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## LEAF GROWTH IN THE SEAGRASS *SYRINGODIUM FILIFORME* KÜTZ.

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### ABSTRACT

Fry, B., 1983. Leaf growth in the seagrass *Syringodium filiforme* Kütz. *Aquat. Bot.*, 16: 361–368.

Field measurements made during the summer of 1982 in the Indian River lagoon, Florida, showed that *Syringodium filiforme* Kütz. displays a consistent pattern of growth. The cylindrical leaves lengthen at initial constant rates from a basal region, slow when approaching maturity, and finally cease growing. Elongation rates of individual blades varied by a factor of 3.6, from 0.86 to 3.11 cm day<sup>-1</sup>, but were usually similar within a factor of 1.5 for leaves growing on the same shoot. Leaf diameter was primarily determined by growth in the basal meristem region and varied from 0.80 to 1.47 mm during growth of an average 40 cm blade. *Syringodium* also partitions growth among leaves in a consistent manner. On an upright shoot that bears 1–3 leaves, growth is almost totally confined to the youngest leaf with a new leaf starting as the previous leaf stops. For productivity studies of *Syringodium*, monitoring growth of the youngest leaves on several leaf shoots will give accurate estimates of mean growth rates.

### INTRODUCTION

*Syringodium filiforme* Kütz. is a western Atlantic seagrass with its center of abundance in the tropical Caribbean (den Hartog, 1970). While *Syringodium* most often grows interspersed among other seagrasses in the Caribbean, it forms large monospecific meadows in the Indian River lagoon on Florida's east coast. *Syringodium* is the dominant seagrass in the lagoon (Thompson 1978), and leaf length may reach 65 cm in waters whose mean depth is about 1 m.

Aerial photography has shown that these *Syringodium* meadows are not uniform, but that the seagrass grows on mounds elevated about 5–20 cm over surrounding sand bottoms. Working in the northern part of the lagoon, Gilbert and Clark (1981) found that total plant biomass averages up to 41 g m<sup>-2</sup>. Ongoing sampling in denser *Syringodium* stands in the central part of

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the lagoon near Fort Pierce shows that plant biomass can exceed  $100 \text{ g m}^{-2}$  and is thus in the upper half of the biomass range reported for *Syringodium* (Zieman and Wetzel, 1980).

I studied *Syringodium* growth for two reasons. First, I wanted to develop a model based on growth rates that would predict leaf turnover rates and leaf age. Second, I wanted to establish how *Syringodium* ages and senesces as a preliminary to a broader study of *Syringodium* decay and export.

## METHODS

To assess growth, individual seagrass blades were measured in the field at 3–5-day intervals during May and June, 1982. Individual short shoots bearing 1–3 leaves were permanently marked at their base with numbered pieces of white Velcro. Leaf length was determined to the nearest mm as the height above a fixed reference located near the sediment surface. The most successful referent used was a 2-m section of 12.8 mm diameter PVC pipe pegged into the sediment at both ends and having a cut slot along its top to accommodate the base of a plastic meter stick.

Using this system, length measurements were reproducible to within  $\pm 3$  mm. Individual leaves on a stem were distinguished over time by recording a variety of characteristics on an underwater slate. These characteristics included leaf color, presence or absence of an intact serrated tip, degree of epiphytism, exterior or interior position relative to other leaves, and height at which the leaf branched from the stem. For simplicity, the height of this branch point has been subtracted out from leaf measurements in this paper so that actual blade length rather than height above the sediment is given.

To follow growth when leaf tips were fragmenting, 1-cm pieces of fine (280  $\mu\text{m}$  diameter) aluminium window screen wire were permanently inserted into leaves. Insertion of these markers did weaken leaves, however, as some senescing leaves eventually broke at the level of the wire.

Leaf widths were measured to the nearest 0.02 mm under a dissecting microscope equipped with an ocular micrometer.

## RESULTS

### *Basal growth*

Numerous marking experiments showed that leaves grow in length from a basal meristem region (e.g., Fig. 1). For growth in width, comparisons of younger and older leaves showed that leaves are also dependent on the basal meristem region and grow little, or not at all, after leaving this region. Thus when young, medium, and old blades were compared, blade width was very similar for equivalent regions such as the flattened tip, the narrowest part of the blade at ca. 0.6 mm below the tip, and for points further back along the blade (Fig. 2). A significant increase in width with increasing leaf age was

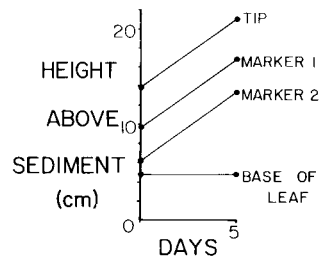


Fig. 1. Growth of a *Syringodium* blade that was marked internally with pieces of thread. Parallel movement of tip and markers indicates that no growth occurred between these points; instead, growth occurs at a lower point near the origin of the leaf.

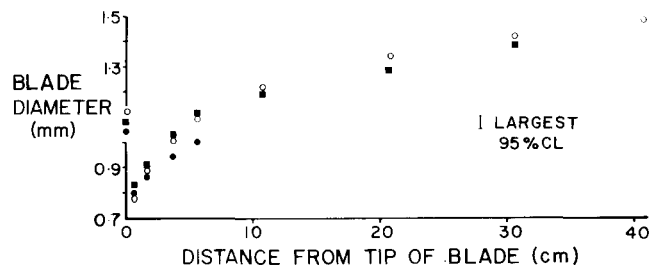


Fig. 2. Tapering of *Syringodium* blades. Points are means of ten blades from the following size categories: small, 4–13 cm (●); medium 23–36 cm (■); and large 45–54 cm (○). Vertical bar shows the largest 95% confidence interval for any of these means.

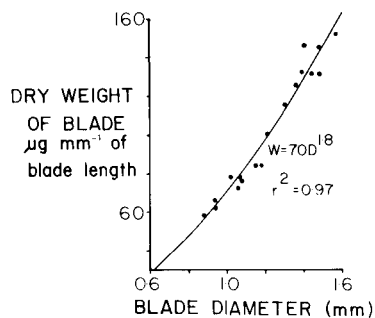


Fig. 3. Relationship between leaf diameter and dry weight for cylindrical *Syringodium* blades. Equation gives least squares fit for 18 samples of epiphyte-free tissue. Flattened leaf tips (mean length = 0.6 cm) were not included in this figure and averaged 26  $\mu\text{g}$  per tip.

apparent only in the region 3–6 cm from the tip. There, medium and old blades were about 0.10 mm wider than young blades (Fig. 2), and young leaves seem to widen from ca. 1.0 to 1.1 mm during maturation outside the basal sheath region.

Measurement of leaf weights showed that these changes in width also entail changes in weight (Fig. 3). Production of leaf material thus increases over time as blade diameter increases.

*Linear growth*

Figure 4 shows three examples of leaf elongation patterns that were observed. Typically, leaves grow at initial constant rates, gradually slow as they near maturity, then finally stop (Fig. 4A). In this example (Fig. 4A), the growth rate was constant at 2.11 cm per day for the first 11 days. In the following 11-day period, growth slowed and finally stopped. An unbroken serrated tip was present through Day 25 so that the two consecutive, identical length measurements at Days 22 and 25 showed that growth had stopped. After Day 25, however, the tip of the leaf began to fragment, and total length could no longer be used to assess growth. Observation of a wire marker inserted in the blade, however, showed that growth after Day 25 continued to be zero for another 20 days of monitoring (Fig. 4A).

Some slight variations in this pattern of monotonic linear growth were

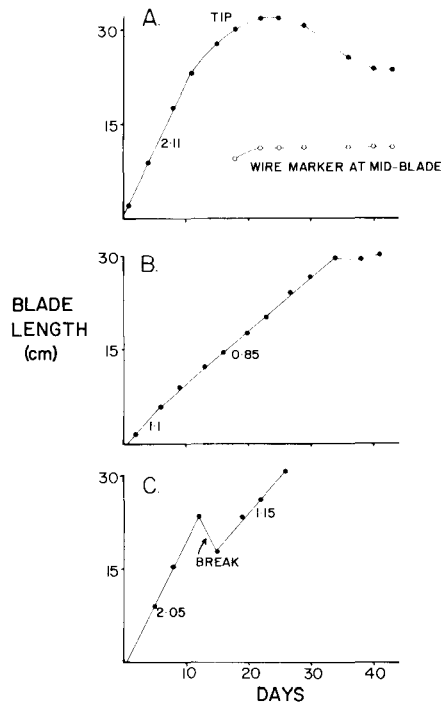


Fig. 4. Three examples of leaf growth taken from field data. Closed circles = height of tip of leaf, open circles = height of inserted wire marker. Numbers give growth rate (= slope of line) in  $\text{cm day}^{-1}$ . (A) Usual growth form. Stationary wire marker after Day 22 indicates cessation of growth while tip was fragmenting. (B) Rare deviation from monotonic linear growth. Initial growth appears slightly faster than later growth. Dashed line shows growth determined by a wire marker as the tip (solid line) was fragmenting. (C) Example of growth slowing after tip fragments; slowing was observed in four out of seven well-documented cases involving natural fragmentation. Growth continued at the initial rate in the other three cases.

observed (Fig. 4B, C). Of 38 blades observed from blade initiation to maturity, 30 blades showed a single linear growth rate until growth began to slow gradually (Fig. 4A). In one case, a lag in initial growth was observed while in seven of the 38 cases, initial growth appeared slightly faster than subsequent growth (Fig. 4B). Additionally, fragmentation influenced growth rates in some cases. In seven cases where linear growth was evident for at least three time intervals before and after a blade was broken, growth rate slowed significantly ( $P < 0.01$ ) in four cases (Fig. 4C). In the remaining three cases, however, growth continued at the same rate following a break.

Altogether, growth was very consistently linear for a major fraction of a blade's lifetime. Of 93 blades monitored during the early part of their growth,  $r^2$  values for linear fits to growth data did not fall below 0.98, and standard errors on linear growth rates were usually  $< 0.1 \text{ cm day}^{-1}$ . Linear growth rates varied from 0.86 to  $3.11 \text{ cm day}^{-1}$  for these blades and averaged  $1.8 \text{ cm day}^{-1}$  overall.

#### *Leaf growth and senescence at a shoot*

*Syringodium* leaves are usually found in clusters of two or three growing from an upright stem that extends above the sediment. The leaves clustered on a stem are in one sense a unit of production; I measured over 30 such units for 40–60 days to establish patterns of growth and senescence.

Figure 5 shows an example of leaf senescence and growth at one upright shoot. The number of leaves present at any measuring day varied from one (Days 0 and 4) to three (Days 18–32). Leaf fragmentation was most often prolonged, as in the case of blade A (35 days), and proceeded in a stepwise manner. Blade B reached a short mature height of  $< 15 \text{ cm}$ ; such short

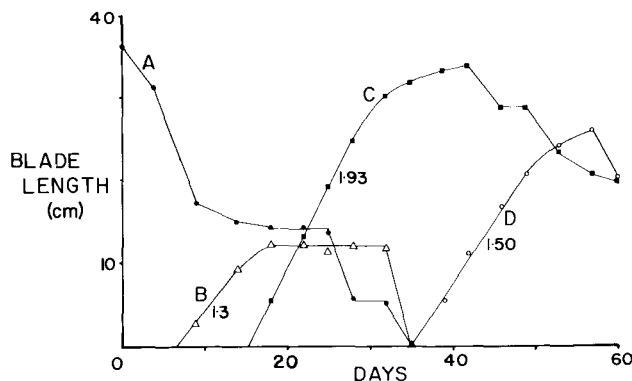


Fig. 5. Fragmentation and growth of four successive seagrass blades at one short shoot. Numbers give growth rate in  $\text{cm day}^{-1}$ . (A) Senescing blade that fragments stepwise from the tip. (B) Slow-growing blade that grows to a short mature height. Senescence occurs at one stroke rather than stepwise. (C) and (D) Successive blades with significantly different initial linear growth rates ( $P < 0.001$ ). Senescence is stepwise.

blades were a minority of those blades whose mature heights could be determined (short blades = 23 out of 160, or 15%). Blades C and D showed more typical mature heights in excess of 25 cm. They also began fragmentation near the time they reached maturity as did other blades that had not been previously broken. It was common for successive blades of a shoot to have significantly different growth rates, as shown in Fig. 5 ( $P < 0.001$  for 1.93 vs. 1.50  $\text{cm day}^{-1}$ ), however, such variations in growth rate for successive blades did not exceed a factor of 1.5.

A regular feature of production dynamics of a shoot was the timing of blade initiation. A new blade started as the growth of the previous blade began to slow and stop its growth. Thus, at the shoot depicted in Fig. 5, blade C began its growth as the growth of blade B slowed, and blade D began as the growth of blade C slowed. (The relationship between blades A and B was not clear in this example due to possible early fragmentation of blade A.) An analysis of 30 clear-cut cases of slowing of blade growth coupled with initiation of blade growth gave the average pattern shown in Fig. 6. After

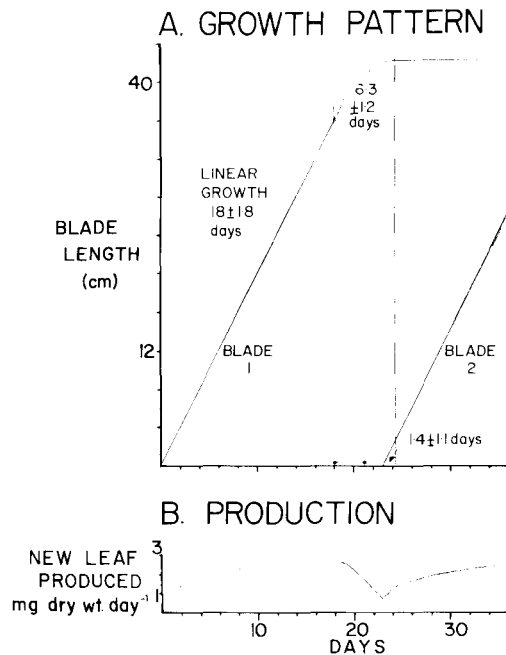


Fig. 6. Average patterns of growth and production in *Syringodium*. (A) Initial growth rate has arbitrarily been assumed = 2  $\text{cm day}^{-1}$ , close to 1.8  $\text{cm day}^{-1}$  average observed in this study. Errors shown are  $\pm$  95% confidence limits for the means which were based on 30 sets of observations. Dotted bar (●—●) above X-axis shows the projected growth of blade 1 if, for modeling purposes, all growth of blade 1 were to occur at the original linear rate and then stop abruptly. (B) Production was calculated by combining Figs. 2 and 3 to give leaf biomass per unit blade length; integration of the resulting curve at 2 cm intervals gave daily estimates of new leaf material produced.

initial linear growth for 18 days, the mean time to cessation of growth was 6.3 days. Initiation of a second blade took place 1.4 days prior to cessation of growth of blade 1 so that growth was continuous.

These mean values show that growth is primarily linear with a period of diminishing growth just prior to initiation of a new blade. For modeling purposes, these data were also evaluated to determine what the growth pattern would be if only linear growth was assumed. Analysis showed that the growth involved during the slow-growth phase prior to cessation of growth was equivalent to  $3.1 \pm 0.55$  (95% C.L.) days of linear growth. The time between the end of this 3.1 days and the initiation of new growth was 1.8 days so that a hiatus of non-growth would be necessary to complete models that employ linear growth.

These considerations of starting and stopping of blade growth have their most dramatic effect in the production of new leaf biomass (Fig. 6). New leaf production increases initially because, although elongation rate is constant, older parts of the leaf are wider and more massive than younger sections of the leaf (Fig. 3). As growth of the older leaf slows, production falls and is only gradually compensated for by growth of the new young leaf. The result is that production of new leaf material is cyclical and in the example shown, ranges from a low of 0.7 to a high of 2.7 mg dry wt. day<sup>-1</sup>.

#### DISCUSSION

The growth of *Syringodium* resembles that of other seagrasses such as *Thalassia*, *Zostera*, and *Halodule* in that (1) growth occurs in the basal meristem region rather than in higher parts of the blade (Fig. 1; Zieman, 1968; Tomlinson, 1974; Sand-Jensen, 1975; Virnstein, 1982) and (2) much growth occurs at constant rates (Fig. 4A; Jacobs, 1979). A major difference between the growth of *Syringodium* vs. some other seagrasses is that essentially only one leaf is actively growing at a time for *Syringodium* shoots; two and possibly more leaves may be growing actively at a *Zostera* or *Thalassia* shoot (Patriquin, 1973; Sand-Jensen, 1975; F. Short, 1982, personal communication).

Two assumptions made in previous models of seagrass growth do not apply to *Syringodium*. The assumptions are that (1) leaf elongation rates decline continuously from an early maximum rate and (2) blades on the same shoot reach the same height (Patriquin, 1973; Jacobs, 1979). For *Syringodium*, elongation rates are usually constant during most of the growth models of Patriquin (1973) and Jacobs (1979) do not conform to patterns of *Syringodium* growth, these models do yield near-asymptotic growth curves very similar to those observed for *Syringodium*.

Knowing the pattern of leaf growth can aid researchers interested in two areas: seagrass productivity and the epiphytic fouling of seagrass leaves. For



*Syringodium*, only the youngest leaves in each of several shoots need be monitored to establish a mean growth rate and thence leaf production. Secondly, when studying the development of fouling communities on seagrass blades, variations in individual leaf growth rates (range = 0.86–3.11 cm day<sup>-1</sup> in this study) should be taken into account. When studying the early successional stages of such leaf fouling communities, leaf growth rates should be monitored so that epiphytic communities of equal ages can be compared.

While this study was conducted during only two early summer months, the patterns of growth were quite consistent. Further sampling in the Indian River lagoon has shown a marked seasonal variation in *Syringodium* growth rates. These rates slow to < 5 mm per day in some winter months, but are near maximal in the late spring and early summer (R.W. Virnstein, 1983, personal communication). The results presented in this study thus pertain to periods of near maximal growth and should be applicable to the tropical regions where growth is thought to be less seasonal and *Syringodium* reaches its maximum abundance.

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