



Effects of shoot age on leaf growth in the seagrass *Thalassia testudinum* in Barbados

Lotus A. Vermeer^{1,3,*}, Wayne Hunte²

¹Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

²Department of Biological and Chemical Sciences, University of the West Indies, Cave Hill, Barbados BB11000, West Indies

³Present address: The Nature Conservancy of California, Santa Cruz Island Preserve, 3639 Harbor Blvd., Suite 201, Ventura, California 93001, USA

ABSTRACT: Effects of shoot age on leaf growth variables of *Thalassia testudinum* were investigated in St. Lawrence Bay, Barbados. Effects were investigated separately within 3 groups of shoots: shoots <1 yr (young shoots, YS), shoots between 1.8 and 2.2 yr (young mature shoots, YMS) and shoots between 4.5 and 6.1 yr (old mature shoots, OMS). Shoot age affected all leaf growth variables, but effects were typically strongest in YS. Leaf width, leaf growth rate, plastochron and maximum leaf length all increased with shoot age, which accounted for 46, 21, 46 and 55% of the variance in YS, respectively. Weak positive effects of shoot age were detectable in YMS and OMS for leaf growth rate, and in OMS for plastochron and maximum leaf length. Number of leaves per shoot increased with shoot age in both mature categories, but the variance explained was low. Shoot age did not affect leaves per shoot in YS. Relative leaf growth rate was negatively correlated with age in YS, not correlated with age in YMS and positively, but weakly, correlated with age in OMS. The possibility of trend reversals between leaf growth variables and shoot age emphasises the need to assess effects of age within discrete age categories. For all leaf growth variables except leaves per shoot, the amount of variance in growth explained by shoot age was substantially higher in YS than in both mature age categories. Results from 2 previous studies and the results of the present study suggest that shoot age effects on leaf growth variables may be common in seagrasses, and that shoot age may have been largely overlooked as a component of the spatial and temporal variation in leaf growth typically observed in seagrasses.

KEY WORDS: *Thalassia testudinum* · Shoot age · Leaf growth · Plastochron

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INTRODUCTION

Studies of environmental effects on seagrass growth are numerous, but few studies (Duarte & Sand-Jensen 1990, Kenworthy & Schwarzschild 1998, Tomasello et al. 2007) have provided data on effects of shoot age on seagrass growth. Duarte & Sand-Jensen (1990) showed that the number of leaves per shoot and maximum leaf length increased with shoot age in the seagrass *Cymodocea nodosa* in the Mediterranean, where shoot age was measured in number of plastochrons (a plastochron refers to the time interval between the formation of successive leaves on a shoot; Erickson & Michellini 1957, Jacobs 1979). Kenworthy & Schwarzschild

(1998) showed that plastochron in *Syringodium filiforme* was shorter in the first year of growth than in older shoots. Tomasello et al. (2007) found that shoot age had a negative effect on rhizome elongation and primary production in *Posidonia oceanica*, and noted that age effects might confound analyses of *P. oceanica* growth performance. Other studies have commented that leaf growth may be influenced by shoot age. For example, Zieman (1968) and Patriquin (1973) remarked that plastochrons may be shorter in very young shoots of *Thalassia testudinum*, and Kaldy et al. (1999) accepted this observation and adjusted for it in generating *T. testudinum* age-frequency distributions. Durako (1995) observed temporal reductions in maxi-

*Email: lvermeer@tnc.org

imum leaf length and leaf area per shoot in *T. testudinum* in Florida Bay. He suggested that the reductions could either be responses to environmental stress or could reflect a shift in population demographics to younger shoots, assuming that shoot age affects leaves per shoot and leaf length in *T. testudinum* as had been documented for *C. nodosa* (see Duarte & Sand-Jensen 1990).

Understanding whether shoot age affects seagrass growth variables is important in understanding spatial and temporal variation in growth. Seagrass beds are often characterised by considerable spatial variation, which is typically attributed to local environmental variation, but could have an age component. For example, in expanding seagrass beds, shoots near the centre of the bed may be older than shoots near the periphery, which could influence differences in growth rates observed (Duarte & Sand-Jensen 1990). Seasonal variation in leaf growth is frequently observed (e.g. Vermeer 2000), and is typically explained by seasonal variation in environmental conditions (e.g. water temperature and light: Barber & Behrens 1985, Alcoverro et al. 1995, Marba et al. 1996), but could partly result from effects of shoot age, if shoot recruitment is seasonal and is strong enough to significantly affect population age structure. Finally, long-term trends of a reduction in leaf growth may indicate reduced viability in response to chronic environmental stress, but could also reflect a shift to a younger age distribution resulting from recolonisation following significant disturbance events (see Durako 1994, 1995). The objective of the present study was to investigate effects of shoot age on plastochron, average leaf growth rate, relative leaf growth rate, maximum leaf length, leaf width and number of leaves per shoot in the tropical seagrass *Thalassia testudinum* in Barbados.

MATERIALS AND METHODS

Study location and shoot tagging. The study was conducted at St. Lawrence, on the south coast of Barbados, West Indies (13° 10' N, 59° 30' W). The site consists of a shallow, sandy lagoon adjacent to a mangrove swamp, and is protected offshore by a coral rubble barrier. The lagoon contains pure stands of *Thalassia testudinum*, pure stands of *Syringodium filiforme*, and mixed stands of *T. testudinum* and *S. filiforme*. Mean low water depth of the seagrass stands at the site is <1 m, and wave action within the lagoon is moderate (maximum bottom velocity is 85 cm s⁻¹; see Patriquin 1973).

Effects of shoot age on *Thalassia testudinum* growth variables were examined separately for mature shoots (>1 yr) and for young shoots (<1 yr). In both cases, *T.*

testudinum shoots were individually tagged and monitored. Shoot tags consisted of a 4 inch nail with a small wire loop (3 cm diameter) wrapped around the nail head, and a small piece of brightly coloured flagging tape affixed to the loop with an identification number unique to each shoot. A shoot was tagged by pulling all of its leaves through the wire loop and inserting the full length of the nail into the substrate such that only the numbered flagging tape protruded from the substrate. The tags were not in physical contact with the shoot, and therefore should not have impeded leaf movement or growth.

Age and growth of mature shoots. The 400 shoots were individually tagged in ten 25 × 25 cm (0.0625 m²) quadrats, each randomly placed and permanently fixed in each of the 10 largest seagrass stands in St. Lawrence Bay. The shoots were monitored for a 6 mo period (February to July 1998). Plastochron (in days) was measured continuously for all tagged shoots at all sites throughout the 6 mo period by monitoring new leaf production every other day, and calculating the time between emergence of 2 successive leaves. The values obtained were averaged for each shoot. Average leaf growth rate per shoot (cm d⁻¹), relative leaf growth rate per shoot (cm new tissue cm⁻¹ old tissue d⁻¹), maximum leaf length (cm), leaf width (cm) and leaves per shoot were measured for all shoots in the final month of the study (July 1998). Average leaf growth rate per shoot and relative leaf growth rate per shoot were measured by punching a hole at the base of each leaf on all shoots in each quadrat and harvesting all marked shoots, with leaves intact, 8 to 12 d following marking. Average leaf growth rate per shoot was measured as the summed length of new leaf material produced over the growth period, divided by the number of leaves on the shoot. Relative leaf growth rate per shoot was measured for each shoot as the summed length of new leaf tissue produced over the growth period divided by the length of existing (old) leaf tissue. Maximum leaf length was measured as the longest leaf on a shoot; and leaf width was measured using the second youngest leaf on each shoot.

At the end of the study (i.e. in August 1998), shoots were excavated with rhizomes intact (i.e. shoots remained attached to the horizontal rhizome), and aged in plastochrons by counting the number of leaf scars on each shoot (vertical rhizome). Of the original 400 shoots, 201 shoots were successfully excavated (i.e. vertical rhizomes and leaves intact) and could therefore be aged. Mean shoot age in plastochrons in the 10 quadrats ranged from 34 to 104 (median: 32 to 115), and differed significantly among quadrats (1-way ANOVA: $F = 10.83$, $p < 0.001$; Kruskal-Wallis test: $H = 57.73$, $p < 0.001$). Quadrats were therefore not pooled to assess effects of age on growth, since apparent

effects of age could have been generated by environmental differences among the sites where the quadrats were located. However, 4 of the 10 quadrats had a 'younger' shoot age distribution (range of means: 34 to 41 plastochrons; range of medians: 32 to 37 plastochrons), and the remaining 6 quadrats had an 'older' shoot age distribution (range of means: 77 to 104 plastochrons; range of medians: 79 to 115 plastochrons). Effects of shoot age on the growth of mature shoots were therefore determined using regression analyses conducted separately for 2 categories of quadrats, those with younger mature shoot age distributions (subsequently termed young mature shoots, YMS), and those with older shoot age distributions (subsequently termed old mature shoots, OMS). Shoot age distributions did not differ among the 4 quadrats with YMS, nor among the 6 quadrats with OMS using either ANOVAs or Kruskal-Wallis tests (quadrats with YMS: $F = 0.77$, $N = 75$, $p = 0.47$; $H = 0.34$, $N = 75$, $p = 0.84$; quadrats with OMS: $F = 1.59$, $N = 126$, $p = 0.18$; $H = 7.40$, $N = 126$, $p = 0.12$). Consequently, any correlations detected between shoot age and leaf growth variables within each of the 2 age categories cannot spuriously arise from environmental effects on the growth variables and differences in shoot age at the different sites (quadrats).

Whenever linear regression analysis detected a significant effect of shoot age on a leaf growth parameter, a stepwise polynomial fitting method was used to determine whether a polynomial curve provided a significantly better fit to the data than the linear model.

Age and growth of young shoots. A total of 200 shoots were randomly selected on the day of their emergence as they emerged from within 10 quadrats near (i.e. within a 2 m radius) the 10 sites used for monitoring the mature shoots, and were individually tagged and monitored during a 1 yr period (August 1997 to August 1998). As for the mature shoots, the emergence of leaves to calculate plastochron was monitored every 2 d over a 6 mo period (August 1997 to January 1998). Average leaf growth rate, maximum leaf length, leaf width and number of leaves per shoot were measured every second day over the same 6 mo period. These growth variables, as well as plastochron and relative leaf growth rate, were also measured at the end of 1 yr (August 1998). At the end of the study (in August 1998), 121 of the original 200 shoots were successfully excavated with rhizomes intact and aged; but chronological age, rather than age in plastochrons, was used to assess age effects on growth. The effects of shoot age on the growth variables were investigated by regression analysis in 2 ways. First, only the growth data obtained on the single sampling occasion at the end of the 1 yr period was used, with each growth

value regressed against the chronological age of the shoot at the time the growth variable was measured. Second, all of the growth data obtained during the 6 mo continuous monitoring was used, with each growth value regressed against the chronological age of the shoot at the time the growth variable was measured. For the single sampling data set, plastochron was measured not only directly by monitoring the emergence of leaves at the end of the 1 yr period, but also by dividing the known chronological age of the shoot by the number of leaf scars on the shoot.

As was the case for mature shoots, whenever linear regression analysis detected a significant effect of shoot age on a leaf growth parameter, a stepwise polynomial fitting method was used to determine whether a polynomial curve provided a significantly better fit to the data than the linear model.

RESULTS

Young shoots (YS)

Shoot age significantly affected most leaf growth variables in shoots <1 yr old (young shoots, YS), as indicated by both the single sampling data set and the continuous sampling data set in the present study. For the former data set, leaf growth rate (Fig. 1A; linear regression analysis: $F = 37.08$, $p < 0.001$), maximum leaf length (Fig. 2A; $F = 144.30$, $p < 0.001$), and leaf width (Fig. 3A; $F = 101.97$, $p < 0.001$) increased linearly with increasing shoot age, with shoot age explaining 21% of the variance in leaf growth rate, 55% of the variance in maximum leaf length and 46% of the variance in leaf width. Leaf plastochron, measured by leaf emergence, increased significantly with increasing shoot age, with age explaining 59% of the variance in plastochron and the increases being fastest in the youngest shoots (Fig. 4A; polynomial regression analysis: $F = 74.74$, $p < 0.001$; relationship significantly better fitted by a quadratic model than a linear model; t -test: $t = 5.70$, $p < 0.001$). Leaf plastochron, calculated by dividing chronological age by the number of leaf scars, also increased significantly with increasing shoot age ($F = 387.26$, $R^2 = 0.787$, $p < 0.001$). Relative leaf growth rate decreased significantly with shoot age, with age explaining 35% of the variance in growth and the decrease being fastest in the youngest shoots (Fig. 5A; polynomial regression analysis: $F = 28.03$, $p < 0.001$; relationship significantly better fitted by a quadratic model than a linear model; $t = 3.52$, $p < 0.001$). There was no effect of shoot age on number of leaves per shoot (Fig. 6A; linear regression analysis: $F = 1.43$, $p = 0.23$). Mean (\pm SE) YS values for leaf growth variables are summarised in Table 1.

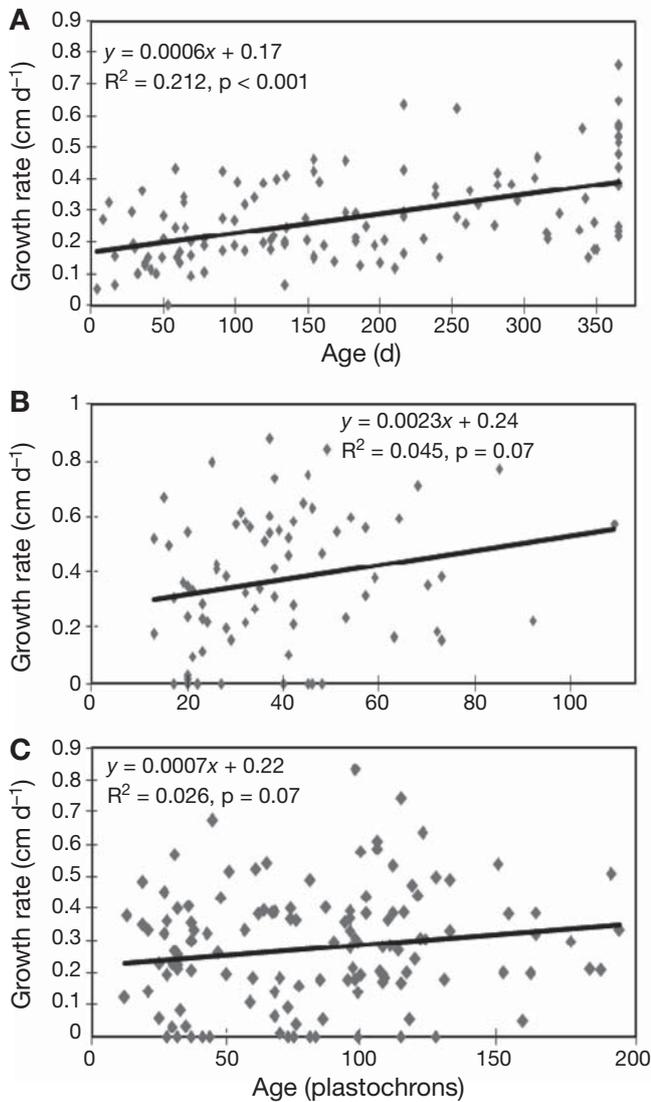


Fig. 1. *Thalassia testudinum*. Regressions and regression equations of average leaf growth rate versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

Similar results were obtained using the continuous sampling data set. Leaf growth rates (linear regression analysis: $F = 110.89$, $R^2 = 0.202$, $p < 0.001$), maximum leaf length ($F = 972.38$, $R^2 = 0.688$, $p < 0.001$), leaf width ($F = 496.24$, $R^2 = 0.529$, $p < 0.001$) and leaf plastochron ($F = 54.12$, $R^2 = 0.252$, $p < 0.001$) all increased significantly with shoot age, and there was again no effect of shoot age on number of leaves per shoot ($F = 0.01$, $R^2 < 0.01$, $p = 0.93$). Data on relative leaf growth rate were not available from the continuous sampling data set.

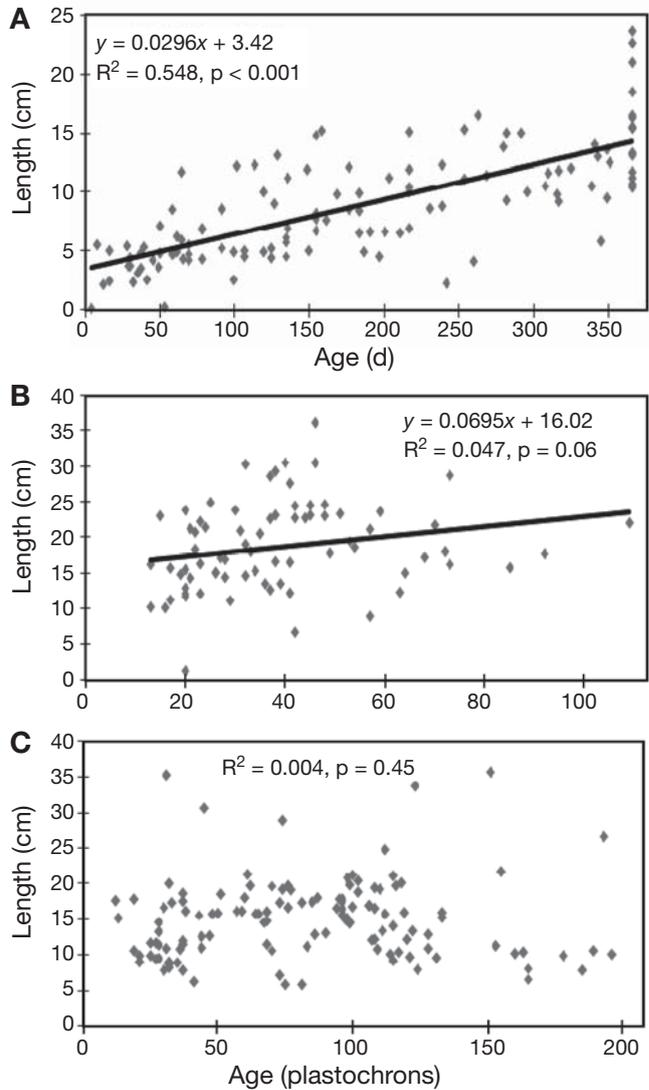


Fig. 2. *Thalassia testudinum*. Regressions and regression equations of maximum leaf length versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

Mature shoots

Young (YMS)

Shoot age also affected leaf growth in YMS, i.e. shoots with mean ages between 34 and 41 plastochrons (chronological age of about 1.8 to 2.2 yr calculated using mean plastochron for shoots in this age category of 19.7 d; see Fig. 4B), although the effects were much weaker than in younger shoots. Mean (\pm SE) YMS values for plastochron and other leaf growth vari-

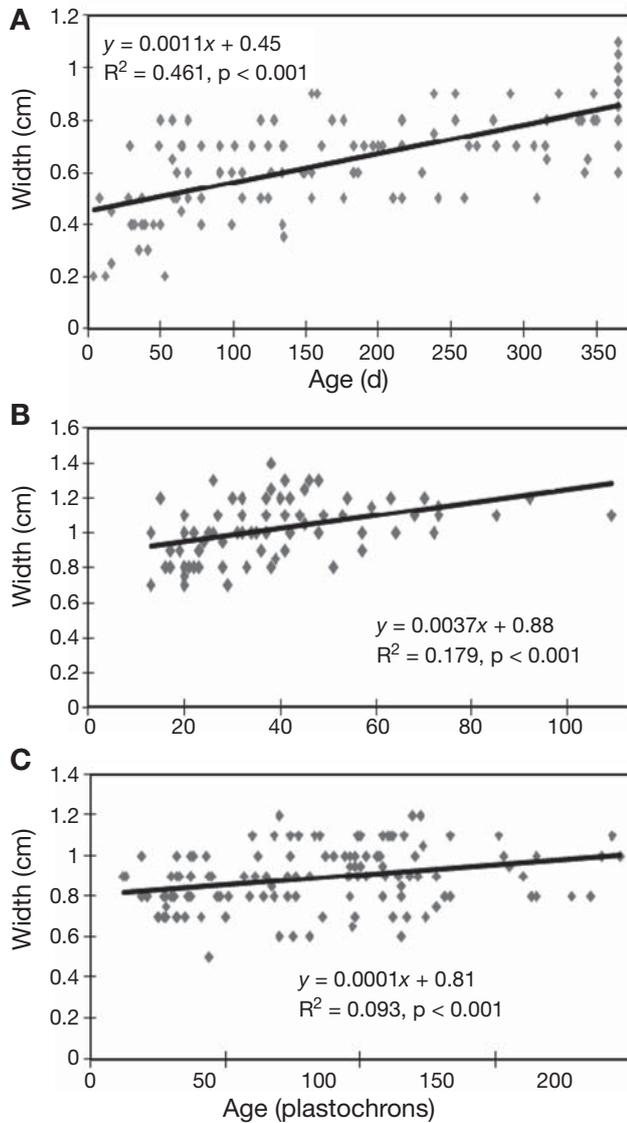


Fig. 3. *Thalassia testudinum*. Regressions and regression equations of leaf width versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

ables are presented in Table 1. There were very weak positive relationships between shoot age and leaf growth rate (Fig. 1B; linear regression analysis: $F = 3.34$, $p = 0.07$), between shoot age and maximum leaf length (Fig. 2B; $F = 3.60$, $p = 0.06$) and between shoot age and leaf plastochron (Fig. 4B; $F = 3.34$, $p = 0.07$). There were stronger positive relationships between shoot age and leaf width (Fig. 3B; $F = 6.75$, $p < 0.01$), with shoot age explaining 18% of the variance, and between shoot age and number of leaves per shoot (Fig. 6B; $F = 6.44$, $p < 0.01$), although shoot age only

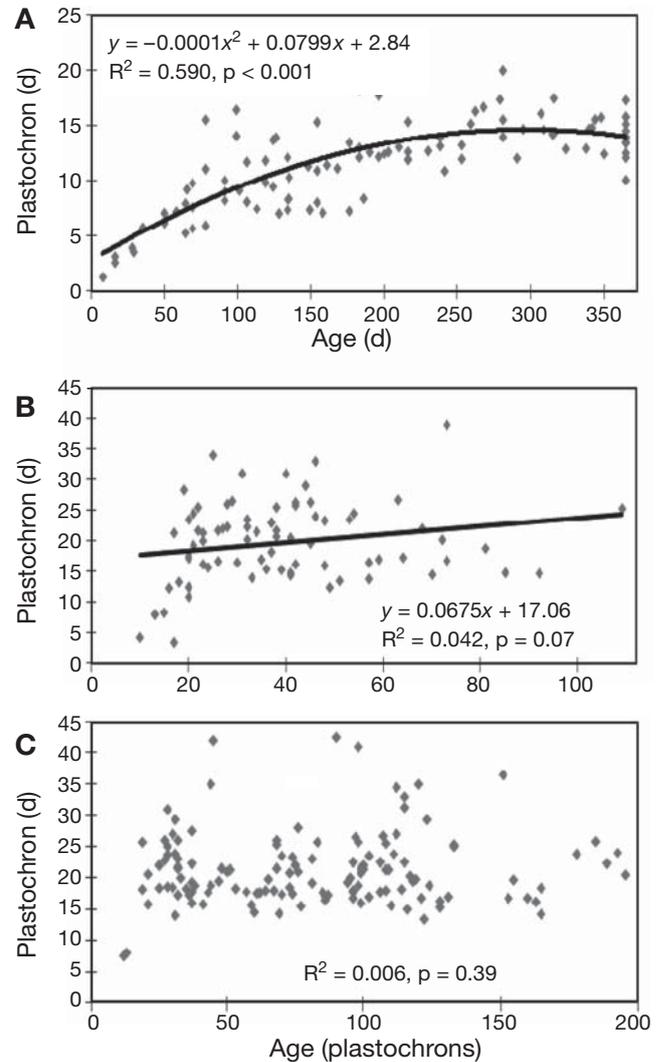


Fig. 4. *Thalassia testudinum*. Regressions and regression equations of plastochron versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

explained 8% of the variance. There was no effect of shoot age on relative leaf growth rate (Fig. 5B; $F = 0.66$, $p = 0.42$).

Old (OMS)

Weak but significant effects of shoot age on leaf growth variables were also detected in the OMS, i.e. shoots with mean ages between 77 and 104 plastochrons (chronological age of about 4.5 to 6.1 yr calculated using mean plastochron for shoots in this age category of 21.4 d; see Fig. 4C). Mean (\pm SE) OMS values

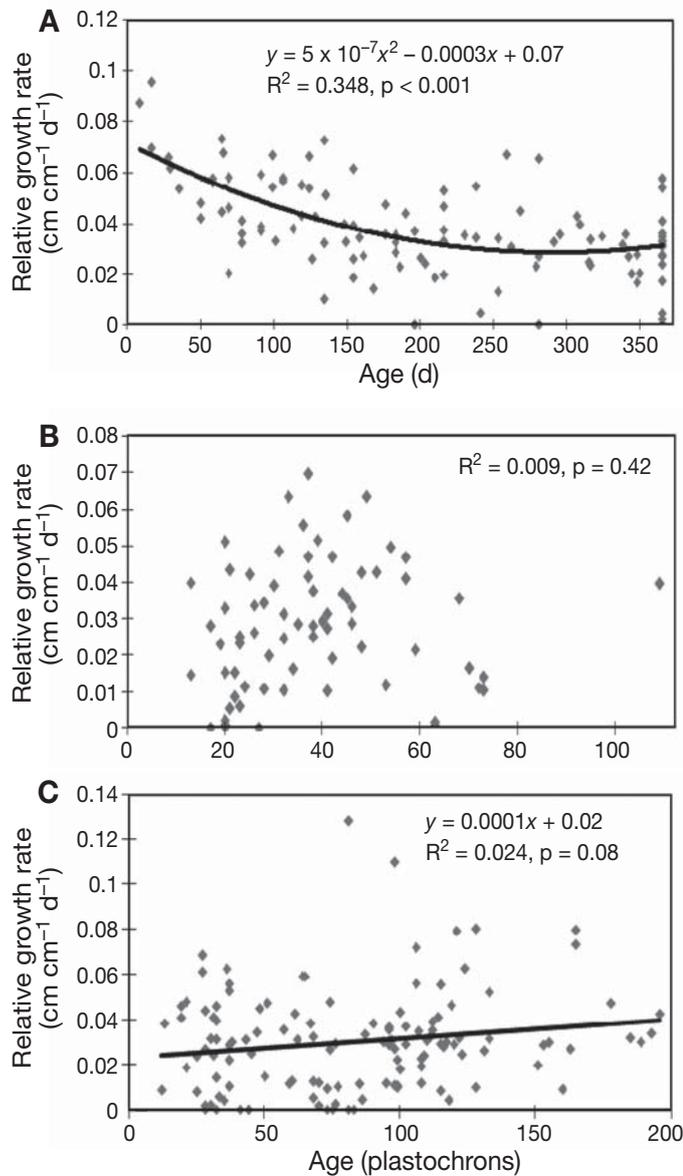


Fig. 5. *Thalassia testudinum*. Regressions and regression equations of relative leaf growth rate versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

for plastochron and other leaf growth variables are presented in Table 1. There were very weak positive relationships between shoot age and leaf growth rate (Fig. 1C; linear regression analysis: $F = 3.19, p = 0.07$), and between shoot age and relative leaf growth rate (Fig. 5C; $F = 3.07, p = 0.08$). There were significant positive relationships between shoot age and leaf width (Fig. 3C; $F = 12.80, p < 0.001$), and between shoot age and number of leaves per shoot (Fig. 6C; $F = 6.44, p < 0.01$), but age explained only 9% of the variance in both

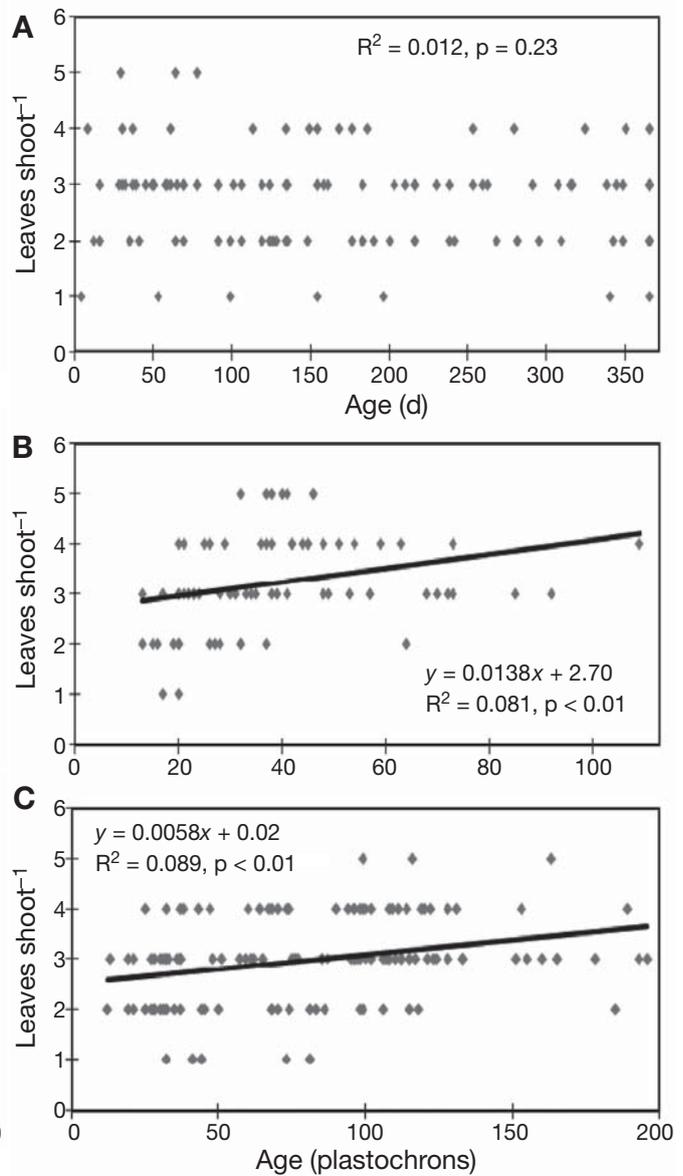


Fig. 6. *Thalassia testudinum*. Regressions and regression equations of number of leaves per shoot versus shoot age for: (A) young (YS; <1 yr), (B) young mature (YMS; mean plastochron = 39) and (C) old mature (OMS; mean plastochron = 79) shoots. Age is in chronological time for YS, and in plastochrons for YMS and OMS. Data for YS are from the single sampling data set

cases. There was no effect of shoot age on either maximum leaf length (Fig. 2C; $F = 0.56, p = 0.45$) or leaf plastochron (Fig. 4C; $F = 0.73, p = 0.39$).

DISCUSSION

The only prior studies of effects of shoot age on leaf growth variables in seagrasses was on a temperate seagrass, *Cymodocea nodosa*, where positive effects of

Table 1. *Thalassia testudinum*. Mean (\pm SE) leaf growth variables for young (<1 yr), young mature (1.8 to 2.2 yr), and old mature (4.5 to 6.1 yr) shoots. LS: leaf scars; GR: average leaf growth rate per shoot; RGR: relative leaf growth rate per shoot

Shoot age	LS (shoot ⁻¹)	GR (cm d ⁻¹)	Length (cm)	Width (cm)	Plastochron (d)	RGR (cm cm ⁻¹ d ⁻¹)	Leaves (shoot ⁻¹)
Young	16.18 \pm 0.66	0.27 \pm 0.01	8.77 \pm 0.42	0.65 \pm 0.02	11.85 \pm 0.38	0.04 \pm 0.002	2.76 \pm 0.08
Young mature	38.89 \pm 2.24	0.33 \pm 0.02	18.72 \pm 0.72	1.02 \pm 0.02	19.68 \pm 0.75	0.03 \pm 0.002	3.24 \pm 0.11
Old mature	82.52 \pm 3.93	0.28 \pm 0.02	14.99 \pm 0.50	0.89 \pm 0.01	21.37 \pm 0.52	0.03 \pm 0.002	2.99 \pm 0.08

shoot age on leaf length and leaf density were detected (Duarte & Sand-Jensen 1990), and on a tropical seagrass, *Syringodium filiforme*, where plastochron was shorter in young shoots (Kenworthy & Schwarzschild 1998). The results of these prior studies and those of the present study suggest that shoot age effects on leaf growth variables may be common in seagrasses and that shoot age may have been largely overlooked as a component of the considerable spatial and temporal variation in leaf growth typically observed in seagrasses.

In the present study, the effects of shoot age on leaf growth were investigated separately within 3 shoot age categories: YS (<1 yr old), YMS (1.8 to 2.2 yr) and OMS (4.5 to 6.1 yr). Plastochron increased (i.e. rate of leaf production decreased) significantly with age for shoots <1 yr old, with the increase being fastest in the youngest shoots. The fact that plastochron decreases with age has important implications for its use in generating age-frequency distributions from which demographic predictions about *Thalassia testudinum* stands are made (the 'reconstruction technique': Duarte et al. 1994). If YS have more leaf scars than they should for their true chronological age, they will be classified as older than they are, i.e. the younger age classes in an age-frequency distribution will be under-represented. This may partially explain why the reconstruction technique often predicts population decline, and has done so in situations in which subsequent field work has recorded population increases (e.g. see predictions by Durako 1994 and field work of Jensen et al. 1996). Kaldy et al. (1999) emphasised that a decrease in plastochron with age would lead to incorrect demographic predictions for *T. testudinum*, and adjusted for this effect in generating *T. testudinum* age distributions. However, the present results suggest that adjustments may be required over a wider age range than previously envisaged. They will certainly be required over the first year, where effects of shoot age on plastochron are strong, but may be required beyond this, given that effects of shoot age on plastochron were weakly detectable in shoots as old as 2 yr in this study.

Several leaf growth variables, apart from plastochron, also change with shoot age. Leaf growth rate increased significantly with shoot age for YS, and weak positive effects were detectable for YMS and

OMS. Maximum leaf length was one of the variables reported by Duarte & Sand-Jensen (1990) to increase with shoot age in *Cymodocea nodosa*, and in this study, maximum leaf length increased significantly with shoot age for YS; weak positive effects of age on length were detectable for YMS, however the effect had disappeared for OMS. The other leaf variable reported to increase with shoot age in *C. nodosa* was number of leaves per shoot (Duarte & Sand-Jensen 1990), and a similar effect was detected for mature shoots of *Thalassia testudinum* in the present study. Number of leaves per shoot increased with shoot age in both mature age categories, but the amount of variance explained was low, and shoot age did not affect leaves per shoot in YS.

Leaf width increased significantly with shoot age in all age categories in the present study, raising the possibility that leaf width can be used as a crude predictor of shoot age in *Thalassia testudinum*. However, although shoot age explained roughly half of the variance in leaf width in YS, the amount of variance it explained for YMS was lower, and even more so for OMS. Environmental factors may therefore be responsible for generating most of the variation in leaf width in older *T. testudinum* shoots. Indeed, studies have shown geographic variation in leaf width in *T. testudinum* (McMillan 1978), and leaf width has been suggested to be a useful indicator of environmental stress in *T. testudinum* (Phillips & Lewis 1983, van Tussenbroek 1996, Vermeer 2000). Durako & Moffler (1985) found that *T. testudinum* leaf width was narrower in female shoots than in male shoots, and sex of a shoot may also be an important factor influencing leaf width variation.

Relative leaf growth rate decreased with increasing shoot age in young *Thalassia testudinum* shoots. Two processes will affect relative leaf growth rate; the first is the rate of production of new leaves on the shoot (which decreases with shoot age in young *T. testudinum* shoots), and the second is leaf growth rate (which increases with shoot age in young *T. testudinum* shoots). The fact that relative leaf growth rate decreases with shoot age in young shoots suggests that the effect of leaf production is stronger than the effect of leaf growth rate in influencing rate of production of

new leaf material on young shoots. Interestingly, there appears to be a trend reversal with respect to relative leaf growth rate as shoot age increases. The fact that there may be trend reversals between leaf growth variables and shoot age with increasing shoot age emphasises the need for future studies of effects of shoot age on growth variables to initially assess the effects within separate age categories.

Given the findings of this study that shoot age affects several leaf growth variables, particularly in younger shoots, implies that shoot age may have been largely overlooked as a potential contributor to the considerable variation typically observed in leaf growth variables in seagrasses. For example, with the variation in age structure observed among sites in the present study, spatial variation in leaf growth variables in seagrass patches may often have a shoot age component. This may be particularly so with respect to 'edge effects' in expanding seagrass patches, where shoots near the edge of the patches may typically be younger than shoots farther from the edge (see Duarte & Sand-Jensen 1990). Beyond this, seasonal variation in leaf growth variables in seagrasses could theoretically have a shoot age component, if shoot recruitment was both seasonal and strong; and long-term changes in leaf growth variables may have a shoot age component, if age distributions are changing over time.

The studies by Duarte & Sand-Jensen (1990) and Kenworthy & Schwarzschild (1998), and our own, are the only 3 to specifically investigate effects of shoot age on leaf growth variables in seagrasses, and have all detected significant effects. This suggests that shoot age effects on leaf growth variables may be a common characteristic of seagrasses, and emphasises the need for further studies to assess the generality of these effects.

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LITERATURE CITED

- Alcoverro T, Duarte CM, Romero J (1995) Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. *Mar Ecol Prog Ser* 120:203–210
- Barber BJ, Behrens PJ (1985) Effects of elevated temperature on seasonal *in situ* leaf productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kutzing. *Aquat Bot* 22:61–69
- Duarte CM, Sand-Jensen K (1990) Seagrass colonization: biomass development and shoot demography in *Cymodocea nodosa* patches. *Mar Ecol Prog Ser* 67:97–103
- Duarte CM, Marba N, Agawin N, Cebrian J and others (1994) Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar Ecol Prog Ser* 107:195–209
- Durako MJ (1994) Seagrass die-off in Florida Bay (USA): changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. *Mar Ecol Prog Ser* 110:59–66
- Durako MJ (1995) Indicators of seagrass ecological condition: an assessment based on spatial and temporal changes. In: Dyer KR, Orth RJ (eds) *Changes in fluxes in estuaries; implications for science to management*. Olsen and Olsen, Fredensborg, p 261–266
- Durako MJ, Moffler MD (1985) Observations on the reproductive ecology of *Thalassia testudinum* (Hydrocharitaceae). II. Leaf width as a secondary sex character. *Aquat Bot* 21:265–275
- Erickson RO, Michelini FJ (1957) The plastochron index. *Am J Bot* 44:297–305
- Jacobs RPWM (1979) Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquat Bot* 7:151–172
- Jensen SL, Robbins BD, Bell SS (1996) Predicting population decline: seagrass demographics and the reconstructive technique. *Mar Ecol Prog Ser* 136:267–276
- Kaldy JE, Fowler N, Dunton KH (1999) Critical assessment of *Thalassia testudinum* (turtle grass) aging techniques: implications for demographic inferences. *Mar Ecol Prog Ser* 181:279–288
- Kenworthy WJ, Schwarzschild AC (1998) Vertical growth and short-shoot demography of *Syringodium filiforme* in outer Florida Bay, USA. *Mar Ecol Prog Ser* 173:25–37
- Marba N, Duarte CM, Cebrian J, Gallegos ME, Olesen B, Sand-Jensen K (1996) Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. *Mar Ecol Prog Ser* 137:203–213
- McMillan C (1978) Morphogeographic variation under controlled conditions in five seagrasses, *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, *Halophila engelmannii* and *Zostera marina*. *Aquat Bot* 4:169–189
- Patriquin DG (1973) Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. *Caribb J Sci* 13:111–123
- Phillips RC, Lewis RR III (1983) Influence of environmental gradients on variations in leaf widths and transplant success in North American seagrasses. *Mar Technol Soc J* 17:59–68
- Tomasello A, Calvo S, Di Maida G, Lovison G, Pirrota M, Sciandra M (2007) Shoot age as a confounding factor on detecting the effect of human-induced disturbance on *Posidonia oceanica* growth performance. *J Exp Mar Biol Ecol* 343:166–175
- van Tussenbroek BI (1996) Leaf dimensions of transplants of *Thalassia testudinum* in a Mexican Caribbean reef lagoon. *Aquat Bot* 55:133–138
- Vermeer LA (2000) Changes in growth and abundance of seagrasses in Barbados, West Indies. PhD thesis, Dalhousie University, Halifax, NS
- Zieman JC (1968) A study of the growth and decomposition of the sea-grass *Thalassia testudinum*. MSc thesis, University of Miami