ARAGONITIC ALGAE IN CALCITE SEAS: EFFECT OF SEAWATER Mg/Ca RATIO ON ALGAL SEDIMENT PRODUCTION

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ABSTRACT: Secular variation in seawater Mg/Ca would have subjected the aragonite-producing codiacean algae to two intervals of low-Mg calcite seas (mMg/Ca < 2) and two intervals of aragonite + high-Mg calcite seas (mMg/Ca > 2) seas since their origin in the Ordovician. It is asserted that the aragonite + high-Mg calcite affinity of modern and Recent tropical seas (mMg/Ca > 2) has enabled the aragonitic Codiciaceae to act as major carbonate sediment producers in these seas. To test this assertion, specimens of the sediment-producing codiacean alga Udotea flabellum were grown in artificial seawaters formulated at mMg/Ca ratios (1.0, 2.5, 5.2) that have occurred in the oceans throughout the geologic history of the Codiciaceae.

While the U. flabellum algae produced exclusively aragonite in both the artificial boundary seawater (mMg/Ca = 2.5) and the artificial aragonite + high-Mg calcite seawater (modern seawater; mMg/Ca = 5.2), the algae produced a portion (25 ± 3%) of their CaCO3 as low-Mg calcite (< 4 mol% MgCO3) in the artificial calcite seawater (mMg/Ca = 1.0), suggesting that their CaCO3 polymorph control can be partially overridden by ambient seawater chemistry.

Primary productivity, calcification, and linear growth of the algae decreased with reductions in ambient Mg/Ca, despite increases in absolute Ca concentration of the seawater. Reduced calcification in the lower Mg/Ca seawaters is probably due to kinetic difficulties of producing aragonite from seawater that favors the nucleation of calcite. The decreased linear growth and primary production are likely associated with reductions in the ambient CO2 available for photosynthesis, resulting from the reduced calcification.

These findings support the assertion that the dominant ecological and sedimentological roles of codiacean algae in Recent tropical seas is facilitated by a seawater Mg/Ca ratio that favors the nucleation of aragonite over calcite. Furthermore, producing aragonite in seawater that favors the nucleation of low-Mg calcite (mMg/Ca < 2) may have reduced the rates of growth and calcification of codiacean algae, making them less competitive for space on the shallow tropical seafloor and more susceptible to predatory grazing, thereby reducing their contribution to carbonate sedimentation.

INTRODUCTION

The polymorph mineralogies of the major reef-building and sediment-producing calcareous marine organisms have tracked transitions in the polymorph mineralogies of ooids and marine cements, the so-called calcite and aragonite seas (Sandberg 1983), throughout the Phanerozoic (Stanley and Hardie 1998, 1999) (Fig. 1). Secular variation in the Mg/Ca ratio of seawater, driven mainly by fluctuations in the rate of ocean crust production and believed to be responsible for the observed calcite–aragonite sea pattern throughout the Phanerozoic (Hardie 1996), would have subjected the codiacean alga to three transitions between high-Mg calcite + aragonite (mMg/Ca > 2) and low-Mg calcite (mMg/Ca < 2) nucleation fields in the oceans since their origin in the Ordovician (Roux 1991a; Stanley and Hardie 1998, 1999) (Fig. 1). It has been proposed that the role of the codiacean alga as major producers of carbonate sediment in Recent tropical seas has been permitted by the molar Mg/Ca of Recent seawater (~ 5.2) remaining within the nucleation field of the aragonite polymorph, thereby supporting the inherent aragonitic mineralogy of these algae (Stanley and Hardie 1998, 1999). This assertion is particularly intriguing in that it connects plate tectonics to carbonate sedimentology, via marine geochemistry and paleobiology (Montañez 2002).

Here I evaluate the relationship between seawater Mg/Ca and algal biomineralization experimentally by growing a modern aragonite-producing codiacean alga, Udotea flabellum, in artificial seawaters formulated at Mg/Ca ratios believed to have existed (Hardie 1996) since the apparent origination of the Codiciaceae in the Ordovician.

This study complements previous work (Ries 2005) showing that the growth and calcification of the codiacean alga Penicillus capitatus, another major sediment producer in Recent tropical seas, was significantly reduced when grown in artificial calcite seawater. Other related work on the subject has revealed that coralline algae (Stanley et al. 2002; Ries in press), echinoids, serpulid worms, crabs, shrimp (Ries 2004), and some species of coccolithophores (Stanley et al. 2005), which naturally secrete high-Mg calcite in modern aragonite seas, actually change their mineralogy to low-Mg calcite when grown in artificial seawaters formulated at Mg/Ca ratios that characterize calcite seas (mMg/Ca < 2).

BACKGROUND

Anatomy

Udotea is an upright-standing, fan-shaped alga whose anatomy can be divided into three basic components: fan; thallus; and holdfast (Fig. 2A).
The thallus (stalk) comprises medullar filaments, which run parallel to the thallial axis, and cortical filaments, which branch laterally from the medullar filaments (Fritsch 1948; Colombo 1978). The cortical filaments are terminated by small swellings, called utricles, which form the external surface of the thallus. The medullar filaments in the fan (Fig. 2A) are heavily branched and lobed (Fig. 2C). These lobate filaments interweave and coalesce to form the apparently continuous surface (cortex) of the mature fan (Fig. 2E) (Fritsch 1948). Both the cortical and medullar filaments have an inner (Fig. 2D, iw) and outer filament wall (ow), which are divided by an organic layer (ol). The two filament walls and the space between them are collectively referred to as the filament sheath (f).

Unlike *Halimeda* and *Penicillus*, the filament sheaths within *Udotea flabellum* lack pores (Bohm et al. 1978). The holdfast (Fig. 2A), consisting of a network of uncalcified filaments that adhere to sand particles, is located at the base of the alga and serves to anchor it in the sediment (Hillis 1991). Offspring algae (Fig. 2B) grow from rhizoids sent out from the holdfast within the sediment.

Photosynthesis occurs within chloroplasts contained in the cytoplasm within the medullar and cortical filaments. *Udotea* is considered the most primitive plant with a C4-like method of photosynthesis, and has called

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**Fig. 2.**—Anatomical detail of the alga *Udotea flabellum*. A) Full-grown plant revealing uncalcified holdfast, calcified thallus, and calcified fan. B) Young alga. C) Vertical section of surface of fan showing cortex and individual utricles. D) Vertical section through cortical layer; u = utricle, p = utricle protrusions, f = filament, ow = outer filament wall, iw = inner filament wall, ol = organic layer within filament wall, CH = chimney system, PD = primary deposit, SD = secondary deposit, ICD = intercellular deposit (after Böhm et al. 1978; Fritsch 1948). E) Cortication of surface of thallus.
into question the terrestrial origin of this CO$_2$-efficient process (Reiskind et al. 1988, 1989; Reiskind and Bowes 1991)

**Calcification**

Calcification in *U. flabellum* occurs as aragonitic needles (< 15 μm long), prisms (0.5 μm long), and serrated crystals (1.0 μm long) precipitated intracellularly within the filament sheath (between the inner and outer filament walls) and intercellularly in the space between the filaments themselves (Fig. 2D). The filament sheath contains an organic layer (ol) that divides the space (Fig. 2D). Aragonite deposited between the outer filament wall (ow) and the organic layer (ol) has been termed primary deposit (PD), while aragonite deposited between the inner filament wall (iw) and the organic layer (ol) has been termed secondary deposit (SD) (Fig. 2D) (Friedman et al. 1972; Borowitza et al. 1974; Borowitza and Larkum 1977; Flajs 1977; Böhm et al. 1978; Borowitza 1984; Kooistra 2002). Mature thalli can contain between 25 and 59 wt % aragonite. While the purpose of algal calcification has been debated, its most common explanation is for rigidity in turbulent hydraulic environments and for protection from grazing predation, especially when combined with acidic, toxic secondary compounds and nocturnal growth (Wray 1977; Paul and Van Alstyne 1988; Hay et al. 1994; Schupp and Paul 1994; Hay 1997; Kooistra 2002).

**Geologic History of Udotea**

The codiacean algae have existed since at least the Ordovician, inasmuch as the Ordovician alga *Dimorphosiphon* demonstrates a level of organization very similar to that of the modern *Halimeda* (Mu 1991). Subsequent to their origin in the Early Ordovician, the Codiaeaceae have exhibited high levels of diversity and abundance in the Silurian–Devonian, the Permian, and the Cenozoic (Chuvashov and Riding 1984; Barattolo 1991; Flügel 1991; Mamet 1991; Mu 1991; Riding and Guo 1991; Roux 1991a, 1991b; Kooistra 2002). However, the acme of diversity and abundance of known aragonitic Codiaeaceae began in the early–middle Cenozoic and has continued until the present (Elliot 1984; Flügel 1988, 1991; Hills 1991), an interval over which the Mg/Ca ratio of seawater has favored the precipitation of aragonite over calcite.

While it is evident that some Codiaeaceae have flourished in purported calcite-sea intervals, our poor understanding of the original polymorph mineralogy and phylogenetic relationships of these ancient groups precludes our meaningful interpretation of them in the context of long-term secular variation in seawater chemistry. This study is concerned with determining the rate of ocean crust production since at least Ordovician time (Mu 1991; Roux 1991a). Modern codiacean algae of the genera *Halimeda, Penicillus,* and *Udotea* are among the most important carbonate sediment producers and bioherm builders in Recent and modern tropical marine environments (Lowenstam 1955; Milliman 1977; Hills-Colinvaux 1980; Weter 1980; Drew 1983; Hudson 1985; Hine et al. 1988; Marshall and Davies 1988; Muller 1988; Orme and Salama 1988; Payri 1988; Phipps and Roberts 1988; Roberts et al. 1988; Hills 1991; Mu 1991).

Rates of carbonate sediment production in Recent codiacean alga-dominated marine environments are estimated to range from 0.18 to 5.9 m $1000$ y$^{-1}$ (Hills 1991). Such rapid rates of carbonate accretion by these algae, attributable to their relatively large size (up to 20 cm in height), short lifespans (1–3 months; i.e., rapid turnover), high rates of growth (up to 2 mm d$^{-1}$), high population densities (76–109 algae m$^{-2}$), and global distribution throughout the shallow tropical environments of the Caribbean and Mediterranean Seas (Hills-Colinvaux 1980), Great Barrier Reef (Drew and Abel 1988), and Indo-Pacific Ocean (Hills 1991), suggest that they could be responsible for much of the aragonite mud deposited in Recent tropical marine environments (Stockman et al. 1967; Neumann and Land 1975; Hills 1991). Carbon and oxygen isotopes support this assertion (Lowenstam and Epstein 1957). However, recent studies have shown that unicellular green algae and cyanobacteria are also capable of producing significant quantities of calcium carbonate sediments (Yates and Robbins 1998, 2001).

It should also be noted that estimates of algal contribution to carbonate sedimentation based solely on recognizable skeletal debris in sediment cores are only between 11 and 29 wt % (Cloud 1962; Bathurst 1975). This may be attributable to the codiacean algae’s lack of discrete anatomical components that are easily recognized in sediment samples. Unlike coral, urchin, and mollusk fragments, most codiacean algae rapidly break down into ambiguous aragonite needles, unidentifiable at the organismal level. Therefore, the quantification of *Udotea’s* contribution to carbonate sediment production, based solely on recognizable skeletal debris, may be low.

**Seawater Chemistry**

The molar Mg/Ca ratio of seawater has fluctuated between approximately 1.0 and 5.2 throughout the Phanerozoic, probably as a function of the rate of ocean crust production (Hardie 1996). As mid-ocean ridge basalt comes in contact with brine, it is converted to greenstone; thereby releasing Ca$^{2+}$ and K$^+$ to the seawater and removing Mg$^{2+}$ and SO$_4^{2-}$ from it. The rate of ocean crust production controls the rate of this ion exchange and, therefore, the relative concentrations of these ions in the oceans. Therefore, high rates of ocean crust production result in relatively low seawater Mg/Ca ratios, as existed during the Cretaceous Period. The secular variation of oceanic Mg/Ca is revealed by the coupling of MgSO$_4$ evaporites with aragonite biotic and abiotic precipitates (favored by low concentrations of Ca relative to SO$_4$ at the point of gypsum saturation and high Mg/Ca ratios, respectively) and the coupling of KCl evaporites with calcite biotic and abiotic precipitates (favored by high concentrations of Ca relative to SO$_4$ at the point of gypsum saturation and low Mg/Ca ratios, respectively) (Sandberg 1983; Hardie 1996; Stanley and Hardie)

Laboratory experiments on the MgCl₂-CaCl₂-Na₂CO₃-H₂O system revealed that ambient Mg/Ca ratio, ionic strength, and temperature determine the precipitation of calcite versus aragonite + high-Mg calcite from seawater (Füchtbauer and Hardie 1976, 1980). The Mg/Ca mole ratio value of 2 (± 0.5) was determined to be the boundary between the calcite (mMg/Ca < 2) and aragonite + high-Mg calcite (mMg/Ca > 2) nucleation fields (Leitmeier 1910, 1915; Lippman 1960; Müller et al. 1972; Folk 1974) for chloride solutions under laboratory conditions approximating modern values of ionic strength (I ≈ 0.7), temperature (28°C), pressure (1 atm total pressure), and atmospheric pCO₂. Ancient Mg/Ca values calculated from established rates of ocean crust production (Hardie 1996) predict that the oceans would have transitioned between the aragonite + high-Mg calcite and low-Mg calcite nucleation fields four times throughout the Phanerozoic, thereby predicting a pattern of aragonite and calcite seas that is consistent with the mineralogical record of ooids and marine cements (Sandberg 1983) and skeletal carbonates (Stanley and Hardie 1998, 1999) throughout the Phanerozoic.

METHODS

Preparation of Artificial Seawater

Three 10-gallon glass aquaria were each filled with 30 L of artificial seawater formulated at molar Mg/Ca ratios of 1.0 (low-Mg calcite nucleation field), 2.5 (boundary nucleation field), and 5.2 (aragonite + high-Mg calcite nucleation field; modern seawater). Excluding the concentrations of Mg and Ca, the artificial seawaters were identically formulated at normal marine values (Bidwell and Spotte 1985). Their ionic strengths were held constant at the modern value of 0.7. Mg/Ca ratios remained within 5% of their initial values throughout the duration of the experiments. The experiments were fertilized with 20.0 mg/L NaNO₃, 1.3 mg/L NaH₂PO₄·H₂O, and 0.025 mL/L EDTA, all within the normal range for nearshore tropical marine waters (Spotte 1979). The aquaria were maintained at 25 ± 1°C using 50-watt electric heaters, illuminated with 10 hours/day of identical irradiance (19 watts), and continuously filtered with Millennium 2000 Wet-Dry Multi-filters (rate of filtration = 600 L/hour).

Specimen Collection

Young _U. flabellum_ algae were collected from the back-reef lagoon of Caye Caulker, Belize. Specimens were stored in plastic bags filled with natural seawater from these locations and transported by airplane to the laboratory at Johns Hopkins University the following day. After transport, the algae were placed in a holding tank of normal salinity for 24 hours to combust all organic matter. The specimens were then dried in an oven at 100°C for 4 hours at 100°C. The total number of offspring algae produced varied among the three seawater treatments (for a total of 120 specimens). These specimens were grown simultaneously and in the same aquaria as those analyzed for their mineralogical attributes. Over the duration of the experiment, most of the parent algae produced offspring algae. The first appearances of offspring algae were noted throughout the experiment. The parent and offspring _U. flabellum_ specimens were scale-photographed every seven days. Linear growth of the offspring algae was measured from the weekly photographs. Average linear growth rates were calculated for the offspring algae over the weeks that they exhibited measurable growth.

After 80 days, the offspring algae were harvested and their ages determined relative to the date of their first appearance. The offspring algae were then dried for 24 hours in an oven set to 100°C, after which their dry weight was measured. The specimens were then baked in an oven at 450°C for four hours to combust all organic matter. The weight of the residual calcium carbonate material was measured and recorded as their total calcification. The difference between the original dry weight of the algae and the weight of their residual mineral material after combustion was recorded as their primary production (that is, the organic matter removed by combustion).

RESULTS

Mineralogical Analysis

Back-scatter electron images of the _U. flabellum_ offspring algae reveal that they all precipitated aragonite needles throughout their organic tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3). The needles are mostly between 1 and 4 μm in length and are packed in apparently random arrangements throughout the tissue, regardless of the Mg/Ca ratio of the artificial seawater in which they were grown (Fig. 3).
intermediate, and highest Mg/Ca treatments had average linear growth rates (± standard error) of 0.104 (± 0.016), 0.195 (± 0.024), and 0.288 (± 0.052) mm d⁻¹, respectively (Table 1).

In the low Mg/Ca (≈ 1.0) seawater, U. flabellum offspring ranged in age from 5 to 24 days. In the intermediate Mg/Ca (≈ 2.5) seawater, U. flabellum offspring ranged in age from 5 to 40 days. In the high Mg/Ca (≈ 5.2) seawater, U. flabellum offspring ranged in age from 6 to 54 days. These differences in the ages among the algae are due to the simultaneous harvest of specimens that vary in their dates of origination.

The ages of the offspring U. flabellum algae were plotted against their total calcification and primary production, resulting in a timeline of these variables representing the lifespan of an “idealized” alga raised in seawater with the given Mg/Ca ratio. This was the only way to obtain a continuous measure of calcification and primary production throughout the life of an alga, because measurement of these variables requires combustion and, therefore, destruction of the specimen. The rates of calcification (Fig. 6) and primary production (Fig. 7) of the algae (Table 1) were calculated as the slopes of the least-squares linear regressions through the respective data.

Rates of calcification and primary productivity increased significantly (p << 0.001) with seawater Mg/Ca. U. flabellum algae grown in the lowest, intermediate, and highest Mg/Ca treatments produced CaCO₃ at average rates (± SE) of 0.116 (± 0.025), 0.305 (± 0.030), and 0.551 (± 0.044) mg d⁻¹, respectively; and organic matter at average rates of 0.087 (± 0.034), 0.138 (± 0.028), and 0.383 (± 0.048) mg d⁻¹, respectively (Table 1).

**DISCUSSION**

The precipitation of mostly aragonitic needles by U. flabellum algae grown in the seawater treatment that favors the abiotic nucleation of low-Mg calcite is significant in that it implies that the algae have biological control over which polymorph of calcium carbonate they precipitate. However, it would be expected that this biologically mediated precipitation of aragonite from seawater that favors the nucleation of aragonite (mMg/Ca < 2) would proceed slower than it would in seawater that naturally favors the nucleation of aragonite (mMg/Ca > 2). This may explain the variation in the rate of calcification of
The observation that the *U. flabellum* alga precipitates most of its calcium carbonate as aragonite in the low-Mg calcite nucleation field suggests that the alga is able to specify the polymorph of calcium carbonate that it precipitates. This may be accomplished via transcellular pumping of cations to maintain an internal nucleation field within the aragonite range (nMg/Ca > 2) or with mechanical and/or chemical templates that specify the nucleation of the orthorhombic aragonite crystal structure (Borowitzka 1984). The precipitation of one-quarter of its mineral component as low-Mg calcite, however, indicates that the alga’s biomineralogical control is somewhat limited, and can be partially superseded by the Mg/Ca ratio of ambient seawater.

A previous study similar to the present one found that the primary productivity, calcification, and linear growth rates of the codiacean alga *Penicillus capitatus* decreased 82%, 91%, and 86%, respectively, when switched from the high Mg/Ca (~ 5.2) seawater to the low Mg/Ca (~ 1.0) seawater (Ries 2005). These results are mostly consistent with the outcome of the present study, which shows that primary productivity, calcification, and linear growth rates of the *U. flabellum* alga decreased 77%, 79%, and 64%, respectively, when switched from the high Mg/Ca to the low Mg/Ca seawater.

The main discrepancy between the two studies concerns linear growth rates, in which case the *Penicillus* algae appears to be more negatively affected by low ambient Mg/Ca ratios than the *U. flabellum* alga. This may be attributable to *Udotea*'s C4-like mode of photosynthesis, which would have sustained the alga’s growth more successfully amid reduced CO₂ liberation resulting from reduced calcification in the low Mg/Ca seawater (Reiskind and Bowes 1991). Likewise, the *Penicillus* algae, which apparently do not use a C4-like mode of photosynthesis, would be more adversely affected by reductions in available CO₂.

The previous study on *Penicillus capitatus* also included a stress–strain biomechanical analysis of the algae which revealed that the stiffness of their thalli decreased when grown in artificial seawater of depressed Mg/Ca, probably because of the observed concomitant reductions in primary productivity and calcification (Ries 2005). This suggests that the *U. flabellum* alga, which exhibits comparably reduced rates of primary production and calcification in reduced Mg/Ca seawater, would also have had a lower stiffness in such seawater.

The results of the present study suggest that *Udotea*, and possibly other aragonite-precipitating codiacean algae, would have been less calcified, thereby resulting in the observed correlation of calcification with primary production and linear growth (Paasche 1968; Borowitzka and Larkum 1976; Borowitzka 1977; Sikes et al. 1980; Reiskind et al. 1988, 1989; Ries 2005; Stanley et al. 2005).

The explanation may concern CO₂ (Ries 2005; Stanley et al. 2005).

Precipitation of CaCO₃ by the *Udotea* alga releases CO₂ to the ambient seawater:

$$2\text{HCO}_3^- + \text{Ca} \rightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}. \quad (1)$$

This CO₂ may fertilize the alga’s photosynthesis:

$$\text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{CH}_2\text{O} + \text{O}_2; \quad (2)$$

**Table 1.** Summary of mineralogy, linear growth, calcification, and primary productivity for *Udotea flabellum* algae raised in the three artificial seawater treatments.

<table>
<thead>
<tr>
<th>Seawater Mg/Ca (mole)</th>
<th>Mineralogy (%calc : %arag)</th>
<th>Linear growth ± SE (mm/day)</th>
<th>Calcification ± SE (mg/day)</th>
<th>Primary production ± SE (mg/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>~ 5.2</td>
<td>0 : 100</td>
<td>0.285 ± 0.052</td>
<td>0.351 ± 0.044</td>
<td>0.383 ± 0.048</td>
</tr>
<tr>
<td>~ 2.5</td>
<td>0 : 100</td>
<td>0.195 ± 0.024</td>
<td>0.305 ± 0.030</td>
<td>0.138 ± 0.028</td>
</tr>
<tr>
<td>~ 1.0</td>
<td>25 : 75</td>
<td>0.104 ± 0.016</td>
<td>0.116 ± 0.025</td>
<td>0.087 ± 0.034</td>
</tr>
</tbody>
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slower growing, smaller, and probably less stiff in the calcite seas of the geologic past. This, of course, assumes that ancient codiacean algae inhabiting such seas were not better adapted than modern codiacean algae at producing aragonite (or perhaps even calcite) in seawater favoring the nucleation of calcite. Such chemically induced reductions in the fitness of these algae would have had significant biological implications for *Udotea* and related codiacean algae. Their slow growth rates and small size would have made them less competitive for space and sunlight on the shallow tropical seafloor. Their reduced calcification and stiffness would have made them more susceptible to predation by grazing fish, which are deterred by the algae’s high CaCO$_3$ content in modern aragonitic seas (Wray 1977; Paul and Van Alstyne 1988; Schupp and Paul 1994). Such reduced calcification, primary productivity, and population density would have decreased the algae’s contribution of biogenic aragonite needles to shallow tropical carbonate platforms during calcite seas.

The negative effects of reduced CO$_2$, with respect to photosynthetic tissue growth, associated with reduced calcification for algae producing aragonite in calcite seas, may have been mitigated by elevated atmospheric pCO$_2$ (Royer et al. 2001; Yates and Robbins 2001) associated with elevated rates of ocean crust production, ultimately believed to be the principal cause of calcite seas. If this is the case, then the low rates of primary production observed in the present study may not be applicable to Codiaeae inhabiting high-CO$_2$ calcite seas of the geologic past. Additional experimental work on the combined effects of seawater CO$_2$ and Mg/Ca are required to explore this issue further.

**CONCLUSIONS**

*U. flabellum* algae, when grown in artificial seawater that favors the abiotic precipitation of low-Mg calcite (nMg/Ca < 2), continue to precipitate most of their calcium carbonate as aragonite needles, thereby suggesting that codiacean algae either control local Mg/Ca by pumping cations or employ a mechanical and/or chemical template to specify precipitation of the aragonite polymorph (Borowitzka 1984). However, the partial precipitation of low-Mg calcite (25 ± 3%) in the calcite seawater suggests that the algae’s mineralogical control is limited and can be partially superseded by the Mg/Ca ratio of ambient seawater.

Rates of linear growth, calcification, and primary production decrease for *U. flabellum* algae grown in seawater that favors the nucleation of low-Mg calcite over aragonite. Slower calcification results in reduced liberation of CO$_2$ available for algal photosynthesis, which may be responsible for the concomitant reductions in rates of linear growth and primary production observed in the experiments (Borowitzka and Larkum 1976; Borowitzka 1977; Ries 2005; Stanley et al. 2005).

The production of aragonite by ancient codiacean algae inhabiting calcite seas, assuming that they found it comparably difficult to grow and...

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**FIG. 5.—** Linear growth rates for *U. flabellum* algae grown in the three artificial-seawater nucleation fields. Algae grown in the calcite nucleation field (nMg/Ca = 1.0), which does not favor their aragonite mineralogy, maintained the slowest linear growth rates ± SE (0.104 ± 0.016 mm d$^{-1}$). Algae grown in the boundary (nMg/Ca = 2.5) and aragonite + high-Mg calcite (nMg/Ca = 5.2) nucleation fields exhibited rates of linear growth (0.195 ± 0.024 and 0.288 ± 0.052 mm d$^{-1}$, respectively) increasing significantly ($p < 0.005$) with ambient Mg/Ca. Error bars correspond to the standard error of the data.

**FIG. 6.—** Calcification by *U. flabellum* algae of increasing age in the three seawater treatments. Average calcification rates are the slopes of the least-squares linear regressions through the data. The solid gray ($y = 0.551x - 5.395$, $R^2 = 0.88$, SE = 0.044), broken black ($y = 0.305x - 1.734$, $R^2 = 0.87$, SE = 0.030), and solid black ($y = 0.116x - 0.665$, $R^2 = 0.61$, SE = 0.025) curves correspond to *U. flabellum* algae raised in the aragonite (nMg/Ca = 5.2), boundary (nMg/Ca = 2.5), and calcite (nMg/Ca = 1.0) seawater treatments, respectively, and reveal average calcification rates that decrease significantly ($p << 0.001$) in that order.

**FIG. 7.—** Primary productivity of *U. flabellum* algae of increasing age in the three seawater treatments. Average primary production rates are the slopes of the least-squares linear regressions through the data. The solid gray ($y = 0.383x - 2.738$, $R^2 = 0.75$, SE = 0.048), broken black ($y = 0.138x + 0.241$, $R^2 = 0.62$, SE = 0.028), and solid black ($y = 0.087x + 0.477$, $R^2 = 0.32$, SE = 0.034) curves correspond to *U. flabellum* algae raised in the aragonite (nMg/Ca = 5.2), boundary (nMg/Ca = 2.5), and calcite (nMg/Ca = 1.0) seawater treatments, respectively, and reveal average calcification rates that decrease significantly ($p << 0.001$) in that order.
calciﬁc seawater as did the modern calciocean algae evaluated in this study, would have reduced the competitiveness of these algae, made them more susceptible to grazing predation, and diminished their contribution to carbonate sedimentation. Likewise, these results support the assertion that the dominant ecological and sedimentological roles of calciocean algae in Recent tropical seas is facilitated by the Mg/Ca ratio of seawater supporting the aragonitic mineralogy of these algae over this interval (Stanley and Hardie 1998, 1999).

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