DOI: 10.1007/s11099-018-0804-x PHOTOSYNTHETICA 56 (4): 1107-1112, 2018

Diurnal temperature-related variations in photosynthetic enzyme activities of two C_4 species of Chenopodiaceae grown in natural environment

T.Y. ORUJOVA, S.M. BAYRAMOV, U.A. GURBANOVA, H.G. BABAYEV, M.N. ALIYEVA, N.M. GULIYEV, and Y.M. FEYZIYEV+

Institute of Molecular Biology and Biotechnologies, National Academy of Sciences, 2a Matbuat ave., AZ1073 Baku, Azerbaijan

Abstract

The effects of the diurnal variations in ambient temperature on some C_3 and C_4 enzymes in the *Salsola dendroides* and *Suaeda altissima* species of Chenopodiaceae family were studied during the intensive vegetation period. Activities of phospho*enol*pyruvate carboxylase (PEPC) and cytosolic aspartate aminotransferase (AsAT) were shown to decrease in both species in the afternoon and evening. The activity of the mitochondrial AsAT decreased in *S. altissima,* remained relatively constant in *S. dendroides* during the day. The activity of alanine aminotransferase was high in the *S. dendroides* species in the morning and evening and decreased in the *S. altissima* species by the evening. Glucose-6-phosphate activated PEPC in both species throughout the day. The study of the redox status-regulated C_3 enzymes showed temperature-related increases in NADP-glyceraldehyde 3-phosphate dehydrogenase activity in both plants, in fructose-2,6-bisphosphatase activity in the *S. altissima* species, and in NADP-MDH activity in the *S. dendroides* species in the afternoon.

Additional key words: C_4 photosynthesis; Chenopodiaceae; photosynthetic enzymes; temperature.

Introduction

High water-use efficiency and CO_2-concentrating mechanism give C_4 photosynthesis an advantage over plants possessing the more common C_3 carbon fixation pathway under extreme environmental conditions, such as high temperatures, high light intensities, limited water availability, nitrogen and CO_2 limitation (Edwards *et al.* 2004, Hibberd and Covshoff 2010, Gowik and Westhoff 2011, Brestic *et al.* 2016). Due to increased water-use efficiency of C_4 plants, soil moisture is conserved, allowing them to grow for a longer period in arid environments. Most C_4 plants constitute the vegetation of tropical areas exposed to high solar intensity and temperature and they are acclimated to these conditions better than C_3 plants. Using the carbon-concentrating mechanism, these plants increase CO_2 concentration at the Rubisco active site and thereby elevate photosynthetic efficiency (Sage *et al.* 2011).

Plants, which utilize the C_4 pathway, typically possess a Kranz leaf anatomy, consisting of functionally distinct photosynthetic cell types: mesophyll (M) cells assimilating CO_2 by organic compounds and bundle sheath (BS) cells reducing carbon by the Calvin cycle (Hatch 1987, Edwards *et al.* 2004). Compared to C_3 plants, C_4 metabolic pathway has a more complex enzymatic system (three enzymes – NAD- and NADP-malic enzymes, and PEP-carboxykinase, involved in C_4 pathway, otherwise the chemistry is similar). Thus, photosynthesis of C_4 species is performed and regulated by enzymes of the C_3 and C_4 pathways: PEPC, NAD- and NADP-malic enzymes (ME), NADP-malate dehydrogenases (MDH), PEP-carboxykinase (PEPCK), aspartate and alanine aminotransferases (AsAT and AlAT, respectively), NADP-glyceraldehyde 3-phosphate dehydrogenase (NADP-GAPDH), *etc*. (Leegod 2002, Gowik and Westhoff 2011). These enzymes

Received 13 February 2017, *accepted* 30 August 2017, *published as online-first* 12 April 2018.
+Corresponding author; phone: +994 12 5105921, e-mail: feyziyev-y@botany-az.org
Abbreviations: AlAT – alanine aminotransferase; AsAT – aspartate aminotransferase; BS – bundle sheath; Chl – chlorophyll; EDTA – ethylenediaminetetraacetic acid; FBPase – fructose-2,6-bisphosphatase; F_v/F_m – maximum quantum efficiency of PSII; Glu-6-P – glucose-6-phosphate; M – mesophyll; MDH – malate dehydrogenase; ME – malic enzyme; 2-ME – 2-β-mercaptoetanol; NADP-GAPDH – NADP-glyceraldehyde phosphate dehydrogenase; PEP(C) – phospho*enol*pyruvate (carboxylase); Tris – tris(hydroxymethyl) aminomethane.
Acknowledgements: This work was supported by the Science Development Foundation under the President of the Republic of Azerbaijan – Grant No. EIF-2012-2(6)-39/19/3.

providing high energetic efficiency for C_4 photosynthesis, respond differently to adverse environmental factors and may perform various functions.

Species belonging to the family Chenopodiaceae are very attractive among C_4 plants. They constitute biodiversity in arid, semiarid, and saline areas. This family is represented by 102 genera and 1,500 species all over the world, including C_3, C_4, and C_3-C_4 plants. There are more C_4 plants in the Chenopodiaceae family (45 genera and 550 species) compared to other dicotyledons (Akhani *et al.* 1997, Pyankov *et al.* 2000, Schüssler *et al.* 2017). More than 100 species of the Chenopodiaceae family are also found in the Azerbaijan flora (Movsumova *et al.* 2014).

In this study, the durinal changes in the activities of some enzymes of C_4 cycle, such as PEPC (EC 4.1.1.31), NAD- and NADP-ME (EC 1.1.1.39 and EC 1.1.1.40, respectively), NADP-MDH (EC 1.1.1.82), AsAT (EC 2.6.1.1), AlAT (EC 2.6.1.2), and redox regulated stromal C_3 enzymes, such as NADP-GAPDH (EC 1.2.1.12), FBPase (EC 3.1.3.46), were studied in the species *Salsola dendroides* and the *Suaeda altissima* of Chenopodiaceae, grown under natural conditions. Both species are NAD-malic enzyme-type C_4 plants (Pyankov *et al.* 2001, Rosnow *et al.* 2014) and are characteristic of the Absheron peninsula (Movsumova *et al.* 2014).

Materials and methods

Plants and growth conditions: Leaves and other photosynthetic organs of matured plants grown under natural conditions at the Absheron peninsula were used as the study material. Sampling was performed during three days of the last week of July, at 3 different times throughout the day, *i.e*. 08:00, 13:00, and 20:00 h. Light intensity, temperature, and humidity at the above sampling times were 47 μmol(photon) m^{-2} s^{-1}, 22 ± 1ºC and 62%; 1,850 μmol m^{-2} s^{-1}, 38 ± 2ºC, and 32%; 25 μmol(photon) m^{-2} s^{-1}, 27 ± 2ºC, and 41%, respectively. Plant materials were stored in liquid nitrogen until further use. No precipitation was recorded on the sampling days. The average values of the separate experimental results were estimated.

Extraction of plant materials: The plant material frozen in liquid nitrogen was thawed, and 200 mg was quickly extracted using a chilled mortar and pestle with 1 ml of medium containing 100 mM Tris-HCl (pH 7.8), 10 mM $MgCl_2$, 1 mM EDTA, 10 mM 2-β-mercaptoetanol, 2 mM phenylmethylsulphonyl fluoride, and 2% (w/v) insoluble polyvinylpyrrolidone. The homogenate was centrifuged at 12,000 × *g* for 5 min. Supernatants were used for the enzyme activity assays.

Enzyme activity: The activities of the photosynthetic enzymes (NADP-MDH, PEPC, NAD-ME, NADP-ME, mitochondrial and cytosolic AsAT, AlAT) were measured using the methods previously described in Pyankov *et al.* (2000) and Alfonso and Brüggemann (2012). The activity of enzymes was followed at 25°C with the *Ultrospec* 3300 spectrophotometer (*Amersham BioSci.*, USA) as the change of absorbance at 340 nm, during the oxidation or reduction of NAD(H) and NADP(H). Assays of the initial and total activities of FBPase and NADP-GAPDH were carried out according to the method of Holaday *et al.* (1992). Enzyme activities were expressed in μmol(substrate) min^{-1} mg^{-1} (protein). Substrates for AsAT, AlAT, NAD (NADP)-ME, NADP-MDH, FBPase, and NADP-GAPDH were Na-aspartate, L-alanine, L-malate, oxaloacetic acid, fructose 1,6-bisphosphate, and phosphoglyceric acid, respectively.

PEPC sensitivity: After extraction of the plant material, supernatant was desalted in a cold *Sephadex G-25* column pre-equilibrated with the extraction buffer. The sensitivity of PEPC to aspartate and Glu-6-P was estimated by adding aspartate or Glu-6-P to make a final concentration of 4 mM and 2 mM, respectively, in the PEP assay medium (Pyankov *et al.* 2000) with minor changes including the use of 100 mM Tris-HCl (pH 7.3), 0.05 mM $NaHCO_3$, and 0.5 mM PEP. The reaction was initiated by adding PEP. PEPC activity was expressed in μmol(HCO_3^-) min^{-1} mg^{-1} (protein).

Protein was measured by the method of Bradford (1976), using bovine serum albumin as the standard.

Fluorescence analysis: Maximum quantum efficiency of PSII, $F_v/F_m = (F_m - F_0)/F_m$ was estimated under field conditions using photosynthesis yield analyzer *Mini-PAM* (*WALZ,* Germany) equipped with *DLC-8* and *2010-A* leaf clips. Chlorophyll (Chl) fluorescence was measured from the leaf surface after 10 min dark-adaptation period. The yield of minimal fluorescence (F_0) from the open state of PSII reaction centers was recorded under modulated (0.6 kHz, 3 μs pulse width) low intensity (630 nm, 0.15 μmol m^{-2} s^{-1}) measuring light. Maximum Chl fluorescence (F_m) from the closed state of PSII reaction centers was initiated by the continuous actinic illumination [6,000 μmol(photon) m^{-2} s^{-1}, white light]. Fluorescence signal was detected through the λ>710 nm long-pass filter.

Statistical analysis: Samples were taken in three biological replicates, and mean values of the results and standard deviation were estimated.

Results

The changes in activities of some C_4 and Calvin cycle enzymes in relation to ambient temperature were studied in *Salsola dendroides* and the *Suaeda altissima* species of the Chenopodiaceae family during the intensive vegetation period in summer (July and August).

The maximum PEPC activity was observed in the morning for both species, but the patterns of the activity decrease occurring during the day were slightly different (Table 1). In the *S. dendroides* and *S. altissima*, afternoon and evening values of PEPC activity decreased 2.5–3.0 and 1.2–1.4 times, respectively, compared to the morning values. This decrease in the enzyme activity might occur due to the incapability of the enzyme to recover its activity after the degradation processes in plants under high temperature and light intensity conditions during afternoon.

Aspartate slightly inhibited the PEPC activity in both plants at various times (Table 1).

Table 1. Effects of aspartate and Glu-6-P on PEPC activity in *Salsola dendroides* and *Suaeda altissima.* Corresponding temperatures are presented in the section Materials and methods.

PEPC activity [μmol(HCO_3^-) min^{-1} mg^{-1}(protein)]				
Species	Time	Control	+Aspartate (4 mM)	+Glu-6-P (2 mM)
S. dendroides	8:00	3.70 ± 0.06	2.80 ± 0.07	4.15 ± 0.09
	13:00	1.40 ± 0.03	1.20 ± 0.03	3.90 ± 0.09
	20:00	1.33 ± 0.07	1.12 ± 0.04	6.08 ± 0.1
S. altissima	8:00	6.40 ± 0.30	6.40 ± 0.10	9.00 ± 0.20
	13:00	5.92 ± 0.20	5.44 ± 0.10	7.50 ± 0.15
	20:00	5.00 ± 0.10	4.50 ± 0.10	6.50 ± 0.10

Different activation patterns of Glu-6-P were observed in two species. Glu-6-P activated PEPC in *S. dendroidies* in the afternoon (~2.7 times) and evening (~4.5 times) contrary to the enzyme in the *S. altissima* species, which was not activated. However, the activation degree of the enzyme was higher (~1.3 times) in the evening than that in the afternoon (~1.2 times).

High morning values of cytosolic AsAT activity in *S. dendroidies* decreased (~2 times) by the evening, whereas mitochondrial AsAT activity remained almost stable during the day (Table 2). However, cytosolic AsAT activity was higher than that mitochondrial one in this plant. Both mitochondrial and cytosolic AsAT activities were high in *S. altissima* leaves in the morning and decreased in parallel during other periods of the day. In contrast, AlAT activity in the *S. dendroidies* was high in the morning and in the evening and comparatively lower in the afternoon. In the *S. altissima*, ~10-fold decrease of this enzyme activity occurred by the evening. Similar changes of the activities of both enzymes, *i.e.*, linear increase in the morning and decrease in the afternoon and evening hours may indicate their concerted actions.

Table 2 shows also temperature-related changes in activities of the decarboxylating NAD- and NADP-ME enzymes in the *S. dendroidies* and *S. altissima* during the day. Afternoon values of NAD-ME activity decreased in both plants compared with the activities observed in other periods of the day. It should be noted that the highest activity of this enzyme in both species was observed in the evening. In contrast, high morning values of NADP-ME activity in both plants significantly decreased in other periods.

Table 2. Diurnal changes in some C_4 enzyme activities in *Salsola dendroides* and *Suaeda altissima*. Enzyme activities are expressed in μmol(substrate) min^{-1} mg^{-1}(protein). Substrates for AsAT, AlAT, NAD(NADP)-ME, and NADP-MDH were Na-aspartate, L-alanine, L-malate, and oxaloacetic acid, respectively. Corresponding temperatures are presented in the section Materials and methods.

Species	Time	AsAT		AlAT	NAD-ME	NADP-ME	NADP-MDH
		Cyt	Mit				
S. dendroides	8:00	7.40 ± 0.15	5.43 ± 0.10	8.03 ± 0.20	0.15 ± 0.02	0.06 ± 0.01	0.07 ± 0.01
	13:00	4.06 ± 0.08	5.86 ± 0.25	5.00 ± 0.10	0.03 ± 0.01	0.02 ± 0.01	0.50 ± 0.02
	20:00	3.90 ± 0.09	5.53 ± 0.15	11.20 ± 0.30	0.40 ± 0.02	0.02 ± 0.01	0.30 ± 0.01
S. altissima	8:00	4.00 ± 0.09	3.50 ± 0.09	3.30 ± 0.04	0.08 ± 0.01	0.020 ± 0.005	0.15 ± 0.03
	13:00	2.50 ± 0.07	2.30 ± 0.04	0.92 ± 0.05	0.03 ± 0.01	0.004 ± 0.001	0.13 ± 0.03
	20:00	1.40 ± 0.03	1.07 ± 0.03	0.30 ± 0.01	0.30 ± 0.02	0.003 ± 0.001	0.22 ± 0.04

In the *S. dendroidies*, NADP-MDH activity appeared to be very low in the morning. But it increased 6–7 times during the day and relatively decreased by the evening. In contrast, no apparent change in this enzyme activity was observed in *S. altissima.* Thus, a high activity was observed in the evening and relatively low activity in other periods (Table 2).

The activities of the redox-regulated enzymes of the Calvin cycle, NADP-GAPDH and stromal FBPase, changed differently in the studied species. The NADP-GAPDH activity appeared to be high both in *S. dendroidies* and *S. altissima* in the afternoon (Table 3).

Table 3. Diurnal changes in stromal FBPase and NADP-GAPDH activities in *Salsola dendroides* and *Suaeda altissima.* Enzyme activities are expressed in μmol(substrate) min^{-1} mg^{-1}(protein). Substrates for FBPase and NADP-GAPDH were fructose 1,6-bisphosphate and phosphoglyceric acid, respectively. Corresponding temperatures are presented in the section Materials and methods.

Species	Time	FBPase initial	FBPase maximal	NADP-GAPDH
S. dendroides	8:00	0.06 ± 0.015	0.16 ± 0.10	3.0 ± 0.1
	13:00	0.04 ± 0.01	0.03 ± 0.25	3.22 ± 0.10
	20:00	0.12 ± 0.02	0.12 ± 0.15	2.26 ± 0.09
S. altissima	8:00	0.10 ± 0.02	0.60 ± 0.09	0.70 ± 0.05
	13:00	1.33 ± 0.04	3.30 ± 0.12	3.21 ± 0.10
	20:00	0.06 ± 0.015	0.36 ± 0.03	2.40 ± 0.09

Nevertheless, the activity of this enzyme in *S. dendroidies* in the morning was ~4 times higher compared with the same activity in *S. altissima.*

Maximum activity of FBPase was found to increase only in the early morning, while remaining unchanged in the afternoon and evening, which was approximately equal to initial values observed in *S. dendroides* (Table 3). However, in *A. altissima*, this activity was higher than the initial activity. The activity of NADP-GAPDH remained stable during the day in *S. dendroidies*, whereas the enzyme activity was lower in the morning and increased in the afternoon and evening in *S. altissima*.

The change of ambient temperature caused negligible changes of leaf fluorescence parameters in the studied plants. The increase of the temperature from the morning (~22ºC) to afternoon hours by ~16ºC was accompanied by a decrease of the relative yield of Chl fluorescence F_v/F_m from ~0.802 to ~0.784 in *S. altissima* and from ~0.764 to ~0.720 in *S. dendroides,* corresponding to a decline of the maximum photochemical efficiency of PSII by ~2.2 and ~6%, respectively. The analysis of the Chl fluorescence parameters in leaves exposed to elevated temperatures showed that the yield of initial fluorescence (F_0) was not changed for the studied temperatures. This indicates that the decrease of F_v/F_m occurred due to a decrease of the efficiency of electron transfer in PSII.

Discussion

Due to their adaptability to the global temperature rise and mineral deficiency, C_4 grasses dominate arid zones. Having a high adaptation potential against adverse environmental factors, such as high temperature, light and water deficiency, C_4 plants are most common in regions frequently subjected to heat and drought.

C_4 photosynthesis in general has a high (20–40°C) temperature optimum (Long 1999, Dwyer *et al.* 2007, Sage *et al*. 2011, Yamori *et al.* 2014). It suggests stability of the reactions included in photosynthesis against daily high temperature and also an effective reparation of the C_4 metabolic pathway. Our study showed that although these plants are habitants of the same geographical territory, activities of the enzymes of C_4 photosynthesis and Calvin cycle altered differently during the day.

The absence of significant changes in maximum photochemical efficiency of PSII indicates that diurnal inhibition of photosynthesis in the studied plants occurred at the level of metabolic reactions, with the participation of redox-regulated enzymes. The present observations emphasized the strong correlation between the modulation of the activity and regulatory properties of PEPC with ambient light and temperature. PEPC is known to be an allosteric enzyme, and its activity is regulated by various metabolite effectors (Chollet *et al.* 1996, O'Leary *et al.* 2011, Chintapalli *et al.* 2014). PEPC activity was previously shown to increase rapidly in the morning and decrease slowly in the evening in sugarcane leaves. Similarly, chloroplast FBPase activity increased with increasing PAR in the morning, reaching a peak between 12:00 and 14:00 h, and then decreased slowly (Du *et al.* 2000). Most PEPC isozymes of plant origin are known to be activated by glucose-6-phosphate and inhibited by feedback inhibitors such as aspartate, L-malate, and glutamate at physiological pH (Chollet *et al.* 1996, Avasthi *et al.* 2011).

Previously it was reported that C_4 PEPC was modulated in leaf discs of *A. hypochondriacus* by the synergistic effects of light and temperature (Avasthi and Raghavendra 2008). Light modulation of C_4 PEPC occurred through phosphorylation (Bailey *et al.* 2007), whereas the effect of temperature was based on the conformational changes in the protein structure (Chinthapalli *et al.* 2003). As it was anticipated, cytosolic AsAT activity decreased along with the decreasing PEPC activity in both plant species (Table 2).

The decrease in the NAD-ME activity in both plants in the afternoon compared to the morning and evening hours is thought to reduce the decarboxylation reaction rate. A positive correlation was observed between daily changes of AlAT and NAD-ME activities in *S. dendroides.* However, AlAT acivity was higher in *S. altissima* in the morning hours. In NAD-ME subtype C_4 plants, PEPC and AsAT are known to be localized in cytosol of mesophyll cells, and implement CO_2 fixation in the form of aspartate. There is evidence that in NAD-ME-type grasses, the form of the enzyme in M cells is cytosolic and the form of the enzyme in BS cells is mitochondrial (Taniguchi and Sugiyama 1990, Taniguchi *et al.* 1995).

The presence of the small activities of NADP-ME and NADP-MDH in both plants is thought to be unrelated to their participation in C_4 photosynthesis.

Temperature caused significant increases in redox-regulated Calvin cycle enzymes, such as NADP-GAPDH. The enzyme activities in *S. altissima* increased sharply at the temperature range of 20–30ºC, while no pronounced

changes were observed at temperatures between 30–35ºC. It suggests a positive correlation between increases in the NADP-GAPDH activity and photosynthetic carbon assimilation in relation to daily temperature.

As seen in Table 3, diurnal alterations in FBPase and PEPC activities correlated negatively. FBPase is involved in cellular energy-exchange processes, including the synthesis of starch and sugars, regulation of the PEPC activity, formation of pyruvate and ATP, proton transport between M and BS cells, and distribution of the energy. So reaction products of FBPase – triose phosphate and hexosephosphate activate PEPC, at the same time providing carbon uptake by PEP in the form of HCO_3^- rather than CO_2 (Gigioli-Guivarc′h *et al.* 1996).

Our results showed that high activities of the studied enzymes were manifested at diferent times of the day. It is proposed to be an adaptive defense property of plants against extreme environmental conditions during the day.

Conclusion: We evaluated daily temperature and light intensity-dependent activities of the enzymes involved in C_3 and C_4 pathways in two species related to C_4 subtypes and detected some variations in their performance. Different and similar regularities established in daily temperature and light intensity-dependent changes of activities of C_4 and C_3 enzymes in two species of Chenopodiaceae family are believed to be adaptive properties developed under adverse environmental conditions that provide maintaining high photosynthetic efficiency and performing protective functions. High temperature, solar intensity, and also salinity and drought, characteristic of the territory, where the research was performed, create extreme conditions for the vegetation. Nevertheless, high diversity of Chenopodiaceae is observed in such a territory. Tolerance of these species against the mentioned factors, especially, high temperature and drought, opens wide opportunities for comparative analysis of adaptive properties of these plants.

References

Akhani H., Trimborn P., Ziegler H.: Photosynthetic pathways in *Chenopodiaceae* from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. – Plant Syst. Evol. **206**: 187-221, 1997.

Alfonso S.U., Brüggemann W.: Photosynthetic responses of a C_3 and three C_4 species of the genus *Panicum* (s.l.) with different metabolic subtypes to drought stress. – Photosynth. Res. **112**: 175-191, 2012.

Avasthi K., Izui K., Raghavendra A.S.: Interplay of light and temperature during the planta modulation of C_4 phospho*enol*pyruvate carboxylase from the leaves of *Amaranthus hypochondriacus* L.: diurnal and seasonal effects manifested at molecular levels. – J. Exp. Bot. **62**: 1017-1026, 2011.

Avasthi U.K., Raghavendra A.S.: Mutual stimulation of temperature and light effects on C_4 phospho*enol*pyruvate carboxylase in leaf discs and leaves of *Amaranthus hypochondriacus*. – J. Plant Physiol. **165**: 1023-1032, 2008.

Bailey K.J., Gray J.E., Walker R.P., Leegood R.C.: Coordinate regulation of phosphoenolpyruvate carboxylase and phospho*enol*pyruvate carboxykinase by light and CO_2 during C_4 photosynthesis. – Plant Physiol. **144**: 479-486, 2007.

Bradford M.: Rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. – Anal. Biochem. **72**: 248-254, 1976.

Brestic M., Živčák M., Kunderliková K., Allakhverdiev S.I.: High temperature specifically affects the photoprotective responses of chlorophyll *b*-deficient wheat mutant lines. – Photosynth. Res. **130**: 251-266, 2016.

Chinthapalli B., Murmu J., Raghavendra A.S.: Dramatic difference in the responses of phospho*enol*pyruvate carboxylase to temperature in leaves of C_3 and C_4 plants. – J. Exp. Bot. **54**: 707-714, 2003.

Chinthapalli B., Chitra D.S.V., Radhavendra A.S.: Temperature modulation of the activity and malate inhibition of the phospho*enol*pyruvate carboxylase from leaves of *Alternanthera pengens*, compared to that of *Lycoperisicon esculentum*. – Am. J. Biosci. **2**: 238-243, 2014.

Chollet R., Vidal J., O'Leary M.H.: Phospho*enol*pyruvate carboxylase:a ubiquitous, highly regulated enzyme in plants. – Annu. Rev. Plant Phys. **47**: 273-298, 1996.

Du Y.-Ch., Nose A., Kondo A., Wasano K.: Diurnal changes in photosynthesis in sugarcane leaves. I. Carbon dioxide exchange rate, photosynthesis enzyme activities and metabolite levels relating to the C_4 pathway and the Calvin cycle. – Plant Prod. Sci. **3**: 3-8, 2000.

Dwyer S.A., Ghannoum O., Nicotra A., von Caemmerer S.: High temperature acclimation of C_4 photosynthesis in linked to changes in photosynthetic biochemistry. – Plant Cell Environ. **30**: 53-66, 2007.

Edwards G.E., Franceschi V.R., Voznesenkaya E.V.: Single cell C_4 photosynthesis versus the dual-cell (Kranz) paradigm. – Annu. Rev. Plant Biol. **55**: 173-196, 2004.

Giglioli-Guivarc'h N., Pierre J.-N., Brown S. *et al*.: The light-dependent transduction pathway controlling the regulatory phosphorylation of C_4 phospho*enol*pyruvate carboxylase in protoplasts from *Digitaria sanguinalis*. – Plant Cell **8**: 573-586, 1996.

Gowik U., Westhoff P.: The path from C_3 and C_4 photosynthesis. – Plant Physiol. **155**: 56-63, 2011.

Hatch M.D.: C_4 photosynthesis in a unique blend of modified biochemistry, anatomy and ultrastructure. – BBA-Rev. Bioenergetics **895**: 81-106, 1987.

Hibberd J.M., Covshoff S.: The regulation of gene expression required for C_4 photosynthesis. – Annu. Rev. Plant Biol. **61**: 181-207, 2010.

Holaday A.S., Martindale W., Alred R. *et al*.: Changes in activities of enzymes of carbon metabolism in leaves during exposure of plants to low temperature. – Plant Physiol. **98**: 1105-1114, 1992.

Leegood R.C.: C_4 photosynthesis: principles of CO_2 concentration and prospects for its introduction into C_3 plants. – J. Exp. Bot. **53**: 581-590, 2002.

Long S.P.: Environmental responses. – In: Sage R.F., Monson R.K. (ed.): C_4 Plant Biology. Pp. 215-249. Academic Press, San Diego 1999.

Movsumova F.G., Babayev H.G., Zeynalova M.H., Feyziyev Y.M.: [Taxonomic composition of *Chenopodiaceae* Vent. family in Absheron flora and its ecological analysis.] – Proc.

Azerbaijan Natl. Acad. Sci. (Biol. Med. Sci.) **69**: 27-35, 2014. [In Russian]

O'Leary B., Park J., Plaxton W.C.: The remarkable diversity ofplant PEPC (phospho*enol*pyruvate carboxylase): recent insights into the physiological functions and post-translational controls of non-photosynthetic PEPCs. – Biochem. J. **436**: 15-34, 2011.

Pyankov V., Ziegler H., Kuz'min A., Edwards G.E.: Origin and evolution of C_4 photosynthesis in the tribe Salsoleae (Chenopodiaceae) based on anatomical and biochemical types in leaves and cotyledons. – Plant Syst. Evol. **230**: 43-74, 2001.

Pyankov V.I., Voznesenskaya E.V., Kuz'min A.N. *et al.*: Occurrence of C_3 and C_4 photosynthesis in cotyledons and leaves of *Salsola* species (*Chenopodiaceae*). – Photosynth. Res. **63**: 69-84, 2000.

Rosnow J.J., Edwards G.E., Roalson E.H.: Positive selection of Kranz and non-Kranz C_4 phospho*enol*pyruvate carboxylase amino acids in Suaedoideae (Chenopodiaceae). – J. Exp. Bot. **65**: 3595-3607, 2014.

Sage R.F., Christin P.A., Edwards E.J.: The C_4 plant lineages of planet Earth. – J. Exp. Bot. **62**: 3155-3169, 2011.

Sage R.F., Kocacinar F., Kubien D.S.: C_4 photosynthesis and temperature. – In: Raghavendra A.S., Sage R.F. (ed.): C_4 Photosynthesis and Related CO_2 Concentrating Mechanisms. Pp. 161-195. Springer Sci+Business Media BV, Dordrecht 2011.

Schüssler Ch., Freitag H., Koteyeva N. *et al.*: Molecular phylogeny and forms of photosynthesis in tribe Salsoleae (Chenopodiaceae). – J. Exp. Bot. **68**: 207-223, 2017.

Taniguchi M., Kobe M., Kato M., Sugiyama T.: Aspartate aminotransferase isozymes in *Panicum miliaceum* L., an NAD-Malic enzyme-type C_4 plant: Comparison of enzymatic-properties, primary structures, and expression patterns. – Arch. Biochem. Biophys. **318**: 295-306, 1995.

Taniguchi M., Sugiyama T.: Aspartate aminotransferase from *Eleusine coracana*, a C_4 plant: Purification, characterization, and preparation of antibody. – Arch. Biochem. Biophys. **282**: 427-432, 1990.

Yamori W., Hikosaka K., Way D.A.: Temperature response of photosynthesis in C_3, C_4, and CAM plants: temperature acclimation and temperature adaptation. – Photosynth. Res. **119**: 101-117, 2014.