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Padina pavonica: Morphology and Calcification Functions and Mechanism

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Abstract

Padina pavonica is one of the common macro-algae that inhabit coastal inter-tidal zones around the world. It is one of the two brown algae known to science today that calcifies. It precipitates $CaCO_3$ in the microscopy form of Aragonite needle shape seen macroscopically as a vertical ventral stripes. Here we will summarize the information available since the beginning of the 20th century, taking into consideration the algal distribution, macro and micro-morphology, cytology, reproduction, $CaCO_3$ bio-mineralization, and a slight reference to the commercial aspects, *i.e.*, its use in the medical and cosmetic industries. This paper discusses the likely advantages that *Padina* gains by the calcification and the effect of pH caused by global climate changes on this calcification. We will describe the distribution of *Padina*, while focusing on the morphology of *P. pavonica*, as described in the literature, occasionally comparing it to another common species in Tel-Baruch—*P. gymnospora*. This review is somewhat prolog for the upcoming research.

Keywords

Padina Pavonica, Morphology, Calcification, Reproduction

1. Getting to Know Padina

Padina pavonica is a brown alga from the Dichtyophyceae family, distributed from warm-temperate to tropical shores, at latitudes of ±30 worldwide, and growing mainly in the Mediterranean Sea and Atlantic Ocean [1] [2]. Today, according to ALGAEBASE.ORG, there are 72 species belonging to the genus *Padina*, most of which were only recently accepted taxonomically, but because of the similarity among them, it is hard to know for sure.

Along the Israeli shores, *Padina* sp. grows mainly on kurkar platforms (abrasion tables) [3], but it can also grow on sand-covered rocks [4]. The environment, whether rocky or sandy, is an extreme one, characterized by very turbulent water, variable salinity, high pH variation, high temperatures and occasional desiccation at ebb time [5]. This alga seems to thrive under such conditions.

Padina's life cycle is considered perennial, but the thallus detaches every winter and regrows in spring [6]. During winter, the alga stays in the form of rhizoids, filamentous thalli or sporelings, until the conditions are suitable for full regrowth [7]. Like most brown algae, it has a haploid-diploid reproduction cycle [8].

Padina is quite unique because it is one of the two calcified brown algae known today (the second one being *Newhousia imbricata*) [2] [9] [10]. $CaCO_3$ is precipitated in the form of needle-shaped aragonite crystals [11]. The aragonite is extra-cellular, mainly on the ventral surface of the thallus [12], and changes from needle shape into lumpy surface in the older part of the thallus, probably due to mechanical erosion [6].

P. pavonica has been well studied since the beginning of the last century and is, environmentally and medically, an important alga, extensively used as a feedstock for the production of biodiesel [13], in heavy-metal biosorption, as a pollution bioindicator [11], a trace metal biomonitor [14], an antioxidant [15], an anticancer drug (by inducing apoptosis of cancer cells) [16], an antibacterial agent [17], and a bioinsecticide [18].

2. Morphology

The *Padina sp.* body contains two parts: the thallus, which is divided into 8, and sometimes more (**Figure 1**), whitish to brownish color fronds, and the holdfast, consisting of flexible rhizoids for surface attachment [4]. The fronds are fan or ear shaped, and can reach up to 15 cm length in summertime, becoming narrower towards the base (**Figure 2(a)**), reaching up to 2 mm width and about 1 cm length [4]. In winter, they are very small or do not grow at all [4].

Figure 1. *Padina* fronds, taken from Shutterstock [44].

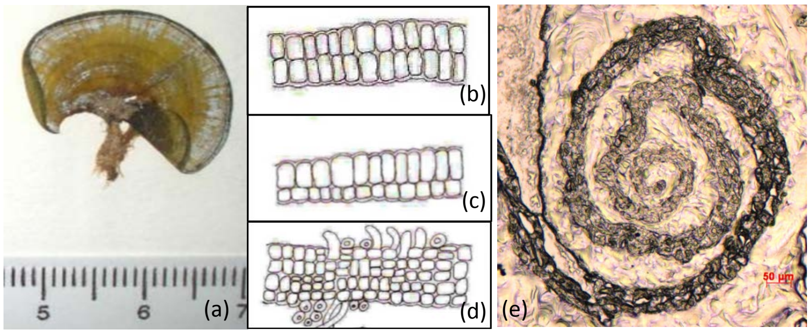

Figure 2. *P. pavonica* cell morphology: (a) The frond (Portuguese Seaweed Website [45]); (b) Transverse section of the upper cell layers; (c) Transverse section of the middle cell layer; (d) Transverse section of the cell layers next to the rhizoids. Scale bar 300 μm [4]; and (e) The inrolled apical margin of the thallus under Axio microscopy and according to the histology protocol.

The apical tip of the fronds is inrolled (**Figure 2(e)**) toward the ventral part of the thallus [11]. The rolling takes place because the dorsal side grows faster than the ventral one, thereby protecting the tender young cells [19]. The growth of the frond begins from a group of marginal meristem cells [9], and expands sideways [4] [20].

The apical region of different *Padina* species is 60 - 70 μm thick and consists of two cell layers, while the base is 90 - 115 μm thick and composed of three to six cell layers [12]. In the case of *P. pavonica*, the thallus is composed of up to three layers at its base [21].

Concentric hair bands 1 - 2 mm wide are found every 2.5 - 3 mm on both sides of the thallus [21], and are more prominent on the dorsal side [19]. Abbas and Shameel [22] found no such hair lines in the species *P. gymnospora* along the coast of Karachi, Pakistan, but Santhanam [23] described concentric hair in both species. *P. pavonica* hairs are 50 - 80 μm long, with a diameter of 6 - 9 μm, are composed of 6 - 12 cells [12], and grow from cells with large nuclei and dense cytoplasm (*P. pavonia*, Carter [19]). This happens to 4 to 8 closed cells at the same time, so that every hair area is composed of several rows [19]. These large condensed cells divide into long hairs, representing the beginning of the reproduction zone, and one of their functions is to protect the forming reproductive cells from sand [19]. The hairs can be broken off in the old thallus [19].

3. Cytology

The outer ventral layer of the thallus (the epidermis) which was measured on *P. pavonica* from Pakistan, contains several dense, brownish chromatophores called phaeoplasts [4]. The upper part is composed of barrel-shaped cells [11 - 23 μm wide (W)] (**Figure 2(b)**), and the lower part (**Figure 2(c)**) is composed of square (23 - 46 * 23 - 34 μm) or rectangular cells [4]. The second layer (the cortex) consist of 1 - 4 layers of large isodiametric, square (23 - 46 * 23 - 34 μm), rarely rectangular cells, set up in transversal rows and having fewer phaeoplasts than the epidermal layer [4].

Toward the holdfast, the peripheral cells change into rhizoidal filaments (**Figure 2(d)**) that attach to a solid surface, such us stone, or are embedded in sand, and the cells between them are double walled [4].

The outer ventral cells, which were measured on *P. pavonica* from Taiwan, are the smallest, *i.e.*, 19 - 38 µm length (L) and 25 - 40 µm height (H). The median cells are the largest, *i.e.*, 62 - 74 µm L and 25 - 45 µm H. The inner dorsal cells are equal or smaller to the middle cells, *i.e.*, 28 - 68 µm L and 25 - 30 µm H [12].

The apical cell line in the inrolled margin is surrounded by distinctly hair-line margins, about 0.4 µm thick each [24]. When an apical cell divides, it grows tangentially into two new daughter cells [19]. The walls of both the dorsal and ventral surfaces appear identical within the inward-rolled margin [24].

Chemically, the thallic tissue is composed of polysaccharides, such as alginates, fucoidans, and cellulose [25], and the phaeoplasts are composed of 14 pigments, including chlorophyll c1, c2, fucoxanthin, fucoxanthol, flavoxanthin, and diatoxanthin [26].

4. Reproduction

Most brown algae have a haploid-diploid life cycle (**Figure 3**) [8]. This is also the case with the genus *Padina*, which has two separate reproductive forms: fronds can have diploidic spores or haploidic gametes [20]. In *Padina pavonica*, fertile sporophytes are much more common than fertile gametophytes [27]. Sporangia are assembled in concentric dark sori, covered by an obvious indusium (a thin membrane that covers the reproduction cells), and arranged between the hair bands (**Figures 4(b)-(d)**). It seems that the indusium is related to the hair lines and covers them too [28].

The reproductive cells are found only on the dorsal side of the thallus [1] [9] [12], usually in an un-calcified area [27]. In *P. pavonica*, there are two stripes of

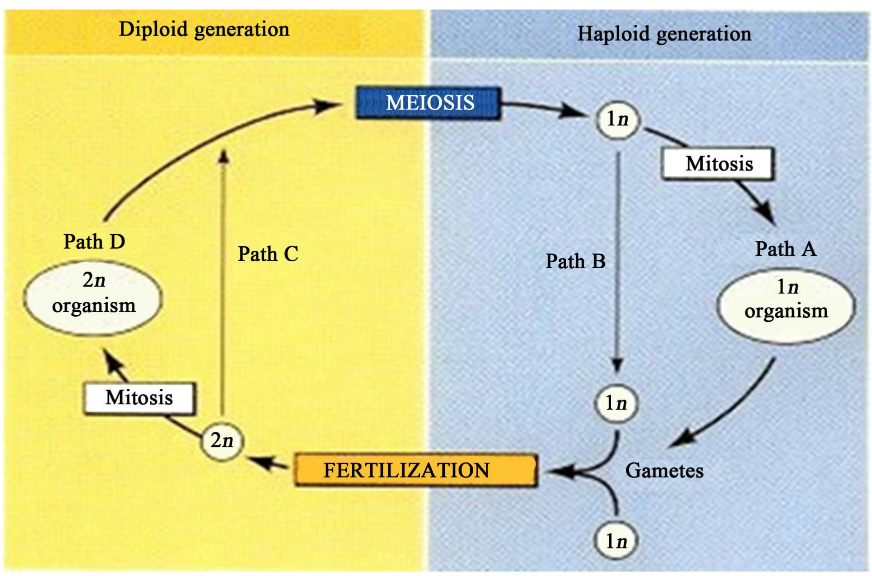

Figure 3. The reproductive haploid-diploid cycle in Phaeophyta [46].

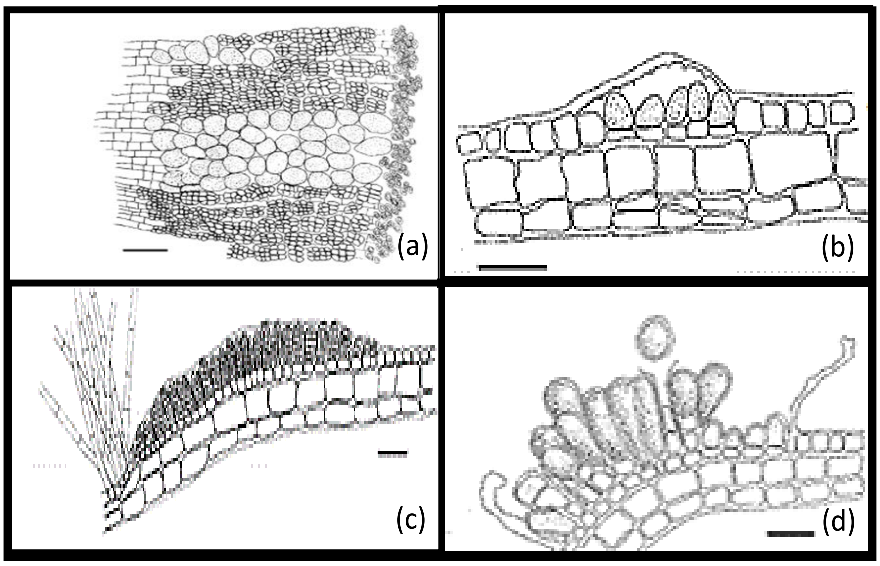

Figure 4. *P. pavonica* reproductive cells. (a) Radial section of monoecious sori; (b) Radial section of the indusium (arrow) over young oogonial sori; (c) Antheridial sori (with basal stalk cells and condensed hair); and (d) The indusium (arrows) torn over mature oogonial sori. Scale bar (a)-(d) 100 μm [27].

reproductive cells and, as seen in **Figure 5(a)** and **Figure 5(b)**, the upper (towards the apical end of the thallus) stripes are thicker than the lower ones, and are sometimes absent all together [20]. Each of the stripes contains perpendicular reproductive cell rows (**Figure 5(c)**) [27]. There is a gradient in the maturation of spores, *i.e.*, the lower stripes mature before the apical ones. These are either in the meiotic division stage or fully developed, while the apical spores are still in the stalk-cell division stage [19].

Gamete expression Specimens can be monoecious, bearing both oogonia and antheridia [9] [12] (**Figure 5(b)**). In such a case, as found in the coasts of south-east Asia and the Mediterranean, antheridia are oval-shaped, 23 - 80 * 57 - 80 μm, and have walls (**Figure 4(c)**) [9]. The oogonial cells are rounded to ovoid and measure 44 - 178 * 39 - 72 μm [27]. In *P. pavonica* from the Iberian coasts [27], the oogonial cells arranged in up to 4 rows, 8 - 10 oogonia per row, and the male sori in rows that contain 8 - 22 antheridia. Their shape can be either ovoid or rectangular, 39 - 78 * 28 - 50 μm. Approximately 2 mm of male gametophytes ends with approximately 90 μm or less of small oogonial sori (**Figure 4(a)**).

Padina can also be dioecious, with antheridia and oogonia on separate fronds [27] (**Figure 5(a)**). In dioecious fronds, female gametophyte sori are arranged in twin parallel stripes, approximately every 2.5 - 3 mm. The upper twin stripes, closer to the apical end, are 290 - 1350 μm wide, and the lower twin stripes, only 230 - 650 μm wide. The sori grow in rows perpendicular to the hair lines. The apical contains 8 to 18 oogonia per row (**Figure 5(c)**), while the lower stripes contain 8 oogonia per row [27]. The Antheridia sorus is white, cylinder-shaped, 23 - 46 μm in height and 18 - 33 μm in diameter, on a basal stalk cell 10 - 21 μm high, and a diameter of 10 - 26 μm [12]. The oogonia sorus is

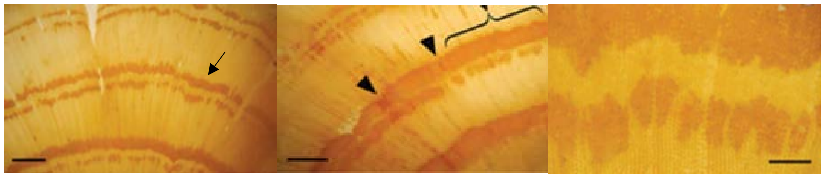

Figure 5. The sorus stripes of *P. pavonica*. (a) Dioecism, female thallus oogonia are arranged as two dark lines (arrow) [27]; (b) Monoecism, Antheridia ({) in between narrow oogonia (arrowheads) [27]. Scale bar (a) and (b), 2 mm; and (c) close-up of the sorus's perpendicular rows. Scale bar 400 μm.

brown, ovoid-shaped, 42 - 91 μm in height and 41 - 63 μm in diameter, with a basal stalk cell 5 - 20 μm in height and 30 - 48 μm in diameter [12].

It seems that temperature is an influential factor on the algal mode of reproduction: in warm waters, *Padina* tends to be mostly dioecious, while in cooler water it is predominantly monoecious. It is noteworthy that *P. gymnospora* appears to have only dioecious or tetrasporic expression [20] [29].

Both oogonia and antheridia originate from the division of cortical cells on a plane parallel to the front surface, and in the case of *P. pavonica*, covered with indusium, as seen in **Figure 4(b)** [27]. When the indusium is torn, it remains connected to the hair bands (**Figure 4(d)**) [28].

Spore expression - Spores can be up to 95 - 175 μm high and 55 - 100 μm in diameter [12]. They form up to 2 layers and have brownish filaments with phaeoplasts between them [9] [12]. The sporangia are born on a basal stalk cell, 6 - 22 μm H and 25 - 52 μm in diameter [12], and when it grows, it forms many-celled sporangia, each cell containing a single spore.

In some *Padina* sp., there is a stage known as the ***Vaughaniella*** stage, in which a prostrate rhizome develops into a branched phase and a new erect thallus. It seems that this stage is perennial, and is not affected by change of season [9] [30]. There are conflicting views among scientists regarding whether such a stage exists in *P. pavonica*. As seen in **Table 1**, Ni-Ni-Win *et al.* [27] consider *P. pavonica* as not having this stage, while Gómez Gómez *et al.* [28] claim that there is a Vaughaniella stage.

It seems that the algae invest more energy in reproduction than in growth, and in an environment that cannot sustain them for too long, *e.g.*, sandy beaches, the algae are smaller and have more gametophytes, because their survival time is shorter, and they can de-attached faster than on solid rocks [7].

5. Species Determination

Determination and identification of *Padina* species only by sight is difficult, and sometime even impossible. In the past, scientists determined if a species was new based on the following morphological features:

1) The structure, position, and arrangement of hair lines and reproductive sori;

2) The presence or absence of rhizoid-like groups of hairs and the presence or absence of indusium;

Table 1. Comparison of morphological features among three-layered species and the two new *Padina* species together with their genetically closest species *P. pavonica* [1]. The significant differences between *P. pavonica* and *P. pavonicoids* marked in red and *P. pavonica* characters are bolded. *According to Carter [19] and Ramon and Friedmann [20]; *pavonica* is dioecious.

Characteristics	*P. ditristromatica*	*P. pavonicoides*	*P. boergesenii*	*P. fraseri*	*P. tristromatica*	*P. pavonica*
			Vegetative characters			
			Thallus			
Shape	Flabelliform	Semicircular or circular	Flabelliform	Flabelliform	Flabelliform	**Semicircular or circular**
Calcification on lower/ upper surfaces	Moderate/heavy	No or light/light	Moderate/moderate	Light/heavy	No or light/light	**No or light/light**
			Number of cell layers			
Marginal portion (inrolled margin)	2 (2)	3 (2)	3 (2)	3 (2)	3 (2)	**3 (2)**
Middle portion	A mixture of 2 and 3	3	3	3	3	**3**
Basal portion	A mixture of 2 and 3	3	3	3	3	**3–4**
			Other characters			
Thickness of cell layers	Same thickness at 3-layer portion; and cells of upper layer twice as tall as those of lower layer at 2-layer portion	Same thickness from the margin to middle portion; central cell layer twice as tall as the surface layers at the basal portion	Cells of lower layer taller than those of upper layer; central cell layer shorter than the surface layers	Central cell layer tallest	Central cell layer shorter than the surface layers	**Central cell layer tallest at 3 layer portion; same thickness at 4-layer portion**
"*Vaughaniella*" *stage*	Absent	Absent	Present	Absent	Absent	**Absent***
			Hair lines			
Arrangement of alternating hair lines between both surfaces	Unequal distance	Equal distance	Equal distance	Equal distance	–	**Equal distance**
Hair lines (lower/ upper surfaces)	Conspicuous/ conspicuous	Moderate/ inconspicuous	Conspicuous/ conspicuous	Conspicuous/ conspicuous	Conspicuous/ inconspicuous	**Moderate/ inconspicuous**
Structures (lower/ upper surfaces)	Broad-depressed/ narrow-undepressed	Broad-slightly depressed/narrow-undepressed	Narrow-undepressed/ narrow-undepressed	Narrow-undepressed/ narrow-undepressed	–/narrow	**Narrow-undepressed/ narrow-undepressed**
			Reproductive characters			
Reproductive system	Dioecious	Dioecious	Dioecious	Dioecious	Dioecious	**Monoecious***
			Sporangial sori			
Position (surface)	Lower	Lower	Lower	Upper	Lower	**Lower**
Structure	Narrow	Narrow	Narrow	Broad	Narrow	**Broad above hair lines, narrow below hair lines**

Continued

Arrangement	Broken lines or patches; above hair lines	Patches; above hair lines	Continuous lines; above hair lines	Continuous or separated lines; between hair lines	Ccontinuous lines; -	**Continuous lines; both sides of hair lines (abutting hair lines)**
Number in row between hair lines	1	1	1	1 - 3		**2**
Location	Half immersed in the cuticle layer	On thallus surface	On thallus surface	On thallus surface	On thallus surface	**On thallus surface**
Fertile zone	Alternate[1]	Alternate[1]	Alternate[1]	Successive[2]	-	**Successive[2]**
Indusium	Present	Present	Absent	Present	Absent	**Present**
Reference			Allender and Kraft [40]	Womersley [41]	Levring [42]	Taylor [43]

[1]Fertile zone separated by sterile zone when both surfaces are viewed together. [2]Sterile zone absent.

3) The characteristics related to degree of calcification [1].

The reason for the difficulties in the identification is the lack of molecular data for the *Padina* species, which recently starting to become clearer as molecular data are starting to be added.

During the last few years, scientists have been using the RUBISCO gene sequence and the maternal *cox3* in order to understand the phylogeny and taxonomy of brown algae [1]. In their study, they identified two new species, one of them is *Padina pavonicoides*, which, according to Ni-Ni-Win *et al.* [1], differs from *P. pavonica* in some features, as shown in **Table 1**. The most significant differences are the monoeciousis, the arrangement of the sporangial sori in continuous lines, and the fact that they are on both sides of the hair lines [27], along with the successive fertile zone in *P. pavonica* [1].

From **Table 1** and from the cross-combination of the two sequences, *cox*3 and *rbcL*, the writers describe the two new species of *Padina*, and that the *P. pavonicoides* is a "sister" to *P. pavonica*. There was a 1.67% - 1.98% divergence between *P. pavonicoides* and *P. pavonica* in *rbcL* sequences, and 5.74% - 9.05% in *cox*3.

In a previous study by Lee and Bae [31], the Dictyotacheae family was divided into two tribes, Dictyoteae and Zonarieae, which according to the *rbcL* sequence and 18s rDNA suggest that *Padina* belongs to Zonarieae rather than the Dictyoteae tribe.

6. Calcification

Padina pavonica deposits needle-shaped aragonite crystals [11] [32] at the rate of approximately 240 $g \cdot m^{-2} \cdot y^{-1}$, which is higher than the other erect calcified algae [10] [32]. At the macro level, the aragonite settles as noticeable bright ventral stripes while the reproductive stripes are in the dorsal lower part, not always in correlation with the aragonite stripes [24]. There is more calcification on the ventral side of the algae than on the dorsal face, although at the margin area, it appears on both sides [24]. At the micro level, the aragonite needles are distributed randomly among the cells, *i.e.*, the intercellular space [24] [33]. The needles are up to 4 μm long and 0.4 μm wide, isolated from sea water by a utricle outer layer. It seems that the needles co-form along with the chloroplast and with the fusion of the utricle, which is closely appressed to the needles [33].

Calcification of the frond amounts to approximately 11% content by dry weight, and is slightly lower in the old and new areas of the thallus, peaking in the middle [24]. It seems that those areas, *i.e.*, mid-thallus, are more calcified than the margin and rhizoid areas [24], and that the aragonite crystals lose their needle shape in the older part of the thallus [33]. Calcification in the dark is slightly less than in the light [24], suggesting that photoperiods could be an influence. It seems to start in the inrolled edge, and since the chloroplasts also occur within this region, it implies an interaction between the initiation of the calcification and that of photosynthesis [24].

CO_2 concentration in the water, which has been increasing since the industrial revolution, lowered the pH levels by 0.1 unit compared with the preindustrial revolution values, and a further decrease of 0.3 - 0.4 units by the year 2100 is predicted [10]. At the coastline, there is also a diurnal fluctuation of pH, ranging from 7.5 up to 9.0. In general, low pH values result in decreasing calcium carbonate saturation levels, and cause sea organisms in general, and *Padina* in particular, to decalcify. The same occurs near underwater CO_2 vents, where the aragonite spines get thinner [10]. *Padina* does not seem to have a problem growing in acid conditions, like those found next to the Panarea vent [34]. In spite of the low pH induced decalcification, it shows resilience under acute pH changes, and this resilience makes it a suitable bioindicator of ocean acidification (OA) in coastal habitats [32]. This resilience occurs because the saturation levels of aragonite in the water is lower (Ω aragonite is 3 - 4, high Ω = low saturation levels) than the magnesium calcite levels (Ω calcite 2 - 3, low Ω = high saturation levels), *i.e.*, it needs less Ca^{2+} saturated in the water to precipitate aragonite than it needs to precipitate calcite, meaning that *Padina* is more resilient to pH changes than calcite precipitating organisms, such us corals and some plankton [10]. In addition, in the presence of Mg^{2+}, as well as other doubly charged ions in the water, the formation of an aragonite form of $CaCO_3$ is more favored than the formation of calcite [35] [36].

7. Calcification under Low pH

At low pH, the aragonite morphology changes until it completely dissolves [6]. Even the calcified epiphytes (*e.g.*, Foraminifera) that grow on the fronds decalcify at low levels of pH caused by high CO_2 levels [6]. Gil-Díaz *et al.* [32] suggested that the calcification process does not stop and that pH levels will dictate only whether the $CaCO_3$ dissolves or calcifies. This implies that the calcification process, though not an obligatory one, is an ongoing process.

When exposed to a low pH environment, along with decalcification, the alga releases phenolic compounds from its cells. It has been suggested that these two responses to acidification make *Padina* more vulnerable to grazers, since reduced $CaCO_3$ makes the alga more palatable, and less phenol makes the thallus more tasty [32].

8. Photosynthesis Related to $CaCO_3$

As ocean acidification progresses and pH levels decrease, photosynthesis rates increase, probably due to the increased availability of CO_2 [10]. Under OA, *P. pavonica* undergoes decalcification, concomitantly losing photo-protective phenolic compounds and decreasing its antioxidant activities [37]. Such processes were also described regarding non-calcareous algae, but unlike them, *P. pavonica* increases its light saturation intensity in order to adjust to the acidic environment [37].

9. The Potential Benefits of $CaCO_3$

Over the years, there have been several suggestions regarding the benefits of *Padina* sp. calcification. Okazaki *et al.* [24] suggest that it gives the algae mechanical support in their high-energy environment, whereas Gil-Díaz *et al.* [32] think that calcification offers protection against grazers. Padilla [38] suggests that it is not protection directly against grazers, but against the tissue damage inflicted by the grazers. Burger and Schagerl [39] suggest that calcification provides protection from excess irradiance [10].

It is possible that all these suggestions are correct and that there is a synergy among the $CaCO_3$ benefits, contributing to the success of *Padina* in her rough habitat.

10. Epilog

In summing up this review, we see a remarkable species that is well-adapted and adjusted to extreme surroundings by benefitting from a particular morphologic phenomenon, *i.e.*, the ability to calcify aragonite needles. This ongoing research underscores the hitherto uncharted aspects of the ecophysiology of *Padina*, such as its optical photoprotective properties and its calcification periodicity.

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