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Sun and shade differences in productivity of reef corals

REEF CORALS are mutualistic symbiotic associations between cnidarians and dinoflagellates. The algae photosynthesise and translocate photosynthate to the animal partner, although the animal is capable of heterotrophic nutrition[1–5]. Some reef corals have wide bathymetric ranges[6,7] and the growth and survival of individuals in the deeper regions of the euphotic zone could result from an increase in the energy efficiency of the symbiotic complex. A number of reports document the laboratory-determined photosynthesis–radiation responses of corals[8–12] and zooxanthellae[13], but because the details of the habitat or depth from which the animals were collected are rarely described, comparisons among results in the literature are difficult. Here we provide evidence for the existence of 'sun' (heliophytic) and 'shade' (sciophytic) differences in the net photosynthesis–radiant flux intensity response of individuals of one coral species from 10 and 25 m depth on the same reef in an atoll lagoon.

Individuals of the foliaceous coral *Pavona praetorta* Dana were collected underwater at the Marine Pier Pinnacle Reef 300 m west of Enewetak Island (site Fred), Enewetak Atoll, Marshall Islands. Immediately after collection, the specimens were placed at the same depth in 1.5-l Perspex containers in which net rates of photosynthesis were determined (Fig. 1). Oxygen production per unit chlorophyll *a* was measured for 5-min intervals as a function of radiant flux intensity, and the data were fitted to the Michaelis–Menten equation by an iterative maximum likelihood solution method, which improves on an initial Lineweaver–Burk estimate[14,15].

The best fit Michaelis–Menten curves for the *Pavona* specimens are plotted in Fig. 1 with 99% confidence limits (one-tailed Student's t test, $n-2$ d.f.) for P_{max} (maximum photosynthetic rate) and K_m (radiant flux intensity at half saturation). By analogy to enzyme kinetics, K_m is a measure of the affinity of the photosynthetic system for radiant energy. The lack of overlap of the confidence limits indicates that the K_m for the 25-m specimens are lower than the value for the 10-m specimen (Table 1). Therefore, relative to their maximum photosynthetic rates, the deep water individuals saturate their photosynthetic machinery at lower radiation intensities than the shallow water individual. This is analogous to the 'sun' and 'shade' differences documented for canopy and understory plants[16] and for phytoplankton acclimatised to high and low light intensities[17,18]. The saturation of deep water individuals at lower radiation intensities is consistent with Margalef's[19] observation of greater A_{450} of pigments from deep water

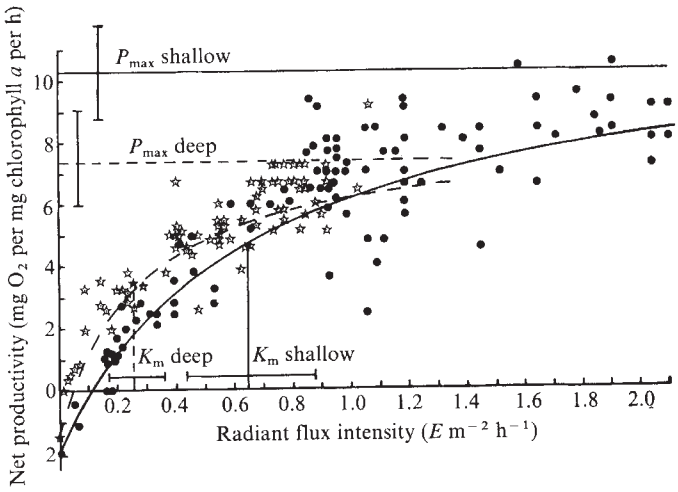

Fig. 1 Photosynthesis–radiation intensity relationships for *Pavona* from 10 m (●) and 25 m (open star). E, einstein ($= 6.02 \times 10^{23}$ quanta). Ideal curves, maximum photosynthetic rates (P_{max}), radiant flux intensities at half saturation (K_m), and their 99% confidence limits are from maximum-likelihood regression analysis[14,15]. 25-m data are from one of the two replicates. Values at zero radiant flux are means: shallow specimen $x = -1.84$, s.d. = 0.29, $N = 71$; deep specimen $x = -1.41$, s.d. = 0.27, $N = 117$. Experiments were run for 26 h *in situ* in Perspex chambers which were stirred continuously and flushed with ambient water at 35-min intervals. The instrument design was modified from that of McCloskey[22]. Oxygen concentrations in the chambers were monitored with silver–platinum electrodes[23] and photosynthetically active radiation (400–700 nm) at the depth of the respirometers was measured with a quantum sensor (Lambda Instruments). These values were recorded continuously on strip chart recorders (Esterline Angus Minigraph). The electrodes were calibrated in air-saturated seawater and a yeast suspension in dilute sucrose solution, according to the tables of Green and Carritt[24], and checked with an independently calibrated commercial oxygen meter (Yellow Springs Model 57). The *in situ* light sensor was calibrated with a factory-calibrated quantum radiometer (Lambda Instruments). After termination of the experiments, the corals were frozen. Chlorophyll was extracted in 90% acetone (20 h, dark, 5 °C). Extinctions were measured in 10-mm cells (Beckman Model DU Spectrophotometer), and total chlorophyll *a* was estimated by the trichromatic equations of Richards[25].

corals compared with conspecifics from shallow water. The measured difference in photosynthetic response is not likely to be due to spectral quality changes in the light between 10 and 25 m, because the 640–670-nm light which affects the red action spectrum peak of photosynthesis[13] amounts to only 2% of the total light flux at 18 m and 0.03% at 25 m (ref. 20), a difference below the resolution range of our *in situ* light meter circuit. We found no difference in temperature between study sites, and von Arx[21] has estimated that atoll lagoons have complete water overturn every 150 h, indicating that temperature stratification is unlikely. Therefore we believe that the differences in photosynthetic response between the two study sites are not temperature related.

Franzisket's[11] data from specimens collected at 3 m indicate K_m values higher than our 25-m specimens and within the range of our 10-m samples, corroborating our interpretation that 'sun' and 'shade' differences exist in the photosynthetic response of corals from high and low light regimes (Table 1). Evidence in support of the phenomenon comes from our *in situ* data for *Plerogyra*, *Porites* and *Acropora* from the Philippines and from Barnes and Taylor's[12] *in vitro* data on *Montastrea annularis* from the Caribbean (Table 1). The 18-m depth specimens have K_m values in the range of our 25-m *Pavona*, the *Montastrea* from 15-m is intermediate between our 25-m and 10-m *Pavona*, and the *Acropora* from 3 m exhibits a K_m in the range of Franzisket's[11] 3-m specimens and our 10-m *Pavona*. The overlap in K_m among the different coral species

Table 1 Half-saturation constants for photosynthesis as fit to the Michaelis–Menten* equation

Species	Depth (m)	K_m ($E\ m^{-2}\ h^{-1}$), Maximum likelihood estimate	One-tailed confidence limits Lower ($P < 0.01$)	Upper
P. praetorta Dana	25	0.26	0.18	0.37
P. praetorta Dana	25	0.14	0.00	0.38
P. praetorta Dana	10	0.63	0.43	0.88
Plerogyra sinuosa Dana	18	0.18	0.10	0.26
Porites lutea Milne Edwards and Haime	18	0.11	0.07	0.15
Acropora cf. *arbuscula* Dana	3	1.23	0.76	1.99
Kaneohe Bay corals, Hawaii† (ref. 11)	3	0.65	0.46	0.86
Montastrea annularis Ellis and Solander[12]	15	0.41	0.21	0.67

Each line represents a 24-h incubation of a single coral.

*Michaelis–Menten equation: $P = (P_{max} \times I)/(K_m + I)$ or $P_{relative} = P_{observed}/P_{max} = I/(K_m + I)$

†Pooled data from four species: (*Fungia scutaria* Lamarck, *Montipora verrucosa* Lamarck, *Porites compressa* Dana and *Pocillopora meandrina* Verrill); regressions run separately were not significantly different ($P > 0.05$).

suggests that, given a particular light regime, the algal photosynthetic efficiency relative to the maximum photosynthetic rate is independent of the coral species that the algae inhabit. In addition, Kawaguti[8] found the compensation light intensity was related to habitat: individuals from deeper or shaded places showed lower values.

The existence of acclimation to ambient light regime in corals suggests that extrapolation from measurements on individuals at one depth to the behaviour of the population over the whole depth range is not valid. Similarly, the efficiency of translocation of photosynthate from alga to animal partner may vary with depth. *In situ* 24-h measurements on individuals from a range of depths and species are needed to begin to resolve the question of the trophic plasticity of corals as a function of habitat.

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Frost sensitivity of *Zea mays* increased by application of *Pseudomonas syringae*

DRIED, powdered corn leaves (*Zea mays* L.) dusted on to the leaves of corn seedlings, will increase frost damage to treated seedlings relative to untreated controls at ~ −4 °C (refs 1, 2). In a preliminary attempt to isolate the entity responsible for this activity, we found that water extracts of corn leaf powder from healthy field-grown plants caused as much increase in frost sensitivity when applied as a spray to seedling corn, as did application of the powder itself when tested as described below. Addition of either streptomycin or tetracycline (1,000 p.p.m.) to these water extracts eliminated their activity, suggesting the possible role of bacteria in this effect.

Corn seedlings for frost sensitivity measurements were grown in sterilised vermiculite in a plant growth chamber (day: 18 h, 30 °C; night: 6 h, 20 °C) to the 3-leaf stage. Plants were watered daily with nutrient solution. Ten or more pots (6 plants per 10-cm pot) were used for each treatment. Unless otherwise noted, treatment was given 24 h before freezing and the plants were held in a mist chamber until 20 min before freezing. Immediately before freezing, all pots were positioned randomly in a controlled temperature chamber at ~ 0 °C. The air temperature was lowered at ~ 0.1 °C min^{-1} to −3.0 °C and then at ~ 0.04 °C min^{-1} to −3.5–−4.0 °C. Maximal differences in frost damage between treated and untreated plants occurred in this temperature range. The air temperature in the chamber was then increased at ~ 1.0 °C min^{-1} to 30 °C. Frost damage was assessed by counting the number of leaves per plant with symptoms of frost injury.

Forty-two bacterial isolates of varying colony colour and morphology were obtained by dilution plating from water extracts of corn leaf powder. Each isolate was grown on nutrient agar, suspended in 0.1 M phosphate buffer, *p*H 7.0, sprayed on to corn seedlings and assayed for the ability to increase frost sensitivity of corn at −3.5 to −4.0 °C. Only one of the 42 isolates was active in increasing the frost sensitivity of corn seedlings. When leaves of corn seedlings were sprayed with suspensions of this isolate in buffer 24 h before freezing > 95% of the leaves were damaged at −3.5 to −4.0 °C, whereas < 8% of the leaves of plants sprayed with buffer alone were damaged at this temperature. On the basis of its response to standard physiological tests[3,4], this isolate was identified as *Pseudomonas syringae* van Hall, a species that includes strains pathogenic to a large number of diverse host plants including corn[5]. We have not observed pathological symptoms even when corn