EFFECTS OF FEEDING PRESSURE AND LOW-LIGHT STRESS ON THE PERFORMANCE OF ANTIHERBIVORE DEFENSES IN THE TWO RED ALGAE *Gracilaria edulis* AND *Gracilaria salicornia* FROM THE MALAY PENINSULAR

[1]SHUKRI ARSAD, [2]CORVIN EIDENS, [3]MARK LENZ AND [4]SITI AISHAH ABDULLAH

[1]*Institute of Oceanography, Universiti Malaysia Terengganu, Malaysia.*
[2]*Justus Liebig Universitat Giessen, Germany.*
[3]*Leibniz-Institute of Marine Sciences, Kiel, Germany.*
[4]*Marine Science Department, Universiti Malaysia Terengganu, Malaysia.*

* *Corresponding author e-mail address: shukri81@umt.edu.my*

Abstract: The objective of this study was to test for the inducibility of an anti-feeding defense in two red macroalgal from the coast of the Malay Peninsular as a response to grazing pressure. Whether the defense capacity in these seaweeds is generally impaired by low-light stress was also investigated. Aquaria with blackened walls connected to a flow-through water system were used as Experimental Units (EUs). Different light regimes were established using layers of black gauze material and clear perspex lids, mounted on top of the EU. The gauze allowed the stepwise reduction of ambient light. Six different light levels with eight replicates each were realised. The growth rates of algal exposed to different light levels were calculated using a linear regression analysis. Using outdoor mesocosm facilities, three fully-factorial experiments were realised during which low-light stress on different algae-grazer combinations was induced: 1) the red algae *Gracilaria edulis* with the sea hare *Aplysia* sp., 2) *G. edulis* with the abalone *Haliotis diversicolor,* and 3) *Gracilaria salicornia* with *H. diversicolor.* For each combination, 48 aquaria were used, while in a control group of another 48 tanks, algae were kept in the absence of herbivores. Following low-light and feeding-stress induction, herbivore consumption on algal material was assessed in feeding assays with living thalli fragments. Negative effects of light reduction on algal growth rates was observed in both experiments with *G. edulis* and in one trial with *G. salicornia,* while general effects of low-light stress on seaweed palatability were absent in our study. By contrast, for some herbivore-algal combinations, significant differences in consumption were detected on previously-grazed and ungrazed algal material, that indicates the presence of an inducible defense. *G. edulis* and *G. salicornia* produced defenses when exposed to grazing by the gastropod *Aplysia* sp. and *H. diversicolor*, respectively. In contrast, *G. edulis* showed no response to *H. diversicolor*. Our findings show that inducible defenses generally exist in the two investigated *Gracilaria* species, but vary with the identity of herbivores. Surprisingly, algal palatability was not affected throughout all low-light regimes, contrasting the widespread notion that defensive traits in seaweeds are dependent on metabolic energy. Thus, it appears that low-light stress effects play only a minor role on the performance of antiherbivore defenses in these two red algae.

KEYWORDS: Antiherbivore defense, red algae, grazers, low-light stress, palatability.

Introduction

Algae are frequently the most abundant primary producers in shallow water along the coast, and fulfill many roles in stream food-webs, contributing to the uptake and transformation of nutrients and providing food for higher tropic levels. Environmental factors, including light, temperature and salinity, play an important role in the growth, reproduction and distribution of marine algae.

Light is an essential resource that limits the growth and biomass of primary producers and relative and absolute levels of light can vary through space and time as a function of natural environmental heterogeneity. Spatial and temporal variability in light levels at different scales are particularly pronounced in the marine environment, because of bank shading and nutrient inputs via farming and industries activities, upwelling, runoff, animal excretion and the local decomposition of organic matter, as well as nutrient uptake by primary producers. These processes will limit the light availability, affecting the variability of the growth and biomass of primary producers.

Herbivory has a profound effect on seaweeds in tropical communities, where 60-97% of the total seaweed production may be removed by herbivores. The herbivorous fishes bite the bottom at rates of 20 000 to 156 00 bites/m^2/day, and either fishes alone or, in some locations, sea urchins alone can remove nearly 100% of algal production (Klumpp & Poulunin, 1989). To persist in marine communities, seaweeds must escape, generate defense or tolerate herbivory (Hay & Fenical, 1988). Four categories of defenses used by marine species are structural, associational, nutritional and chemical defenses.

Although difficult to assess, the production of defenses is believed to be costly because defenses utilise resources that could have been allocated to growth or reproduction (Herms & Mattson, 1992). Constitutive defenses require expenditure of resources even when consumers are absent and the benefits of protection are not realised. In contrast, inducible defenses allow costs to be deferred until enemies have been detected, at which time the costs can be offset by the benefits of protection. Induced resistance may therefore minimise costs by keeping defenses low until they are needed (Harvel, 1990; Baldwin, 1994). Most studies on inducible defenses focussed only on factors that initiate antiherbivore responses. However, if induction of antiherbivore defenses is costly in terms of metabolic energy, the defenses should also decrease when low-light stress increases.

The objective of this study was to test for the inducibility of an anti-feeding defense in two red macroalgae from the coast of the Malay Peninsular as a response to grazing pressure. Additionally, whether the defense capacity in these seaweeds is generally impaired by low-light stress was investigated.

Material and Methods

The organisms

Two red macroalgae species *Gracilaria edulis* and *Gracilaria salicornia*, which are known to produce secondary metabolites, were chosen for the experiments and were collected at two different sites along the coast of Peninsular Malaysia. First, Middle Bank, Penang, west coast Peninsular Malaysia (01°26.048'N; 104°00.029'E), with mainly sandy mud bottom and a maximum depth of 1.5 m. The red algae *G. edulis* is the most abundant algae in the Middle Bank area and is found at an average depth of 0.5 m. The second site was Tanjung Kopok, located in the south of Peninsular Malaysia (05°23.781'N;100°20.251'E), where *G. salicornia* appears as scattered sub-dominants species, which grows on sandy bottoms. Environmental data such as water temperature and Total Dissolved Solid (TDS) were determined using multiparameter YSI 550 during the sampling. In the laboratory, the algae were cleaned and kept in large storage tanks with a flow-through system and aeration until the start of the experiment. In addition, two grazer gastropoda were used in our experiments: the sea hare *Aplysia* sp. with two mixed species of *Aplysia oculifera* and *Aplysia dactylomela,* and the abalone *Haliotis diversicolor. H. diversicolor* was bought from an abalone farm in Thailand and stems originally from Taiwan. The abalone readily consumes *Gracilaria fisherii.* The sea hare *Aplysia* sp. was collected in the upper sublitorral around Bari Kecil Bay, where it was observed that *Aplysia* sp. consumed the red algae *Laurencia* sp.

Determination of the Light-Compensation Point

All experiments were conducted at the coastal laboratory of University Malaysia Terengganu (5°24'N; 103°5'E) on the east coast of Peninsular Malaysia, between June and September 2007. The light-compensation point experiments were conducted to know what levels of low light are stressful for the algae. The entire experimental set-up was positioned underneath a clear-filtered plastic roof so that algae were exposed to the natural diurnal light rhythm. Light-compensation point determination for individual algal species was performed prior to each experiment. The algae were kept in the hatchery under different light regimes within a flow-through system for one week. Each six litre (6 L) aquarium was equipped with 100 g of algal material and completely filled with seawater. Clear perspex lids were mounted on top of the aquaria where they were fixed with different numbers of layers of gauze (mesh size 1 mm): one, five, six, seven, and eight. The side walls of each aquarium were wrapped with black plastic to exclude scattered light. Each light level was replicated two times, while two replicates were left without gauze. After three days of acclimatisation, the concentration of dissolved oxygen in the aquaria was then measured without a flow-through system three times a day (8am, 12pm and 5pm) for a three-day period. The minimum number of gauze layers at which a significant diurnal pattern in oxygen concentration was not observed was considered as the light regime closest to the compensation point of the respective algal species.

Assessment of growth rates during the light-limitation phase

The growth rates of *G. edulis* and *G. salicornia* individuals exposed to different light levels were calculated as: growth rate in percentage = [Wa/Wb] x 100 - 100, Where 'Wa' indicates weight of an algae after light limitation and Wb weight of an algae before light limitation, kept in the absence of grazers, multiplied by 100 minus 100 is the growth in percent.

Light Limitation Phase

During the light limitation experiments, the inducibility of a chemical defense in two red macroalgae was tested for as a response to grazer and an attempt was made to determine whether this defense capacity was affected by low-light stress. Three light-limitation phases were realised with different algae-grazer combinations. The algae-grazer combinations were: 1) *G. edulis* with *Aplysia* sp., 2) *G. edulis* with *H. diversicolor* and 3) *G. salicornia* with *H. diversicolor.*

To minimise the intrusion of fouling organisms, seawater from Mengabang Telipot Bay was filtered using a sand-filter system prior to its passage through the aquaria. This part of the study was also run underneath a clear-filtered plastic roof and aquaria with blackened walls connected to a flow-through water system were used as experimental units (EUs). Different light regimes were established using layers of black gauze material with a mesh size of 1 mm. Six different light levels with eight replicates each were realised; the ambient-light regime (no gauze), the light regime at the compensation point, one level above and three levels below the compensation point. Each aquarium was filled with 25 g of algal material and one grazer was added to induce a chemical defense if such a defense is present in the algal species under investigation. The algal material and grazers were weighed at the beginning and at the end of the study. The algal materials were blotted dry with paper tissue. For the ungrazed treatment, six different light levels were used with eight replicates each, with 25g algal biomass and without any grazers, to test whether algal growth rates were affected by the different light regimes. In total, 96 EUs were used, 48 in which algae were exposed to grazers and 48 EUs with ungrazed algae. These experiments were maintained for 2 weeks and the stress induction was stopped as soon as algal material showed signs of degradation. Physical parameters

in the aquaria, such as temperature, salinity, dissolved oxygen, pH and the numbers of grazers were observed and kept constant. Growth rates of the algae and their epibiontic cover were monitored by naked-eye observations weekly.

Feeding assays tested for seaweed palatability

Following the light-limitation phase, the algal test pieces were removed from the aquaria, blotted dry with paper tissue and individually weighed (TOLEDO scale, precision 0.0001g) before and after the feeding assays. For these, we used either fresh algal pieces, both grazed and ungrazed algae, or agar-based artificial food pellets made from freeze-dried algal material to identify chemical defense traits and effects of the different light levels. To avoid grazer adaptations to food quality, we used the same grazer species but different starved individuals in the feeding assays than in the stress induction. Feeding assays were conducted in a total of 96 aquaria (48 aquaria each for grazed and ungrazed algae respectively) with seawater which was changed twice per day. Consumption of a grazer on a single algal piece was calculated as: gram consumption per gram grazer = $(Ab – Aa)/G$, where 'A' indicates weight of the alga, and 'b' and 'a' indicates measurements at the beginning and end of the feeding assays, respectively, as well as the weight of the grazer, 'G'. The consumption of artificial food pellets was calculated as the difference in pellet weight at the beginning and the end of the assay. Feeding assays with *H. diversicolor* and *Aplysia* sp. were conducted during 16 hour (at night) and 24 hours, respectively, because *H. diversicolor* was most active at night. It was observed that *Aplysia* sp. was active both day and night.

Statistical analysis

We tested for the normality of the data with Shapiro-Wilks-w-test and for homogeneity of variances with the Levene's test. Data were transformed using natural logarithm when necessary; if the transformation was unsuccessful, non-parametric tests were used. The effect of light limitation and pattern of light dependent on palatability was analysed using a two-way ANOVA when data were parametric and homogeneous. The Tukey's HSD post-hoc test determined the sources of any significant differences. The growth rates data were transformed using $\log^{10}$ because the effect of light limitation on algal growth rates using a linear regression analysis was tested.

Results

The light-compensation point of Gracilaria edulis and Gracilaria salicornia

The absence of a diurnal rhythm in oxygen production indicates light conditions under which photosynthesis ceased (Fig. 1 and 2). The minimum number of gauze layers at which this occurs was taken as the light regime closest to the compensation point. The light-compensation points were different between algae: eight gauze layers for *G. edulis* and six gauze layers for *G. salicornia*.
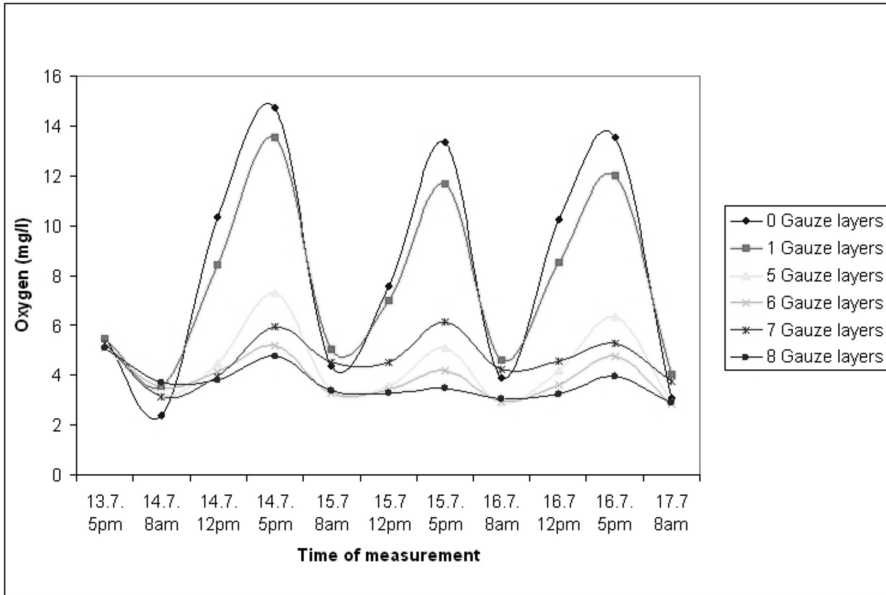
Figure 1. Oxygen production and light-compensation point of *Gracilaria edulis* under different light regimes. The experimental units were placed underneath a clear plastic roof and were exposed to natural-light conditions.
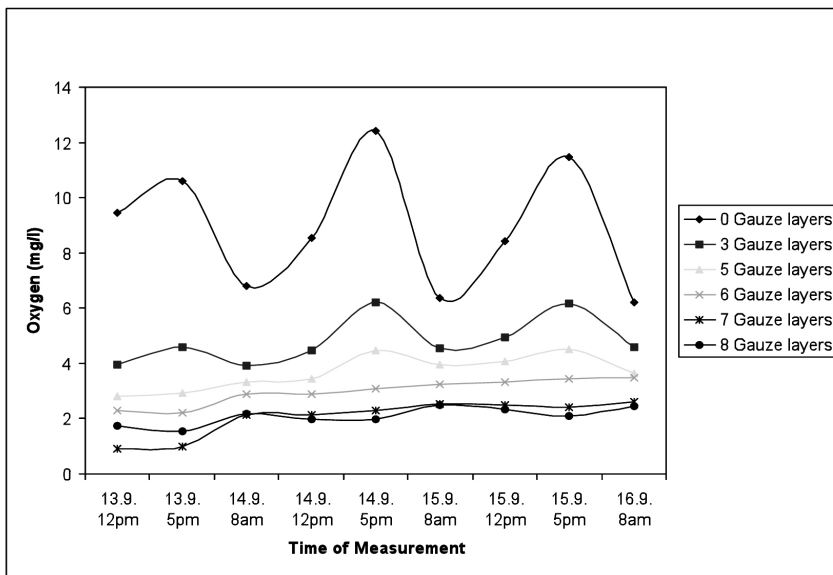

Figure 2. Oxygen production and light-compensation point of *Gracilaria salicornia* under different light regimes. The experimental units were placed underneath a clear plastic roof and were exposed to natural-light conditions.

Growth rates

Temporary low-light stress had a significant effect on the growth rates of the two red algae *G. edulis* and *G. salicornia* in two weeks under photoperiod of 12:12 h light:dark regime. The growth rates of *G. edulis* in the two different experiments, and *G. salicornia* exposed to different light levels show significant difference: 1) *G. edulis*: $r^2 = 0.74$, n = 5 for each light level, $P < 0.001$, 2) *G. edulis*: $r^2 = 0.62$, n = 8 for each light level, $P < 0.001$ and 3) *G. salicornia*: $r^2 = 0.70$, $n = 8$ for each light level, $P < 0.001$ (Fig. 3, 4 & 5). They show that growth was a linear function of light availability with light explaining 70% of the variation in the data for all three species. The growth rates varied more than 10% at 1046 μmol photon s^{-1} m^{-2} (100% light transmission) and negative growth rates were detected at lower than 126 μmol photon s^{-1} m^{-2} (12% light transmission).

Table 1. Measurement of initial light intensity at Kuala Terengganu three times a day (8am, 12pm and 5pm) during sunny climate conditions. With zero gauze layers 1046 μmol s^{-1} m^{-2} was measured which indicated 100 % light transmission.

Number of gauze layers	Light intensity (μmol photon s^{-1} m^{-2})	Light transmission (%)
0	1046	100
2	406	38.8
4	162	15.5
5	82	7.8
6	44	4.2
7	36	3.4

Algal growth rates as a function of light transmission *Gracilaria edulis*
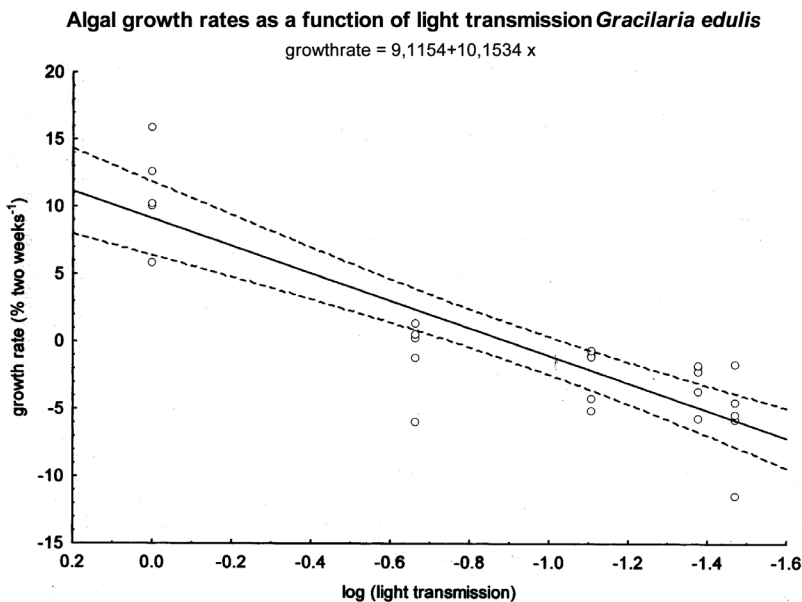
growthrate = 9,1154+10,1534 x

Figure 3. Growth rates of *Gracilaria edulis* under different light-transmission regimes during light-limitation phase. Each level of light transmission had five replicates.
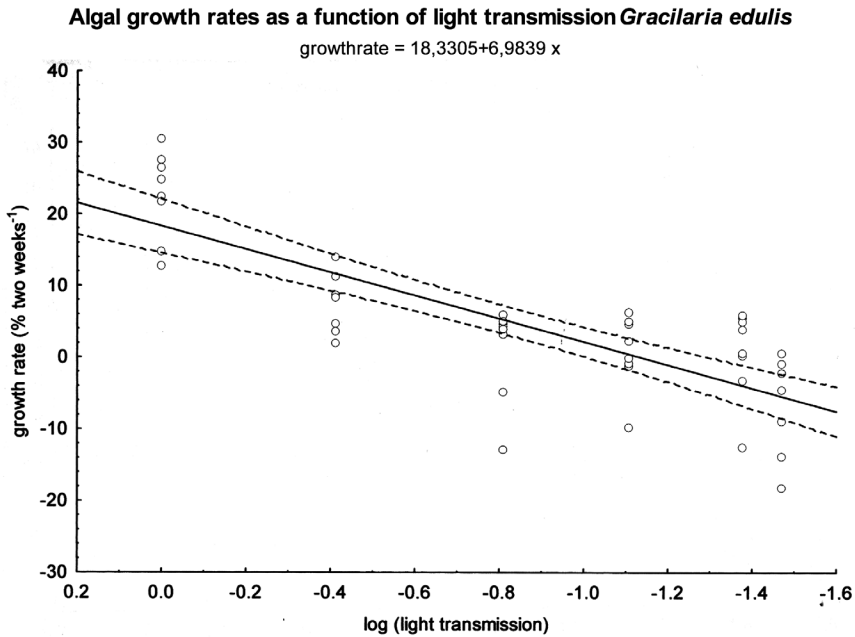
Algal growth rates as a function of light transmission *Gracilaria edulis*

growthrate = 18,3305+6,9839 x

Figure 4. Growth rates of *Gracilaria edulis* under different light-transmission regimes during light-limitation phase. Each level of light transmission had eight replicates.
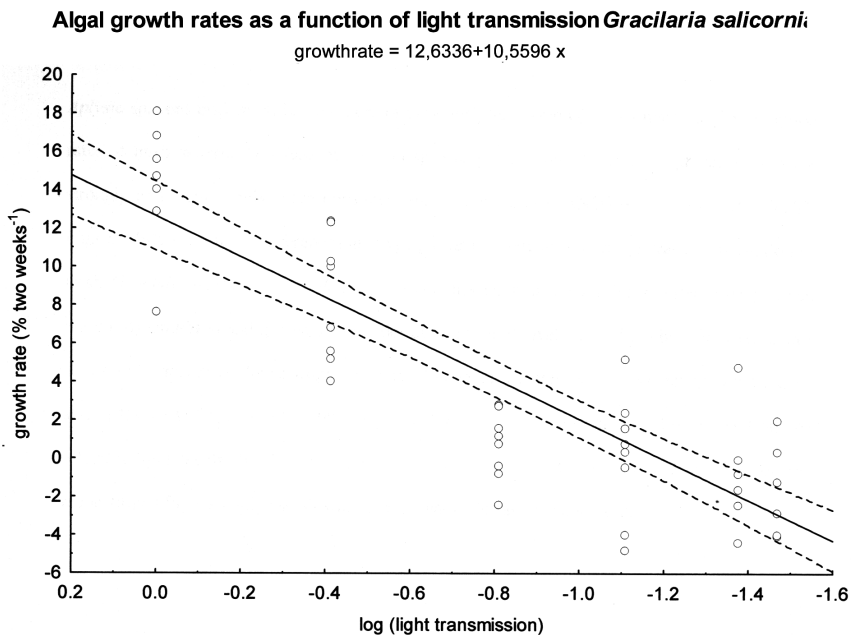
Algal growth rates as a function of light transmission *Gracilaria salicorni*

growthrate = 12,6336+10,5596 x

Figure 5. Growth rates of *Gracilaria salicornia* under different light-transmission regimes during light-limitation phase. Each level of light transmission had eight replicates.

Feeding assays with fresh algal material

Aplysia sp. consumed significantly more of previously-ungrazed *G. edulis* material. Consumption rates of fresh material *G. edulis* by *Aplysia* sp. was significantly different, ungrazed algae were strongly and significantly more consumed than grazed algae (ANOVA: $F = 15.6$, $P < 0.001$; Fig.6), while significant differences among light levels were absent. In contrast, consumption of fresh *G. edulis* material by *H. diversicolor* did not show any significant differences between previously-ungrazed and grazed algae under different light levels (Fig. 7). When *H. diversicolor* feed on *G. salicornia*, the gastropod consumed more of the previously-ungrazed than the grazed algae (ANOVA: $F = 29.6$, $P < 0.001$; Fig. 8) and did not distinguish among algal pieces from the different light levels. In all three cases, *Aplysia* sp. and *H. diversicolor* did not feed on the reconstituted food, so only assays with living algal material were analysed.
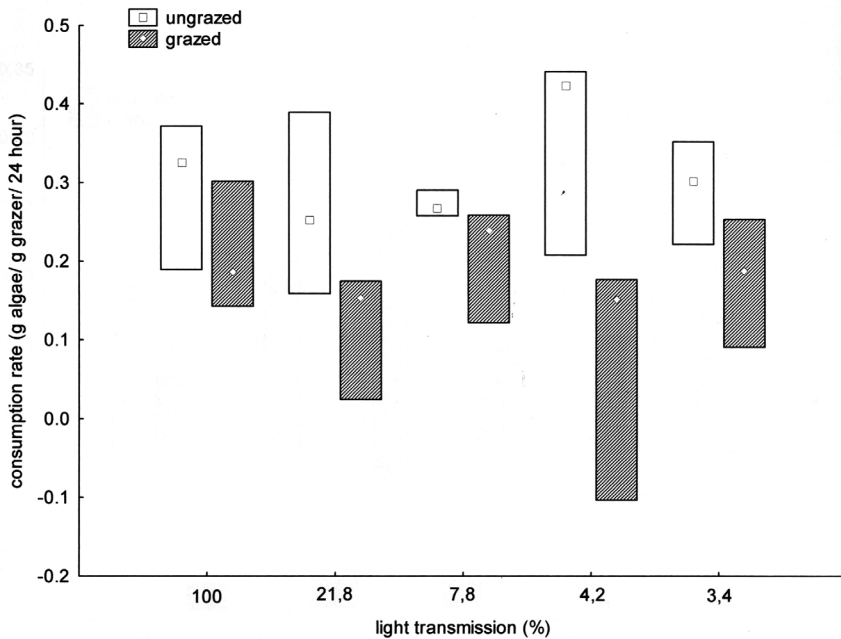

Figure 6. Median (SE) Consumption of living *G. edulis* by *Aplysia* sp. as a function of light transmission and grazing history in feeding assays after light-limitation phase. The boxes show interquartiles (n = 3 replicates for each treatment).
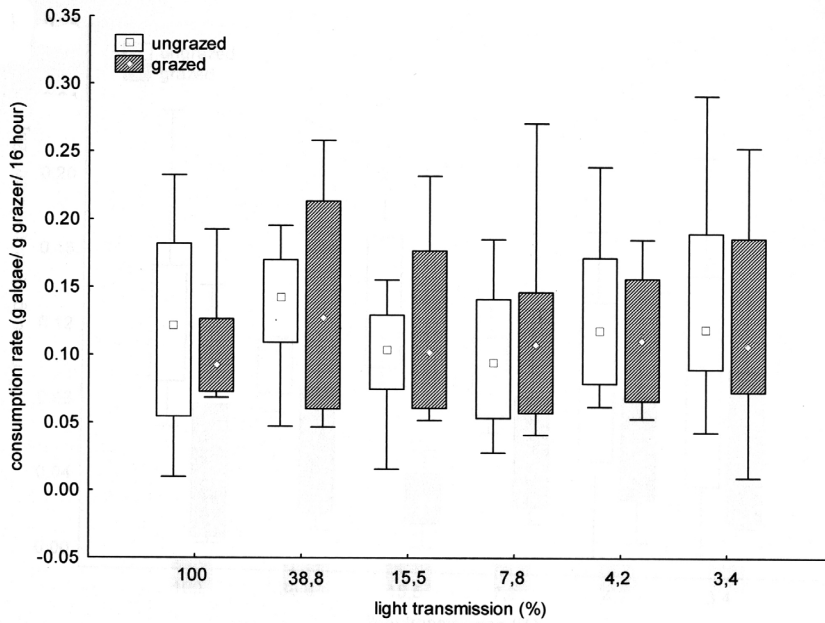
Figure 7. Median (+95% CI) Consumption of living *G. edulis* by *H. diversicolor* as a function of light transmission and grazing history in feeding assays after light-limitation phase. The boxes show interquartiles and whiskers represent non-outlier range (n = 8 replicates for each treatment).

Figure 8. Median (+95% CI) Consumption of living *G. salicornia* by *H. diversicolor* as a function of light transmission and grazing history in feeding assays after light-limitation phase. The boxes show interquartiles and whiskers represent non-outlier range (n = 8 replicates for each treatment).
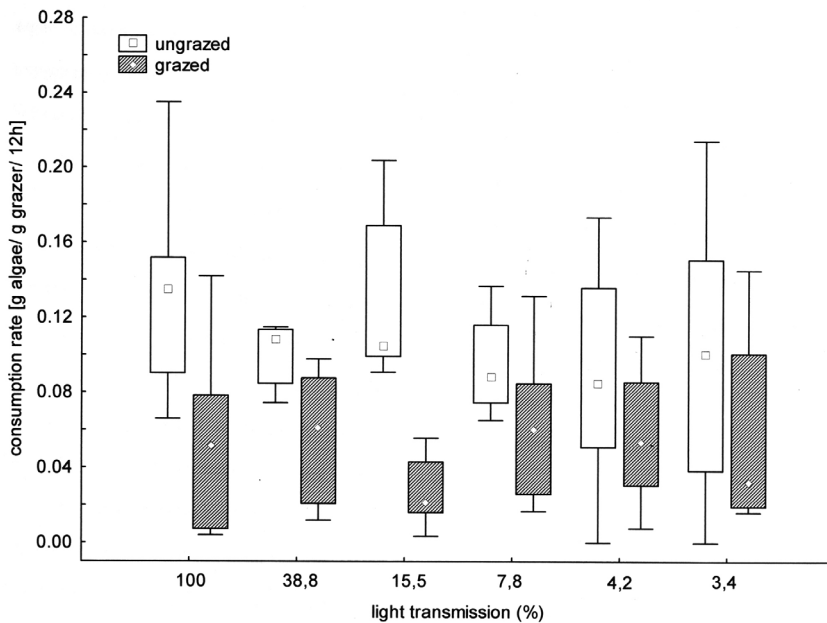
Discussion

Effects of low-light stress on algal growth rates

Our study demonstrated that algal photosynthesis was affected by decreasing light availability. From the determination of the light compensation points, we assumed that the algae experience stress when the oxygen production and respiration were balanced. In normal conditions, when the algae received enough light, the oxygen productions were higher than respiration. In contrast, oxygen productions were lower than respiration when the algae received less light.

We observed negative effects of light reduction on growth rates in two cases; with *G. edulis* and one time with *G. salicornia*. Algae which received less light were obviously darker than algae which received enough light. Therefore, it was assumed that these algae produced more pigments to compensate for the reduced energy supply. The changes in pigmentation in these red algae suggest that reduced light intensity may be the key factor causing increased densities of these pigments at low-light conditions in the related red algae *Gracilaria tikvahiae* (Lapointe et al., 1984) and *Hypnea musciformis* (Durako & Dawes, 1980). Pigment levels, in part, regulate photosynthetic capacity of seaweeds (Ramus, 1981) so light history must be considered in comparative physiological seaweed studies. Differences in growth rates between high and low light levels might have also been exaggerated relative to natural communities due to the reduction of light intensity in this study. Each EU was covered with different gauze layers that only allow the penetration of light intensity approximately between the 406 and 36 μmol photon s^{-1} m^{-2}. Bothwell et al. (1994) showed that growth was inhibited by ultraviolet radiation in the initial stages of algal community development. Therefore, under natural conditions, growth rates at high light-intensity levels might be inhibited by natural ambient-light intensity, thereby diminishing differences between growth rates measured at high and low light intensity. Some *Gracilaria* species require less than 100 μmol photon s^{-1} m^{-2} for optimal growth (Bird et al., 1979; Beer & Levy, 1983), while others require higher light intensity (Lapointe, 1981; Lapointe et al., 1984). Environmental factors, including temperature, salinity and light, play an important role in the growth, reproduction and distribution of marine algae (Gessner, 1970; Gessner & Schramm, 1971; Luning, 1981; Lobban & Harrison, 1994). Our findings of a high influence of light intensity on growth of *G. edulis* and *G. salicornia* is a good example of environmental factors, which may be more ecologically important than the main effects (of single factors) themselves. Lapointe et al. (1984) found a similar pattern for the red algae *Gracilaria tikvahiae*. They demonstrated that light was the most important factor affecting growth and photosynthesis in *Gracilaria* in their study.

Effects of low-light stress on palatability

Most reports about inducible defenses in seaweeds are from the group of brown algae, particularly the Fucales (Van Alstyne 1988; Cronin & Hay 1996; Pavia & Toth 2000; Toth & Pavia 2000; Sotka et al., 2002; Taylor et al., 2002; Rohde et al., 2004; Macaya et al., 2005), while three recent studies report chemical defenses in red algae (Weidner et al., 2004; Ceh et al., 2005; Diaz et al., 2006). In our study, there were no significant effects of low-light stress on the palatability of two red algae but significant differences in palatability were detected between previously-grazed and ungrazed algal material. The red algae *G. edulis* and *G. salicornia* produced defenses when exposed to grazing by the gastropod *Aplysia* sp. and *H. diversicolor,* respectively. In contrast, *G. edulis* showed no response to the gastropod *H. diversicolor.* These findings show that the defense mechanisms induced by grazing of different grazer species are variable while algal palatability was not light-dependent.

Effects of gastropod grazing on the palatability of G. edulis

Grazing by the gastropod *Aplysia* sp. lowered the palatability of the red algae *G. edulis* within a time period of two weeks. The grazing impact of *Aplysia* sp. was severe. When *G. edulis* were treated in light limitation algae in the presence of grazers were damaged severely by gastropod feeding, while those without grazers always grew well. These repulsive effects were observed in feeding assays with fresh material, adding additional evidence that inducible anti-herbivore defenses are not taxonomically restricted to brown algae. The red algae *G. edulis*, treated with gastropod *H. diversicolor*, however showed no significant differences in palatability between previously grazed and ungrazed material. There are different explanations for this. (1) *Aplysia* sp. consumed larger amounts of *G. edulis* than *H. diversicolor*: consumption by *Aplysia* sp. was 50% higher than consumption by *H. diversicolor*. Thus, to avoid being killed by *Aplysia* sp., *G. edulis* induced defense while this was not the case with *H. diversicolor* therefore. The higher grazing pressure by *Aplysia* sp. could explain the induction of defenses on *G. edulis* in our experiment. We observed that *Aplysia* sp. was very mobile and could easily feed on different parts of the algae during the light limitation phase. In contrast, grazing pressure by *H. diversicolor* was too low to induce a defense in *G. edulis*. (2) These different effects could be explained due to mechanistic understanding is critical to evaluating induced and other defenses, as induction of chemical changes does not always translate to reduced palatability. For example, when the brown alga *Fucus vesiculosus* was grazed by amphipods, the alga's phenolic levels increased by a statistically significant 100%; however, this had no effect on feeding by the amphipods and did not lead to amphipods choosing ungrazed over grazed plants (Duffy & Hay, 1994). We did not asses chemical compound of these algae, which could explain these feeding patterns. Neither did we asses tissue toughness and so we cannot exclude morphological plasticity. (3) For *G. edulis* treated with *H. diversicolor*, the absence of significant differences in palatability may be explained by the variability in responses of herbivores to different compounds (Hay & Fenical, 1988). For example, more than 400 different compounds have been reported in the genus *Laurencia*. Most repel fish, but others have no effect on them, and may repel other grazers (Hay & Fenical, 1988). We assume that the specific chemical defenses in *G. edulis* are active against *Aplysia* sp. but not against *H. diversicolor*. Feeding by *H. diversicolor* was either not affected or was even stimulated by the same compounds that deter *Aplysia* sp.. *Haliotis diversicolor* that has limited mobility may preferentially feed on nutrient-rich plants or parts of plants in order to optimise their fitness. It was not possible to show that the feeding differences were exclusively generated by chemistry since feeding assays with food pellets were not employed. (4) Complex ecological interactions could ultimately increase the fitness of the algae or the grazer. Seaweeds can attract grazers that clean the alga of epiphytes or possible competitors (Stachowicz 2001). Such positive interactions between seaweeds and herbivores have been described for many aquatic systems (Underwood et al., 1992; Kerffoot et al., 1998; Jones et al., 1999).

Grazing effects in Gracilaria salicornia palatability

The feeding assay with fresh material showed that ungrazed pieces of *G. salicornia* were preferred by the gastropod *H. diversicolor* over grazed pieces, indicating that an anti-herbivore defence was induced here. However, no significant effect of the light treatments were detected indicating that palatability of *G. salicornia* was not light dependent. As tissue toughness or the concentrations of chemical compound were not measered, it was not possible to determine whether the induced defences were morphological or chemical or a combination of both.

Absence of light effect on algal palatability

For all three feeding assays, no significant differences in palatability were detected between seaweed material that experienced different levels of light transmission. Any pattern of light dependency in palatability was not observed. This is surprising, because stressed algae which receive less light should be more susceptible to grazers than nonstressed ones as inferred by environmental stress theory. Theories of environmental stress-induced increases in palatability in terrestrial plants have proposed increases in nutritive value or decreases in the defensive traits as mechanisms responsible for a change in palatability. The environmental stress theory (EST) is based on the premise that a stressed organism is less able to acquire resources and will allocate a greater proportion of these reduced resources to maintenance, compared to an unstressed organism. The capacity of the red algae *G. edulis* and *G. salicornia* to induce defenses against grazers under both stressed and nonstressed conditions could be explained by resource availability model (RAM). RAM is a chemical defense theory which suggests that plant species produce levels and types of defenses based on the resources-richness of the environment in which they evolved. RAM suggests that plant species that evolved in low-resources environments will be inherently slow growing because of limitation imposed by low-resource acquisition, will be long-lived, and will allocate a large proportion of resources to defenses because any tissue lost to an herbivore will be expensive to replace. Chemical compounds and growth rates for grazed algae were not assessed, so RAM could not be excluded.

Conclusion

It was shown that two red macroalgae *G. edulis*. and *G. salicornia* off the Peninsular Malaysia induced anti-herbivore defenses in response to grazing by the gastropod *Aplysia* sp. and *H. diversicolor*. Findings indicate that inducible defenses generally exist in the two investigated Gracilaria species, but vary with the identity of herbivores. Surprisingly, algal palatability was not affected throughout all low-light regimes, contrasting the widespread notion that defensive traits in seaweeds are dependent on metabolic energy. However, it appears clear that low-light stress effects play only a minor role on the performance of antiherbivore defenses in these two red algae. It is suggested that palatability of these algae are not affected by low-light stress and inducible defenses can also be an effective mechanism to affect the abundance and distribution of various tropical seaweed species in Malaysia. Furthermore, it was demonstrated that light reduction affected photosynthesis and growth in these algae. The palatability of these two algae was not light-dependent.

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