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Photosynthetic acclimation to elevated CO_2 in relation to leaf saccharide constituents in wheat and sunflower

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Abstract

Wheat (*T. durum* cvs. HD 4502 and B 449, *T. aestivum* cvs. Kalyansona and Kundan) and sunflower (*Helianthus annuus* L. cv. Morden) were grown under atmospheric (360±10 $cm^3\ m^{-3}$, AC) and elevated CO_2 (650±50 $cm^3\ m^{-3}$, EC) concentration in open top chambers for entire period of growth and development till maturity. Leaf net photosynthetic rate (P_N) of EC-grown plants of wheat measured at EC was significantly decreased in comparison with AC-plants of wheat measured at EC. Sunflower, however, showed no significant depression in P_N in EC-plants. There was a decrease in ribulose-1,5-bisphosphate carboxylase (RuBPC) activity, its activation state and amount in EC-plants of wheat, whereas no significant decrease was observed in sunflower. The above different acclimation to EC in wheat and sunflower was related with saccharide constituents accumulated in the leaves. Under EC, sunflower accumulated in the leaves more starch, whereas wheat accumulated more sugars.

Additional key words: dry matter production; feedback inhibition; ribulose-1,5-bisphosphate carboxylase activity; RuBPC content; starch; stomatal conductance; sugars.

Introduction

Atmospheric CO_2 concentration (AC) has risen from pre-industrial concentration of 280 $cm^3\ m^{-3}$ to over 360 $cm^3\ m^{-3}$ and is rising at a rate of over 1.5 $cm^3\ m^{-3}$ per year (Keeling and Whorf 1992, Bowes 1996, Makino and Mae 1999). Because net photosynthetic rate (P_N) of C_3 plants, which constitute more than 90 % of terrestrial species, is limited by the supply of CO_2 at its present concentration in the atmosphere, a rise in AC increases P_N in short-term studies (Lemon 1983). Photosynthetic response decreases under long-term exposure to elevated CO_2 (EC) environment (Peet *et al.* 1986, Sage *et al.* 1989) and has been attributed to photosynthetic acclimation or adjustment. Photosynthetic acclimation is a change in photosynthetic efficiency of leaves due to long-term exposure to EC. Photosynthetic acclimation is clearly revealed by comparing P_N of AC- and EC-grown plants at the same concentration of CO_2 (Drake *et al.* 1997, Ghildiyal and Sharma-Natu 2000). Acclimation to EC usually results in down-regulation of CO_2 fixation although long-term positive changes in P_N have also been reported in some species (Sage *et al.* 1989, Ziska *et al.* 1991, Kalina and Ceulemans 1997, Ghildiyal *et al.* 1998, Fernández *et al.* 1999, Ghildiyal and Sharma-Natu 2000). The physiological basis of such genotype differences in photosynthetic acclimation to EC is not clear. Plants showing little or no down-regulation of P_N under long-term exposure to EC may be able to utilise the beneficial effect of EC on P_N and consequently productivity.

One of the factors that may influence photosynthetic acclimation to EC is the imbalance in the supply and demand of saccharides resulting in end product inhibition (Neales and Incoll 1968, Herold 1980). Plant species differ in the type of saccharides that accumulate in leaves. Sunflower is a starch accumulator (Potter and Breen 1980, Mitra and Srivastava 1993), whereas wheat accumulates more of sugars in the leaves (Azcón-Bieto 1983, Sharma-Natu and Ghildiyal 1993, Ghildiyal and Sharma-Natu 1995). The present study, therefore, has been undertaken on the photosynthetic acclimation to EC in cultivars of two species of wheat and in sunflower that differ in the saccharide constituents accumulated in the leaves.

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Abbreviations: AC, atmospheric CO_2 concentration; EC, elevated CO_2 concentration; g_s, stomatal conductance; P_N, net photosynthetic rate; RuBPC, ribulose-1,5-bisphosphate carboxylase.

Materials and methods

Two cultivars each of *Triticum durum* L. (HD 4502 and B 449) and *Triticum aestivum* L. (Kalyansona and Kundan) and one cultivar of sunflower (*Helianthus annuus* L. cv. Morden) were used. They were grown in atmospheric (360 ± 10 cm^3 m^{-3}, AC) and elevated (650 ± 50 cm^3 m^{-3}, EC) CO_2 concentrations inside the open top chambers (200×160 cm) for entire period of growth and development till maturity. The construction of the open top chambers was based on the design of Leadley and Drake (1993). Standard cultural practices were followed (Singh 1983). HD 4502 is a small grain cultivar with more grains per ear than the bolder grain cultivar B 449 having fewer grains per ear. Cultivar Kalyansona has more grains whereas cv. Kundan is a bold grain type. Date of anthesis in the main shoot (MS) was recorded on the tags placed on each plant.

P_N of the flag leaf (uppermost fully expanded leaf) of main shoot (MS) of AC- and EC-grown plants was measured between 10:00 and 11:00 h, at anthesis stage using the *Li-Cor 6200* (*Li-Cor*, Lincoln, NE, USA) portable photosynthetic system. The incident photosynthetic photon flux density during gas exchange measurement was saturating (>1 200 µmol m^{-2} s^{-1} upon the leaf surface). P_N of AC- and EC-grown plants was measured not only at their respective growth CO_2 concentrations but also P_N of AC-plants was measured at EC and P_N of EC-plants at AC. At around 11:00 h comparable leaves were sampled for sugar and starch estimation, plunged into boiling 95 % ethanol for 2 min, and preserved. Contents of reducing, non-reducing, and total sugars and of starch were determined as described by Ghildiyal and Sinha (1977). Dry matter per plant of AC- and EC-plants was determined at maturity. There were at least three replications for each observation.

Leaf samples for RuBP carboxylase (RuBPC) activity and content were taken around 11:00 h and stored in liquid nitrogen. RuBPC was rapidly extracted following the method of Servaites *et al.* (1984). The RuBPC activities were estimated by RuBP dependent incorporation of $^{14}CO_2$ into an acid stable product. 'Initial' activities were measured at 25 °C by injecting 50 mm^3 of 5 mM RuBP and 25 mm^3 of soluble leaf extract into an assay mixture containing (final concentrations) 50 mM Tris-HCl (pH 8.0), 20 mM $MgCl_2$, 0.1 % (m/v) bovine serum albumin, and 10 mM $NaH^{14}CO_3$ (74 kBq per assay) in a total volume of 0.5 cm^3. The reaction was terminated after 60 s by addition of 100 mm^3 of 6 M acetic acid; the material was dried at 65 °C, and the acid-stable ^{14}C was estimated by liquid scintillation counting. 'Total' activities were determined in a similar way except that 25 mm^3 of the soluble leaf extract and 425 mm^3 of assay mixture were incubated together for 10 min at 25 °C before 50 mm^3 of 5 mM RuBP were added. From the initial and total activities the % activation of the enzyme was calculated (Servaites *et al.* 1984). RuBPC content was determined using SDS-PAGE (Laemmli 1970, Servaites *et al.* 1984). LSU and SSU bands of RuBPC were quantified by using laser densitometer (*LKB Ultrascan XL*, *Pharmacia*). Soluble protein content was determined by the method of Bradford (1976).

Results

P_N was higher in EC-plants than in AC-plants when measured at their respective growth CO_2 concentrations in all the five genotypes examined in this study (Table 1). Enhancement was maximal in sunflower. In durum wheat the cv. HD 4502 and in aestivum wheat the cv. Kalyansona, that have more grains per ear, showed a larger enhancement of P_N in EC. Photosynthetic acclimation was determined by comparing P_N of AC- and EC-grown plants measured at the same concentration of CO_2. Such comparison revealed a decrease in P_N in EC-plants in wheat cultivars and no significant down-regulation of P_N under EC in sunflower (Table 1). The stomatal conductance (g_s) of EC-plants was lower than that of AC-plants when measured at the respective growth CO_2 concentrations (Table 1). However, when measured at the same CO_2 concentration, the differences in g_s in AC- and EC-plants were not significant except for B 449 and Kundan measured at AC.

The content of sugars in the leaves of EC-plants was significantly larger than that of AC-plants for all the genotypes of wheat (Table 2). The increase in sugar content was mostly due to increase in non-reducing sugars in EC plants. Only in HD 4502, the content of reducing sugars was also increased under EC. There was no significant increase in leaf starch content under EC compared to AC in wheat cultivars. However, in sunflower the content of reducing sugars was increased more than the content of non-reducing sugars in the leaves of EC-plants. Sunflower, however, accumulated significantly higher amount of starch in EC-plants than in AC-plants (Table 2). The decrease of P_N in EC-plants compared to AC-plants when compared at the same CO_2 concentration (photosynthetic acclimation) was probably associated with the net accumulation of non-reducing sugars in these genotypes (Fig. 1). Sunflower accumulated least amount of non-reducing sugars in the leaves and showed less down-regulation of P_N under EC. The accumulation of starch in the leaves was not associated with a decrease in P_N under EC. Sunflower cv. Morden showed the highest accumulation of starch in the leaves and the least decrease in P_N under EC (Fig. 1).

RuBPC initial activity was decreased significantly

Table 1. Net photosynthetic rate, P_N [μmol(CO_2) m^{-2} s^{-1}] and stomatal conductance, g_s [mol(H_2O) m^{-2} s^{-1}] in the leaves of wheat and sunflower cultivars grown in ambient (AC) and elevated (EC) CO_2 concentrations. LSD at 5 % *p*; NS = not significant.

Plant	Cultivar	Measurements	P_N AC	EC	LSD	EC/AC	g_s AC	EC	LSD
T. durum	HD 4502	AC at AC, EC at EC	16.02	24.39	4.52	1.52	0.173	0.121	0.023
		at AC	16.02	13.12	2.78	0.82	0.173	0.179	NS
		at EC	32.30	24.39	4.93	0.76	0.135	0.121	NS
	B 449	AC at AC, EC at EC	21.83	27.85	4.54	1.27	0.281	0.196	0.056
		at AC	21.83	15.64	3.68	0.72	0.281	0.248	0.030
		at EC	40.58	27.85	3.32	0.69	0.206	0.196	NS
T .aestivum	Kalyansona	AC at AC, EC at EC	19.57	27.30	4.14	1.39	0.203	0.174	0.027
		at AC	19.57	16.77	2.18	0.86	0.203	0.208	NS
		at EC	35.95	27.30	6.79	0.76	0.185	0.174	NS
	Kundan	AC at AC, EC at EC	17.25	22.57	3.87	1.31	0.165	0.139	0.016
		at AC	17.25	9.27	1.81	0.54	0.165	0.135	0.023
		at EC	33.41	22.57	9.12	0.68	0.151	0.139	NS
Helianthus	Morden	AC at AC, EC at EC	14.38	38.67	2.51	2.68	0.176	0.146	0.025
		at AC	14.38	13.08	NS	0.91	0.176	0.169	NS
		at EC	40.44	38.67	NS	0.96	0.144	0.146	NS

Table 2. Sugar and starch contents [g kg^{-1}(d.m.)] and initial and total RuBPC activity [μmol(CO_2) kg^{-1}(f.m.) s^{-1}], its activation state [%], and content [g kg^{-1}(f.m.)] in the leaves of wheat and sunflower cultivars grown under ambient (AC) and elevated (EC) CO_2 concentrations. LSD at 5 % *p*; NS = not significant.

Plant	Cultivar	Saccharides	AC	EC	LSD	RuBPC	AC	EC	EC/AC
T. durum	HD 4502	Reducing sugars	20.58	32.42	10.82	Initial activity	77.65	57.66	0.74
		Non-reducing sugars	24.72	34.65	8.17	Total activity	108.65	128.32	1.18
		Total sugars	45.30	67.07	18.86	Activation [%]	71.46	44.93	0.63
		Starch	96.00	106.00	NS	Content	8.40	6.54	0.77
	B 449	Reducing sugars	11.84	11.49	NS	Initial activity	134.32	99.32	0.74
		Non-reducing sugars	10.68	34.88	12.89	Total activity	194.31	201.31	1.04, NS
		Total sugars	22.52	46.37	12.18	Activation [%]	69.12	49.34	0.71
		Starch	130.20	140.00	NS	Content	10.01	8.09	0.80
T .aestivum	Kalyansona	Reducing sugars	19.56	17.73	NS	Initial activity	72.65	44.33	0.61
		Non-reducing sugars	29.31	43.49	10.17	Total activity	100.32	116.65	1.16
		Total sugars	48.87	61.22	10.22	Activation [%]	72.41	38.00	0.52
		Starch	140.00	150.00	NS	Content	7.85	5.60	0.71
	Kundan	Reducing sugars	9.79	10.41	NS	Initial activity	70.66	61.32	0.86
		Non-reducing sugars	22.93	51.38	16.65	Total activity	83.65	91.65	1.09, NS
		Total sugars	32.72	61.79	15.63	Activation [%]	84.47	66.90	0.79
		Starch	149.77	162.66	NS	Content	11.02	9.70	0.88
Helianthus	Morden	Reducing sugars	14.74	27.15	7.94	Initial activity	58.66	61.99	1.06, NS
		Non-reducing sugars	18.86	23.60	NS	Total activity	70.99	65.32	0.92, NS
		Total sugars	33.60	50.75	19.20	Activation [%]	82.63	94.90	1.14
		Starch	134.00	202.00	30.74	Content	7.62	7.30	0.96

in EC-grown wheat cultivars whereas its total activity was greater in EC-plants of HD 4502 and Kalyansona (Table 2). In B 449 and Kundan, no significant difference in total activity of AC- and EC-plants was observed. In sunflower, 'initial' and 'total' RuBPC activities were not significantly affected by EC. The RuBPC activation was significantly decreased under EC in wheat genotypes. In sunflower, no significant effect on RuBPC activation was observed under EC. RuBPC content decreased significantly under EC in wheat cultivars but not in sunflower (Table 2). Among the genotypes examined, sunflower showed the greater response to EC in terms of dry matter per plant and least down-regulation of P_N under EC (Table 3).

Discussion

In the present study P_N of EC-plants of both wheat and sunflower was higher than that of AC-plants when P_N was measured at their respective growth CO_2 concentrations. However, for comparing the photosynthetic efficiency of AC- and EC-plants, P_N should be measured at identical condition (Drake *et al.* 1997). P_N of AC- and EC-plants was therefore compared at the same CO_2 concentration. This revealed a decrease in P_N of EC-plants of wheat compared to AC-plants. Such change in photosynthetic properties and consequently in photosynthetic efficiency of leaves due to long-term exposure to EC is called photosynthetic acclimation (Sage 1994). Sunflower, however, did not show such a down-regulation of P_N (or negative acclimation of P_N) under EC. No significant down-regulation of P_N under EC in sunflower, therefore, resulted in its greater dry matter response to EC.

Table 3. Per cent response of wheat and sunflower cultivars to elevated CO_2 (EC) in terms of dry matter production and photosynthetic acclimation. LSD at 5 % p; NS = not significant.

		Dry matter per plant	Decrease in P_N (acclimation)
T. durum	HD 4502	32.40	22.22
	B 449	22.40	28.35
T. aestivum	Kalyansona	24.59	14.30
	Kundan	12.35	46.20
Helianthus	Morden	45.65	9.04, NS

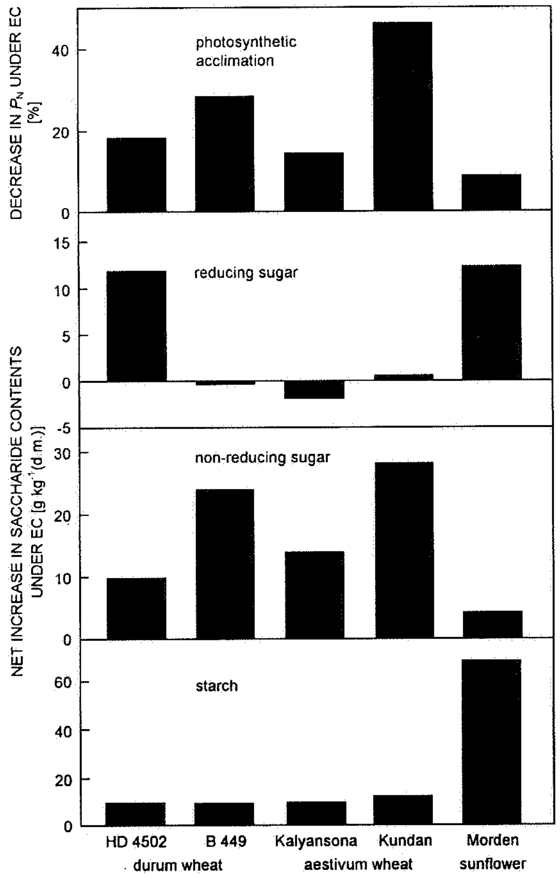

Fig. 1. Photosynthetic acclimation [% decrease in P_N under EC] in relation to net increase in content of leaf saccharides under EC.

The decrease in P_N under EC compared to AC in wheat may not be explained entirely on the basis of g_s in the present study. The g_s was lower in EC-plants compared to AC-plants when measured at the respective growth CO_2 concentrations, yet P_N was high in EC-plants because of high AC. In the present study, when comparison of g_s of AC- and EC-plants was made at the same CO_2 concentration, g_s generally did not differ significantly whereas P_N was decreased in EC-plants. Drake *et al.* (1997) using the ratio of intercellular and ambient CO_2 concentrations, C_i/C_a as an index of the limitation of photosynthesis have reported that mean range of C_i/C_a is nearly identical for both AC- and EC-plants in 26 species examined. They suggest that g_s is reduced in EC, but it does not limit photosynthesis at EC more than it does at AC. Furthermore, a comparison of P_N at the same C_i (when the stomatal factor is eliminated) shows that P_N is lower in EC-plants indicating photosynthetic acclimation at the metabolic level (Sage 1994, Sharma-Natu *et al.* 1997).

The photosynthetic CO_2 fixation is a manifestation of the reaction catalysed by RuBPCO. A decrease in RuBPC content and activity under long-term CO_2 enrichment has been reported in many plant species (Sage *et al.* 1989, Rowland-Bamford *et al.* 1991, Jacob *et al.* 1995, Sharma-Natu *et al.* 1997, Vu *et al.* 1997). In the present study, the RuBPC activity, state of activation, and amount of RuPBC remained unaffected by CO_2 enrichment in sunflower whereas a decrease was observed in wheat. Campbell *et al.* (1988) observed in soybean that RuBPC activity and RuBPC protein content remained unaffected in EC-plants relative to AC-plants.

The present study indicated that the different acclimation to EC in terms of P_N and RuBPC in wheat and sunflower might be due to differences in the saccharide constituents that accumulated in the leaves. Wheat accumulated in leaves mostly sugars, whereas sunflower accumulated mainly starch. Accumulation of sugars may inhibit P_N by decreasing the flux of P_i into the chloroplast (Sharkey 1990, Stitt 1996) and through repressing the expression of photosynthetic genes including those encoding small and large subunits of RuBPCO (Sheen 1994, Koch 1996, Van Oosten and Besford 1996, Cheng *et al.* 1998, Gesch *et al.* 1998). The decrease in RuBPC activity, activation state, and amount observed in wheat in the present study can therefore be explained on the basis of the above mentioned sugar accumulation in the leaves. On the other hand, a starch accumulator that continues to recycle P_i for photosynthesis consequently may sustain P_N unless starch granules start shading and disrupting the chloroplast (Vu *et al.* 1989). This may probably happen at extreme level of accumulation. RuBPC amount, activity, and activation state were, therefore, not significantly affected in sunflower. The less sensitivity of P_N to accumulation of starch has also been reported in mungbean (Ghildiyal and Mitra 1988, Ghildiyal and Sharma-Natu 1995) and soybean (Potter and Breen 1980). Plant species showing little or no down-regulation of P_N under EC, such as soybean (Xu *et al.* 1994), mungbean (Ghildiyal *et al.* 1998), potato (Sage *et al.* 1989), and radish (Usuda and Shimogawara 1998) are starch accumulators. Therefore the accumulation of excess saccharides in a form that is less inhibitory may decrease the down regulation of photosynthesis under EC and enable plants to utilise the beneficial effect of EC on photosynthesis and production more efficiently.

References

Azcón-Bieto, J.: Inhibition of photosynthesis by carbohydrates in wheat leaves. – Plant Physiol. **73**: 681-686, 1983.

Bowes, G.: Photosynthetic responses to changing atmospheric carbon dioxide concentration. – In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 387-407. Kluwer Academic Publ., Dordrecht – Boston – Lancaster 1996.

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

Campbell, W.J., Allen, L.H., Jr., Bowes, G.: Effects of CO_2 concentration on Rubisco activity, amount, and photosynthesis in soybean leaves. – Plant Physiol. **88**: 1310-1316, 1988.

Cheng, S.H., Moore, B.d., Seemann, J.R.: Effects of short- and long-term elevated CO_2 on the expression of ribulose-1,5-bisphosphate carboxylase/oxygenase genes and carbohydrate accumulation in leaves of *Arabidopsis thaliana* (L.) Heynh. – Plant Physiol. **116**: 715-723, 1998.

Drake, B.G., Gonzàlez-Meler, M.A., Long, S.P.: More efficient plants: A consequence of rising atmospheric CO_2? – Annu. Rev. Plant Physiol. Plant mol. Biol. **48**: 609-639, 1997.

Fernàndez, M.D., Pieters, A., Azkue, M., Rengifo, E., Tezara, W., Woodward, F.I., Herrera, A.: Photosynthesis in plants of four tropical species growing under elevated CO_2. – Photosynthetica **37**: 587-599, 1999.

Gesch, R.W., Boote, K.J., Vu, J.C.V., Allen, L.H., Jr., Bowes, G.: Changes in growth CO_2 result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase oxygenase small subunit gene expression in expanding and mature leaves of rice. – Plant Physiol. **118**: 521-529, 1998.

Ghildiyal, M.C., Mitra, S.: Photosynthesis in relation to saccharides in mungbean leaves. – Photosynthetica **22**: 127-128, 1988.

Ghildiyal, M.C., Sharma-Natu, P.: Photosynthesis in relation to saccharides in wheat and mungbean leaves. – In: Mathis, P. (ed.): Photosynthesis: from Light to Biosphere. Vol. V. Pp. 667-669. Kluwer Academic Publ., Dordrecht – Boston – London 1995.

Ghildiyal, M.C., Sharma-Natu, P.: Photosynthetic acclimation to rising atmospheric carbon dioxide concentration. – Indian J. exp. Biol. **38**: 961-966, 2000.

Ghildiyal, M.C., Sharma-Natu, P., Khan, F.A.: Photosynthetic acclimation to elevated CO_2 in relation to saccharides content in wheat and mungbean leaves. – Indian J. exp. Biol. **36**: 217-220, 1998.

Ghildiyal, M.C., Sinha, S.K.: Physiological analysis of heterosis in *Zea mays* L. I. Changes in sugars and starch contents in relation to grain development. – Indian J. exp. Biol. **14**: 899-904, 1977.

Herold, A.: Regulation of photosynthesis by sink activity – the missing link. – New Phytol. **86**: 131-144, 1980.

Jacob, J., Greitner, C., Drake, B.G.: Acclimation of photosynthesis in relation to rubisco and non-structural carbohydrate contents. – Plant Cell Environ. **18**: 875-884, 1995.

Kalina, J., Ceulemans, R.: Clonal differences in the response of dark and light reactions of photosynthesis to elevated atmospheric CO_2 in poplar. – Photosynthetica **33**: 51-61, 1997.

Keeling, C.D., Whorf, T.P.: Atmospheric CO_2 – modern record Mauna Loa. – In: Boden, T.A., Sepanski, R.J., Stoss, F.W. (ed.): Trends' 91 – A Compendium of Data on Global Change Highlights. Pp. 14-17. Carbon Dioxide Information Analysis Centre, Oak Ridge National Laboratory, Oak Ridge 1992.

Koch, K.E.: Carbohydrate-modulated gene expression in plants. – Annu. Rev. Plant Physiol. Plant mol. Biol. **47**: 509-540, 1996.

Laemmli, U.K.: Cleavage of structural proteins during the assembly of the head of bacteriophage T4. – Nature **227**: 680-685, 1970.

Leadley, P.W., Drake, B.G.: Open top chambers for exposing plant canopies to elevated CO_2 concentration and for measuring net gas exchange. – Vegetatio **104/105**: 3-15, 1993.

Lemon, E.R.: CO_2 and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide. – Westview Press, Washington 1983.

Makino, A., Mae, T.: Photosynthesis and plant growth at elevated levels of CO_2. – Plant Cell Physiol. **40**: 999-1006, 1999.

Mitra, S., Srivastava, G.C.: Photosynthesis as influenced by assimilate level in sunflower (*Helianthus annuus* L.). – J. Agron. Crop Sci. **171**: 20-25, 1993.

Neales, T.F., Incoll, L.D.: The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis. – Bot. Rev. **34**: 107-125, 1968.

Peet, M.M., Huber, S.C., Patterson, D.T.: Acclimation to high CO_2 in monoecious cucumbers. II. Carbon exchange rates, enzyme activities, and starch and nutrient concentrations. – Plant Physiol. **80**: 63-67, 1986.

Potter, J.R., Breen, P.J.: Maintenance of high photosynthetic rates during the accumulation of high leaf starch levels in sunflower and soybean. – Plant Physiol. **66**: 528-531, 1980.

Rowland-Bamford, A.J., Baker, J.T., Allen, L.H., Jr., Bowes, G.: Acclimation of rice to changing atmospheric carbon dioxide concentration. – Plant Cell Environ. **14**: 577-583, 1991.

Sage, R.F.: Acclimation of photosynthesis to increasing atmospheric CO_2: The gas exchange perspective. – Photosynth. Res. **39**: 351-368, 1994.

Sage, R.F., Sharkey, T.D., Seemann, J.R.: Acclimation of photosynthesis to elevated CO_2 in five C_3 species. – Plant Physiol. **89**: 590-596, 1989.

Servaites, J.C., Torisky, R.S., Chao, S.F.: Diurnal changes in ribulose-1,5-bisphosphate carboxylase activity and activation state in leaves of field-grown soybeans. – Plant Sci. Lett. **35**: 115-121, 1984.

Sharkey, T.D.: Feedback limitation of photosynthesis and the physiological role of ribulose-1,5-bisphosphate carbamylation. – Bot. Mag. (Tokyo) **2**: 87-105, 1990.

Sharma-Natu, P., Ghildiyal, M.C.: Diurnal changes in photosynthesis in relation to ribulose-1,5-bisphosphate carboxylase activity and saccharides content in wheat leaves. – Photosynthetica **29**: 551-556, 1993.

Sharma-Natu, P., Khan, F.A., Ghildiyal, M.C.: Photosynthetic acclimation to elevated CO_2 in wheat cultivars. – Photosynthetica **34**: 537-543, 1997.

Sheen, J.: Feedback control of gene expression. – Photosynth. Res. **39**: 427-438, 1994.

Singh, C.: Modern Techniques of Raising Field Crops. – Oxford & IBH Publishers, New Delhi – Calcutta 1983.

Stitt, M.: Metabolic regulation of photosynthesis. – In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 151-190. Kluwer Academic Publishers, Dordrecht – Boston – London 1996.

Usuda, H., Shimogawara, K.: The effects of increased atmospheric carbon dioxide on growth, carbohydrates, and photosynthesis in radish, *Raphanus sativus*. – Plant Cell Physiol. **39**: 1-7, 1998.

Van Oosten, J.-J., Besford, R.T.: Acclimation of photosynthesis to elevated CO_2 through feedback regulation of gene expression: Climate of opinion. – Photosynth. Res. **48**: 353-365, 1996.

Vu, J.C.V., Allen, L.H., Jr., Bowes, G.: Leaf ultrastructure, carbohydrates and protein of soybeans grown under CO_2 enrichment. – Environ. exp. Bot. **29**: 141-147, 1989.

Vu, J.C.V., Allen, L.H., Jr., Boote, K.J., Bowes, G.: Effect of elevated CO_2 and temperature on photosynthesis and Rubisco in rice and soybean. – Plant Cell Environ. **20**: 68-76, 1997.

Xu, D.Q., Gifford, R.M., Chow, W.S.: Photosynthesis acclimation in pea and soybean to high atmospheric CO_2 partial pressure. – Plant Physiol. **106**: 661-671, 1994.

Ziska, L.H., Hogan, K.P., Smith, A.P., Drake, B.G.: Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. – Oecologia **86**: 383-389, 1991.