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Intrinsic factors influence the attachment of fragments of the green alga *Caulerpa filiformis*

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Abstract

Asexual reproduction via fragmentation is an integral component of the life history of many marine organisms. In south-eastern Australia the green macroalga *Caulerpa filiformis* (Suhr) Hering is abundant on many rocky shorelines and fragments are very abundant in the water column. We examined some of the factors that may influence the growth and successful reattachment of fragments of *C. filiformis* that potentially contribute to its success. Field surveys revealed that *C. filiformis* fragments were of variable morphologies (from small fronds to entire thalli) and sizes (0.1–60 cm in length). All fragments of *C. filiformis* were viable propagules that survived and grew well in the laboratory. However, some fragments grew more than others, in particular larger sizes (7.5 cm class) of certain morphologies (fragments that consisted only of a single frond). Rhizoids were produced by all fragments, but again, larger fragments produced more rhizoids than smaller fragments. The force required to detach fragments was proportional to the number (but not size) of rhizoids, demonstrating the importance of rhizoids for attachment. The rate of attachment of fragments was also fast, usually within 12 h, but the longer these fragments were attached to a substratum the greater the force required to dislodge them. Interestingly, fragments only produced rhizoids if they were resting on a substratum which may explain the small proportion of fragments with rhizoids in the field (<5%). Ultimately, the long term success of *C. filiformis* fragments was low as only 1.6% of fragments attached within 24 h and none of these persisted for longer than 2 days. Nonetheless, the abundance and viability of fragments of *C. filiformis* available to attach suggest that asexual fragmentation is a successful reproductive strategy in this seaweed.

Keywords: Asexual reproduction; Dispersal; Fragmentation; Invasive; Rhizoid; Seaweed

1. Introduction

Asexual reproduction by fragmentation is an important method of propagation for many marine organisms, including corals (Highsmith, 1982), sponges (Maldonado and Uriz, 1999), zooanthids (Karlson, 1988) and macroalgae (Collado-Vides, 2002). Indeed, for many reef-building corals, fragmentation is the predominant mode of reproduction (Highsmith, 1982; Lasker, 1990; Smith and Hughes, 1999). Coral fragment survivorship can be size-dependent (e.g. Smith and Hughes, 1999) but is frequently unrelated to size (e.g. Lasker, 1990; Bruno, 1998). In marine algae, fragmentation is common across the three divisions (Deysher and Norton, 1982; Kilar and McLachlan,

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1986; Smith and Walters, 1999; Walters et al., 2002) and is not only important for range expansion and establishment but can also facilitate invasion (Deysher and Norton, 1982; Ceccherelli and Cinelli, 1999; Schaffelke and Deane, 2005; Wright, 2005; Wright and Davis, 2006).

The green algal genus *Caulerpa* contains approximately 70 species, of which at least three (*C. taxifolia*, *C. racemosa* and *C. brachypus*) are highly invasive (Piazzi et al., 2001; Jacoby et al., 2004; Verlaque et al., 2004). Several other *Caulerpa* species (*C. filiformis*, *C. scalpeliformis* and *C. sertularioides*) show dramatic increases in distribution and abundance (May 1976; Davis et al., 1997; Scrosati 2001), but these increases may not be permanent, especially if facilitated by environmental fluctuations (such as El Niño; Scrosati 2001). *Caulerpa* can reproduce both sexually and asexually, however, sexual reproduction has rarely been documented (Žuljevic and Antolic, 2000; Panayotidis and Žuljevic, 2001). Although the relative contribution to propagation of either mode of reproduction is not yet understood for the majority of invasive *Caulerpa* species, asexual reproduction in *Caulerpa* by fragmentation appears to be common and important for range expansion (Ceccherelli and Cinelli, 1999; Smith and Walters, 1999; Ceccherelli and Piazzi, 2001; Wright and Davis 2006).

Fragments of *Caulerpa* are generated by environmental factors, such as wave action and/or herbivory (Žuljevic et al., 2001), and by recreational and commercial fishing practices (Sant et al., 1996) and are transported by various anthropogenic activities (Walters et al., 2006). Regardless of their origin, fragments of some *Caulerpa* species, for example *C. taxifolia* and *C. racemosa*, can survive and reattach in the field (Ceccherelli and Cinelli, 1999; Ceccherelli and Piazzi, 2001; Wright and Davis, 2006). Furthermore, these fragments need not be large to persist. Fragments as small as 5 mm can survive, attach and grow, although short-term fragment survivorship in the laboratory is typically size-dependent (Smith and Walters, 1999, Walters et al., 2002). However, size-dependency of longer term growth and survivorship of fragments in the field appears more variable semi-colon between references (Walters and Smith, 1994, Walters et al., 2002).

In south-eastern Australia, *Caulerpa filiformis* is abundant on intertidal and shallow subtidal rocky shores, especially on wave exposed coastlines in the Sydney region (Pillman et al., 1997), where it can form extensive patches hundreds of metres in area (author's personal observations). *C. filiformis* was first recorded in Sydney in 1923 and observations since suggested a marked increase in abundance, replacing other species by the 1970s (May, 1976). It has been proposed that *C. filiformis* was recently introduced into Australia from South Africa (May, 1976), but rDNA ITS sequencing suggests that this is not the case (Pillman et al., 1997). Regardless, *C. filiformis* is listed as an invasive species by New South Wales Fisheries (Pollard and Pethebridge, 2002) and despite its apparent increase in distribution and abundance, little is known of the factors determining its success.

Given the lack of knowledge of the demographic factors underlying the apparent expansion of *C. filiformis* in south-eastern Australia and the very high abundance of fragments we have observed, we examined a possible role for fragmentation in the observed high local abundance of this species. We first describe the types, sizes and abundance of fragments in the water column, which allowed us to assess the relative contribution of different morphological components of this alga to the fragment pool. Common fragments types and sizes were then used to test whether fragments of *C. filiformis* have similar attachment characteristics to those of fragments from other marine algae, in particular *Caulerpa*, that successfully propagate via fragmentation (Fralick and Mathieson, 1972; Walters and Smith, 1994; Ceccherelli and Cinelli, 1999; Smith and Walters, 1999; Ceccherelli and Piazzi, 2001; Žuljevic et al., 2001; Walters et al., 2002; Wright 2005). We tested if 1) a high proportion of *C. filiformis* fragments (>50%) can regenerate, 2) larger fragments survive and grow more than smaller fragments, and 3) viable fragments attach in a short period of time (e.g. less than a week). Furthermore, we examined the role of specialised structures in the attachment process, specifically rhizoids (Walters and Smith, 1994), and tested the effect of substratum availability on the production of rhizoids by comparing settled and suspended fragments. Finally we discuss the potential importance of the above intrinsic characteristics to *C. filiformis* attachment in the field.

2. Methods

2.1. Description of study organism

Caulerpa (Chlorophyta) are coenocytic multinucleate green algae that have no internal compartmentalisation but deal with thallus rupturing by rapid healing. *Caulerpa* thalli are made up of prostrate stolons, upright fronds and anchoring rhizoids. *C. filiformis* has multiple flat, non-ramulated fronds up to 60 cm in length that are typically unbranched (but see Fig. 1). Fronds arise from a horizontal stolon which, along with rhizoids, facilitate attachment of the thallus to the substratum. An interesting morphological feature of *C. filiformis* is the ringed structure at the node, seen as the constricted section at