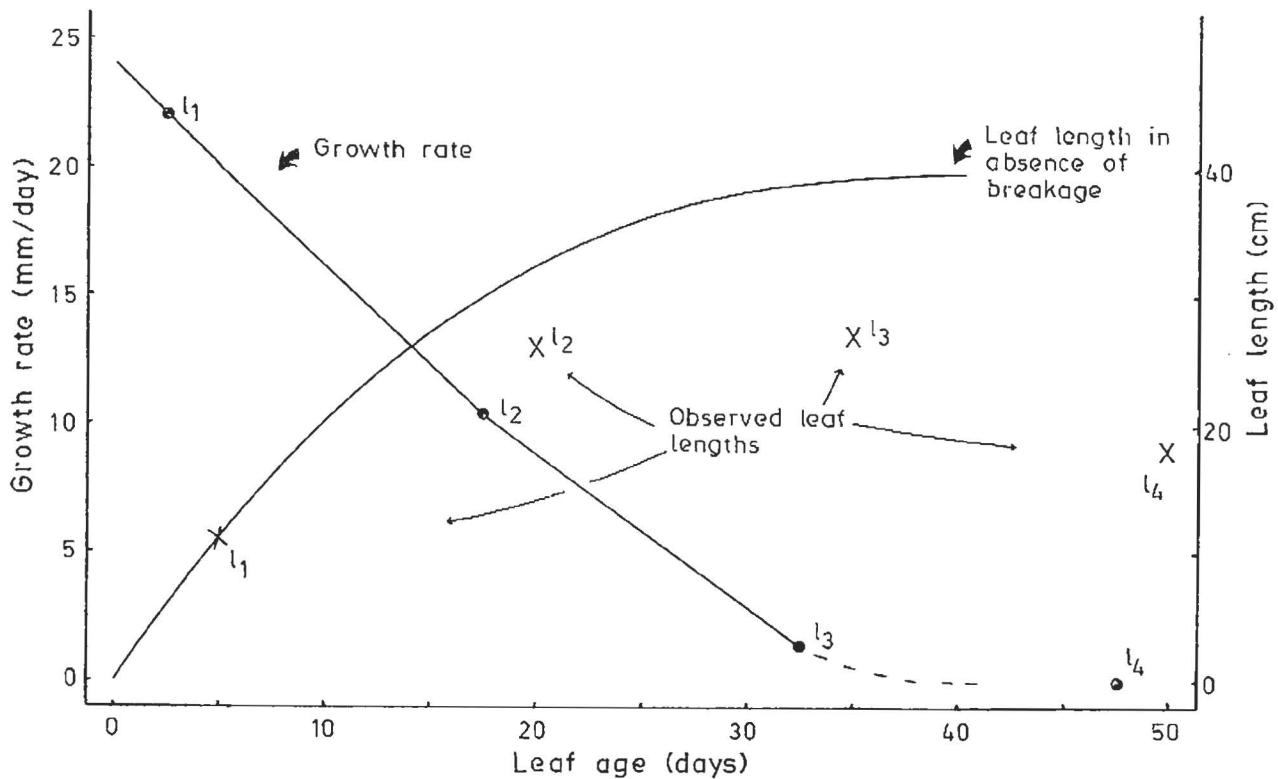

FIG. 5. Growth of an individual leaf. Projected from observed growth rates of four leaves (l_1, l_2, l_3, l_4) on a shoot

average length of leaf tissue produced per shoot per day. Comparison of the ratios $I_s/I_{s\ Bath}$, $L_{5\%}/L_{5\%\ Bath}$, and G/G_{Bath} in Table I indicates that variation in wave action has much less effect on the average maximum leaf length than on the number of leaves per shoot. Thus 'average growth rates' estimated from the leaf length-growth relation are comparable in the physiological sense. This is self-evident from the data in Fig. 3, and is suggested also by studies in which a high degree of correlation ($r_s = 0.96$, $P < 0.001$) was found between L_{10} and a strictly physiological characteristic, the concentration of ammonium(+amino acid)—N in the rhizomes (Patriquin, 1971). I_s may be estimated from the G-$L_{5\%}$ relation by multiplying the estimate of G by 3.5 (the mean of the two average no. leaves per shoot values of the Series 2 stands, Table I); the relation between I_s and $L_{5\%}$ is then given by

$$I_s = 0.735\ L_{5\%} - 3.22$$

where I_s is in mm/day and $L_{5\%}$ is in cm.

The production of leaf tissue per shoot is given by

$$P_s = I_s\ x\ w\ x\ c$$

where P_s is production in mg leaf tissue/shoot per day, w is the average leaf width in cm and c is the dry weight of epiphyte-free leaf tissue in mg/cm^2. Multiplication of P by the number of shoots per unit area gives the production per unit area. Alternatively, dividing P_m (estimated from the P/SC ratio) by P_s gives an estimate of the number of shoots per m^2, a statistic that is often difficult to obtain by direct count. At one stand, the number of shoots per m^2 estimated by a count of shoots in a 1/8 m^2 area was 488, while the number estimated by dividing P_m by P_s was 463.

AGE, GROWTH RATES AND PRODUCTION OF UNDERGROUND PARTS

Shoots of *Thalassia* have distinct leaf scars (Fig. 6). Assuming a 15 day periodicity in development of new leaves, the age of a shoot can be estimated by counting the leaf
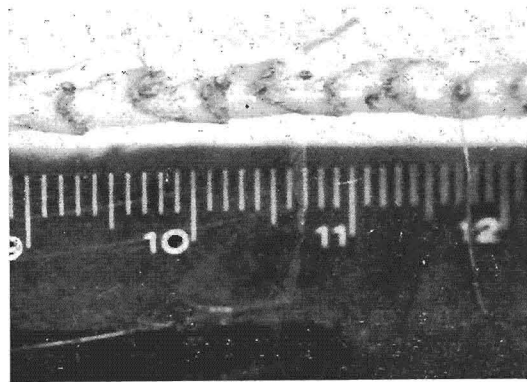

FIG. 6. A portion of an erect shoot with dead leaf tissue removed to show leaf scars

scars and leaves, and multiplying this number by 15 days. Tomlinson and Vargo (1966) observed that meristematic tissue is restricted to the rhizome apex, and concluded that growth and branching of the rhizome are restricted to the apical region of the rhizome. Hence an estimate of the growth rate of the rhizome may be obtained by dividing the length of the rhizome between two shoots by the difference in the ages of the two shoots.

Observations of the difference in ages between shoots on 10 rhizome fragments suggest there is a periodicity in branching of rhizomes. Of 21 pairs of adjacent shoots examined, 10 pairs differed in the number of leaf scars+leaves by 1, and 11 pairs differed by 2. Since leaf scars and leaves can be counted in only whole numbers, these observations suggest that the difference in age between adjacent shoots does not vary greatly and usually is some figure between 15 and 30 days. The average difference in number of leaf scars+leaves between adjacent shoots was 1.52 which is equivalent to an average difference in age of 22.8 days. Estimates of the average difference in age of adjacent shoots on 5 rhizome fragments with 5 or more shoots, and estimated average growth rates of the rhizomes are given in Table III. These and the above data indicate a periodicity in branching of the rhizome of the order of 24 days.

Since shoots are generally separated by 9, 11 or 13 internodes (Tomlinson and Vargo, 1966), new scale leaves bust be produced at intervals of less than 15 days. Several of the rhizome fragments and associated shoots examined included growing tips of the rhizomes. The shoot next to the apex on these fragments (Fig. 7) had 6 or 7 leaves including scale-leaves and "intermediates "(Tomlinson and Vargo, 1966) between scale-leaves and foliage leaves. The shoot next to the youngest differed in the number of leaf scars+leaves from the youngest by 1 or 2, as described above. Since the interval between development of new shoots is estimated as approximately 24 days, the
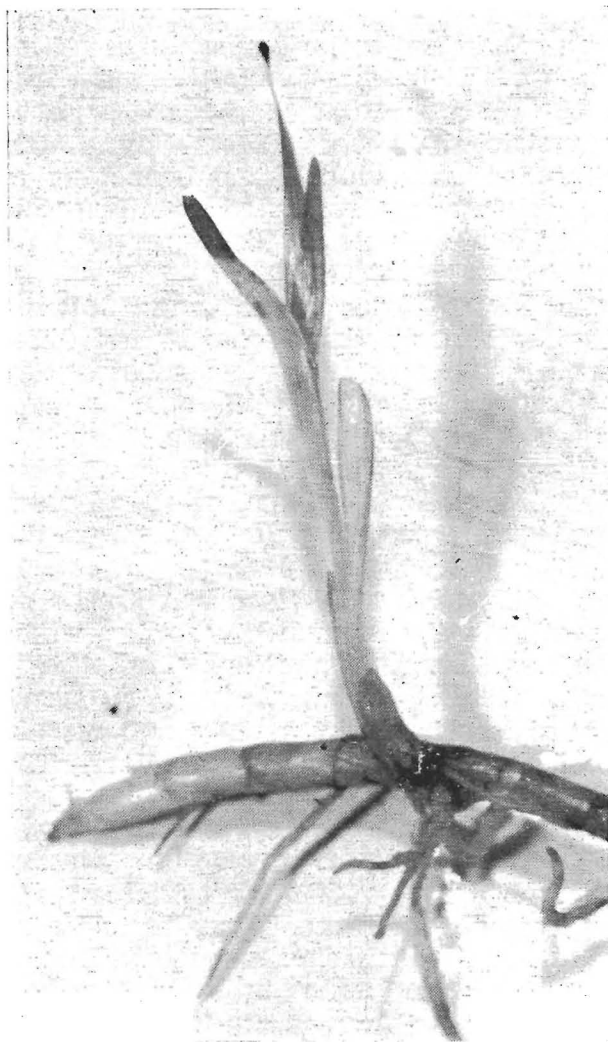

FIG. 7. Rhizome growing tip and young erect shoot. X 1

first 6 or 7 leaves must be produced within this interval. Presumably the change from a less than 15 day periodicity in development of scale-leaves as on the rhizome to a 15 day periodicity in development of foliage leaves as on shoots is completed by the time of development of the 6th or 7th leaf. In aging a shoot the first 7 leaf scars should thus be considered to represent 24 days growth, and each subsequent leaf-scar or leaf can be considered to represent 15 days growth. Preliminary studies, made at 17 different *Thalassia* stands, indicate that except in very young stands it is common to find shoots at least 4½ years of age, and not uncommon to find shoots 8 to 10 years of age. The oldest shoot observed was 10.5 years of age. There are large differences in the spacing of leaf-scars (i.e. in shoot growth rates), and these may reflect differences in sedimentary conditions. In an area where it was evident that accretion of sediment was occurring rapidly, the average distance between leaf scars was 3.2 mm, while in an adjacent area which appeared to be quite stable (well developed epifauna), the average distance was 0.30 mm.

Production of shoot and rhizome tissue may be estimated as

$$P_m = n \times G \times c$$

where P_m is the production (g dry wt shoot or rhizome tissue/m² per day), n is the number of shoots or rhizome growing tips per m², G is the average growth rate of shoots or rhizomes (cm/day), and c is the dry wt (g/cm) of shoots or rhizomes. To determine c it may be neccessary to remove roots from shoots and rhizomes because of adherent sediment, and thus production of root tissue would not be included; this is probably small in any case. It is generally difficult to remove underground parts from the substrate in intact condition. Average growth rates of shoots and rhizomes may be estimated by determining the average internodal distance on fragments of shoots and the average intershoot distance on rhizome fragments, and dividing by 15, 24 days. The number of rhizome growing tips may be estimated by digging up the substrate

under a given surface area and counting the growing tips exposed and which float to the surface.

Because shoot apices may lie well under the substrate surface, a significant amount of leaf tissue may be produced underground that is not included in the estimate of leaf tissue production above the substrate. This material is decomposed under the sediment surface, and thus should be included in estimates of underground production. Assuming one new leaf is produced on each shoot every 15 days, production of leaf tissue underground may be estimated as

$$P_m = (n \times w \times l \times c)/15 \text{ days}$$

where P_m is production (g dry wt leaf tissue per m² per day), n is the number of shoots per m², w is the average leaf width (cm), l is the average depth of the shoot apices below the substrate surface (cm) and c is the dry weight (g/cm²) of epiphyte-free leaf tissue (Fig. 4).

Estimates of the total plant tissue production at a Barbados *Thalassia* stand and a Bermuda *Thalassia* stand are given in Table IV. It can be seen that there may be significant production of leaf tissue underground; production of shoot and rhizome tissue was less than 1/7 of the total production in these stands.

DISCUSSION

Development of techniques for estimating age, growth rates and production of marine angiosperms is obviously dependent on an understanding of the vegetative morphalogy of the plant concerned. The vegetative morphology of the temperate water counterpart of *Thalassia, Zostera marina* L., has been studied in detail and estimates of the age, growth rate and production of this plant have been made (Petersen, 1914; Setchell, 1929). Critical morphological studies of other marine angiosperms are required. Several of the relationships reported in the present paper are implicit in the conclusions of Tomlinson and Vargo (1966) regarding the development of *Thalassia*. For example they refer to branching of the rhizome as a well ordered," "rhythmic" process, and Tomlinson (1970)

remarked that the regular intervals at which branching occurs seem "to be determined entirely by the time which has lapsed since a previous branching." It is nos surprising then that the present study indicated a periodicity in branching of the rhizome. Tomlinson's concept of separate autonomies of the rhizome and shoot is well illustrated by the difference in periodicity in development of scale-leaves on the rhizome and foliage leaves on the shoots.

Since the periodicity in foliage leaf development appears to be constant throughout the range of *Thalassia* distribution (represented by the Florida stands of Zieman, 1968, and the Bermuda and Barbados stands of the present study), the methods of estimating age and production of underground parts should be applicable to *Thalassia* throughout its range. However the methods of estimating growth rates and production of leaves are based on empirical relations which may vary from place to place, and perhaps with depth.

According to the hypothesis stated in the Introduction, maximum leaf length is determined in part by the rate of infestation of leaves by calcareous epiphytes. Thus one might expect a significant difference in the growth rate-maximum leaf length relation between areas in which the rate of infestation by calcareous epiphytes varies significantly. The degree of epiphyte infestation was significantly less at Bermuda than at Barbados. However, the I_s of the Bermuda stand predicted from the Barbados I -$L_{5\%}$ relation, 2.7 cm/day, is in good agreement with the observed I , 2.8 cm/day. There did appear to be somewhat more "scollaping" of the leaves — Thomas *et al.* (1961) attribute this to grazing — at Bermuda than at Barbados. Still, the agreement may not be entirely coincidental. There must be some negative feedback between leaf length and growth rate; leaf length per se influences growth rate through photosynthesis, and growth rate influences leaf length. Differences in the lengths of other sea grasses, for example as reported for *Zostera* (Ostenfeld, 1908), *Syringodium* and *Diplanthera* (Phillips, 1960; Strawn, 1961) are probably also related

to variations in growth rate. Even without knowledge of the quantitative relation of growth rate to maximum leaf length, the maximum length is a useful and easily obtained statistic.

The production-to-standing crop ratio of the Bermuda stand, 0.0034, is close to the ratios of the Barbados stands. In general there tends to be poorer growth of calcareous epiphytes in calm water than in turbulent water (Land, 1970). This would tend to result in higher P/SC ratios in calm water conditions. On the other hand, leaves tend to remain attached longer under calm conditions, and this would tend to result in smaller ratios. While the relation between production and standing crop (wet weight including epiphytes) is theoretically complicated, it may be reasonably constant.

All observations at Barbados and Bermuda were made on stands at depths less than 2 m, and there was probably little variation in the amount of light reaching these stands. Jones (1968) found that oxygen production by *Thalassia* is influenced mainly by standing crop and the length of day with illumination greater than 20 ly/hr. Hence it may not be reliable to use relationships observed for shallow water stands for estimating growth and production of deep water stands.

It may be possible to correlate growth of *Thalassia* leaves with a leaf statistic that is not influenced by variation in environmental parameters, at least not on a proximate basis. A suggested statistic is the average length of the youngest leaves on a number of shoots; the original tips are almost invariably present on these leaves. If the growth rate patterns of all leaves on a shoot are similar, which seems likely, then there should be a high degree of correlation between growth rate and this statistic. If this is so, then it would be possible to work out other production-leaf statistic relations in any area without having to make growth rate measurements.

At a time when increasing pressures are being put on coastal ecosystems, means of rapidly assessing the various parameters of these systems are urgently required. The relationships described, or similarly determined relationships, provide a basis for conveniently estimating the following. (1) Rates of primary production by *Thalassia*. (2) N_2 fixation in *Thalassia* beds — studies by Patriquin (1971) indicate that a minimum of the order of 11.5 mg N_2 are fixed per gram of *Thalassia* leaf tissue produced; thus multiplication of production by this factor gives a minimum estimate of the N_2 fixation associated with *Thalassia* stand. (3) Rates of production of sessile organisms such as calcareous algae, serpulids and foraminifera on *Thalassia* leaves — these can be estimated by multiplying the quantity of the organisms per cm^2 of old leaf tissue by the production of *Thalassia* expressed in terms of cm^2 leaf tissue produced. (4) Sedimentation rates — variation in spacing of leaf scars may reflect variation in sedimentation rates; this requires further study. (5) Rates of development of *Thalassia* stands — by determining the age of underground parts of *Thalassia* it is possible to estimate rates of succession in the early stages of *Thalassia* community development. Together with a knowledge of the growth rates of rhizomes, this information provides a basis for predicting the time required for *Thalassia* to colonize denuded or previously uncolonized areas.

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NOTE ADDED IN PROOF Dr. P. B. Tomlinson pointed out to the author that the parameter "T" (p. 115 and Table II) is referred to as the "plastochrone interval" by developmental biologists. The youngest 3 foliage leaf primordia are not included in the counts reported in the present paper; see: Tomlinson, P. B. 1972. On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae) IV. Leaf anatomy and development. Bull. Mar. Sci. Gulf and Carib., *22:* 75-93. Dr. Tomlinson suggested also that in the Florida region there may be seasonal variations in some of the parameters discussed in the present paper.

TABLE I

Leaf growth rate and production data of Series 2 stands and a Bermuda stand

| | SERIES 2 | | BERMUDA |
| | BATH | ST. LAWRENCE | |
WAVE ACTION	Strong	Moderate	Gentle
No. shoots	25	12	13
No. leaves	80	46	54
Period of observation	5 days	5 days	43 hr
No. new leaves emerged during period of observation	8	5	2
Non-growing leaves, % of total	12.5	19.6	29.6
Avg no. leaves per shoot	3.20	3.83	4.15
Avg width (mm)	14.0	15.1	7.28
c (mg/cm^2)	5.38 c	5.54 c	4.28 o
G (mm/day)	7.12	5.31	6.76
I_s (cm/shoot per day)	2.28	2.04	2.81
P_s (mg/shoot per day)	17.2	17.0	8.75
P/SC	0.00375	0.00360	0.00343
$L_{5\%}$ (cm)	36.0	31.5	41.0
$I_s/I_{s\,Bath}$	1.00	0.89	1.23
$L_{5\%}/L_{5\%\,Bath}$	1.00	0.87	1.30
G/G_{Bath}	1.00	0.74	0.95

c   estimated,   o   observed.

TABLE II

Growth rate-leaf length data for estimation of T

| SHOOT | YOUNGEST LEAF WITH TIP | | NEXT YOUNGEST LEAF WITH TIP | | OTHER LEAVES | | T (days) |
	Length (cm)	G (mm/day)	Length	G	Length	G	
Bath 1 ...	11	15.0	27	13.8	15	2.0	11.3
Bath 2 ...	8.5	10.4	23	8.6	8.5	0.6	15.7
Bath 3 ...	18.5	11.4	33.5	7.6	24	0	16.8
Bath 4 ...	19	9.0	36	8.4	26.5	0	19.7
SL 5	17	12.0	30	8.0	1.6 *	—	14.0
					11	0	
SL 6	22.5	12.0	33	6.0	5 *	—	13.3
					9	0.4	

*   Leaf emerged after marking.

TABLE III

Data for estimation of frequency of rhizome branching and rhizome growth rate

No. shoots on rhizome fragment	Leaves+leaf scars on youngest shoot	Leaves+leaf scars on oldest shoot	Distance between youngest and oldest shoots (cm)	Estimated difference in age between successive shoots (days)	Estimated avg growth rate of rhizome (mm/day)
8	15	26	45	23.6	2.7
7	11	21	36	25.0	2.4
5	7	13	28	22.5	3.1
5	7	14	26	26.3	2.5
5	19	26	31	26.3	3.0

TABLE IV

Underground production at two *Thalassia* stands

	Barbados	Bermuda
Shoots/m²	488	1611
Avg distance between leaf scars	2.1 mm	1.5 mm
Avg growth rate of shoots	0.14 mm/day	0.10 mm/day
Dry wt of shoots	0.041 g/cm	0.032 g/cm
PRODUCTION OF SHOOT TISSUE	0.28 g/m² per day	0.52 g/m² per day
Rhizome growing tips/m²	73	196
Avg intershoot distance	6.8 cm	5.2 cm
Avg growth rate of rhizomes	2.8 mm/day	2.2 mm/day
Dry wt of rhizomes	0.037 g/cm	0.035 g/cm
PRODUCTION OF RHIZOME TISSUE	0.76 g/m² per day	1.5 g/m² per day
Depth of shoot apices (range)	18 to 25 cm	4 to 10 cm
Assumed avg depth of shoot apices	21.5 cm	7 cm
Avg width of leaves	10.2 mm	7.3 mm
Dry wt of leaves	4.8 mg/cm²	4.3 mg/cm²
PRODUCTION OF LEAF TISSUE UNDERGROUND	3.4 g/m² per day	2.4 g/m² per day
TOTAL UNDERGROUND PRODUCTION	4.4 g/m² per day	4.4 g/m² per day
LEAF TISSUE PRODUCTION (above ground)	3.1 g/m² per day	14.1 g/m² per day