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# The Spreading of the Introduced Seaweed *Caulerpa taxifolia* (Vahl) C. Agardh in the Mediterranean Sea: Testing the Boat Transportation Hypothesis

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Several experiments with the green alga *Caulerpa taxifolia* (Vahl) C. Agardh were performed to test the hypothesis that boat transportation could explain its rapid and wide spreading along the Mediterranean coasts. In particular, studies were made of its desiccation resistance, drought tolerance, and survival capacity under simulated conditions prevailing in boat anchor lockers or in fishing net heaps. For comparative purposes, identical studies have been carried out with *Caulerpa prolifera* (Forskål) Lamouroux. Dehydration rates were very similar for both species, with lost of 50% of their original relative water content in 1 h, at 23 °C temperature and 70–75% of relative air humidity, and complete desiccation in 5 h. Rehydration of plants with different degrees of dehydration was also very rapid but not always complete; thalli of *Caulerpa taxifolia* recovered as much as possible after 50 min of dehydration. Restoration of productivity was highly affected by dehydration in both species, being negative in plants of *C. taxofolia* desiccated to a relative water content (RWC) lower than 60%, and in plants of *C. prolifera* desiccated below 50% of their original RWC. However, *C. taxifolia* resisted long periods of emersion, up to 10 days, when kept in darkness, at 18 °C temperature, and at high air humidity (85–90%). These results indicate that *C. taxifolia* is able to survive long periods of time on board boats when kept in conditions similar to those prevailing in an anchor locker or in a heap of fishing nets, and confirms that boat mediated transport is possible.

## Introduction

Since the accidental introduction of *Caulerpa taxifolia* (Vahl) C. Agardh in 1984, to the coasts of Monaco (Meinesz and Hesse 1991), this alga has been found in several places all along coasts of the Mediterranean Sea (Meinesz *et al.* 1993). A very small fragment of the thallus of *C. taxifolia* is perfectly capable of regrowing into a whole plant (Meinesz 1992). Once *C. taxifolia* is planted, local spreading is ensured by stolon growth, forming dense meadows of up to 14 000 blades and 350 m of stolon per square meter (Meinesz *et al.* 1995), which replace the highly diverse autochthonous photophilic algal communities and seagrass beds (Verlaque and Fritayre 1994, Villèle and Verlaque 1995).

Sexual reproduction has never been observed in Mediterranean specimens of *C. taxifolia* (Meinesz and Hesse 1991, Meinesz *et al.* 1995), and natural vegetative dispersal by drifting algae, although important (Meinesz 1992, Pou *et al.* 1993), is not able to account for rapid large scale dispersal. Most new colonies of *C. taxifolia* appear in harbours and coves several tens (and even hundreds) of miles away from the nearest colonized sites suggesting that boat transport is playing an important role in the spreading of *C. taxifolia* (Meinesz 1992, Meinesz *et al.* 1993).

Exposure to air is thought to be the main factor affecting the survival of *C. taxifolia* once on board ships. Thus, the goal of the present study is to test the hypothesis of boat transportation of *C. taxifolia* by means of its resistance to desiccation and its survival capacity under the particular conditions prevailing in anchor lockers or in fishing net heaps. In addition, and for comparative purposes, identical studies have been carried out with the indigenous Mediterranean species, *Caulerpa prolifera* (Forsskål) Lamouroux.

## Materials and Methods

Plants of *Caulerpa taxifolia* were collected by SCUBA diving at Cap Martin, Alpes-Maritimes, France (lat. 42°45'15" N; long. 7°29'40" E), at 9 m depth, in September and November 1993, while plants of *Caulerpa prolifera* were collected at Cases d'Alcanar, Tarragona, Spain (40°31'53" N; 0°31'2" E), at 3 m depth, in October 1993. Collected plants were carried to the laboratory in insulated and aerated tanks. Thalli portions (whole blades) 7 to 10 cm long were cut and cleaned of epiphytes 24 hours before each experiment.

Dehydration and rehydration processes were measured as relative water content variation (% RWC), and calculated as in equation 1, where the intermediate weight was the weight of the dehydrated sample, and the fresh weight the initial weight of the humid sample after carefully removing the surface water with blotting paper. Dry weight was determined after drying the plants to constant weight at 60 °C for at least 24 h.

$$100 \times \frac{(\text{intermediate weight} - \text{dry weight})}{(\text{fresh weight} - \text{dry weight})} = \%\ \text{RWC} \qquad \text{(eq. 1)}$$

Dehydration was followed on 6 blades exposed to air that were weighed every 10 min, during the first part of the process, and thereafter, every 20 to 60 min, under controlled laboratory conditions of 23 °C (± 1) and 70–75% humidity. Rehydration experiments tested the ability of the algae to recover their initial water content in plants dehydrated to different degrees under the laboratory conditions mentioned above. For this purpose, plants were replaced in seawater after a certain period of exposure to air, and taken out in groups of 6 at time intervals ranging from 10 min to some hours, and immediately weighed. Two experiments were conducted with different initial water contents obtained by drying for two periods:

1) with plants of *C. taxifolia* (n = 102) and *C. prolifera* (n = 60) totally desiccated after 24 h to a RWC of 2.5%, and

2) with plants of *C. taxifolia* (n = 36) desiccated for 50 min to a RWC of 70%.

Tolerating dehydration can be an alternative to avoiding tissue dehydration for survival after prolonged emersion (Levitt and Bolton 1991). To measure drought tolerance, plants with different degrees of desiccation were resubmersed for 24 h to achieve their maximum possible rehydration, and then their productivity was measured in indoor incubators. Incubations were performed with 6 replicates in 325 mL glass bottles for 2 h at saturating irradiance of 330 µmol photon $m^{-2} s^{-1}$ and 20 °C temperature under constant magnetic stirring. Seawater used in the incubations was previously filtered with glass fiber filters (Whatman GFC). Light was provided by cool light lamps (Osram 30 W) and irradiance measured with a Li-cor Data-logger and a spherical quantum sensor Li-1000 SPQA. Dissolved oxygen concentration was determined with an Orbisphere 2607 oxygen measurement system to 0.01 mg/L.

In order to simulate the conditions prevailing in the anchor lockers or in heaps of fishing nets, specimens of *C. taxifolia* were placed in a darkened incubator at 18 °C and 85–90% air humidity, and their productivity was later tested. Experimental procedure was as outlined above, but separate blades were left emersed for almost two weeks, taking 10 blades out every 2 days: 6 replicates were used to measure their oxygen production, the other 4, were returned to the aquaria to observe growth. This experiment was performed twice, once in November 93, and again in January 94.

## Results

Dehydration rates of *Caulerpa taxifolia* and *C. prolifera* were similar and can be fitted to negative exponential curves (Fig. 1). Both species lost 50% of their original RWC after approximately 1 h of exposure to air at 23 (± 1) °C, and 73% (± 3) relative humidity, reaching complete desiccation in 5 h. Both species also showed the same rehydration rates and pattern when plants previously dehydrated for 24 h were resubmersed in seawater (Fig. 2). Plants recovered about 60% of their relative water content very rapidly, in less than 10 min, but this process stopped at that level and plants did not further rehydrate, even after 24 h of resubmersion in seawater. However, less desiccated plants of *C. taxifolia*, i. e. 40 to 50 min of exposure to air (with a initial RWC of 70 ± 10%), rehydrated almost completely (91 ± 6%) in only 5 min (Fig. 2).

Restoration of productivity was highly affected by dehydration in both species (Fig. 3). *Caulerpa prolifera* showed a complete recovery in productivity in thalli with initial RWC above 70% (10.87 ± 2.43 mg $O_2$ g odw $h^{-1}$). Conversely, *C. taxifolia*, was more sensitive and highly hydrated thalli with a RWC of 90%, experienced a marked drop (1/3) in their productivity (rates of 15.90 ± 4.43 mg $O_2$ g odw $h^{-1}$, in intact thalli, compared to 5.61 ± 1.26 mg $O_2$ g odw

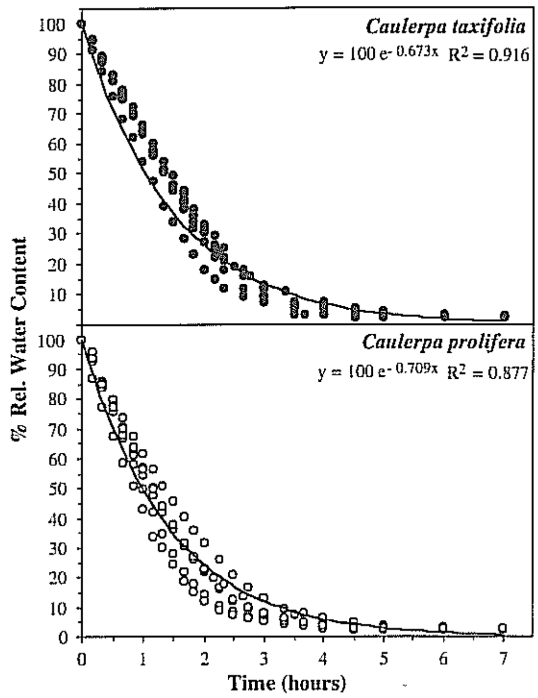


Fig. 1. Dehydration time-course of *Caulerpa taxifolia* and *Caulerpa prolifera* under continuous emersion (n = 6).

$h^{-1}$). Values for net productivity began to be negative in thalli of *C. taxifolia* desiccated to a RWC lower than 65%, while first negative values appeared for *C. prolifera* in thalli that had lost about 50% of their original RWC.

The photosynthesizing capacity of *C. taxifolia* extended for several days when the thalli were exposed to air in complete darkness and constant high air humidity (85–90%) (Fig. 4). Productivity values remained positive even after 10 days of emersion (first negative values appearing the 12th day). Further monitoring of the plants used in the experiments in aquaria revealed that thalli with positive values of productivity continued to grow normally for at least several weeks, while thalli showing negative values of productivity in the assays, leached and decomposed in a few days. Furthermore, the decrease observed in productivity is not related to plant dehydration, since the RWC of the thalli remained constant during the whole experiment (Fig. 4).

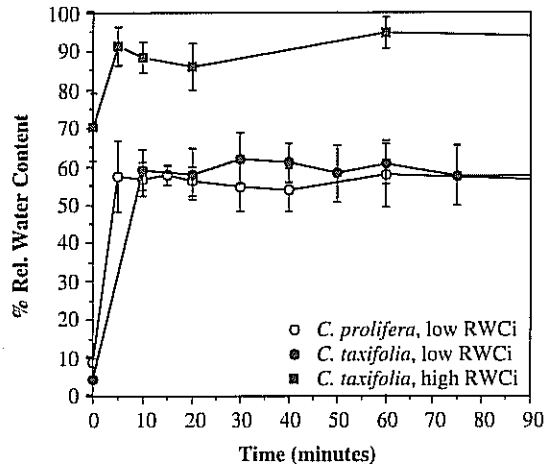


Fig. 2. Rehydration rates of *Caulerpa taxifolia* after exposure to air for 24 h (2.5% RWCi) and 50 min (70% RWCi) and of *Caulerpa prolifera* after a 24 h period of exposure to air. Plotted data are means of 6 replicates ± S. D. RWCi, initial relative water content.

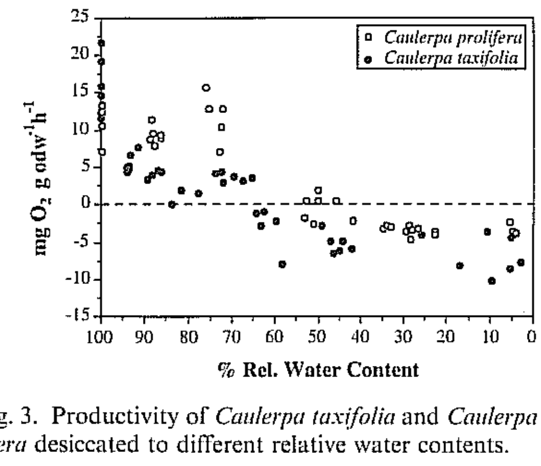


Fig. 3. Productivity of *Caulerpa taxifolia* and *Caulerpa prolifera* desiccated to different relative water contents.

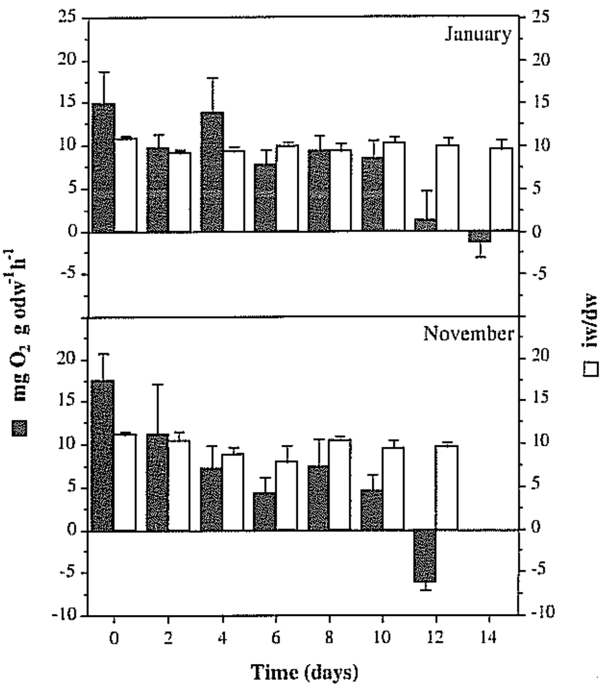


Fig. 4. Productivity and water content of *Caulerpa taxifolia* subjected to emersion in darkness at high air humidity levels in samples collected in January and November. iw/dw, ratio between the initial weight of the samples before resubmersion (iw) and its dry weight (dw). Plotted data are means of 6 replicates ± S. D.

## Discussion

The results of this study have shown that neither *Caulerpa taxifolia* nor *C. prolifera* are specially adapted to resist dehydration. The characteristics of *C. taxifolia* and *C. prolifera* regarding resistance to air exposure agree to the expected ecological requirements of both species, which exclusively occur in the sublittoral (Meinesz 1972; Littler *et al.* 1989; Meinesz and Hesse 1991). Thus, desiccation resistance and drought tolerance (*sensu* Brown 1987) of *C. taxifolia* and *C. prolifera* are markedly lower than numerous intertidal benthic macroalgae (Oates and Murray 1983, Beer and Kautsky 1992, Lipkin *et al.* 1993), and other sublittoral Mediterranean macroalgae adapted to short periods of regular emersion (Delgado *et al.* 1995, Einav *et al.* 1995). The siphonaceous nature of *Caulerpa* may have an effect in accelerating the desiccation process and could be responsible for the high observed dehydration rates.

Since totally desiccated thalli of *C. taxifolia* never rehydrate completely (60% of its original RWC, at its most), it is obvious that they are damaged as a consequence of air exposure. This damaging effect is also supported by the incapacity of *C. taxifolia* thalli that had lost at least 25–30% of their original RWC to recover photosynthesis after resubmersion. Nevertheless, resistance to emersion increases drastically when *C. taxifolia* is kept emerged in conditions similar to those met in anchor lockers or within heaps of fishing nets. In this case, thalli do not suffer any dehydration due to the high air humidity. Under these specific conditions, *C. taxifolia* is able to regain positive photosynthetic capacity even after 10 days of emersion and to continue growing normally thereafter (at least for a whole month). This should not be seen as an extraordinary ability since other intertidal and high sublittoral seaweeds have been shown to resist even much longer periods of emersion in nature (Rodríguez-Prieto 1992, Delgado *et al.* 1995).

Concluding, the results obtained here indicate that, despite the fact that *Caulerpa taxifolia* is not adapted to resist desiccation, it is able to survive several days under the conditions prevailing in a boat anchor locker or in a heap of fishing nets, strengthening the hypothesis of boat mediated spreading of *C. taxifolia* in the Mediterranean Sea.

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