

Organic carbon isotopic fractionation by marine plankton in the temperature range -1 to 31°C

Isotopic fractionation
Organic carbon
Photosynthesis
Plankton
Metabolism

Fractionnement isotopique
Carbone organique
Photosynthèse
Plancton
Métabolisme

M. R. Fontugne, J.-C. Duplessy.

Centre des Faibles Radioactivités, Laboratoire mixte CNRS (Centre National de la Recherche Scientifique)/CEA (Commissariat à l'Énergie Atomique), 91190 Gif-sur-Yvette.

Received 21/5/80, in revised form 6/9/80, accepted 10/9/80.

ABSTRACT

Organic carbon isotopic ratios of marine plankton have been measured on 86 samples from the North Atlantic and Indian Oceans. These new data confirm that the $^{13}\text{C}/^{12}\text{C}$ ratio of organic carbon is characteristic of well defined surface water masses. Significant correlation between sea surface temperature and carbon isotopic composition shows clearly the thermal effect on carbon isotopic fractionation by plankton. Two linear relations between the isotopic composition of plankton and sea surface temperature have been established; their temperature coefficients are equal and agree with theoretical and experimental ones. Results are discussed in relation to metabolism of phytoplankton species.

Oceanol. Acta, 1981, 4, 1, 85-90.

RÉSUMÉ

Fractionnement isotopique du carbone organique par le plancton marin entre -1 et 31°C

La composition isotopique du carbone organique du plancton marin a été mesurée sur 86 échantillons provenant des océans Indien et Atlantique Nord. Ces nouvelles mesures confirment que le rapport $^{13}\text{C}/^{12}\text{C}$ du carbone organique du plancton présente des valeurs caractéristiques pour des masses d'eau superficielles bien définies. Une corrélation significative entre la température de l'eau de surface et la composition isotopique du carbone organique du plancton montre clairement l'importance de l'effet thermique sur le fractionnement isotopique du carbone par le plancton. Deux relations linéaires entre la composition isotopique du plancton et la température ont été établies; leurs coefficients de température sont identiques et en parfait accord avec les coefficients théoriques et calculés à partir de culture. L'ensemble des différents résultats est discuté en fonction du métabolisme des espèces phytoplanctoniques.

Oceanol. Acta, 1981, 4, 1, 85-90.

INTRODUCTION

Mineral carbon assimilation during photosynthesis results in the fractionation of stable carbon isotopes. This carbon isotope discrimination is mainly due to enzymatic reactions, which catalyze initial carboxylation (Ribulose 1-5 biphosphate carboxylase [RuBPC] for C_3 plants and marine phytoplankton). The range of carbon isotopic fractionation between organic tissue of marine phytoplankton and CO_2 or HCO_3^- dissolved in seawater can

reach more than 20‰ (Craig, 1953; Sackett *et al.*, 1965). Sackett *et al.* (1965) related the variations of the organic carbon isotopic ratio ($^{13}\text{C}/^{12}\text{C}$) of marine plankton to sea surface temperature variations, and determined a temperature coefficient of $0.23\text{‰ per }^{\circ}\text{C}$. In the laboratory, Degens *et al.* (1968 *a*), using marine phytoplankton culture grown under controlled environmental conditions (0.03% CO_2 in air), showed that an increase of water temperature reduces the isotopic discrimination by $0.35\text{‰ per }^{\circ}\text{C}$. Libby (1972), by

Table 1

MD 13 Osiris III cruise : location of stations, sea surface temperature $\delta^{13}\text{C}$ of plankton organic carbon.
Campagne MD 13 – Osiris III : position des stations, température des eaux de surface $\delta^{13}\text{C}$ du
carbone organique du plancton.

Surface water mass	Station	Latitude	Longitude	T (°C)	$\delta^{13}\text{C}$	Mean	
						$\delta^{13}\text{C}$	σ
	1	19°27'2 S	61°36'2 E	27.44	-20.71		
	2	18°38'3 S	65°31'6 E	27.38	-20.39		
	3	17°31'6 S	70°59'7 E	27.36	-19.64		
	4	16°51'6 S	74°40'3 E	27.73	-19.11		
	5	16°34'6 S	76°35'7 E	27.24	-19.23		
	6	16°08'6 S	79°39'8 E	26.94	-19.53		
	7	15°08'8 S	85°22'8 E	27.61	-19.66		
	8	15°03'7 S	85°55'7 E	27.55	-20.14		
	9	14°58'8 S	86°33'5 E	27.59	-19.60		
	10	14°11'0 S	86°58'8 E	27.95	-19.21		
	11	13°36'8 S	87°17'2 E	27.94	-19.47		
South Equatorial Current	12	12°58'7 S	88°28'2 E	27.32	-19.82	-19.79	0.24
	13	12°07'4 S	88°31'6 E	27.69	-19.45		
	14	11°41'1 S	87°55'2 E		-19.91		
	16	09°52'6 S	88°48'3 E	28.26	-19.99		
North Equatorial Counter current	17	08°58'7 S	88°49'4 E	28.33	-20.48	-20.39	0.18
	18	07°59'0 S	88°57'0 E	28.92	-20.13		
	19	06°46'5 S	89°09'9 E	29.36	-20.52		
	20	06°00'8 S	89°12'6 E	29.15	-20.41		
North Equatorial Current	21	04°48'2 S	90°02'3 E	29.36	-19.40	-19.48	0.10
	23	01°16'0 S	89°09'0 E	29.59	-19.42		
	24	00°06'5 N	89°51'3 E	29.49	-19.65		
	25	01°24'8 N	90°03'0 E	29.47	-19.43		
	26	02°38'1 N	90°31'8 E	29.99	-19.48		
	27	04°27'9 N	90°35'1 E	29.27	-19.90		
	29	06°05'7 N	93°37'3 E	29.37	-19.86		
Adaman Sea	30	06°16'6 N	94°26'7 E	29.42	-20.00	-19.99	0.28
	31	06°43'4 N	95°49'6 E	29.67	-19.90		
	32	07°39'0 N	96°12'0 E	29.04	-20.24		
	33	08°43'0 N	95°08'9 E	29.39	-20.10		
	34	10°12'5 N	95°03'0 E	29.23	-19.97		
	35	11°09'0 N	93°41'0 E	29.60	-19.87		
	36	11°45'6 N	94°09'0 E	29.96	-20.63		
	37	12°43'0 N	94°46'0 E	29.56	-19.93		
	38	12°46'0 N	96°04'0 E	29.63	-19.50		
39	13°34'4 N	95°56'2 E	29.79	-19.88			
Gulf of Bengal	41	14°30'5 N	93°07'6 E	29.37	-19.51	-19.63	0.12
	42	16°24'5 N	93°24'2 E	29.82	-19.67		
	43	17°11'7 N	93°05'0 E	29.63	-19.44		
	44	18°21'6 N	91°01'3 E	29.64	-19.70		
	45	18°28'3 N	89°51'4 E	30.46	-19.51		
	46	17°23'7 N	90°29'1 E	29.85	-19.73		
	47	16°10'0 N	91°00'0 E	29.61	-19.71		
	48	15°09'0 N	91°43'0 E	29.69	-19.74		
	49	13°58'7 N	92°11'7 E	29.80	-19.52		
	50	12°24'0 N	92°03'7 E	29.42	-19.78		
	52	10°13'8 N	91°59'0 E	28.93	-20.05		
	53	09°07'3 N	90°25'4 E	29.26	-20.10		
	54	07°42'0 N	90°11'1 E	29.27	-19.96		
	55	07°41'0 N	87°49'6 E	28.87	-19.43		
	56	07°30'1 N	76°43'0 E	28.56	-20.14		
	57	08°21'5 N	75°58'0 E	28.87	-20.00		
	58	09°24'9 N	75°26'1 E	29.36	-19.78		
West coast of India	59	10°28'0 N	75°14'0 E	29.85	-19.38	-19.29	0.08
	60	11°29'7 N	74°32'2 E	30.12	-19.27		
	61	12°18'7 N	73°59'4 E	30.26	-19.19		
	62	13°11'0 N	73°26'0 E	30.15	-19.32		
Arabian Sea	63	14°01'8 N	73°01'1 E	30.42	-18.76	-18.98	0.21
	64	13°58'3 N	71°53'2 E	30.72	-19.01		
	65	16°32'5 N	67°53'5 E	31.12	-19.27		
	66	17°56'7 N	63°09'8 E	30.47	-19.08		
	67	19°13'3 N	60°40'9 E	29.77	-18.80		
	A1	16°27' N	67°17' E	29.03	-19.00		

Table 1 (continued).

Surface water mass	Station	Latitude	Longitude	T (°C)	$\delta^{13}\text{C}$	Mean	
						$\delta^{13}\text{C}$	σ
Upwelling	68	20°41'9" N	59°34'1" E	26.49	-20.47		
	69	19°18'0" N	58°26'0" E	28.02	-19.68		
Upwelling	70	17°44'0" N	57°40'4" E	26.31	-20.15		
Gulf of Aden	{ 71	16°52'6" N	55°07'1" E	28.74	-20.16		
	{ 72	15°04'0" N	52°13'0" E	28.68	-21.83		
	{ A2	15°00' N	55°02' E	26.97	-20.39		
Red Sea	{ A3	15°56' N	41°35' E	31.26	-17.58		
	{ A4	21°15' N	38°02' E	29.65	-18.53		

N.B. : A1, A2, A3 and A4 are unpublished MD 10 Osiris II data.

theoretical calculations, found a temperature coefficient of 0.36‰ per °C for carbon isotope fractionation between cellulose and CO_2 . Wong and Sackett (1978), working with several phytoplankton species cultures, determined temperature coefficients ranging from -0.13 to $+0.36\text{‰}$ per °C. Whelan *et al.* (1973) and Christeller *et al.* (1976), measuring carbon isotope discrimination by RUBP carboxylase, found a temperature effect respectively of 1.4‰ and 0.22‰ per °C. These different results obtained on laboratory cultures of isolated distinct species thus exhibit a large scattering of temperature coefficients for carbon isotopic fractionation by phytoplankton.

Nevertheless, plankton samples collected by Degens *et al.* (1968*b*) in the Pacific Ocean and by Fontugne and Duplessy (1978) in the Indian Ocean, revealed no relationship between seawater temperature ranging from 15 to 31°C and the $^{13}\text{C}/^{12}\text{C}$ ratio of organic carbon of marine plankton. Sackett *et al.* (1973) found that plankton shows a "limited linear dependence" between the $^{13}\text{C}/^{12}\text{C}$ ratio and the temperature of surface seawater below 15°C. Data reveal a disagreement between temperature coefficients obtained by theoretical or experimental calculations and natural observations.

We present here new carbon isotopic measurements on plankton samples for seawater temperature ranging from 6 to 31°C. These results confirm the link between the $^{13}\text{C}/^{12}\text{C}$ ratio and well defined water masses (Fontugne, Duplessy, 1978), and indicate a temperature dependence of carbon isotopic fractionation by marine plankton. In fact, two relationships $\delta^{13}\text{C}$ -T with the same temperature coefficient for carbon isotopic fractionation have been established, exhibiting the occurrence of two planktonic populations with different metabolisms, and agree well with theoretical calculations (Libby, 1972).

MATERIALS AND METHODS

Sixty-six plankton samples were collected in the Indian Ocean during the cruise MD 13-Osiris III (May-June 1977) of the French M/S "Marion Dufresne". Fifteen plankton samples were also collected in July 1977 in the North Atlantic Ocean, during the Faegas II cruise

of the R/V "Jean Charcot". Hydrographic profiles were made at each station; salinity measurements were made on board during the MD 13 Osiris III cruise, and shortly after the end of the cruise Faegas II in the Laboratoire d'Océanographie Physique of the French Museum National d'Histoire Naturelle, using a Guildline 8400 salinometer.

Samples were collected above the thermocline when it occurred (generally between 0-40 m) with a zooplankton net 202 mesh and 0.25 m² section. These natural samples were mixtures composed of a variety of forms, and may even contain partially remineralized organic materials. No attempt was made to separate the phytoplankton because the zooplankton reflects nicely the isotopic composition of its diet (Sackett *et al.*, 1965; Degens *et al.*, 1968*b*; Smith, Epstein, 1970; Deuser, 1970). All samples were dried on board at 60°C, and then stored in the dark at 4°C. In the laboratory, plankton aliquots are decarbonated with dilute HCl (0.1 N), dried again and burnt in an oxygen flow, using the procedure described by Lerman *et al.* (1970) and Fontugne (1978). Any traces of nitrous oxide obtained at the same time as the CO_2 were removed by heating on copper turnings at 400°C.

Results are expressed as:

$$\delta^{13}\text{C} = \left[\frac{^{13}\text{C}/^{12}\text{C} \text{ sample}}{^{13}\text{C}/^{12}\text{C} \text{ standard}} - 1 \right] \times 1000.$$

The standard used is the Chicago PDB1. The calibration of our laboratory standard was obtained through the isotopic standards NBS20 and NBS21. Isotopic ratios were measured with a "Micromass 602D" mass spectrometer.

RESULTS AND DISCUSSION

The location of samples, surface seawater temperatures and carbon isotopic ratios are reported in Tables 1 and 2. During the Osiris III cruise in the Indian Ocean, the hydrologic pattern is quite well defined and the isotopic composition of plankton organic carbon is characteristic (Table 1) of a well defined surface water mass and

Table 2

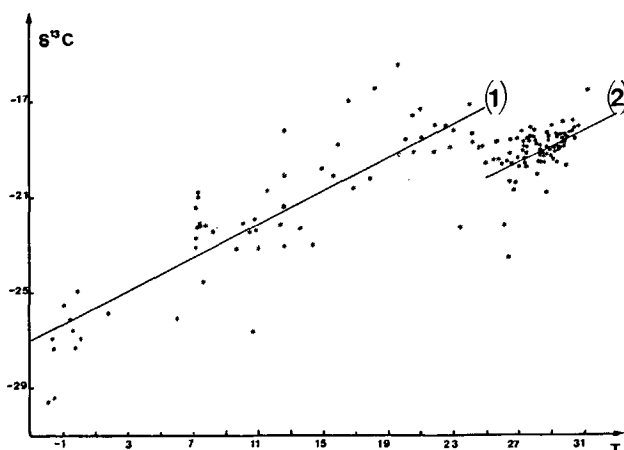
Faegas II cruise: location of stations, sea surface temperatures and $\delta^{13}\text{C}$ of plankton organic carbon.

Campagne *Faegas II*: position des stations, température des eaux de surface, $\delta^{13}\text{C}$ du carbone organique du plancton.

Station	Latitude	Longitude	T	$\delta^{13}\text{C}$
1	52°20,9 N	35°14 W	11.09	-24.15
2	52°42,5 N	36°05,5 W	11.46	-23.00
3	57°56,9 N	29°06 W	10.19	-23.12
4	59°48,4 N	27°55,4 W	9.75	-24.16
5	60°23,3 N	26°00 W	10.56	-23.43
6	62°00,9 N	24°29,2 W	10.81	-22.93
7	66°35,9 N	10°30,5 W	6.04	-27.07
8	64°52 N	8°30 W	7.67	-25.57
9	61°42 N	9°11 W	10.87	-23.38
10	58°38,8 N	14°00,7 W	12.66	-24.07
11	59°48,6 N	15°51,8 W	12.69	-19.21
12	60°56,2 N	17°44,5 W	12.69	-21.09
13	61°20 N	18°25,5 W	12.61	-22.37
14	62°27,4 N	20°24,7 W	12.46	-23.17
15	62°56,8 N	21°37 W	11.64	-21.67

changes from one water mass to another, marking hydrologic discontinuities. Within well defined water masses, the isotopic ratio of plankton collected during the day is not significantly different from that of plankton collected at night. These new observations confirm previous results obtained by Fontugne and Duplessy (1978). On the other hand, in the North Atlantic Ocean, the mixing of warm water from the Irminger Current and Polar cold water from the Greenland Current (Tchernia, 1979) fails to reflect a well defined hydrologic pattern; consequently, no relationship between $\delta^{13}\text{C}$ of plankton and surface water masses was observed.

Correlation coefficients for cruises MD 13 Osiris III and *Faegas II* (respectively $r=0.32$ for 66 samples, $r=0.80$ for 15 samples) point to a significant correlation between $\delta^{13}\text{C}$ of plankton and sea surface temperature.



Figure

Organic carbon isotopic composition compared with surface seawater temperature:

(1) $\delta^{13}\text{C}=0.35 T-27$; (2) $\delta^{13}\text{C}=0.35 T-30$.

Variation de la composition isotopique du carbone organique du plancton en fonction de la température des eaux de surface.

Nevertheless, the sampling was not altogether representative of the whole range of seawater temperature variations, especially for low temperatures, so we added (Fig.) data of natural plankton $\delta^{13}\text{C}$ available in literature (Sackett *et al.*, 1965; Degens *et al.*, 1968b; Deuser, 1970; Fontugne, Duplessy, 1978). A strong positive correlation ($r=0.83$) for the whole of the data had been obtained again between $\delta^{13}\text{C}$ of plankton organic carbon and surface seawater temperature, but we noticed a maximum for $^{13}\text{C}/^{12}\text{C}$ ratios for temperature reaching 25°C. Such a values distribution with a maximum near 25°C cannot be explained by a single $\delta^{13}\text{C}$ -temperature linear relationship. To check the true significance of such a correlation, we made a partition of values for different ranges of seawater temperature ($T < 10^\circ\text{C}$, $T < 15^\circ\text{C}$, ..., $T < 25^\circ\text{C}$).

Coefficients of correlation, levels of significance and temperature coefficients are reported in Table 3. For classes characterized by seawater temperature below 10, 15, 20, 25°C, the correlation remains always highly significant, while for classes 15-31°C and 20-31°C the correlation does not exist, but reappears strongly for class 25-31°C. Furthermore, we obtain two identical slope relationships (1), (2) on both sides of the maximum at 25°C, which constitute the best fit of the points

$$\delta^{13}\text{C}=0.35 t-27, \quad t < 25^\circ\text{C} \quad (1)$$

$$\delta^{13}\text{C}=0.35 t-30, \quad t > 25^\circ\text{C}. \quad (2)$$

Table 3

Linear regression parameters and correlation coefficients between $\delta^{13}\text{C}$ and seawater temperature for different temperature classes.

Paramètres de régression et coefficients de corrélation entre $\delta^{13}\text{C}$ et température pour différentes gammes de températures.

Temperature classes	Number of samples	Correlation Coefficient	Level of significance 0.05	Slope of the curve
$T < 5^\circ$	12	0.57	0.576	0.81
$T > 5^\circ$	150	0.82	0.159	0.18
$T < 10^\circ$	24	0.867	0.388	0.528
$T > 10^\circ$	138	0.553	0.166	0.139
$T < 15^\circ$	39	0.822	0.300	0.41
$T > 15^\circ$	123	0.002	0.174	0.001
$T < 20^\circ$	47	0.873	0.273	0.438
$T > 20^\circ$	115	0.099	0.185	0.036
$T < 25^\circ$	65	0.873	0.241	0.350
$T > 25^\circ$	97	0.541	0.202	0.351
$T < 31$	162	0.83	0.16	0.22

The temperature coefficients (0.35‰ per $^\circ\text{C}$) are consistent with that obtained by Christeller *et al.* (1976) from carbon isotopes fractionation by RUBP carboxylase, and agree with the experimental temperature coefficient (0.35‰ per $^\circ\text{C}$) obtained from phytoplankton culture by Degens *et al.* (1968 a) and the theoretical value calculated by Libby (1972).

The occurrence of two relationships suggests the existence of two phytoplankton populations on either side of the seawater temperature (20-25°C). In fact, this range of temperature is characterized by a replacement of subtropical phytoplankton by species (such as cyanophyceae) more adapted to high temperature. A similar observation has been described by Sackett *et al.* (1973) near the Antarctic convergence, which constitutes a hydrologic front linked to a boundary between different phytoplankton regimes. These results allow us to explain the lack of correlation found by Degens *et al.* (1968 *b*) and Fontugne and Duplessy (1978): their sampling ranging from 15 to 30°C was a mixture of two different populations.

Nevertheless, we notice for both relationships a wide scattering, which means that carbon isotopic variation in plankton cannot be explained by thermal effect alone. The scattering may be related to small metabolism differences of phytoplankton species, probably linked to chemical properties of seawater (concentration of minor nutrients).

The large difference of carbon isotope fractionation for the two populations suggests difference of mineral carbon assimilations, and is probably due to structurally and catalytically distinct RUBP carboxylases (Estep *et al.*, 1978 *a*).

Some authors (Beardall *et al.*, 1976; Estep *et al.*, 1978 *b*; Raven, Glidewell, 1978) suggest the occurrence of an initial carboxylation using HCO_3^- as substrate by phosphoenol pyruvate (PEP) carboxylases (C_4 pathway). The C_4 pathway is characterized by high $\delta^{13}\text{C}$ values of organic tissue (Smith, Epstein, 1971; Bender, 1971; Lerman *et al.*, 1974) and occurs generally in warm climate upper plants. In warm seawater, where high HCO_3^- concentrations occur, conditions would be propitious for a C_4 pathway on plankton, but we noticed a decrease of $\delta^{13}\text{C}$ of plankton above 25°C. This fact

does not appear consistent with a C_4 pathway which would enrich carbon 13 content of the phytoplankton. Nevertheless, our results indicate that phytoplankton has its own mineral carbon fixation pathways which change on both sides of the 25°C isotherms.

To conclude, new results on natural plankton establish clearly the temperature effect on carbon isotopic fractionation, and explain the apparent lack of correlation for seawater temperature above 15°C.

The relationship between $\delta^{13}\text{C}$ of plankton and well defined water masses is observed again, and may be explained because each water mass is characterized by its peculiar temperature and distribution of phytoplanktonic species. We notice the occurrence of two planktonic populations with different metabolisms. The same temperature coefficient for the two populations, and the lower $\delta^{13}\text{C}$ values for plankton of warmer seawater, suggest that the difference of metabolism may be related to different CO_2 fixation by different subunits of RUBP carboxylase, rather than to a C_4 pathway.

Acknowledgements

We are grateful to J. Labeyrie for his constant encouragement. Thanks are due to P.-L. Blanc for help in finalizing the manuscript. We thank C. Copin, E. Nicolas and L. Gamberoni for hydrologic data, Captain Paquet and the crew of R/V "Jean Charcot", Captain Burdin and the crew of M/S "Marion Dufresne" for their active participation.

Logistic and financial support from Les Terres Australes et Antarctiques Françaises is gratefully acknowledged. The laboratory work was supported by the French Centre National de la Recherche Scientifique through "ATP Océanographie Chimique".

REFERENCES

- Beardall J., Mukerji D., Glover H. E., Morris I., 1976. The path of carbon in photosynthesis by phytoplankton, *J. Phycol.*, **12**, 409-417.
- Bender M. M., 1971. Variation in the $^{13}\text{C}/^{12}\text{C}$ ratio of plants in relation to the pathway of photosynthetic carbon dioxide fixation, *Phytochemistry*, **10**, 1239-1244.
- Christeller J. T., Laing W. A., Troughton J. H., 1976. Isotope discrimination by ribulose 1-5 biphosphate carboxylase, *Plant Physiol.*, **57**, 580-582.
- Craig H., 1953. The geochemistry of the stable carbon isotopes, *Geochim. Cosmochim. Acta*, **3**, 53-92.
- Degens E. T., Guillard R. R. L., Sackett W. M., Hellebust J. A., 1968 a. Metabolic fractionation of carbon isotopes in marine plankton. I: Temperature and respiration experiments, *Deep-Sea Res.*, **15**, 1-9.
- Degens E. T., Behrendt M., Gotthart B., Reppmann E., 1968 b. Metabolic fractionation of carbon isotopes in marine plankton. II: Data on samples collected off the coasts off Peru and Ecuador, *Deep-Sea Res.*, **15**, 11-20.
- Deuser W. G., 1970. Isotopic evidence for diminishing supply of available carbon during diatom bloom in the Black Sea, *Nature*, **225**, 1069-1071.
- Estep M. F., Tabita F. R., Parker P. L., Van Baalen C., 1978 a. Carbon isotope fractionation by ribulose 1.5 biphosphate carboxylase from various organisms, *Plant Physiol.*, **61**, 680-687.
- Estep M. F., Tabita F. R., Van Baalen C., 1978 b. Purification of ribulose 1.5 biphosphate and carbon isotope fractionation by whole cells and carboxylase from *Cylindrotheca* sp. (Bacillariophyceae), *J. Phycol.*, **14**, 183-188.
- Fontugne M. R., 1978. Étude de la composition isotopique du carbone organique du plancton marin. Application à la paléocéanographie, *Thèse 3^e cycle, Univ. Bordeaux I*.
- Fontugne M. R., Duplessy J.-C., 1978. Carbon isotope ratio of marine plankton related to surface water masses, *Earth Planet. Sci. Lett.*, **41**, 365-371.
- Lerman J. C., Mook W. G., Vogel J. C., 1970. ^{14}C in tree rings from different localities, in: *Radiocarbon variation and absolute chronology*, Nobel Symposium 12, edited by I. U. Olsson, Almqvist and Wisell, Stockholm and Wiley-Interscience, New York, 273-301.
- Lerman J. C., Deleens E., Nato A., Moysse A., 1974. Variation in the carbon isotope composition of a plant with Crassulacean acid metabolism, *Plant Physiol.*, **53**, 581-584.
- Libby L. M., 1972. Multiple thermometry in paleoclimate and historic climate, *J. Geophys. Res.*, **77**, 4310-4317.
- Raven J. A., Glidewell S. M., 1978. C_4 characteristics of photosynthesis in the C_3 alga *Hydrodictyon africanum*, *Plant Cell Environment.*, **1**, 185-197.
- Sackett W. M., Eadie B. J., Exner M. E., 1973. Stable isotope composition of organic carbon in recent Antarctic sediments, *Actes du 6^e Congrès International de Géochimie organique, Rueil-Malmaison, France*, 661-671.
- Sackett W. M., Eckelmann W. R., Bender M. L., Be A. W. H., 1965. Temperature dependence of carbon isotopic composition in marine plankton and sediments, *Science*, **148**, 235-237.
- Smith B. N., Epstein S., 1970. Biochemistry of the stable isotopes of hydrogen and carbon in salt marsh biota, *Plant Physiol.*, **46**, 730-742.
- Smith B. N., Epstein S., 1971. Two categories of $^{13}\text{C}/^{12}\text{C}$ ratio for higher plants, *Plant Physiol.*, **47**, 380-383.
- Tchernia P., 1979. *Océanographie régionale*, École Nationale Supérieure des Techniques Avancées, Paris.
- Whelan T., Sackett W. M., Benedict C. R., 1973. Enzymatic fractionation of carbon isotopes by phosphoenolpyruvate carboxylase from C_4 plant, *Plant Physiol.*, **51**, 1051-1054.
- Wong W. W., Sackett W. M., 1978. Fractionation of stable carbon isotopes by marine phytoplankton, *Geochim. Cosmochim. Acta*, **42**, 1809-1815.