

FUNCTIONAL-MORPHOLOGICAL RELATIONSHIPS IN *SARGASSUM POLYCERATIUM* (PHAEOPHYTA): PHENOTYPIC AND ONTOGENETIC VARIABILITY IN APPARENT PHOTOSYNTHESIS AND DARK RESPIRATION¹

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ABSTRACT

Phenotypic and ontogenetic changes in apparent photosynthesis and dark respiration for Sargassum polyceratum Mont. were related to the differential allocation of resources into blades, stems, vesicles, and fertile branches as well as anatomical parameters of surface area, volume, and blade density from a population in the Content Keys, Florida. Three divergent phenotypes were evaluated during four phases of ontogeny: maximum growth (October), peak reproduction (December), senescence (April), and stasis (July). Photosynthetic and respiratory rates changed throughout the year, at different stages of morphogenesis, and among different phenotypes. Photosynthesis was highest during active growth, decreased during reproduction and senescence, and was lowest during stasis. In contrast, respiration was higher during peak reproduction and stasis. Temporal, phenotypic, and ontogenetic changes in apparent photosynthesis were best explained by interactions among anatomical features, growth stages, and source-sink relationships of metabolic reserves and pigments. Surface area: volume (SA:V) ratios played a secondary role. Photosynthetic performance of mature axes decreased with the allocation of resources away from blades to air bladders and fertile branches. Apparent productivity and development of fertile branches on phenotypes were not correlated. High respiratory rates, SA:V ratios, blade areas, and low blade densities occurred on developing axes and were consistent with adaptations to low light fields. Sargassum polyceratum, because of its morphological differentiation, is a relatively complex, physiologically variable alga.

Key index words: Fucales; functional morphology; ontogeny; Phaeophyta; phenotype; photosynthesis; respiration; Sargassum

Phenotypic and ontogenetic changes in photosynthesis and respiration are of ecological significance. Seaweeds exhibit differences in photosynthesis as a function of age (Küppers and Kremer 1978, Ramus and Rosenberg 1980, Wheeler 1980), growth stage (Jensen 1966, Rhee and Briggs 1977, Prince 1980),

or morphological form (Littler and Littler 1983, Hanisak et al. 1988). Morphological and physiological adaptations to depth (Dring 1981, Coutinho and Yoneshigue 1988, Peckol and Ramus 1988), canopy and understory habitats (Dayton 1975) or conditions of crowding (Hay 1981, Kilar 1984) enable seaweeds to live in a wide range of light environments. An alga's structural form and net production have been equated with survival strategies that represent trade-offs between the capacities for rapid growth, reproduction, and environmental tolerance (Littler and Littler 1980, Steneck and Watling 1982). Net photosynthesis and specific growth rate frequently correlate with surface area: volume ratios (SA:V) whether comparisons examine a broad spectrum of algae (Littler 1980, Littler et al. 1983) or divergent forms of a single species (Littler and Littler 1983, Hanisak et al. 1988).

Sargassum is a structurally dominant genus in shallow waters throughout Florida and the Bahamas (Taylor 1960) and, unlike most macroalgae, is morphologically differentiated and relatively complex; it exhibits specialized anatomical features such as leaf-like blades, stems, vesicles (air bladders), fruiting branches, and a holdfast (attachment structure). In Florida, *S. polyceratum* is a pseudoperennial (*sensu* Sears and Wilce 1975) with growth maximal from mid-fall to mid-winter and minimal in the mid-summer (Prince 1980). Reproduction begins immediately after the initiation of growth. The "great variability in form, size, and texture of leaves" of this species has long been noted (Britton and Millspaugh 1920) and attributed to ontogenetic forms (Kilar and Hanisak 1988) and polymorphisms in local populations (Kilar and Hanisak 1989). As a structurally specialized, phenotypically variable species, *S. polyceratum* is a superb organism to study the ecological relevance of intraspecific thallus-form variation.

Our study represents an extension of traditional approaches that applies morphometric and physiological techniques to anatomically defined forms of *Sargassum polyceratum*. Three polymorphs were examined seasonally for (1) apparent photosynthesis and dark respiration, (2) the partitioning of biomass into blades, vesicles, stems, and fertile branches, and (3) the anatomical parameters of surface area, vol-

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ume, and blade density in order to reach a better understanding of the relationship of morphology, physiology, and ontogeny on the ecology of *Sargassum*.

MATERIALS AND METHODS

Plants were collected on the northern side of the western island of Content Keys (24°48' N, 81°30' W), Florida (Florida Keys), within an area studied by Croley and Dawes (1970). A broad zone of *Sargassum polyceratum* Mont. is present from just below mean low water to a depth of 5 m. The site receives moderate wave activity (Tanner 1960) and tidal fluctuations are diurnal with a maximum range of 1 m (NOAA 1987).

During seasonal life-history phases of maximum growth (October), maximum reproduction (December), senescence (April), and stasis (July) (Kilar and Hanisak 1988), three phenotypes of *Sargassum polyceratum* were collected: plants with (1) recurved, undulate, ovate blades, (2) flat, ovate blades, and (3) flat, linear blades; hereafter, referred to as curly, broad, and thin individuals, forms, or phenotypes, respectively. These phenotypes represent ends of morphological continua (Kilar and Hanisak 1989). The best examples of each phenotype (i.e. qualitatively, plants with the highest and lowest length-width ratios or recurved blades) were measured for anatomical features and algal productivity.

Apical tips, 4–6 cm, were removed from mature and developing axes ($n = 75$ ea.), cleaned of obvious epiphytes, and placed into 37.8 L aquariums for 24 h. Fifteen tips of each age (mature or juvenile) were measured for surface area, volume, and blade density (no. of blades per cm of stem). Surface area (cm^2) was determined separately from blades, stems, vesicles, and fertile branches using a LI-COR Area Meter (Model LI 3100-1 + 1). Volume was determined for each apical tip and measured by the displacement upward of water in a 10 mL graduated cylinder with a microburette (± 0.01 mL).

Photosynthesis and dark respiration were determined in wide-mouth, 1-L glass jars between 0900 and 1400 h. Ten tips per treatment (i.e. two age classes for each of the three phenotypes) were incubated between 2.5–4.5 h in clear polycarbonate trays at ambient seawater temperatures at 25% (July) or 13% (October, December, April) incident light—within the range of light saturation but not photoinhibition (unpubl. data). Respiration was assessed from jars sealed in two layers of aluminum foil. Dissolved oxygen was determined (± 0.01 ppm) using an Orbisphere Model 2610 Oxygen Analyzer and expressed in units of $\text{mg C fixed} \cdot \text{g}^{-1} \text{dry wt} \cdot \text{h}^{-1}$. Methods concerning the selection of specimens, handling incubations, and oxygen analysis are that of Littler (1979) and Littler and Arnold (1980).

Data analysis included parametric and nonparametric statistical techniques. Tests for homogeneity of variances (Bartlett's test) were done to verify the assumption of equality of populational variances. Data were transformed when necessary and analyzed by 2- or 3-Way ANOVA (Model I) with interactions and, if applicable, a Student-Newman-Keuls multiple range test (S-N-K) was used. A nonparametric analysis of variance test, Kruskal-Wallis Test (KWAL), was performed when departures from homogeneity occurred or sample sizes were < 30 . A Sum of Square Simultaneous Test Procedure (SS-STP) was used to separate group means (Pimentel and Smith 1986). If SS-STP failed to distinguish groups resulting from a significant KWAL test, then Mann-Whitney U tests were performed.

RESULTS

Temporal trends. Apparent photosynthesis and respiration varied with time (Table 1). Photosynthesis was highest in the fall during active growth and lowest in the summer during stasis. For pooled data (adult and juvenile axes), photosynthetic rates de-

creased significantly from times of active growth, reproduction, senescence, and stasis, respectively. Statistically, the same pattern was not observed when data from adult and juvenile axes were viewed separately (Fig. 1). Respiration rates showed a different pattern, with high rates occurring in December and July (Table 1, Fig. 1). SA:V ratios were highest during maximum growth, decreased while reproductive, and further decreased during senescence and stasis (Table 1). Blade density and area were higher in October; otherwise, they were similar in April, July, and December.

Phenotypic trends. Curly phenotypes exhibited a higher photosynthetic rate than the thin ones, while the broad phenotype was not different from either the curly or thin (Table 1). Respiration was highest in broad-bladed forms, followed by the thin, then the curly forms. Neither the SA:V ratio nor blade density correlated well with patterns of photosynthesis and respiration. Blade density appeared more influential; for example, curly individuals had the highest photosynthetic rate and blade density and the lowest SA:V ratio. The opposite was true for the thin-bladed plants. Blade area was similar among phenotypes. Significant interactions among main effects (Table 1) indicated that a variety of factors was influencing these patterns of photosynthesis and respiration.

Developmental trends. Photosynthetic rates of mature and juvenile axes were similar; however, respiration rates were higher in developing axes. Significant differences in SA:V ratio, blade density and blade area occurred between the two groups, with immature axes exhibiting a higher SA:V ratio and blade area, and a lower blade density (Table 1).

Mature axes. Plant productivity and the presence or absence of specialized anatomical features appear intimately related. During periods of rapid growth and peak reproduction, photosynthetic rates were greater in the thin-bladed plants than the broad or curly (Oct: KWAL, $P < 0.009$, Mann-Whitney, $P < 0.05$; Dec: KWAL, $P < 0.001$, SS-STP, $P < 0.05$; Fig. 2). At these times, thin and broad phenotypes developed more blade area (Fig. 3). Curly forms were more reproductive in December (KWAL, $P < 0.001$, SS-STP, $P < 0.05$) and had a greater number of vesicles in October (KWAL, $P < 0.002$, SS-STP, $P < 0.05$). During senescence and stasis, plants with curly blades outperformed those with broad or thin blades (Apr: KWAL, $P < 0.004$, SS-STP, $P < 0.05$; Jul: KWAL, $P < 0.001$, SS-STP, $P < 0.05$; Fig. 2) and had more blade area than those with thin blades (Table 2). In contrast, thin and broad phenotypes were more reproductive (KWAL, $P < 0.001$, SS-STP, $P < 0.05$), and the thin-bladed form had more vesicles than curly-bladed plants (KWAL, $P < 0.001$, SS-STP, $P < 0.05$, Fig. 3).

Concurrent with shifts in anatomical features were changes in SA:V ratios and blade densities (Table 2, Figs. 4, 5). In October and December, the thin

TABLE 1. Significance levels derived from three-way ANOVA tables for apparent photosynthesis, dark respiration, SA:V ratio, blade density, and blade area for thin (t), broad (b), and curly (c) phenotypes of *Sargassum polyceratum* in April (a), July (j), October (o) and December (d) for mature (m) and immature (i) axes. Groups are arranged in ascending order (left to right) and a line delimits similar groups (S-N-K, $P < 0.05$).

Source	P	Groupings			
Photosynthesis: (mg C·g ⁻¹ dry wt·h ⁻¹) after log transformation					
Time	<0.001	j	a	d	o
Phenotype	0.015	t	b	c	
Age	0.121	i	m		
(T × P)	<0.001				
(T × A)	<0.001				
(P × A)	0.023				
(T × P × A)	0.001				
Respiration: (mg C·g ⁻¹ dry wt·h ⁻¹) after log transformation					
Time	<0.001	o	a	d	j
Phenotype	<0.001	c	t	b	
Age	<0.001	m	i		
(T × P)	<0.001				
(T × A)	0.001				
(T × P × A)	<0.001				
Surface/volume: (cm ² ·cm ⁻³) after arcsine transformation					
Time	<0.001	a	j	d	o
Phenotype	<0.001	c	b	t	
Age	<0.001	m	i		
(T × P)	<0.001				
(T × A)	0.002				
(P × A)	<0.001				
(T × P × A)	<0.001				
Blade density: (no·cm ⁻¹ of stem) after log transformation					
Time	<0.001	d	a	j	o
Phenotype	0.015	t	b	c	
Age	0.121	i	m		
(P × A)	0.002				
(T × P × A)	<0.001				
Blade area: (cm ²) after log transformation					
Time	0.013	d	a	j	o
Phenotype	0.110	t	b	c	
Age	<0.001	m	i		
(T × P × A)	<0.001				

and broad phenotypes had higher SA:V ratios than curly-bladed plants which had a higher blade density (October). In April and July, the curly and broad individuals had higher SA:V ratios than the thin phenotype, and blade densities were alike. SA:V ratios can explain photosynthetic patterns among the thin and curly forms but not with the broad-bladed plants that had the highest measures of SA:V and leaf density (e.g. October, Table 2) but showed intermediate rates of photosynthesis. It follows that neither the SA:V ratio nor blade density explains phenotypic trends as measured.

Respiration rates varied with blade morphology

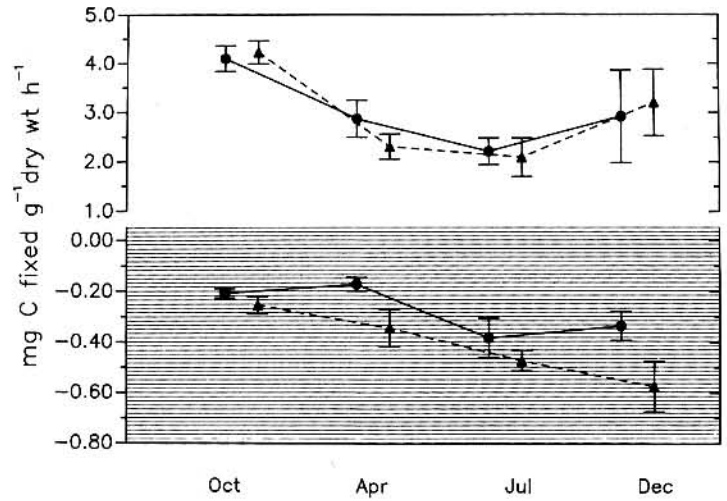


FIG. 1. Temporal patterns in apparent photosynthesis and dark respiration for apical tips of developing (▲) and mature (●) axes of *Sargassum polyceratum* (October–December). Error bars are 95% confidence limits around the mean. $n = 30$ tips per treatment.

within sampling periods (KWAL, $P \leq 0.02$), with no consistent correlation with anatomical measurements. In December, respiration was highest in the curly phenotype, followed by thin, and then broad-bladed, plants (SS-STP, $P < 0.05$): a pattern correlated with reproduction, vesicle production, and blade density (Fig. 3) and negatively correlated with blade area and SA:V ratio (Table 2). In April, the same respiratory pattern resulted; however, thin and broad phenotypes were more reproductive and had more vesicles, lower blade areas, and reduced SA:V ratios. In July, broad and curly individuals had higher rates than the thin form (SS-STP, $P < 0.05$): a pattern which reflected SA:V ratios.

Developing axes. Photosynthetic and respiratory trends were not fixed among phenotypes and sampling periods, or with their adult counterparts, or with any anatomical features (Fig. 2). To illustrate, in October, photosynthetic and respiratory rates were alike among blade morphologies (KWAL, $P > 0.21$), but blade density and the SA:V ratio were lower in broad-bladed forms (Table 2). In December, all phenotypes were morphologically equivalent; however, curly-bladed individuals were more productive (KWAL, $P < 0.009$, SS-STP, $P < 0.05$); a pattern opposite that shown for adult axes. Respiration rates varied (KWAL, $P < 0.02$), with the broad-bladed plants having lower rates than the thin-bladed but not the curly-bladed morphologies (Mann Whitney, $P < 0.05$).

DISCUSSION

Sargassum polyceratum is a structurally complex, phenotypically variable species with concomitant variability in net productivity. Photosynthetic and respiratory rates change throughout the year, at different stages of development, and among different phenotypes. Apparent photosynthesis is highest during active growth, decreases during reproduction

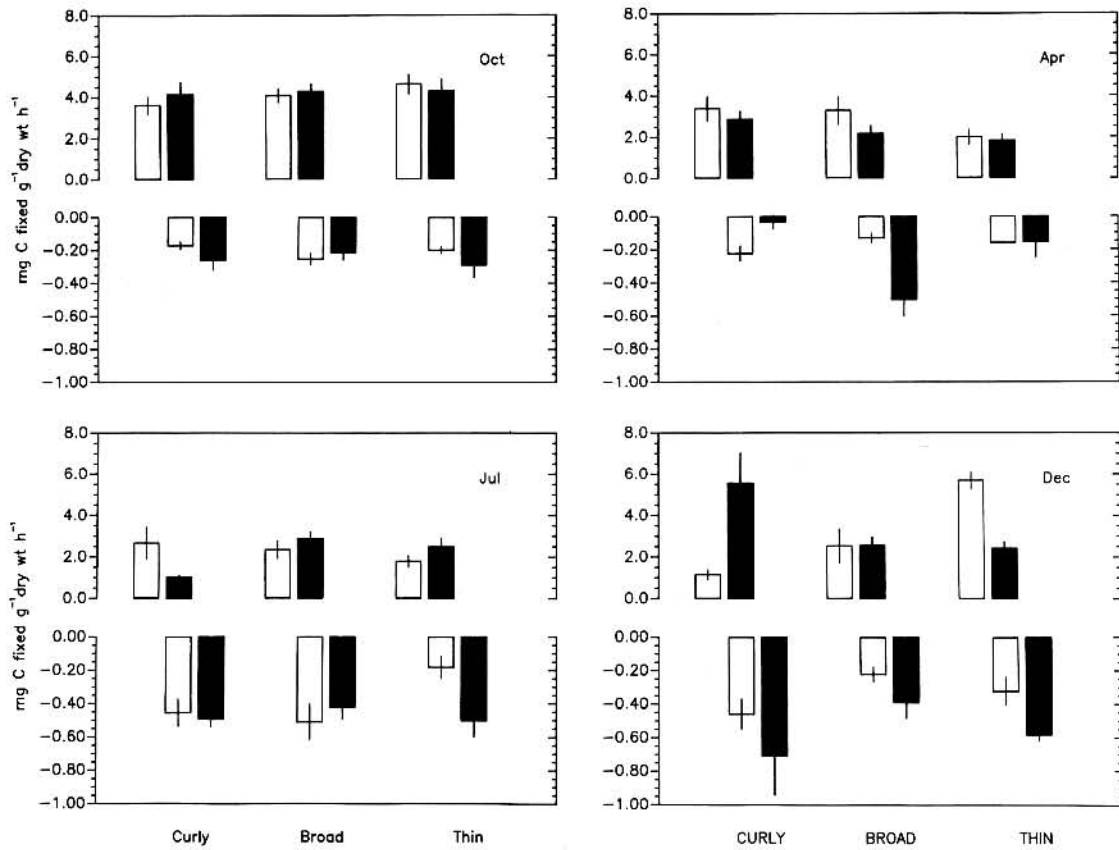


FIG. 2. Developmental and temporal patterns in apparent photosynthesis and dark respiration for three phenotypes (curly, broad, thin) of *Sargassum polyceratum*. Error bars are 95% confidence limits around the mean. $n = 10$ tips per treatment. Dec = maximum reproduction; Apr = senescence; Jul = stasis; and Oct = maximum growth. Developing axes = dark bar, mature axes = open bar.

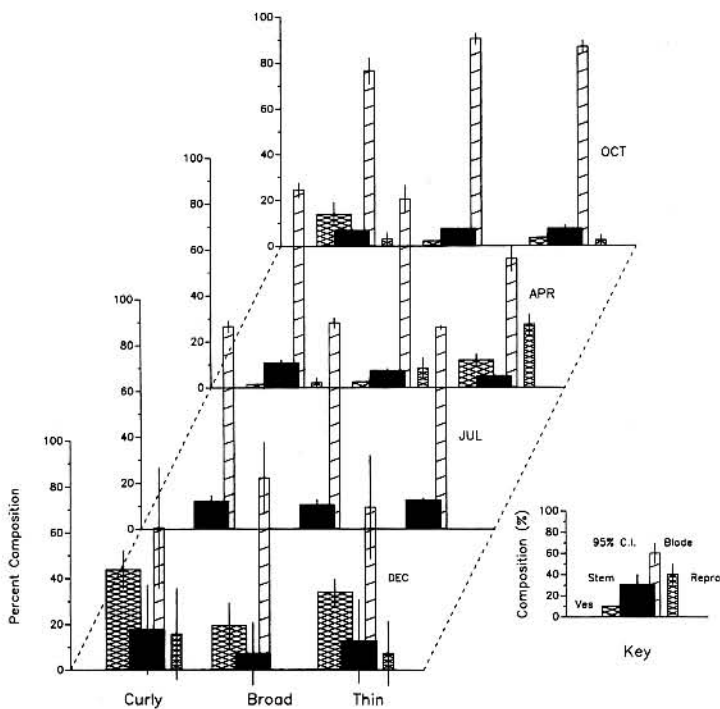


FIG. 3. Seasonal composition (%) of morphological features based on surface area for the three phenotypes (curly, broad, thin) of *Sargassum polyceratum* during April, July, October, and December. Error bars are 95% confidence limits around the mean. $n = 15$ tips per treatment.

and senescence, and is lowest during stasis. Similar patterns have been reported for *S. pteropleuron* (Prince 1980) and *S. filipendula* (Dawes 1987). Annual trends in respiration that tracked those of photosynthesis have been shown by Prince (1980). Our data do not show similar trends. Instead, high respiratory rates correlate well with the times of production of photosynthetic reserves and pigments.

Anatomical features and ontogenetic events explain photosynthetic rates. With the onset of reproduction, photosynthesis decreases, and vesicles and receptacles develop at the expense of blades, a pattern observed for each phenotype. The resulting lower photosynthetic activity agrees with the cytological and manometric comparisons of Fagerberg et al. (1979); blades have a 62% greater photosynthetic potential and 61% more thylakoid membrane surface area than stems. It has been suggested (Dawes, pers. commun.) that physical parameters may be better correlated to photosynthetic performance if production is related to differences in chlorophyll *a* and accessory pigment composition. The synthesis of photosynthetic pigments also may act to decrease apparent photosynthesis. In the fall and winter months, lower incident light and higher ambient nutrient concentrations have been shown to increase photosynthetic pigments (Ramus et al. 1976a, b, 1977, DeBoer and Ryther 1978, Rosenberg and Ra-

TABLE 2. Nonparametric analysis of variance table (KWAL) evaluating phenotypic patterns in blade area and blade density, and apical-tip SA:V ratio for adult and juvenile axes. Groups are arranged in ascending order (left to right) and a line delimits similar groupings (SS-STP or Mann-Whitney U tests [*], $P < 0.05$). c = curly, b = broad, and t = thin phenotypes.

	Period	Juvenile			Adult		
		KWAL (P)	Groupings		KWAL (P)	Groupings	
Blade area	Oct	0.69			<0.001	c	t b*
	Apr	0.03	c	b t*	<0.001	t	b c
	Jul	0.31			0.31		
	Dec	0.53			<0.001	c	t b
Blade density	Oct	0.003	b	t c*	<0.01	b	t c*
	Apr	0.63			0.13		
	Jul	0.20			0.34		
	Dec	0.28			0.92		
SA:V ratio	Oct	<0.001	b	t c	<0.001	c	t b
	Apr	0.23			<0.01	t	c b
	Jul	0.13			<0.01	t	c b
	Dec	0.22			<0.01	c	t b*

mus 1982); the pigments work to limit the decrease in net photosynthesis in the face of decreasing light and temperature (Moon and Dawes 1976, Brinkhuis 1977, Durako and Dawes 1980).

Respiration rates are highest during peak reproduction and stasis. Previously, Dawes (1987) reported a physiological "slowdown" or decrease in apparent photosynthesis (he did not measure respiration) to occur prior to reproduction in mature, pre-reproductive plants. Reduced photosynthetic rates probably reflect elevated respiratory rates that accompany the production of mannitol and alginic acid during reproduction (Prince 1980, Daly and Prince 1981). As respiratory rates among pheno-

types are not correlated with reproduction, these high rates may be short-lived and restricted to a transition period between vegetative and reproductive phases. As annual trends are similar in mature and developing axes (Fig. 1), respiration rates are affected throughout the plant. During stasis, carbohydrates are most abundant in *Sargassum* (Dawes 1987). At this time, plants often form inflated areas on upright axes that probably contain reserve products. More study is needed before further interpretation of these trends can be made.

Patterns of SA:V ratios bear little correlation with photosynthesis but still play a functional role. Most macroalgae are structurally uniform, temporally

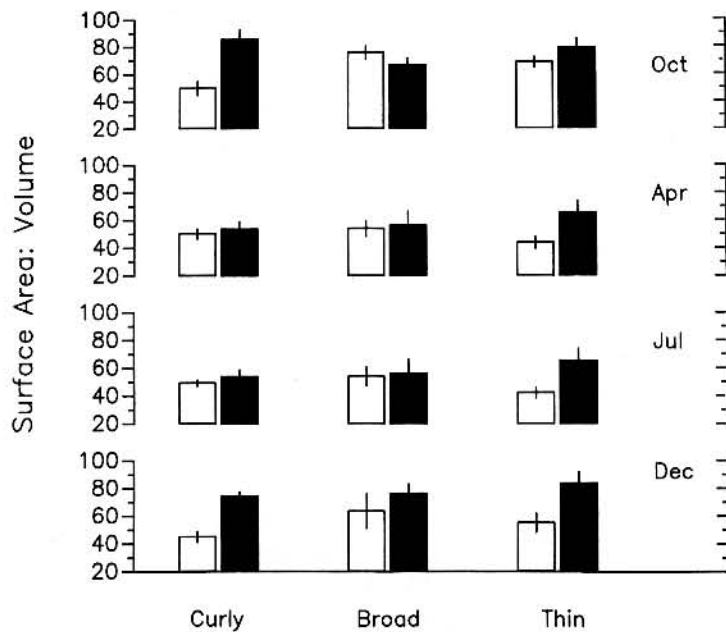


FIG. 4. SA:V ratio for the three phenotypes (curly, broad, thin) of *Sargassum polyceratum* during April, July, October, and December. Error bars are 95% confidence limits around the mean. n = 15 tips per treatment. Developing axes = dark bar, mature axes = open bar.

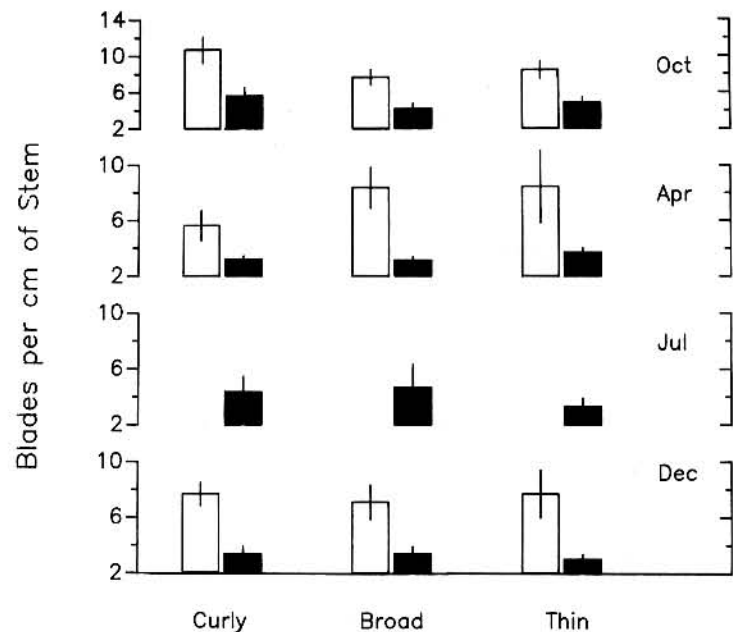


FIG. 5. Blade density for the three phenotypes (curly, broad, thin) of *Sargassum polyceratum* during April, July, October, and December. Error bars are 95% confidence limits around the mean. n = 15 tips per treatment. Developing axes = dark bar, mature axes = open bar.

predictable, and morphologically stable within a habitat. Among these seaweeds, net photosynthesis and specific growth rates correlate well with SA:V ratios. Among long-lived species, structural complexity (e.g. in Laminariales) and intra- and inter-individual variability may increase, reflecting different environmental pressures (disturbance, competition, predation) on growth and reproductive cycles (Kilar and Hanisak 1989). For example, the storage of photosynthate (Chapman and Craigie 1977, 1978), mechanical support of uprights (Kain 1976, Koehl 1982), or early fruiting (Harper 1977) may be more important to plant fitness than rapid growth or the maximizing of SA:V. In *Sargassum*, SA:V plays a secondary role as productivity is not correlated with the development of receptacles on phenotypes and SA:V effects on production are not independent of blade-density effects or the development of specialized anatomical features. Caution should be used in generalizing relationships between SA:V ratios and metabolic activities (see Dahl 1973, 1976), since this study shows that in highly differentiated algae, the interpretation is more complex. Turf forms, with overlapping diffusion gradients and self shading, also are not as productive as their SA:V ratios would suggest (Littler and Arnold 1980). Also, large kelps with source-sink translocation to photosynthetically incompetent portions (Titlyanov and Peshekhod'ko 1973) show no correlation between SA:V ratio and apparent photosynthetic capacity.

Developing axes have greater blade areas and SA:V ratios than mature axes, representing possible adaptations to low light. Previously, the acclimation of the photosynthetic apparatus of *Sargassum* to low light fields has been shown to take place through the accumulation of photosynthetic pigments (Titlyanov et al. 1983); the lower parts form most pigments (chlorophyll *a* and *c*), make full use of weak light, and use, with great efficiency, the strong light from infrequent flashes. Difference in photosynthetic performance between perennial bases (mature, older parts of the plant) and annual axes could be similarly explained (Dawes and Tomasko 1988). All major groups of algae accommodate to photon flux density and increase in antenna pigment contents with decreasing incident light (Ramus et al. 1976a, b, 1977). Also, *Sargassum* has been compared with terrestrial plants with small blades or sun leaves in shallow, well-lit water and larger blades or shade leaves in deeper water (Hay 1986). Blades of mature versus juvenile axes or distal versus proximal location follow a similar developmental pattern, where blades closest to the perennial stem and holdfast are larger in size. In *S. polyceratium*, blade size diminishes with age and stage of development (Kilar and Hanisak 1988), a possible adaptation to increase blade productivity when blade numbers are decreasing. Smaller blades have high SA:V ratios that are frequently correlated with nutrient uptake (Rosenberg

and Ramus 1982) and growth (Littler and Littler 1980).

Blade senescence and loss have been reported from the field and in culture (Norton 1977, Taniguchi and Yamada 1978, Terawaki et al. 1984). The loss of older blades is consistent with the theory that *Sargassum* lacks conductive tissues. That is, if photosynthate diffuses from blades and stems to meristematic areas, then the usefulness of older blades diminishes as the meristem grows. However, translocation is reported in *S. pallidum* (Turn.) C. Ag. (Titlyanov and Peshekhod'ko 1973) and probably occurs in most species (for anatomy, see Hansteen 1892, Simons 1906). As to why older blades are removed rather than maintained, the cost of removal appears less than the expense of adding vesicles to support their weight or maintaining some older cell-structures.

Developing axes have high respiratory rates. In contrast, Titlyanov et al. (1983) and Gao and Umezaki (1988) report decreased respiratory rates in the lower parts of *Sargassum*. The later observations are compatible with blade senescence and loss; hence, they do not represent a contradiction. High rates of respiration in developing axes are attributed to active growth, pigment production, and reserve product formation.

In summary, seasonal changes in net production coincide with ontogenetic changes in metabolism and allocation of biomass into blades, stems, vesicles, and fertile branches. Physiological processes in *S. polyceratium* resulting in the senescence and loss of blades, and the production and accumulation of photosynthetic reserves, or morphological features such as an anatomically differentiated thallus or blade SA:V modifications, represent highly specialized adaptations and a 'division of labor strategy.' With complex algae, like *Sargassum*, such specialization of plant parts requires the examination of functional/morphological relationships on a fine scale (i.e. within plant). For example, productivity studies (Littler and Arnold 1980) and translocation work (Lobban 1978) on *Macrocystis pyrifera* (L.) C. Ag. suggest that the photosynthetically active blades function as sources of photosynthate that is moved to the sporophyll blades (Littler and Arnold 1980). Morphologically differentiated fronds on the same thalli of *Halidrys dioica* Gardner and *Egregia menziesii* (Turn.) Aresch. have significantly different photosynthetic performances (Littler and Arnold 1980), as do undifferentiated juvenile fronds vs. mature fronds of *E. menziesii* (Littler and Littler 1980). Also, individual blades of *M. pyrifera* (Clendenning 1971) and *Laminaria digitata* (Huds.) Lamour. (King and Schramm 1976, Küppers and Kremer 1978) show steeply rising photosynthetic rates with increasing distance from the basal holdfast.

Therefore, whole-plant models of the functional morphology (Littler and Littler 1980), which pre-

dict relatively low overall photosynthetic rates for highly differentiated algae such as *Sargassum* (due to a preponderance of structural tissue and sink organs), should be applied on a finer scale of resolution when used to compare and interpret the functional-anatomical features within complex thalli. Such an approach to the understanding of relationships among structurally differentiated and physiologically specialized plant structures should prove challenging, since presumably all metabolic function is ultimately related to structure at some anatomical, cytological, or biochemical level.

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