



Photosynthetic responses of an intertidal alga to emersion: The interplay of intertidal height and meteorological conditions

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ABSTRACT

The photosynthetic response of juvenile stages of the brown alga *F. distichus* subsp. *edenatus* (Fueales, Heterokontophyta) was examined at different tidal heights at an intertidal site located on the Gaspé Peninsula, Québec, Canada. During the low tide, we used pulse-amplitude modulated (PAM) fluorometry to examine the effective quantum yield (Φ_{PSII}) and the non-photochemical quenching (NPQ) of furoid juveniles at five intertidal levels spanning a vertical distance of 1.2 m. Observations were made under four different meteorological conditions, defined as “sunny–windy,” “sunny–calm,” “cloudy–windy” and “cloudy–calm.” Rates of evaporation were measured at the same time. A gradient of responses was generally found: at the highest two levels, Φ_{PSII} declined over time with concomitant increases in NPQ. At the lowest levels, there was no decline of Φ_{PSII} over time and just a slight increase in NPQ, except under “sunny–windy” conditions when responses were similar to the higher levels. This combination of sun and wind created the most severe meteorological conditions in terms of physiological responses whereas the least intense meteorological condition was “cloudy–calm” during which only the highest level showed a decrease in quantum yields. Evaporation rates were much greater at the two highest levels and during windy conditions, suggesting that desiccation is a major stressor during emersion and is partly responsible for the smaller size and lower density of algae at the two highest levels.

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1. Introduction

The periodic exposure to air during low tide (i.e., emersion) creates a vertical gradient in certain abiotic stressors, and the relationship between these gradients and the zonation of intertidal organisms has long been a subject of interest (Coleman, 1933; Doty, 1946; Swinbank, 1982; Underwood and Denley, 1984). Most past efforts have focused on determining the ecological factors responsible for the upper and lower vertical limits of species (e.g., Schonbeck and Norton, 1978, 1980; Underwood, 1980), and it is generally believed that the upper limits are set directly by physical factors whereas the lower limits are set indirectly by physical factors acting on competitors or consumers (Dayton, 1975; Jenkins et al., 1999; but see Underwood and Denley, 1984).

Less attention has, however, been directed towards the performance of intertidal species relative to variation in stressors within the limits of their vertical distribution (Beer and Eshel, 1983; Chapman, 1995; Garbary, 2007; Nielsen et al., 2006; Raffaelli and Hawkins, 1996; Wahl et al., 2011). Although tidal height is an easily measured variable, the exact relationship between it and emersion

stressors is complex as the influence of tides, waves and local topography can influence the duration of the period of emersion in complex manners (Druehl and Green, 1982; Harley and Helmuth, 2003; Helmuth and Hofmann, 2001; Scrosati and Heaven, 2008). In addition, the timing of low tide during the day will also influence the severity of emersion stressors (Dethier and Williams, 2009; Helmuth et al., 2002), especially in regions with mixed semi-diurnal tide cycles. Finally, emersion stressors are ultimately determined by the meteorological conditions experienced during the period of low tide. Although intuitively obvious, this factor has been largely ignored, especially over the shorter spatial scales of day-to-day variation in the weather.

Stressors can be broadly defined as limiting or disruptive, depending on whether the stress involves a lack of resources or damage to the organisms, respectively (Davison and Pearson, 1996), and both can potentially occur when intertidal organisms are exposed during low tide. Although certain disruptive stressors can produce immediate lethal effects, it is more likely that patterns of vertical distribution are the result of the accumulated sub-lethal effects on the physiological processes underlying growth. In intertidal seaweeds, photosynthesis is the fundamental physiological process underlying growth (Beer and Eshel, 1983; McLachlan, 1974) and, as such, has been the focus of numerous studies assessing the influence of intertidal stressors. To study the photosynthetic performance of intertidal algae, researchers have often relied on techniques that measure the

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evolution of oxygen (e.g., Beer and Eshel, 1983; Brenchley et al., 1997; Smith et al., 1986) or the uptake of ^{14}C -bicarbonate (e.g., Johnston and Raven, 1986; Quadir et al., 1979), but difficulties in assessing responses to stressors in the field have largely prevented detailed studies of physiological responses under natural conditions. Instead, such studies have usually been conducted in the laboratory where there is more control but less realism (e.g., Johnson et al., 1974; Madsen and Maberly, 1990a; Major and Davison, 1998). Those ecophysiological experiments that have been conducted in the field (e.g., Cheshire et al., 1996; Hanelt and Nultsch, 1995) have been handicapped by cumbersome equipment or the need for destructive sampling, which has limited the scope and resolution of the research.

Fortunately, pulse-amplitude modulated (PAM) fluorescence provides a rapid, non-intrusive, and extremely sensitive way to examine photosynthesis under field conditions (Beer et al., 1998, 2000; Gómez et al., 2004; Gorbunov et al., 2000; Lamote et al., 2007; Nielsen and Nielsen, 2008). This technique, which relies on the natural fluorescence of chlorophyll, is not in itself a direct measure of photosynthesis, but instead assesses the function of the photosynthetic apparatus, especially photosystem II (PSII) (Schreiber et al., 1995). The use of this technique thus permits an examination of the dynamic properties of photosynthesis, especially the potential for changes in composition and function (e.g., photoadaptation), and responses to environmental damage (e.g., photoinhibition) when changes in the environment exceed the rate or limits of acclimation.

Over the past ten years, PAM fluorometry has been used successfully in the study of marine algae, but most studies have examined subtidal species (e.g., Häder et al., 1996; Hanelt et al., 1997; Leverenz et al., 1990; Magnusson, 1997). Studies on intertidal algae (Beer et al., 1998; Davison and Pearson, 1996; Gylle et al., 2009; Gómez et al., 2004; Lamote et al., 2007; Nielsen et al., 2006) and microalgae (Consalvey et al., 2004; Honeywill et al., 2002; Kromkamp and Forster, 2003) have generally supported earlier results of declines in photosynthesis during emersion (reviewed in Davison and Pearson, 1996), presumably due to the high light conditions and desiccation that can produce photoinhibitory stress in algae. Most of these studies have, however, only focused on the photobiology of the adult stages with no examination of juvenile stages in the field (but see Lamote et al., 2007; Pang et al., 2007). This lack of information on the photobiology of juveniles is understandable as the challenge of conducting physiological studies in the field is further constrained by the small size of juvenile stages (Davison et al., 1993). Still, given that the distributional limits of adults depend, in part, on the survival of juvenile stages (supply and settlement of propagules can also be equally important; Johnson & Brawley, 1998), an understanding of the ecology of juvenile stages is essential.

In an earlier study (Lamote et al., 2007), we examined the physiological responses of the earliest life stages (microscopic zygotes and germlings) of three furoid algae (*Ascophyllum nodosum*, *Fucus vesiculosus*, and *F. distichus* subsp. *edentatus*) outplanted within and among the different intertidal zones defined by the distribution of adults of these three species. We found that physiological performance of early stages generally varied consistently with the distribution of adult stages, but that meteorological conditions had a strong effect, except in protected microhabitats. Here we examine similar physiological responses of one of these species, *F. distichus* subsp. *edentatus* (henceforth *F. distichus*), within the tidal zone in which its natural recruitment occurred, focusing on larger juvenile stages that had reached a macroscopically visible size in the field (from 3 to 18 cm in length). We specifically measured their photosynthetic response to the collective stressors experienced during exposure to air during daytime low tides (i.e., emersion). As this physical environment may vary in space and time, we examined this response spatially across a vertical gradient and temporally under different meteorological conditions. The different intertidal heights represented a predictable gradient of the stressors associated with emersion (e.g., desiccation), but the severity of this gradient should ultimately depend

on the meteorological conditions occurring during low tide, which are less predictable. Our primary goal was to determine how physiological performance would vary under different environmental conditions (i.e., meteorological conditions) across the physical gradient of shore height.

2. Methods

The study was conducted in the intertidal zone at Pointe-Mitis (48°41'N, 68°2'W) near Mont-Joli, Québec, Canada, a northwest-facing, semi-sheltered shore consisting of a series of rocky ridges interspersed with consolidated boulder fields. Furoid algae, including *Ascophyllum nodosum* (L.) Le Jolis, *Fucus vesiculosus* L., and *F. distichus* subsp. *edentatus* (Pyl.) Powell, are the most common macroalgae in the boulder fields and on the lower portions of adjacent ridges. Perennial algae are not able to colonize the more exposed rocky surfaces (e.g., the sides and tops of ridges) due to scouring by ice during winter (Archambault and Bourget, 1983).

For this study we selected a 2-m high, 10-m long rock wall located in the low intertidal zone. The wall was oriented towards the northwest and was partially protected from the full effects of wave action by a rocky ridge some 10 m offshore. The wall was generally smooth and flat except for prominent crevices that ran vertically to divide the surface into distinct sections. We selected 3 adjacent sections of the wall, each approximately 3 m² in area.

The selection of this site was made to facilitate certain aspects of the study. First, we wanted to reduce environmental variation due to the aspect or orientation of the rock surface (e.g., north-facing vs. south-facing surfaces) – the wall provided a consistent surface and slope where just the effect of tidal height could be examined. Second, we wanted to minimize the effects of herbivory – the lack of crevices and holes eliminated the refuges that herbivorous gastropods use at this site (Addy and Johnson, 2001). Third, we wanted an area that had consistent recruitment of juvenile stages – we had observed massive colonization of these areas by furoid algae late in the summers of 1998 and 1999. The timing of these events coincides with the onset of reproduction by *Fucus distichus* (Lamote and Johnson, 2008), and the specific identity of the juveniles examined in this study was confirmed after the experiment when the species matured (i.e., the following season). Finally, we needed to be able to move quickly among locations to make the necessary measurements.

On each section, five levels separated vertically by 30 cm were marked with stainless steel screws. Level 1 (the highest) began at 30 cm from the top of the wall at the level where the upper limit of colonization had been observed in previous years. Level 5 (the lowest; approximately 0.5 m above chart datum) was just above a persistent stand of adult *F. distichus*. In late summer of 2000, we determined photosynthetic states during low tide. As desiccation is a key determinant of photosynthetic performance in algae (e.g., Davison and Pearson, 1996; Gessner and Schramm, 1971; Madsen and Maberly, 1990a), we measured evaporation rates across this short but sharp physical gradient. We also estimated the density and size of furoid juveniles during a 2-month (August–September) period.

Photosynthetic responses were examined *in situ* by pulse-amplitude modulated (PAM) fluorometry, using a PAM 2000 portable fluorometer (Walz GmbH, Effeltrich, Germany). The fluorescence responses were measured directly from individual algae greater than 5 mm in length, using a measuring modulated light intensity of approximately 0.1 $\mu\text{mol}\cdot\text{photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which was sufficiently low as to not produce any significant photosynthesis. Each measurement provided the following fluorometric parameters: (1) F_0 and F_m , the minimal and maximal fluorescence yields after a 15-min dark adaptation, and (2) F_0' and F_m' , the minimal and maximal fluorescence yields after light adaptation. F_0 is observed when all PSII reaction centers are open as occurs after dark-adaptation whereas F_m is observed when all the PSII reaction centers are closed. The parameter F_0' corresponds to the minimal fluorescence yield in the dark of a light-adapted sample

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