Temperature extremes reduce seagrass growth and induce mortality

C.J. Collier *, M. Waycott [1]

School of Marine and Tropical Biology, James Cook University, Townsville 4817, Australia

ABSTRACT

Extreme heating (up to 43 °C measured from five-year temperature records) occurs in shallow coastal seagrass meadows of the Great Barrier Reef at low tide. We measured effective quantum yield (ϕ_{PSII}), growth, senescence and mortality in four tropical seagrasses to experimental short-duration (2.5 h) spikes in water temperature to 35 °C, 40 °C and 43 °C, for 6 days followed by one day at ambient temperature. Increasing temperature to 35 °C had positive effects on ϕ_{PSII} (the magnitude varied between days and was highly correlated with PPFD), with no effects on growth or mortality. 40 °C represented a critical threshold as there were strong species differences and there was a large impact on growth and mortality. At 43 °C there was complete mortality after 2–3 days. These findings indicate that increasing duration (more days in a row) of thermal events above 40 °C is likely to affect the ecological function of tropical seagrass meadows.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Low tides are a strong driving force in intertidal and shallow water coastal communities defining community and species boundaries and periodically exerting a major ecosystem stress (Anthony et al., 2007; Erftemeijer and Herman, 1994; Helmuth, 1998; Mellors et al., 2008; Stapel et al., 1997). Tidal exposure is highly predictable, but climatic conditions can influence the magnitude of tidal changes through barometric pressure and wind. Furthermore, in shallow coastal habitats during low tides, solar radiation and air temperature combine to heat shallow water to temperatures far exceeding oceanic temperature (Berkelmans, 2002; Feder and Hofmann, 1999; Jimenez et al., 2012; Massa et al., 2009; Rasheed and Unsworth, 2011; Seddon et al., 2000). Exposure to extreme low tide events are a natural phenomena, and due to daily variation in the height of low tide and its timing, exposure to these temperatures is short-term and would rarely last longer than a few days (Anthony and Kerswell, 2007). Global climate change could transform this phenomenon into a regular and highly stressful event for shallow water communities as water and air temperature are predicted to rise, and an increase in the frequency and intensity of extreme climatic events is expected (Bernstein et al., 2007).

Seagrasses are marine flowering plants (Les et al., 1997), which are globally distributed and well recognised for the ecosystem services they provide such as high rates of productivity, coastal nutrient cycling, and supporting diverse ecosystems as a habitat and food source (Orth et al., 2006). Most seagrass species have relatively high light requirements compared to algae and phytoplankton, and this usually constrains them to shallow waters (Dennison et al., 1993) except for some deepwater specialists (Duarte, 1991). Declining water quality and reduced light penetration have further constrained seagrass colonisation depths to even shallower waters (Abal and Dennison, 1996; Dennison et al., 1993) where vulnerability to thermal extremes is highest (Anthony and Kerswell, 2007; Jimenez et al., 2012).

Thermal optima associated with high rates of photosynthesis and growth ranges from approximately 15 to 33 °C, with the species-specific optimums generally reflecting their geographic distribution (Berry and Bjorkman, 1980; Bulthuis, 1983; Coles and Jokiel, 1977; Collier et al., 2011; Masini and Manning, 1997; Perez and Romero, 1992). During low tide, these thermal optima are likely exceeded for shallow water habitats. Extreme events occurring during low tide have been linked to seagrass loss (Massa et al., 2009; Rasheed and Unsworth, 2011); however, the contribution of thermal stress *per se* to loss is not known due to a lack of temperature threshold data.

Seagrasses are affected by thermal stress in a number of ways. Water temperature affects the balance between carbon uptake (photosynthesis) and carbon consumption (respiration) (Bulthius, 1987; Perez and Romero, 1992). The photosynthetic apparatus is highly sensitive to temperature, with temperature sensitive

* Corresponding author. Tel.: +61 7 4781 5745.
    E-mail address: Catherine.collier@jcu.edu.au (C.J. Collier).
  [1] Current address: School of Earth and Environmental Sciences, Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, Adelaide, South Australia 5001, Australia.

processes occurring throughout the photosynthetic pathways (Buxton et al., 2012; Jones et al., 1998). Increases in photosynthesis occur within their physiological optimum, but this is followed by sharp reductions in photosynthetic efficiency after temperatures exceed optimum thresholds (Bulthuis, 1983; Campbell et al., 2006; Perez and Romero, 1992; Ralph, 1998). Sensitivity to elevated temperature is variable among species, with tropical species tolerating higher temperatures than subtropical and temperate species (Campbell et al., 2006; Collier et al., 2011). Following extreme or prolonged thermal stress, seagrass mortality results: however, *in situ* observations of seagrass mortality typically occur after the thermal event, making it difficult to directly link changes in physiological processes to mortality (Marbá and Duarte, 2010; Massa et al., 2009; Rasheed and Unsworth, 2011).

We measure seagrass responses to simulated low tide temperature extremes (35 °C, 40 °C and 43 °C). This is an extension of the work presented by Campbell et al. (2006) who measured dark and light-adapted yield at high temporal frequency on similar species to determine response times. In this study we link the photosynthetic responses to changes in growth and mortality. The work was conducted in outdoor aquaria in naturally varying light conditions, enabling us to measure the interactive effects between light intensity and thermal stress.

2. Methods

2.1. Field measures

Water temperature was measured within the seagrass canopy at four island locations spread over approximately 400 km in the northern Great Barrier Reef, Australia: Low Isles (16° 23.0′, 145° 33.9′), Green Island (16° 45.5′, 145° 58.4′); Dunk Island (17° 56.8′, 146° 08.5′); and Magnetic Island (19° 10.73′, 146° 50.47′). The maximum tidal range at these locations is from *c.a.* 3 to 4 m during spring tides. All are intertidal meadows but they differ in the extent to which the meadows drain at low tide ranging from +0.6 m above lowest astronomical tide (LAT) at Low Isles to +1.0 m at Magnetic Island (i.e. exposing with a smaller drop in sea level), while the remaining 2 sites are approximately +0.8 m above LAT. Temperature loggers (Thermodata iBtag G) were fastened to star pickets at canopy height and recorded water temperature every 90 min. These were exchanged quarterly, and some technical complications resulted in small data gaps throughout.

2.2. Experimental studies

Short-term temperature spike experiments were carried out at Orpheus Island in August–September, 2008. Seagrass was collected from Juno Bay, Fantome Island in the Palm Island group on the Great Barrier Reef, Australia, located between the two most southern field sites. Seagrasses were collected 3–14 days before the initiation of the experiments and stored in outdoor (under a 12.5% Photosynthetic Photon Flux Density, PPFD-reducing roof) flow-through aquaria. Four seagrass species were collected from the same reef flat: *Thalassia hemprichii* was collected from the upper intertidal zone which fully dries on each low tide; *Cymodocea rotundata* was collected on the landward side of the reef flat, where a shallow pool of water (~10 cm deep) is retained even on spring low tides; *Halodule uninervis* and *Halophila ovalis* were growing in a mixed community and collected together at the most seaward edge of the reef flat. The seagrasses were collected using a 17 cm diameter stainless steel corer, where the corer was pushed into the sediment and a plug of seagrass was carefully lifted out and placed into a plastic plant pot lined with a plastic bag. The end of the bag was pulled up over the seagrass and tied at the top to maintain humidity within the bag. The pots were stored in large plastic containers for transport to the aquaria. The seagrasses were kept in large aerated flow-through outdoor aquaria prior to the experiments.

Due to equipment limitation, three separate experiments were conducted, one for each of the temperature treatments: 35 °C, 40 °C and 43 °C. Each experiment had a separate ambient and temperature spike treatment, and they were conducted one after another i.e. the experiments were seven days each and therefore, the start time was usually 8 days after the previous. The ambient and temperature spike treatment (either 35 °C, 40 °C or 43 °C) were run simultaneously, and controls were repeated for each experiment (see statistical analysis below for further clarification). This set-up enables us to compare responses between the ambient water temperature, and the temperature elevation run at the same time, but we are unable to statistically compare plant responses among the different temperature spike treatments (e.g. between 35 °C and 40 °C). The experiments were conducted outdoors in 60 L plastic tubs under a solid mostly transparent roof, which attenuated 12.5% of incoming light. There were four replicate tanks of each of the ambient and temperature treatments for the 40 °C and 43 °C experiments and five for the 35 °C. A constant flow-through was maintained in each tank from water sourced directly from the adjacent bay, Pioneer Bay on Orpheus Island. The flow rate was *c.a.* 3 L min^{-1} and was reduced to *c.a.* 1 L min^{-1} during heating. All tanks had bubblers (without a diffuser) placed in the centre of the tank and these created vigorous bubbling to mix water and ensure water flow over leaves.

Water bath heaters were fastened to each tank. They were turned on at 9:30 am and off at 14:00 but due to a time-lag in heating the water the experimental temperatures were reached after *c.a.* 2 h at 11:30 am. On the 7th day, the water in both the ambient and temperature spike treatments was held at ambient temperature.

PPFD was recorded using 2π light loggers (Submersible Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems Pty Ltd, New Zealand). A single light logger was placed in one of the ambient temperature tanks. PPFD was recorded every 30 min. Water temperature was recorded in one ambient and one temperature treatment tank every 30 min using Thermodata iBtag G$_i$. Thermometers were placed in each tank to monitor and control temperature throughout the experiment.

A number of morphological characteristics were measured prior to the initiation of the experiments; the number of shoots in each pot (or leaves for *H. ovalis*), the number of leaves per shoot (excepting *H. ovalis*), and the percentage of necrotic (blackened) leaf tissue were measured. Leaf growth was measured using the leaf marking technique (Short and Duarte, 2001). Leaves were marked on the morning of day one and measured at the end of day seven. The whole pot of seagrass was harvested, the growth of each marked shoot was measured, scraped free of epiphytes and later dried at 60 degrees for 48 h and dry weight measured.

Effective quantum yield (ϕ_{PSII}) was measured using a Diving PAM fluorometer (WALZ GmBH) on day 1, 2, 4, 6, which were temperature spike days, and day 7 when the temperature spike treatment was held at ambient. All measures were made between 11:30 and 14:00. Measures were made by fitting a dark adaptation clip to a young but mature leaf and immediately initiating a rapid light curve in less than 10 s (Ralph and Gademann, 2005). The leaf was held 5 mm from the tip of the fibre-optic cable. The initial yield measurement was used for determination of the effective quantum yield of photosystem II (PSII) calculated from $(F'_m - F)/F'_m (\phi_{PSII})$. Other rapid light curve data are not presented here.