

## DESICCATION PROTECTION AND DISRUPTION: A TRADE-OFF FOR AN INTERTIDAL MARINE ALGA<sup>1</sup>

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For marine algae, the benefits of drying out are often overshadowed by the stresses involved. Here we used laboratory and field experiments to examine both the costs and benefits of desiccation in the intertidal turf alga *Endocladia muricata* (Endlicher) J. Agardh. Laboratory experiments showed that when *Endocladia* is dry, photosynthesis stops, but thermotolerance increases to the point that the alga is protected from heat-induced mortality. Drying rates measured in a wind tunnel, combined with tidal data and measured wave splash, indicate that a substantial fraction of the year is spent “drying out” (~30% of the total time available for photosynthesis). During these periods, the rate of drying determines how much time is spent hydrated and potentially engaged in photosynthesis, but also vulnerable to high temperatures. Turf algae such as *Endocladia* dry from the edge of a clump inward. Consequently, the clump center remains hydrated longer than the clump edge. The resulting regionalization of a clump results in notable patterns of frond mortality (“fairy rings,” and zoned patterns of frond bleaching) within the *Endocladia* zone.

**Key index words:** desiccation protection; desiccation tolerance; *Endocladia muricata*; fairy rings; marine algae; thermotolerance

**Abbreviations:** ETR, electron transport rate; LT50, lethal temperature 50% mortality; PAM, pulse amplitude modulated; RH, relative humidity; RWC, relative water content

Desiccation increases thermotolerance for a wide variety of taxa, from insects to plants to microbes (Rothschild and Mancinelli 2001, Alpert and Oliver 2002). This protective role of desiccation is well known for resting stages and species that survive long periods of desiccated inactivity (see reviews by Crowe et al. 1992, Gaff 1997, Crowe et al. 1998, Alpert 2000, Hoekstra et al. 2001, Rascio and La Rocca 2005). Drying also increases thermotolerance in desiccation-tolerant intertidal marine algae (Kanwisher 1957, Biebl 1972, Smith and Berry 1986, Kübler and Davison 1993, Davison and Pearson

1996) that may be exposed to hot, dry conditions on a daily basis during low tide. Despite the abundant physiological work demonstrating the potentially beneficial role of desiccation, ecological experiments on the interaction between temperature and desiccation in intertidal algae have focused exclusively on the disruptive effects of desiccation (Hodgson 1981, Matta and Chapman 1995, Beach and Smith 1997). Consequently, the perspective of intertidal ecologists is dominated by the perceived stresses associated with desiccation (Schoenbeck and Norton 1978, Dromgoole 1980, Hodgson 1981, Oates and Murray 1983, Pena et al. 1999, Williams and Dethier 2005). The protective role of desiccation has received much less attention. Here we examine both the costs and benefits of desiccation in *E. muricata*.

*Endocladia* dries to a dormant and heat-resistant state during most periods of low tide. Because desiccation increases thermal tolerance at the cost of decreased photosynthesis, we will refer to this pair of desiccation-induced changes as a “trade-off.” Note that there is no active mechanism of control; *Endocladia* lacks a cuticle and loses water passively (Bell 1995, Hunt 2006). However, the notion of a trade-off indicates that desiccation has both positive and negative effects, which co-occur and must be considered together. In this context, we measured photosynthetic rates at different degrees of desiccation (costs) to pair with measurements of increased thermotolerance (benefits). We discuss how these laboratory measurements may explain patterns of frond growth and mortality seen in the field.

*Endocladia* grows as an aggregation of individuals into a thick mat or “turf” that blankets the substratum on high intertidal rocks along the Pacific coast of North America. This turf morphology is common among high-intertidal algal species worldwide (Stephenson and Stephenson 1972), and the canopy formed by these turf species is a key component of the upper intertidal habitat. For example, in central California, more than 60 species of algae and small animals shelter in the *Endocladia* turf (Glynn 1965). The turf also shelters itself, and positive interactions among neighboring fronds (such as decreased desiccation within the center of a clump) enable turfs to survive where isolated individuals cannot (Hay 1981, Taylor and Hay 1984, Scrosati and DeWreede 1998).

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At low tide, desiccation proceeds from the clump edge inward, so all clumps are regionalized into zones of decreasing desiccation toward the clump center. Using a wind tunnel, we measured differential drying times within a clump and compared times spent drying out to the total time spent hydrated (and potentially engaged in photosynthesis) under field conditions. Field hydration times were calculated from measurements of wave splash and predictions of tidal emersion. Approximately 30% of the time available for photosynthesis is spent "drying out." Thus, the desiccation environment of a frond is profoundly affected by the rate of drying, which depends on the location of the frond within the clump. When coupled with thermal limits that depend on desiccation, these differential drying rates lead to predictable patterns of frond growth and temperature-induced mortality within a clump.

#### MATERIALS AND METHODS

**Treatment of samples.** All *Endocladia* samples were collected from the high-intertidal zone (1–1.5 m above MLLW, NTDE 1983–2001) at Hopkins Marine Station, Pacific Grove, California (36.62° N, 121.91° W), and kept submerged in flowing seawater overnight. Algae were removed from the rock with a sharp putty knife to keep the holdfasts intact. Samples collected on December 13 and 14, 2003, were heated for 1 h in either a wet or dried state in a drying oven (Isotemp 500; Fischer Scientific, Pittsburgh, PA, USA). Wet samples were placed in a covered petri dish containing a small amount of seawater to ensure that the thallus remained hydrated without being submerged. "Dry" samples were dried at room temperature with a fan to 10%–15% relative water content (RWC) prior to treatment and placed in a covered petri dish during heat shock, but without any water. RWC is defined following Slayter (1967) as:

$$\text{RWC} = \frac{\text{desiccated weight} - \text{dry weight}}{\text{fresh weight} - \text{dry weight}} \times 100\% \quad (1)$$

$$= 100 - \% \text{ desiccation.}$$

where fresh weight is the weight when fully hydrated, desiccated weight is the weight of the sample when RWC is calculated, and dry weight is the oven-dried weight (50°C).

During heat exposure, the oven temperature was recorded each minute with an iButton temperature logger (Thermochron, 0.5°C resolution; Dallas Semiconductor, Dallas, TX, USA), and thallus temperature was measured with a small (40 gauge) thermocouple (Omega Engineering Inc., Stamford, CT, USA) placed near the center of the algal clump. The oven was preheated to the test temperature (between 25°C and 65°C). Dried thalli reached oven temperature within 15 min, while wet thalli reached oven temperature within 10 min. The difference was presumably due to evaporative water loss, as "dried" thalli (10%–15% RWC) continued to lose water until they equilibrated with the lowered humidity within the heated oven. Because they were contained at 100% relative humidity (RH), wet thalli could not evaporatively cool. In both cases, the 1 h exposure included this equilibration period. Following the 1 h heat shock, the samples were allowed to recover for 36 h in flowing seawater before survivorship was determined.

In addition, the survivorship of wet *Endocladia* heated for different lengths of time was determined for samples collected between October 20 and November 7, 2005. For these samples, heat stress was applied to individual fronds using an aluminum heating block. The temperature of the block was kept constant

at each end by a heater embedded at one end and tubes cooled by a water bath at the other. In this way, a temperature gradient was established within the block and samples could be held at various temperatures, depending on their placement within the gradient. Fronds were heated in the block within 1.5 mL microcentrifuge tubes that were capped, with a small amount of water in the bottom. Each tube was then inserted into a hole in the block, where fronds were held at temperatures between 30°C and 45°C for 0.5, 1, 2, and 4 h. The fronds were allowed to recover, as above, before survivorship was measured.

**Vital assay.** Survival or death of fronds was determined by measuring the photosynthetic ability of experimental samples. After heat exposure and subsequent recovery, rapid light curves were constructed for dark-adapted samples using a pulse-amplitude-modulate (PAM) fluorometer (Diving PAM; Heinz Walz GmbH, Effeltrich, Germany). Electron transport rates (ETR = quantum yield  $\times$  PAR  $\times$  0.5  $\times$  absorbance) were averaged for three saturating but not photoinhibitory light levels (Fig. 1, PAR fluxes of 500, 650, and 1,000  $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ). Absorbance was measured using a Li-Cor 1800 spectroradiometer (Li-Cor, Lincoln, NE, USA), and the PAR light source on the PAM was calibrated using a Li-Cor 190 PAR sensor. Samples were considered dead if ETR had not recovered above 25% of fresh sample ETR. Conclusions remained unchanged regardless of whether the discriminating percentage was chosen to be 25% or 60% of fresh-sample ETR because <4% of post-heat-shock samples were in the range of 25%–60% of fresh ETR. (Note that because the assay is a ratio, it is acceptable to measure only the relative ETR at a constant light intensity: absorbance and calibrated PAR values are not essential.) Samples collected in 2005 were assayed with a more rudimentary PAM (PAM 210; Heinz Walz GmbH) at the single light level of  $\sim 750 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  PAR.

To test for further recovery of ETR, 15 individuals classified as alive and 15 individuals classified as dead were assayed after an additional 24 h submerged in seawater. In all 15 samples classified as dead, there was neither substantial recovery of ETR nor a change in survival classification. In contrast, ETR

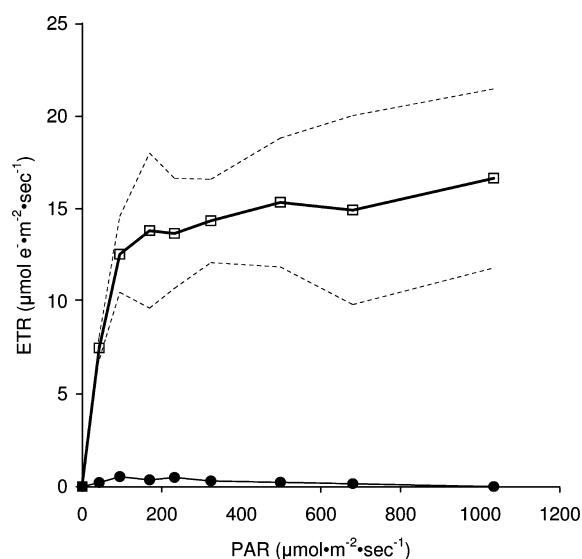


FIG. 1. Rapid light response curves for dark-adapted, hydrated *Endocladia*. Open squares are values for pretreatment samples (dashed lines are 95% confidence intervals for the data [not the mean]). Filled circles are a typical response curve for nonphotosynthesizing *Endocladia* (e.g., either "dead" or desiccated). ETR, electron transport rate.

continued to approach fresh ETR in all 15 samples classified as alive.

Survivorship curves were fit to the data using probit regression (Finney 1964) in MatLAB (MathWorks, Natick, MA, USA).

**Thermotolerance of settled spores.** Spore thermotolerance was also determined in both wet and dried states. To induce sporulation, spore-bearing thalli of *Endocladia* collected on August 8, 2005, were dried to <20% RWC at room temperature (20°C–23°C) in airflow from a fan. Thalli were then rehydrated in autoclaved filtered seawater in a large petri dish, and spores were soon released upon rehydration. During spore release, the dish was placed within a darkened incubator at 13°C (average ambient seawater temperature in Pacific Grove in August) and agitated every hour to keep the spores in suspension. After 8 h, numerous spores had been released, and the suspension was swirled gently and distributed into petri dishes, resulting in approximately equal numbers of spores in each dish from 10 parent thalli. Spores from these 10 thalli were used in all experiments. Spores were incubated for 3 d at 13°C under fluorescent light (15 W warm white bulb G.E., Fairfield, CT, USA) with a daily light period of 14 h. The water was changed daily, and the spores were allowed to dry at room temperature (~20°C to 23°C). Drying the cultures daily kept them free of ciliates, which otherwise would consume the colonies.

After 3 d, the spores were subjected to heat within a drying oven as above. Prior to heat stress, water in the dry-treatment petri dishes was poured out, and the spores (which adhered to the dish) were dried with a fan with the plate in a vertical orientation at room temperature. In wet spores, the water was poured off, and a film of water remained, which kept the spores moist. Both groups of spores were in a covered petri dish during heating. Following heat-stress, the spores were allowed to recover in autoclaved seawater for 48 h before survivorship was determined.

Individual groups of spores were marked and counted, and the group followed through treatment. Spores were classified as alive if they retained their reddish pigmentation (largely due to water-soluble phycobiliproteins [Lee 1999] that could diffuse away when the enclosing membranes were damaged). Spores that lost pigment were pronounced dead. A pilot study determined that spores retaining their pigment for 48 h continued to retain pigment for at least 4 d, while spores without pigment failed to recover and often deteriorated noticeably in this time. The fraction of all spores surviving within a dish ( $n = 87$ –150) was used as the estimate for survivorship.

**Duration of field drying times.** We made the following assumptions to estimate the height of wave splash at this site: the average height of the wave splash that first wets a site at the upper limit of *Endocladia* was measured at 20 sites after Harley and Helmuth (2003) as average distance above the still-water level when a site was first splashed. Briefly, temperatures were measured with iButton temperature loggers (Thermochron, 0.5°C resolution; Dallas Semiconductor), and the time of first wave splash was indicated by a rapid decrease in temperature. The measured wave splash was calculated as the vertical distance the iButton was above the still-water elevation at the time of the first wave splash. We assumed the waves on a falling tide were the same size as on a rising tide. Because measuring wave splash in this manner was only possible when the logger temperature was substantially above the water temperature, the resulting record had many gaps, and a wave gauge (Seabird SBE-26) ~0.1 km offshore was employed to give a continuous record in the following manner. The average significant wave height measured by the wave gauge offshore of the rocks protecting this site was 0.9 m, and we scaled the continuous wave height record for 1999–2005 by the ratio of the average measured wave splash (0.2) and the offshore average signifi-

cant wave height (0.9) to obtain a continuous estimate of wave splash at this site (Hunt 2006).

## RESULTS

**Desiccation increases thermotolerance.** The survivorship curves for both saturated (RWC ~100%) and desiccated (RWC < 15%) thalli collected at the upper limit of *E. muricata* at Hopkins Marine Station are shown in Figure 2. The temperature where 50% mortality occurred (LT50) was 35°C for wet thalli, while for dry thalli the LT50 was substantially hotter (47°C). *Endocladia* can survive hotter temperatures for shorter amounts of time (Fig. 3). This experiment was performed to determine the interdependence between LT50 and duration of heat stress.

The thermotolerance of 3-day-old spores showed a similar increase in survival when they were dehydrated, although the magnitude of the effect was less (Fig. 4). The LT50 of wet spores was 34°C–35°C, comparable to wet adult thalli, while the LT50 of dry spores was 39°C, substantially below that of dry thalli (47°C). The haploid tetraspores and the diploid carpospores showed similar patterns of thermotolerance.

**Photosynthesis during drying.** The rate of photosynthesis is negligible when thalli are dehydrated below 30% RWC (Fig. 5). This result corroborates the findings of Britting and Chapman (1993) for this species.

Within a 4 cm diameter clump, the clump edge dries more quickly than the clump center (Fig. 6), and for a moderate windspeed of  $1 \text{ m} \cdot \text{s}^{-1}$ , the clump center is moist and capable of photosynthesis (RWC > 30%) for ~1 h longer than the clump edge. Under these conditions, within 2 h the entire

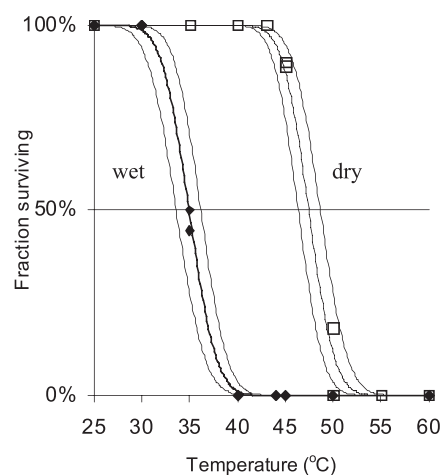


FIG. 2. Survival curves for dry (<15% RWC) and wet (100% RWC) *Endocladia* following 1 h temperature stress and 36 h recovery. LT50 values for wet and dry *Endocladia* are 35°C and 47°C, respectively. The 95% confidence limits of the probit regression are shown. RWC, relative water content.

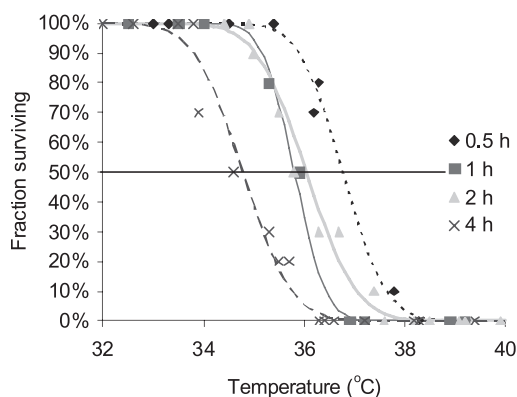


FIG. 3. Survivor curves for wet (100% RWC) *Endocladia* for different durations of heat stress. RWC, relative water content.

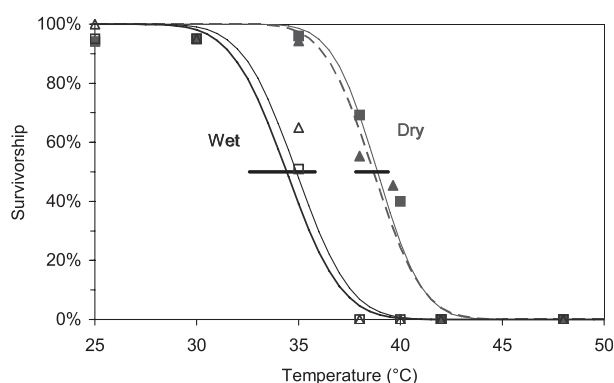


FIG. 4. Survivorship for 3-day-old spores of *Endocladia muricata* after 1 h exposure to heat stress and 48 h of recovery. Carpospores (squares, solid lines) are diploid, and tetraspores (triangles, dashed lines) are haploid; both are dispersal phases. Survivorship after desiccation is shown by filled symbols (▲, ■). Hydrated survival is shown by outlined symbols (△, □). LT50 is ~35°C when wet and 39°C when dry, regardless of life-history phase. Error bars for LT50 estimates (horizontal lines) of hydrated and desiccated spores show 95% confidence limits.

clump (both center and edge) is dried such that photosynthesis is stopped. This is the equilibrium state of *Endocladia* during emersion, which is seen as the long-term asymptote of the drying curve. The maximal possible desiccation (the equilibrium RWC) depends on ambient relative humidity (Fig. 7). For typical conditions in Pacific Grove, California, the relative humidity in the intertidal zone is between 40% and 60%, and this results in an equilibrium RWC of 5%–15% (Fig. 7). Thus, *Endocladia* survives substantial desiccation, often on a daily basis.

**Duration of field desiccation.** Between August 1999 and August 2005, *Endocladia*'s average upper limit (at 1.4 m above MLLW) was above the measured still-water level for 87% of the time (data from Monterey Tidal Observations, NOAA). However, if splashing due to waves is considered, the amount of time spent high and dry is reduced considerably. If wave splash is estimated from offshore wave height

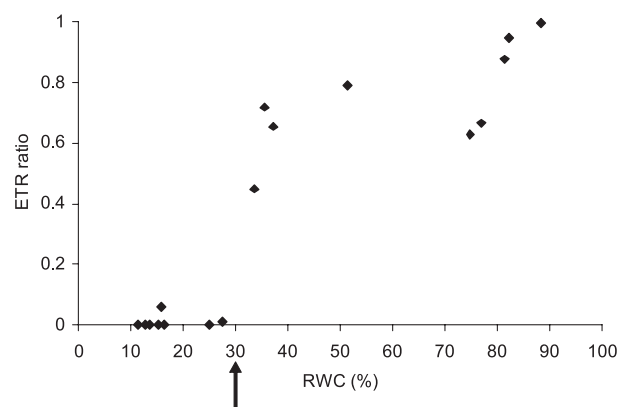


FIG. 5. Ratio of electron transport rate (ETR) during desiccation. Each point is a separate thallus. Thalli dried below 30% relative water content (RWC; arrow) have negligible rates of photosynthesis, compared to fully hydrated thalli.

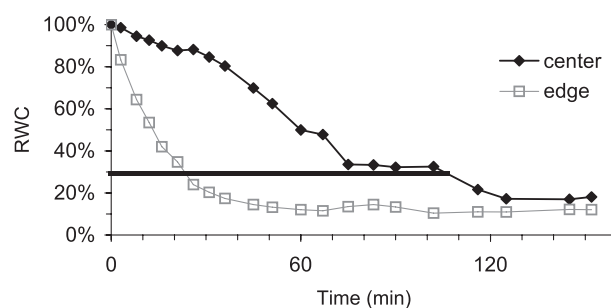


FIG. 6. Drying curves for central (◆) and exterior (□) portions of a 4 cm diameter clump of *Endocladia* measured in a wind tunnel under  $1 \text{ m} \cdot \text{s}^{-1}$  wind speed and no solar irradiation. The clump edge dries faster than the clump center, and under such conditions, fronds near the clump center experience longer periods engaged in photosynthesis with relative water content (RWC) above 30% (horizontal line is shown at RWC = 30%). Under these conditions, most of the clump is dried within 2 h, although small basal portions of fronds may remain moist.

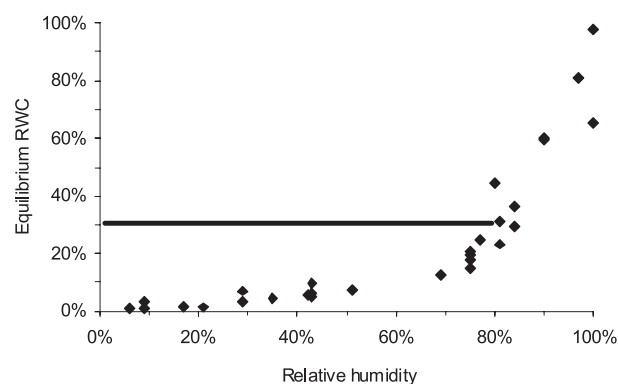


FIG. 7. Equilibrium relative water content (RWC) as a function of ambient relative humidity (RH). Humidity was controlled by saturated salt solutions, and the RWC was measured after 2 d equilibrating in a closed container above the solution. Each point is a separate thallus. Photosynthesis is negligible below 30% RWC (line shown); therefore, below ~80% RH, *Endocladia* dries to photosynthetic dormancy at room temperature.

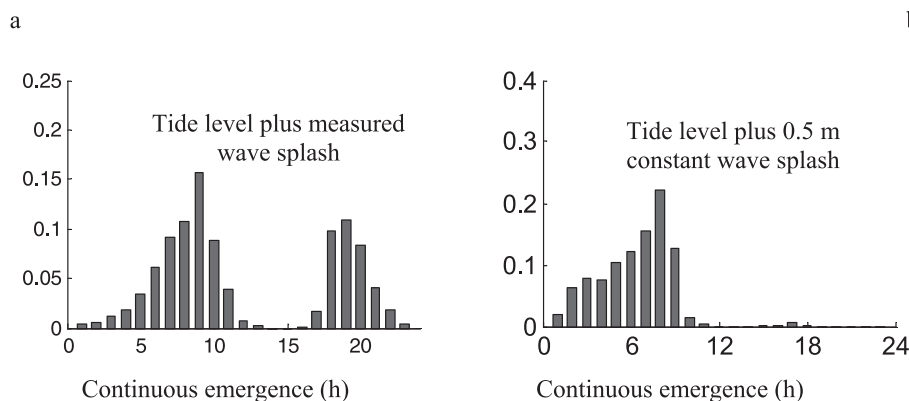


FIG. 8. Frequency histograms for continuous emergence with measured wave splash (a) and constant 0.5 m wave splash (b) above the still-water level. For example, 15% of the emergence periods lasted for 9 h when measured waves (a) were considered.

and added to still-water level, the time *Endocladia* is dried is reduced to 75%, and if a constant wave splash of 0.5 m is assumed (likely an overestimate, as the average wave splash is 0.2 m, see Materials and Methods), the fraction of time dry drops to 50%. Thus, even considering wave splash, *Endocladia* at its upper limit spends a substantial fraction of the year above the water.

Furthermore, *Endocladia* at the upper limit is exposed to air for long uninterrupted periods. The duration of emergence is shown in Figure 8 as a frequency distribution. The frequency is the proportion of emergence events that last for a specified duration. The bimodal distribution obtained with measured wave heights (Fig. 8a) results because this study site experiences mixed, semidiurnal tides. During some periods of the tidal cycle, every high tide wets the site, while at other times only one high tide per day is high enough to wet the site. Infrequently, emersion lasts longer than a day (1% of the periods of emergence with measured waves), and the maximum continuous emergence was 4.6 d, in May 2002. The unimodal distribution obtained with constant 0.5 m waves indicates that under these conditions the upper limit is almost always splashed during both daily periods of high tide.

#### DISCUSSION

The thermotolerance of *E. muricata* markedly increases when thalli are dried, both for mature thalli and for recently settled spores, and photosynthesis stops when thalli are dried below 30% RWC. Thus, due to the dependence of thermotolerance on desiccation, there is a trade-off between survival and the potential for growth. This trade-off is manifest within an *Endocladia* clump: compared to interior fronds, the outer fronds dry more quickly and therefore experience both less time exposed to potentially lethal temperatures and less time hydrated and engaged in photosynthesis. The ecological importance of this trade-off relies on two conditions: first, increased survival of dry thalli, and second, enhanced growth of fronds that remain moist longer.

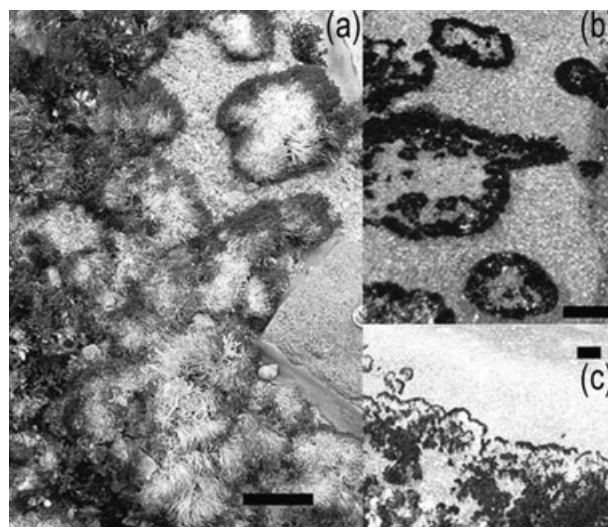


FIG. 9. (a) *Endocladia* bleaching pattern during widespread bleaching event of July 3, 2003. The central bleached portion subsequently died. (b, c) *Endocladia* "fairy rings," are a common sight in the central California intertidal zone. Scale bars are 5 cm.

*Increased survival when dry.* The maximum temperature of *Endocladia* we have measured in Pacific Grove, California, is 41°C, on April 26, 2004 (in this case the crispy-dry alga survived). This temperature exceeds the thermal limit (LT50 = 35°C) of both mature thalli and spores when they are hydrated. It is also above the thermal limit of dry spores (LT50 = 39°C), but well below the thermal limit of dry thalli (LT50 = 47°C). The maximum temperature of wet *Endocladia* we have measured is 37°C (on July 3, 2003). In this case, there was widespread bleaching, and the alga died (see Fig. 9a). Thus, in Pacific Grove, California, dried thalli appear to be at minimal risk of thermal mortality, while hydrated thalli do experience lethal temperatures.

*Increased growth when wet.* Within a clump, central fronds remain moist longer (Fig. 6), and they appear to grow faster than peripheral fronds: Outer fronds of high-intertidal *Endocladia* clumps do not bear sporangia, and they are often much shorter



than the fronds of the clump interior. Within the clump centers, reproductive portions of the fronds are shed seasonally (personal observation), and this biomass must be regenerated. If growth rates (neglecting tissue loss) were the same at the clump edge and at the center, the seasonal loss of material from central fronds would cause these fronds to elongate more slowly. In clumps with minimal frond mortality (so frond age is not a dominant factor), the slower rate of elongation would lead to central fronds that are shorter than peripheral fronds. However, the opposite size trend is observed: fronds are usually longer in the clump center, which suggests that these fronds may grow faster.

A notable pattern of bleaching in the middle of individual fronds also suggests that mortality is desiccation dependent. During the widespread bleaching (and subsequent mortality) event of July 2003, we were perplexed to find that the middle length of the fronds often bleached, while the tips and very base retained their pigment (Fig. 10). These individuals later appeared to have healthy frond tips, but the fronds eventually broke below the bleached portion and regrew from the unharmed basal region.

The July 2003 event was the only widespread bleaching of *Endocladia* that we observed during 5 years of weekly observation (2000–2005). This bleaching was different than the summer “yellowing” and inflating of tetrasporophyte fronds. When these yellowing fronds are viewed under a microscope, maturing tetraspores are visible. In contrast, the bleaching in 2003 was pure white. Tetraspores had lost their pigment, and female gametophytes (and attached carpogonia) were also bleached white. In light of the markedly different thermotolerance between wet and dry thalli, we suggest that the frond tips might have been protected because they had dried. The frond base was close enough to

the rock and shaded to the point that it remained cool enough to survive even when wet. However, the middle length of the frond died because it was both wet and less shaded, and therefore it reached its lethal temperature.

A second pattern of mortality also indicates the importance of desiccation-enhanced thermotolerance. Numerous events that prove lethal to interior fronds leave a fringe of *Endocladia* surviving—only the outermost fronds survive in a “fairy ring” (Fig. 9). Many fairy rings were generated by the thermal bleaching event noted above, which preferentially killed central fronds (Fig. 9a). Although we observed fairy rings caused by desiccation protection, other mechanisms (such as the clump center filling with trapped sediment) may also generate similar patterns.

The surviving outer fronds in a fairy ring often are the source for vegetative recolonization of the clump center. Thus, these outer fronds may serve a dual purpose: they may slow the drying rate of the inner, reproductive fronds (increasing the time they are hydrated and engaged in photosynthesis), as well as acting as a source for recolonization via vegetative growth in the event of a thermal catastrophe. The clump periphery appears to have an ecological function similar to the persistent basal crust of turf species (Hay 1981), and it may be a generally important function of the turf form in species that lack a prominent basal crust.

*Duration of natural exposure: the magnitude of the trade-off.* Time spent drying out is a large portion of the total time *Endocladia* spends hydrated and potentially engaged in photosynthesis. During most periods of low-tide emergence, peripheral clumps are dried to a dormant state. That is, >98% of emergence events considering measured wave splash (or >90% for 0.5 m waves: an overestimate of wave splash, see Materials and Methods) lasted more than 2 h, which is roughly the time it takes for the peripheral regions of *Endocladia* clumps to dry out in typical wind conditions (Fig. 6). The central portions of large clumps, however, may remain wet for much longer, and this can greatly extend the time available for photosynthesis.

Considering only daylight hours ( $\text{PAR} > 100 \text{ W} \cdot \text{m}^{-2}$ ), ~10% of the year is spent drying during the 2 h following emergence (10% for measured waves, 13% for modeled 0.5 m waves). Since *Endocladia* is below the elevation of wave splash for only 25%–50% of the year, this time spent drying represents a substantial fraction of the total time spent hydrated and potentially engaged in photosynthesis (~30% for measured waves and ~15% for 0.5 m modeled waves). The slower drying rate at the clump center relative to the clump edge results in a large increase in the time available for photosynthesis.

*Endocladia* is noteworthy in that it experiences >90% absolute desiccation [Alpert's (2005) criterion

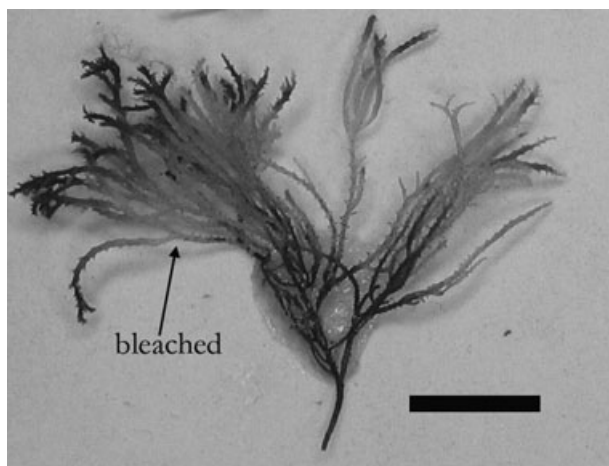


FIG. 10. Bleaching pattern seen on fronds (July 3, 2003). The bleached portion subsequently died and broke off. Scale bar is 5 cm.

for “desiccation tolerant” or “anhydrobiotic” species], often on a daily basis. Here we have shown how the simultaneously protective and disruptive effects of desiccation may lead to ecological trade-offs and notable patterns within these aggregating turf algae.

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