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# Reproductive biomass allocation in three *Sargassum* species

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**Abstract.** Allocation of biomass to sexual reproductive (receptacle) tissue and vegetative (holdfast) tissue differed absolutely and relatively in three *Sargassum* species that form the bulk of the intertidal algal canopy in the northern Gulf of California. *Sargassum herporhizum* devoted a greater proportion of its thallus mass into its rhizoidal holdfast than did *S. sinicola* var. *camouii* or *S. johnstonii*, whose holdfasts are solid, more compact, and composed of a lower percentage of water. Conversely, more sexual receptacle tissue was produced by these two species with small holdfasts during the spring reproductive period. *Sargassum sinicola* var. *camouii*, which is the only species of the three that becomes fertile in the fall, produces a comparable amount of sexual tissue during this second period of reproduction. Removal of *Sargassum* from single-species patches showed that canopy regrowth by *S. herporhizum* with its encroaching rhizoidal holdfast was more rapid and complete than that of the other two species, which invest most of their reproductive efforts into sexual propagules that can disperse long distances. *Sargassum herporhizum* also displayed a more rapid and complete recovery of canopy cover in patches cleared of thalli and in control patches following the annual summer dieback. These two divergent modes of reproductive biomass allocation suggest that ability to encroach upon nearby open sites and ability to colonize distant discrete islands of suitable habitat represent two distinct reproductive strategies requiring different patterns of biomass allocation. Moreover, for energetic reasons, a species may not be able to excel at both modes of reproduction.

Vegetative growth and sexual reproduction impose very different demands on the energy budgets of plants. Plants producing large numbers of sexual structures (flowers and seeds) generally produce fewer vegetative reproductive structures (rhizomes and runners) (Harper 1977; Werner 1979). Plants commonly invest most of their reproductive biomass to vegetative or sexual structures, but not to both. The best evidence of this apparent tradeoff in the ability of a plant to invest in one or the other of the two modes of reproduction (but not both) comes from studies of terrestrial and freshwater plant communities. Divergent patterns of reproductive biomass investment have been shown in closely related sets of species such as *Solidago* (Werner 1979), *Ranunculus* (Sarukhán 1976), *Polygonum* (Hickman 1977), *Smyrnium* (Lovett Doust 1980), and *Typha* (Grace and Wetzel 1982). Although marine algae display intra- and interspecific variation in the proportion of reproductive biomass allocation to sexual and vegetative structures, the existence of a tradeoff in allocation abilities has rarely been demonstrated (Russell 1979).

Species of *Sargassum*, a brown alga common on tropical and some temperate shorelines, allocate biomass differentially to different modes of reproduction. Intertidal benthic *Sargassum* reproduce vegetatively through lateral encroachment of basal holdfasts and sexually through the shedding of fertile, receptacle-bearing branches that may float and disperse propagules great distances (Deysher and Norton 1982). Some evidence suggests that a tradeoff exists in the production of vegetative and sexual tissue. Norton (1977) showed that vegetative branches grow five times faster than branches bearing sexual structures (receptacles). Free-floating *Sargassum* plants in the Sargasso Sea forgo sexual reproduction entirely (Parr 1939) in a habitat where selection operates against sexual propagules that must settle on hard substrates. This paper reports on biomass allocation in three intertidal *Sargassum* species that make up most of the intertidal algal canopy in the northern Gulf of California.

## Materials and methods

All investigations were carried out at Station Beach near Puerto Peñasco, Sonora, Mexico in the northern Gulf of California (see McCourt, 1983, 1984a, 1984b, for details of study site). Average sea surface temperatures in this region range from 14° C in winter to nearly 30° C in summer. The spring tide range exceeds 7 m and uncovers a large expanse of coquina reef with numerous tide pools up to a meter or more deep and many meters wide. The three species of *Sargassum* that occur here are *S. johnstonii* Setchell & Gardner, *S. herporhizum* Setchell & Gardner, and *S. sinicola* Setchell & Gardner. Two varieties of the last species are known, one generally subtidal (var. *sinicola*), the other intertidal (var. *camouii*) (Norris and Yensen in press). In this paper, *S. sinicola* will refer only to the variety *camouii*. The species are distributed in a zonation pattern in tide pools and across the intertidal zone as a whole (McCourt 1984a) and are most abundant in winter and spring (McCourt 1984b).

Vegetative reproductive investment was measured as proportion of the plant thallus in the holdfast. Allocation of biomass to holdfasts and upper branch system was measured by using material collected from small patches (0.01 to 0.04 $m^2$) in the midst of pure stands of each species. Measurements were adjusted to 0.01-$m^2$ patch size for statistical analyses. Plant material was collected from the patches by scraping the substrate with a putty knife, which removed holdfasts and attached branches nearly intact. Each patch contained 50 to 100 stipes. Samples from each patch were collected from tide-pool populations of each species in February 1978 (five patches per species), April 1980 (four patches per species), and February 1981 (four patches per species). These months were times of near-peak canopy cover for the three species.

Samples were preserved in 3% formalin-seawater, later rinsed in fresh water in the laboratory, dissected into holdfast and upper branch subsamples, and cleaned of epiphytes and pieces of coquina. Samples were blotted dry and weighed to determine wet mass.

Holdfast subsamples from patches in 1980 and 1981 were dried for 2 days at 104° C, after which dry mass was measured.

Branch subsamples from patches in 1980 and 1981 were divided into two approximately equal parts. One part was weighed for wet mass, then placed in the drying oven for 2 days at 104° C and weighed to measure for proportion dry mass, which was used to estimate the dry mass of the original branch subsample (proportion dry mass × wet mass of branch subsample).

Thalli in saved portions of branch subsamples from 1980 patch removals were sorted into fertile and nonfertile portions, blotted dry, and weighed. Total wet mass of fertile branch tissue in a patch was calculated (proportion fertile tissue × total wet mass of the branch subsample). Ten sections of fertile branch tissue (1–2 cm long) from each patch were cut off, blotted dry, and weighed. Number of receptacles on each section was counted, and number per gram wet mass (receptacle density) calculated.

To measure sizes of fertile and nonfertile stipes throughout the year, collections of stipes from *Sargassum* plants in Station Beach tide pools were made approximately monthly from September 1979 to March 1982. Two collections were also made in April 1979. Stipes were collected form plants in pools along a transect parallel to the shore at a level of +0.6 m above mean low water. One stipe per plant was detached at the branch point on the main axis to avoid destruction of the entire plant. Lengths of 25 stipes per species from each sampling date were measured to the nearest 0.5 cm (in summer when plants were scarce sample sizes ranged from zero to 20). Presence or absence of sexual receptacles was noted for each stipe, which was recorded as fertile or nonfertile, respectively.

Receptacle densities in March 1981 were calculated by treating stipe collections for that date as a "patch." Ten sections per species were cut from fertile branches. Receptacle density was determined for each stipe section. *Sargassum sinicola* is the one species of the three that is fertile in autumn (McCourt 1984b). Receptacle densities were calculated for this species based on stipe collections from October 1979 and November 1980.

The length (l) and width (w) of 100 randomly selected receptacles per species were measured. Twenty-five receptacles of *S. johnstonii* and *S. sinicola* were measured from each of the four patches in 1980; 100 receptacles from the sole fertile patch of *S. herporhizum* were measured. Volume (V) was calculated for each receptacle based on an assumed cylindrical shape ($V = \pi(w/2) \cdot l$). The volume ($mm^3$) of receptacle tissue per gram fertile branch tissue was calculated for each patch (mean number receptacles$\cdot g^{-1}$ fertile branch × mean receptacle volume in $mm^3$). The total volume of receptacles produced in each patch was also estimated (mean receptacle volume ($mm^3$)$\cdot g^{-1}$ fertile branch × total g fertile branches$\cdot$patch$^{-1}$).

The four patches per species cleared of thalli in April 1980 were monitored for 1 year to measure canopy regrowth. From color slides, percent cover of *Sargassum* canopy for cleared patches and four nearby control patches for each species was calculated at approximately monthly intervals. Slides were displayed on a grid of 100 dots arranged in a regular square array (10 rows, 10 columns). The sum of the dots on each slide where a species occurred was used as the percent canopy cover for that species.

Statistical analyses were performed using BMDP computer programs described by Dixon and Brown (1979) and some procedures in Sokal and Rohlf (1969). Data were log-transformed when necessary to achieve homogeneity of variances; proportion data were arcsine-transformed before analysis. Preliminary two-way analyses of variance (ANOVA) showed some differences between data collected in different years. However, because no interaction effects were significant in the analyses, the data were pooled for further tests (one-way ANOVA) of differences between species.

## Results

The proportion of total wet and dry mass devoted by *S. herporhizum* to holdfast tissue was two to three times the proportion devoted to holdfast tissue by the other two species (Table 1). *Sargassum herporhizum* produced less vegetative branch tissue (wet and dry mass) and more holdfast tissue (wet mass) per unit area in pure stands than the other two species (Table 1). Holdfast dry mass was equal across species (Table 1).

**Table 1.** Biomass allocation by three *Sargassum* species in small patches in tide pools at Puerto Peñasco, Sonora, Mexico. Numbers are mean ± standard error. Numbers in same row with different superscripts are significantly different ($P < 0.05$, ANOVAs and LSD tests on means)

| Biomass Measurement | *Sargassum* species | | |
|---|---|---|---|
| | *herporhizum* | *johnstonii* | *sinicola* |
| Percent total plant mass in holdfast | | | |
| Wet, $n = 13$ | $34.3 \pm 2.5^a$ | $9.0 \pm 1.2^b$ | $8.9 \pm 1.8^b$ |
| Dry, $n = 8$ | $33.6 \pm 3.3^a$ | $10.9 \pm 2.4^b$ | $17.5 \pm 5.6^b$ |
| Mass of structures (g) | | | |
| Holdfast | | | |
| Wet, $n = 13$ | $12.9 \pm 1.5^a$ | $6.6 \pm 1.2^b$ | $6.5 \pm 1.4^b$ |
| Dry, $n = 8$ | $1.7 \pm 0.4^a$ | $0.8 \pm 0.2^a$ | $1.9 \pm 1.8^a$ |
| Branches | | | |
| Wet, $n = 13$ | $24.5 \pm 2.4^a$ | $66.3 \pm 8.8^b$ | $68.8 \pm 10.8^b$ |
| Dry, $n = 8$ | $3.6 \pm 0.7^a$ | $7.5 \pm 1.2^b$ | $8.0 \pm 1.5^b$ |
| Percent dry mass in structure | | | |
| Holdfast, $n = 8$ | $12.4 \pm 0.5^a$ | $17.8 \pm 1.1^b$ | $25.3 \pm 1.6^c$ |
| Branches, $n = 8$ | $14.3 \pm 0.4^a$ | $14.7 \pm 1.4^a$ | $15.9 \pm 0.4^a$ |

Table 2. Percentages, numbers, and mean lengths (±SD) of fertile and nonfertile *Sargassum* stipes in combined Station Beach collections, 1979–1982. Fertile stipes of each species were significantly longer than nonfertile stipes ($P < 0.001$, Mann-Whitney test with normal two-tail approximation)

| Species | Fertile | | Nonfertile | |
|---|---|---|---|---|
| | Percent ($n$) | Mean Length, cm | Percent ($n$) | Mean Length, cm |
| *S. herporhizum* | 5.4 (31) | 17.42±8.44 | 94.6 (538) | 7.96±4.18 |
| *S. johnstonii* | 23.8 (124) | 18.75±7.81 | 76.2 (397) | 10.76±6.73 |
| *S. sinicola* | 41.1 (231) | 20.21±8.69 | 58.9 (331) | 12.28±6.54 |

Table 3. Average production of fertile branch tissue in tide-pool patches by three *Sargassum* species. $n = 4$ patches per species; each patch contained 50 to 100 stipes. Numbers in same column with different superscripts are significantly different ($P < 0.05$, ANOVA, LSD tests on means, arcsine transformed percentages)

| Species | Mean Wet Mass (±*SE*), g | Mean % Total Mass (±*SE*) |
|---|---|---|
| *S. herporhizum* | 0.29±0.26$^a$ | 6.87±13.21$^a$ |
| *S. johnstonii* | 5.26±0.50$^b$ | 65.06± 7.11$^b$ |
| *S. sinicola* | 22.79±8.76$^c$ | 74.16± 3.86$^b$ |

Table 4. Means±standard errors for receptacle volume, density (number per g fertile branch) across years, volume density (volume per g fertile branch), and total volume (mm$^3$) per patch for three *Sargassum* species. Sample size ($n$) in parentheses

| Receptacle Measurement | *Sargassum* species | | |
|---|---|---|---|
| | *herporhizum* | *johnstonii* | *sinicola* |
| Volume (mm$^3$) | 0.52± 0.07<br>(100) | 1.37± 0.09<br>(100) | 4.22± 0.28<br>(100) |
| Density | | | |
| Spring 1980 | 396.54±54.31<br>(10) | 462.51±19.70<br>(40) | 133.56± 8.07<br>(40) |
| Spring 1981 | 256.83±29.61<br>(10) | 488.46±41.87<br>(10) | 138.89±16.40<br>(10) |
| Fall 1979 | – | – | 127.12± 5.65<br>(10) |
| Fall 1980 | – | – | 140.83±12.51<br>(10) |
| Volume density | 64.66<br>(4) | 658.25<br>(4) | 538.62<br>(4) |
| Total volume per patch | 463.21<br>(4) | 24,812.07<br>(4) | 26,201.99<br>(4) |

Assuming that the caloric cost of producing a structure is proportional to the percent dry mass of the structure (Hickman and Pitelka 1975), the species differed significantly in cost of producing their holdfasts (Table 1). *Sargassum sinicola* holdfasts cost the most to produce, *S. herporhizum* the least. The cost of producing branches was uniform across species (Table 1).

*Sargassum johnstonii* holdfasts and branches contained the same percentage of dry matter ($P > 0.05$), whereas *S. herporhizum* holdfasts contained less and *S. sinicola* holdfasts more dry matter per gram wet mass than their respective branches ($P < 0.05$, paired $t$ tests on data in Table 1).

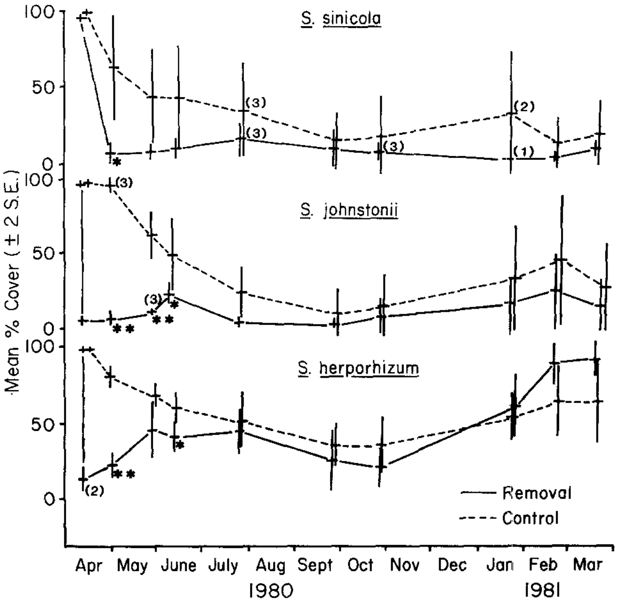

Fig. 1. Changes in canopy cover of *Sargassum* in tide pool removal and control patches from spring 1980 to spring 1981. $n = 4$ patches per species on each date unless otherwise indicated in parentheses; $n < 4$ due to wind distortion of water surface making photographs unusable. Differences between removals and controls: * = $P < 0.05$; ** = $P < 0.01$, ANOVA on arcsine-transformed percent cover

Pooled across all collections, fertile stipes of each species were longer than nonfertile stipes (Table 2). In individual monthly collections of each species with mixtures of fertile and nonfertile stipes, fertile stipes were either equal in length or significantly ($P < 0.05$, Mann-Whitney tests) longer than nonfertile stipes.

*Sargassum sinicola* has two fertile periods during the year (spring and fall) and therefore had the highest number and percentage of fertile stipes in the combined collections (Table 2). Percentage of fertile stipes in combined collections of *S. johnstonii* was about half that for *S. sinicola*, and *S. herporhizum* scored lowest in this measure of sexual biomass production.

*Sargassum sinicola* and *S. johnstonii* produced more grams of fertile branch tissue per patch than *S. herporhizum* (Table 3). Over half the total branch tissue produced by the former two species was fertile, compared to less than 10% for *S. herporhizum*.

Statistical analysis of receptacle production in patches was complicated by the near or complete absence of receptacle tissue in three of the four patches of *S. herporhizum*. For this reason receptacle densities were first compared for *S. johnstonii* and *S. sinicola* only (two-level nested ANOVA, patches within species) (Table 4). There was significant ($P < 0.01$) variation among patches, and *S. johnstonii* produced a significantly ($P < 0.01$) higher receptacle density than *S. sinicola*.

Three of the four *S. herporhizum* patches contained virtually no receptacles in April 1980. However, the mean receptacle density of stipe sections from the one fertile patch of *S. herporhizum* was not significantly ($P > 0.08$) different from that of stipe sections from the four patches of *S. johnstonii*, but was significantly ($P < 0.001$) greater than mean density for *S. sinicola* stipe sections (pairwise $t$ tests on data in Table 4).

Receptacle volume and density for the three species in each patch in 1980 were used to estimate volume of receptacle tissue produced per gram of fertile branch (volume density) and total receptacle volume per patch (Table 4). *Sargassum sinicola* and *S. johnstonii* produced a significantly ($P<0.01$) higher receptacle volume per fertile gram of branch tissue and per patch than *S. herporhizum* (ANOVA and LSD test on means, Table 4).

Less than 1 month following thalli removal in patches (by early May) *S. herporhizum* canopy cover had recovered to a greater extent than that of the other two species (Fig. 1). In fact, mean canopy cover in *S. herporhizum* cleared patches was significantly greater than in cleared patches of the other two species on every date sampled after the initial clearing ($P<0.05$; ANOVA on arcsine-transformed data for each date, LSD tests on means). Poorest regrowth was shown by *S. sinicola*, which recovered to less than 20% after 3 months. Regrowth appeared to be from remnants of holdfast embedded in the coquina and was augmented in *S. herporhizum* by encroachment of haptera from plants adjacent to the cleared patch. Settlement of new plants in cleared patches or in nearby areas was not observed.

The levels of canopy cover in the cleared patches of all three species converged with those in their respective control patches during the course of the summer dieback (Fig. 1). Canopy cover in *S. sinicola* and *S. johnstonii* cleared patches was lower than that of their respective controls in the subsequent spring, whereas *S. herporhizum* cleared patches actually surpassed the controls in canopy cover a year after removal.

## Discussion

The data on the three *Sargassum* species show interspecific differences in biomass allocation between closely related species. Species tend to devote reproductive biomass into vegetative or sexual tissue but not both. *Sargassum herporhizum* invests mostly in vegetative reproductive structures (holdfast haptera) and engages in relatively little sexual reproduction, whereas the other two species display a reversed pattern of reproductive tissue production. The patterns of biomass investment in the three *Sargassum* represent two divergent strategies: receptacle production for long-distance dispersal (Deysher and Norton 1982), and haptera production for encroachment into nearby areas.

Few studies have addressed the issue of reproductive biomass allocation in marine algae. Russell (1979) suggested that the "heavy receptacles" of *Fucus vesiculosus* L. are an adaptation of plants to disturbed habitats. He argued that production of more receptacle tissue results in more propagules, which are better able to colonize newly opened space in habitats subject to heavy surf. In protected areas where less space is opened up by disturbance, less receptacle tissue is produced and relatively more tissue is devoted to vegetative fronds that enable a plant to compete better against other algae.

The pattern of tradeoff in biomass allocation in *Sargassum* has also been reported for many vascular plants (Werner 1979). Two species of aquatic cattail (*Typha*) studied by Grace and Wetzel (1982) exhibit some similarities to the *Sargassum* species. *Typha latifolia* (L.) and *T. angustifolia* (L.) occur in ponds in a zonation pattern, with *T. latifolia* in shallower water. *Typha latifolia* devotes a larger proportion of its biomass to vegetative rhizomes and is a competitive dominant over the other species in shallow habitats. *Typha angustifolia* occurs in deeper water, devotes more tissue to sexual structures, and is assumed to be more of a fugitive species. *Sargassum* species in tide pools at Puerto Peñasco also exhibit a zonation pattern, but it is *S. herporhizum*, the middle species in the zonation pattern, that specializes in reproduction through vegetative rhizome-like haptera. The species producing the greatest amount of sexual biomass, *S. sinicola* and *S. johnstonii,* occur in the deepest and shallowest parts of pools, respectively (McCourt 1984a). The habitat of these two *Sargassum* species may be more patchy than that of *S. herporhizum* due to occasional desiccation stress of *S. johnstonii* at pool edges and burial of *S. sinicola* by sand in the deeper parts of pools. *Sargassum herporhizum* may be the competitive dominant on continuous patches of coquina at intermediate depths not subject to sand burial or desiccation; however, removals of plants in monospecific stands in pools does not result in immediate invasion by either *S. johnstonii* or *S. sinicola.*

Occurrence of sympatric species such as *Typha* or *Sargassum* on an environmental gradient (for these plants a depth gradient) may lead to a divergence of reproductive strategies. Investment of biomass into vegetative rhizomes at the expense of sexual structures will affect a plant's competitive abilities on the gradient and lead to a zonation pattern in which the superior space competitor occurs in shallow, light-rich habitats.

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