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POSSIBILITY OF HIGHER GREEN PLANTS HETEROTROPHIC NUTRITION

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SUMMARY

The latest study proposed a new look into the nutrition of higher green plants as a base for a brief analytical review of the scientific literature. The paradigm originated based on the utilization and absorption of organic compounds, which comprise the soil organic matter of green vascular plants. From the trophological point of view, green vascular plants are facultative heterotrophic (mixotrophic) organisms. Heterotrophic plant feeding is an additional feeding that makes plants more resistant to adverse environmental conditions. The plants' consumption and assimilation of organic compounds have a direct impact on the biochemical and biophysical processes occurring in these vascular plants. As a result of organic compound utilization, plant growth and development accelerate. The natural consequence of these provisions: in the process of the biological carbon cycle in ecosystems, the circulation of organic compounds (universal structural and functional units), which can be used repeatedly at various trophic levels of ecological systems (to build primarily plant biomass), plays an essential role. The heterotrophic feeding pathway of green vascular plants is one of the auxiliary ways to regulate plant productivity.

Keywords: Higher green plants, mixotrophy, heterotrophy, rhizoexudates, soil organic matter, mycotrophy, rhizosphere biota, phytosymbionts

Key findings: Green vascular plants are facultative heterotrophs, but more precisely, mixotrophs. Green plants' nutrition seems inherited from the early stages of biosphere evolution. The concept of organic plant nutrition should make it possible to restore the functioning of the soil-plant trophic system and can serve as a theoretical basis for the justification of the biological farming system.

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INTRODUCTION

The fundamental question of plant physiology and its applied sciences is linked to plant nutrition and its functional dependence on environmental conditions (Kravkov, 1978). Plant nutrition has always received study consideration (Linovsky, 1846; Pryanishnikov, 1963; Krupenikov, 1981). Thus, in ancient and medieval times, plant nutrition resembles animal nutrition. The plants, assisted by the roots, can absorb available nutrients from the soil. Then the plants process these nutrients or

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depolymerize—large organic molecules get digested. At that time, no valid theories on plant nutrition flourished. Suggestions cropped up that soil fertility is a special substance found in the soil or the ’fat’ of the ground (*terrae adeps*). In the 16th–18th centuries, scientists sought to explain the effect of organic fertilizers on plant growth and development. Thus, B. Palissy (1510–1589) suggested that pet manure has a beneficial effect on the plants due to its nitrogen compounds content. In turn, O. de Serres (1539–1619) reasoned that the favorable effect of manure on plants is explained by its warmth. From the 17th century to the middle of the 18th century became the period for an intensified search for the ’growth principle’ of plants. Plants were also originally thought to consume only water from the soil (the so-called ’water’ hypothesis of plant nutrition). This assumption came about due to the well-known experiments of J.B. van Helmont (1580–1644) and H.L. Duhamel du Monceau (1700–1782). At the end of the 17th century, J. Woodward (1833–1884) concluded that plants need some soil components, and not only water. Later, J. Tull (1674–1741) established that ’small earth-like particles’ serve as food for plants, and air and water help to isolate these particles from the soil (Krupenikov, 1981).

In the 18th century, a base was established for the 'humus' nutrition hypothesis of plants (Waksman, 1937; Krasilnikov, 1958; Krupenikov, 1981). The plant humus nutrition hypothesis brought great success for agriculturists because it was well-supported by practice. The hypothesis proved green vascular plants feed on organic compounds found in manure and soil humus. The idea of J.A. Külbel (1741) was also supported by the Swedish scientist, J.G. Wallerius (1709–1785) who, based on his experimental data, concluded that humus (*nutritiva*) is the food for plants, and the other soil components (*instrumentalia*) play a supporting role, i.e., clay helps to fix and retain organic matter in the soil, and lime helps dissolve the certain components of soil organic matter (SOM). The Russian agrarian scientist, I.I. Komov (1788), also argued that organic matter is necessary for plants just like it is necessary for animals.

The knowledge of plant nutrition prospered during the period from the end of the 18th century to the beginning of the 19th century (Waksman, 1937; Krasilnikov, 1958; Krupenikov, 1981). Thus, in 1771, J. Priestley (1733–1804) discovered the ability of green plants to secrete oxygen in the light, which began the photosynthesis study. In 1782, J. Senebier (1742–1809) called the carbon dioxide consumption by plants in light ’carbon nutrition’. However, this scientist believed that plants consume carbon dioxide from the soil solution by their roots, but not from the air. At the end of the 18th century, J. Ingenhaus (1730–1799) found that certain gaseous substances enter the leaves from the air, from which plants synthesize organic matter in light. At the turn of the 18th and 19th centuries, the Swiss Plant Physiologist N.T. de Saussure (1767–1845) finally proved that plants synthesize their organic substances from carbon dioxide and water and excrete oxygen. He also discovered respiration in plants and presented the theory of gas exchange during photosynthesis stoichiometry. With this, N.T. de Saussure believed that plants consume nitrogen from the air and soil, and biota litter in the form of ammonia and other water-soluble compounds of this chemical element, and in turn, the inorganic substances are extracted by plants mainly from the soil.

Despite the discovery of photosynthesis, the idea that humus (SOM) is a source of carbon for plants sustained its existence in the 19th century (Waksman, 1937; Guminsky, 1968; Gold *et al*., 2008). Prof. A.D. Thaer, an agronomist at Berlin University, Germany played a significant role in the development and scientific substantiation of the humus plant nutrition hypothesis. He believed that since humus is the product and state of life, thus, without humus, life is impossible. Prof. A.D. Thaer's hypothesis coexisted peacefully with the hypothesis of carbon nutrition of plants due to photosynthesis. In fact, the hypothesis of the plant humus nutrition was accepted by such outstanding scientists of the 17th–18th century in the likes of J.J. Berzelius, E. Mitscherlich, and Sir H. Davy. Interestingly, one of the discoverers of photosynthesis, N.T. de Saussure experimentally established the flow of humic substances into plants. The researcher believed that when humic substances penetrate the roots of plants, they are chemically modified and thus assimilated (Waksman, 1937; Guminsky, 1968; Gold *et al*., 2008). The hypothesis of humus nutrition of plants found its followers in Russia, as well. They include Prof. M.G. Pavlov at Moscow University, physicist and Doctor of Medicine, as well as the Chemist H.R. Hermann at Moscow, who also believed that plants were nourished by a ’humus extract’ (Waksman, 1937).

In the 1940s, the works of two eminent scientists, J.B.J.D. Boussingault and J. von-

Liebig appeared. Their works disproved the hypothesis concerning the plant humus nutrition that caused a crushing blow but did not eliminate it (Waksman, 1937). Despite that, the studies of N.T. de Saussure and J.B.J.J. Bussengo receive support from the brilliant arguments of J. von-Liebig (1803–1873). Likewise, in support of de Saussure and Bussengo studies, the works with aquatic cultures of other naturalists, showed that plants can synthesize their constituent organic substances in the absence of organic compounds in the nutrient medium (Gold *et al*., 2008; Chozin *et al*., 2017; Bhat *et al*., 2018; Gaballah *et al*., 2021). Nevertheless, the idea that plant nutrition is closely related to soil organic matter continued to exist until the end of the 19th century and found followers even in the 20th and 21st centuries (Krasilnikov, 1958; Guminsky, 1968; Popov, 2004; Gold *et al*., 2008).

Why do photosynthetic organisms, such as green vascular plants, need to consume and assimilate organic compounds? What are the higher plants: obligate autotrophs or mixotrophs? In this connection, the study sought to characterize the significance of consumption and assimilation of organic compounds by green vascular plants based on the analysis of the factual material presented in the modern scientific literature and the theoretical positions of Academician Ugolyov (1991).

ANALYSIS OF THE PROBLEM

From the end of the 19th century to the present, an enormous volume of facts on the consumption of organic compounds of natural, artificial, and even synthetic origins by higher green plants existed (Popov, 2004, 2006). At the start of the 20th century, Shulov (1913) created a few variants of the vegetation method (methods of fluid solutions and sterile cultures), where he proved the ability of higher plant roots to assimilate organic compounds, including some proteins. Soviet academician Palladin (1924), referring to the nutrition of green vascular plants, believed that plants can feed on existing organic compounds. Moreover, such nutrition can go alongside assimilating carbon from the atmosphere. Krasilnikov (1958) wrote that it is difficult to agree with the concept that plants throughout their evolutionary history, tapping their roots for SOM, would not have acquired the ability to assimilate some organic compounds. Smirnov (1970) convincingly demonstrated that isolated roots of higher plants, deprived of assimilating above-ground organs, cannot grow without the organic compounds as a carbon source in the nutrient medium. According to Ivanov (1973), the organic compounds of plant root excretions can be recycled by the same and adjacent plants of the phytocoenosis.

Ugolov (1991) reported that the feeding patterns of living organisms (prokaryotes, protists, fungi, plants, and animals) are common, and there are no completely autotrophic organisms. From the evolutionary point of view (Calvin, 1959; Ugolyov, 1991), specialized photosynthetic organisms, including plants, appeared last after heterotrophs, so green vascular plants must retain some or other pre-existing types of digestion. The most striking example to confirm the heterotrophic nutrition of higher green plants are the insectivorous plants, i.e., *Droseraceae*, *Lentibulariaceae*, *Nepenthaceae*, and *Sarraceniaceae,* as well as the higher phytoparasitic plants, i.e., *Viscaceae*, *Orobanchaceae*, *Cuscutaceae*, and *Rafflesiaceae* (Popov and Chertov, 1993; Nam, 2015). However, in these cases, the presence of extracellular and membrane digestion is particularly evident.

Another example of heterotrophic plant nutrition is mycosymbiotrophism, which is widespread. About 80% of terrestrial plant species are mycotrophic (Calvin, 1959; Selivanov, 1981; Karatygin, 1993; Wang and Qiu, 2006; Akhmetzhanova *et al*., 2012). The arbuscular mycorrhiza, widespread in terrestrial ecosystems, is also formed in aquatic plants, particularly in *Lobelia dortmanna* L., helping adapt to the use of mineral-poor subaquatic bottom (Markov, 2017). Moreover, the extent of mycorrhizal infection and the number of detected mycorrhizal taxa decreased along the trophic gradient from oligotrophic to mesotrophic lakes (Moora *et al*., 2016). Under natural conditions, mycotrophic nutrition is the main channel of nitrogen and phosphorus compounds supplied to vascular plants through the consumption of these elements in the form of organic compounds (Harley and Smith, 1983), as well as the consumption of organic compounds: in exchange for sugars produced by plants, fungi supply them with physiologically active substances. Another important feature of mycotrophic plants is the plant cell digestion of some parts of the fungi (Selivanov, 1981).

Even in nonmycorrhizal plants, two other types of consumption and assimilation of allochthonous organic compounds occur. Thus, plants can depolymerize the food substrate, in particular, some SOM components, either with the help of root excretions or rhizosphere microorganisms (Pauchon and de-Barjac, 1960). Besides, heterotrophic organoids (more precisely, endosymbionts) — mitochondria and autotrophic chloroplasts — are present within one cell of higher plants. In addition, during seed germination, supplying the developing embryo with organic compounds comes from the endosperm (monocotyledonous plants) or the cotyledons (dicotyledonous ones).

Several authors reported a significant excess in the free-living microorganisms around root hairs, the so-called rhizosphere effect (Krasilnikov, 1958; Pauchon and de-Barjac, 1960; Mishustin, 1975; Woldendorp, 1978; Haider and Martin, 1979). Rhizospheric microorganisms actively participate in the SOM transformation, in its destruction (depolymerization) and mineralization, and contribute to the assimilation of organic compounds and other nutrients by plants (Estermann and McLaren, 1991). Krasilnikov (1958) considered that plants receive vitamins and other active substances from rhizosphere microorganisms.

At present, there exists mutualism between plants and microorganisms as rhizophagy, the essence of which consists of the following: initially, symbiotic prokaryotes grow in the rhizoexudate release zone (White *et al*., 2018). Then the microorganisms inpour into the meristem cells of the root tips, settling in the periplasmic spaces between the cell wall and the plasma membrane. In the periplasmic spaces of root cells, bacteria get transformed into protoplasts without walls, exposed to oxygen (superoxide) produced by NADPH oxidases (N_{OX}). Oxygen oxidizes some of the bacteria, effectively extracting nutrients from them. Surviving bacteria in the epidermal cells of the root causes the root hairs to lengthen, and these microorganisms come out from them, restoring their cell walls and cellular texture.

The possibility of complex organic molecules entering plants through the root system and their further assimilation by plants is now a well-proven fact (Popov, 2004). From the end of the 19th century to date, there proliferates a vast number of facts about the consumption by green plants of organic substances of natural, artificial, and even synthetic origin (Nefedov, 1897; Kursanov, 1946; Kursanov *et al*., 1948; Khristeva, 1951, 1955; Aleshin and Tyuneev, 1956; Ratner *et al*., 1963; Tokarskaya, 1956; Krasilnikov, 1958; Kononova and Diakonova, 1960; Ratner and Ukhina, 1961; Khristeva and Luk'yanenko, 1962; Ratner and Smirnov, 1966; Schnitzer and Poapst, 1967; Klimova and Komissarov, 1971; Aleksandrova, 1972; Flaig, 1978; Pospishil *et al*., 1981; Ryzhikov *et al*., 1991; Popov and Shishova, 2001; Gold *et al*., 2008). Organic substances consumed by plants can be roughly divided into several groups, i.e., a) mono- and oligomers-components of biological macromolecules (glucose, sucrose, amines, amino acids, heterocyclic compounds, glycerol, and carboxylic acids), b) heterogenic oligo- or polymers, which are physiologically active substances (hormones, plant growth stimulators and inhibitors, vitamins, antibiotics, proteins, including enzymes), and c) chemically isolated from natural bodies, the so-called humic substances, which are being a complex mixture of heteropolymers in a colloidal state, oligo- and monomers, having a pronounced positive effect on plant growth and development.

An analogy can be drawn between the functioning of the digestive system of obligate heterotrophic organisms (especially with intracavitary digestion) and that of the plant root system (Popov and Chertov, 1993). In both cases, strong acidification of the food substrate (both by gastric juice and by root exudates) and, thus, activation of hydrolytic enzymes leading to depolymerization of large organic compounds was observed. Notably, at certain stages of digestion, there is an excretion of amino acids in the intestines of animals to stimulate intestinal microorganisms (Ivanov, 1973). Perhaps this also explains the presence of amino acids in root exudates. In other words, the root system is the 'exogastric' of plants. Photosynthetic plants can be considered facultatively heterotrophic organisms with extracellular symbiont digestion and symbiont feeding. The fact that organic substances with a relatively high molecular weight enter plants indicates the presence of intracellular vesicular digestion as well (Popov and Chertov, 1993).

The study opines that the SOM trophic function is, firstly, a supplier of a variety of mono-, oligo-, and polymeric compounds, which are consumed and assimilated by plants. Secondly, organic compounds facilitate the entry and transport of mineral nutrition elements into green plants. In the ecosystem, apart from the well-known biological carbon cycle (Figure 1A), there occurs a second one, the organic molecules cycle (Figure 1B) (Popov and Chertov, 1993). A consequence of the organic matter cycle is the existence of a double-trophic chain in phytocenoses (natural and anthropogenic) in which the utilization by

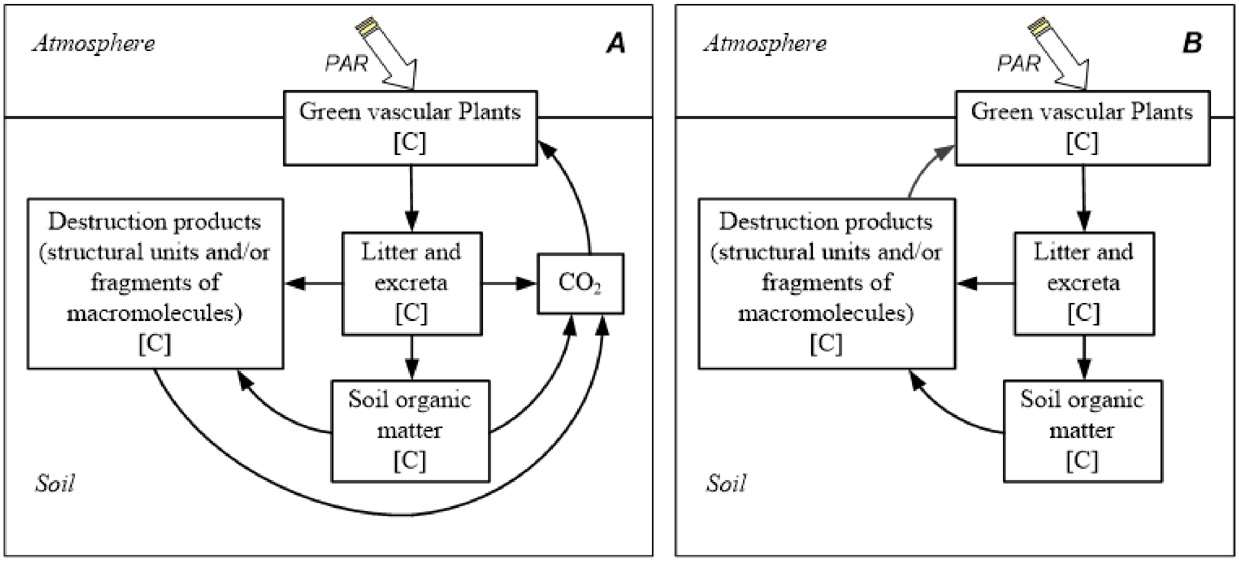

Figure 1. Biological carbon cycles: PAR — physiologically active radiation, a) the well-known biological carbon cycle, and b) the second biological carbon cycle, the cycle of organic compounds (bound carbon [C]).

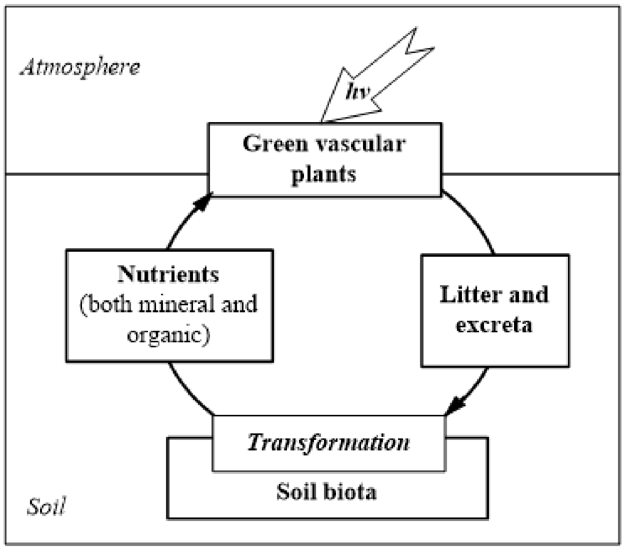

Figure 2. Double-trophic relationship between plants and soil.

the soil biota of plant litter and excreta is accompanied by the creation of a food source for plants, including certain organic compounds (Figure 2) (Popov, 2006).

If the theory about the exceptionally large role of the biological cycle in the functioning of the ecosystem as the fastest and cheapest way of natural recycling of organic materials in wildlife is true, then one can presume that the way of feeding plants is some organic macromolecule blocks, formed by transforming of SOM components through soil biota and mycorrhizal fungi. Such nutrition allows plants to 'save' energy by using organic molecules, which can be both structural and functional units. In principle, this approach is a return at a new scientific and methodological level to A. Thayer's hypothesis of plant's humus nutrition. The authors believe that mineral nutrition is characteristic, firstly, of structurally and functionally simplified (reduced) ecosystems of the pioneer stages of succession (when vegetation overgrows geologically 'young' land surfaces) and, secondly, of agroecosystems. The predominance of organic nutrition is a characteristic feature of highly organized, persistent climax ecosystems. The presence of the above mechanism in plant nutrition increases the number of functional relationships in soil-plant systems and is a factor in increasing the stability of the ecosystem (Popov and Chertov, 1993; Popov and Shishova, 2001).

The proposed view on the role of organic compounds in plant nutrition allows a more reasonable approach to the assessment of modern agriculture. The continuing increase in the production of mineral fertilizers and various biocides, combined with repeated mechanical soil tillage, practically relegates the soil to the level of a hydroponic system with broken trophic links and with changed in the composition of soil biota and the SOM qualitative composition. Such process is a waste; in addition, it leads to an increase in the costs concerning agricultural production. This path is costly; it leads to increased outlays (including fossil fuel energy) in all links of farming. Hence, the ideas of biological (ecological, alternative, green) farming are based on the restoration of the soil-plant system functioning, discarding the maximizing of crop yields in favor of the principles of sustainable agriculture with minimized tillage, improving the crop production quality, and restoring the trophic functions of agro landscapes, are continually being pursued (Kant, 1988; Dudkin and Lobkov, 1990; Zhuchenko, 2000, 2008). The concept of organic plant nutrition can serve as a theoretical basis for the justification of the biological farming system.

CONCLUSIONS

The possibility of organic molecules entering green vascular plants through the root system and their further assimilation proves factual. In other words, higher plants are facultative heterotrophs, more precisely, mixotrophs. As the authors believe, the mixotrophic nutrition of green vascular plants is the predominant type of nutrition, which provides significant energy and structural gains at the ecosystem level. It seems that a similar mechanism of plant nutrition has been inherited from the earliest stages of biosphere evolution.

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