

CO₂ increase, a direct cause of coral reef mass bleaching?

L'élévation du CO₂, une cause directe du blanchiment de masse des récifs coralliens ?

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ABSTRACT

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Reef mass bleaching is a very serious threat to this major Earth ecosystem. Global Warming is generally invoked. The direct involvement of CO₂ increases in the reef mass bleaching has not yet been fully addressed. Here I present experimental results on the synergistic effects of light, temperature and CO₂ on the symbiotic sea anemone *Anemonia viridis*. Photosynthetic state was measured by chlorophyll fluorescence fast kinetic rise, allowing determination of the classical stress indicator, the so-called Fv/Fm ratio. Evidence is provided here showing that CO₂ acts very much like temperature. Present CO₂ increase has an effect equivalent to a warming of 0.4°C, more probably 1.2°C. Hence CO₂ increase appears as a main cause of reef bleaching. Given expected future CO₂ levels, reefs must be considered as in very great danger.

RÉSUMÉ

Pêcheux M. - [L'élévation du CO₂, une cause directe du blanchiment de masse des récifs coralliens ?] Mar. Life, 12 (1-2) : 63-68.

Le blanchiment de masse des récifs de coraux est une très sérieuse menace pour cet écosystème majeur de la Terre. Le réchauffement global est généralement invoqué. L'effet direct de l'accroissement de CO₂ n'a pas été examiné en détail. Je présente ici les résultats expérimentaux des effets synergétiques de la lumière, de la température et du CO₂ sur l'anémone de mer symbiotique *Anemonia viridis*. L'état de l'appareil photosynthétique a été mesuré par la cinétique rapide de la fluorescence de chlorophylle permettant la détermination de l'indicateur classique de stress Fv/Fm. Il apparaît que le CO₂ agit de manière semblable à la température. L'actuel accroissement de CO₂ a un effet équivalent à 0,4°C, plus probablement 1,2°C. Ainsi, l'accroissement de CO₂ est probablement le facteur principal du blanchiment des récifs. Etant donné les niveaux futurs de CO₂, les récifs doivent être considérés comme en très grand danger.

INTRODUCTION

Unexplained reef mass bleaching first appeared in the early 80's (see review in Williams, Bunkley-Williams, 1990; Smith, Buddemeier, 1992; Goreau, Hayes, 1994; Glynn, 1996; Brown, 1997; Hoegh-Guldberg, 1999; Pêcheux, *subm./online*). This worldwide phenomenon has been increasing in frequency and magnitude since then. Bleaching affects all reefal photosynthetic symbioses, corals

being the most spectacular, with consequent but variable mortality. Although certainly global, its causes are not completely understood yet. The Global Warming of 0.5°C (Houghton *et al.*, 1996) when mass bleaching began is generally invoked as bleaching occurs preferentially during Summers with "above average" temperature, but evidence of new maxima all over the tropics is still needed, and good counter-examples exist, notably large foraminifers (Williams *et al.*, 1997).

Bleaching is due to the expulsion of the symbionts and/or the loss of their pigments, hence the name. The fact that it affects a great diversity of photosynthetic symbioses (corals, sea anemones and others cnidarians, mollusks, sponges, foraminifers, ascidians in association with either dinoflagellates, diatoms, chlorophytes or cyanobacteria) points to some fundamental limitations of photosynthesis, the two main causes being photoinhibition and photorespiration. The increase of CO_2 from 280 ppm in preindustrial times to 360 ppm today (Houghton *et al.*, 1996) is a global change affecting all shallow seawaters (Brewer *et al.*, 1997; Peng *et al.*, 1998). Photosynthetic symbionts are particularly limited in uptake of inorganic carbon from the seawater medium. But, in contrast to others phototrophs, in corals (Allemand *et al.*, 1998) and large foraminifers (Kuile *et al.*, 1989), photosynthesis decreases as CO_2 rises, surely because of weakening of HCO_3^- pumping by the host which uses pH gradient, and thus promotes photorespiration. It is also well known that photosystem II (PS II) photochemistry is strongly modulated by HCO_3^- at the QA-QB site (Diner *et al.*, 1991; Govindjee, van Rensen, 1993). Analysis of the literature indicates that photoinhibition is very important in bleaching: involvement of light (clear sky and calm, transparent waters during events, preferential occurrence on upper sides), xanthophylls ratio change *in situ* (Amarsali *et al.*, 1997), and in warming bleaching experiments, early thylakoid disruption (Salih, personal communication) and fall of Fv/Fm (Iglesias-Prieto *et al.*, 1992; Fitt, Warner, 1995; Iglesias-Prieto, 1997; Jones *et al.*, 1998; Tsimilli-Michael *et al.*, 1998).

It is also already known that, without any other stress, corals reduce calcification with lowering of calcium carbonate saturation (Gattuso *et al.*, 1999; Kleypas *et al.*, 1999), like calcifying marine plankton (Riebesell *et al.*, 2000). Bleaching also affects non-calcifying organisms, such as sea anemones and sponges. Marine microalgae are indeed directly sensitive to CO_2 level (Tortell *et al.*, 1997; Goldman, 1999).

A small environmental change is responsible for bleaching during maximum Summer stresses. Experiments with coral and large foraminifers showed that high CO_2 is a bleaching factor (Pêcheux, in preparation). In order to quantify the effect of CO_2 in synergy with light and temperature, the photochemical state was measured on tentacles of a symbiotic sea anemone after systematic incubation of one hour under four light levels, five temperatures and four CO_2 levels.

MATERIAL AND METHODS

Six clones of *Anemonia viridis* (Forskål, 1775) (non-purple tips morph) were collected in May 1998 at half metre depth in Villefranche-sur-Mer Bay, South-Eastern France. Temperature was about 15.7°C, the Summer maximum is 29-30°C. Before experiments,

they were kept in culture in a 100 litres aquarium for one to three weeks at 25°C, 100 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ Life-Glo fluorescent tube, 12 h light: 12 h dark and at 8.25 ± 0.05 pH, fed twice a week with various feeds. They are still healthy after one year of culture.

Experimental protocol

Experiments were run in a pseudo-random order of light and temperature. Tentacles, 1 to 2 cm long, were cut and put individually in 16 tubes of 5 mL seawater at 25°C, 8.25 pH. This preparation was done under dim light ($\approx 10\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and took five minutes at most. It was seen in preliminary experiments that cut tentacles in tubes stay healthy (*i.e.* no strong decline of Fv/Fm, and before any microscopic signs of deliquescence) for at least four days under culture conditions, or for two days under stress (32°C, 500 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). They were kept in the dark for 25 minutes, with control measurements of chlorophyll fluorescence during the last ten minutes. Seawaters were then replaced by pCO_2 -controlled pHs of 7.80, 8.10, 8.40 or 8.70 ± 0.02 ones, with four replicates per pH treatment. Extremes are like those observed exceptionally in reef lagoons (see Pêcheux, *subm.*). These decanted, unfiltered seawater mediums were the same from the beginning to the end of the experiments, kept in CO_2 -tight plastic 1.5 litre bottles in darkness, adjusted when needed before runs from small drifts (generally less than 0.03 pH) with addition of the same stock of 5.0 or 9.5 pH seawaters. Different pHs were obtained by either adding commercial 95% CO_2 gas or by bubbling in closed circulation with air bathed through a commercial NaOH- $\text{Ca}(\text{OH})_2$ solution. pH was measured with a Bioblock 3301 model, with 0.01 precision, 0.02 accuracy, calibrated with Radiometer Copenhagen 7.00 and 9.16 IUPAC NBS buffers. The NBS pHs of 8.70, 8.40, 8.10, 7.80 used in the experiment correspond to CO_2 levels of respectively about 85, 230, 570 and 1270 ppm at 25°C, given NBS pH/seawater Hansson pH conversion, a measured salinity of 38.75 (sea gravimeter, temperature and Dikson, Goyet (1994) equations), an alkalinity of 2,603 $\mu\text{eq}\cdot\text{kg}^{-1}$ (using the standard salinity-alkalinity Mediterranean relationship) and DOE (1994) equations.

Samples were incubated at a temperature of either 25, 28, 30, 32 or 34°C ($\pm 0.2^\circ\text{C}$ maximum range, measured with a mercury ASTM ERTGO thermometer, 0.1°C accuracy) and light (measured with a Sekonic M38) of either 50, 160, 500 or 1,600 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (except at 28°C-1,600 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 70 minutes. Two 10 minutes cycles of chlorophyll fluorescence measurements were performed, one after 50 minutes, with 10 ± 1 seconds of predarkening, the second beginning at 1 hour with 1-minute predarkening. Results with ten seconds predarkening are essentially similar to the others. Without changing the seawater medium, further measurement was made after 30 minutes in darkness at 25°C.

Chlorophyll fluorescence measurements

Measurements of the polyphasic rise of chlorophyll fluorescence were done with a Plant Efficiency Analyser (Hansatech Instruments Ltd, King's Lynn Norfolk, PE 4NE, UK) at 12 bits precision, with recording every 10 μ s the first 2 ms, then every ms up to 1 s, and every 100 ms thereafter. Maximum LED excitation light intensity was used, around 6,000 μ E.m⁻².s⁻¹, peak at 650 nm. Preliminary experiments had shown that under culture conditions a standard one minute predarkening allows full opening of PS II traps, without starting the dark adaptation. As in corals and large foraminifers, the maximum fluorescence level (Fm) is often reached after a few seconds, up to 5 seconds, a characteristic of reef symbioses (Tsimilli-Michael *et al.*, 1998).

The fast kinetics of chlorophyll fluorescence increase was analysed according to established model (Strasser *et al.*, 1995; Tsimilli-Michael *et al.*, 1998). Here I focus only on the primary photosynthetic efficiency parameter Fv/Fm (Baker, 1996), calculated from the ratio of the variable (Fv) to maximum (Fm) chlorophyll-a fluorescence, and corresponding to the ratio of exciton trapped by the PS II per photon absorbed by chlorophyll antenna, measured here in light-adapted state.

RESULTS

First, the influence of light is preponderant (figure 1). After one hour of incubation in light, Fv/Fm displays a classical down-regulation. It is remarkably well correlated with the logarithm of light level ($Fv/Fm = -0.352 \log \text{light} + 1.254$, $r^2 = 0.908$, $p < 0.0001$, $n = 304$). As in land plants (Epron, 1997; Spunda *et al.*, 1998), temperature and CO₂ effects are superimposed on this light trend. Under dim (50 μ E.m⁻².s⁻¹) light, Fv/Fm rises slightly at first with temperature, then declines above 30°C ("Monday morning effect") (figure 1a). It is well known that weak light acts in an antagonist manner to high temperature (Havaux, Strasser, 1990). Under mid-level (160 and 500 μ E.m⁻².s⁻¹) light, Fv/Fm increases somewhat linearly with temperature. This trend is very weak under full, noon (1,600 μ E.m⁻².s⁻¹) light, as values are very low ("Sunday afternoon effect"). The influence of CO₂, as recorded through pH, has exactly the same pattern as does temperature, although with more variance (figure 1b).

The parallelism between temperature and CO₂ effects allows one to establish an equivalence between them, by comparing their Fv/Fm slopes of regression. For example, at 160 μ E.m⁻².s⁻¹, acidification by CO₂ of one pH unit has the same effect as 3.7°C warming. The rise of atmospheric CO₂ from 280 ppm to 360 ppm (Houghton *et al.*, 1996) has induced a worldwide acidification of surface seawater, of -0.0853 pH unit (22% increase of proton concentration) from 8.315 down to 8.229 for mean reef seawater (25°C, 36S, 2,380 μ Eq. Alk.kg⁻¹, and Dickson, Goyet (1994)

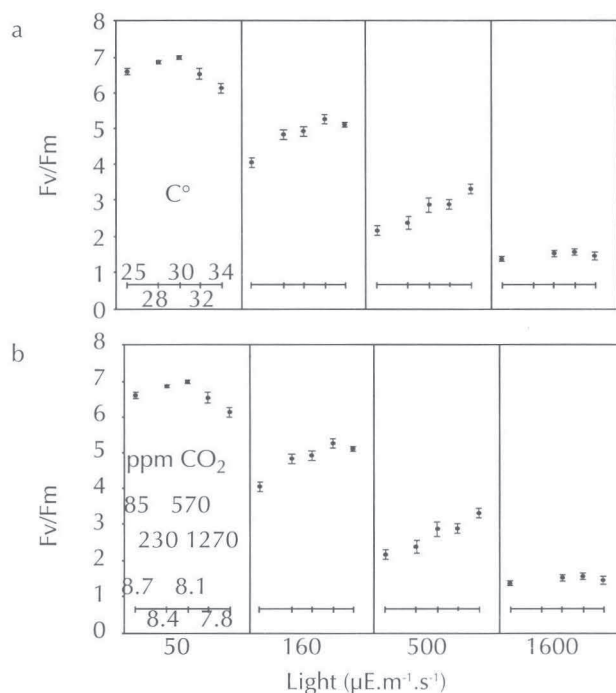


Figure 1 - For each light level, Fv/Fm \pm SE as a function of: (a), temperature (CO₂/pH conditions pooled, $n=16$ each point); and (b), CO₂/pH (temperature conditions pooled, $n=20$ each point). With increasing temperature, at 50 μ E.m⁻².s⁻¹, Fv/Fm increases up to 30°C, then decreases (both $p < 0.0001$). At 160 μ E.m⁻².s⁻¹, it increases up to 32°C ($p < 0.0011$) then it decreases slightly ($p=0.44$). At 500 μ E.m⁻².s⁻¹ there is only an upward trend ($p < 0.0001$). At 1,600 μ E.m⁻².s⁻¹, the positive trend is non-significant ($p=0.38$). With acidification by CO₂ (note inverted pH scale), at 50 μ E.m⁻².s⁻¹, Fv/Fm increases with CO₂, from 8.7 down to 8.1 pH ($p=0.016$; 0.0035 with values corrected from temperature deviations from mean in order to reduce dispersion) then decreases at pH 7.8 although not significantly ($p=0.72$; 0.57). It increases at 160 μ E.m⁻².s⁻¹ ($p=0.019$; 0.0015) but not down to pH 7.8 ($p=0.83$; 0.57). At 500 μ E.m⁻².s⁻¹, there is an overall increase ($p=0.023$; 0.0049), but mostly between 8.4-8.1 pH ($p=0.014$; 0.0036) not 8.7-8.4 pH ($p=0.47$; 0.30) nor 8.1-7.8 pH ($p=0.97$; 0.97). At 1,600 μ E.m⁻².s⁻¹, the positive trend is non significant ($p=0.69$; 0.68). / Pour chaque niveau de lumière, Fv/Fm \pm SE en fonction de : (a), la température (les conditions de CO₂/pH réunies, $n=16$ chaque point) ; et (b), le CO₂/pH (les conditions de température réunies, $n=20$ pour chaque point). Avec l'accroissement de température, à 50 μ E.m⁻².s⁻¹, Fv/Fm augmente jusqu'à 30°C, puis décroît (chaque fois $p < 0.0001$). À 160 μ E.m⁻².s⁻¹, il augmente jusqu'à 32°C ($p < 0.0011$) puis décroît légèrement ($p=0.44$). À 500 μ E.m⁻².s⁻¹ il y a seulement un accroissement régulier ($p < 0.0001$). À 1 600 μ E.m⁻².s⁻¹, la tendance positive est non significative ($p=0.38$). Avec l'acidification par le CO₂ (noter l'échelle inversée du pH), à 50 μ E.m⁻².s⁻¹, Fv/Fm augmente avec le CO₂, du pH 8,7 à 8,1 ($p=0,016$; 0,0035 en utilisant les valeurs corrigées de la déviation de température par rapport à la moyenne afin de réduire la dispersion) puis décroît à pH 7,8 bien que de manière non significative ($p=0,72$; 0,57). Il augmente à 160 μ E.m⁻².s⁻¹ ($p=0,019$; 0,0015) mais pas au pH 7,8 ($p=0,83$; 0,57). À 500 μ E.m⁻².s⁻¹, il y a seulement un accroissement régulier ($p=0,023$; 0,0049), mais surtout entre les pH 8,4 et 8,1 ($p=0,014$; 0,0036) et non entre 8,7 et 8,4 ($p=0,47$; 0,30) ni 8,1 et 7,8 ($p=0,97$; 0,97). À 1 600 μ E.m⁻².s⁻¹, la tendance positive est non significative ($p=0,69$; 0,68).

Table 1 - Temperature equivalence of stress due to actual CO₂. For each light level, temperature equivalence of CO₂ rise stress, calculated by the ratio of the two slopes of regression of Fv/Fm versus pH and versus temperature, multiplied by the mean actual acidification of -0.0853 pH unit. Due to reversed trends ("Monday morning effect"), only data without 32-34°C and pH 7.8 were used at 50 µE.m⁻².s⁻¹, and without 34°C and pH 7.8 at 160 µE.m⁻².s⁻¹. Although confidence intervals are very great for all data, temperature equivalence increases significantly with the logarithm of light: $Teq=0.0889 \log \text{light}+0.112$, $r^2=0.973$, $p=0.014$. / Équivalence en température du stress causé par l'actuelle augmentation du CO₂. Pour chaque niveau de lumière, l'équivalence en température du stress causé par l'actuelle augmentation du CO₂ est calculée en divisant la pente de régression de Fv/Fm versus pH par celle de la température, et multiplié par l'actuelle acidification moyenne de -0,0853 pH. Afin de ne pas inclure les tendances inverses ("Monday morning effect"), les données sans 32-34°C et pH 7,8 ont été utilisées à 50 µE.m⁻².s⁻¹, et sans 34°C et pH 7,8 à 160 µE.m⁻².s⁻¹. Bien que la précision de chacune des données soit faible, l'équivalence de température s'accroît significativement avec le logarithme de la lumière : $Teq=0,0889 \log \text{light}+0,112$, $r^2=0,973$, $p=0,014$.

Light (µE.m ⁻² .s ⁻¹)	n	Slope pH	Slope T	Teq (°C)
50	32	-0.02667	0.00893	0.255
160	48	-0.06542	0.01771	0.315
500	80	-0.05467	0.01291	0.361
1,600	64	-0.00583	0.00128	0.388

equations). This acidification corresponds in this case to an equivalent warming of $Teq=0.315^\circ\text{C}$. Moreover, this equivalence increases with light level (table I). As mass bleaching occurs when the sky is clear, the value for full sun is taken as the reference value ($Teq\approx 0.4^\circ\text{C}$). A similar calculation leads to the equivalence of the CO₂ increase with a 4.9% light change. This Teq value is probably underestimated. As can be clearly seen at 500 µE.m⁻².s⁻¹, the CO₂ level has an effect essentially within the natural range of pH 8.1 and 8.4 (560 and 230 ppm CO₂). Using only values at 8.1-8.4 pH yields $Teq\approx 1.2^\circ\text{C}$.

DISCUSSION

The above data establish that, first, in a light-adapted state, PS II efficiency is enhanced by temperature and CO₂ over a range relevant for mass bleaching. It suggests that bleaching originates in greater photochemistry *sensu lato* instead of photoinhibition. But this is a short term effect: reef symbiotic systems kept at high temperature are overwhelmed within a few hours or days and Fv/Fm begins to decrease instead. Relaxation in darkness at 25°C for 30 minutes after incubation showed a decreasing trend with temperature, as in corals (Fitt, Warner, 1995; Warner *et al.*, 1996; Jones *et al.*, 1998), and, with longer delay (about a day), also with pH. This "boom then bust" effect can arise with secondary photoinhibition, following from an imbalance between photochemistry and dark reactions (Jones *et al.*, 1998). Alternatively, the Fv/Fm increase with temperature and CO₂ might be due to a reduction of the protective non-photochemical quenching, already invoked in bleaching (Warner *et al.*, 1996).

Secondly, and despite much research on the effect of CO₂ on marine ecosystems (Bazzaz 1990;

Raven, Johnston, 1994; Kleypas *et al.*, 1999; Riebesell *et al.*, 2000), it was unexpected that CO₂ would have so strong an effect, and moreover that it was so similar to that of temperature. In fact, this points to some identical mechanism of action. I speculate that the temperature effect is mediated by internal CO₂, perhaps at the QA-QB PS II site. Whatever the precise mechanisms of coral reef host/symbiont rupture, the line of argument that CO₂ is a bleaching factor is based on the following:

- slight temperature increase induces bleaching, as is well known both in the laboratory and in the field;
- as summarised above, it originates in photo-synthetic mechanisms, the best indicator of which is Fv/Fm;
- as shown in this paper, CO₂ has the same effect on Fv/Fm as does temperature.

In long term bleaching experiments with corals and large foraminifers, slight increases of CO₂, as do most environmental changes, favour bleaching, although in a complex way. Similar values of Teq (0.6 to 1.2°C) were found, often with greater sensitivity between 8.1 and 8.4 pH, when Fv/Fm is around the triggering level for bleaching (0.275±0.050) (in preparation).

The CO₂ level in the future decades, 500 to 700 ppm, will induce a seawater acidification of -0.20 to -0.32 pH unit, equivalent, according to these data, to a stress of 2.8°C to 4.5°C, in addition to Global Warming. This is a tremendous change. Given observed damage to reefs (Wilkinson, 1998), 90% to 99% of photosynthetic symbiotic organisms may die, and reefs as they are known today will disappear, if my interpretation is correct. Thus, strong mitigation of anthropogenic CO₂ increase is urgent.

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