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**THE GENESIS OF PHOTOSYNTHESIS TYPES AS THE BASIS OF ECOLOGICAL EXPANSION OF HALOPHYTIC PLANTS***Bogdan Chmelnskiy Melitopol State Pedagogical University*

The C<sub>3</sub>, C<sub>4</sub>, and CAM photosynthesis types are considerably differed by CO<sub>2</sub> absorption intensity, its biochemistry, saturation level, water productivity, biological productivity, and other different features, which secure the plants survival at stress and extreme conditions. The aim of current research was to discover the photosynthesis peculiarities at halophytic plants species (*Salicornia europaea* L., *Halimione pedunculata*, *Artemisia santonica* L., *Plantago lanceolata* L.) by salinity at model and natural conditions, and to generalize data in historical aspect. It was constituted that *S. europaea* L. was characterized by C<sub>3</sub> photosynthesis passage which was switched on CAM CO<sub>2</sub> fixation under soil salinity conditions till 4-4,5 %, but glycophyte *A.santonica* was immanent C<sub>4</sub> assimilation way of aspartate type.

Analysis of literature data and own research allows to find out that in majority the C<sub>3</sub> photosynthesis dependence from environmental factors described by determinate curve with matched mathematical expression. It was suggested to generalize the data by Lagrange polynomial. The obtained results proved that the pattern of photosynthesis evolution is: C<sub>3</sub> → C<sub>4</sub> → CAM with commute possibilities: C<sub>3</sub> → CAM; C<sub>4</sub> → CAM.

*Key words: genesis, photosynthesis, halophytic plants, different ecological groups, salinity.*

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**ГЕНЕЗИС ТИПОВ ФОТОСИНТЕЗА КАК ОСНОВА ЭКОЛОГИЧЕСКОЙ ЭКСПАНСИИ ГАЛОФИТНЫХ РАСТЕНИЙ***Мелитопольский государственный педагогический университет имени Богдана Хмельницкого*

C<sub>3</sub>, C<sub>4</sub>, и CAM-типы фотосинтеза значительно отличаются по интенсивности поглощения CO<sub>2</sub>, биохимическим показателям, уровню насыщенности, водной продуктивности, биологической продуктивности и другим особенностям, которые обеспечивают выживание растений при стрессах и экстремальных условиях. Цель исследования – установить особенности фотосинтеза галофитных видов (*Salicornia europaea* L., *Halimione pedunculata*, *Artemisia santonica* L., *Plantago lanceolata* L.) в модельных и естественных условиях и обобщить данные в историческом аспекте. Было установлено, что *S. europaea* L. характеризовался C<sub>3</sub> типом фотосинтеза, который было трансформирован в фиксацию CO<sub>2</sub> по CAM-типу при условиях солености до 4-4,5 %, причем гликофиту *A. santonica* был свойственен C<sub>4</sub> путь ассимиляции аспартатного типа.

Анализ литературных данных и собственного исследования позволило определить, что в большинстве случаев зависимость C<sub>3</sub> фотосинтеза от внешних воздействующих факторов должно быть описано определенной кривой с соответствующим математическим уравнением. Нами было предложено обобщить данные при помощи полинома Лагранжа. Полученные результаты доказали, что схема эволюции фотосинтеза может быть представлена как: C<sub>3</sub>→C<sub>4</sub>→CAM с возможностью замены: C<sub>3</sub>→CAM; C<sub>4</sub>→CAM.

Ключевые слова: генезис, фотосинтез, галофитные виды, различные экологические группы, соленость.

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**ГЕНЕЗИС ТИПІВ ФОТОСИНТЕЗУ ЯК ОСНОВА ЕКОЛОГІЧНОЇ ЕКСПАНСІЇ ГАЛОФІТНИХ РОСЛИН**

C<sub>3</sub>, C<sub>4</sub>, і САМ-типи фотосинтезу значно відрізняються за інтенсивністю поглинання CO<sub>2</sub>, біохімічним показникам, рівню насиченості, водній продуктивності, біологічній продуктивності та іншим особливостям, які забезпечують виживання рослин при стресах і екстремальних умовах. Мета дослідження - встановити особливості фотосинтезу галофітних видів (*Salicornia europaea* L., *Halimione pedunculata*, *Artemisia santonica* L., *Plantago lanceolata* L.) в модельних і природних умовах та узагальнити дані в історичному аспекті. Було встановлено, що *S. europaea* L. характеризувався C<sub>3</sub> типом фотосинтезу, який було трансформовано в CO<sub>2</sub> фіксацію за типом САМ при солоності до 4-4,5 %, причому для глікофіту *A. santonica* був характерний C<sub>4</sub> шлях асиміляції аспартатного типу.

Аналіз літературних даних і власного дослідження дозволило визначити, що в більшості випадків залежність C<sub>3</sub> фотосинтезу від зовнішніх чинників повинно бути описано певною кривою з відповідним математичним рівнянням. Нами було запропоновано узагальнити дані за допомогою полінома Лагранжа. Отримані результати довели, що схема еволюції фотосинтезу може бути подана як: C<sub>3</sub>→C<sub>4</sub>→САМ з можливістю заміни : C<sub>3</sub>→САМ; C<sub>4</sub>→САМ.

*Ключові слова:* генезис, фотосинтез, галофітні види, різні екологічні групи, солоність.

Nowadays, depending on anatomical-morphological peculiarities, localizations of places and mechanisms of carboxylation and decarboxylation, the composition specificity of fermentative complexes, composition of primary, intermediate and eventual assimilation products distinguish such ways of photosynthesis: C<sub>3</sub>, C<sub>4</sub>, CAM. They are characterized by different time and evolutionary formation what allow them to occupy certain niches. For all photosynthesis types the role of Calvin cycle is equal. Its intermediate products are proceeding in sugars, and all of the last functional chains are examined as auxiliary. Under-buildings are very important for plants species at stress and lethal conditions.

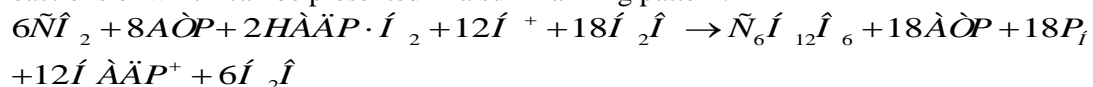
Chemical mechanism of CO<sub>2</sub> fixation was decoded only after using of radio-active indicators method. S. Ruben (Ruben, 1940) made this in 1939-1943 using of (<sup>14</sup>C) carbon radio-active isotope with a half-decomposition period of 20 min. Though experiments did not give presentation about chemical nature of matters which took part in CO<sub>2</sub> assimilation an author was succeeded to pull out a few new principal positions:

1 – CO<sub>2</sub> assimilation is begun with the carboxylation reaction of aldehydic group of unknown matter – RH;

2 – the difficult cycle of regeneration of CO<sub>2</sub> acceptor was registered in plants;

3 – at CO<sub>2</sub> assimilation these processes play an important role (Edwards, 1986).

Finally all of these questions were decided by M. Calvin with the employees of the Californian University at application of <sup>14</sup>C carbon radio-active isotope with a half-decomposition period of 5720 years (Calvin, 1962). The duration of “life period” of carbon isotope allowed detail research of sequence of biochemical transformations of CO<sub>2</sub> fixing products. Calvin cycle includes three phases (carboxylation, renewal, and regeneration), 13 reactions of which can be presented in a summarizing pattern:



Owing to formation of 3C-carbon intermediate compound, this got the name of C<sub>3</sub> - photosynthesis, and plants are characterized the specific anatomic-morphological and physiological-biochemistry peculiarities. According to equation on renewal of one CO<sub>2</sub> molecule to the carbohydrates level in Calvin cycle it is expended the 3 ATP molecules and 2



NADP·H<sub>2</sub> molecules. They are synthesized in the previous – light stage of photosynthesis. In some papers (Carpilov, 1970; Magomedov, 1969; Hatch, 1966) it was discovered the primary CO<sub>2</sub> assimilation by the maize, amaranth, millet, for them was registered the <sup>14</sup>C accumulation in the carboxyl groups of oxaloacetic, apple, and asparagine acids.

This CO<sub>2</sub> assimilation way got the name of C<sub>4</sub>-photosynthesis, with inherent for plants the structural and functional peculiarities. By C<sub>4</sub>-acids degradation method it was succeeded to set, that the primary acceptor function for them is fulfilled the 2-phosphotolpyrovinogradnic acid. It which with participation of carboxylase enzyme (PEP-carboxylase) joins CO<sub>2</sub> with formation of oxaloacetic acid. The last as a result of renewal forms apple acid, or after an amination is an aspartate, on the basis of what Daunton in 1970 suggested to divide them into „malate” or „aspartate” forms (Downton, 1970). These reactions take a place in mesophyll cells and formed C<sub>4</sub>-intermediate products, which are transported in the cover cells. There it is decarboxylated, dehydrogenated, deaminated, providing the Calvin cycle by substrates (secondary carboxylation). 3-carbon substances (PVA, 3 PGA and alanine) go back into mesophyll cells for participating after the transformations row in primary carboxylation. Based on carboxylation method of cover cells these plants are divided into 3 types (Govindghy, 1987; Hatch, 1976):

1. NADP-malic enzyme type, in the cover cells at presence of NADP-ME, which decarboxylize apple acid with formation of CO<sub>2</sub> and NADP-H<sub>2</sub> – substrates for Calvin cycle.

2. PEPR-kinase type, at which CO<sub>2</sub> after decarboxylation in the secondary carboxylation included by PEPK-kinase.

3. NAD-malic enzyme type, at which decarboxylation NAD-ME is carried out in mitochondria with the subsequent including of CO<sub>2</sub> in Calvin cycle.

At the end of 60th – beginning of 70th years of XX century some publications describe crassula acid metabolism (CAM-photosynthesis) regards C<sub>4</sub>-fotosynthesis (Kennedy, 1974; Lioret, 1964; Moyses, 1978; Ranson, 1960). For plants with the CAM-photosynthesis researchers found out such peculiarities:

- 1 – their stomas are opened at night and closed in the day time;
- 2 – fixing of atmospheric CO<sub>2</sub> takes place at night with the considerable accumulation of free apple acid;
- 3 – the last is produced in vacuoles;
- 4 – in the day time apple acid is decarboxylized and CO<sub>2</sub> due to light energy remakes into saccharose and spare glucan (starch) in the reactions of C<sub>3</sub>-photosynthesis;
- 5 – in next dark period the part of spare glucan disintegrates with formation of PEP-molecules-acceptors for dark CO<sub>2</sub> fixing. Maintenance of spare glucan falls down at night and apple acid rises; in the day time there are opposite changes. The primary and secondary carboxylations divide not only spatially (as at C<sub>4</sub>-photosynthesis), but also in temporally (primary – at night, secondary – in the day time).

O.M. Volkov proved that when photosynthesis begins the assimilation intensity directly correlates with lighting. E.P. Votchal investigated photosynthesis and gas interchange simultaneously with water balance, transpiration, leaves temperature, maintenance and high-quality composition of pigments with registration of dynamics of geophysical factors (Votchal, 1939). K.A. Purievich suggested that:

- 1 – in photosynthesis process not more than 2,5% of effulgent energy is used, which falls on a green leaf;
- 2 – for photosynthesis the mass and energy conservation law could be applied;
- 3 – in the photosynthesis process squirrel and fats can be synthesized (Purievich, 1913).

V.M. Lyubimenko found out the light-admired nature and shade-hardiness of tree species and other plants. Subsequent fundamental researches of photosynthesis physiology were conducted in Institute of physiology and genetics of the Ukrainian National Academy of Sciences.

Basic properties of plants with different types of CO<sub>2</sub> assimilation are generalized in Table 1.

Table 1.

Characteristic features of plants with different types of CO<sub>2</sub> assimilation.

Feature	C <sub>3</sub> -plants	C <sub>4</sub> -plants	CAM-plants
Anatomy of leaves	Palisade spongy parenchyma, low concentration of organelle in spongy cages	Presence „cants”- anatomy with organelle plenty in the cover cells	Considerable modifications, mesophyll is well expressed, large vacuoles in store tissue
Chloroplasts	Granulated	In mesophyll - granulated; in cover cells – granulated and non-granulated	Granulated
Chlorophyll „a”/”b”	2,8 ± 0,4	3,9 ± 0,6	2,6 ± 0,5
Minimum charges (theoretical) on CO <sub>2</sub> renewal (CO <sub>2</sub> : ATP : NADP • H <sub>2</sub> )	1 : 3 : 2	1 : 5 : 2	1 : 6 : 2
Carboxylic enzymes	RBPK	PEPK + RBPK	PEPK- at night; RBPK- in day time
Maximal intensity of photosynthesis, mg of CO <sub>2</sub> /dm <sup>2</sup> ·hour	15 - 55	70 - 120	Certainly: 1-5 Sometimes: 11-15
Size of diffusive resistances for CO <sub>2</sub> , s/sm	r <sub>s</sub> – 0,5-3 r <sub>ms</sub> – 1-10	r <sub>s</sub> – 3-7 r <sub>ms</sub> – 0,2-1,5	r <sub>s</sub> – 7-11 r <sub>ms</sub> – 0,1-1,5
Primary products of assimilation of CO <sub>2</sub>	C <sub>3</sub> -acids (3 PGA)	C <sub>4</sub> - acids (oxaloacetic, apple, asparagines)	3 and PGA – on light; apple – in darkness
Photorespiration	It is	It isn't	It isn't
Light saturation of photosynthesis, cal/sm <sup>2</sup> ·min.	0,40-0,45	Does not occur, even at light, 1-1,2	In the light limit, 0,85-1,1
Carbon-acid compensative point	30-70	0-10	In darkness 0-200, At light 0-5
Transpiration coefficient	450-950	250-350	50-55
Accumulation of dry matter, t/h·year	30-35	60-80	5-10



Temperature optimum of growing processes, °C	20-25	35-48	40-50
Evolution of carbon metabolism	C <sub>3</sub>	C <sub>3</sub> → C <sub>4</sub>	C <sub>3</sub> → CAM

### RESULTS AND DISCUSSIONS

The analysis of table contest let to define as concrete regions as a time of year, most favorable or unfavorable, for plants with the different types of photosynthesis. Thus, for the plants with C<sub>3</sub> photosynthesis the west and north conditions of Ukraine promote in a greater measure, C<sub>4</sub> – at central and east regions and in spring – South of Ukraine, CAM is extreme south conditions and sultry summer periods of each regions.

Coloring is one of functional properties of plant organism, the light-dependence function of which because of pigments capable to take in radiation (Jones, 1992; Kosakivska, 2003). Due to optical properties of pigments the transformation of effulgent energy in other forms is possible. They are necessary for biochemical metabolism in vital functions of plant organism. The content and composition of pigments is the genetically predefined indication, depends on ontogenesis and environment conditions, like salinity. Change of maintenance and contest of pigments is sensible indicator of environment factors. B.P. Stroganov used leaves reaction on salt for determination of plants adaptation to salinity and diagnostics of salt-tolerance. At the same time there is not clear idea about salinity influence on pigments dynamics at plants (Bohnert, 1995). Some suggested that increase of concentration of soil solution stipulates the considerable lower of pigments maintenance, others have opposite opinion. From literature analysis some contradictions are marked:

- 1 – in experiments with plants of different salt-tolerance and systematic;
- 2 – in different rates, levels and types of soil salinity;
- 3 – in using of different measuring units of pigments maintenance (*mg pigments · g of raw mass<sup>-1</sup>*; *mg pigments · g of dry mass<sup>-1</sup>*; *mg pigments · 1 liter of solution*; *mg pigments · area unit<sup>-1</sup>* et cetera), that very complicates comparison of experimental results;
- 4 – in synchronization of absence and clear control of environment factors at growing plants;
- 5 – in different explanations of adaptive mechanisms of plants to salinity.

Due to specificity of experimental objects (small sizes, numerous modification of organs etc.) the determination of pigments maintenance we expected at a *mg pigment · g of dry matter<sup>-1</sup>*. Our results simply testify substantial influence of soil salinity on pigments maintenance and composition of photosynthetic organs. Thus, the changes specific is stipulated by the plant species, the ontogenetic development stage of it and the soil salinity rate.

At the beginning of vegetation at control plants maintenance of pigments is most in *Plantago lanceolata* and prevails on the green pigments sum on 24,1% in *Salicornia europaea*; 30,5% – *Halimione pedunculata* and in 2,2 times – *Artemisia santonica*. Thus, a difference on chlorophyll “a” is evened to 32,2%, 31,5% and 42,3% accordingly, and on chlorophyll “b” – 52,2%; 26,1%; 11,1% accordingly. On the sum of yellow pigments this difference was 30%; 39% and 45%. Such situation is stipulated that *Plantago lanceolata* as a mesophyte insensitively passes the individual development stages in spring, at that time when in halophytes this process takes a place considerably slower. In later for all of control plants on the dynamics of pigments maintenance it is characterized the general conformity – the lowering of green pigments maintenance in midsummer, when the external factors action

arrives at maximal values, on a background of the insignificant increase of yellow pigments and renewal, but on occasions the greater pigments accumulation, according to their level in spring. On this background it is gradually registered the increase of yellow pigments maintenance, which is connected with the action of high tension factors in summer, and in autumn – by the plants senescence and worsening of environment condition. The least pigments amount during of all vegetation is characterized the plants of *Artemisia santonica*, which are differ the adaptive mechanisms specificity to the external factors action.

Salinity in any vegetation period results in diminishing of green and increase of yellow pigments. At increase of soil solution concentration in spring the general maintenance of green pigments is lowered at ehalophytes on 10,2%; crynohalophytes – 12,9%; glycohalophytes – on 4,5%. The experimental plants *Plantago lanceolata* at salt stress catastrophically lose green coloring and maintenance of green pigments lower in 2-3% according control.

Salinity in spring stipulates the decline of “a” and “b” chlorophyll maintenance in *Salicornia europaea* on 12,4% and 9,7% accordingly; *Halimione pedunculata* – 15,3% and 10,3%; *Artemisia santonica* – 15,2% and 12,5%, but for *Plantago lanceolata* leaves value of this parameter evened 2-3%. Diminishing of green pigments takes a place on a background the increase of yellow pigments, which is accompanied the deceleration of chlorophyll biosynthesis and strengthening of yellow pigments synthesis. The content maintenance of yellow pigments at experimental plants rises in *Salicornia europaea* on 2 %; *Halimione pedunculata* – 5,7%; *Artemisia santonica* – 7,8%.

Salinity in the vegetation middle has some other influence (plants are well developed, and pigments maintenance is less), but changes character broadly speaking is analogical the plants with salinity in spring. A peculiarity is that *Plantago lanceolata* experimental plants do not maintain the cooperative factors action of external environment and salt stress and die off. For all of the halophytes it is characterized the chlorophyll adaptive process and increase of yellow pigments maintenance. On a background of general decline of green pigments maintenance at the control *Salicornia europaea* plants on 4,2%; *Halimione pedunculata* – 7,6%; *Artemisia santonica* - 8,8% diminishing of chlorophyll of “a” and “e” at experimental plants accordingly evened 13 and 11,5%; 12,2 and 6,8%; 11,9 and 8,4%. Thus the amount of yellow pigments grew accordingly on 3,2; 12,3 and 20,1%. The carotinoid function are to extend the photosynthesis action spectrum, but in the stress conditions it was shifted to protective function, because it was able to react with the excited molecules of chlorophyll, taking away the energy from them, what is warned their photooxidation. Energy of photoexcitation molecules of chlorophyll passes to carotinoid; chlorophyll acquires the normal energetic state followed by energy release.

Salinity of plants in autumn, when halophytes are characterized insensitive vital functions takes a place on a background of high pigments maintenance (their level is evened, or, even, exceeds this parameter in spring) and it is accompanied diminishing of green and considerable increase of yellow pigments. For ehalophytes the chlorophyll diminishing of “a” evened 13,2%, “b” – 11,6% and increase of yellow pigments on 44%; for crynohalophytes according to 15,9; 11,2 and 15,5%; glycohalophytes – 14,2; 14,0 and 28,6%.

The great interest is presented on pigments maintenance the “red” plants of *Salicornia europaea*, which occur between the green plants and on hills they form the “red” associations. “Red” plants are more compact, less sizes and have less water maintenance on a background of higher concentration of cellular sap. The researches are set, that these plants appear later green, when the environment factors, including salinity level, arrive at critical



and before-stress values. In some research (Yeo, 1998, Puyrko, 2001) it is shown that the high level of chlorides salinity stipulates the accumulation of without-plastid pigments – anthocyanins even at these plants, in which it quite do not meet at a vegetation at normal condition. The substance for the anthocyanins biosynthesis is the metabolism intermediate products: organic acids, keto-acids, amino acid and other. Accumulation of anthocyanins as intermediate catalysts in oxidative metabolism assists to activating of oxidizing processes and promotes an energetic level at plants at salinity. The accumulation of anthocyanins is also instrumented in neutralization of toxic matters due to glycolic aglycans, which have the toxic abilities (Waisel, 1972).

The special actuality is acquired by the study of changes dynamics of pigments maintenance at salt stress in connection with that in the first photosystem (PS I) the sun radiation absorption takes a place mainly by “*a*” chlorophyll, and in the second one (PS II) – by as “*a*” chlorophyll as “*b*” chlorophyll. PS I contains 150-200 chlorophyll molecules on the molecule of reactionary center (P-700), but correlation of “*a*”/“*b*” chlorophyll arrives at 5 and anymore. Typical complex PS II of higher plants contains 250-300 molecules of chlorophyll on the molecule of P-680 and has correlation of “*a*”/“*b*” chlorophyll about 2-3 and carries out water oxidization (Yeo, 1998). Among existing at the higher plants the pigment-protein complexes (PS I, PS II and LGC II) a pool of light-gathers is most. In the complement of LGC II nearly enters half of chlorophyll all on earth. This complex takes the sun energy and gives over it to the reactionary centers of PS II that is the initial link of photosynthetic process on the whole.

#### CONCLUSIONS

Change of pigments maintenance and content under the stress is stipulated the intensities correlation of their synthesis and hydrolysis. We noted more considerable changes at stress in “*a*” than “*b*” chlorophyll and explain this by labiality of first which serves as substance for a biosynthesis of the second one. Greater stability of “*b*” chlorophyll at stresses is explained by continuation of its biosynthesis from “*a*” chlorophyll on a background of stopped biosynthesis of “*b*”.

The increase of yellow pigments maintenance at stresses explained the chlorophyllase activating and stopping of green pigments synthesis. Substance of  $\text{CH}_3\text{CO-COA}$  is directed for the biosynthesis of other plastid (yellow) and without-plastid (anthocyanins) pigments. Thus, salinity stipulates the considerable changes of maintenance and contest of pigments in halophytic plants and diminishing maintenance of green pigments at salt stress.

The concentration of yellow pigments rises in both cases. Salinity (more than 4,5%) stipulates level of chloride in “red” euhalophytes, possibly due to the biosynthesis of anthocyanins. We suggested that every species of plants grows in certain ecological conditions due to adaptation properties of major process of vital functions – photosynthesis which forms the basis of biological productivity and determines size and quality of yield of xerothermic plants.

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