

## Herbivory effects on the morphology of the brown alga *Padina boergesenii* (Phaeophyta)

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Many coral reef benthic algae exhibit morphological plasticity enabling them to persist in diverse habitats under different environmental pressures. Morphological plasticity has been previously observed in the brown alga *Padina jamaicensis*, which displays a foliose morphology under low grazing pressure and a turf morphology in habitats with medium to high herbivory levels. To determine whether a different species of *Padina*, *P. boergesenii*, exhibits morphological plasticity regulated by herbivory, we excluded macroherbivores from experimental plots containing *P. boergesenii* thalli on a rocky reef off Santa Marta in the Colombian Caribbean. The experiment used exclusion cages to test for effects of herbivores and was carried out in two contrasting oceanographic seasons: upwelling (low water temperature and high water transparency) and rainy (higher temperature and low water transparency). The morphology of *P. boergesenii* was significantly affected by herbivory but only during the upwelling season. *Padina boergesenii* rapidly changed from a turf morphology to a fan-shaped form and increased in size when protected from herbivores in full cages in a period of less than a week. Thalli exposed to macroherbivores in open plots did not shift to a foliose morphology, and neither did thalli investigated during the rainy season, independent of herbivore treatment. Our results show that herbivory plays an important role in controlling the morphology and may affect life history processes of the alga *P. boergesenii* but suggest that plant response to herbivory may be a seasonal process. This suggests that there are important climatic (e.g. trade winds inducing upwelling) and oceanographic factors (e.g. water temperature) limiting algal abundance and that these factors may mediate morphological plasticity of algae. Therefore, reductions of grazing are not enough to promote morphological plasticity during the rainy season.

KEY WORDS: Caribbean, Herbivory, Macroalgae, Morphological plasticity, *Padina boergesenii*, Seasonality, Upwelling

### INTRODUCTION

Morphological plasticity has been observed in red, brown, and green algae and has been related to changes in the intensity of environmental factors such as of wave exposure, light, herbivory, and life history stages (Steneck & Adey 1976; Lubchenco & Cubitt 1980; Lewis *et al.* 1987; de Ruyter van Steveninck *et al.* 1988a; Littler & Littler 1988; Coen & Tanner 1989; Collado-Vides 2002; Scrosati 2002; Stewart & Carpenter 2003; Monro & Poore 2005). Individuals that can show continuous but reversible changes in morphology may reduce risk of predation and therefore may have a greater chance of survival. Furthermore, morphological plasticity may incur a selective advantage if fitness is increased by changing phenotype (Piersma & Drent 2003). There are important ecological implications for algae showing morphological plasticity, including, for instance, exploitation of a variety of habitats and resources. Changes in the intensity of wave exposure, light, and herbivory may induce rapid responses in algal morphology and size. For example, the brown alga *Padina sanctae-crucis* Børgesen [previously known as *P. jamaicensis*

(Collins) Papenfuss] shifted from a turf morphology to a foliose, fan-shaped morphology in 96 h when grazing pressure was reduced, allowing the alga to persist in habitats of different grazing pressure (Lewis *et al.* 1987). However, other algae of the same family Dictyotaceae [e.g. *Lobophora variegata* (Lamouroux) Womersley ex Oliveira], which exhibit a wide range of different morphologies, did not show important changes in morphology when the regulating factors were altered (de Ruyter van Steveninck *et al.* 1988b). The morphological plasticity in the latter case may be related to genotypic differences of the populations (de Ruyter van Steveninck *et al.* 1988b; Coen & Tanner 1989).

*Padina boergesenii* Allender & Kraft is a common species of intertidal and shallow subtidal habitats in the area of Santa Marta, Colombian Caribbean (Diaz-Pulido & Diaz-Ruiz 2003). The foliose, fan-shaped morphology is generally found in habitats and microhabitats where grazing pressure is reduced, such as rocky intertidal zones, sand plains, damselfish territories, or between branches of hard corals (G.D.-P., personal observation). The foliose morphology rarely occurs in shallow rocky reefs where herbivore pressure (mainly by surgeonfishes, parrotfishes, damselfishes, and seaurchins) is intense. In contrast, the turf morphology of *P. boergesenii* is quite common below the intertidal down to 6-m depth (G.D.-P., personal observation). These observations and the experi-

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ments by Lewis *et al.* (1987) inspired us to examine whether the morphology of *P. boergesenii* is also regulated by herbivory, allowing us to explore how common is this trait within the genus *Padina*. Since the abundance and composition of algal assemblages are quite seasonal in the area of Santa Marta, we explored whether the effects of herbivory on the alga depended on the two main oceanographic seasons: the dry, upwelling season and the rainy, non-upwelling season.

## MATERIAL AND METHODS

### Study area

The experiment was carried out on a rocky reef at El Morro islet, in the El Rodadero Bay, located 5 km south from the city of Santa Marta, Colombian Caribbean (11°15'N; 74°13'W). This rocky reef is characterised by a steep slope from the intertidal down to 4–5-m depth. Between 5 to 7 m, the reef extends horizontally and is dominated by algal turfs and scarce massive colonies of hard corals. Algal turfs are dominated by species of *Ceramium*, *Gelidium*, *Jania*, *Ectocarpus*, *Chaetomorpha*, *Enteromorpha*, *Cladophoropsis*, *Griffithsia*, *Polysiphonia*, and *Padina* (turving form).

The climate of the area of Santa Marta can be divided in two main climatic and oceanographic seasons: a dry, upwelling season and a wet, non-upwelling season. During the dry season (December to April–May) there is a decrease in rainfall and an upwelling of colder (mean 25°C but as low as 21°C), saline (mean 37 psu), clear, and nutrient-rich waters. The upwelling is driven by an increase in the intensity of trade winds in combination with the orientation of the coast and the narrow continental shelf. During the rainy season (May–June to November), inputs of riverine and estuarine water influence the area resulting in higher temperature (mean 27°C but as high as 31°C), lower salinity (mean 36 psu but as low as 24 psu), higher turbidity, and pulses of nutrients (Zea 1993; Diaz-Pulido & Garzón-Ferreira 2002). Sea surface temperature collected weekly during the course of the experiments in April–May 1997 (end of upwelling season) and August–September 1997 (rainy season) were significantly lower in the upwelling season (mean = 26.4°C,  $s_x = 0.5$ ) than in the rainy season (mean = 28.5°C,  $s_x = 0.4$ ;  $t = 3.366$ ,  $v = 13$ ;  $P = 0.005$ ). Transparency of the water column was significantly higher in the upwelling (mean = 4.4 m,  $s_x = 0.1$ ) than in the rainy season (mean = 3.3 m,  $s_x = 0.2$ ;  $t = -4.386$ ,  $v = 13$ ;  $P = 0.001$ ).

Qualitative observations on the type of macroherbivores and quantitative data on grazer rates by fishes at the experimental site at the time of this study and during both seasons (unpublished data), showed that the surgeonfishes *Acanthurus coeruleus*, *A. chirurgus*, and *A. bahianus*; the parrotfishes *Sparisoma viride*, *Scarus vetula*, and juveniles of *Scarus crocensis* and *Scarus taeniopterus*; and the damselfish *Stegastes dorsopunicans* were the most common vertebrate grazers during both experimental periods. Surgeonfishes exerted the highest grazing pressure on benthic algae at the experimental site (67% of the total number of bites), followed by parrotfishes (18%) and damselfishes (15%, unpublished data). Large invertebrate herbivores, such as the black searchin *Diadema antillarum*, were commonly observed at the experimental site.

### Experimental design

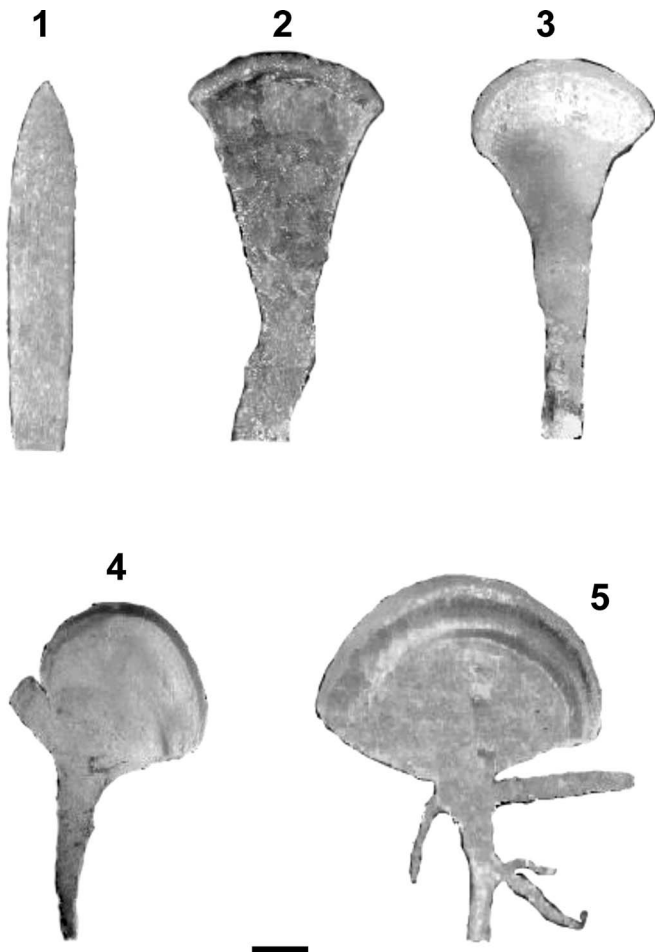
To test the effects of herbivory on the morphology of *P. boergesenii* and to determine whether those effects depended on the oceanographic seasons, we carried out a nested, fully factorial experimental design, with two fixed factors: (1) herbivore exclusions, with three levels: open, uncaged plots; caged plots; and partial-caged controls; and (2) season, with two levels: end of upwelling (May 1997) and rainy (August–September 1997). These sampling dates are representative of each of the oceanographic seasons, although a stronger test of seasonality would require more intensive sampling. Within each treatment combination there were three replicate plots (or cages) and, within each plot, a variable number (3–16) of *P. boergesenii* thalli were collected randomly. Thalli were nested within plots.

Open (uncaged) plots were marked with aluminium frames of 50 × 50 cm, anchored to the substrate with brass bolts. Bolts were anchored in holes made with a pneumatic drill, cemented with epoxy (Sikadur 32 primer™), and fastened with a terminal nut. Caged plots were made with an anchored frame (as above) and a removable cage. The frames had a Velcro cover on the upper side. The aluminium cage (50 × 50 × 50 cm), covered with polypropylene mesh size of 12 × 12 mm (to exclude macroherbivores), had Velcro on the base to secure the cage to the anchored frame. The use of Velcro allowed easy removal of the cages for *in situ* measurements (Thayer 1985). Partial cages were identical to full cages except that two of the sides of the cage were removed to allow free access of herbivorous fishes and sea urchins. These partial cages were used to control for cage artefacts (e.g. controlling effects of internal currents and light reduction) (Thayer 1985; McCook 1996). The cages, partial cages, and uncaged plots were placed outside of territories of damselfishes. The experiment was left for 3 weeks in each season, and cages were cleaned weekly to remove fouling organisms.

To determine morphological changes of *P. boergesenii*, we randomly collected thalli of *P. boergesenii* within each treatment combination by scrapping areas of algal turfs of approximately 4 cm<sup>2</sup>. Sampling was done once a week during 3 weeks, for each of the two main oceanographic seasons (upwelling: 16, 23, and 30 May 1997; rainy: 22 and 29 August and 5 September 1997). No samples were taken at the beginning of the experiment because of logistic problems. Thalli were then measured under a compound microscope in the laboratory. When the foliose, fan-shaped morphology was visible to the naked eye on the experimental plots, length and width of randomly selected plants were measured directly *in situ* with a calliper. Specimens and slides were deposited in the herbarium of the first author (D.P.) and at INVEMAR (Santa Marta, Colombia).

### Data analyses

Width and length of plants were analysed on the final date of each oceanographic season, using a factorial ANOVA model, with herbivore exclusion treatments and seasons as fixed factors and plots as replicates. Plants were nested within plots, and the nested factor mean square was used for the *F*-tests. Width and length gave significant interactions between herbivore exclusion treatments and seasons; therefore, these were then analysed for herbivore treatment effects within season



**Figs 1–5.** Morphological changes of *Padina boergesenii* when excluded from herbivores during the upwelling season. Scale bar = 0.3 mm.

**Fig. 1.** Filamentous turf form at the beginning of the experiment (7 May 1997; DP pl –210).

**Fig. 2.** Thalli with in-rolled margin, 7 d from the beginning of the experiment (16 May 1997; DP pl –211).

**Fig. 3.** Thalli with apical calcification, 14 d (23 May 1997; DP pl –212).

**Figs 4–5.** Foliose, fan-shaped form with blade showing concentric bands, at the end of the experiment (30 May 1997; DP pl –213), 21 d.

and season effects within herbivore treatments, using one-way ANOVAs and Tukey's *post hoc* comparisons (Underwood 1997). Data were checked for homogeneity of variance, and normality of residuals was confirmed (using Cochran's test and probability plots, respectively).

## RESULTS

### Morphological and morphometric changes

The morphology of *P. boergesenii* was significantly affected by herbivory during the upwelling season. *Padina boergesenii* shifted from a turfing morphology to a foliose, fan-shaped form when excluded from herbivores in a period of less than a week. *Padina boergesenii* remained as a turfing species under natural (ambient) grazing pressure (i.e. open, uncaged

**Table 1.** Factorial ANOVAs for the effects of herbivore exclusion and sampling period (season) on length of *Padina boergesenii*.<sup>1</sup>

Source	Sum of squares	<i>v</i>	Mean square	<i>F</i> -ratio	<i>P</i>
Herbivory (H)	902.287	2	451.144	15.555	<0.001
Season (S)	1345.385	1	1345.385	46.389	<0.001
H*S	1268.829	2	634.414	21.874	<0.001
Plot (H*S)	348.031	12	29.003	4.456	<0.001
Error	924.167	142	6.508		

<sup>1</sup> One-way ANOVA and Tukey's test within levels of treatments indicate the following: Cage treatment effects within season for length: Within upwelling season (30 May 1997): Cage > Partial = Uncaged; Within rainy season (05 Sep. 1997): Cage = Partial = Uncaged. Season effects within cage treatments: Within caged plots: Upwelling (30 May 1997) > Rainy (05 Sep. 1997); Within partial cages: Upwelling (30 May 1997) = Rainy (05 Sep. 1997); Within uncaged plots: Upwelling (30 May 1997) = Rainy (05 Sep. 1997).

plots; Fig. 1). At the beginning of the experiment, *P. boergesenii* thalli were filamentous, generally less than 0.32-mm width, without calcification or reproductive structures (although we occasionally observed tetrasporangia in the turf form). *Padina boergesenii* modified the morphology within full cages after 7 days (Fig. 2). The main branches became wider, followed by the secondary branches; then the frond margin rolled in, the upper side of fronds began to calcify from the apical part toward the holdfast, and several concentric bands became evident before the third week of the experiment (Figs 3–5).

There were strong interactions between herbivore treatments and seasons for both length and width of *P. boergesenii* (Tables 1, 2). The width and length of plants growing inside the full cages were significantly higher ( $P < 0.001$ ) than those growing in open plots and partial cages but only during the upwelling season (Figs 6, 8; Tables 1, 2). *Padina boergesenii* grew 14 times more when protected from herbivores within full cages than in the other two herbivore treatments during the upwelling (e.g. sampling from 30 May). In contrast, *P. boergesenii* remained in the turfing stage during the rainy season (August–September). Plants collected during the rainy season were shorter than plants of the upwelling season. No significant differences were observed in width of the plants between herbivore treatments during the rainy season (Figs 7, 9) at any of the three dates (Tables 1, 2), excepting August 29, where plant length from full cages was significantly smaller than those from open plots, contrary to the expected (Fig. 7). Some *Cerithium* spp. snails and hermit crabs were observed within full cages at this time, apparently because of reduction in predation pressure inside cages. However, the difference in thalli length was small, over 1 mm, and is much less than other effects.

## DISCUSSION

In this study we experimentally demonstrated that the brown alga *P. boergesenii* showed morphological plasticity that is regulated by herbivory. Significant changes in shape and increases in width, length, and cover were rapidly observed when the algae were excluded from macroherbivores in full

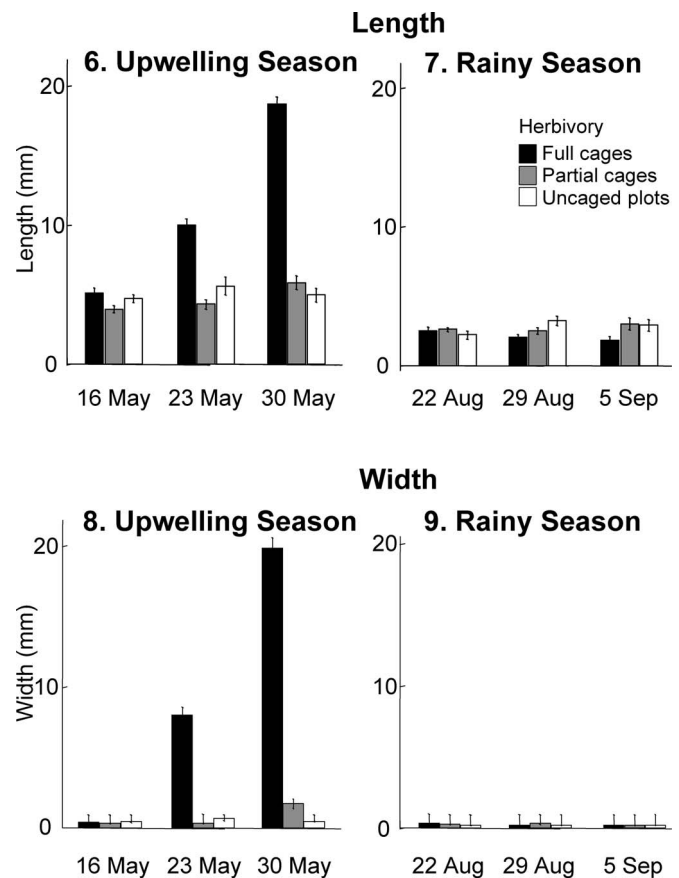
**Table 2.** Factorial ANOVAs for the effects of herbivore exclusion and sampling period (season) on width of *Padina boergesenii*.<sup>1</sup>

Source	Sum of squares	<i>v</i>	Mean square	<i>F</i> -ratio	<i>P</i>
Herbivory (H)	2125.081	2	1062.540	39.451	<0.001
Season (S)	1306.504	1	1306.504	48.509	<0.001
H*S	2137.334	2	1068.667	39.679	<0.001
Plot (H*S)	323.197	12	26.933	2.376	0.008
Error	1609.886	142	11.337		

<sup>1</sup> One-way ANOVA and Tukey's test within levels of treatments indicate the following: Cage treatment effects within season for width: Within upwelling season (30 May 1997): Cage > Partial = Uncaged; Within rainy season (05 Sep. 1997): Cage = Partial = Uncaged. Season effects within cage treatments: Within caged plots: Upwelling (30 May 1997) > Rainy (05 Sep. 1997); Within partial cages: Upwelling (30 May 1997) = Rainy (05 Sep. 1997); Within uncaged plots: Upwelling (30 May 1997) = Rainy (05 Sep. 1997).

cages during the upwelling season. These results are in agreement with the observations of Lewis *et al.* (1987), who found that the reduction of grazing pressure resulted in a rapid morphological shift from a turf morphology to a foliose morphology in the alga *P. sanctae-crucis*. These results suggest that morphological plasticity may be common in the genus *Padina*. The morphological change (Figs 1–9) and increase in macroalgal cover (authors, personal observation) in response to herbivore exclusion supports the argument that herbivory is an important process controlling the morphology, abundance, and distribution of many tropical seaweeds (Hay 1981; Littler & Littler 1984; Lewis *et al.* 1987; Littler & Littler 1988; Coen & Tanner 1989; Steneck & Dethier 1994; Diaz-Pulido & McCook 2003). In addition to herbivory, there are other factors that may affect or that have been related to the morphological plasticity and abundance of algae in tropical ecosystems, such as light, wave exposure, temperature, nutrients, and life history stages (Littler & Littler 1988; Steneck & Dethier 1994; Diaz-Pulido & Garzón-Ferreira 2002). At our study site, it seems that herbivory is a critical process regulating morphological plasticity in the alga *P. boergesenii* but only during the dry, upwelling season.

The morphological response of *P. boergesenii* to herbivory was different in the two seasons, and this may suggest that morphological plasticity follows a seasonal pattern. As mentioned before, there was a significant shift in morphometrics during the upwelling, but we did not observe important form shifts when excluded from herbivores during the rainy season. This suggests that there are climatic and oceanographic factors (e.g. wind-driven upwelling, water temperature) limiting algal abundance and that these factors may mediate morphological plasticity of *P. boergesenii*, as has been suggested for the red alga *Rissoella verruculosa* in the Mediterranean (Benedetti-Cecchi *et al.* 2006). Therefore, reduction of grazing pressure is not enough to promote the foliose morphology. Foliose morphology apparently does not take place unless the environmental conditions (e.g. temperature and nutrients) are favourable during the upwelling. Algal populations and communities in the study area are highly seasonal, and such variation has been linked to climatic (wind) and oceanographic dynamics (temperature and salinity; Bula-Meyer 1990; Diaz-Pulido & Garzón-Ferreira 2002). During the rainy season, the



**Figs 6–9.** Length and width of *Padina boergesenii* thalli by herbivore treatment, date, and season. Data are means  $\pm 1 s_x$ ;  $n = 3$  plots.

**Fig. 6.** Length during the upwelling season, May 1997.

**Fig. 7.** Length during the rainy season, Aug.–Sep. 1997.

**Fig. 8.** Width during the upwelling season, May 1997.

**Fig. 9.** Width during the rainy season, Aug.–Sep. 1997.

abundance of algal populations is low, but it increases with the upcoming of relatively cold waters during the upwelling. The difference in plant response to herbivory according to season suggests an important link between natural history processes and environmental variability and illustrates that some environmental pressures (e.g. herbivory), when released, do not necessarily involve higher morphological development or morphological plasticity. There are additional factors that may be equally or more important (e.g. climatic and oceanographic) in regulating the abundance of tropical benthic algae.

Observations on herbivory at the studied reef indicated that the main macroherbivores are parrotfishes, surgeonfishes, and damselfishes, with some *D. antillarum* urchins. Preliminary results from a study looking at variations in grazing rates by parrotfishes, surgeonfishes, and damselfishes in the study area suggested that herbivory pressure is highly variable at small temporal scales (15 min), thus obscuring changes between seasons of the year. Despite this short-term variability, herbivorous fishes continuously grazed algal turfs during both seasons (Almanza *et al.* 1998). It is likely that the size of *P. boergesenii* was smaller during the rainy season because of increased herbivory or that the alga was in a dormancy state in the turfing form due to nonoptimal conditions during the

rainy season. These factors might explain the observed patterns. However, more intensive studies addressing the seasonality of grazing pressure and the relationship to life histories of tropical reef algae are required (Rogers *et al.* 1997).

Our experiment showed that *P. boergesenii* responded rapidly to changes in herbivory levels, particularly in thalli morphology and growth. Thus, thallus shape provides a field indicator of grazing status but only during the upwelling season, when narrow, turf-forming thalli indicate herbivory control, while broader blades indicate low herbivory pressure.

Morphological plasticity in *P. boergesenii* may have important ecological and evolutionary implications. It may be a strong adaptive strategy allowing the alga to thrive successfully in habitats with variable environmental pressures. These environmental pressures include high herbivory and adverse oceanographic conditions such as those occurring during the rainy season (e.g. high temperature or low water quality). Phenotypic plasticity in tropical and temperate algae has been suggested not only as a response to variable levels of herbivory, light and wave action (Steneck & Adey 1976; Lewis *et al.* 1987; Littler & Littler 1988; Fowler-Walker *et al.* 2006; Stewart 2006) but also as an important attribute of algae with high invasive potential (e.g. *Caulerpa*). Species of *Caulerpa* use resources opportunistically by modifying morphology and physiology, allowing them to colonise a wide range of habitats (Collado-Vides & Robledo 2002). Morphological plasticity may be an important trait contributing to the dominance of *P. boergesenii* in many tropical shallow reefs, like in our study area. The fact that after exclusion of herbivores *P. boergesenii* changed their phenotype to the nonresistance foliose one may suggest that herbivore-specific phenotype may be costly to maintain. However, energetic costs of maintaining the turfing morphology have not been explored.

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