Bot. Bull. Acad. Sin. (2003) **44:** 107-112

d^{13}C values of marine macroalgae from Taiwan

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(Received April 18, 2002; Accepted January 10, 2003)

Abstract. The natural abundance of stable carbon isotope values ($\delta^{13}C$) of organic matter of marine macroalgae collected from Taiwan and its offshore islands (Penghu Islands) were analyzed in this study. These values ranged from -10.5 to -29.5‰. The highest $\delta^{13}C$ value came from green algae (-10.5‰, *Ulva pertusa* while most algae exhibited values in the -14 to -19‰ range. On average, the $\delta^{13}C$ values of red algae (-17.7‰) are slightly more negative than those of green (-16.5‰) and brown (-13.6‰) algae. The carbon isotope record from organic matter of marine algae and its implications for marine algae physiology are also discussed.

Keywords: Marine macroalgae; $\delta^{13}C$; Taiwan.

Introduction

Carbon isotope fractionation is associated with photosynthesis, and non-photosynthetic physical-chemical processes can also discriminate, e.g. lipid synthesis from carbohydrates (Farquhar et al., 1989). The carbon isotope composition of plants is employed to indicate photosynthetic pathways in terrestrial plants (Bender, 1968; Troughton, 1979). The $\delta^{13}C$ values for terrestrial C_3, C_4, and CAM plants range from -22 to -38‰, -11 to -19‰, and -13 to -34‰, respectively. The lower $\delta^{13}C$ values in the range for CAM plants refers to facultative CAM plants functioning as C_3 plants. Carbon isotope combinations measured in marine algae range between -8.8‰ and -34.7‰, potentially leading to the mistaken impression that both C_3 and C_4 photosynthetic pathways are present (Raven et al., 1982; Stephenson et al., 1984; Dunton and Schell, 1987).

Many studies on the pathway of CO_2 assimilation during photosynthesis in plants have demonstrated that differences arise in metabolism of the carbon isotopes ^{13}C and ^{12}C (Park and Epstein, 1960, 1961; Bender, 1968, 1971; Tregunna et al., 1970; Smith and Epstein, 1971; Troughton, 1979; Farquhar et al., 1989; Sackett, 1991; Johnston and Raven, 1992; Maberly et al., 1992; Raven, 1993). With terrestrial C_3 and C_4 plants, the degree of discrimination against $^{13}CO_2$ is distinctive and falls in two clearly separable ranges (Bender et al., 1973; Smith et al., 1973; Yeh and Wang, 2001). The ranges for both C_3 as well as C_4 plants can largely be explained by variations in $\delta^{13}C$ values of source CO_2 and/or in environmental conditions, in addition to probable species effect (Yeh and Wang, 2001). However, with plants which assimilate CO_2 via the CAM pathway, the extent of discrimination stretches over the entire range covering both in C_3 and C_4 plants (Bender et al., 1973; Osmond et al., 1973). Other work has shown that much of the isotope discrimination during photosynthetic CO_2 uptake is by ribulose-bisphosphate carboxylase-oxygenase (RUBISCO) in terrestrial C_3 plants (Park and Epstein, 1961; Whelan et al., 1973) while the carboxylation catalyzed by phosphoenolpyruvate carboxylase (PEPCase) shows only a slight isotopic discrimination in terrestrial C_4 plants (Whelan et al., 1973). Since these are the two known carboxylases involved in photosynthetic CO_2 assimilation, CO_2 assimilation can be assessed via PEPCase or RUBISCO or both in a given tissue by studying the $\delta^{13}C$ value of the tissue. Reiskind and Bowes (1991) report that phosphoenolpyruvate carboxykinase (PEPCK) fixes CO_2 in the "C_4-like" marine green algae *Udotea flabellum*, and are involved in the high rates of dark CO_2 fixation in diatoms and brown algae. Thus, an index of CO_2 assimilation in an organism can be theoretically obtained by knowing the $\delta^{13}C$ value.

For subtidal algae two carbon sources are available for photosynthesis: CO_2 and HCO_3^-. The marine macroalgae with $\delta^{13}C$ values lower than -30‰ are mainly subtidal red algae, with some shaded intertidal red algae and a few green algae, and those examined in the laboratory rely on diffusive CO_2 entry (Raven, 1997; Raven et al., 2002). Some red algae with very low $\delta^{13}C$ values and diffusive CO_2 entry live in warmer, high intertidal habitats, with significant CO_2 gain from the atmosphere. Marine benthic organisms with very positive $\delta^{13}C$ values are mainly green macroalgae and seagrass, with some red and brown macroalgae, with a high $\delta^{13}C$ that can be accommodated by CO_2 use without discrimination in favor of $\delta^{13}C$ (Raven et al., 2002). All of these organisms are able to use HCO_3^-.

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Most species of marine benthic photolithotrophs have $\delta^{13}C$ values ranging from -10 to -30‰ The $\delta^{13}C$ value cannot distinguish between HCO_3^- and CO_2 use although other evidence suggests that most of these organisms can use HCO_3^-. The photosynthesis of organisms with $\delta^{13}C$ values more positive than that of CO_2 in seawater (-10‰) must involve HCO_3^- use. It is mainly unknown what proportion of the different carbon sources are taken up by the different species of macroalgae, which obviously complicates the interpretation of the data. A more extensive investigation of the $\delta^{13}C$ values in marine algae from Taiwan was undertaken to understand more fully the carbon isotope record and its implications for marine algae physiology.

Materials and Methods

Marine macroalgae were collected from Taiwan and its offshore islands (Penghu Islands) (Figure 1). Collection sites for the algae examined are cited where data on $\delta^{13}C$ are given.

The samples were initially dried in an oven at 50°C. The dried samples were pulverized in an agate mortar with a pestle. For carbonate-containing samples, each of the powdered samples was treated with hydrochloric acid (1.2 M) for 48 h, or until effervescence stopped, to remove carbonates. The completely decalcified sample was washed with distilled water and then dried at 50° C. Around 4 mg of the powder sample was placed in a Pt crucible admixed with purified CuO. The CuO had been treated with pure oxygen gas of slightly greater than one atmosphere pressure at about 1100° C for one week. The crucible with the mixture was combusted at 1100° C under vacuum in a quartz reaction vessel (Yeh et al., 1995). The CO_2 was separated from other combustion products by condensation and evaporation under the control of liquid nitrogen and dry ice. The carbon-isotope compositions of the CO_2 samples were determined in an isotope ratio mass-spectrometer (McKinney et al., 1950). The isotope radio mass spectrometer employed in this study was a VG SIRA-10. The results are reported in $\delta^{13}C_{PDB}$ values (Craig, 1957). The overall reproducibility is better than 0.1 permil at the 90% level of confidence (Yeh et al., 1995). The statistic is derived from results of repeated analysis of a spectrographic graphite powder standard for more than two decades and random reanalysis of a sample. Normally, one aliquote of the graphite standard was analyzed after every six samples were.

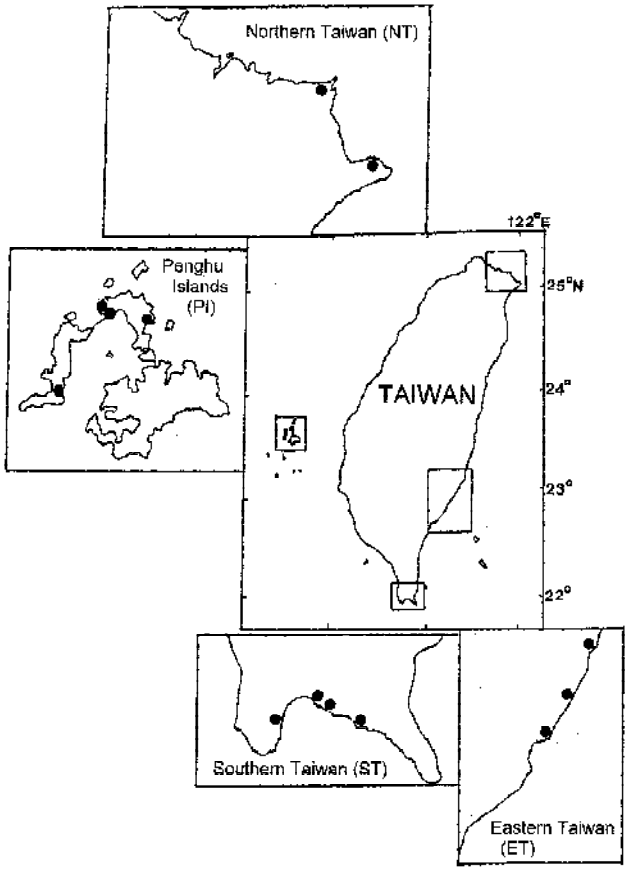

Figure 1. Map showing collecting localities (•) in Taiwan and its offshore islands (Penghu Islands).

Results and Discussion

There is a large range of $\delta^{13}C$ values for the marine macroalgae studied here (Figure 2) and elsewhere (Figure 3) (Craig, 1953; Parker, 1964; Smith and Epstein, 1970; Smith and Epstein, 1971; Black and Bender, 1976; DeNiro and Epstein, 1981; Fry et al., 1982; Kerby and Raven, 1985; Raven et al., 1987; Dauby, 1989; Fenton and Ritz, 1989; Surif and Raven, 1990; Wiencke and Fischer, 1990; Raven, 1991; Raven and Johnston, 1991; Ye et al., 1991; Fischer and Wiencke, 1992; Raven and Osmond, 1992; Maberly et al., 1992; Raven et al., 1994; Raven et al., 1995; Raven et al., 2002). The $\delta^{13}C$ values of the marine algae obtained in this study range from -11.7 to -29.5‰ (Table 1). For the Chlorophyta, the values range from -10.5 to -21.2‰ (Figure 2) with a mean of -16.5‰ For the Phaeophyceae, the values range from -11.7 to -15.8‰ (Figure 2) with a mean of -13.6‰ For the Rhodophyta, the values range from -12.4 to -29.5‰ (Figure 2) with a mean of -17.7‰ The highest $\delta^{13}C$ value is from the green algae *Ulva pertusa* (-10.5‰) whereas most algae exhibit the $\delta^{13}C$ values in the -13.4 to -17.2‰ range (Figure 2). Fry et al. (1982) reported high $\delta^{13}C$ values for a number of marine algae, which corresponds to results presented herein. On average, the $\delta^{13}C$ values of red algae are slightly more negative than those of green and brown algae. Black and Bender (1976), Fry et al. (1982), Maberly et al. (1992) and Raven et al. (1995) also reported some marine red algae with relatively low $\delta^{13}C$ values. The cultivated alga, *Halymenia microcarpa*, in this study is somewhat more reduced in ^{13}C than samples of this alga collected subtidally (Table 1). The work of Wiencke and Fischer (1990) involved algae cultured in the laboratory, with possibly a less constrained source inorganic $\delta^{13}C$ values than is found in the sea. The $\delta^{13}C$ val-

ues of the inorganic carbon in the source is crucial in interpreting discrimination. In the sea, values are believed to fairly constant, but they may be variable locally; variation is particular likely in culture. The implication is that the inorganic carbon in the culture tank may be more negative ^{13}C than the sea. No relationship is apparent between the $\delta^{13}C$ of the algae and their phylogeny.

The $\delta^{13}C$ values for the marine algae in Figure 2 indicate that these algae discriminate against ^{13}C in their assimilation of carbon. These values are in good agreement with the results from tropical and subtropical algal values (Figure 3)(Craig, 1953; Park and Epstein, 1961; Parker, 1964; Black and Bender, 1976; Fry et al., 1982). Since terrestrial C_3 plants have $\delta^{13}C$ values between -22 and -38‰and some of the marine algae in Table 1 show a similar range, we could conclude that these marine algae $\delta^{13}C$ are comparable to terrestrial C_3 plants (Kerby and Raven, 1985).

The $\delta^{13}C$ values of the marine macroalgae from previous works (including work on cultured algae) are shown in Figure 3. Apparently, two groups can be delineated for the Chlorophyta, and the values range from -8.8 to -21.3 ‰and from -25.7 to -32‰ Only one group can be distinguished for the Phaeophyceae and Rhodophyta, and the values range from -8.8 to -38.3‰and from to -9.6 to -34.7 ‰respectively. The $\delta^{13}C$ value range of marine algae do

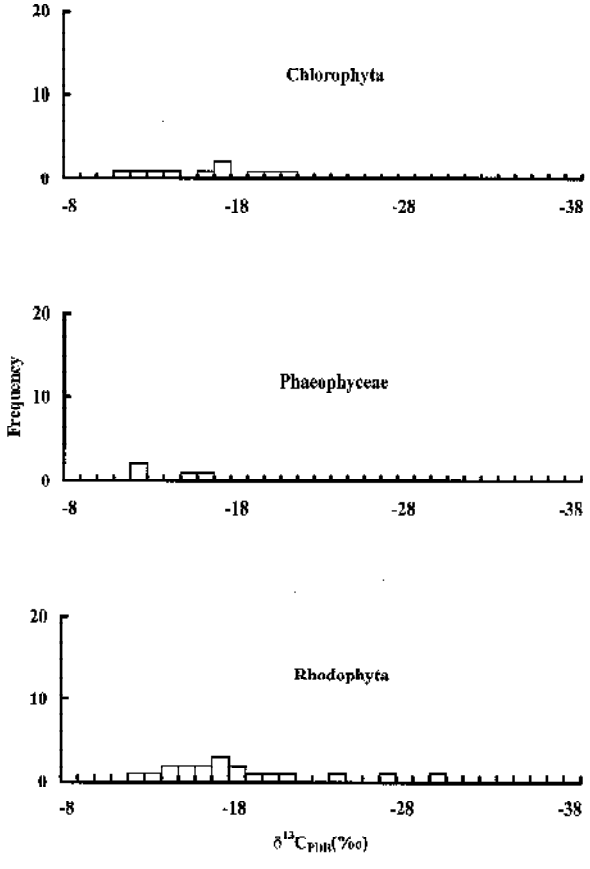

Figure 2. $\delta^{13}C$ values of marine green, brown and red macroalgae from Taiwan.

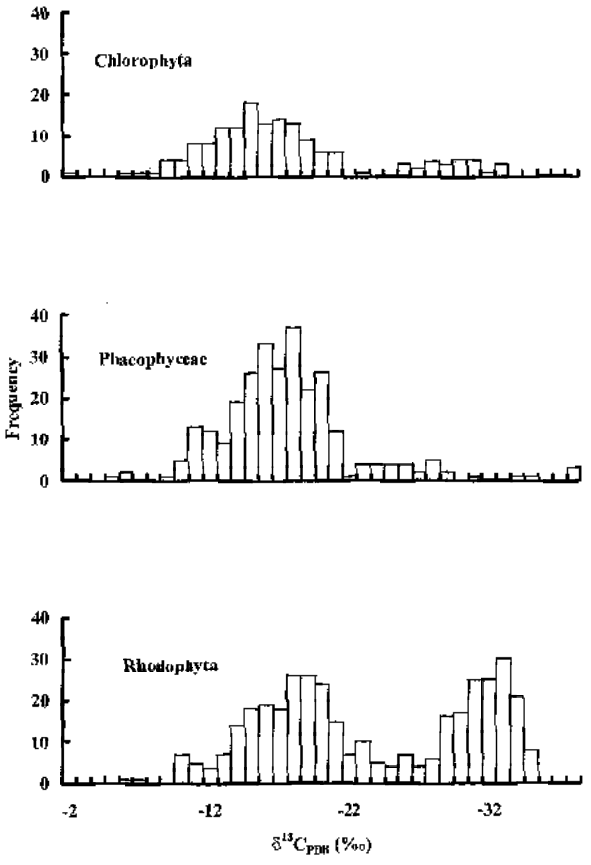

Figure 3. $\delta^{13}C$ values of marine green, brown, and red macroalgae from previous works. Data from Craig (1953), Parker (1964), Smith and Epstein (1970), Smith and Epstein (1971), Black and Bender (1976), DeNiro and Epstein (1981), Fry et al. (1982), Kerby and Raven (1985), Raven et al. (1987), Dauby (1989), Fenton and Ritz (1989), Surif and Raven (1990), Wiencke and Fischer (1990), Raven (1991), Raven and Johnston (1991), Ye et al. (1991), Fischer and Wiencke (1992), Raven and Osmond (1992), Maberly et al. (1992), Raven et al. (1994), Raven et al. (1995), Raven et al. (2002).

not fit into the photosynthetic pathways type in terrestrial plants. It would be helpful to point out that no seaweed is known to perform CAM (except for a few fucoid brown algae where the contribution to organic C is only a few percentage points) and only one seaweed (*Udotea flabellum*) is known to have C_4-like photosynthesis although with PEPCK as its (C_3+C_1) carboxylase, this enzyme has a much greater $^{13}C/^{12}C$ discrimination than does PEPC (Raven et al., 1995). However, some marine algae in Table 1 do not fit into the range commonly observed with terrestrial plants. In particular *Ulva pertusa*, a green algae, has a $\delta^{13}C$ of about -10.5‰(Table 1). Other marine algae, *Colpomenia sinuosa*, *Padina sanctae-crucis*, *Enteromorpha intestinalis* and *Acetabularia* sp., have similar $\delta^{13}C$ values (-8.8, -9.5, -8.8 and -9.4‰)(Figure 3), which, when compared to terrestrial plants, are at the upper extreme of $\delta^{13}C$ values for C_4 plants and below the lower extreme for C_3 plants (Bender, 1968). Thus, a definite conclusion on the major pathway of CO_2 assimilation in these

organisms cannot be reached, except to state that they should be a subject of future research with emphasis on C_4-type metabolism utilizing the major detectable carboxylase PEPCK, which uses phosphenolpyruvate and ADP and produces oxaloacete and ATP.

Most $\delta^{13}C$ values for marine algae clearly correspond to either limitation by CO_2 diffusion or by a low-discrimination HCO_3^- active transport process. In a few cases, however, no such process seems to be limiting, and neither CO_2 diffusion nor HCO_3^- active transport are limiting.

Table 1. $\delta^{13}C$ values of marine algae from Taiwan and its offshore islands (Penghu Islands).

Species	$\delta^{13}C_{PDB}$ (‰)	Date	Site[a]
Chlorophyta			
Monostromataceae			
Monostroma latissimum Wittrock	-16.9	5/10/95	PI, mid-littoral
Ulvaceae			
Enteromorpha intestinalis (L.) Nees	-17.3	5/10/95	PI, mid-littoral
Enteromorpha sp.	-18.7	5/11/95	PI, mid-littoral
Ulva conglobata Kjellman	-16.3	5/11/95	PI, mid-littoral
Ulva fasciata Delile	-13.4	2/1/93	NT, upper littoral
Ulva pertusa Kjellman	-11.8	6/24/95	PI, mid-littoral
Ulva pertusa Kjellman	-10.5	6/24/95	PI, mid-littoral
Codiaceae			
Codium mamillosum Harvey	-14.2	12/20/93	NT, sublittoral
Halimedaceae			
Halimeda macroloba Decaisne	-21.2	4/28/89	ST, tidal pool
Halimeda opuntia (L.) Lamouroux	-19.7	1/1/79	ST, tidal pool
Phaeophyceae			
Dictyotaceae			
Padina arborescens Holmes	-11.7	5/15/93	NT, sublittoral
Scytosiphonaceae			
Colpomenia sinuosa (Mertens ex Roth) Derbés & Solier	-12.0	5/19/95	NT, sublittoral
Sargassaceae			
Sargassum ilicifolium (Turner) C. Agardh	-15.8	5/10/95	PI, tidal pool (Vesicle)
	-14.7		(Leaf)
Rhodophyta			
Galaxauraceae			
Galaxaura marginata (Ellis *et* Solander) Lamouroux	-16.2	5/15/95	ET, tidal pool
Tricleocarpa cylindrica (Ellis *et* Solander) Huisman *et* Borowitzka	-16.5	5/15/95	ET, tidal pool
Liagoraceae			
Liagoropsis schrammi (P. Crouan & H. Crouan) Dotty & Abbott	-18.0	5/15/95	ET, low littoral
Yamadaella caenomyce (Decaisne) Abbott	-18.2	5/15/95	ET, upper littoral
Gelidiaceae			
Pterocladia capillacea (S. Gmelin) Bomet	-15.2	12/20/93	NT, sublittoral
Gracilariaceae			
Gracilaria arcuata Zanardini	-16.8	5/15/95	ET, tidal pool
Gracilaria coronopifolia J. Agardh	-17.1	5/15/95	ET, tidal pool
Gracilaria salicornia (C. Ag) Dawson	-27.4	5/15/95	ET, tidal pool
Halymeniaceae			
Halymenia microcarpa (Montagne) P. Silva	-29.5	5/18/95	ST, cultivated in pond
Halymenia microcarpa (Montagne) P. Silva	-23.8	5/19/95	NT, sublittoral
Prionitis ramosissima (Okamura) Kawaguchi	-18.6	12/20/93	NT, sublittoral
Corallinaceae			
Amphiroa foliacea Lamouroux	-13.7	4/9/85	ST, tidal pool
Hydrolithon onkodes (Heydrich) Penrose & Woelkerling	-12.7	7/1/92	ET, mid-littoral
Neogoniolithon brassica-florida Setchell & Mason	-12.4	9/8/91	PI, tidal pool
Hypneaceae			
Hypnea spinella (C. Ag.) Kützing	-19.8	5/19/95	NT, sublittoral
Hypnea japonica Tanaka	-21.2	12/20/93	NT, sublittoral
Rhodomelaceae			
Acanthophora specifera (Vahl) Børgesen	-13.9	5/15/95	ET, upper-tidal pool
Laurencia niponica Yamada	-15.1	5/15/93	NT, sublittoral
Laurencia sp.	-15.5	5/9/95	PI, mid-littoral

[a]NT: northern Taiwan; , ST: southern Taiwan; ET: eastern Taiwan; PI: Penghu Islands.

Acknowledgments. This study was supported by National Science Council Grant NSC 86-2116-M-001-012. We thank Miss H. T. Yang and C. H. Lu for technical assistance. Comments of Drs. Chi-Ming Yang and J. A. Raven and an anonymous reviewer contributed to the betterment of this manuscript, and we are grateful.

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臺灣產海藻之穩定性碳同位素研究

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從臺灣各地及澎湖所採得的海藻，進行其有機物的穩定性碳同位素（$\delta^{13}C$）的分析。所得到海藻 $\delta^{13}C$ 值的範圍從 -10.5 到 -29.5‰。其中以綠藻的 *Ulva pertusa* Kjellman 的 $\delta^{13}C$ 值最高 (-10.5‰)，其他海藻的 $\delta^{13}C$ 值大部份分佈在 -14 至 -19‰間。就平均值而言，紅藻的 $\delta^{13}C$ 平均值 (-17.7‰) 比綠藻的 -16.5‰及褐藻的 -13.6‰ 稍小。在本文中亦對海藻穩定性碳同位素的值與海藻生理方面的關係稍做討論。

關鍵詞：海藻；穩定性碳同位素；臺灣。