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Developmental morphology of *Acanthophora nayadiformis* (Rhodophyta, Ceramiales): Sympodial growth and propagule germination

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Abstract

The *A. nayadiformis* thallus is peculiar due both to its morphological organization and to the production of specialized vegetative propagules resembling turions of aquatic dicotyledons. Propagules have proved to be useful culture inocula for morphogenetic research. They germinate quickly when cultured under optimal conditions, growing in a polar fashion, producing uprights from their distal buds and axes with rhizoids from the proximal ones. The thallus growth pattern in *A. nayadiformis* at first involves a monopodial arrangement of determinate branches followed by ramisympodial growth at all thallus levels with an unpredictable model. There is not, in fact, a fixed 'sympodial unit' which reiterates itself in the ramisympodia, thus giving rise to great morphological diversity. Both irradiance and temperature have a significant effect on propagule bud growth rate, but not on their developmental morphology. In contrast, changes in the apex morphogenetic trend, such as transformation from the stolon apex into the upright kind and sympodial growth, are promoted by long-day conditions and largely suppressed under short-day regimes. The short-day inhibition of upright growth seems to be a specialized mechanism for over-wintering in a resistant vegetative phase.

Key words: Acanthophora, *Ceramiales, daylength, propagule, seaweed morphology, sympodium.*

Introduction

Acanthophora nayadiformis (Delile) Papenfuss (Rhodophyta, Ceramiales), the only species of the genus occurring in the Mediterranean Sea, is a perennial species that at our latitude is present in winter and spring with the prostrate rhizomatous system only; the upright fronds sprout in May–June and grow until October when they begin to decay (Cecere et al., 2000).

A. nayadiformis has proved to be an interesting taxon because of the morphological organization of its thallus and the production of specialized vegetative propagules. Since the Ceramiales have uniform reproductive features, morphological characters are crucial for diagnostic and taxonomic investigation. A detailed study carried out by Cecere and Perrone (2002) on the morphology of *A. nayadiformis* from the Gulf of Taranto highlighted that the great morphological variability of the thallus was caused by sympodial branching taking place at all thallus levels. Moreover, different kinds of buds with distinct origin and development can contemporarily be present on the same thallus.

While sympodial branching in vascular plants concerns the organization of whole organs (i.e., inflorescences and branches) in the dasyacean thalli it has been described at the cellular level (Parsons, 1975). Norris and colleagues (1984) proposed the term 'cellulosympodial' for this kind of growth. On the contrary, they defined as 'ramisympodia' branch systems made by a series of determinate axes arising from intercalary positions on determinate branches, as described in some Crouanieae (Ceramiaceae) and Delesseriaceae.

Among the Rhodomelaceae, sympodial growth was observed for the first time in *A. nayadiformis* (Cecere & Perrone, 2002), whereas it is well known in the Ceramiaceae, Dasyaceae and especially Delesseriaceae (Ceramiales) (Wynne & Daniels,

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1966; Wollaston, 1968; Gordon-Mills & Kraft, 1981; Womersley & Shepley, 1982; De Clerk et al., 2002). In the Rhodomelaceae, a few species have been described as having a growth pattern resembling sympodial growth (Falkenberg, 1901; Hommersand, 1963; Wynne, 1985; Masuda & Selivanova, 1989; Masuda et al., 1998), but such a growth pattern has been misinterpreted due merely to an overtopping of the main axis by laterals with more rapid growth.

Vegetative propagules have been described in a few floridean species, mostly Ceramiales (Hawkes, 1990; Murray & Dixon, 1992), but none are homologous to the *A. nayadiformis* propagules. Similar propagules are not present in the other species of the genus, and were found in the *exiccata* of *A. nayadiformis* from all geographic areas. Therefore, they have been proposed as a taxonomic character at species level (de Jong et al., 1999; Cecere & Perrone, 2002).

On the basis of both field observations and *in vitro* propagule cultures, this work aims to investigate the developmental morphology of *A. nayadiformis*, and the factors that could act as triggers for the intervening sympodial growth. For the best understanding of the terminology used in describing the results of this research, both definitions and descriptions previously reported in the literature will be summarized together with the new observations.

Materials and methods

Field observations

Monthly collections were carried out by SCUBA diving from January to December 2000 from the attached populations of *A. nayadiformis* at the Cheradi Islands (Mar Grande, Taranto, Italy, 40°28′ N, 17°13′ E, Ionian Sea). Samples were preserved in 5% formalin – seawater and brought to the laboratory, where both their morphological characteristics and developmental dynamics were observed. Representative specimens are kept in the herbarium of IAMC CNR-Taranto Section.

Cultures

Propagule-bearing thalli were collected between July and August 2003; infertile specimens were selected for the experiments. Mature propagules, useful as culture inocula, detached spontaneously, and were deposited on the bottom of the vessel.

Experimental material was incubated for 1 – 2 min in 0.5% POVIDONE (polyvinylpyrrolidone-iodine complex) (Smit & Bolton, 1999) then rinsed in sterile seawater, incubated for 10 min in 50 ppm chloramphenicol, then rinsed again in sterile seawater.

Preliminary cultures were performed to assess how light and temperature could affect the growth rate of propagule primordia. As an experimental unit, 16 propagules in 200 ml Petri dishes (mean wet weight: 22.4 mg) were chosen; four replicates for each test were prepared. Plain seawater from the collection site, filtered through Millipore filters (MF – 3μ), was used as the base of the culture medium; 0.1 mM NH_4NO_3 as an enrichment, and 6 ppm GeO_2 to control diatom proliferation were always added (Lewin, 1966). The medium was replaced every 4 d; cultures were run for 40 d in growth chambers under fluorescent light (Cool-White 40 W tubes); PAR was measured by means of a QRT1 light and temperature sensor (Hansatech, UK).

To evaluate the individual effects of both light intensity and temperature on propagule germination, the experimental units were kept in culture (two separate experiments) under the following conditions: (i) 26°C ± 1°; 15, 30, 60 or 120 μmol m^{-2}s^{-1} PAR (the maximum value in our growth chambers); 16 h:8 h light-dark photoperiod; (ii) 10, 18, 26, 34°C ± 1°; 120 μmol m^{-2}s^{-1} PAR; 16 h:8 h light-dark photoperiod.

This long-day photoperiod corresponded to the natural one during the *A. nayadiformis* life cycle at the collection site. The wet weight of each experimental unit was measured every week using a triple beam balance; the % Daily Growth Rate (DGR) was calculated according to the following formula: DGR = ln (Nt/No) x 100 / t. Data were analysed with one-way ANOVA, and differences between the variables were determined by Fischer's Least Significance Difference (LSD).

Both long day (LD) and short day (SD) cultures were performed with the aim of evaluating the morphogenetic effects of the daylength. Culture conditions were as follows: (i) SD cultures: 8 h:16 h light-dark photoperiod; 120 μmol m^{-2}s^{-1} PAR; 26°C ± 1°; (ii) 12 h:12 h cultures: 120 μmol m^{-2}s^{-1} PAR for the first 8 h, and 10 μmol m^{-2}s^{-1} PAR for the remaining 4 h; 26°C ± 1°; (iii) LD cultures: 16 h:8 h light-dark photoperiod; 120 μmol m^{-2}s^{-1} PAR for the first 8 h, and 10 μmol m^{-2}s^{-1} PAR for the remaining 8 h; 26°C ± 1°.

PAR at 10 μmol m^{-2}s^{-1} was chosen as a value lower than the compensation irradiance in *A. nayadiformis* (Petrocelli & Felicini, 1997) to exclude the effect of light quantity. Propagules were grown for 60 d. At the end of the experiment, both stolon apices which turned into the upright kind and those that shifted to the sympodial kind were counted. The homogeneity of the response in terms of apex transformations to different light regimes was statistically evaluated by the chi-squared test.

Both morphological and anatomical observations were carried out on fresh material, liquid preserved specimens and cultured thalli. Sections were made by hand or on a Leitz Kryomat microtome (Ernst Leitz Gmbh®, Wetzlar, Germany). Sections were stained with 1% aniline blue acidified with 0.5% HCl, and mounted with 50% glycerol–seawater. Slide preparations were observed under an Olympus BX–41 microscope (Olympus, Melville, NY, USA) and photographed with a digital camera (Nikon Coolpix 990).

Results

The sympodial construction of the thallus

A. nayadiformis (Figure 1) grows uni-axially from a dome-shaped transversely dividing apical cell. A monopodial pattern of growth controls development of the entire first basal part of the plant; lateral branches are of two kinds, determinate and indeterminate. Determinate laterals, trichoblasts and spines, originate from every segmental cell according to a one-fourth right-handed spiral. Trichoblasts are deciduous colourless mono-siphonous laterals pseudo-dichotomously branched (Figure 2); early in development, but after the periaxial cell formation, their basal cells give origin to the second kind of determinate branches, the so-called 'spines' (Figure 3). These are polysiphonous laterals, subulate when young, approx. 1 mm long, and divergent at right angles to the axis when mature (Figures 4, 5, 7, 10). There are few indeterminate lateral branches of first order, 2–3, originating early from the basal part of the main axis; those of second, and rarely of third order, form in the axils of every spine from primordia identical to the terminal bud, and develop like the main axis (Figure 5). Axillary branches are always spirally arranged according to the arrangement of both trichoblasts and spines.

In most thalli the growth pattern of both the main axis and lateral branches shifts to the sympodial, but with an unpredictable model. Buds able to develop into branches that substitute main axes and initiate sympodial growth are not the axillary buds as in flowering plants, but those endogenously generated on the adaxial side of the last-formed (youngest) spine and termed 'spiny primordia' (cf. Cecere & Perrone, 2002) (Figure 6).

While the first spiny bud is forming, the main apex aborts. Once initiated, sympodial growth characterizes all subsequent development of the distal two tiers of the thallus. There is not, however, a fixed 'sympodial unit' that reiterates itself in the ramisympodia, thus giving rise to the great morphological diversity of the *A. nayadiformis* thalli. The sympodial units continuing the main axis growth (the 'continuation shoots', according to the flowering plant terminology) can be axes bearing 1–4 or more spines (Figure 4). Lateral spiny buds, arising secondarily from some or all mature spines, may also develop into either elongated or short branches, that can in turn branch (Figure 7). Lateral sympodial branches are usually spirally arranged when every spine forms its own spiny bud (Figure 8). When they arise alternately on only two spines of opposite orthostichies, the axes appear quite distichous with respect to the second order branches (Figure 9). A subtending spine can bear a single bud, an axillary monopodial bud, or a spiny sympodial one; the simultaneous presence of both buds has never been observed. As the sympodial units grow successively, they become shorter and shorter, so that the distal parts of the thallus appear crowded.

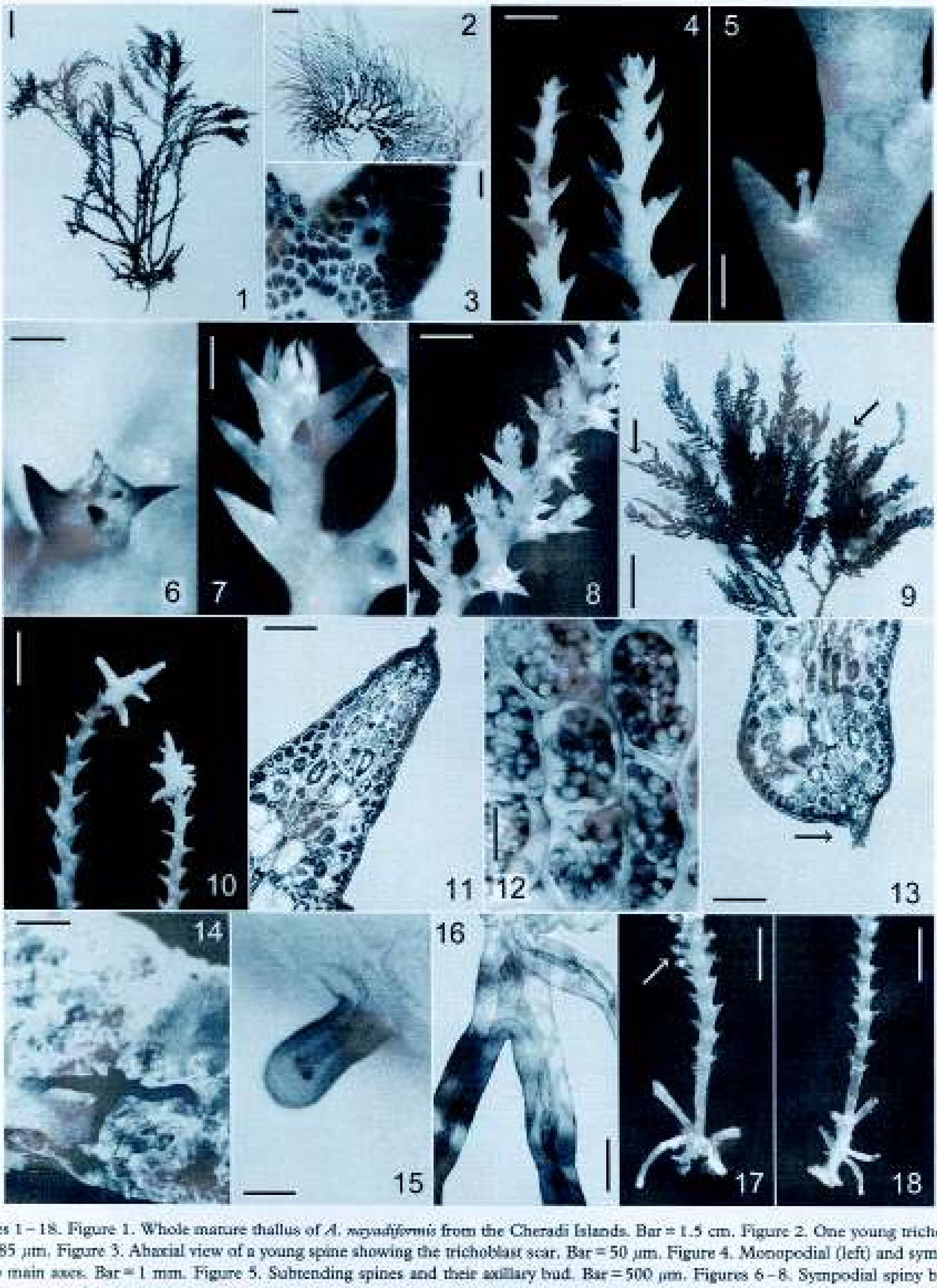
Other indeterminate branches can form secondarily on mature plants; they originate from distinct terete buds near the base of the spines (extra-axillary), and develop monopodially into terete spineless stolons with blunt apices. The gross morphology of *A. nayadiformis* can be further complicated by a number of adventitious ramisympodia regenerated from broken thallus parts.

Propagule structure and germination

Propagule production occurs early in thallus development, since propagules are already present on young monopodial branches. On mature thalli most propagules form from sympodial branches. Both gametophytes and tetrasporophytes produce propagules to the same extent.

The *A. nayadiformis* propagules are apical parts modified as swollen cone-shaped darkly pigmented bodies. Propagules bear up to 5 dwarf spines and as many terete primordia of stolons, while the main apex is also transformed into a terete bud. Mature propagules measure 1–1.5 mm in length and 400–600 μm in diameter (Figure 10). Their structure is basically the same as that of the thallus (Figure 11), however the inner cortical cells are bigger and filled with large floridean starch granules (Figure 12). Their basal poles are abruptly constricted and end in an abscission zone consisting of elongated hyaline cells (Figure 13).

Propagules are undoubtedly suitable structures to ensure prompt attachment onto the substratum (Figure 14). In summer–autumn their germination occurs soon after their abscission, while propagules shed in late autumn over-winter in a fairly dormant state and, in May–June, begin to germinate just as the new frond begins to sprout from the perennial bases (cf. Cecere & Perrone, 2002). In the field, plantlets derived from propagules are distinguishable from sporelings by the way in which they attach to the substratum. The first are attached by means of rhizoids arising from stolons (Figures 15–17), the second form an attachment disk which becomes



Figures 1 – 18. Figure 1. Whole mature thallus of *A. nayadiformis* from the Cheradi Islands. Bar = 1.5 cm. Figure 2. One young trichoblast. Bar = 85 μm. Figure 3. Abaxial view of a young spine showing the trichoblast scar. Bar = 50 μm. Figure 4. Monopodial (left) and sympodial (right) main axes. Bar = 1 mm. Figure 5. Subtending spines and their axillary bud. Bar = 500 μm. Figures 6 – 8. Sympodial spiny buds in different stages of development. Figure 6, bar = 200 μm; Figure 7, bar = 500μm; Figure 8, bar = 2 mm. Figure 9. Pseudo-distichous pattern of branches (arrows). Bar = 2 cm. Figure 10. Apices transformed into propagules. Bar = 1.2 mm. Figure 11. Longitudinal section of the distal part of a propagule. Bar = 200 μm. Figure 12. Inner cortical cells filled with large floridean starch granules. Bar = 150 μm. Figure 13. Longitudinal section of the proximal part of a propagule. Arrow indicates the abscission zone. Bar = 200 μm. Figure 14. Propagule in the field attached to the natural substratum. Bar = 800 μm. Figure 15. Budding of a rhizoid from a stolon outer cortical cell. Rhizoid remains in open connection with its mother cell. Bar = 10 μm. Figure 16. Tri-furcate rhizoid. Bar = 8 μm. Figure 17. Wild plantlet from propagule. Arrow indicates sympodial growth. Bar = 1.5 mm. Figure 18. Wild sporeling. The plantlet is still entirely monopodial. Bar = 1.5 mm.

corticated (Figure 18). The growth patterns of the two kinds of germlings are the same, with a short terete stipe continued by a monopodial axis. Sympodial growth is detectable in the sporelings when thalli are about 3 – 4 cm long, usually in June – July, whereas apices of plantlets from propagules shift to sympodial growth and branch earlier, when axes are about 2 cm long (Figure 17).

In culture, propagule germination starts with the development of the pre-existing terete buds that develop as terete naked stolons for 0.3 – 0.5 cm (Figure 19). The blunt apices of the most distal axes soon start to produce primary determinate branches, trichoblasts and spines, becoming apices of upright fronds. Sooner or later the youngest spines initiate sympodial branching from endogenous spiny buds. Axes from the proximal part of the propagule continue their growth as terete irregularly branched stolons, usually producing rhizoids (Figure 20).

Both irradiance and temperature had a significant effect on propagule bud growth rate (Tables I and II), but had little effect on their developmental morphology. Growth rate was proportional to both temperature and irradiance; the differences between the tests were highly significant ($p < 0.0001$). Analysed data did not show differences between the replicates. Both low temperature and low irradiance strongly limited growth; at 10°C and at 15 μmol $m^{-2}s^{-1}$ PAR, growth increments did not reach 50%. Under these conditions, the axes did not grow in length enough to transform into uprights. By contrast, the highest irradiances tested led to the transformation of the apices of the proximal stolons into uprights. At the highest irradiance used and at 26°C, a % DGR > 4 was observed.

During germination, the propagule body became slender and, after approx. 15 d, starch granules disappeared. Sometimes, new propagules were precociously produced by young 'germlings' growing in all the conditions supporting apical transformation (Figure 21).

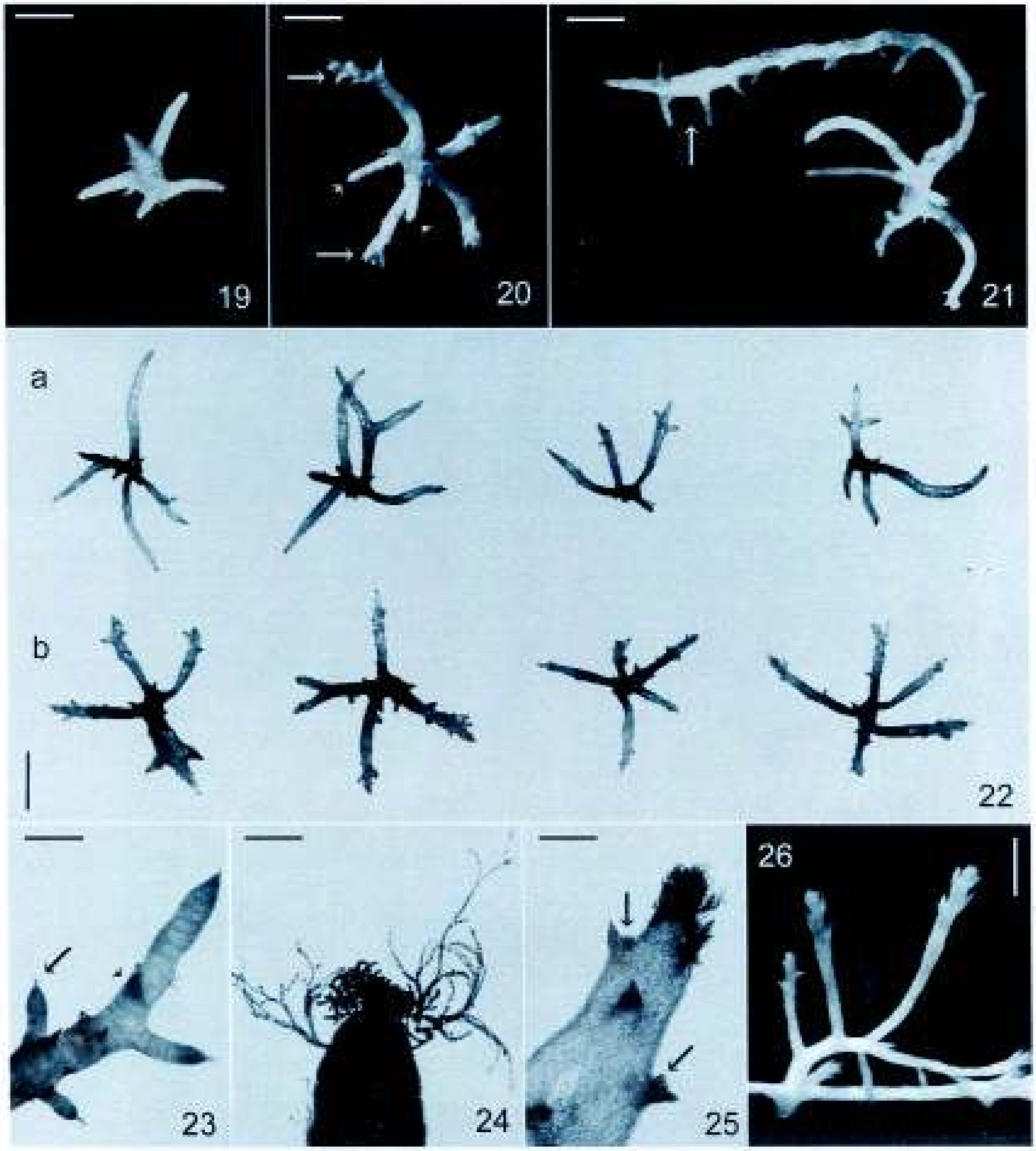
The results of the different daylength regimes tested are shown in Table III. In the four replicates of each experimental unit, a homogeneous photoperiodic response was obtained ($\chi^2 = 1.531$; $p = 0.6751$). Therefore, data were put together into a contingence table, and the chi-squared test was performed in order to evaluate the effect of the three different photoperiods on apex differentiation. In both SD and 12 h:12 h cultures, stolon apices rarely changed into the upright kind (Figures 22a, 23); results were not significantly different ($\chi^2 = 1.6716$; $p = 0.1960$). In LD cultures, on the other hand, almost all the apices were transformed into the upright kind (Figures 22b, 24, 25), and a high percentage of them (89.3%) very soon initiated sympodial growth, even from the first spine born. By transferring SD grown plantlets to the LD regime, apices very soon turned into the upright kind (Figure 26).

Discussion

As regards their ontogeny *A. nayadiformis* has a peculiar kind of ramisympodia, never before observed in other macroalgal thalli. A distinctive type of bud, the 'spiny primordium', is able to establish sympodial branching; it forms endogenously in the adaxial side of a spine from the fifth pericentral cell, the last formed in the branch. It should be noted that the origin of this bud is the same as that of the carpogonial branch in *Acanthophora* (Cecere & Perrone, 2002).

A great diversity characterizes ramisympodium development and arrangement, because there is no unique sympodial unit reiterating itself in both main and lateral axes. In *A. nayadiformis*, sympodial branching leads to specimens being more robust and branched, thus increasing their photosynthetic efficiency under various light conditions. Other than the Ceramiales, very few taxa really show ramisympodial growth such as *Plocamium* Lamouroux (Plocamiales) (Womersley, 1971) and *Lomentaria umbellata* (Hooker et Harvey) Yendo (Rhodymeniales) (Hooker, 1855, as *Chylocladia umbellata* Hooker et Harvey; Adams, 1994). In these genera, the sympodial unit shows heteroblastic growth and reiterates itself, as in some Delesserioideae such as *Kurogia* Yoshida and *Zinovaea* Wynne (Yoshida, 1979), and *Sympodophyllum* Shepley et Womersley (Shepley & Womersley, 1960). Genera such as *Nereiginpha* Kylin (Dumontiaceae) (Kylin & Scottsberg, 1919) and *Nereocaulon* Zanardini (Furcellariaceae) (Zanardini, 1865; Codomier, 1967) have also been described as sympodially branched. Their thallus is constructed by cylindrical axes bearing determinate amplexicaul leafy branchlets. The growth pattern resembles that of most monocotyledons, in which the last leaf overtops the tip, but there is no true evidence of aborting main apices.

Among the cormophytes, there are no similar models of development, except the 'fuzzy' morphology of the aquatic riverweeds Podostemaceae, in particular *Tristicha trifaria* (Bory ex Willd.) Spreng. and *Indotristicha ramosissima* (Wight) van Royen. These are alga-like plants with a body often described as a thallus. Many scientists regard the podostemads as not fitting into the classical root-shoot model (CRS model) of angiosperms (Rutishauser, 1997), while others recognize homologies with the corresponding organs of the angiosperms and detail the unusual sympodial growth of the above species (Jäger-Zürn, 1997). Some analogies with podostemad organography can be recognized in the



Figures 19 - 26. Propagule germination in culture. Figure 19. Initial step of stolon development. Bar = 1.2 mm. Figure 20. Fifteen-day old germinated propagule (top view). Distal apices are transformed into the upright kind and some of them are already sympodial (arrows); proximal apices continue to grow as stolons (arrowheads). Bar = 1.2 mm. Figure 21. Germinated propagule that has precociously formed a new propagule (arrow). Bar = 1.2 mm. Figure 22. (a) Fifteen-day old SD grown plantlets from propagules; all the axes are stolons. (b) Fifteen -day old LD grown plantlets from propagules; most of the axes are uprights shifting into sympodial growth. Bar = 3 mm. Figure 23. Magnification of a SD grown plantlet axis (stolon). Note the few short trichoblasts (arrows) and the dwarf spines (arrowheads). Bar = 300 μm. Figure 24. Magnification of an apex of the upright kind with typically well developed trichoblasts. Bar = 100 μm. Figure 25. Magnification of a LD grown plantlet axis with trichoblasts, spines and axillary buds (arrows). Bar = 300 μm. Figure 26. Sixty-day old SD grown plantlet transferred to a LD regime for 10 days. Note the transformation of the apices into the upright sympodial kind. Bar = 1.2 mm.

A. nayadiformis thallus organization. As in *Tristicha trifaria* and *Indotristicha ramosissima* the 'ramuli', which represent the distal parts of sympodial branches, are regarded as subtending leaves bearing axillary buds; similarly, in *A. nayadiformis* the 'spines' could be regarded as either homologous subtending leaves bearing monopodial axillary buds or as branches bearing sympodial intercalary buds.

Vegetative propagules have proved to be useful culture inocula for morphogenetic research in *A. nayadiformis*. When cultured under optimal culture conditions they 'germinate' quickly; their buds grow

Table I. Effect of temperature on propagule growth (mg_{ww}) (initial biomass = 22.4 ± 2.8 mg_{ww}) after a 40-day culture at 120 μmol m^{-2} s^{-1} PAR and 16 h:8 h light-dark regime. In parentheses are the confidence limits at $p = 0.01$ ($n = 64$).

	Temperature (°C ± 1°)			
	10	18	26	34
Mean biomass	27.9 (± 3.9)	75.8 (± 8.4)	129.0 (± 11.4)	111.7 (± 17.2)
% Increase	24.55	238.39	475.89	398.66
% DGR	0.549	3.047	4.377	4.017

Table II. Effect of irradiance on propagule growth (mg_{ww}) (initial biomass = 22.4 ± 2.8 mg_{ww}) after a 40-day culture at 26°C and 16 h:8 h light-dark regime. In parenthesis are the confidence limits at $p = 0.01$ ($n = 64$).

	PAR (μmol $m^{-2}s^{-1}$)			
	15	30	60	120
Mean biomass	31.8 (± 4.2)	72.8 (± 7.1)	95.2 (± 9.1)	126.6 (± 8.8)
% Increase	41.96	225.00	325.00	465.18
% DGR	0.876	2.946	3.617	4.329

Table III. Effect of day length on apex transformation after a 60-day culture ($n = 64$).

Light-dark regimes	N° total apices	N° upright apices	% Sympodial apices
8 h:16 h (SD)	271	1	0
12 h:12 h	270	3	0
16 h:8 h (LD)	280	268	89.3

in a polar fashion as do those of vascular plant scions, producing uprights from distal parts and stolons from the proximal ones. A similar polarity has been previously described in the regeneration of thallus explants from *Pterocladiella capillacea* Santelices et Hommersand (Gelidiaceae) (Felicini & Perrone, 1994, Felicini et al. 2002), *Schottera nicaeensis* Guiry et Hollenberg (Phyllophoraceae) (Perrone & Felicini, 1972, as *Petroglossum nicaeense* (Duby) Schotter; Perrone & Felicini, 1981), *Chondrachantus acicularis* (Roth) Fredericq (Gigartinaceae) (Perrone & Felicini, 1976, as *Gigartina acicularis* (Wulf.) Lamour.) and *Solieria filiformis* Papenfuss (Solieriaceae) (Perrone et al., 1991; Perrone & Cecere, 1997).

Thallus polarity has proved to be affected by light intensity in *A. nayadiformis*, with too high a light intensity also inducing proximal stolons to change into uprights, a phenomenon that has also been observed in the above species. Low temperature, low irradiance and a short-day regime affected both bud growth rate and morphogenesis, in that the first two conditions slowed down the growth rate so much that new axes did not grow in length enough to transform themselves into uprights. Short-day conditions (the 12 h:12 h regime also acts as SD in this species) did not permit even the longest stolons to change into uprights. This behaviour justifies the occurrence of propagules with long stolons during winter – early spring, and their quick development into upright fronds in late spring. By contrast, cultured propagules reached the highest growth rates at the highest tested values of both temperature and irradiance, in accordance with previous field observations on intertidal *vs* subtidal populations showing that intertidal plants grew faster and reached a larger size than subtidal ones (Cecere et al., 2000).

The finding that apex transformation (and sympodial growth) was promoted by LD conditions, and largely suppressed under both 12 h:12 h and SD regimes supports the hypothesis that *A. nayadiformis* is a long-day plant with a critical daylength greater than 12 h. The sprouting of uprights occurring in late spring from the over-wintering prostrate system could be another LD response. The LD regime matches the seasonal growth and reproduction pattern of *A. nayadiformis* in its native environment, the Mediterranean Sea, and limits its distribution area north of the Tuscan Archipelago (Tyrrhenian Sea) (Papi et al., 1992) through both the Red Sea and Indian Ocean up to the equator (de Jong et al., 1999). On the other hand, the SD inhibition for apex transformation seems to be a specialized mechanism for over-wintering in a resistant vegetative phase at our latitude.

Most of the photoperiodic responses reported in the literature involve a change of phase in a heteromorphic life history, usually through either the formation or release of spores by the diploid generation; in red algae, tetrasporogenesis is often stimulated by SD (Dring, 1984). The initiation of uprights from prostrate perennial systems is another common response to photoperiod, which can be interpreted as a change of vegetative phase. In red algae with a winter life cycle, the production of upright thalli has also proved to be a SD response (Felicini & Perrone, 1972; Rietema & Breeman, 1982; Rueness & Åsen, 1982; Dring, 1988; Perrone & Felicini, 1993). Since these responses resemble the breaking of dormancy in woody plants, it is possible that processes similar to the onset of dormancy are also under photoperiodic control in some macroalgae. In *Schottera nicaeensis* changes in apical morphogenetic trends analogous to those observed in *A. nayadiformis* have also been shown to be controlled by daylength (Perrone & Felicini, 1988; Perrone & Felicini, 1993).

A. nayadiformis propagules have no homologs among the macroalgae. By contrast, they are very similar to the turions of most aquatic dicotyledons. Turions are winter buds, dormant organs often formed as a response to unfavourable ecological conditions. They are greatly modified shoot apices, spherical to club-shaped, consisting of dwarf dark green leaves filled with storage substances and closely packed around the axis (Sculthorpe, 1967). *A. nayadiformis* propagules resemble turions of *Hydrilla verticillata* (L.f.) Royle (Cook & Lüönd, 1982) and some carnivorous plants, such as *Aldrovanda vesiculosa* Linnaeus and *Utricularia vulgaris* Linnaeus (Adamec, 1999). In these species, turions play the role of seeds.

In the *A. nayadiformis* population, propagule-bearing thalli represent the vast majority of specimens, and this suggests that propagules rather than sexual reproduction play a crucial role in both population maintenance and increase. Moreover, the earlier occurrence of female gametophytes and their higher incidence compared with male gametophytes (Cecere et al., 2000), together with the very low spore vitality and germination potential (both carpo- and tetraspores), suggest that in the course of time *A. nayadiformis* has improved its propagation strategy due to declining fertility. It must also be underlined that plantlets deriving from dormant propagules grow only at the beginning of the favourable season, whilst sporelings arise later in summer. They are also more robust than sporelings, and reach sympodial branching earlier.

Both the peculiar thallus organization and the likeness of propagules to turions lead us to compare the *A. nayadiformis* architecture with that of more evolved plants and, even though such a comparison may seem hazardous, it makes the cormophytes-thallophytes borderline less marked.

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