

Global Photosynthesis and its Regulatory Role in Natural Carbon Cycle

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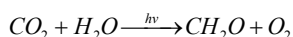
Abstract

Main features of global photosynthesis operating in global carbon cycle are considered. Global photosynthesis has all the basic features of normal photosynthesis of C3 type, excepting those that characterize ontogenetic changes. They include: the existence reciprocal processes assimilation and photorespiration, the possession of the key enzyme Rubisco having carboxylase/oxygenase activity, the existence of oscillatory mechanism switching over assimilation to photorespiration and back, carbon isotope fractionation in CO₂ assimilation and photorespiration with opposite signs of isotope effects and some others. Considering these features of global photosynthesis, its functioning in global carbon cycle is analyzed. The photosynthetic mechanism forming carbon isotope composition of "living matter" and sedimentary organic matter is suggested. It is shown that environmental conditions of photosynthesis in the location plays a dominant role in forming carbon isotope composition of the above objects. The difference in environmental conditions determines facial isotopic shifts. The analysis of natural isotopic data confirms this conclusion. It allows saying that carbon isotopic difference between oils and organic matter is inherited from the difference between lipid fraction and other part of biomass of "living matter" that was the source of initial biogenic material. It is shown that global photosynthesis performs in global carbon cycle a regulatory role ensuring cycle's movement to the ecological compensation point. The regulatory role is based on the ability of photosynthesizing organisms to respond to the increased oxygen concentration in the course of evolution by reducing assimilation and increasing photorespiration. The achievement of ecological compensation point means that oxygen atmosphere was stabilized and further accumulation of organic matter in the Earth's crust stopped.

Keywords: CO₂ assimilation; Environmental factors; Facial isotopic shifts; Global photosynthesis; Living matter; Oscillatory pattern; Photorespiration; Sedimentary organic matter

Introduction

To understand the global carbon cycle, it is necessary to find out the meaning of the two terms - "global photosynthesis" and "living matter". "Living matter" - is a term, introduced by Vernadsky in 1926 [1], which he defined as the total biomass of all living on Earth organisms. Global photosynthesis is the process of synthesis of organic matter from carbon dioxide and water under sunlight, carried by all living on the Earth organisms with special photosynthetic apparatus. Formally, the global equation of photosynthesis can be written as it is written for any photosynthetic organism.



Since the global photosynthesis involves all of the photosynthesizing organisms living on the Earth, then given they constitute the beginning of all food chains, the total biomass of all living organisms, including photosynthesizing biomass and biomass of all consumers in trophic chains, can be regarded as a product of global photosynthesis. According to Vernadsky, it is the "living matter".

Another product of global photosynthesis is an oxygen molecule in the Earth's atmosphere. With a good approximation it can be regarded as such if to neglect the quantity of oxygen, which was in atmosphere prior to photosynthesis emergence [2].

What is common and what is the difference between global photosynthesis from regular photosynthesis of individual organism?

The regular photosynthesis of individual organism is described in detail in the literature [3]. What is common and what is the difference between global photosynthesis and regular photosynthesis of individual organism? At first we'll see the common features. Considering that each photosynthesizing organism has CO₂ assimilation and

photorespiration, let's assume that the same ability inherent in global photosynthesis. The first is responsible for the total biomass growth on the Earth, while the second is used in oxidation of part of the assimilated carbon to cover the energy costs of organisms partly to ensure adaptation of them to environmental conditions and to supply other metabolic needs. Part of respiration flux is used for biosynthesis of total biomass.

Assimilatory and photorespiratory metabolic fluxes of global metabolism are in reciprocal relations, i.e., the increase one of them is accompanied by a decrease of the other [4]. The contribution of the fluxes to the total biomass growth depends on CO₂/O₂ concentration ratio. The increase in CO₂ concentration intensifies CO₂ assimilation, whereas the increase in O₂ concentration is followed by the intensification of photorespiration and by subsequent decrease of total biomass.

The main difference between global photosynthesis and that of photosynthesizing organism is in that it does not account for the changes associated with ontogenesis. It means that global photosynthesis doesn't depend on time, but depends on the environmental conditions in a given place at a given moment. As compared with photosynthesis of individual organism, global photosynthesis can be imagined as an instant photo taken at the moment. These images, taken in different locations of the Earth at the same time, will be different depending on the conditions of photosynthesis in these locations only.

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The control over the ratio of assimilatory and photorespiratory fluxes in a photosynthesizing cell, is carried out, as known, by the key enzyme of photosynthesis is ribulose biphosphate carboxylase/oxygenase (Rubisco) having carboxylase and oxygenase function and has a working feedback mechanism [5]. Functions oscillate, switching over depending on the ratio of CO_2/O_2 in the environment. The switching time determines the duration carboxylase and oxygenase phases [6] and contribution to the biomass of both processes. We accept that the same principle lies in the basis of the synthesis of the total photosynthetic biomass on the Earth.

Each photosynthesizing organism has a so-called CO_2 compensation point, which corresponds to the state when the quantity of carbon assimilated in photosynthesis is equal to the quantity of carbon oxidized in the photorespiration. The state below the compensation point makes the physical existence of the organism is impossible, while the excess of the assimilated carbon over the oxidized means the growth of the biomass. Global photosynthesis has the same feature. The analog of CO_2 compensation point in global photosynthesis termed as ecological compensation point. It corresponds to the state when the total amount of the assimilated carbon (total photosynthesizing biomass) becomes equal to the amount of organic material returned back completely to the oxidized inorganic form. Above this point the excess of carbon assimilated in photosynthesis turns into organic matter deposited in the Earth crust. With oxygen growth in the course of photosynthesis evolution the carbon cycle system spontaneously strives to ecological compensation point. On achieving this point the system goes into stationary state. Oxygen and carbon dioxide begin to oscillate around the steady meaning. It means that in the course of evolution oxygen reached its maximal meaning, while carbon dioxide its minimal meaning [7]. Thus, the oxygen and carbon dioxide concentrations in the environment, as well as the ecological compensation point are determined by the features of photosynthesis itself [8,9].

Carbon isotope fractionation in global photosynthesis

Following the adopted logic we assume that CO_2 assimilation and photorespiration in global photosynthesis are followed by carbon isotope fractionation like photosynthesis of an individual organism. CO_2 assimilation results in enrichment of total biomass in ^{12}C isotope whereas photorespiration leads to accumulation in biomass of ^{13}C .

Let's see what affects carbon isotope composition of "living matter" on the Earth. The "living matter", as said, consists of photosynthesizing and heterotrophic parts. The latter includes biomass of all organisms forming trophic chains. Since the photosynthesizing biomass is a source of the whole "living matter", it can be regarded as a product of photosynthesis. If so, in the equation of global photosynthesis CH_2O will denote the "living matter".

From numerous isotopic studies of heterotrophic assimilation it was found that this assimilation isn't accompanied with noticeable carbon isotope fractionation [10,11] and isotope composition of consumer's biomass is determined by carbon isotope effect at the stage of photosynthesizing assimilation. It allows concluding that the "living matter" should be of the same isotope composition as its photosynthesizing part.

Besides carbon isotope fractionation associated with photosynthesis, in cells of any "living matter", regardless of whether it is heterotrophic or photosynthetic, the intracellular carbon isotope fractionation takes place. This leads to a natural redistribution of carbon isotopes between fractions. The lipid fraction of biomass turns to be 3-5‰ "lighter" than other fractions (lignin, protein and carbohydrate) [12]. This is a

result of a specific way of biosynthesis of lipid components in a cell that occurs through structural C_2 -fragments and is accompanied by a carbon isotope effect [13,14].

The enrichment in a "light" isotope begins to occur immediately after the death of the organisms in the course of sedimentation in water column and in burial of biogenic material in the sediment. The most frequent case is the burial in a subaqueous environment, which is considered below. Microbial and chemical oxidation of biogenic material commences already in the water column and in the sediment. Of the major biochemical fractions the lipid one is the most stable to oxidation. That's why the initially small lipid fraction in the "living matter" begins to increase with oxidation development. This is clearly manifested in the shift of the isotopic composition of organic matter relative to the source of carbon of biogenic material. At all stages of sedimentation and diagenesis there was a steady enrichment of organic matter in ^{12}C , which indicates an increase in the relative proportion of total carbon of the lipid component [15,16]. But it doesn't mean structural and chemical stability of the lipid fraction components.

Depending on carbon isotope composition of sedimentary organic matter two main factors determining carbon isotope composition: Sedimentary organic matter is an intermediate product on the way of biogenic material transformation to the final oxidized inorganic carbon forms in global carbon cycle [17]. As we use carbon isotopic technique to study carbon turnover, carbon isotope composition of sedimentary organic matter is of special interest. Carbon isotope composition of sedimentary organic matter is determined by two reasons:

- 1) The difference in photosynthesis conditions leading to different values of carbon isotope effects. This in turn determines different carbon isotope composition of "living matter" at different locations;
- 2) The uneven oxidation of the fractions in different locations leads to a change relative to the initial ratio of the fractions and to the emergence of additional isotopic shifts. As a result, the variance in the carbon isotope composition between organic matter and initial biogenic material emerges.

To assess the influence of these two reasons, let's see first the scale of natural variations of carbon isotope composition of photosynthesizing organisms at different environmental conditions. Different natural parameters effect on carbon isotope composition of biomass. They are concentration of CO_2 and O_2 in the environment, pH values of the water in aquatic environment, salinity, light intensity, temperature, water availability, mixing and aeration, temperature and other parameters derived from the above [17-19]. The scale of isotopic variations covers range up to 20‰. After the burial of biogenic material the isotopic differences associated with uneven fractions oxidation begin to show. But their value, as said before, can't exceed 5‰, i.e., maximal isotopic differences between fractions observed in living organisms. The case corresponds to the full oxidation of all fraction excepting lipid one. Evidently, this case is very unlikely. It allows concluding that photosynthesis conditions play a dominant role. Another conclusion is in that carbon isotope composition of sedimentary organic matter mainly depends on environmental parameters in photosynthesis.

Environmental factors exerting an impact on carbon isotope composition of sedimentary organic matter. Mechanism of formation of carbon isotope composition of "living matter" and sedimentary organic matter: As it follows from the above, isotopic differences of sedimentary organic matter should reflect isotopic differences of the "living matter" in the relevant period. From the above

the environmental factors exerting an impact on photosynthesizing organisms have the same effect on the carbon isotope composition of organic matter.

Below we show the examples of impact of different environmental parameters on carbon isotope composition of photosynthetic biomass. Natural observations and *in vitro* experiments showed that the carbon isotopic variations depending on CO₂ concentrations in the environment may achieve 25‰ [20]. It was also found [21] that the ¹²C enrichment of biomass turned out to be much less than the carbon isotope effects of RuBP carboxylation on the enzymes isolated from the biomass of these organisms. The effects were about 60-65‰. Such a great difference was found later to be mainly a result of photorespiration [22].

Environmental factors have different effects on carbon isotope composition of biomass. Among them the variations of CO₂ concentration in the environment exerts the strongest effect. High CO₂ concentrations results in ¹²C enrichment of biomass in the *in vitro* experiments [11,20,23]. Similarly pH manifests itself in aquatic environment. The low pH values, corresponding to high CO₂ concentrations, provided ¹²C accumulation in biomass of marine alga *Cyclotella*, whereas high pH values resulted in abrupt enrichment in ¹³C [24,25]. In nature one can see the same picture [17].

The effect of environmental oxygen concentration on carbon isotope composition of biomass was firstly considered to be insignificant [26,27], since the role of photorespiration was underestimated and the reciprocal relation of assimilation and photorespiration was unknown. Later the role of carbon isotope effect of photorespiration was recognized as important [22,28] and some researchers have indicated the role of oxygen concentration on photorespiratory function of Rubisco [23,29]. It was shown that low O₂ content caused the observed enrichment of organic matter ¹²C [30].

Numerous data showed that the environmental parameters, directly or indirectly affecting the CO₂ uptake by photosynthesizing cells or facilitating CO₂ availability, result in ¹²C enrichment of biomass. The parameters are: water salinity [31], water availability [32], temperature [27], cell density per volume unit [11], mixing and aeration of water [33,34]. But total effect of these parameters as a rule doesn't exceed several per mille.

Light intensity exerts an impact on carbon isotope composition as well [35]. The isotopic shifts under low intensity have multidirectional character, but at high intensity isotopic shifts are always followed by ¹³C enrichment of biomass up to 5‰ [36]. In nature so-called mid-day ¹³C enrichment of biomass is also associated with maximum light intensity [37]. The exposed leaves of plants reveal the accumulation of ¹³C as compared with shadowed leaves [38]. The effect of light intensity on carbon isotope composition of biomass can be explained by its impact on carboxylase/oxygenase activity of Rubisco. Under intense illumination CO₂ the supply of Rubisco becomes insufficient to provide effective work of Calvin cycle. In this case photosynthesizing organisms use instead of CO₂ another substrate O₂, involving photorespiratory pathway [39]. It is followed by ¹³C enrichment of biomass.

Figure 1 illustrates the principal scheme, explaining the mechanism of influence of different environmental factors on carbon isotope composition of living matter and, hence, sedimentary organic matter. It illustrates the impact of CO₂/O₂ concentration ratio in the environment. In the point 1, RuBP acceptor fixes CO₂ and carbon isotope fractionation occurs resulting in ¹²C enrichment (+) of the assimilated carbon. In the point 2 glycine decarboxylation occurs followed by carbon isotope fractionation resulting in ¹³C enrichment (-) of the assimilated carbon. Switching over the enzyme from assimilatory function to photorespiratory occurs by RuBP carboxylase/oxygenase.

The mechanism takes into account that global photosynthesis fractionates carbon isotopes like a photosynthesizing cell, including isotope fractionation in assimilation and photorespiration. Note that these processes are in reciprocal relations and oscillate.

The key element of this mechanism is Rubisco engine, switching over assimilation to photorespiration function and back. In assimilatory phase the mechanism provides ¹²C accumulation in biomass (Figure 1). In this phase the total biomass on the Earth and the amount of sedimentary carbon in the Earth's crust increases. In photorespiratory phase the mechanism provides ¹³C accumulation in biomass (Figure 1). Total biomass on the Earth and the amount of sedimentary carbon in the Earth's crust decreases.

From the Figure 1 it becomes clear why the environmental parameter CO₂/O₂ ratio exerts the stronger effect on carbon isotope composition of biomass as compared with others. It is the result of the fact that it is connected directly with Rubisco engine. In contrast,

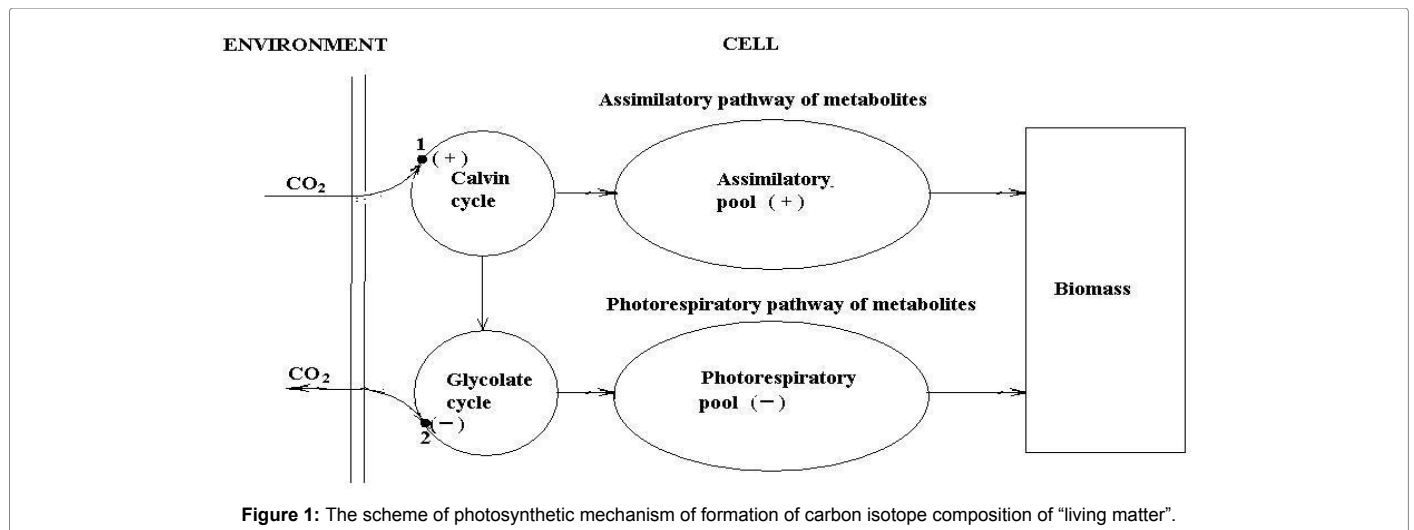


Figure 1: The scheme of photosynthetic mechanism of formation of carbon isotope composition of "living matter".

the relatively small isotopic variations due to other parameters are explained by indirect impact of them. In general, the relatively small scale of isotopic variations observed in photosynthesis is due to a strong coordination of different photosynthetic processes in a cell to ensure optimal conditions for Calvin cycle functioning.

It was shown [3,40] that the coordination includes energy (ATP) and reducing equivalents (NADPH) formation coupled with electron transport chain associated with photosystem II. Thus, various environmental parameters determine CO₂/O₂ ratio inside a cell. The latter controls carboxylase/oxygenase activity of Rubisco and determine assimilation and photorespiration and, hence, carbon isotope composition of biomass.

Global photosynthesis in space and time

Global photosynthesis is manifested in space and in time in the form of facial isotopic shifts and temporal isotopic shifts of sedimentary organic matter correspondingly [41]. The difference between these two terms is the same as the difference between a photograph and a video. Facial isotopic shifts reflect the conditions of photosynthesis at this time in this location. That is why we attribute them to organic matter in rocks of the same age. As shown before, the main environmental parameter, exerting an impact on carbon isotope composition of organic matter, is the CO₂/O₂ concentration ratio in the surrounding.

It is known that in the course of photosynthesis evolution the CO₂/O₂ ratio on the Earth permanently changed from maximal value at the photosynthesis origin to minimal value at the ecological compensation point [7]. The changes of the ratio in the course of evolution were a saw tooth with gradual decrease of the average value to the ecological compensation point. It means that if to compare samples of organic matter separated by large time intervals they would correspond to different CO₂/O₂ ratios and have different values of carbon isotope composition.

Facial isotope differences: Following the above definition we assert that a set of environmental parameters makes within a cell a certain ratios of assimilatory and photorespiratory fluxes, which form carbon isotope composition of “living matter” and further of sedimentary organic matter. It was confirmed by many researchers, who disclosed distinctive links of organic matter with the assumed zones of organisms’ habitats differing in CO₂/O₂ ratios and corresponding to marine, fresh water, terrigenous and salt marshes’ conditions [42-44]. They evidence that the initial isotopic discrepancies are remained, despite of transformations, and inherited at different stages of organic matter transformations [16,44]

The correspondence of zones with different CO₂/O₂ ratios to isotopic differences of carbon isotope composition can be traced not only for organic matter but for oils as well. As said before, oils origin is associated with the lipid fraction of the “living matter” which is enriched in ¹²C relative to other parts of biomass. If compared the difference between carbon isotope composition of “living matter” and its lipid fraction with the corresponding difference in the carbon isotope composition of organic matter and genetically related oil, it is easy to see that both values are very close. It allows concluding that the latter difference is inherited from the “living matter”. From this fact it follows that no noticeable carbon isotope fractionation occurs in oil generation and the role of kinetic isotope effect of C-C and C-H bonds cleavage in oil formation is strongly overestimated [45,46].

It follows from this standpoint that the observed ¹²C enrichment of oils is a result of initial enrichment of lipid fraction due to intracellular

carbon isotope fractionation [15,47]. One more important point should be explained. It is the cause of the dependence of carbon isotope composition of fractions and metabolites of “living matter” on isotope effect of photosynthesis. The thing is that carbon isotope effect of photosynthesis arises at the entry into any photosynthesizing cell. It means that all intracellular isotope effects that appear later and result in carbon isotope heterogeneity of biomass, including isotopic shifts its fractions and metabolites, should be summarized with photosynthesis effect and hence should reflect photosynthesis conditions. Thus the facial isotopic differences reflect a variety of photosynthesis conditions on the Earth at the same time.

Temporal isotope differences: If two samples of organic matter relating to the rocks of different ages and this time interval comprise one or more orogenic cycles, it is necessary to take into account the change in CO₂/O₂ ratio arising due to photosynthesis evolution. Naturally, it is more correct to compare temporal isotope differences for the samples of the same faces.

Data of Hayes et al. [48] disclose distinctive ¹³C enrichment of sedimentary marine organic matter relating to different intervals of geological time. They studied carbon isotope discrimination (the difference in carbon isotope composition of organic matter and carbonates, $\epsilon = \delta^{13}\text{C}_{\text{org C}} - \delta^{13}\text{C}_{\text{carb C}}$):

Neoproterozoic	from 800 to 750 Ma	$\epsilon < -32\text{‰}$
	from 685 to 625 Ma	$-32 < \epsilon < -28\text{‰}$
Phanerozoic	less than 625 Ma	$-28 < \epsilon < -22\text{‰}$

Distinct reduction of carbon isotope discrimination with time was found.

The same regularity one can find by studying carbon isotope composition of oils and their fractions in time comprising Neoproterozoic and Phanerozoic [49]. The study disclosed a similar change of carbon isotope composition of oil fractions C₁₅₊ as was seen before for organic matter. Carbon fractions become “heavier” with time (isotope discrimination become less). It should be emphasized that oil, despite to organic matter, reflects the average trend of carbon isotope composition in time, since during migration from source rock to reservoir, oil absorbs hydrocarbons from different sources. But in each case the general trend to ¹³C enrichment remains.

Figure 2 illustrates four steps of ¹³C enrichment of the fraction C₁₅₊ of oils occurring in Phanerozoic. Vertical bars are standard deviations, which increase with decreasing age. Arrows indicate Cambrian-Ordovician, Triassic-Jurassic, and Paleogene-Neogene boundaries where ¹³C enrichment occurs.

The ¹³C enrichment is associated with a 4-fold increase in oxygen content in the atmosphere in the course of 4 orogenic cycles [49].

Regulatory role of global photosynthesis

Global photosynthesis performs in global carbon cycle a regulatory role ensuring cycle’s movement to the ecological compensation point. The regulatory role is based on the ability of any photosynthesizing organisms to respond to the increased oxygen concentration by reducing assimilation and increasing photorespiration. The interaction of CO₂ assimilation and photorespiration occurs by negative feedback mechanism [4]. Any increase in oxygen concentration causes an intensification of photorespiration which is followed by enrichment of biomass in ¹³C. The similar changes in global photosynthesis are associated with corresponding ¹³C enrichment of sedimentary organic matter. The formation of the mechanism of adaptation which emerged

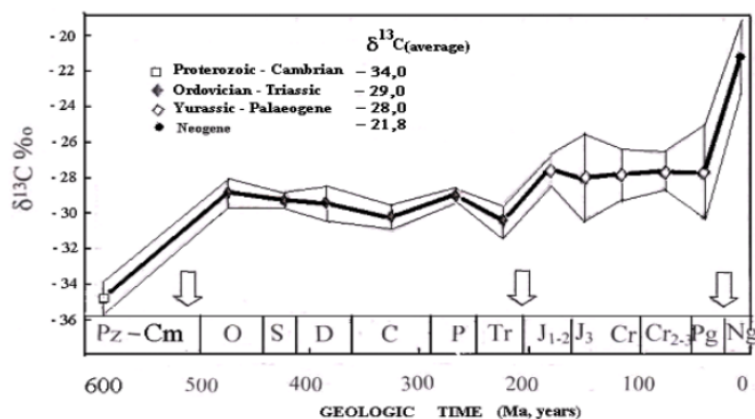


Figure 2: The change of the average carbon isotope composition ($\delta^{13}\text{C}$, ‰) for saturate fraction C_{15+} of crude oils.

with advent of photosynthesis to resist oxygen action (the mechanism of photorespiration) later was transformed into mechanism of adaptation to all stressors.

How long oxygen content in the atmosphere could increase? The analysis allows concluding [7] that the rise of oxygen could last as long as the amount of the reduced carbon derived in photosynthesis doesn't become equal the amount of carbon return back into oxidized inorganic form. This state is called the ecological compensation point, when the system achieves steady state. In case of deviation from this state under the action of any reason, the system spontaneously returns back to the initial state. Miocene was likely the time when the ecological compensation point was achieved. Two facts give indirect arguments in favor of this conclusion. First is the emergence of C_4 plants having a new mechanism of CO_2 -assimilation. The second is the last wave of oil generation indicating the formation of rocks rich in organic matter. Both arguments evidence about low environmental concentration of CO_2 and high concentration of O_2 and indicate the end of orogenic cycle. Further any signs of orogenic cycles were not detected. The long-term orogenic cycles were completely replaced by short-term climatic oscillations. It was reflection of the fact that the equilibrated system became sensitive to collisions of separate lithospheric plates [7].

Conclusions

Global photosynthesis has all the features typical to the normal photosynthesis of individual organism of C_3 type, excepting ontogenetic features. They include: the existence of reciprocal processes assimilation and photorespiration, the possession of the key enzyme Rubisco having carboxylase/oxygenase activity, the existence of oscillatory mechanism switching over assimilation to photorespiration and back, carbon isotope fractionation in CO_2 assimilation and photorespiration with opposite signs of isotope effects and some others.

Taking into account these features of global photosynthesis, the mechanism of formation of carbon isotope composition of "living matter" and of sedimentary organic matter in the frames of global carbon cycle model is suggested. The main photosynthetic enzyme Rubisco, having carboxylase/oxygenase activity, plays the key role in this mechanism.

The analysis of the natural carbon isotope data in conjunction with the mechanism of global carbon cycle functioning shows that environmental conditions of photosynthesis play a dominant role in formation of carbon isotope composition of "living matter" and

sedimentary organic matter as well. Among them the content of CO_2 and O_2 in the environment are the most important. Many others environmental parameters (pH, salinity, mixing, water availability, etc.) exert an impact via their influence on the CO_2/O_2 ratio inside a cell. The role of the intracellular carbon isotope fractionation in formation of carbon isotope composition of the total carbon of "living matter" and sedimentary organic matter is insignificant.

Facial isotopic shifts of sedimentary organic matter are determined by effect of photosynthesis depending on environmental conditions in habitats. The fractions of sedimentary organic matter undergo the same isotopic shifts as organic matter itself. The isotopic difference between oils and organic matter of the source rocks is inherited from the difference between lipid fraction and other part of biomass of the assumed "living matter" in the related habitat. The isotopic difference between lipid fraction and other part of biomass is a result of intracellular carbon isotope fractionation in cells of "living matter".

The temporal isotopic differences of sedimentary organic matter are due to the change in CO_2/O_2 ratio in the environment arising owing to evolution of photosynthesis during the period separating sampling of organic matter. Of course, samples should be taken from the same facies.

It is shown that global photosynthesis performs in global carbon cycle a regulatory role ensuring cycle's movement to the ecological compensation point. The regulatory role is based on the ability of photosynthesizing organisms to respond to the increased oxygen concentration in the course of evolution by reducing assimilation and increasing photorespiration. The achievement of ecological compensation point means that oxygen atmosphere was stabilized and further accumulation of organic matter in the Earth's crust stopped.

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