Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga
*Mastocarpus papillatus* Kützing

Emily Carrington Bell

*Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA*

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**Abstract**

The upper limits of vertical zonation for intertidal macroalgae are largely determined by the algae's ability to withstand temperature and desiccation stress when exposed to air at low tide. However, very little is known about the processes that determine thallus temperature and desiccation rates in the field. This study provides a quantitative analysis of the effects of the physical environment (i.e. sun, wind, air vapor density) on the temperature and rate of desiccation of the intertidal macroalga *Mastocarpus papillatus* Kützing. Wind tunnel experiments measure directly the influence of single physical factors on thallus temperature and desiccation, and demonstrate how thallus temperature and thallus hydration are coupled. Under most physical conditions, fully hydrated thalli readily evaporate water and are consequently below air temperature. Desiccated thalli, however, have no water for evaporative cooling and can greatly exceed air temperature, particularly when wind velocity is $<0.4 \text{ m} \cdot \text{s}^{-1}$.

In addition, the effects of thallus morphology on thallus temperature and desiccation are examined. Increasing thallus thickness decreases the rate of desiccation, while increasing the degree of thallus dissection (i.e. branching) increases both the rate of desiccation and the rate of heat dissipation. Thus, while thallus temperature and desiccation are ultimately controlled by the physical environment, they can be influenced by thallus morphology.

**Keywords:** Desiccation; Intertidal; Macroalga; *Mastocarpus*; Morphology; Temperature

1. Introduction

Bell (1993) suggests that the red alga *Mastocarpus papillatus* Kützing is typical of high intertidal macroalgae in that it is photosynthetically active when exposed to air, with rates increasing with thallus temperature but decreasing markedly as
the thallus dries out. Furthermore, the rate of recovery of photosynthesis upon reimmersion in seawater is dependent on the thallus temperature prior to immersion. Thus thallus heating and desiccation influence growth by affecting both emersed and immersed rates of photosynthesis. In addition, the survival of a macroalga is threatened when extreme thallus temperatures are encountered during low tide.

While the effect of temperature and desiccation on the physiology of macroalgae is well documented (see Bell, 1993), there is very little quantitative information on the thallus temperatures and desiccation rates that actually occur during low tide. How often are macroalgae exposed to extreme temperatures or levels of desiccation? During low tide, do they remain hydrated long enough to fix a significant amount of carbon? Clearly the answers to such questions require a knowledge of the physical properties of a thallus, as well as how it interacts with its environment.

A number of studies have enumerated properties of a thallus that can influence its desiccation rate. As reviewed by Dromgoole (1980), it has been suggested that thallus water content, cell wall thickness, and biochemical composition may all affect the rate of thallus desiccation. A low ratio of thallus surface area to volume and overlapping branches can also slow the rate of desiccation (Schonbeck & Norton, 1979; Dromgoole, 1980).

The above studies were designed to investigate interspecific differences in thallus desiccation with the goal of explaining patterns of intertidal zonation, and to this end they measured desiccation under controlled laboratory conditions. It is clear, however, that the physical environment to which algae are exposed in the field can have a profound influence on their rate of desiccation. For example, Beer & Eshel (1983) found that the drying rate of Ulva sp. was three times higher at noon than it was in the morning. Maberly & Madsen (1990) observed similar variations in the drying rate of Fucus spiralis measured under six different daytime conditions varying in air temperature, irradiance, and relative humidity. While these studies highlight the importance of the physical environment in determining desiccation rates in nature, they do not isolate which aspect of the environment may be most important.

On the central coast of California, air temperatures to which algae are exposed in the intertidal can range from 2 to 35°C (Hodgson, 1981; pers. obs.). How closely coupled are thallus temperature and air temperature? As was briefly alluded to by Dromgoole (1980), this coupling can be influenced by the level of thallus hydration. Intertidal macroalgae can have very low resistances to water loss, losing water from their surfaces about 84% as fast as water is lost from a free water surface (Schonbeck & Norton, 1979). Because the process of evaporating water from a surface involves the removal of energy from the surface, it is possible that the temperature of thalli with high rates of desiccation could be substantially lower than air temperature.

The purpose of this study is to analyze quantitatively the effects of the physical environment on the temperature and rate of desiccation of an intertidal macroalga. Wind tunnel experiments were used to measure directly thallus tempera-
ture and desiccation under various combinations of physical factors. These experiments provide a quantitative measure of how a single physical factor, such as wind velocity or solar irradiance, can influence thallus temperature and desiccation, and how thallus temperature and thallus hydration are coupled.

In addition, this study examines the role of thallus morphology in determining thallus temperature and desiccation during low tide. The transfer properties of terrestrial leaves have been shown to be dependent on leaf shape (Parkhurst et al., 1968; Vogel, 1970; Balding & Cunningham, 1976; Smith & Nobel, 1977; Gurevitch, 1988) and size (Nobel, 1978; Woodhouse et al., 1983). Smaller and highly dissected leaves typically have thinner boundary layers and are, therefore, able to transfer heat and mass more effectively than large or non-dissected leaves. In this manner, the temperature and desiccation rate of a thallus during low tide may depend on aspects of its morphology.

This study shows that thallus temperature is intimately tied to its hydration. Under most physical conditions, fully hydrated thalli have high rates of evaporative water loss, and are, therefore, generally below air temperature. If the exposure to air is long enough for thalli to completely desiccate, however, evaporation is no longer possible and thalli can greatly exceed air temperature. Thallus temperature and desiccation are ultimately controlled by the physical environment, but can be influenced by thallus morphology.

2. Materials and methods

2.1. Algal material

*Mastocarpus papillatus* Kützing is an intertidal red alga commonly found in the middle to high intertidal zones on the Pacific Coast of North America (Abbott & Hollenberg, 1976). Thalli may reach 15 cm in length and exhibit a variety of branching patterns, from a few broad to many narrow branches (Carrington, 1990). The surfaces of the thalli are covered with papillae which can vary in spatial density (number per area) and size among growth forms. Thalli were collected at low tide near Agassiz Beach at Hopkins Marine Station (HMS), Pacific Grove, CA (36°37' N, 121°54' W). Only female gametophytes, the predominant erect form at HMS, were used in this study. Thalli were kept in the laboratory in aerated filtered seawater at 15°C for 12–24 h before use in any experiment.

2.2. Thallus temperature and desiccation in the laboratory

2.2.1. Wind tunnel and instrumentation

The wind tunnel was 60 by 60 cm in cross-section and 3.6 m in length, the floor of which was constructed from plywood and the sides and top from 5 mm thick Plexiglas. A variable speed fan drew air through the tunnel at a maximum mainstream velocity of 7 m·s⁻¹. Flow was collimated at each end of the tunnel.
by an array of polystyrene egg crate louvers (10 cm length, 1.25 cm grate size; AIN Plastics, Salinas, CA).

Thalli were placed on a small granite rock in the working section of the wind tunnel (2 m downstream from tunnel entrance; Fig. 1). The rock was $25 \times 19 \times 9$ cm ($1 \times w \times h$) in size and had a relatively flat horizontal upper surface. Granite is the natural substratum for *M. papillatus* at HMS and for much of the central coast of California.

Wind velocity was measured with an R1D-type anemometer (model HH-615, Omega Engineering, Stamford, CT, modified for voltage output) at a fixed position $\approx 30$ cm downstream and 30 cm to the side of the rock (Fig. 1). Based on an empirical relationship established by Bell (1992), the measured wind velocity was converted to an equivalent free stream velocity 1 cm above the thallus surface.

Irradiance was provided by up to three 500 W flood lamps (Model PAR64, Sylvania, Danvers, MA) shining through the top of the wind tunnel. Thermal loading of the top of the tunnel was reduced by suspending the flood lamps over a

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Fig. 1. Wind tunnel and instrumentation used for thallus temperature and desiccation experiments. (A) Side view of the entire tunnel. (B) Close up view of the working section from the top.
3 cm deep bath of water (constructed from 7 mm thick Plexiglas). Total shortwave irradiation (W m$^{-2}$) reaching the thallus surface was measured with a LiCor pyranometer (model LI-200SB, Lincoln, NE; calibrated for use with artificial light, see Bell, 1992).

A sling psychrometer (Weksler Instruments, Freeport, NY) measured wet bulb and dry bulb temperature to the nearest 0.5°C. The two temperatures were used to determine ambient relative humidity from a standard psychrometric table.

Thallus temperature was measured to the nearest 0.1°C with a modified thermocouple (AWG 40 thermocouple wire threaded through the sawed-off tip of a 29 gage hypodermic needle, see Bell, 1992). A total of five thermocouples, arranged haphazardly in the broader, distal half of the thallus, were used to estimate average thallus temperature.

Air and rock temperatures were measured with larger, conventional thermocouples (AWG 24, 0.51 mm diameter). The thermocouple measuring air temperature was placed 3 cm above the granite surface and was shaded from direct irradiation. A shallow (5 mm) groove cut in the granite rock housed the rock temperature thermocouple. The thermocouple wire was secured in the groove with cement so that the temperature-sensing junction was 1–2 mm below the surface.

Thallus desiccation during the experiments was determined from periodic measurements of thallus weight. Weight measurements were complicated by the fact that the thallus could not be easily removed from the wind tunnel once the thermocouples were in place. As a solution to this problem, a platform was designed to support the thallus and lie flush with, but not touching, the granite rock in the wind tunnel (Fig. 1). The circular platform (7 cm diameter) was made of 4 mm thick Plexiglas, which was covered with shards of granite (roughly 1 cm$^2$ by 0.4 cm). A nylon screw placed on the upstream edge of the platform secured the base of the thallus stipe. The support to the platform passed through a channel cut in the rock and was mounted on a digital balance (model S-300D, Fisher Scientific, Springfield, NJ) in place of the standard weighing plate. By taking into account the constant weight offset of the platform and thermocouples, accurate measurements of thallus weight were achieved. The five thermocouples monitoring thallus temperature were anchored in place with modelling clay, as any change in position of these wires (caused by the wind) would alter the offset of the weight measurements. High wind velocities caused fluctuations in the balance readings, thus it was necessary to turn off the fan motor briefly to read the balance. The balance was allowed to equilibrate for ≈15 s before each reading was made.

Thallus desiccation was expressed in terms of relative water content (RWC), where

\[
RWC = \frac{\text{desiccated wt} - \text{dry wt}}{\text{fresh wt} - \text{dry wt}} \times 100\%.
\]  

(1)

Fresh weight was determined after blotting surface water from a fully hydrated
sample. Dry weight was determined after drying for 48 h at 60°C after wind tunnel experiments on the thallus were completed. All weights were measured to the nearest 0.01 g.

2.2.2. Physical factors influencing thallus temperature and desiccation

Four experiments were designed to evaluate the general trends in thallus temperature and desiccation as a function of a single environmental parameter (wind, irradiance, or air vapor density) while the other parameters were held as constant as was practical. Three to six replicate thalli were used for each experiment. Thalli were “typical” in that they did not exhibit an extraordinary degree of dichotomous branching and spanned a broad range of thickness. It is assumed that these thalli provide a good representation of the response of *M. papillatus* thalli to physical factors. Separate experiments (described in the following section) were designed to evaluate more specific effects of thallus morphology on temperature and desiccation. Each experiment consisted of a series of "runs", where environmental parameters were held constant during each run, but the single parameter of interest was varied between runs. Thus, a response curve was constructed by assimilating the analyses of thallus temperature and desiccation rates from each run of an experiment.

Each run started with a fully hydrated thallus placed in the wind tunnel under constant physical conditions. The run was terminated when the water lost by the thallus was \( \leq 0.01 \) g during a 10-min interval. Thus the duration of each run depended on the physical parameters to which the thallus was exposed, as well as the drying properties of the thallus itself. Thallus, air, and rock temperatures were sampled by a datalogger (model 21X, Campbell Scientific, Logan, UT) every second and averages were stored every 15 s (or every 30–60 s for longer runs). Thallus weight was measured every 2 min at the beginning of the run, then less frequently (every 5 or 10 min) as the rate of thallus desiccation slowed, for a total of 10–20 weight measurements.

For the analysis of thallus temperature during each run, the difference between air temperature and thallus temperature (the average of five thermocouples) was calculated. This difference was plotted as a function of time \( t \) in minutes, and modeled as a sigmoidal function:

\[
T_{\text{thallus}} - T_{\text{air}} = a + b \left( \frac{1}{1 + \exp \left( \frac{c - t}{d} \right)} \right)
\]  

(2)

The constants \( a-d \) were determined using a least-squares curve-fitting program (TableCurve, Jandel Scientific, Corte Madera, CA). Constant \( a \) corresponds to the initial difference between air temperature and thallus temperature (when the thallus was wet), and \( a + b \) corresponds to the final difference between air temperature and thallus temperature (when the thallus was dry). Constants \( c \) and \( d \) describe the rate and timing of the transition from wet thallus to dry thallus. Specifically, \( c \) is the time at which the point of inflection occurs in the sigmoidal
function and is therefore a measure of the time required to reach the wet thallus-dry thallus transition. \( d \) defines the rate at which the transition is made.

The rate of desiccation of a thallus can be represented as the flux density of water vapor across a gradient (Campbell, 1977):

\[
E = \frac{\rho'_{\text{thallus}} - \rho_{\text{air}}}{r_m}
\]

where \( E \) is the rate of water loss (in g \( \cdot \) s\(^{-1} \)) divided by the area over which water transport occurs (taken as the projected thallus area in m\(^2\)). \( \rho'_{\text{thallus}} \) is the water vapor density at the thallus surface, \( \rho_{\text{air}} \) is the water vapor density of the surrounding air (both in g \( \cdot \) m\(^{-3} \)), and \( r_m \) is the resistance to mass transfer in s \( \cdot \) m\(^{-1} \). \( r_m \) describes the transfer of water vapor from the thallus to the air, and is dependent on wind velocity and the pattern of flow around the thallus as well as the resistance of the thallus to water loss. For this reason, \( r_m \) is a useful parameter for describing desiccation as a function of wind velocity and thallus morphology. \( r_m \) can be solved for by rearranging Eq. 3.

The prime in \( \rho'_{\text{thallus}} \) denotes that the thallus surface is saturated, thus water vapor density at the thallus surface can be calculated from thallus temperature and relative water content, as described in the Appendix. On the other hand, \( \rho_{\text{air}} \) is not necessarily at saturation and is therefore dependent on relative humidity, RH, and air temperature, \( T_{\text{air}} \):

\[
\rho_{\text{air}} = RH \rho'_{\text{air}}
\]

\( \rho'_{\text{air}} \) is the saturation vapor density of air and is dependent on \( T_{\text{air}} \), as described in the Appendix. \( \rho_{\text{air}} \) was assumed to be constant during the entire run and was therefore calculated from relative humidity and air temperature measurements made at the beginning of each run.

The flux of water per area, \( E \), decreased exponentially over time, and it was therefore necessary to calculate \( r_m \) over short time intervals. A total of 10 calculations were made that spanned the length of each run. Each calculation was made using thallus temperatures averaged over three weight measurements, thus calculations made early in a run spanned 6 min, but those made later in the run spanned a longer period of time (up to 30 min). The average relative water content was also calculated over each time interval.

Effect of air vapor density. The effect of changes in air vapor density on thallus temperature and desiccation was evaluated for three thalli. As indicated by Eq. 4 and the Appendix, the density of water vapor in air is governed by the temperature and relative humidity of the air. Various air vapor densities were achieved by adjusting the flow-through heating system in the laboratory: warming the air decreased its relative humidity but had a net effect of increasing its vapor density. It was not practical to vary either parameter (\( T_{\text{air}} \) or RH) independently. Each of the three thalli were run at air temperatures of 20, 25, and 30°C (±0.5°C) with relative humidities of 55, 49, and 41% (±2%), respectively, for a total of
nine runs. These conditions correspond to air vapor densities of 9.8, 11.2 and 12.1 g·m\(^{-3}\), respectively. Wind velocity was 2.5 m·s\(^{-1}\) for all runs, while irradiance was 660 W·m\(^{-2}\). Thalli were rehydrated completely in seawater between runs. The estimate of the temperature difference between a wet thallus and air \((a)\) from each run were compared to the difference in wet bulb and dry bulb temperatures (i.e. the *wet bulb depression*) of the sling psychrometer reading. The wet bulb depression provided a useful index for analysis because it also depends on air vapor density (Campbell, 1977):

\[
T_{\text{wet}} - T_{\text{dry}} = \frac{-1}{\gamma(\rho'_{\text{wet}} - \text{RH}\rho'_{\text{dry}})}
\]

where \(T_{\text{wet}}\) and \(T_{\text{dry}}\) are the wet and dry bulb temperatures, respectively, and \(\gamma\) is the psychrometric "constant" (equal to 0.495 g·m\(^{-3}\) C\(^{-1}\) at 20°C). \(\rho'_{\text{wet}}\) and \(\rho'_{\text{dry}}\) are the saturation vapor densities at \(T_{\text{wet}}\) and \(T_{\text{dry}}\), respectively. The expression \(\text{RH}\rho'_{\text{dry}}\) is the density of water vapor in the air. In this study, the wet bulb depression is defined as \(T_{\text{wet}} - T_{\text{dry}}\) and therefore is less than or equal to zero.

**Effect of wind velocity.** Four thalli were used to evaluate the effect of changes in wind velocity on thallus temperature and desiccation. Each of the four thalli were run at four to seven different wind velocities ranging from 0 to 6.7 m·s\(^{-1}\) (haphazardly ordered) for a total of 21 runs. The other environmental parameters were held constant for all runs: irradiance at 660 ± 10 W·m\(^{-2}\), air temperature at 25 ± 1°C, and relative humidity at 45 ± 5%. The resistance to mass transfer \((r_m)\) and the difference between thallus and air temperatures (both \(a\) and \(a + b\) of Eq. 2) were calculated for each run, and were then plotted as a function of wind velocity. Thirteen runs from the irradiance response experiments (those at an irradiance of 660 W·m\(^{-2}\), as described below) were also included in this wind response analysis. A power curve was used to model the variation in \(r_m\) as a function of wind velocity, fit using a least-squares iterative search algorithm (Statgraphics, STSC, Inc., Rockville, MD).

**Effect of irradiance.** Two irradiance response experiments were conducted: one with high wind velocity (6.4 m·s\(^{-1}\)) and one with low wind velocity (0.15 m·s\(^{-1}\)). For the high wind experiment, six thalli were run at four to seven haphazardly ordered irradiances ranging from 0 to 1000 W·m\(^{-2}\) (an approximate value for summer midday sun), for a total of 34 runs. Four different thalli were used for the low wind experiment, run at irradiances ranging from 0 to 800 W·m\(^{-2}\) for a total of 20 runs. In both experiments, air temperature was held constant at 25 ± 1°C and relative humidity was 45 ± 5%.

### 2.3. Morphological determinants of thallus temperature and desiccation

**Morphological parameters.** Thirteen morphological parameters that could potentially affect thallus temperature and desiccation were measured for 44 *M.*
papillatus thalli. (1) Fresh weight was measured to the nearest 0.01 g and (2) length to the nearest mm. (3) Thallus thickness including papillae and (4) thickness excluding papillae were measured with vernier callipers to the nearest 0.05 mm. (5) The density of papillae was estimated to the nearest 10 papillae per cm². The branching morphology of each thallus was measured in terms of (6) the total number of dichotomous branches, as well as (7) the branching order, i.e. the number of levels where the branches were produced. For example, a thallus with one branching order has a total of one branch, a thallus with two orders has three branches, a thallus with three orders has seven branches, etc. A perfectly dichotomous thallus with n orders has 2ⁿ−1 branches. (8) Projected area measured to the nearest 0.01 cm² and (9) perimeter to the nearest 0.01 cm were obtained by digitizing thallus tracings (SigmaScan, Jandel Scientific, Corte Madera, CA). The perimeter measurements were divided by thallus projected areas to provide estimates of thallus dissection (i.e. the amount of edge per unit area).

A relative measure of (10) surface area (SA) was obtained using a modified version of the spectrophotometric technique of Hoegh-Guldberg (1988). A thallus was briefly dipped in a solution prepared with 400 ml filtered seawater, a small amount of detergent (0.10% Triton X100 w/v) and 0.4 g of methylene blue. The thallus was shaken 10 times, then immersed in 30 ml of filtered seawater. Absorbance of the eluted dye solution at 663 nm was measured on a diode array spectrophotometer (model 8452A, Hewlett-Packard, Palo Alto, CA). Five replicate elutions were performed on each thallus.

Three morphological parameters were derived from the directly measured parameters. (11) Thallus fresh weight per projected area (weight/area) described the effective thickness of the thallus. (12) Surface area per fresh weight (SA/weight) was an index of the surface area to volume ratio of the thallus. (13) Surface area per projected area (SA/area) provided an estimate of the roughness of the thallus surface.

Many of these parameters describe the same morphological trait, such as thallus "roughness" or "thickness". A matrix of correlation coefficients was constructed for the thirteen parameters in order to identify groups of highly correlated (thus redundant) parameters (SigmaStat, Jandel Scientific, Corte Madera, CA). Representative parameters were selected from each group and were used as independent variables in the multiple regression analyses described below.

**Experimentation.** Each of the 44 thalli was run under two conditions: at a low wind velocity of 0.15 m·s⁻¹ and a high wind velocity of 6.4 m·s⁻¹. Irradiance was maintained at 660 ± 10 W·m⁻², air temperature at 25 ± 1°C and relative humidity at 45 ± 5%. Each run was analyzed for the difference between thallus and air temperature and the resistance to mass transfer as described in the previous section. At each wind velocity, morphological parameters were used as the independent variables in stepwise multiple regression analyses (SigmaStat) to account for the variation in each of four dependent variables: the temperature difference between a wet thallus and air, the temperature difference between a
dry thallus and air, the time at which the transition from wet thallus to dry thallus occurred (parameters \(a\), \(a + b\), and \(c\) in Eq. 13, respectively), and the resistance to mass transfer. Thus, a total of eight multiple regressions were performed. The criterion for entry of a variable was \(p < 0.05\) for an \(F\) test of the hypothesis that the coefficient of the entered variable is zero.

2.4. Thallus temperature in the field

As a test of the validity of the wind tunnel experiments, thallus temperatures were measured during low tide in the field on the afternoons of October 20 and 23, 1991. These days were selected haphazardly, but are representative of warm sunny and cool sunny days, respectively. The site was near Agassiz Beach at HMS where a healthy population of \(M.\ papillatus\) was growing. Instrumentation was set up on a horizontal site as soon as the tide had receded. The temperatures of ten thalli were measured by single thermocouples and a thermocouple shaded from direct sunlight measured air temperature at the height of the canopy surface. Wind velocity was measured 4 cm above the canopy surface, and solar irradiance was measured at the level of the canopy. The datalogger sampled wind velocity every second, and stored the average and maximum at 1-min intervals. Thallus temperatures, air temperature, and solar irradiance were sampled every 5 s, and average values were stored at 1-min intervals. Recordings were made for 2–3 h, until the sun was no longer shining directly on the site. Relative humidity was measured every 30–50 min.

It was not practical to measure thallus weight during the field measurements without disrupting the temperature measurements. Instead, relative water content was estimated from samples of five nearby thalli every 30–50 min. The nearby thalli were haphazardly selected and immediately weighed. Thalli were subsequently hydrated and then dried to determine fresh and dry weight, respectively, and relative water content was calculated using Eq. 1.

On October 23, the final relative water content of each thallus that was used for temperature measurements was determined. This was possible because the thalli had not dried to the point of shrinking onto the temperature probe, so it was not necessary to rehydrate the thalli in order to remove the probe. At the termination of the measurements the temperature probes were removed, the thalli were immediately brought into the laboratory, and relative water contents were determined as described above.

3. Results

3.1. Thallus temperature and desiccation in the laboratory

Typical time courses of temperature and desiccation for the same thallus run under two different wind conditions are shown in Fig. 2. Relative water content decreased exponentially in both cases, but the rate of water loss was higher at the
Fig. 2. Time course of air, rock and thallus temperature (left axes) and thallus desiccation (right axes) in the wind tunnel. Irradiance = 660 W m$^{-2}$. (A) Thallus exposed to high wind (6.4 m s$^{-1}$). (B) The same thallus exposed to low wind (0.15 m s$^{-1}$).

higher wind velocity (Fig. 2a). While air and rock temperatures were fairly stable over time, thallus temperature was initially below air temperature, then rapidly increased mid-way through the run to a temperature above that of the air. Because air temperature was controlled to only ±1°C, it was useful to express thallus temperature in terms of its deviation from air temperature for further analyses and comparisons.

Two different thalli run under the same conditions showed similar patterns of temperature variation with time, but differed in the timing of temperature increase (Fig. 3a). The same thalli also differed in their rate of desiccation: the thallus that surpassed air temperature faster also dried out faster (Fig. 3b). However, if $T_{\text{thallus}} - T_{\text{air}}$ is plotted versus relative water content instead of time, the two thalli follow the same temperature pattern: below air temperature when relative water content is >30%, in transition from 30 to 10% RWC, and above air temperature at 10% RWC and below (Fig. 3c). All other runs showed similar patterns of thallus temperature with relative water content.

The sigmoidal function (Eq. 2) provided a satisfactory description of the difference between thallus and air temperature over time (e.g. Fig. 3a, $r^2 = 0.98$–0.999; minimum $n = 120$ for each run). Because thallus temperature was linked to relative water content, the constant $a$ corresponds to the difference in thallus and air temperature for a "wet" thallus (100–80% RWC) and $a + b$ corresponds to
Fig. 3. Two thalli run under the same physical conditions, illustrating the interdependence of thallus temperature and relative water content. Wind velocity = 6.4 m·s⁻¹, $T_a = 25°C$, RH = 0.45, irradiance = 660 W·m⁻². Solid line is a thick thallus, dashed line is a thin thallus. The thin thallus heats up and dries out faster than the thick thallus (A and B), but the two thalli show similar trends in thallus temperature with respect to relative water content (C).

The temperature difference for a "dry" thallus (≤10% RWC). On average, the wet thallus-dry thallus transition occurred at 23% RWC ($SD = 7.6$; high and low wind runs combined, $n = 88$).

The difference between thallus and air temperature for a wet thallus (i.e. the constant $a$) varied with air vapor density in the same manner as the wet bulb depression of the sling psychrometer (Fig. 4). Wet thallus temperature ranged between 4 and 10°C below air temperature, but generally fell within 1°C of the wet bulb temperature. Dry thalli, on the other hand, were ≈2°C above air temperature and showed no trend with wet bulb depression. Because wet thallus temperature was so sensitive to air vapor density, it was necessary to correct the estimates of $a$ for the variation in air temperature and relative humidity between runs for the other experiments. For example, estimates of $a$ from runs with a wet bulb depression of $-8°C$ were roughly 2°C lower than estimates from runs with a wet bulb depression of $-6°C$, when all other physical parameters were held...
Fig. 4. The difference between thallus and air temperature varies with wet bulb depression for wet thalli (●), but not for dry thalli (▲). Solid diagonal line is y = x. Wind velocity = 2.5 m·s⁻¹, irradiance = 660 W·m⁻².

constant. To remove this source of variation from the data, estimates of $T_{\text{thallus}} - T_{\text{air}}$ were corrected to an air temperature of 25°C and a relative humidity of 0.5, corresponding to a wet bulb depression of −7°C. For the correction, it was assumed that the deviation of $a$ from the wet bulb depression was constant for all wet bulb depressions. Thus, if an $a$ of −6.5°C were measured at a wet bulb depression of −8°C (a difference of 1.5°C), it was assumed that an $a$ of −5.5°C would have been measured had the wet bulb depression been −7°C (again a difference of 1.5°C). This correction was never > 2°C. Dry thallus estimates ($a + b$) were not corrected, as they did not vary with air vapor density.

Both wet and dry thallus temperatures were highly dependent on wind velocity, but only at wind velocities < ≈ 0.4 m·s⁻¹ (Fig. 5). At higher wind velocities, wet thalli were consistently 5–7°C below air temperature and dry thalli were 1–3°C above air temperature. At very low wind velocities (< 0.2 m·s⁻¹), even wet thalli heated up to nearly 5°C above air temperature, and dry thalli exceeded air temperature by 15°C. It is because thallus temperatures were highly responsive to

Fig. 5. Difference between thallus and air temperature as a function of wind velocity for a wet thallus (●) and a dry thallus (▲). Irradiance = 660 W·m⁻². Lines are sigmoidal curves (Table Curve, $r^2 = 0.88$ for both curves).
low wind velocities but not to high wind velocities, that the remaining wind tunnel experiments were conducted under wind conditions typical of each regime: at 0.15 m·s⁻¹ and 6.4 m·s⁻¹.

At high wind velocity, the temperatures of wet thalli ranged between 5 and 8°C below air temperature and showed little dependence on shortwave irradiance ranging from 0 to 1000 W·m⁻² (Fig. 6). Dry thallus temperature increased by ≈2°C over the same range of irradiances.

In contrast, irradiance had a much greater effect on thallus temperature at low wind velocity (Fig. 7). Over the range of irradiances from 0 to 800 W·m⁻², wet thalli increased from ≈5°C below air temperature to 1°C above air temperature. Dry thalli increased from ≈0.5°C below air to 17°C above air temperature over the same range of irradiances.

The resistance to mass transfer, \( r_m \), increased nonlinearly with decreasing thallus relative water content during each run. However, its inverse, \( 1/r_m \), was found to decrease nearly linearly with decreasing RWC, approaching zero when the thallus was near full desiccation (Fig. 8). A linear regression provided a good description.
of the variation in $1/r_m$ with relative water content during a run, with $r^2$ typically > 0.85 (4 plants, 28 runs total, $n = 7$–10 for each regression). Because the change of $1/r_m$ with relative water content (i.e. the slope of the regression line, $1/r_m/RWC$) was constant during a run, this value provided a useful index for the comparison of $r_m$ between runs (rather than $r_m$ itself). This mass transfer index ($1/r_m/RWC$) increased with increasing wind velocity (Fig. 9), and was described by the power curve mass transfer index = 0.000849 (wind velocity)$^{0.46}$ ($r^2 = 0.88$, $n = 24$). Note that it was often difficult to estimate $1/r_m$ at high relative water contents because temperature measurements were unstable at the onset of each run.

3.2. Morphological determinants of thallus temperature and desiccation

The 13 morphological parameters measured for $M. papillatus$ thalli were not entirely independent, as indicated by the correlation matrix in Table 1, and were, therefore, not appropriate for use as independent variables in multiple regression analyses. There was a pattern to the correlations, however, with parameters

Fig. 9. Mass transfer index increases with increasing wind velocity. Each symbol represents one of four thalli. Irradiance = 660 W·m$^{-2}$.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>1</th>
<th>8</th>
<th>10</th>
<th>13</th>
<th>12</th>
<th>3</th>
<th>11</th>
<th>4</th>
<th>2</th>
<th>9</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh weight</td>
<td>1</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>8</td>
<td>0.638**</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA</td>
<td>10</td>
<td>0.667**</td>
<td>0.581**</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA/area</td>
<td>13</td>
<td>0.188</td>
<td>−0.179</td>
<td>0.649**</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA/weight</td>
<td>12</td>
<td>−0.518*</td>
<td>−0.365</td>
<td>0.025</td>
<td>0.411</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thickness (w/papillae)</td>
<td>3</td>
<td>0.745**</td>
<td>0.186</td>
<td>0.614**</td>
<td>0.517*</td>
<td>−0.391</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight/area</td>
<td>11</td>
<td>0.831**</td>
<td>0.190</td>
<td>0.499*</td>
<td>0.407</td>
<td>−0.511*</td>
<td>0.877**</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thickness (w/o papillae)</td>
<td>4</td>
<td>0.624**</td>
<td>0.213</td>
<td>0.330</td>
<td>0.290</td>
<td>−0.307</td>
<td>0.562**</td>
<td>0.682**</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>2</td>
<td>0.453</td>
<td>0.441</td>
<td>0.326</td>
<td>0.050</td>
<td>−0.155</td>
<td>0.311</td>
<td>0.289</td>
<td>0.337</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perimeter/area</td>
<td>9</td>
<td>−0.454</td>
<td>−0.528*</td>
<td>−0.345</td>
<td>−0.014</td>
<td>0.112</td>
<td>−0.195</td>
<td>−0.273</td>
<td>−0.313</td>
<td>−0.655**</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Branches</td>
<td>6</td>
<td>0.054</td>
<td>0.246</td>
<td>0.141</td>
<td>−0.097</td>
<td>−0.208</td>
<td>−0.056</td>
<td>−0.027</td>
<td>−0.106</td>
<td>−0.509*</td>
<td>0.436</td>
<td>—</td>
</tr>
<tr>
<td>Branching orders</td>
<td>7</td>
<td>−0.139</td>
<td>0.094</td>
<td>0.105</td>
<td>−0.040</td>
<td>−0.086</td>
<td>−0.133</td>
<td>−0.191</td>
<td>−0.255</td>
<td>−0.515*</td>
<td>0.632**</td>
<td>0.817**</td>
</tr>
<tr>
<td>Papillary density</td>
<td>5</td>
<td>0.115</td>
<td>0.187</td>
<td>0.028</td>
<td>0.191</td>
<td>0.179</td>
<td>0.286</td>
<td>0.287</td>
<td>0.259</td>
<td>−0.171</td>
<td>0.298</td>
<td>0.323</td>
</tr>
</tbody>
</table>

** denotes significant correlation at $p = 0.01$; * denotes $p = 0.05$ (sequential Bonferroni test, Rice (1989)). Numerical headings correspond to the order in which the parameters were described in the Materials and methods section. Shaded regions indicate highly correlated parameters that describe a common morphological trait. Parameters in bold were selected for use as independent variables in multiple regression analyses.
describing similar morphological traits showing a high degree of interdependence. For example, the perimeter/area, number of branches, and number of branching orders were initially assumed to be measures of thallus “dissection”. An examination of the correlation matrix revealed that these parameters (along with thallus length) were indeed interrelated and to some extent could be considered to be interchangeable indexes of thallus dissection. Similarly, the two direct measures of thallus thickness (with and without papillae) and the derived parameter, weight/area, were a priori considered to be measures of the overall “thickness” of a thallus. These three parameters are also tightly correlated. Two of these parameters were also highly correlated with various parameters describing the thallus surface: surface area/weight, surface area, and surface area/area. As a whole, these five parameters could be considered to be indexes of “roughness”, although the segregation of roughness and thickness parameters was not distinct. Thallus fresh weight, area and surface area were intercorrelated and described thallus “size”. Papillar density was not correlated with any other measured aspect of morphology at the \( p = 0.05 \) level.

Based on these correlation patterns, a single parameter was selected to represent each morphological trait in the multiple regression analyses. Specifically, area, SAIarea, weight/area, and branching orders were selected to represent thallus size, roughness, thickness, and dissection, respectively. The selection of these four parameters was based on meeting the criterion of independence, but was otherwise arbitrary.

Thallus dissection was entered into each of the four regression equations where the difference between thallus and air temperature was a dependent variable (both wet and dry thalli; Table 2). In each case, the correlation was negative such that an increase in thallus dissection was associated with a reduction in \( T_{\text{thallus}} - T_{\text{air}} \). In the two regressions involving wet thallus temperature, parameters describing thallus roughness and thickness were also entered into the equation, explaining up to 51% of the variation in the dependent variable.

Thallus dissection accounted for most of the variation in the mass transfer index, while roughness and size explained a less substantial amount of the variation. However, these parameters only explained maximally 28% of the overall variation in the mass transfer index. In contrast, thallus thickness (as described by weight per area) accounted for 69 and 83% of the variation in the time to reach the wet thallus-dry thallus transition at low and high wind, respectively. In both cases, thicker thalli remained “wet” for a longer period. Other parameters explained a significant, but less substantial proportion of the variation, accounting for up to an additional 8% of the overall variation in the time required to reach the desiccated state.

3.3. Thallus temperature in the field

The temperatures of the 10 thalli measured in the field followed similar trends over time, but varied between individuals (ranging over 10°C). For simplicity, only two thalli representing the extremes in temperature are presented here. On
Table 2
Effect of thallus morphology on thallus temperature and desiccation. Results of eight stepwise multiple regression analyses (four dependent variables, each measured at two wind velocities)

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Wind</th>
<th>Step</th>
<th>Independent variable</th>
<th>Morphological trait</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet thallus - air temperature</td>
<td>Low</td>
<td>1</td>
<td>SA/area (+)</td>
<td>Roughness</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>Branching orders (-)</td>
<td>Dissection</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1</td>
<td>Weight/area (1-)</td>
<td>Thickness</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>SA/area (-)</td>
<td>Roughness</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>Branching orders (-)</td>
<td>Dissection</td>
<td>0.51</td>
</tr>
<tr>
<td>Dry thallus - air temperature</td>
<td>Low</td>
<td>1</td>
<td>Branching orders (-)</td>
<td>Dissection</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1</td>
<td>Branching orders (-)</td>
<td>Dissection</td>
<td>0.30</td>
</tr>
<tr>
<td>Time to wet thallus - dry thallus transition</td>
<td>Low</td>
<td>1</td>
<td>Weight/area (+)</td>
<td>Thickness</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>Area (+)</td>
<td>Size</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1</td>
<td>Weight/area (+)</td>
<td>Thickness</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>Branching orders (-)</td>
<td>Dissection</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>SA/area (-)</td>
<td>Roughness</td>
<td>0.90</td>
</tr>
<tr>
<td>Mass transfer index</td>
<td>Low</td>
<td>1</td>
<td>Branching orders (+)</td>
<td>Dissection</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>Area (-)</td>
<td>Size</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1</td>
<td>Branching orders (+)</td>
<td>Dissection</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>SA/area (+)</td>
<td>Roughness</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Low wind = 0.15 m·s⁻¹, high wind = 6.4 m·s⁻¹. In the independent variable column, symbol in parentheses denotes positive or negative coefficient. The morphological trait described by the independent variable was determined from the segregation pattern of the correlation matrix in Table 1.

October 20, 1991, air temperature was unseasonably high and wind velocity was very low during the first 80 min of the measurements, then gradually increased (Fig. 10a). The difference between thallus and air temperature was influenced by the wind: $T_{thallus} - T_{air}$ increased when wind velocity was low at 0–10 min, and decreased when the wind picked up at 80–90 min.

Relative humidity ranged from 33 to 41%, corresponding to wet bulb depressions of $\approx$ −10°C (Fig. 10a). All thalli were warmer than the wet bulb temperature. Nearby thalli were at 46% RWC 45 min after the initiation of the measurement, and at 20% RWC after 105 min ($S = 12\%$ and 8%, respectively, $n = 5$).

In contrast to October 20, the weather conditions on October 23, 1991 were cooler and windier (Fig. 10b). There was less variation in thallus temperature, with the warmest and coolest of the ten thalli differing by $<3°C$. Relative humidity was 64–71%, corresponding to a wet bulb depression of −3 to −4°C. In general, thallus temperatures did not exceed air temperature. Upon termination of the measurements, thallus relative water contents ranged from 13 to 56%. The thalli shown in Fig. 10b were at 21% (dashed line) and 59% (solid line) relative water content at the end of the measurement period.
4. Discussion

4.1. Thallus temperature and desiccation in the laboratory

Thallus resistance to water loss. Unlike higher plants, *M. papillatus* thalli are unable to regulate their water status, as they have no impermeable cuticle and no stomates with which to control the rate of water loss and no root and vascular system with which to replenish evaporated water. Thus hydrated *M. papillatus* thalli lose water at a rate that is primarily determined by the physical environment.

How readily does a wet thallus conduct water vapor to the boundary layer? The resistance to mass transfer, $r_m$, incorporates the water vapor transfer properties of both the boundary layer and the thallus. Specifically, $r_m$ is equal to the sum of the
resistances of the thallus, $r_{\text{thallus}}$, and the boundary layer, $r_{\text{bl}}$, to the diffusion of water vapor:

$$r_m = r_{\text{thallus}} + r_{\text{bl}}.$$  

(6)

While neither of these two resistances were measured directly in this study, they can be inferred from the observation that hydrated thalli approach the wet bulb psychrometer temperature at high wind velocity. Applying Gates's (1968) extensive analysis of the effect of transpiration on leaf temperature, hydrated thalli at high wind velocities can approach the wet bulb psychrometric temperature only if there is negligible internal resistance to water transport. This implies that fully hydrated thalli have essentially zero internal resistance to water loss and is consistent with the observations of Schonbeck & Norton (1979).

Further, for a given wind velocity (thus a constant boundary layer resistance), the internal thallus resistance varies with $r_m$ (Eq. 6). As relative water content decreases, $1/r_m$ decreases linearly, and the internal thallus resistance must consequently increase. Thallus resistance increases only gradually with the initial desiccation of a hydrated thallus, but then increases very rapidly as RWC approaches zero. When the thallus is fully desiccated, internal thallus resistance to water loss is infinite.

Because boundary layer resistance is constant for a given wind velocity, the observed decrease in $1/r_m$ with decreasing relative water content during a run must be due to increasing internal thallus resistance. Similarly, because internal thallus resistance is constant for a given relative water content, the observed increase in the mass transfer index with increasing wind velocity is due to a decrease in boundary layer resistance (by decreasing the thickness of the boundary layer). In general, the resistance to mass transfer is lowest when the sum of the boundary layer and internal thallus resistances are low, i.e. when both relative water content and wind velocity are high. A high resistance to mass transfer is the result when either (or both) of these resistances increase. For a given physical environment, a lower resistance to mass transfer increases the rate of evaporation, and consequently, lowers thallus temperature.

**Evaporation.** While the resistance to mass transfer depends primarily on wind velocity and thallus relative water content, the overall rate of evaporative water loss is a complex function of the physical environment. A thorough evaluation of the influence of the physical environment on the transpiration of leaves is provided by Gates (1968), thus only the general trends are discussed here.

Because of the high latent heat of vaporization of water, the evaporation of water is associated with a large energy flux away from the thallus. Thus, thallus temperatures well below air temperature are often the result of high rates of evaporation, and negative values of $T_{\text{thallus}} - T_{\text{air}}$ can be used as an index of evaporation rate. In this light, it can be seen that evaporation increases with increasing wind velocity, and decreasing air vapor density (Figs. 4 and 5).
The effect of irradiance on evaporation is less clear. An increase in irradiance increases energy flux to the thallus, which increases thallus temperature and consequently increases the rate of evaporation (by increasing $P_{\text{thallus}}$). However, the cooling provided by increased evaporation does not outweigh the warming effects of increased irradiation, resulting in a slight increase in thallus temperature to be associated with an increase in evaporative cooling.

Overall, evaporation rates are highest when a thallus is fully hydrated and is exposed to high wind velocity, high shortwave irradiance, and low air vapor density.

*Thallus temperature.* The upper temperature tolerance of *M. papillatus* has been estimated to be 35°C (Bell, 1993). Under what conditions do thalli reach this thermal limit? Average daytime air temperatures at HMS are typically 10–20°C, but can reach as high as 35°C on occasion. Thallus temperature must therefore equal or exceed air temperature if the lethal limit of 35°C is to be reached. Because of the large amount of cooling provided by evaporation, this is likely to be a rare event for hydrated thalli, as they exceed air temperature only when high irradiance is combined with very low wind velocity (Figs. 4–7). However, under these conditions the increase in thallus temperature relative to air temperature is modest; air temperature must be at least 30°C before hydrated thalli are at risk of overheating.

The scenario is much different for dry thalli, however, where no evaporative cooling is available. Instead, dry thalli must rely on convective heat transfer and thermal radiation to dissipate heat. The efficiency of convective heat transfer increases with increasing wind velocity (Holman, 1986), thus dry thalli are very close to air temperature when wind velocities are $>0.4 \text{ m} \cdot \text{s}^{-1}$. At lower wind velocities, however, thalli must rely on the process of thermal radiation as a means of dissipating heat. If irradiation is high when wind velocity is very low, the temperature of a dry thallus can soar to nearly 20°C above air temperature. Under these conditions, *M. papillatus* thalli can critically overheat when exposed to air temperatures well below their thermal tolerance.

When thalli are newly exposed to air by the receding tide, they are fully hydrated and, from the above discussion, are likely to be at or below air temperature. Whether a thallus ever substantially exceeds air temperature before it is reimmersed in water depends on whether it ever reaches the wet thallus-dry thallus transition ($\approx 23\% \text{ RWC}$) during the course of the low tide. This is clearly dependent on the physical conditions which affect the rate of evaporative water loss, but is dependent on biotic factors as well. For example, Bell (1992) has shown that placing a thallus within an aggregation prolongs the hydrated state. This is most likely due to a reduction in wind velocity within the aggregation, thereby reducing the rate of evaporative water loss. Reduced desiccation within an aggregation has also been observed in other species (e.g. Hay, 1981 and Taylor & Hay, 1985).
4.2. Morphological determinants of thallus temperature and desiccation

The length of time a thallus remains in the hydrated state is also dependent on its morphology. It is interesting to note, however, that thallus morphology (primarily dissection) explained < 30% of the variation in the mass transfer index at both low and high wind velocities. Thus, thallus morphology has only a small influence on the rate of evaporation under given physical conditions. Morphology does, however, strongly influence the rate of desiccation. This can be readily seen when two thalli with the same projected area are considered, differing only in thickness (and consequently, mass per area). Under the same physical conditions, the two thalli lose water by evaporation at the same rate, but the thicker thallus has a larger pool of water to evaporate. Thus the reduction in relative water content for the thicker thallus is less severe, and it takes longer for the thicker thallus to desiccate to the dry thallus state.

The difference between dry thallus temperature and air temperature depended on thallus dissection; temperature decreases with increasing dissection at both high and low wind velocities (Table 2). This was probably due to an increase in convective heat transfer when a greater proportion of the thallus is near a leading edge, as has been found in broad leaves and copper plates (Vogel, 1970; Gurevitch, 1988). Boundary layer thickness typically increases with increasing distance from an edge; by introducing new edges into a solid sheet (or thallus), the boundary layer is reduced and the convective transfer of heat is enhanced. Because convective heat and mass transfer both involve transfer across a boundary layer, it is not surprising that thallus dissection can also influence the mass transfer index, as the same general principles apply to both processes (Campbell, 1977; Holman, 1986).

Thallus roughness was also found to influence the mass transfer index at high wind velocity. This may have been a consequence of increased mixing (turbulence) in the boundary layer in the presence of roughness elements (Nowell & Church, 1979). Alternatively, it may simply reflect a relative increase in surface area over which mass transport can occur.

When thalli are colder than air temperature, convective heat transfer actually warms the thallus. The observed decrease in wet thallus temperature with increasing dissection at low wind velocity is therefore counter to the trend observed with dry thalli. This need not imply that thallus dissection has the opposite effect on convective heat transfer in wet thalli versus dry thalli. Rather, this decrease in temperature with increasing dissection likely reflects the relative magnitudes of evaporative cooling versus convective heating of wet thalli. The increase in mass transfer afforded by increased dissection outweighed the concomitant increase in convective heat transfer. Similarly, differential effects on mass and convective heat transfer may explain the positive correlation of roughness with wet thallus temperature at low wind velocity, but a negative correlation at high wind velocity.

Forty-five percent of the variation in wet thallus temperature at high wind velocity was explained by thallus roughness and thickness. This may have been
due to the enhanced evaporative cooling provided by increased roughness, or a large amount of fluid initially trapped between papillae. However, while the percentage of the variation in temperature explained was large, the range in variation was quite small ( < 3°C; Bell, 1992). It is, therefore, unlikely that these morphological effects on wet thallus temperature are of much biological significance.

4.3. Thallus temperature in the field

How well do wind tunnel experiments compare with thallus temperatures in the field? For the thallus temperature measurements made in October, 1991, wind velocity was measured 4 cm above the canopy surface. Using the boundary layer profiles measured over the same site by Bell (1992), the velocity at 1 cm above the canopy is approximately half of that at 4 cm. The wind measurements of Fig. 10 must therefore be divided by two to compare the field data to the wind tunnel data.

Thalli were wet and wind velocity was extremely low during the first 90 min of the October 20 measurements. Thallus temperatures were well above the wet bulb depression, and varied widely. This is consistent with the wind tunnel measurements for low wind velocity: wet thalli become uncoupled from the wet bulb temperature and the difference between thallus and air temperature is very sensitive to changes in wind velocity. The broad range in thallus temperature noted in these field measurements may be due to microhabitat differences in wind velocity.

The difference between thallus and air temperature dropped markedly at 80–90 min. While there was only a slight increase in the average wind velocity at the site, there was a sharp increase in the maximum wind velocity. This may indicate that relatively transient increases in wind velocity can perhaps provide an effective means of cooling a thallus that is exposed to low average wind velocity. Transient increases in wind are likely not to be as important at high average wind velocities, where thallus temperature is not as responsive to changes in wind (Fig. 5).

Average and maximum wind velocities were higher on October 23. In agreement with the wind tunnel experiments at higher wind velocity, wet thallus temperatures were below air temperature, were closer to the wet bulb temperature, and showed less variation between individuals. Later in the day, thallus temperature diverged for the two individuals shown. This may be due to the difference in hydration in the two thalli at the end of the measurements: the one that was desiccated was increasing in temperature while the one with enough water for evaporative cooling was decreasing in temperature.

The data from October 20 are important for two reasons. First, they document that wind velocity in the field can indeed be low enough for even hydrated thalli to exceed air temperature. Secondly, it documents that thalli can be exposed to physical conditions that test their thermal tolerances. Air temperatures near the canopy were \( \approx 35°C \) for nearly 2 h, and thalli exceeded this temperature. However, the low winds and high air temperatures of October 20 were truly
exceptional, and it is likely that on more typical days a thallus must first dry out before encountering potentially lethal temperatures.

In summary, the extent to which thallus temperature is coupled to air temperature is largely dependent on complex interactions of the thallus with its physical environment. Similar effects have been observed in terrestrial plants, such as cacti, kudzu, and the broad leaves of trees (e.g. Lewis & Nobel, 1977; Nobel, 1978; Forseth & Ehleringer, 1982; Woodhouse et al., 1983; Forseth & Teramura, 1986). The most striking contrast between *M. pupillatus* and higher plants, however, is the low resistance to water loss of fully hydrated thalli. Whereas higher plants rarely drop below air temperature when exposed to full sun, this is likely to be a common occurrence for *M. pupillatus* thalli. Once thalli dry, however, they behave much like higher plants with closed stomates and can exceed air temperatures when exposed to high shortwave irradiance.

Overall, this study indicates that thallus temperature during low tide is not necessarily equal to air temperature. Rather, thallus temperature can be as much as 10°C below or above air temperature, depending on the hydration of the thallus and the physical environment.

Increasing thallus thickness is one morphological strategy to prolong the hydrated state of a thallus during low tide. This potentially could have important consequences for the growth and survival of a thallus, as photosynthesis in air requires thallus hydration, and extreme temperature stress generally requires desiccation. For example, a thicker thallus may fix more carbon during a low tide because it remains hydrated longer, while a dissected morphology may be at less risk of overheating because it is more effective at dissipating heat. The importance of morphology on thallus growth and survival will ultimately depend on the duration of a low tide, as well its coincidence with physical factors such as low winds and high shortwave irradiation. For example, if thalli are usually submersed during periods of high irradiance, then photosynthesis in air (and its dependence on thallus temperature and hydration) is likely to have little effect on the growth of a thallus. Thus, the effect of morphology on thallus temperature and desiccation and, in turn, growth and survival, must be evaluated under the physical conditions a thallus is likely to encounter during low tide.

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Appendix

The water vapor density at the thallus surface, $\rho'_\text{thallus}$, is that over a saturated salt solution and is calculated from thallus temperature according to the perfect gas law (Campbell, 1977):

$$\rho'_\text{thallus} = \frac{p_{\text{thal}}}{4.62(T_{\text{thal}} + 273.15)}$$

(7)

where $p_{\text{thal}}$ is thallus vapor pressure in kPa. The concentration of salt in the thallus has the effect of lowering thallus vapor pressure below that of pure water, $p_0$:

$$p_{\text{thal}} = p_0 - \delta$$

(8)

where $\delta$ is the vapor pressure lowering in kPa and is dependent on thallus salt concentration and thallus temperature. $p_0$ was approximated from thallus temperature using the equation of Campbell (1977):

$$p_0 = \exp\left(52.576 - \frac{6790.5}{T_{\text{thal}} + 273.15} - 5.0281 \ln(T_{\text{thal}} + 273.15)\right).$$

(9)

Thallus salt concentration was expressed as salinity ($S$), and was assumed to be equal to sea water (34) for a fully hydrated thallus, and increases as thallus relative water content decreases:

$$S = \frac{34}{(\text{RWC})}.\quad \text{(10)}$$

The vapor pressure lowering, $\delta$, was calculated from thallus temperature and salinity ($S$) from equations fit to the data of Arons & Kientzler (1954, assuming $S = 0.03 + 1.805$(Chlorinity); Spiegler, 1977):

$$\delta(S, T) = 0.1333(k_1 S + k_2 S^2),$$

where

$$k_1 = 5.387 \times 10^{-4} + 2.316 \times 10^{-4} T + 2.632 \times 10^{-7} T^3;$$

$$k_2 = 9.713 \times 10^{-6} + 7.085 \times 10^{-7} T + 6.142 \times 10^{-10} T^3.$$ \quad \text{(11)}

These equations are valid for use for temperature between 0 and 50°C and salinity between 0 and 290 (corresponding to RWC of 100 and 11%, respectively).

The saturation vapor density of air, $\rho'_\text{air}$, was calculated from Eq. 7, substituting $p_0$ for $p_{\text{thal}}$ and $T_{\text{air}}$ for $T_{\text{thal}}$. $p_0$ was calculated according to Eq. 9, again substituting $T_{\text{air}}$ for $T_{\text{thal}}$. 
References


