Book Chapter

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 in- ter-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 mi- cro-morphology, cytology, reproduction, $CaCO_3$ bio-mineralization, and a slight reference to the commercial aspects, *i.e.*, its use in the medical and cos- metic 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

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 *Pa- dina*, 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 (abra- sion 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 turbu- lent 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 win- ter and regrows in spring [6]. During winter, the alga stays in the form of rhizo- ids, filamentous thalli or sporelings, until the conditions are suitable for full re- growth [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].

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 nar- rower 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].

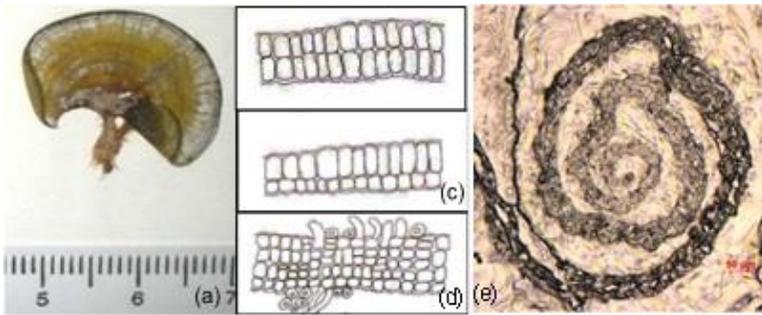Figure 1: *Padina* fronds, taken from Shutterstock [44].

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 repro- ductive cells from sand [19]. The hairs can be broken off in the old thallus [19].

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 cor- tex) 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 algi- nates, fucoidans, and cellulose [25], and the phaeoplasts are composed of 14 pigments, including chlorophyll c1, c2, fucoxanthin, fucoxanthol, flavoxanthin, and diatoxanthin [26].

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 reproductive cells and, as seen in **Figure 5(a)** and **Figure 5(b)**, the upper (to- wards 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 perpendicu- lar reproductive cell rows

(**Figure 5(c)**) [27]. There is a gradient in the matura- tion of spores, *i.e.*, the lower stripes mature before the apical ones. These are ei- ther in the meiotic division stage or fully developed, while the apical spores are still in the stalk-cell division stage [19].
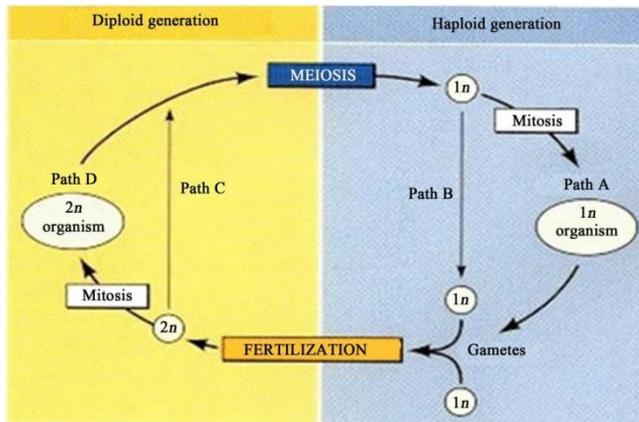

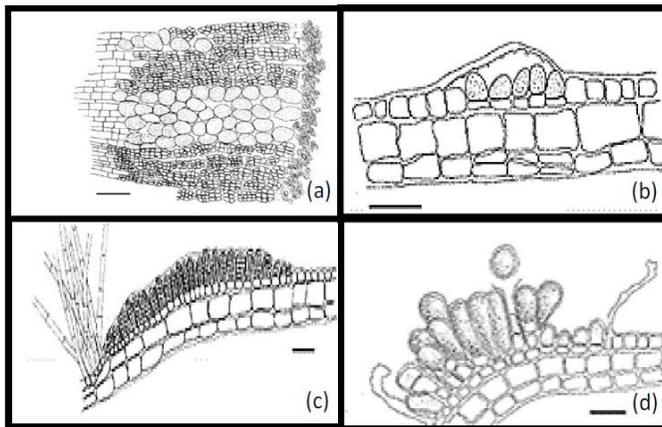**Figure 3:** The reproductive haploid-diploid cycle in Phaeophyta [46].

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 oogoni- al sori. Scale bar (a)-(d) 100 μm [27].

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, cylind- er-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 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].
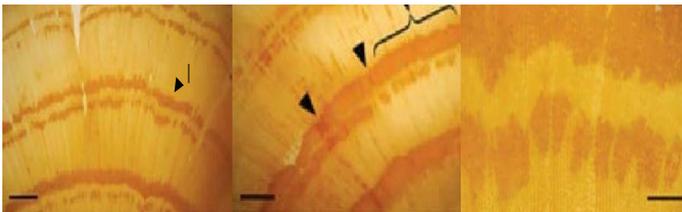

Figure 5: The sorus stripes of *P. pavonica*. (a) Dioecism, female thallus oogonia are ar- ranged as two dark lines (arrow) [27]; (b) Monoecism, Antheridia ({) in between narrow oogonia (arrowheads) [27]. Scale bar (a) and (b), 2 mm; and (c) close-up of the sorus's perpendicular rows. Scale bar 400 µm.

It seems that temperature is an influential factor on the algal mode of repro- duction: in warm waters, *Padina* tends to be mostly dioecious, while in cooler water it is predominantly monoecious. It is noteworthy that *P. gymnospora* ap- pears 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 thal- lus. 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 beach- es, 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].

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;
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 se- quence and the maternal *cox3* in order to understand the phylogeny and tax- onomy 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 con- tinuous 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. pavoni- coides* 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 Dictyo- teae tribe.

Calcification

Padina pavonica deposits needle-shaped aragonite crystals [11,32] at the rate of approximately 240 g·m^{-2}·y^{-1}, which is higher than the other erect calcified algae [9,32]. 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 in- fluence. It seems to start in the inrolled edge, and since the chloroplasts also oc- cur within this region, it implies an interaction between the initiation of the cal- cification 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 carbo- nate saturation levels, and cause sea organisms in general, and *Padina* in partic- ular, to decalcify. The same occurs near underwater CO_2 vents, where the arago- nite 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 ara- gonite 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 le- vels), *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].

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 decal- cify at low levels of pH caused by high CO_2 levels [6]. Gil-Díaz *et al.* [32] sug- gested 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 re- duced $CaCO_3$ makes the alga more palatable, and less phenol makes the thallus more tasty [32].

Photosynthesis Related to CaCO3

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 phe- nolic compounds and decreasing its antioxidant activities [37]. Such processes were also described regarding non-calcareous algae, but unlike them, *P. pavoni- ca* increases its

light saturation intensity in order to adjust to the acidic environment [37].

The Potential Benefits of CaCO3

Over the years, there have been several suggestions regarding the benefits of *Pa- dina* sp. calcification. Okazaki *et al.* [24] suggest that it gives the algae mechani- cal 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 protec- tion 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.

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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