# INTERPRETING DIURNAL VARIATIONS OF CARBON ISOTOPE CHARACTERISTICS IN PLANTS WITHIN A CONCEPTUAL FRAMEWORK BASED ON AN OSCILLATORY MODEL OF CARBON METABOLISM CASE STUDY - CASTOR BEAN (.*RICINUS COMMUNIS* L.)

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*Abstract: Within a conceptional framework based on carbon metabolism oscillatory model (CMOM), diurnal variations of $\delta^{13}C$ values of water-soluble organic matter (WSOM), and water-insoluble organic matter (IOM) in leaves, stem and phloem sap of castor bean plants (Ricinus communis L.), experimentally investigated by Gessler et al. (2008), are discussed. It is shown that carbon for the synthesis of the IOM fraction components is provided by carbohydrate pool formed in carboxylase phase of photosynthetic oscillations and is enriched with $^{12}C$ due to carbon isotope effect in ribulosebisphosphate (RuBP) carboxylation. Carbon source for the synthesis of the WSOM fraction components is predominantly linked with carbohydrate pool formed in oxygenase phase of photosynthetic oscillations. They are enriched with $^{13}C$ due to carbon isotope effect in glycine dehydrogenase reaction.* As *a result, IOM fraction is always more enriched in $^{12}C$ in comparison with WSOM fraction. IOM fraction appears to be the main source of organic matter for the phloem sap. The organic substances of the sap are mainly used by plants to synthesize heterotrophic organ biomass thus determining the $^{13}C$ enrichment of heterotrophic organs (roots, seeds, wood) of plants in relation to autotrophic (leaves, needles) ones. In accordance with CMOM, the variations of $\delta^{13}C$ values of WSOM and IOM fractions could be used for photosynthesis and assimilate transport and partitioning studies in real-time mode during the day.*

*Key words: carbon isotope characteristics, oscillatory model of photosynthesis, duirnal dynamics, water-soluble and water-insoluble foliar fractions, phloem sap.*

The application of isotope data within a conceptional framework based on carbon metabolism oscillatory model (CMOM) turned to be an effective instrument to study and explain various biological and ecological problems. They reflect plant response to stress conditions [10], greenhouse effect and global reasons for climate change on the Earth [15, 16], photosynthesis and assimilate transport in conifers in the vegetation period [25], dependence of wheat productivity on environmental factors [17], salinity effect on isotope characteristics of plants of various types [19], etc.

Recently, A. Gessler and co-authors [7] have published a very comprehensive research in which they had studied diurnal variations of some isotopic characteristics in castor bean plants *(Ricinus communis),* including $\delta^{13}C$ of water-soluble organic matter (WSOM) and water-insoluble organic matter (IOM) of leaves, stem and phloem sap organic matter. They have interpreted daily variations of the characteristics mentioned above on the basis of steady-state model [23].

As it was shown before [15, 25], both models result in conflicting conclusions on many aspects of plant physiology due to differences of initial postulates. E. g., the nature and intramolecular isotopic pattern of metabolites, temporal organization of cell processes, nature of isotopic discrepancies of autotrophic and heterotrophic organs in plants, other problems of assimilate synthesis and transport are explained quite differently.

The experimental data on diumal variations of the above isotope characteristics in castor beans obtained by A. Gessler and co-workers [7] provide important information on the temporal organization of photosynthesis but, in our opinion, it cannot be extracted and explained properly by means of a steady-state model. Therefore, we tried to reconsider the data obtained through an oscillatory model in order to elucidate additional information concerning assimilate partitioning in this experiment and to illustrate the possibilities that OMCM application opens for photosynthesis studies.

The principal differences of the initial postulates of both concepts should be emphasized first. Accepting, in accordance with the steady-state model, that Calvin cycle functions in a permanent regime, Gessler and co-workers [7], following Tcherkez et al. [23], claimed that $^{13}C$ enrichment of C-3 and C-4 atoms in glucose resulted from carbon isotope fractionation in aldolase reaction of the cycle; and $^{12}C$ enrichment of C-l atom emerged in transketolase reaction of cycle due to the exchange of C-l and C-3 atoms at the repeating cycle turns. However, there are no other experimental arguments in favor of carbon isotope fractionation in the cycle besides the fact of glucose isotope heterogeneity as it is, that has another explanation [15].

Oscillatory concept based on the label randomization in the cycle, observed in the experiments with $^{14}C0_2$ [4], claims that no carbon isotope fractionation occurs in Calvin cycle. J.M. Hayes supports this idea when compares Calvin cycle work with an isotope mixer [9]. Even in the cases when isotopically different substrates would feed Calvin cycle, transketolase and transaldolase reactions would shuffle atoms and isotope distribution in the cycle metabolites would become uniform after some turns [12, 15].

As a result, an oscillation model gives quite different interpretation for isotope heterogeneity of glucose. Accepting photosynthesis as oscillations consisting of the assimilation phase (carboxylase phase of Rubisco function) and the photorespiration phase (oxygenase phase of Rubisco function), it explains uneven carbon isotope distribution of glucose as a result of isotope fractionation in glycine decarboxylation reaction during the oxygenase phase of cycle oscillations [12, 15].

The reason for isotope discrepancies in different fractions and organs of plant also has different explanation within the frameworks of both concepts. According to the steady-state hypothesis, these discrepancies arise in metabolic reactions following RuBP carboxylation in $C0_2$ assimilation. Like G. Tcherkez and co-authors [23], Gessler et al. [7] consider that during the light period the reserve starch pool is formed. As a result of destruction in the dark, the pool generates sucrose enriched in $^{13}C$. On the other hand, triosophosphates formed in Calvin cycle in the light and exported from chloroplasts into cytoplasm, have "light"' carbon isotope composition and form glucose enriched in $^{12}C$. Thus, according to the authors, sucrose pools arising during the light and dark periods and bearing different carbon isotope ratio provide the basis for circadian rhythms and, in particular, give rise to the observed carbon isotope differences for WSOM and IOM foliar fractions of castor beans.

However, the authors' assertion that the initial starch destruction is followed by carbon isotope effect resulting in $^{13}C$ enrichment of sucrose contradicts with experimental data of P.H. Abelson and T.C. Hoering [1] who did not find any noticeable effect of C isotope fractionating during starch destruction up to its transformation into pyruvate (a product of glucose destruction in Embden - Meyerhof - Pamas pathway).

On the contrary, in accordance with the oscillatory hypothesis, two isotopically different carbohydrate pools really emerge in photosynthesis, but as a result of oscillations, since in their different phases, carbon isotope fractionation with opposite trends occurs [12, 15]. In accordance with this concept, the reason for isotope discrepancies in WSOM

and IOM of castor beans leaf fractions results from their connection with these two pools and temporal organization of photosynthetic metabolism, as well. For a better insight, take into consideration that IOM leaf fraction predominantly consists of lipid, protein and lignin components which are produced on the basis of "light'' carbon pool synthesized in carboxylase phase of Rubisco function, whereas WSOM fraction mainly consists of components (labile carbohydrates, organic acids, some amino acids) synthesized in oxygenase phase of Rubisco function. Although it should be marked (see below) that some "light" components can participate in IOM fraction formation, too.

Prior to the analysis of $5^{13}C$ diurnal variations of castor beans characteristics obtained by Gessler and co-authors [7] within the frameworks of the oscillation model, it is crucial to outline the problem. According to the model, carbon metabolism in photosynthesis is an oscillating process. Carbon fluxes in the Calvin cycle change their direction depending on whether Calvin cycle works in the direction of $C0_2$ assimilation and glucose synthesis or in the direction of photorespiration that partially oxidizes substrate formed in assimilation phase and produces $C0_2$. This cycle state switching is due to the dual ability of Rubisco to function either as carboxylase, or as oxygenase [18,21,22]. It is essential that in each phase carbon isotope effects opposite in their sign appear. As a result, two carbohydrate pools different in carbon isotope composition are formed.

Addressing Gessler and co-authors' work [7], let us first see the ranges of diurnal variations of the examined isotope characteristics in castor beans. They are shown in Figure 1. At each vertical segment depicting the range of $\delta^{13}C$ variations, the maximum and minimum points corresponding to light and dark periods as well as the point corresponding to average $\delta^{13}C$ value for 24 hours, are given.

As it follows from Figure 1, the ranges of $\delta^{13}C$ variations of the foliar WSOM and IOM fractions do not overlap. The carbon of foliar IOM fraction is enriched in $^{12}C$ relative to the carbon of foliar WSOM fraction. The range of $\delta^{13}C$ of phloem sap organic matter variations almost completely coincides with the range of $\delta^{13}C$ characterizing IOM fraction and only small part of it overlaps with the range of $\delta^{13}C$ variations of WSOM fraction. The main issue in question is the cause for $^{12}C$ enrichment of WSOM fraction in relation to IOM fraction.

In the frameworks of the oscillatory model and considering the known plant cell biochemistry, the difference in the ranges of the foliar WSOM and IOM fractions has a simple interpretation. Most of the IOM fraction components of lipid, protein and lignin origin are synthesized at the expense of carbon feeding glycolytic chain. The latter is bound to "light" carbohydrate pool and is produced in carboxylase phase of Rubisco function. This explains the enrichment of IOM fraction in $^{12}C$. Most of the cell structures, e. g., enzymes, membranes are built of these components.

The great amount of WSOM fraction components are labile carbohydrates, organic acids and other photorespiratory products. They are derived in the oxygenase phase and bound to "heavy" carbohydrate pool [5,12]. That is why they are enriched in $^{13}C$. The extent of $5^{13}C$ enrichment depends on a number of carbon flux turns in photorespiratory loop. The carbon of this pool is in part exported with phloem sap to the points where the growth of heterotrophic tissues occurs. This is the reason for the enrichment of heterotrophic organs in $^{13}C$ as compared with that of autotrophic ones. Many investigators have observed this fact long ago but have failed to give a satisfactory explanation so far [3, 6, 8, 24].

Figure 1 shows that the diurnal variation range of $\delta^{13}C$ for WSOM fraction and phloem sap almost coincide. It should be expected, as it was shown by A.A. Kursanov [20], that labile sugars, being the prevalent component of the "heavy" pool, are not only main transport agents, but also the key carbon source for plants' heterotrophic tissues. Thus,

the coincidence of the $\delta^{13}C$ diumal variations of WSOM fraction and phloem sap organic matter composition supports the above assertion and apparently is a reflection of that fact. The observed carbon isotope differences between the WSOM and the IOM leaf fractions clearly indicate their link with the assumed oscillations.

WSOM fraction, as shown further, includes some components whose synthesis is bound to the pool formed in carboxylase phase of oscillations, but, as derived from the averaged values of $\delta^{13}C$ for the whole fraction, their contribution is insignificant (Figure 1).

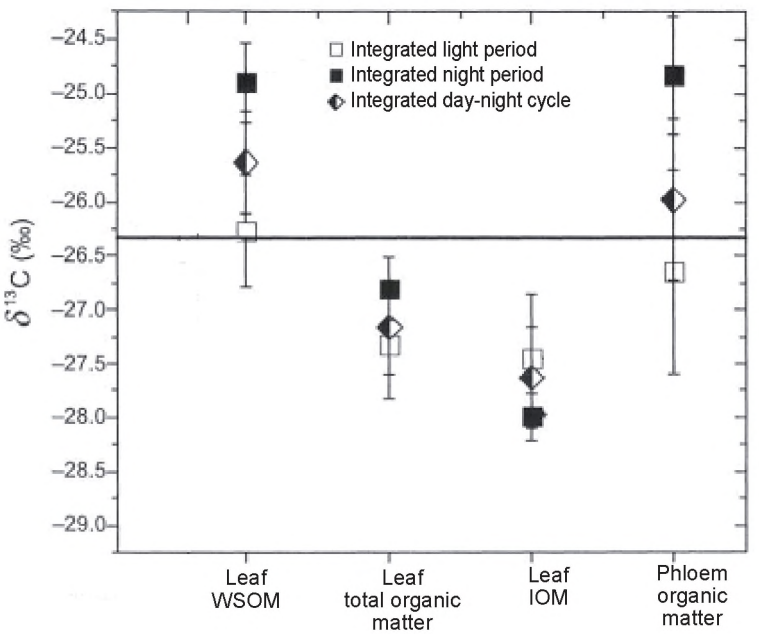


**Fig-1** . The range of $5^{13}C$ diurnal variations of foliarwater-soluble organic matter (WSOM), total and water-insoluble organic matter (IOM) as well as the phloem sap organic matter for castor bean *(Ricinus communis)* The figure was replotted from the paper by A. Gessler et al. [7]

Figure 2 shows sampling points on the castor beans plant where leaf samples from the canopy and stem samples along the shoot were taken [7].

Further on, it seems worthwhile to consider experimental dynamics of $\delta^{13}C$ diumal variations of WSOM fraction, observed by Gessler and co-authors [7]. As per Figure 3a, each point characterizing $\delta^{13}C$ of the foliar WSOM fraction and disposed at different height in canopy has its own specific $\delta^{13}C$ value. According to the oscillation concept, it means that the specific conditions of photosynthesis at each point in the canopy are determined by various parameters (light intensity, exposure, gas exchange, water availability, etc.). All these parameters change along the shoot in the canopy. Each point (leaf) is characterized by its own diumal curve. Moreover, the curves are similar in shape and synchronous. The leaves corresponding to the higher level of $\delta^{13}C$ enrichment are located at the top of the canopy and vice versa.

All environmental factors mentioned above influence $C0_2/0_2$ ratio and hence affect the balance of $C0_2$ contribution in assimilation and photorespiration thus determining isotope composition of leaf biomass.

In this connection, the study of A.M. Borland and co-authors [5] should be mentioned. A great isotopic difference (about 5-6‰) was found between shaded and exposed leaves of *Clusia minor* L. (C3-CAM plant). The exposed leaves were enriched in $^{13}C$ as opposed to shaded ones. The difference became even greater in the conditions of limited water availability (in dry season). The analysis of these and other results brought about the explanation [10] that the exposure and water deficit stimulate photorespiration and cause the enrichment in $^{13}C$. Therefore, we consider that in case of castor beans, $^{13}C$ enrichment of leaves from the bottom to the top of the canopy could be explained by the increased contribution of photorespiration.

Close similarity and synchronism of $\delta^{13}C$ diurnal curves for WSOM fraction in various leaves (Figure 3a) point out the same character of the processes occurring in them and the existence of the common mechanism of synchronization at the plant level. The analysis of $\delta^{13}C$ diurnal variation curves for WSOM fraction (Figure 3a) reveals that with the morning photosynthesis onset the fraction carbon is getting enriched in $^{12}C$. It reaches maximum at noon and then relative stabilization takes place. The latter continues up to 16:00. Afterwards, a rapid $^{13}C$ enrichment of carbon fraction occurs until it reaches the level corresponding to the $\delta^{13}C$ values of dark period.

No distinct isotopic variations of WSOM carbon were observed in the dark. The oscillatory concept explains such a shape of isotopic curves as follows.

The most interesting fact — an obvious $^{12}C$ enrichment of WSOM fraction observed in the light period - is explained by the entry of some soluble components into the fraction. They are synthesized in the carboxylase phase at the onset of photosynthesis. They mightbelowmolecularweight Calvin cycle products, suchaserythrose phosphates, or phosphoenolpyruvate, which is an intermediate product of lignin synthesis. Both of them are also linked to the pool of "light'' carbohydrates that is formed in carboxylase phase of oscillations.

To distinguish two carbon fluxes associated with "light" and "heavy" carbohydrate pools, one flux was named assimilatory flux, while the other is photorespiratory one [10]. Low-molecular metabolites of glycolytic chain synthesized there in gluconeogenetic phase in the light period appear to be another source of $^{12}C$-enriched ("light")

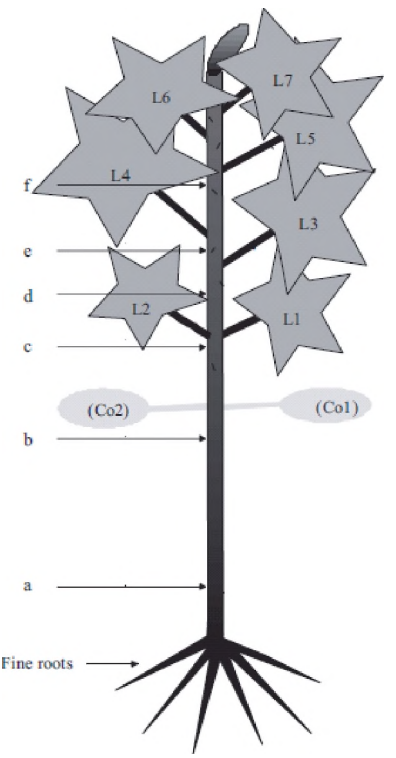


**Fig. 2.** The scheme of a castor bean plant *(R. communis)* with places of sampling indicated. Carbon isotope composition of WSOM and IOM fractions was separated from fully developed leaves (L1-L7). Samples of phloem sap organic matter were taken along the stem (a-f) at six time points during a diel course. For the analysis of stem's total organic matter, samples were taken from the same six positions. The figure was replotted from Gessler et al. [7]

components. They are soluble and also can participate in WSOM fraction. However, it should be emphasized that in spite of some contribution of "light" components associated with assimilatory flux to the WSOM fraction, the total carbon of the fraction always retains its "heavy" isotope composition. As one can see from Figure 1, the ranges of WSOM and IOM do not overlap anywhere and the fractions are easily distinguishable from one another.

Due to the pronounced differences in $\delta^{13}C$ diurnal curve shapes in the light and dark periods and due to their reproducible character in time the circadian rhythms may be readily displayed. This is a crucial aspect since it might be used in the studies of the photosynthesis to follow its diurnal dynamics.

Let us decipher $\delta^{13}C$ diurnal curves for the IOM fraction the same way as before. From Figure 3b, one can see the same periodicity in the curve behavior as in the previous case. It is not surprising since the external factors determining curves' behavior in both cases appeared to be the same. Diurnal dynamics for each leaf level in the canopy is described by similar and separate curve. At the top level of the canopy, the curve corresponds to greater $^{13}C$ enrichment of IOM fraction as compared to the curve corresponding to the bottom level of the canopy.

The ranges of $\delta^{13}C$ diurnal variations between the curves at the top and at the bottom of the canopy for IOM and WSOM fractions are clearly distinct. The range for WSOM carbon is much greater than that for IOM carbon. It can be interpreted through the fact that WSOM carbon is impacted by both carbon isotope effect of $C0_2$ assimilation and that of photorespiration whereas IOM carbon is only influenced by the isotope effect of $C0_2$ assimilation.

The amplitude of $\delta^{13}C$ variations (Figures 3a and 3b) is another feature differing diurnal curves for WSOM and IOM fractions. The range for WSOM curves is much greater than that for IOM ones. As per the oscillation model, most of WSOM fraction components are synthesized via substrates of the Calvin cycle in the carboxylase phase when transketolase and transaldolase reactions randomize atoms and alleviate isotopic discrepancies.

Comparing $\delta^{13}C$ diurnal curves for WSOM and IOM fractions (Figures 3a and 3b), one can reveal an extra difference in curves' behavior. It refers to the inverse character of the curves. The shifts of $\delta^{13}C$ diurnal curves for WSOM fraction precisely correspond to those of IOM fraction but in the opposite direction, i.e. isotopic changes are of opposite signs. The idea of a reciprocal relationship between $C0_2$ assimilation and photorespiration was put forward in the work of A.A. Ivlev and co-workers [10]. Later it was experimentally confirmed in the work of M.J. Andre [2] as a relationship between $C0_2$ consumption in assimilation and 02 consumption in photorespiration. It has been named the "mirror effect".

Besides the leaf fractions, Gessler and co-workers [7] have examined diurnal isotopic variations of the stem carbon and organic carbon of phloem sap (Figures 4a and 4b). Sampling was done at various heights along the stem.

The analysis of $\delta^{13}C$ diurnal curve dynamics characterizing stem carbon (Figure 4a) shows that it resembles the behavior of $\delta^{13}C$ diurnal curves for the foliar WSOM fraction. They have the same range of $\delta^{13}C$ variations and reveal distinct enrichment in $^{12}C$ at the onset of photosynthesis. Each sampling point is defined by a separate curve. However, the curves' shapes are found to be somewhat different from those describing foliar WSOM fraction. There is no stability interval between 12:00 and 16:00 and a maximum of $^{12}C$ enrichment occurs at 19:00 instead of 12:00. These peculiarities of the diurnal curves are explained by the oscillation concept in the following way. Stem tissues include both

WSOM and IOM fractions. The addition of IOM fraction results in different diurnal dynamics in comparison to the foliar WSOM fraction. The same explanation works for a slight shift of $\delta^{13}C$ values for the stem carbon to more negative values.

It is interesting to note that the diurnal curve for the point "a" at the stem base (Figure 1) corresponds to the most $^{12}C$-enriched isotope level whereas the diurnal curve corresponding to the fine roots, disposed even lower than the point "a", fit into the most $^{13}C$-enriched level (Figure 3a). It entirely confirms the previous conclusion that heterotrophic tissues of plants (fine root tissue in particular) are synthesized mainly at the expense of WSOM fraction enriched in $\delta^{13}C$.

The organic matter of phloem sap mainly represents the part of WSOM fraction with admixture of soluble components enriched in $^{12}C$ (see above) exported from leaves. That is why the dynamics of $\delta^{13}C$ diurnal curves have much in common with those of the diurnal curves for the foliar WSOM (Figure 4a). First of all, there is a distinct enrichment in $^{12}C$ in response to the onset of photosynthesis. The major difference between the diurnal curves for the foliar WSOM fraction and those for phloem sap is as follows. In case of the phloem sap, the diurnal curves for various points on the stem dispose very close to each other whereas in case of the foliar WSOM, the range of the diurnal curve variations corresponding to various points is much wider (compare Figures 3a and 4b).

A very limited range of $\delta^{13}C$ diurnal curve variations for the phloem sap is an evidence of good mixing of assimilates coming from different leaves. It means that at the given moment carbon isotope composition of the phloem sap along the stem is the same.

All curves are similar in shape and have a common peak corresponding to $^{12}C$ enrichment at 12:00. It may evidence for a good synchronization of the metabolite syntheses in various leaves with the assimilate transport.

It should also be noted that

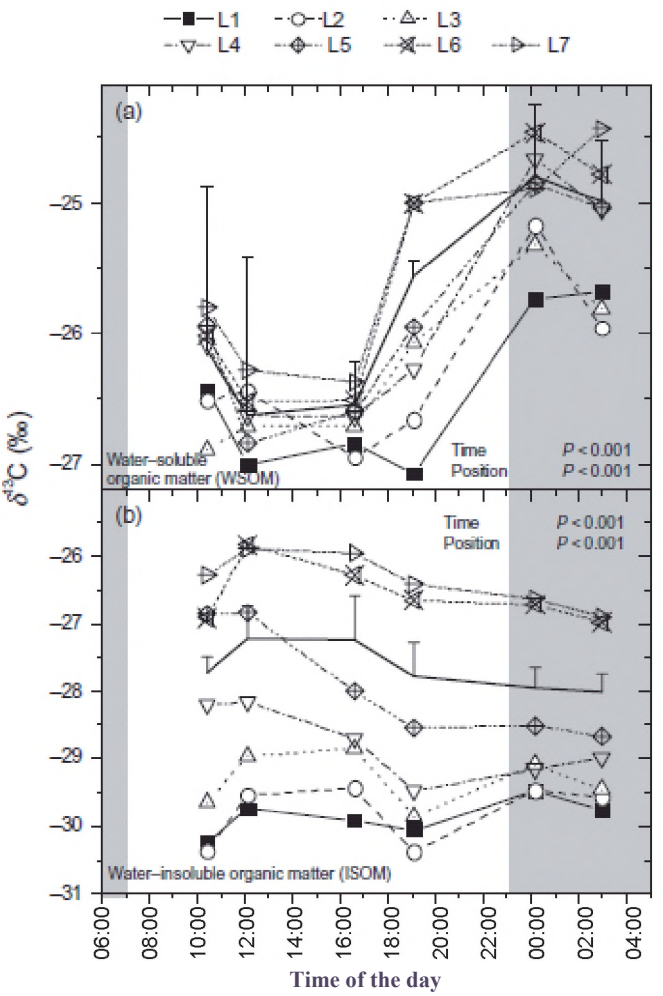


**Fig. 3.** $\delta^{13}C$ Diurnal variations of foliar water-soluble organic matter (WSOM) (a), and water-insoluble organic matter (IOM) (b) in all seven leaves (L1-L7) of *R. communis*. The solid curve indicates the canopy weighted mean values. The figure was replotted from Gessler et al. [7]

the amplitude of $\delta^{13}C$ diumal curve variations for the phloem sap is slightly wider than the corresponding range for the foliar WSOM fraction and the range itself is shifted to the "light" $\delta^{13}C$ values. The latter is a result of WSOM fraction mixing with the soluble low-molecular components synthesized in the carboxylase phase of photosynthetic oscillations.

The only aspect that remains unclear is why $\delta^{13}C$ value of the phloem sap from the point "e" does not follow this common rule. Its diumal curve does not coincide with the other curves.

## Conclusions

The use of the oscillation model of photosynthesis for the interpretation of $\delta^{13}C$ diumal curves for WSOM and IOM fractions of leaves, for the total carbon of the stem at different points and for the phloem sap, observed by A. Gessler and co-workers [7], makes it possible to conclude the following:

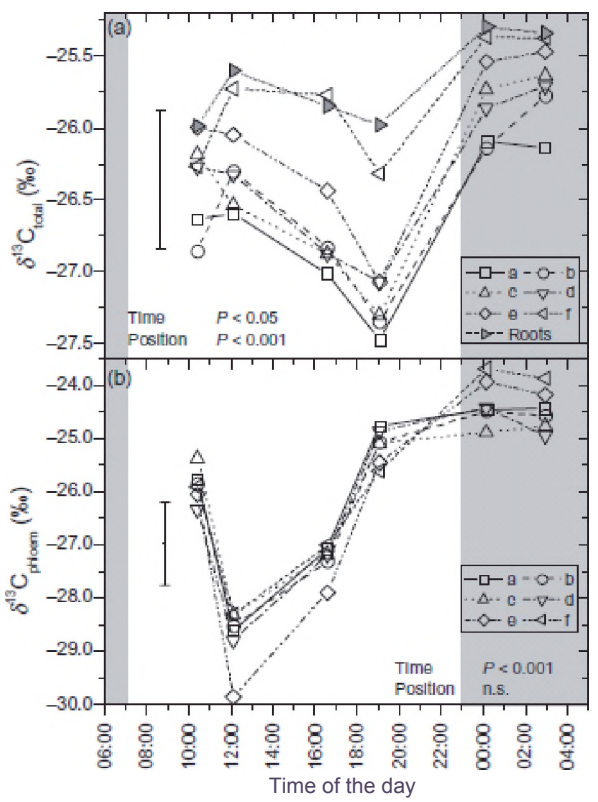


**Fig. 4.** $\delta^{13}C$ Diurnal variations of stem and fine roots total carbon (a) and phloem sap organic matter (b) along the axis (a-f) of *R. communis* during the diel course. Position "a" denotes a sampling site at the stem base; "f" is the uppermost position on the stem. The figure was replotted from Gessler et al. [7]

1. The carbohydrate pool formed in the carboxylase phase of photosynthetic oscillations is the basic carbon source for the leaf IOM fraction synthesis. As a result, IOM carbon is enriched in $^{12}C$.

2. The carbohydrate pool formed in the oxygenase phase of the photosynthetic oscillations is the basic carbon source for the leaf WSOM fraction synthesis. As a result, WSOM carbon is enriched in $^{13}C$.

3. At the onset of photosynthesis, a part of the low-molecular soluble components synthesized in the carboxylase phase of photosynthetic oscillations with their "light" carbon isotope composition falling into WSOM fraction causing its enrichment in $^{12}C$ which reaches maximum at noon and then decreases up to the end of photosynthesis. It makes it possible to use $\delta^{13}C$ diumal curves for studies of WSOM fraction dynamics in photosynthesis.

4. The phloem sap is predominantly formed at the expense of the foliar WSOM fraction and its carbon isotope

composition is enriched in $^{13}C$ as well. Since the phloem sap supplies substrates for the synthesis of heterotrophic tissues, it explains the $^{13}C$ enrichment of heterotrophic plant organs as compared to autotrophic ones. $\delta^{13}C$ diumal curves for the phloem sap, like those for the foliar WSOM fraction, reflect the impact of mixing with soluble components synthesized in the carboxylase phase and enriched in $^{12}C$. Hence, they also may be used in the research of photosynthesis dynamics.

5. Bearing in mind the relative methodological simplicity of the techniques for the phloem and foliar WSOM fraction sampling, the $\delta^{13}C$ diumal curves may be used as a fine instrument for the studies of the circadian rhythm in photosynthesis in the real-time mode.

6. Carbon isotope composition of the phloem sap may be also used in assimilate transport studies.

**References**


1. *Abelson P.H., Hoering T.C.* Carbon isotope fractionation in fonnation of amino acids by photosynthetic organisms // Proc. Nat. Acad. Sci. USA. 1961. Vol. 47. P. 623-629.

2. *Andre M.J.* Modelling 180 and 160 unidirectional fluxes in plants: 1. Regulation of preindustrial atmosphere // BioSystems. 2011. Vol. 103. P. 239-251.

3. *Batheller C., Badeck F-W, Couzi Ph., Harscoet S., Mauve C.* Divergence in $\delta^{13}C$ of dark respired C02 and bulk organic matter occurs during transition between heterotrophy and autotrophy in *Phaseolus vulgaris* plants // New Phytologist. 2008. Vol. *Ill.* P. 406-418

4. *Bassham J.A., Calvin M.* The Path of Carbon in Photosynthesis. Prentice-Hall, Englewood Cliffs, New Jersey 1957. P. 39-66.

5. *Borland A.M., Griffiths H., Broadmeadow M.S., Fordham M.C., Maxwell C.* Carbon isotope composition of biochemical fractions and the regulation of carbon balance in leaves of the C3-Crassulenean acid metabolism intermediate *Clusia minor* L. growing in Trinidad // Plant Physiol. 1994. Vol. 105. P. 493-501.

6. *Cernusak LA., Tcherkez G., Keitel C., Cornwell W. K, Santiago L.S., Knohl A., Barbour MM., Williams D.G., Reich P.B., Ellsworth D.S., Dawson T.E., Griffiths H.G., Farquhar G.D., Wright I.J.* Why are non-photosynthetic tissues generally $^{13}C$ enriched compared with leaves in C-3 plants? Review and synthesis of current hypotheses // Funct. Plant Biol. 2009. Vol. 36. P. 199-213.

7. *Gessler A., Tcherkez G., Peuke A.D., Ghashghaie J.G., Farquhar G.D.* Experimental evidence for diel variations of the carbon isotope composition in leaf, stem and phloem sap organic matter in *Ricinus communis //* Plant. Cell Environ. 2008. Vol. 31. P. 941-953.

8. *Gessler A., Keitel C., Kodama N., Weston Ch., Winters A J, Keith H., Grice K, Leuning R., Farquhar G.D.* $\delta^{13}C$ of organic matter transported from the leaves to the roots in *Eucalyptus delegatensis:* short-term variations and relation to respired $C0_2$ // Funct. Plant Biol. 2007. Vol. 34. P. 692-706.

9. *Hayes J.M.* Fractionation of carbon and hydrogen isotopes in biosynthetic processes // In: Review in mineralogy and geochemistry Vol. 43. Stable isotope geochemistry / Eds. J.W. Valley, D.R. Cole / Mineralogical Society of America. Washington DC, 2001. P. 226-275.

10. *Ivlev A.A.* Contribution of photorespiration to changes of carbon isotope characteristics in plants affected by stress factors // Russ. J. Plant Physiol. 2004. Vol. 49. № 2. P. 271-280.

11. *Ivlev A.A.* Isotope effect in glycine dehydrogenase reaction is the cause for intramolecular carbon isotope heterogeneity of starch glucose synthesized in photorespiration // Biophysics. 2005. Vol. 50. P. 1079-1086.

12. *Ivlev A.A.* Isotope fractionation and cell mechanisms of carbon metabolism in a photosynthesizing cell. Moscow: Publlishing house of RSAU-MTAA, 2008. 74 p.

13. *Ivlev A.A.* Oscillatory character of carbon metabolism in photosynthesis: arguments and facts //Biol. Bull. 2010. Vol. 37. P. 211-220.

14. *Ivlev A.A.* Possible reasons for climate change on the Earth // Adaptation of Russia's agriculture to varying weather and climate conditions. Moscow: Publlishing house of RSAU-MTAA, 2010. P. 85-89.

15. *Ivlev A.A.* Oscillatory nature of metabolism and carbon isotope distribution in photosynthesizing cells // Photosynthesis - fundamental aspects / ed. M.M. Najafpour. Croatia: Intech Publishers, 2012. P. 341-366.

16. *Ivlev AA,, Voronin VI.* The mechanism of carbon isotope fractionation in photosynthesis and carbon dioxide component of the greenhouse effect // Biol. Bull. 2007. Vol. 34. P. 603-609.

17 .*Ivlev A.A. DubinskvA.Ju., Pichouzkin VI.* Metabolic carbon isotope effects and production process in cultivated plants in the light of oscillation concept of photosynthesis // Biol. Bull, (in press)

18. *Ivle\'A.A., Igamberdiev A.Y, Dubinskv A.Yu.* Isotopic composition of carbon metabolites and metabolic oscillations in the course of photosynthesis // Biophysics. 2004. Vol. 49. Suppl. 1. P. 3-16.

19. *Ivlev A.A., Pichouzkin VI., Tarakanov I.G.* The salinity effect on carbon isotope composition of plant biomass // Advanced Study in Biol, (in press)

20. *Kursanov A.A.* Assimilate transport in plants. Moscow: Nauka, 1976. 644 p.

21. *Roussel M.R., Igamberdiev A.Y.* Dynamics and mechanisms of oscillatory photosynthesis //BioSystems. 2011. Vol. 103. № 2. P. 230-238.

22. *Roussel M.R., Ivlev A.A., Igamberdiev A.Y.* Oscillations of the internal C02 concentration in tobacco leaves transferred to low C02 // J. Plant Physiol. 2007. Vol. 164. P. 1188-1196.

23. *Tcherkez G,, Farquhar G,, Badeck F,, Ghashghaie J.* Theoretical consideration about carbon isotope distribution in glucose of C3-plants // Funct. Plant Biol. 2004. Vol. 31. P. 857-877.

24. *Terwilliger I H u a n g J.* Heterothrophic whole plant tissue show more $^{13}C$ - enrichment than their carbon source//Phytochemistry. 1996. Vol. 43. P. 1183-1188.

25. *Voronin VI., Ivlev A.A., Oskolkov V* Boettger T. Intra-seasonal dynamics in metabolic processes of $^{13}C/^{12}C$ and $^{18}0/^{16}0$ in components of Scots pine twigs from southern Siberia interpreted with a conceptual framework based on the Carbon Metabolism Oscillatory Model // BMC Biology. 2012. Vol. 12. P. 76-83.

# ИНТЕРПРЕТАЦИЯ СУТОЧНЫХ ВАРИАЦИЙ ИЗОТОПНЫХ ХАРАКТЕРИСТИК РАСТЕНИЙ В РАМКАХ ОСЦИЛЛЯЦИОННОЙ МОДЕЛИ ФОТОСИНТЕЗА НА ПРИМЕРЕ КЛЕЩЕВИНЫ *(RICINUS COMMUNIS* L.)

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*Аннотация: в рамках осцилляционной концепции фотосинтеза анализируется суточная динамика величин $\delta^{13}C$ углерода фракции водорастворимого органического вещества (ВОВ) и фракции водонерастворимого органического вещества (ВНОВ) листа клещевины, общего углерода стебля и органического вещества сока флоэмы, изученных в экспериментальной работе Гесслера с соавт. [7]. Показано, что источником углерода для синтеза компонентов фракции ВНОВ является углеводный фонд, возникший в карбоксилазной фазе фотосинтетических осцилляций и обогащенный изотопом $^{12}C$ благодаря изотопному эффекту углерода в реакции карбоксилирования рибулозобисфофата (РиБФ). Преимущественным источником углерода для синтеза компонентов фракции ВОВ является углеводный фонд, образовавшийся в оксигеназной фазе фотосинтетических осцилляций и обогащенный $^{13}C$ бла-*

*годаря изотопному эффекту глициндегидрогеназной реакции в этой фазе осцилляций. В итоге фракция ВНОВ всегда несколько обогащена изотопом $^{12}C$ относительно фракции ВОВ. Фракция ВОВ является главным источником органических веществ сока флоэмы. Эти вещества используются растением для синтеза биомассы нефотосинтезирующих (гетеротрофных) органов. В этом, по нашему мнению, главная причина наблюдаемой обогащенности гетеротрофных органов растений (корней, семян, древесины) изотопом $^{13}C$ относительно автотрофных (лист, хвоя). Различия изотопного состава углерода фракций ВНОВ и ВОВ могут быть использованы для изучения фотосинтеза и транспорта ассимилятов в режиме реального времени суток.*

*Ключевые слова: изотопные характеристики углерода, осцилляторная модель фотосинтеза, суточная динамика, водорастворимая и водонерастворимая фракции листа, сок флоэмы.*

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