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Why overgrowth of intertidal encrusting algae does not always cause competitive exclusion

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Abstract

Encrusting algae are well-known to be able, for long periods, to withstand shading and overgrowth by other organisms. How this is achieved remains a mystery. It had been proposed that connections with unshaded (non-overgrown) parts of the thallus may allow transfer of nutrients to the shaded part. From this model, I proposed and tested the hypothesis that shaded patches of the intertidal red alga, *Hildenbrandia rubra*, would survive overgrowth longer, or better, when connected to unshaded thallus than when experimentally separated from surrounding alga. Experimental treatments were shading (black or transparent 80 mm perspex discs or no cover) and scraping (scraped around the disc to remove contacts, a control for effects of scraping, no treatment). The 9 orthogonal combinations of cover and scraping were applied to 3 independent, random replicates (i.e. 27 plots) in each of four randomly chosen sites.

In all 4 sites, over 13 months, shaded *H. rubra* survived in greater abundance (as % cover) where in contact with surrounding thallus. In one site, there was no effect of shading unless the thallus was isolated. In two sites, shading reduced cover, but was more deleterious where the thallus was isolated. In the fourth site, there were artefacts due to a perspex cover, but still less cover of alga where it was isolated.

This encrusting alga can withstand a long period of complete shading, provided there is connection to unshaded thallus. Interpreting or predicting overgrowth interactions in terms of competitive outcomes is therefore dependent on consideration of whether the overgrown species is actually being affected. It also depends on the duration of overgrowth and, as shown here, the extent to which connectivity with unshaded thallus is effective at preventing or reducing any consequences. Observations and experiments that do not ascertain these are difficult to interpret.

Keywords: Alga; Competition; Encrusting; Intertidal; Overgrowth; Shade

1. Introduction

Because space is such a limiting resource in many habitats, overgrowth of organisms is often detrimental to those that are overgrown (e.g. for marine examples, Connell, 1961; Dayton, 1971, 1975; Denley and Underwood, 1979; Sebens, 1986; for terrestrial examples, Clements et al., 1929; Black, 1958; Raynal and Bazzaz, 1975; reviewed by Schoener, 1983). On rocky surfaces, access to adequate space is crucial for the survival (or growth or reproduction) of many organisms. They need space for attachment (e.g. Connell, 1961; Suchanek, 1985) or to get adequate access to resources of light or the water-column (e.g. Jackson, 1979). Overgrowth is therefore one of the most widespread mechanisms by which species compete (Jackson, 1979; Sebens, 1986). Some species have evolved

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complex defences against being overgrown, including "fighting", at the margins where overgrowth can occur (e.g. Wellington, 1980) or have biochemical defences against potential competitors (e.g. Jackson and Buss, 1975; Keats et al., 1977; Figueiredo et al., 1996). Some species benefit because grazers remove the overgrowers, allowing persistence of otherwise excluded species (e.g. Steneck, 1986; Dethier, 1994). There are even cases where one species survives because the superior competitor is itself eliminated by being overgrown. Thus, the alga *Pterocladia capillacea* survives under the canopy formed by *Eisenia arborea* which shades and suppresses *Halidrys dioica* that would otherwise overgrow and eliminate the *P. capillacea* (Kastendiek, 1982).

Given all the competition by overgrowth that occurs, it is surprising that some two-dimensional, encrusting algae are so widespread and persistent. Unless they have chemical defences (Steinberg et al., 1998) or external agents (grazing, disturbance) preventing potential overgrowers from becoming established, it would seem that they ought to be less widespread in nature. Apart from internal defences or external grazing, the "inferior" encrusting species may be able to persist for very long periods of time underneath a competitor simply because they store sufficient reserves of energy to last until a new disturbance removes the overgrower.

Alternatively, encrusting species of algae may be able to survive being overgrown provided the spatial scale (rather than the temporal scale) is not too large. Wetherbee (1979), Miles and Meslow (1990) and Steneck (1986) have suggested mechanisms in the plants that would allow circulation of nutrients. In theory, therefore, in any individual, parts of the body not being overgrown could sustain parts that had been shaded. So, provided overgrowth does not occur simultaneously over the whole of its thallus, an alga may survive indefinitely. This mechanism has not been demonstrated experimentally. For numerous encrusting species, Dethier and Steneck (2001) investigated growth of shaded and undshaded portions of thallus. They obtained some evidence of differences in viability of the species examined, suggesting some communication between shaded and unshaded portions of thallus. Samples were very small. No results were statistically significant and analyses were potentially compromised by non-independence of data (the shaded and unshaded portions of the same thallus were treated as though they were independent). Regardless of these findings, their study did not investigate the role of isolation from surrounding tissue in processes of competitive overgrowth.

Observations over many years have demonstrated that the encrusting alga, *Hildenbrandia rubra*, is very widespread at mid- and low-shore levels of intertidal rock-platforms in New South Wales (Dakin, 1953; Underwood, 1980, 1981). In many areas, it is overgrown by foliose algae. Most of this overgrowth does not result in its disappearance and it can survive for quite long periods under other plants (see particularly Underwood, 1980). Such overgrowth (and that by barnacles; Denley and Underwood, 1979, Underwood et al., 1983) is patchy and discontinuous. *H. rubra* can also survive more widespread smothering by sand, but this rarely lasts for more than a few weeks before the sand is removed by waves (Underwood and Chapman, 1998). Finally, when grazers are removed, foliose algae very quickly recruit and grow over *H. rubra* (Underwood, 1980; Underwood and Jernakoff, 1981).

These observations suggest that persistent abundance of *H. rubra* is not maintained by chemical defence. Overgrowth in the absence of grazers is rapid and effective, although *H. rubra* can slow down the colonization of foliose algae by some months (Underwood, 1980, Fig. 1). Nor does it persist in low-shore habitats because grazers prevent overgrowth (Underwood and Jernakoff, 1984). If it is removed, it recruits and grows slowly (Underwood, 1980), so is not surviving by rapid recruitment, as found for some other encrusting species (Adey and Vassar, 1975; Dethier, 1981; Figueiredo et al., 1997; Airoldi, 2000).

Two possibilities remain. First, despite overgrowth by foliose algae being widespread and persistent, it is possible that they do not completely block off the light. Many encrusting species can cope well with reduced intensities of light (Littler and Littler, 1980; Vadas and Steneck, 1988; Steneck and Dethier, 1994). Second, connectivity and transport of materials around the thallus make overgrowth effective only if the area overgrown is large. This paper describes experiments to test the consequences of the second model under circumstances where the first does not apply. I predicted that complete shading of patches of *H. rubra* would result in a decline in its abundance (as percentage cover of the substratum) and ''health'' or physiological well-being (as amount of chlorophyll in the algae) as an index of biomass or physiological activity. I then predicted that the negative effect of overgrowth would be smaller or zero where the shaded portion of the alga was in contact with surrounding, unshaded portions of thallus. Overgrowth would have larger negative effects where the patch of algae was completely shaded. Experimental tests of these hypotheses are described here.