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Phototropic growth in a reef flat acroporid branching coral species

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SUMMARY

Many terrestrial plants form complex morphological structures and will alter these growth patterns in response to light direction. Similarly reef building corals have high morphological variation across coral families, with many species also displaying phenotypic plasticity across environmental gradients. In particular, the colony geometry in branching corals is altered by the frequency, location and direction of branch initiation and growth. This study demonstrates that for the branching species *Acropora pulchra*, light plays a key role in axial polyp differentiation and therefore axial corallite development – the basis for new branch formation. *A. pulchra* branches exhibited a directional growth response, with axial corallites only developing when light was available, and towards the incident light. Field experimentation revealed that there was a light intensity threshold of 45 μmol m^{-2} s^{-1}, below which axial corallites would not develop and this response was blue light (408–508 nm) dependent. There was a twofold increase in axial corallite growth above this light intensity threshold and a fourfold increase in axial corallite growth under the blue light treatment. These features of coral branch growth are highly reminiscent of the initiation of phototropic branch growth in terrestrial plants, which is directed by the blue light component of sunlight.

Key words: axial polyp differentiation, coral morphology, light quantity, light quality, *Acropora pulchra*.

INTRODUCTION

Patterns of morphological change are common among many organisms and potential benefits can be linked to environmental heterogeneity (Via et al., 1995; Pigliucci, 2005). In plants, variations in crown architecture as a response to uneven light environments results in maximizing light capture and photosynthesis in shaded habitats and minimizing photoinhibition in high light habitats (Pearcy et al., 2005). Many scleractinian corals have highly variable colony morphologies (e.g. Willis, 1985; Bruno and Edmunds, 1997; Muko et al., 2000) with branching corals showing morphological plasticity in response to differing environmental conditions, such as water motion (Kaandorp et al., 2005) and ambient light levels (Muko et al., 2000). Changes in colony geometry of branching corals are influenced by the frequency, location and direction of new branch initiation and growth. Most acroporid branching species have specialized corallite structures, axial corallites, which are formed as a consequence of polyp differentiation at the branch tip, and are an area where linear branch extension occurs (Oliver et al., 1983; Oliver, 1984; Veron, 2000). The differentiation of an existing radial polyp into an axial polyp and the resulting axial corallite formation leads to the initiation of a new branch and therefore a new direction of growth (Oliver, 1984). The developmental signals of axial corallite formation and possible environmental cues involved in this axial corallite development are unknown.

Corals form a symbiosis with photosynthetic dinoflagellates (genus *Symbiodinium*), which may be a critical factor in the success of scleractinian corals in the nutrient-poor tropical oceans (Muscatine and Porter, 1977). Given the central role of photosynthesis in supplying the energetic needs of corals and their symbionts, light plays a key role in the biology and development of corals. Similar to plants, corals need sufficient external light intensities to have enough energy for survival, growth and reproduction (Chalker et al., 1983; Anthony, 1999) while minimizing the chances of photoinhibition and photodamage (Jones and Hoegh-Guldberg, 2001). It is common for terrestrial plants to use plant geometry and physiology to optimize their photosynthetic response (reviewed by Herbert, 1996). Similarly, scleractinian corals can manage the availability of light to their symbiotic dinoflagellate through a range of mechanisms, such as polyp contraction (Brown et al., 2002; Levy et al., 2003), use of antioxidant enzymes (Brown et al., 2002) and light absorption by fluorescent and non-fluorescent pigments (Salih et al., 2000; Dove, 2004). With changing light levels, the symbiotic dinoflagellates can change in density within the host and change the amount of photosynthetic pigments they contain (e.g. Falkowski and Dubinsky, 1981; Iglesias-Prieto and Trench, 1997). Colony morphology is also important for maintaining optimal light levels within the colony (Anthony et al., 2005), and fine-scale changes in mesostructure (e.g. septa, columella and dissepiments) can have major influences on the amplification of low light levels (Enriquez et al., 2005). Colony morphology of branching coral species can be highly complex (Kaandorp et al., 2005) and branching corals may use their colony morphology to optimize within-colony irradiance levels (Kaniewska et al., 2008).

As colony morphology represents a strategy for manipulating within-colony light levels, light may be an important environmental cue in axial corallite development, as it would influence the direction of new branch growth. Phototropism, where an organism will alter growth patterns in response to light direction, is common among plants (Iino, 1990). Terrestrial plants also have differing responses to various wavelengths of light. Phytochrome photoreceptors in green plants respond to far red light and initiate stem elongation in response to low light levels (Khattak et al., 2004). Plants also have blue light receptors, cryptochromes, which elicit a directional growth response

towards light (Ahmad et al., 1998). In corals, changes in light quality and intensity result in changes in photosynthesis (Kinzie and Hunter, 1987), *Symbiodinium* growth rates (Kinzie et al., 1984), GFP-like protein concentrations (D'Angelo et al., 2008) and coral settlement behaviour (Petersen et al., 2005).

The underwater light environment for corals is different from that of terrestrial plants, as light attenuates with depth as a result of absorption and scattering by dissolved and suspended material, as well as phytoplankton (Kirk, 1994). Light attenuation in the water column is not uniform across the spectrum, the blue part of the spectrum experiences the least attenuation whereas longer wavelengths attenuate quickly with depth. The spectral attenuation is affected by water type, as attenuation will occur more rapidly in turbid waters (Kirk, 1994). The coral–algal complex contains pigments that absorb in the blue and red region for light harvesting (Iglesias-Prieto and Trench, 1997) and there are also host pigments that absorb in the green spectrum (Dove, 2001). In order for the coral to respond to a possible light cue and change growth morphology, it must be able to detect changes in light by possessing light-sensing photoreceptors. To date only blue-light-sensing photoreceptors, cryptochromes that are also found in plants, have been found in corals (Gorbunov and Falkowski, 2002; Levy et al., 2007). In addition, physiological and biochemical responses to blue light have been documented (Levy et al., 2006). Given that the underwater environment is dominated by the blue part of the light spectrum, it can be expected that if a light cue exists for axial corallite development, and therefore branch initiation in acroporid branching corals, it will operate in the blue part of the light spectrum.

Acropora pulchra Brook 1891, is a complex branching coral common in shallow waters. It develops distinct axial polyps which deposit axial corallites, a corallite structure from which branch extension occurs, at the tip of the branches. The aim of this study was to determine if light serves as a cue for axial corallite development, and to understand the role of light intensity and quality in this development.

MATERIALS AND METHODS

Effect of light availability on axial corallite development

To investigate the relationship of light availability on axial corallite development, the effect of directional light was tested in outdoor aquaria at Heron Island Research Station, Great Barrier Reef, Australia. The aquaria were maintained at ambient temperatures and under natural light conditions, with light in the aquaria measured regularly using a light meter with a manufacturer-calibrated sensor (Li-cor, LI-192S, Lincoln, NE, USA). Same-sized sea water flow-through aquaria that were continuously flushed with water obtained from the reef crest were used for each treatment. The three tested conditions were: side light, top light and open (control). The open aquaria allowed sunlight entry from all sides, but had light shade cloth above the aquaria to reduce the intensity of the midday sun (effectively equalizing the light through out the day). The side-light and top-light aquaria were covered in black plastic, except for a single side or top (respectively) left open. Branches (96 cm×7–8 cm long) were collected from 12 healthy *Acropora pulchra* colonies on Heron Island reef flat (23°33′S, 151°54′E), Great Barrier Reef, Australia. Axial corallites were removed from the branches by cutting with side cutters approximately 1 cm from the branch tip. Branches were photographed and branch lengths were recorded. In each aquarium, branches (24 per treatment) were suspended, using plastic-coated wire, in the middle of the aquarium. In the side-light aquaria the branches were hung parallel to the water surface and in the top light aquaria the branches were hung vertically. In the control aquaria branches were hung both horizontally and vertically, as controls for both treatments. In all treatments, equal numbers of branches were positioned so that the previous axial corallite end faced towards and away from the light direction, to account for the chance of predetermined growth due to original branch directional growth.

Branches were left to grow in aquaria for 8 weeks. A pilot study demonstrated that this was enough time for *A. pulchra* branches to develop axial corallites (data not shown). After 8 weeks, branch lengths were measured and branches were re-photographed to record direction of axial corallite development (proximal or distal or both), lateral branch growth and overall branch health. The amount of axial corallite growth at the cut surfaces at both ends of a branch was calculated from the photographs.

Effect of light quantity and quality on axial corallite development

To test the influence of light quantity and quality on axial corallite development, light intensity and quality were manipulated in a field experiment. Branches (288×7 cm to 8 cm) were collected from 16 healthy *Acropora pulchra* colonies on Heron Island reef flat (23°33′S, 151°54′E), Great Barrier Reef, Australia. The axial corallites were removed from the branches by cutting with side cutters approximately 1 cm from the branch tip. Two branches were placed 1 cm (distal end down) into underwater cement in diagonally opposite cells, of 12 cm×12 cm four-cell seedling trays. A replicate consisted of one seedling tray (two branches; Fig. 1). The branches were photographed and initial branch lengths were recorded. The seedling trays were attached to one of four underwater frames (Fig. 1) for exposure to a range of light treatments. Each frame had four replicates of light quantity treatments of 0, 30, 50, 80 and 100% light reduction (using shade cloth or opaque black plastic), and four replicates of light quality treatments of clear (acetate sheet), blue (408–508 nm), red (618–700 nm) and green (482–554 nm) filters (nos 132, 124 and 026, respectively, from LEE Filters, Burbank, CA, USA; Fig. 2). Each of the 36 treatments per frame were widely spaced and randomly assigned, to minimize effects of potential differences in flow among positions. The materials used for the various treatments were made into open bottomed boxes approximately 15 cm square with sides of approximately 3 cm. These were fixed to wire mesh (10 cm square) and suspended above the seedling trays to leave approximately 3 cm of the coral branch bases exposed to light and water movement (Fig. 1). This would minimize water flow differences among positions within the frame and allow some light for branches in dark treatments, to avoid branch mortality.

The frames were placed at 4 m depth at Harry's Bommie (23°27.625′S, 151°55.759′E), Heron Island. This nested experimental design resulted in four independent frame replicates for all treatments, and in each frame there were four replicates per treatment.

Coral branches were left to grow for 8 weeks, after which branch lengths were recorded and the amount of vertical axial corallite growth at the cut surfaces was determined by calculating the difference between initial and final branch lengths. Branches were also photographed as a record of the potential lateral encrusting growth at the base, new lateral branch formation and overall branch health (including recovery from handling effects).

Ambient downwelling irradiance (photosynthetically active radiation, PAR) next to the frames was recorded underwater *in situ* using underwater light loggers (Odyssey, Z412, Christchurch, New Zealand). The logger, a 2π cosine-corrected light sensor was calibrated against a manufacturer-calibrated sensor (Li-cor, LI-192S). In addition, a spectral scan was performed underwater at 4 m at the site of the experiment, on a cloudless day at noon, using a

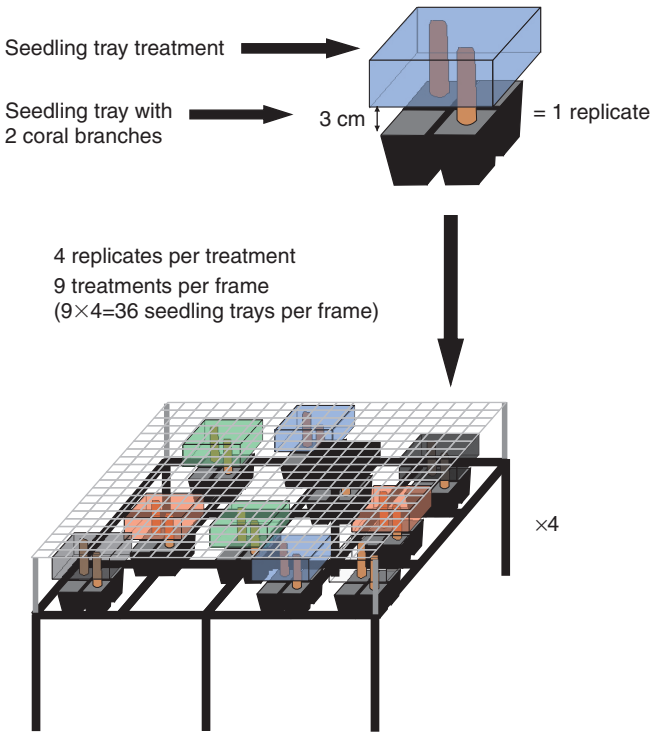

Fig. 1. Experimental design of the four frames deployed at Harry's Bommie (4 m) at Heron Island (23°27.625′S, 151°55.759′E), Great Barrier Reef. Arrows point to individual seedling trays (replicates) each containing two *Acropora pulchra* branches. These were exposed to randomly positioned treatments of 0, 30, 50, 80 or 100% light reduction, or clear, blue, red or green filters.

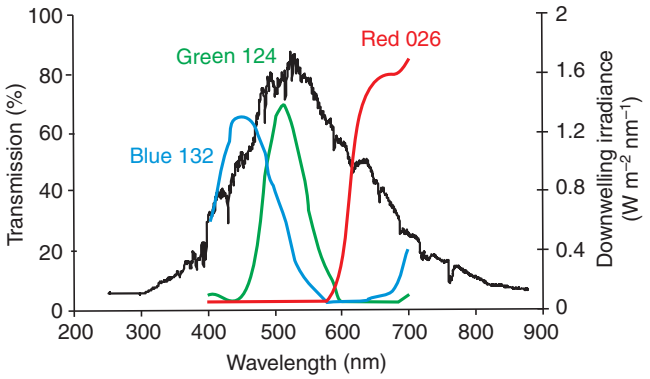

Fig. 2. Underwater spectral scan (black line) of ambient PAR at Harry's Bommie (4 m), Heron Island (23°27.625′S, 151°55.759′E), at the site where experimental frames with corals were deployed. Coloured lines represent transmission characteristics of the coloured filters used in the experiment; blue (LEE Medium Blue 132), green (LEE Dark Green 124) and red (LEE Bright Red 026).

USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA; bandwidth of 200–850 nm in a custom-made underwater housing) *via* an attached optic fibre.

RESULTS

Effect of light availability on axial corallite development

In all treatments, axial corallites were developed irrespective of the direction of the previous axial corallite, if light was available from that direction (Fig. 3). Cut branch surfaces that were facing away from available light did not develop axial corallites, but live tissue was regenerated over the exposed skeleton (Fig. 3).

The maximum recorded irradiance at any time in control aquaria, and where light was present in treatment aquaria, was 680 µmol m^{-2} s^{-1}. In unlit areas of the treatment aquaria, the maximum irradiance at any time was 33 µmol m^{-2} s^{-1}. Horizontally positioned branches had a twofold greater axial corallite growth for cut surfaces facing the light compared with cut surfaces facing away from the light (one-way ANOVA, $F_{3,83}$=9.25, P<0.001). In the vertically positioned branches there was also a twofold greater axial corallite growth for cut surfaces facing the light as compared to cut surfaces facing away (one-way ANOVA, $F_{3,87}$=28.68, P<0.001). Axial corallites only developed in control aquaria and in treatment aquaria towards the direction of light (Fig. 4). The values reported for growth of cut surfaces facing away from the light was associated with tissue and polyp regeneration over the exposed skeleton, but at no stage were axial corallites developed. The mortality rate of branches was <10%, branches recovered quickly from handling and tissue grew over the plastic coated wire as well as cut areas with exposed skeleton.

Effect of light quantity and quality on axial corallite development

During this study the mean daily ambient irradiance level was 225.9±5.8 µmol m^{-2} s^{-1} (mean ± s.e.m.), whereas the mean maximum daily irradiance was 409.2±10.2 µmol m^{-2} s^{-1} (mean ± s.e.m.). A spectral scan at the site of the experiment together with the spectral characteristics of the filters showed that there was 15% less PAR under the red filter than under the blue and green filters. This was confirmed by PAR measurements performed *in situ* under the three coloured filters at 4 m. The transmission rate of the clear filter was 95% in the PAR region.

Differences in axial corallite growth among light reduction treatments were detected (nested ANOVA, $F_{52,42}$=2.78, P<0.001). Assuming the mean daily ambient irradiance during the length of the experiment reported above, light reduction treatments of 0, 30, 50, 80 and 100% would equate to a mean daily ambient irradiance of 226, 158, 113, 45 and 0 µmol m^{-2} s^{-1}, respectively. The greatest axial corallite growth was found in the control treatment, where there was a threefold increase in axial corallite growth compared to the 30% and 50% light reduction treatments. There was a twofold increase in axial corallite growth between the 30% and 50% light reduction treatments and the 80% and 100% light reduction treatments (Fig. 5A). The values reported for the 80% and 100% light reduction treatments corresponded to growth associated with live tissue and polyp regeneration over the exposed skeleton, but no axial corallite development.

Differences in axial corallite growth were detected among light quality treatments (nested ANOVA, log transformed data, $F_{39,31}$=1.83, P=0.043). Axial corallite regeneration occurred in the control, clear and blue filter treatments, but not in the green and red filter treatments (Fig. 5B). Again, the values reported for the green and red treatments corresponded to growth associated with live tissue and polyp regeneration over the exposed skeleton, but no axial corallites developed. There was little effect of handling on the branches as a consequence of the fixation into the seedling trays, as most of the branches grew laterally over the cement, and in light reduction treatments it was common for secondary lateral branch formation to occur at the base of the branch where light was available. The overall mortality rate of branches in the field experiment was 31%. This mortality was mostly due to branch destruction by wave action.

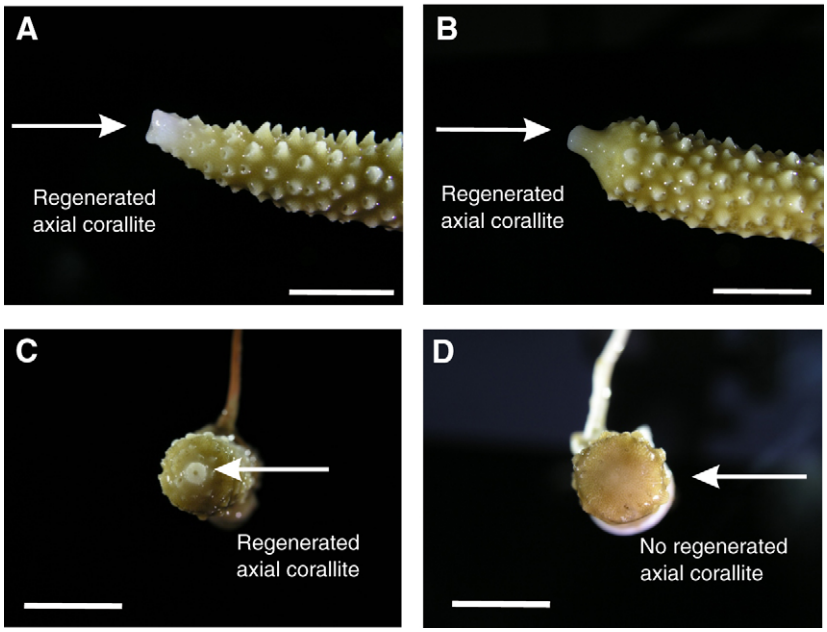

Fig. 3. *Acropora pulchra* axial corallite development after 8 weeks. (A) Axial corallite developed at previous tip end of branch. (B) Axial corallite developed at previous basal end of branch. (C) Axial corallite clearly developed at basal end of branch. (D) Tissue regeneration over cut surface without axial corallite development. Scale bar, 1 cm.

DISCUSSION

The exposure of higher plants to uneven light environments often results in the bending of the growing axes of a plant towards the direction of higher light levels (Iino, 1990). Here we found a similar response for the reef-building coral *Acropora pulchra*, where the growth of axial corallites towards available light provides evidence that light is an important cue for the development of this coral structure and is therefore similar to plant directional morphogenesis. This confirms previous findings that axial corallites in *Acropora formosa*, which were exposed to shaded environments, did not grow and eventually reverted back to radial corallites (Oliver, 1984). In addition, in the current study there was development of axial corallites at the distal end of a branch, where previous axial corallites were not present. This shows that this is not just regeneration of an axial corallite, but a developmental response towards light. There were no differences in growth rates between axial corallites regenerated at the proximal end and newly developed ones at the distal end of the branch (data not shown).

In most acroporid coral species branch extension only occurs in axial corallites (Oliver et al., 1983; Oliver, 1984), where the highest growth rate is present (Fang et al., 1989), therefore the position where a radial corallite differentiates into an axial corallite will determine the direction of the new branch growth. Growth towards light (positive phototropism) is advantageous for photosynthetic organisms such as corals and their symbionts (Porter et al., 1984). In terrestrial plants, shade avoidance is well known, with a complex set of physiological behaviours triggered by specific wavelengths of light resulting in an increased likelihood of light availability (Iino, 1990). The underwater light environment experienced by corals is different from the terrestrial light environment that many plants are exposed to. One of these differences is that in water the light field as a function of depth, becomes more diffuse and omni directional (Kirk, 1994). However, the acroporid species investigated in this study grows on reef flats and shallow reef slopes and is therefore exposed to more directional light, with exposure to almost direct sunlight at low tide. Therefore the directional light environment for this branching coral may be comparable to that of terrestrial plants. The directional growth towards light found in this study is similar to the terrestrial plant shade-avoidance strategy. As linear branch extension occurs in the axial corallite for most acroporid coral species, it can be argued that branch extension and secondary branch development in a colony is towards the light, as shaded parts of the *A. pulchra* colony and branches do not develop axial corallites.

In the field experiment, variability in light intensity influenced the axial corallite regeneration. The existence of a threshold, above which an axial corallite is regenerated, may represent a minimum light level, below which is considered as potential shade areas, and therefore the coral does not develop an axial corallite, to preclude growth in the direction of low light. It has been suggested that photosynthetic organisms acclimate to a mean irradiance as opposed to instantaneous irradiances (Chabot et al., 1979; Falkowski and Raven, 1997). The threshold here was found to be <80% light reduction, which at 4 m at Harry's Bommie represents a mean daily light level of $<45\,\mu mol\,m^{-2}\,s^{-1}$. An optimal irradiance level for corals is where the light harvested equals the turnover rate of photosystems, quantified by the subsaturating irradiance of the photosynthesis–irradiance relationship (Falkowski and Raven, 1997). This has been estimated for foliose corals to be between 150–370 $\mu mol\,m^{-2}\,s^{-1}$ (Anthony et al., 2005), whereas a hypothetical lower limit for reef distribution has been suggested to be $50\,\mu mol\,m^{-2}\,s^{-1}$ (Kleypas et al., 1999). The threshold for axial corallite development seems to adhere to the latter value. *Acropora pulchra* is a shallow-water species, which is most abundant between 0–5 m (Wallace, 1999; Veron, 2000) and has therefore adapted to higher irradiance levels. Values below $45\,\mu mol\,m^{-2}\,s^{-1}$ could be considered as potential shade areas by this species, although this threshold value may not be optimal for many coral species with a larger depth range.

A spectral scan at the site of the field experiment (Fig. 2) revealed that there was still a substantial amount of red light present at the site. Light attenuation will vary across water types where the depth of the ocean floor is greater than the depth of the light penetration, and water types where the ocean floor depth is less than the light penetration potential (Mobley, 1994; Ackelson, 2003). In such optically shallow waters the inherent optical property of the water column will be affected by the benthic substrate (Boss and Zanevald, 2003). This could explain the spectral scan in Fig. 2, as the site has a large percentage cover of sand, and so the light is highly reflected and less attenuation occurs at that depth compared to attenuation

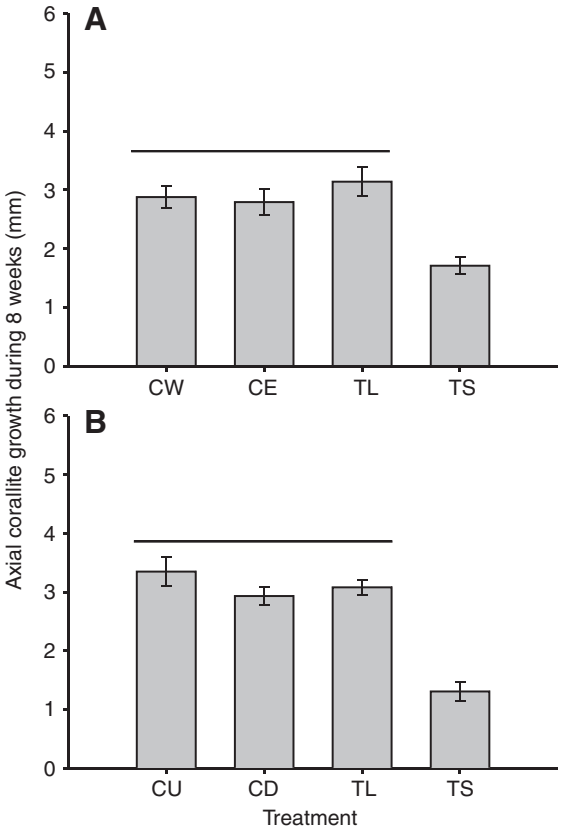

Fig. 4. *Acropora pulchra* axial corallite growth as a function of light availability in (A) horizontally positioned branches (23 branches in control treatment and 20 branches in side-light treatment) and (B) vertically positioned branches (22 branches in control treatment, 23 branches in top-light treatment). Error bars represent standard error of the mean. CW and CE are horizontally positioned branches from control aquaria with light available from all directions, where CW refers to the cut end facing west (the light direction in treatment aquaria); CE refers to the cut end facing east (away from the light direction in treatment aquaria). CU and CD are vertically positioned branches from control aquaria where CU refers to the cut end facing up (the light direction in treatment aquaria) and CD to the cut end facing down (away from the light direction in treatment aquaria). TL and TS are branches from treatment aquaria where TL refers to the cut end facing the light direction and TS to the cut end facing away from the light. Results of *post-hoc* tests (Fisher LSD test) for differences between different treatments are indicated; horizontal lines link groups that do not significantly differ (P>0.05) from each other.

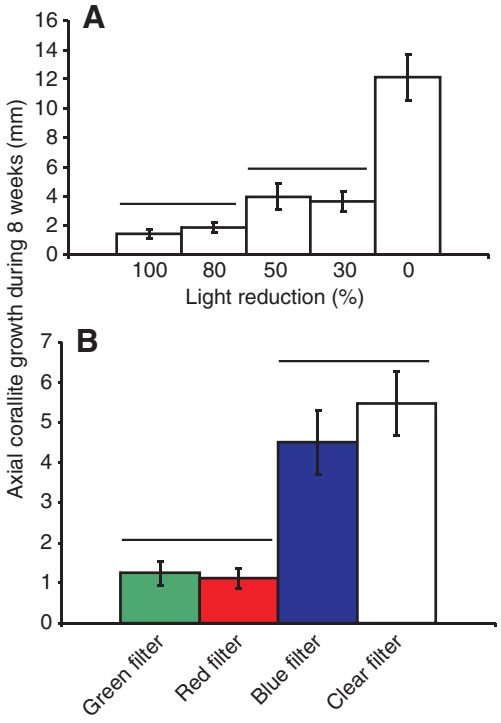

Fig. 5. Axial corallite growth in *Acropora pulchra* (16 replicates for each treatment but nested within frame, N=4) as a function of (A) light intensity (0, 30, 50, 80 or 100% light reduction) and (B) light quality (blue, red, green or clear). Error bars represent the standard error of the mean. Results of *post-hoc* tests (Fisher LSD test) for differences between different treatments are indicated; horizontal lines link groups that do not significantly differ (P>0.05) from each other.

across wavelengths that might occur in other water types such as oceanic waters (e.g. Maritorena et al., 1994; Boss and Zanevald, 2003; Voss et al., 2003; Zanevald and Boss, 2003).

In higher plants, phototropism – the directional growth and bending towards light – is triggered by blue light (Iino, 1990) and is mediated by cryptochrome photoreceptors (Ahmad et al., 1998). In the current study, a similar phototropic behaviour was found in reef-building corals, where axial corallite growth was only initiated by blue light (408–508 nm), adding to the similarities between the two photosynthetic organisms. The difference between axial corallite growth under the clear filter compared to the 0% light reduction treatment (Fig. 5) is probably due to minor fouling of the clear filter, which occurred despite regular cleaning of the filters. Considering that blue wavelengths of light are dominant in the water column (Kirk, 1994), and evidence of the same blue photoreceptors (cryptochromes) in corals (Gorbunov and Falkowski, 2002; Levy et al., 2007) as in terrestrial plants, it is understandable that the axial corallite development occurred in the blue light treatment. Apart from phototropism, plants have many behavioural responses to blue light, including leaf and cotyledon expansion, petiole elongation, promotion of flowering and inhibition of hypocotyl elongation (Ahmad et al., 1998). Similarly corals have many reported physiological responses to blue light and this study adds another blue light response. Other studies have shown that coral polyp tentacle behaviour responded to the blue zone of the spectrum (Levy et al., 2006), coral larvae can have settlement preferences for areas treated with blue light (Petersen et al., 2005), coral respiration rates can increase in response to the blue part of the spectrum (Kinzie and Hunter, 1987), symbiotic dinoflagellates can have higher growth rates under blue light (Kinzie et al., 1984) and blue light can regulate GFP-like protein concentrations (D'Angelo et al., 2008). The species used in this study, however, is a reef flat species, living high up in the water column where the smallest attenuation of red and green light occurs. If any coral were to respond to red or green wavelengths, it should be a reef flat species. It is expected that if coral species migrated down the water column during evolution, then basic responses such as phototropic growth, should still be sensitive to the red and green parts of the spectrum. This was not the case for *Acropora pulchra*, which perhaps reflects the fact that this coral species, has over time evolved to migrate up the water column to the reef flat, instead of, from the reef flat down the water column.

Overall, the growth of *Acropora pulchra* branches over an 8 week period in this field study was comparable to that reported for *Acropora formosa* transplantation experiments. For *A. formosa* at 5 m, the mean yearly extension rate was 8 cm per year (Oliver et al., 1983),

which for 2 months, would be 1.3 cm assuming a constant light regime. In another study, extension rates of white axial corallite tips in *A. formosa* were on average 0.75 cm over 30 days (Oliver, 1984) which for 8 weeks would be 1.5 cm. The current study measured regeneration growth of axial corallites and linear extension from these cut surfaces. Axial corallite extension in full light conditions was, on average, 1.2 cm over 8 weeks (Fig. 5). Considering that branches in this study had to invest energy to repair the cut surfaces at the top and redevelop axial corallites, these are comparable values.

In the field experiment, light was available to the middle part of the branch, but not the proximal and distal end of the branch. Overall, the available energy should have been sufficient to support regeneration at the cut surface and further growth of the branch if the treatment conditions stimulated tip growth. This was the case, for even in the 100% light reduction treatment there was regeneration and repair of tissue at the cut surface, but no axial corallite development was induced. In light-reduction treatments in the field experiment, parts of the branch near the base exposed to light grew and extended towards the light, either as a new secondary branch or lateral encrusting growth over the base of the cement.

This study showed that axial corallite development and therefore branch initiation in *Acropora pulchra*, shows a directional growth response towards light, reminiscent of the phototropic response in terrestrial plants. Similar to plants this growth response was triggered by the blue part of the spectrum, which also is the dominant light environment for corals. These results indicate that perhaps light is one of the critical factors structuring coral colony architecture in *A. pulchra*, which may also be true for many shallow water acroporid coral species.

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