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Aspects of carbon monoxide production and oxidation by marine macroalgae

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ABSTRACT: Rates of macroalgal carbon monoxide (CO) production were compared among 5 taxa representing 3 major phylogenetic groups (Phaeophyta, Chlorophyta, Rhodophyta). CO production varied substantially from a minimum of about 20 ng CO gdw^{-1} h^{-1} for *Fucus vesiculosus* to >4000 ng CO gdw^{-1} h^{-1} for *Laminaria saccharina*. None of the macroalgae examined contained significantly elevated CO concentrations within their pneumatocysts (float bladders), so the variability among taxa reflects other intrinsic properties. An *in vitro* evaluation of *Ascophyllum nodosum* indicated that CO production varied as a function of temperature, desiccation and illumination. CO production increased strongly for live fronds over an ecologically relevant range (5 to 23°C), but decreased at 45°C. For non-living desiccated wrack, CO production increased consistently from 5 to 47°C. Short-term desiccation of living algae decreased CO production substantially, but long-term changes in water content appeared not to markedly alter CO production relative to fresh material. Illumination strongly increased CO production relative to dark incubations, with similar responses for living and non-living material. CO oxidation (presumably bacterial) was observed for most living algae during incubations with exogenous CO at concentrations of 100 ppm, suggesting that a microbe-alga association might limit in part CO fluxes. Extrapolation of CO production rates indicates that macroalgae likely contribute only a minor fraction (<1%) of global marine CO emissions to the atmosphere (about 10 Tg yr^{-1}).

KEY WORDS: Carbon monoxide · Biogeochemistry · Trace gas

INTRODUCTION

Though present at only 60 to 300 parts per billion (ppb), carbon monoxide (CO) plays a major role in atmospheric chemistry (Logan et al. 1981, Crutzen & Gidel 1983). Specifically, CO regulates hydroxyl radical (OH) concentrations, which in turn affect greenhouse gases such as methane and ozone (Guthrie 1989). Fugelstvedt et al. (1996) and Daniel & Solomon (1998) have suggested that the combined direct and indirect effects of CO on atmospheric chemistry result in short-term cumulative radiative forcing that may be equal to or greater than the forcing due to nitrous oxide.

Anthropogenic sources (including fossil fuel combustion and biomass burning) dominate the contemporary global CO budget, accounting for about 60% of total emissions (about 2600 Tg yr^{-1}; Khalil 1999). Marine contributions to the CO budget (about 10 Tg yr^{-1}) have not been assessed in detail and remain somewhat uncertain (Khalil 1999). Published estimates have been derived from pelagic CO fluxes based in part on CO concentrations in the water column and models of gas exchange (e.g., Conrad 1988). The role of coastal systems has largely been ignored.

Although coastal marine ecosystems account for only a small fraction of oceanic surface area, they contribute disproportionately to the budgets of several major trace gases. Capone (1991) estimated that near-shore systems (estuaries, salt marshes) produce about 10% of

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the total marine nitrous oxide. Likewise, salt marshes, estuaries and other near-shore environments emit a large fraction of the sulfur gases (dimethyl sulfide, carbonyl sulfide, carbon disulfide) produced in marine systems (Kelly & Smith 1990). In addition, inter- and sub-tidal macroalgae form substantial amounts of halomethanes, especially methyl iodide, which contribute to atmospheric halogen budgets (Wever 1991).

Macroalgal CO production is also potentially important. For instance, the brown macroalga *Nereocystis luetkeana* has long been known to contain elevated (>1 to 10%) CO concentrations in its pneumatocysts (float bladders), and results from a limited survey of macerated algal tissues indicate that CO production for some species may be significant (Loewus & Delwiche 1963, Chapman & Tocher 1966). Although controls of macroalgal CO production have not been addressed in any detail, photochemical oxidation of emergent and submerged tissues and thermal decomposition of emergent tissues exposed to elevated temperatures likely affect production as is the case for terrestrial plants (Fischer & Lüttge 1978, Seiler et al. 1978, Conrad 1988, Tarr et al. 1995, Schade & Crutzen 1999).

For terrestrial plants, CO production on a dry weight and leaf-surface-area basis is high, resulting in perhaps 100 Tg CO yr^{-1} globally. Relatively high CO production rates have also been reported for a freshwater chlorophyte, *Chlorella fusca*, with key controls including temperature, illumination and chlorophyll content (Bauer et al. 1980).

The study reported here documents for the first time CO production rates for freshly collected brown (Phaeophyta), green (Chlorophyta) and red (Rhodophyta) macroalgae occurring inter- and sub-tidally on the Maine coast. Rates varied substantially among taxa and responded to a number of parameters including illumination, desiccation, and temperature. Rates for some taxa, e.g., *Ascophyllum nodosum*, were sufficiently high to suggest that dense stands of macroalgae might represent locally significant CO sources. However, extrapolation of even the highest observed rates suggests that macroalgae contribute only a small fraction of the estimated global marine CO budget (=1%). Nonetheless, all of the macroalgae examined in this study supported a CO-oxidizing microbiota that may use alga-derived CO as a source of substrate for maintenance or growth.

MATERIALS AND METHODS

Macroalgal sources and collection. Five taxa were collected during fall from the inter- and sub-tidal region adjacent to the Darling Marine Center, Walpole, Maine, USA. These included *Ascophyllum nodosum* and *Fucus vesiculosus* (intertidal, Phaeophyta), *Laminaria saccharina* (subtidal, Phaeophyta), *Ulva lactuca* (sub-tidal, Chlorophyta), and *Chondrus crispus* (sub-tidal, Rhodophyta). *A. nodosum* and *F. vesiculosus* were collected intact from patches adhering to a rock substrate; *L. saccharina* samples were obtained from a colony consisting of blades 10 to 20 cm in length adhering to a dock; *U. lactuca* grew adjacent to the *L. saccharina* samples and was harvested as intact 'sheets'; intact *C. crispus* was obtained from small patches on rock surfaces and included both normally pigmented and a bleached, white form. All samples appeared healthy and non-senescent, with the exception of *A. nodosum* samples obtained from partially desiccated wrack or debris at or above the mean high-tide level. Algal samples were transported moist to the laboratory and used within about 18 h of collection. During any lag before initiating CO flux assays, samples were stored in sealed containers at 4°C.

CO production assays. Rates of CO production or oxidation were determined using 3 to 5 g (fresh weight, gfw) samples that were transferred to 120 cm^3 glass jars subsequently sealed with neoprene stoppers. The algal samples were blotted to remove excess water, but were otherwise visibly moist. After sealing the incubation jars, 1 cm^3 headspace sub-samples were removed at 2 to 3 min intervals by needle and syringe for assay of CO content using a Trace Analytical RGA-3 equipped with a mercury vapor detector (for additional details, see King 1999, 2000). Unless otherwise noted, all incubations were conducted in darkness at ambient laboratory temperatures (about 20 to 23°C). Additional CO production assays were conducted by incubating jars and algae at 5, 23 and 45°C. Both fresh and naturally desiccated *Ascophyllum nodosum* were used for these assays.

The response of CO production to desiccation was determined using freshly collected non-senescent *Ascophyllum nodosum*. Fronds collected shortly after exposure on a falling tide were separated into 2 treatments. For one treatment, *A. nodosum* was maintained in darkness in a sealed plastic container at ambient laboratory temperature. The second treatment consisted of algal fronds maintained similarly but left exposed to the atmosphere and subject to air-drying. Rates of CO production were measured for 3 to 5 gfw sub-samples obtained from each treatment at the beginning of the incubation and at intervals of 6 and 24 h thereafter.

In addition, the impact of natural air-drying and aging was estimated by measuring CO production rates as described above for samples of *Ascophyllum nodosum* obtained from 'wrack' that had accumulated in rock crevices near the mean high water level. This

material was black in color, stiff in texture and of uncertain age. For comparison, CO production was assayed using partially dried material of a known age obtained by incubating approximately 1 kg of freshly collected non-senescent *A. nodosum* on a rock surface for 6 wk at a position above the mean high water level. This material was exposed to natural regimes of light, temperature and precipitation. Sub-samples (about 20 gfw) were obtained at intervals for CO production assays as described above.

Responses to light regimes of CO production by fresh non-senescent and naturally dried *Ascophyllum nodosum* were determined by incubating 10 to 20 gfw algal samples in a chamber consisting of a 1 l quartz beaker modified with ports for obtaining headspace samples by needle and syringe. The beaker containing algae was inverted and sealed into an aluminum-foil-lined plastic tray using modeling clay and a layer of organic-free sand. Assays without algae indicated that the clay-sand seal was effective and that blank CO production rates were negligible during assays >60 min. The chambers were incubated with the following conditions: (1) foil-covered for darkness; (2) uncovered and exposed to a vertical light source consisting of a 1000 W sodium vapor lamp; and (3) uncovered and exposed to natural sunlight. Ultraviolet radiation (280 to 320 nm) and photosynthetically active radiation (PAR) inside the chamber were measured using an Eppley radiometer and LiCor (Lincoln, NE) sensor interfaced with a Licor model 1000 datalogger. Intensities of UV and PAR were varied by adjusting the height of the chamber relative to the lamp source.

All of the above assays were conducted in triplicate unless otherwise indicated. All CO production rates were normalized and expressed on a gram dry weight (gdw) basis by drying samples at 105°C for 24 h. Where appropriate, differences among samples or treatments were analyzed using analysis of variance and Systat or Statview software for Macintosh.

CO oxidation assays. Fresh non-senescent macroalgal samples were incubated in 120 cm^3 sealed jars as described above. CO was added at a final concentration of 100 ppm to the headspace of each sample. Headspace sub-samples were removed at intervals by needle and syringe for assay of CO content using a Varian 3400 (Varian Instruments, Inc.; Walnut Grove, CA) gas chromatograph equipped with a flame ionization detector and a methanizer to convert CO to methane. A molecular sieve 5A column (1 m × 0.3 cm OD) was operated at 80°C with a carrier gas of nitrogen flowing at 20 ml min^{-1}. Assays were conducted in triplicate for each algal species with incubations at ambient laboratory temperature in the dark. Surface sterilized controls were used to assess the contribution of microbial epiphytes to the observed CO uptake rates. Fresh *Ascophyllum nodosum* was immersed in 10 mM mercuric chloride for 5 min, after which the tissue was rinsed twice for 5 min each with sterile seawater.

RESULTS

Macroalgal CO production

CO accumulated rapidly in all assays (Fig. 1), but production rates varied substantially among taxa (Table 1), with a range of values approximately 24-fold among the 3 Phaeophyta (20 ± 3 to 4820 ± 2160 ng CO gdw^{-1} h^{-1}). Rates for the chlorophyte (150 ± 40 ng CO gdw^{-1} h^{-1}) *Ulva lactuca* were intermediate among those of the phaeophytes. CO production by pigmented *Chondrus crispus*, a rhodophyte, was low (30 ± 3 ng CO gdw^{-1} h^{-1}) and comparable to values for *Fucus vesiculosus*, while values for non-pigmented *C. crispus* were approximately 6-fold higher (190 ± 50 ng CO gdw^{-1} h^{-1}).

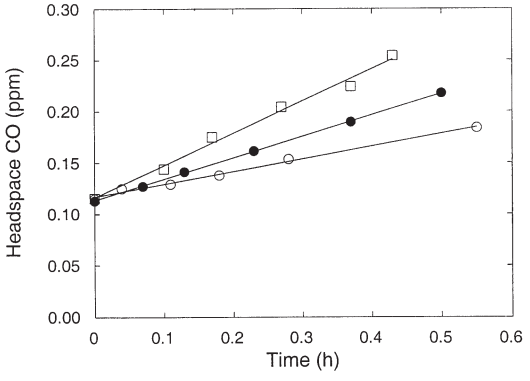

Fig. 1. Time course of CO production by *Ulva lactuca* incubated at room temperature in darkness. Different symbols represent individual samples

Table 1. CO production rates for various macroalgal species incubated in darkness at ambient laboratory temperature. All values are means of triplicate determinations (±1 SE)

Species	Rate (ng gdw^{-1} h^{-1})
Laminaria saccharina	480 ± 220
Ascophyllum nodosum	250 ± 75
Fucus vesiculosus	20 ± 3
Ulva lactuca	150 ± 40
Chondrus crispus	30 ± 3
C. crispus (bleached)	190 ± 50

Responses to temperature, desiccation and illumination

CO production rates for fresh *Ascophyllum nodosum* increased 6.5-fold from 5 to 23°C, but then decreased (36.5%) at 45°C (Fig. 2). In contrast, for dry *A. nodosum* CO production increased continuously from 5 to 47°C (Fig. 2). In the latter case, rates varied consistent with the Arrhenius relationship (rate = $Aexp^{-\Delta H/RT} + c$, where A and c are fitting constants, R is the universal gas law constant, T is the absolute temperature, and ΔH is the activation enthalpy), and an activation enthalpy of about –40 kJ mol^{-1}.

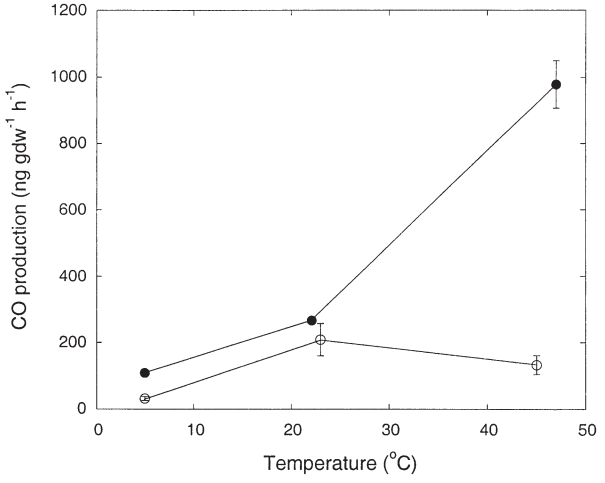

Fig. 2. Response of CO production by *Ascophyllum nodosum* incubated in darkness to various incubation temperatures. Open symbols represent fresh, living samples; closed symbols represent desiccated, non-living samples. All data are means of triplicate assays ± 1 SE

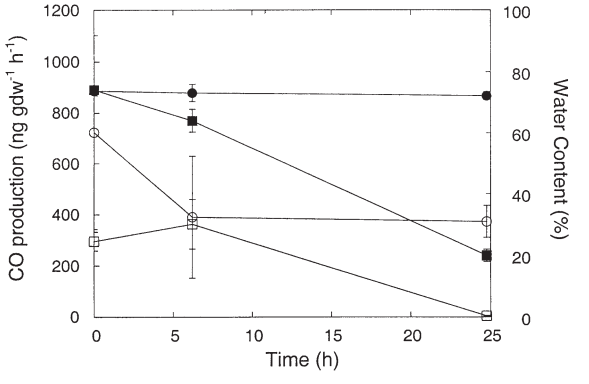

Fig. 3. Response of CO production by *Ascophyllum nodosum* incubated in darkness to short-term air-drying. Open and closed circles represent CO production rates for control and air-dried algal samples, respectively; open and closed squares represent water contents for control and air-dried samples, respectively. All data are means of triplicate assays ± 1 SE

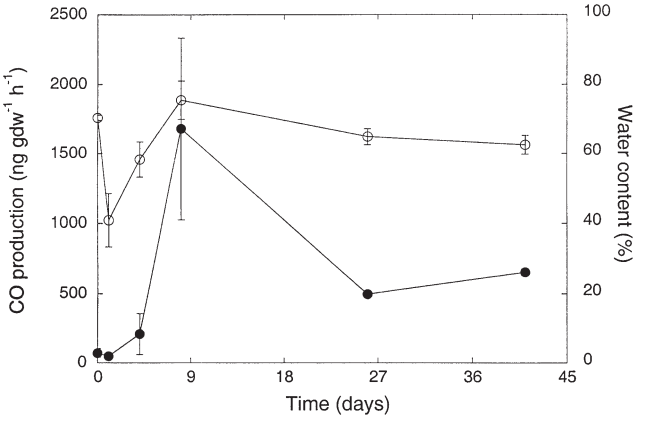

Fig. 4. Time course for CO production (open symbols) and water contents (closed symbols) of freshly harvested *Ascophyllum nodosum* incubated for 6 wk in the supra-tidal zone. Production assays were conducted in darkness. All data are means of triplicate assays ± 1 SE

CO production rates for fresh *Ascophyllum nodosum* maintained in a sealed container to prevent desiccation did not vary significantly during a 24 h interval through which water contents were essentially constant (Fig. 3). Although initial CO production values for this treatment were high and quite variable, rates at 6 h and 24 h were comparable to rates obtained during an initial multi-species comparison (Table 1). CO production rates after 6 h of air-drying were comparable to initial values and values for the sealed treatment (Fig. 3). However, after 24 h of air-drying, water contents dropped substantially (from 74.3 to 20.1%) as did CO production rates (from 300 ± 40 to 4 ± 1 ng CO gdw^{-1} h^{-1}). In contrast, naturally air-dried *A. nodosum* wrack (water content 23.5%) of an unknown age collected from the supratidal zone produced CO at rates of 110 ± 30 ng CO gdw^{-1} h^{-1}.

During an incubation of fresh *Ascophyllum nodosum* in the supratidal zone for 6 wk, CO production rates were low initially, though within the range of values measured at other times for *A. nodosum*. Production increased to a peak value of 1680 ± 650 ng CO gdw^{-1} h^{-1} at 8 d (Fig. 4). Rates decreased subsequently by 60 to 70%. During the 6 wk incubation, water content dropped from an initial value of 70.3% to a minimum of 40.9% (Day 1) and then rose to values between 58 and 76%. Increases in water content reflected an extended period of frequent precipitation.

Fresh and desiccated *Ascophyllum nodosum* responded similarly to a shift from darkness to low light levels from a 1000 W sodium vapor lamp (290 µE PAR, 3.2 W m^{-2} UV), with CO production rates increasing 3.7-fold and 3.4-fold, respectively (Fig. 5). Shifts from darkness to ambient sunlight (approximately 1200 to 1400 µE PAR, 18 to 20 W m^{-2} UV) also enhanced CO

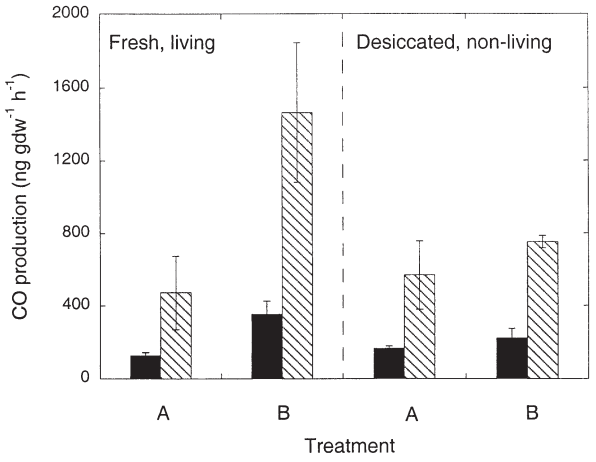

Fig. 5. Rates of CO production by *Ascophyllum nodosum* incubated sequentially in darkness and light. Treatment A represents a shift from dark to illumination by a 1000 W sodium vapor lamp (PAR = 290 µE); Treatment B represents a shift from dark to illumination by ambient sunlight (PAR is about 1200 µE). All data are means of triplicate assays ± 1 SE

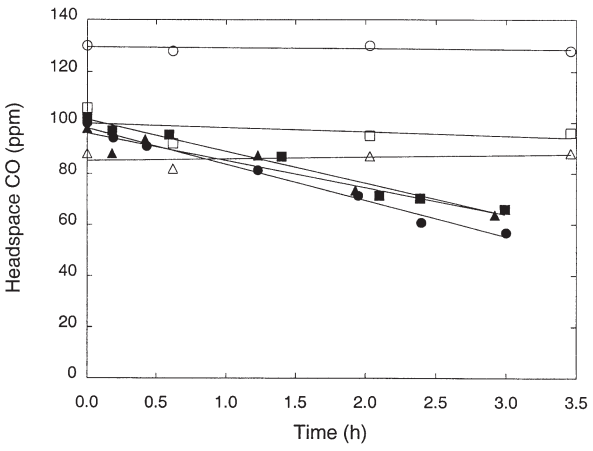

Fig. 6. Time course of CO added at final concentrations of approximately 100 ppm to the headspace of jars containing *Ascophyllum nodosum* (closed symbols) and mercuric chloride surface-sterilized *A. nodosum* (open symbols) incubated in darkness at room temperature. Different symbols represent individual samples

production, with increases of 4.1-fold and 3.4-fold for fresh and desiccated algal samples, respectively. Dark CO production rates for the 2 sets of incubations (dark to low light and dark to ambient sunlight) differed somewhat, especially for fresh *A. nodosum*; however, the observed differences were within ranges observed for a variety of other incubations and reflected inherent variability among samples.

CO oxidation

CO added to final concentrations of about 100 ppm was consumed readily (Fig. 6) and by all taxa. Uptake was typically linear for decreases of 20 to 50%, thus facilitating estimates of maximum uptake velocities. With 1 exception, CO oxidation rates (Table 2) were comparable to or greater than CO production rates. Values tended to be higher for the phaeophytes, but due to substantial variability among replicates, trends among taxa were not discernible. However, a distinctly notable difference was apparent for samples of unpigmented and pigmented *Chondrus crispus*, since the former did not consume CO at all, while the latter did. CO uptake was completely inhibited by surface sterilization of *A. nodosum* with a 10 mM mercuric chloride treatment (Fig. 6).

Table 2. CO oxidation rates for various macroalgal species at an initial CO concentration of 100 ppm. All values are means of triplicate determinations (±1 SE)

Species	Rate (ng gdw^{-1} h^{-1})
Fucus vesiculosus	2680 ± 380
Laminaria saccharina	1110 ± 1110
Ascophyllum nodosum	70 ± 85
Ulva lactuca	660 ± 660
Chondrus crispus	240 ± 120

DISCUSSION

Each of the macroalgal species examined in this study produces CO, although rates vary substantially among taxa (Table 1). Reasons for the variability are unclear, but appear unrelated to phylogenetic status, habitat or morphology. Further, none of the phaeophytes investigated accumulates CO within its pneumatocysts, so elevated CO production (as in *Laminaria saccharina*) cannot be attributed to the presence of an usually high source. Similar rates and variability among taxa have been reported in more limited surveys by Loewus & Delwiche (1963), although these authors used macerated tissues that had been stored frozen (–10°C) prior to use.

The potential global impact of macroalgal CO production clearly depends on the magnitude of CO production per unit mass (integrated over time and *in situ*) and on total biomass. Global macroalgal biomass has been estimated to be approximately 10^{13} gdw (Wever 1991). Using an average dark CO production rate determined at 23°C for the various macroalgae included in this study, and applying a multiplier of 5 (an overestimate to maximize production; see above) to

account for differences in light-dark responses, yields a value of about 0.4 µg CO gdw^{-1} d^{-1} for a regime of 12 h light d^{-1}. Though strictly an approximation, this rate suggests that the potential global macroalgal CO source is about 0.04 Tg CO yr^{-1}, assuming that all of the CO produced is emitted to the atmosphere. In order to contribute significantly (=10%) to the estimated 10 Tg CO yr^{-1} flux from the oceans to the atmosphere, average macroalgal CO production gdw^{-1} would have to be some 25-fold greater than values reported here or elsewhere.

Although at best minor on a global scale, macroalgal CO production might contribute significantly to CO dynamics at local to regional scales. This could occur as a result of direct CO production as described here, or through production of dissolved organic matter that undergoes subsequent photochemical degradation (Najjar et al. 1995). However, since most of the research on marine CO dynamics has emphasized pelagic rather than coastal systems, additional effort is needed to assess the scales at which macroalgal processes may be important.

A substantial increase in average macroalgal CO production beyond the rates reported seems unlikely. Results from this study indicate that CO production responds to several major parameters, including temperature, desiccation and illumination. Although changes in these parameters can enhance CO production, *in situ* temperatures for most macroalgal populations are less than 23°C, suggesting that the average rate calculated here would be an upper limit. In addition, results from incubating *Ascophyllum nodosum* at 45°C indicate that CO production may decrease for temperatures >25 to 30°C (Fig. 2). Elevated temperatures increase CO production from senescent, dry *A. nodosum*, but the amount of biomass represented by such material is relatively small, as is the period during which elevated temperatures might occur.

The temperature response of senescent, dry *Ascophyllum nodosum* is consistent with that of terrestrial plants (e.g., Schade & Crutzen 1999) and soil organic matter (Conrad & Seiler 1982, 1985a,b), although activation energies for CO production from soil organic matter (70 to 100 kJ mol^{-1}) are higher than those observed here. This suggests that macroalgal organics are less susceptible to thermally driven CO production than bulk soil organics. In contrast, the response of fresh *A. nodosum* differs from that of soils in that it appears to be similar to biologically or enzymatically determined reactions. While an enzymatic process may account for CO production in live macroalgae, an alternative explanation may be that increases in temperature beyond 20 to 25°C decrease the chemical reactivity of CO precursors (e.g., polyphenolics) that are not so affected in senescent material.

Desiccation also appears to decrease CO production by live *Ascophyllum nodosum* (Fig. 4), at least during short-term intervals. Although this differs from patterns for terrestrial plants (Tarr et al. 1995), controls of the response may be similar to those for the response to elevated temperature. However, since CO production for senescent desiccated material collected *in situ* is comparable to that for live material, desiccation does not appear to result in long-term losses of activity, and likely does not have any substantial effect on the magnitude of CO emission to the atmosphere. Further, desiccation of intertidal forms that occurs upon exposure to the atmosphere during low tides would reduce, not increase, the global source estimate calculated above.

Responses of both live and non-living *Ascophyllum nodosum* (Fig. 5) to illumination agree with reports for *Chlorella fusca* and various terrestrial plants, in that light stimulates CO production (e.g., Fischer & Lüttge 1978, Bauer et al. 1980, Tarr et al. 1995, Schade & Crutzen 1999). There is little doubt that photochemical reactions play a major role in determining rates of macroalgal CO production, although some activity occurs in darkness. For some taxa (especially intertidal forms) at some times (e.g., low tide) photochemical reactions may result in relatively high CO production rates. However, the responses reported here likely overestimate the effect of illumination *in situ*, since partial shading for many species and strong absorption of UV (the most potent wavelengths for CO photoproduction) in the water column would limit interception of light relative to that possible in the *in vitro* assays described here. Accordingly, the preceding estimate of the global macroalgal CO source, which incorporates a light-dark CO production ratio of 5, likely represents an upper limit for the effect of light-mediated activity.

Net macroalgal CO production may also be constrained *in situ* by CO-oxidizing epimicrobiota. Significant rates of dark CO uptake have been observed for all but an unpigmented form of *Chondrus crispus* (Table 2), suggesting that CO oxidizers may be a common component of macroalgal epiphytic microbiota. Although results of this study do not demonstrate conclusively that CO oxidation was microbial, net CO oxidation by plants has been previously reported only at elevated CO levels (>100 ppm) during illumination. Further, surface sterilization completely inhibited CO uptake (Fig. 6), most likely by reducing the activity of bacterial epiphytes. In addition, CO-oxidizing bacteria have been readily enriched from the macroalgae used in this study.

One isolate appears closely related to the genus *Stappia* (G.M.K. unpubl.), which has a cosmopolitan distribution, but which has not been reported to oxidize CO (Rüger & Höfle 1992, Uchino et al. 1998). Previously, marine CO oxidation has been attributed to an

indirect or cometabolic activity of ammonia-oxidizing bacteria (e.g., Jones 1991). Macroalgal CO production may thus affect the diversity of marine CO oxidizers and play a role in various algal-microbe interactions, perhaps introducing some specificity for microbial epiphyte colonization by increasing the competitiveness of carboxydotrophic bacteria.

In conclusion, CO production by macroalgae appears to be a common phenomenon, and not one simply related to the presence of CO in pneumatocysts. CO production rates vary as a function of temperature, desiccation and illumination following patterns similar to terrestrial plants. In addition, macroalgal CO production may support an epimicrobiota that appears capable of oxidizing CO at significant rates and perhaps attenuating CO fluxes. However, net macroalgal CO production likely accounts for only a small fraction of the annual global emission of CO to the atmosphere.

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