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AUSTRALIAN JOURNAL OF PLANT PHYSIOLOGY

Volume 27, 2000

An international journal of plant function

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the Australian Academy of Science

Aust. J. Plant Physiol., 2000, **27**, 1119–1130

Effects of elevated CO_2 concentration on photosynthetic acclimation and productivity of two potato cultivars grown in open-top chambers

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Abstract. In two subsequent years, an early maturing potato cultivar with low leaf area index (LAI) and a late cultivar with high LAI were grown at concentrations of 350 and 700 μL CO_2 L^{-1} in open-top chambers. The average increase of tuber dry matter yield by elevated CO_2 was 27% in 1995 and 49% in 1996. During the first weeks after planting, elevated CO_2 stimulated the light-saturated rate of photosynthesis (A_{max}) of both cultivars by 80%. However, A_{max} under elevated CO_2 declined to the level of the low-CO_2 treatment in the course of the growing season. In 1995 this convergence due to acclimation of photosynthesis was completed within 6 weeks, but in 1996, acclimation proceeded until the end of the growing season. Photosynthetic acclimation was accompanied by a reduced Rubisco content, and was correlated more closely with accumulation of sucrose than of starch. From fluorescence measurements it was concluded that, in contrast to the carboxylation efficiency, the efficiency of photosynthetic reactions centers was not affected by acclimation to elevated CO_2. The faster photosynthetic acclimation in 1995 coincided with overall lower values of A_{max}, crop growth rate and growth response to elevated CO_2. It is shown that the indeterminate growth pattern of potato with its large sink capacity does not preclude acclimation. The effect of acclimation on yield was quantified by computer simulations. The simulated results indicated that photosynthetic acclimation reduced the positive effect of elevated CO_2 on tuber yield by 50%.

Keywords: acclimation, climate change, elevated CO_2, photosynthesis, open-top chambers, potato, simulation model, *Solanum tuberosum*, source–sink.

Introduction

An elevated atmospheric CO_2 concentration stimulates the productivity of a broad range of agricultural crops (Kimball 1983; Lawlor and Mitchell 1991). However, the range of values obtained for the stimulation of Net Primary Production (NPP) by elevated CO_2 is often very large, even within species (e.g. 7–97% for wheat; Poorter 1993). In the comparison between species and cultivars it is essential to pay attention to the growing conditions. Interaction between temperature, light and phenology is quite decisive for the overall effect (Grashoff *et al.* 1995; Morison and Lawlor 1999). In a closed canopy of winter wheat, doubled CO_2 stimulated daily net photosynthesis by 5% in early spring, but 40% in late spring (Dijkstra *et al.* 1999).

Other important crop-specific properties such as the length of the vegetative stage (Acock *et al.* 1985), the time until canopy closure and start of senescence (Curtis *et al.* 1989; Grulke *et al.* 1990), the ability to store carbon in storage pools (Ammerlaan and de Visser 1993) and the use of carbohydrates as an energy source for nitrogen fixation (Ryle *et al.* 1992*a*, *b*) all have a significant influence on yield response to climate change. The initial stimulation of photosynthesis can be reduced by direct feedback inhibition due to accumulation of chemical intermediates and, in the longer term, by a decrease of the transcripts that encode for the nuclear-encoded small subunit of Rubisco (Rbcs) and other proteins involved in photosynthesis (Van Oosten and Besford 1994). It has been proposed that an increase in hexose sugars leads, via hexokinase-related signaling, to a repression of Rbcs and other genes leading to a decrease in Rubisco. An extensive review on this subject has recently been published by Moore *et al.* (1999).

Abbreviations used: A_{max}, photosynthetic rate of a leaf at light saturation; BSA, bovine serum albumin; F_m, maximum fluorescence during a saturating light pulse; F_o, minimum fluorescence in the dark; fw, fresh weight; LAI, leaf area index; OTC, open-top chamber; PAR, photosynthetically active radiation; Rbcs, small subunit of Rubisco; Rubisco LSU, large subunit of Rubisco; SDS, sodium dodecyl sulfate; SLA, specific leaf area; Φ_{PC}, efficiency of energy transfer to open photosystem II reaction centres.

10.1071/PP99205 0310-7841/00/121119

Initial effects of CO_2 on photosynthesis and growth are thus often not sustained as a consequence of decreased leaf Rubisco content (Webber *et al.* 1994; Van Oosten and Besford 1995). Regulation of photosynthesis by this feedback mechanism is relatively well understood at the physiological level (Stitt 1991), but the consequences for productivity at the whole-plant and canopy levels are still speculative (Farrar and Williams 1991; Stitt and Knap 1999). The concept that photosynthetic acclimation is mainly expressed in determinate 'sink-limited' plants and absent in indeterminate or 'source-limited' plants is probably an oversimplification (Morison and Lawlor 1999). Potato is an excellent species to test the hypothesis related to this issue, that developmentally restricted capacity for growth or storage would lead to a feedback control on photosynthesis. Potato is not only an indeterminate plant; it also develops such large sinks that yield is expected to be limited by assimilate supply only, unless export is hampered by a blockage of phloem loading, or in the case that tuber filling is not as source-dependent as usually assumed. This was discovered in another major storage crop, sugar beet, that showed an unexpected sink control of CO_2 stimulation despite the large sink capacity of its tap root (Demmers-Derks *et al.* 1998).

Potato contains substantial genetic variation for tuber filling, reflecting phenological differences in sink activity. This makes comparison of potato cultivars an appropriate model system for study of sink–source interactions and acclimation under elevated CO_2. However, data from experiments with potato are scarce. The reported effects of CO_2 doubling on potato yield vary between slightly negative (Goudriaan and de Ruiter 1983) to a positive effect of 39% (Wheeler *et al.* 1991). In a Free Air CO_2 Enrichment (FACE) experiment, a potato crop grown in the field under otherwise natural conditions was exposed to elevated CO_2 by means of a sophisticated fumigation device (Miglietta *et al.* 1998), and plants were exposed to a gradient of CO_2 concentrations ranging from ambient to 460, 560 and 660 μmol mol^{-1}. An average increase in yield of 10% for each step of 100 μmol mol^{-1} increase in CO_2 was observed. Similar stimulation numbers have been reported in a recent paper on potatoes in open-top chambers (OTCs) (Sicher and Bunce 1999).

Strong accumulation of starch in leaves of potato plants that were grown under elevated CO_2 has been observed (Goudriaan and de Ruiter 1983; Sicher and Bunce 1999). Attempts were made to relate this phenomenon to photosynthetic acclimation by Ludewig *et al.* (1998), but their results showed an inverse correlation between starch content of leaves and photosynthetic acclimation. It thus seems that not starch but an intermediate sugar is responsible for acclimation (Stitt and Knapp 1999). The occurrence of acclimation itself is often difficult to distinguish from senescence (Miglietta *et al.* 1998). Overall, the results obtained with potato suggest that photosynthetic acclimation is a complex process involving potentially interactive effects of elevated CO_2 with source–sink relationships and with the canopy energy balance.

We hypothesize that the effect of elevated CO_2 on potato yield is determined by the summed effect of two mechanisms, both of which affect early and late cultivars to different extent. First, CO_2 affects source strength by increasing photosynthesis and growth of biomass and leaf area index (LAI). The increase in LAI itself will enhance light interception and thereby cause additional growth stimulation, but mainly in early maturing cultivars because only they are characterized by low LAI at ambient CO_2. Elevated CO_2 will increase light interception in early cultivars, both by faster canopy closure and by less vulnerability to leaf losses during the stage of senescence. The second mechanism through which elevated CO_2 affects early and late cultivars differentially is by the interaction of CO_2 with sink strength. Late cultivars have higher tuber production rates, which provide them with a more durable sink for the enhanced carbohydrate production under elevated CO_2, so photosynthetic acclimation is expected to be less in late cultivars than in early ones. Because the 'source mechanism' described above favours early cultivars, and the 'sink mechanism' favours late ones, the overall effect of elevated CO_2 on yield of potato will be determined by the summed effect. Interactions with environmental conditions will determine whether acclimation effects have a negative effect on yield or not.

The work presented in this paper aims at quantifying both mechanisms and thereby identifying the one of major importance. The importance of inter-annual variation in temperature and irradiance with respect to the complex interaction between acclimation, senescence and yield is illustrated. We complete our analysis by using a simulation model to quantify the consequences of the photosynthetic acclimation for tuber yield and to assess any possible improvement of the CO_2 effect.

Materials and methods

Experimental set-up

Two OTC experiments were carried out in 1995 and 1996, on light clay soil (pH 7.5, organic matter content 6%), in Wageningen, the Netherlands (51°58′ N, 5°40′ E). The experiments were performed in a factorial set-up, with two levels of CO_2 and two cultivars, in three replicates, giving 12 OTCs in all, and a fifth treatment consisting of six ambient plots. The two cultivars of potato (*Solanum tuberosum* L.) were the early maturing cultivar Gloria and the late maturing cultivar Elles. Single eye pieces were cut from sprouted tubers in April, and placed in containers filled with white sand and supplied daily with a nutrient solution prepared according to Steiner (1961). After emergence, the young single stem sprouts were uprooted and transplanted in OTCs in the field on 16–17 May 1995 and 13 May 1996 (days of the year 136–137 and 133, respectively). Additional potato sprouts were planted in a 0.75-m-wide border outside the OTCs to prevent irradiation from the sides. CO_2 was supplied via tubes on the soil surface and via an airbag at 1.3-m height. Additional tubes on the soil surface were used for irrigation whenever the topsoil dried out visibly. Dry soil had a

mineral nitrogen content of 4.68 g kg^{-1}. In addition, 15 g m^{-2} K_2O and 51.7 g m^{-2} $Ca(H_2PO_4)_2$ were added to the soil in late October. Nitrogen was supplied at the beginning of April (17.5 g m^{-2}), the beginning of June (15.0 g m^{-2}) and the beginning of July (4.0 g m^{-2}). The plantlets were planted 0.20 m apart with a spacing of 0.25 m between rows, giving a total density of 20 plantlets m^{-2}. Each plot consisted of 40 or 41 plants. Plots were watered through a drip-irrigation system. The experiments were set up as randomized block designs with three replicates. The CO_2 concentration was maintained at 350 μL L^{-1} in the low-CO_2 treatment and 700 μL L^{-1} in the high-CO_2 treatment.

Statistical analyses

Statistical analysis was carried out separately for the 1995 and 1996 experiments. All measurements were analysed using analysis of variance (ANOVA) corresponding to the two-factorial randomized block designs used; the ambient plots were not included in the ANOVAs.

Open-top chambers

The OTCs were constructed as equilateral hexagons with side width and length of 0.87 m, height of 1.95 m, and a volume of 3.8 m^3. Ground area inside the chamber was 1.95 m^2. Chambers were made from 3-mm polycarbonate (Lexan®; GE Plastics Europe BV, Bergen op Zoom, The Netherlands), without chamber supports. A frustum of 0.25 m at an angle of 45° was added on top. The material was 88% transparent for PAR, but absorbed all UV-B below 385 nm. Air was blown into the chamber by a blower, through a series of manifolds and pipes placed in the soil before planting. Air entered the chamber through small straight upward pipes. A windbreaker, mounted over the pipes, reduced the wind speed from 30 m s^{-1} in the pipes to less than 2 m s^{-1} at soil level. A second air-inlet system was a circular flexible transparent PVC tube, at about 2/3 of the OTC height, well over the canopy. Chamber air was replaced 3.6 times min^{-1}. Temperature and CO_2 concentration were measured in all chambers every 6 min. Pure CO_2 was added at the ventilator inlet and thoroughly mixed inside the OTC. CO_2 concentration was measured and adjusted when needed. Average low-CO_2 levels were 335 to 380 μL L^{-1} in both years, and high-CO_2 levels were 712 to 720 μL L^{-1} in 1995, and 720 to 746 μL L^{-1} in 1996. There was a higher average radiation level in 1995 than in 1996: 19.4 compared to 16.8 MJ global radiation m^{-2} d^{-1}, respectively. The average temperature in 1995 was 16.8 compared to 15.1°C in 1996. In both years, the temperature in OTCs was on average 2.1°C higher than in the ambient plots. Plants were irrigated using perforated flexible PVC tubes.

Measurements

The following measurements were carried out: (1) ground cover; (2) biomass of organs and leaf area; (3) leaf photosynthesis; (4) efficiency of electron transport; and (5) leaf chemical composition (starch, sucrose and Rubisco content).

(1) Fractional light interception was assumed to be equal to fractional ground cover by green foliage, which itself was visually estimated at weekly intervals from two different observation angles per plot, and linearly interpolated to daily values. Full light interception was reached around day 175. In 1996, full light interception was delayed for cultivar Gloria because of infestation by *Verticillium dahliae*, which occurred especially in OTCs where Gloria was grown at elevated CO_2. The data were not considered in the analyses.

(2) On 24 July 1995 and 22 July 1996 (days of the year 205 and 203), i.e. before crop senescence, half of the area of each plot was harvested (first harvest). Border effects for the remaining area were avoided by placing shade cloth in the OTC at the borders of the harvested areas. The final harvests for both cultivars were on 14 August 1995 and 12 August 1996 (days 226 and 224). At each harvest, dry and fresh weight (fw) of leaves, stems and tubers were determined.

(3) In order to measure photosynthesis and perform chemical analyses, samples of single leaves were taken weekly from the end of May until the final harvest, in three replicates. Leaf samples were taken at random from the youngest full-grown leaves. The leaves were cut with the petiole immersed in water to prevent air blocking the xylem. This procedure did not affect the photosynthetic rates compared with the same leaves of uprooted plants. In fact we observed that, under high light conditions, leaves from uprooted young plants were more sensitive to turgor loss and a decrease of photosynthetic rates than cut leaves. The change between the measured maximum photosynthetic rates just after sampling and 1.5 h later was monitored routinely during 2 weeks in the initial growth stage. Light-saturated photosynthesis remained stable within a range of 5% for cut leaves and 10% for uprooted plants.

Photosynthesis measurements were carried out with a top leaflet placed in a small leaf chamber. The upper side of the leaf was illuminated by an EFN A1/230 halide lamp (Philips, Eindhoven, The Netherlands). Long-wave irradiance was filtered by a short wavelength band pass filter (Schott 115). Different irradiance levels were obtained by fractionally filtering with neutral grey filters. Photosynthesis was light-saturated at 1200 μmol m^{-2} s^{-1}. Average conditions in the leaf chamber were air temperature of 22.6°C and vapour pressure deficit of 0.57 kPa. Rates of photosynthesis were calculated from the measured concentrations of CO_2 and vapour in the ingoing and outgoing air stream and the flow rate of the stream by the procedure described by von Caemmerer and Farquhar (1981). Three leaves per treatment were measured yielding six independent data sets. Leaves were gradually adapted to increasing light intensity starting at 200 μmol m^{-2} s^{-1} with steps of 250 μmol m^{-2} s^{-1} at time intervals of 5 min. Light-saturated photosynthesis was measured at 350, 700 and 1300 μL L^{-1} [CO_2].

(4) After 30-min dark adaptation, single leaves were clamped in a small cuvette, flushed with humidified air. Minimum fluorescence in the dark (F_o) and maximum fluorescence during a saturating light pulse (F_m) was measured with the PAM 101 chlorophyll fluorometer (Walz, Effeltrich, Germany). The saturating light closes all open traps of photosystem II, yielding the maximum fluorescence. The efficiency of energy transfer to open photosystem II reaction centres (Φ_{PC}) was estimated as $\Phi_{PC} = (F_m - F_o)/F_m$.

(5) Two side leaflets of the leaf used for photosynthesis measurements were frozen in liquid nitrogen and stored at –80°C for further chemical analyses. Proteins were extracted by grinding leaves (approximately 1 g fw) in a precooled mortar in liquid nitrogen. Five mL of ice-cold buffer [60 mM TRIS–HCl pH 8.0, 500 mM NaCl, 10 mM EDTA, 30 mM β-mercaptoethanol, 0.1 mM phenyl methyl sulfonyl fluoride and 1% sodium dodecyl sulfate (SDS)] was added per g of the resulting powder. The suspension was thoroughly vortexed, boiled for 10 min, centrifuged (12 000 *g*, 20°C, 10 min) and the supernatants stored at –80°C. Control experiments demonstrated that the pellet contained no detectable protein. Protein patterns were visualized by applying 0.5 μL of the protein extracts on a 12% SDS polyacrylamide gel and staining with Coomassie brilliant blue (R250).

Quantification of the large subunit of Rubisco (Rubisco LSU) was performed by densitometry of the protein bands using BSA as a standard. Absolute protein concentrations of Rubisco LSU were calculated using BSA as a standard on each gel. Relative amounts of Rubisco LSU were compared to the total leaf protein extract added to the polyacrylamide gels.

Starch and sucrose content were determined on the same leaf material. Sucrose was extracted in 33 mM Na_2HPO_4/16.7 mM citrate, pH 5 at 4°C. Sucrose was measured as glucose after hydrolysis by yeast invertase. Glucose determination was performed by the glucose oxidase method according to Maas *et al.* (1995). Starch was measured as the amount of glucose in the ethanol-insoluble fraction, after enzymatic cleavage by amyloglucosidase (Pharr and Sox 1984).

Simulation model

The potato crop growth model applied in the present study has been described by Spitters and Schapendonk (1990). Light interception by the canopy is calculated as a function of the LAI following Beer's law (describing the exponential extinction of light in a certain medium). Thermal time determines how photosynthates are allocated to leaves, stems, roots and tubers. Death rate of leaves due to senescence depends on the maturity class of the cultivar. For the present analysis, the constant light use efficiency of the original model was replaced by a calculation of photosynthesis based on the biochemical model of Farquhar *et al.* (1980). The effects of acclimation on yield were estimated by comparing simulation runs with input data of non-acclimated A_{max} values and input data of acclimated A_{max} values.

Results

Ground cover and leaf area dynamics

Ground cover in spring was similar for all treatments (Fig. 1). The plots without OTCs (ambient) produced more leaves than the treatments in the OTCs, and maintained a higher LAI until the end of the season. In 1996, senescence started late, which coincided with lower temperatures and lower irradiances in that year compared with 1995 (Fig. 2). At the first harvest at the end of July (d 203–205), the weight of leaves (green and dead) and LAI were not significantly affected by elevated CO_2 concentration (Tables 1 and 2) for both cultivars. The late cultivar, however, produced twice the

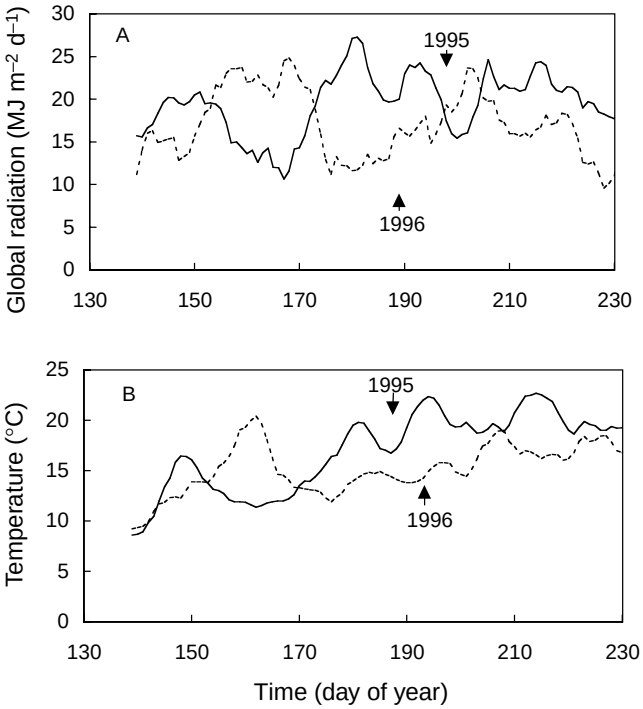

Fig. 2. Seasonal course of daily global radiation and daily average temperature. The curves show 7-d moving averages.

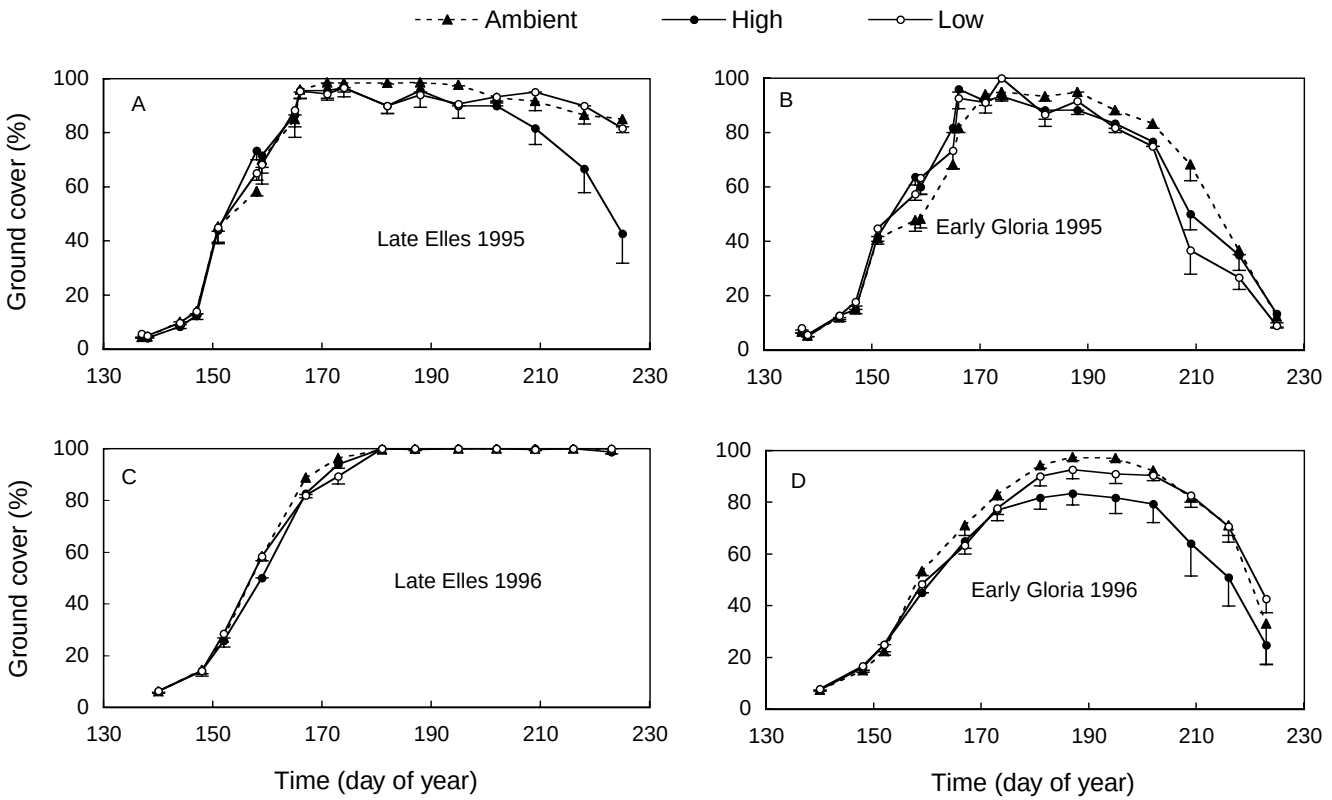

Fig. 1. Seasonal course of ground cover by green foliage in 1995 and 1996. Vertical bars indicate standard errors (n = 3).

leaf weight of the early cultivar, making it less vulnerable to leaf senescence. At final harvest, green leaf weight was higher under elevated CO_2 in the early cultivar and lower in the late cultivar (significant interaction at $P < 0.05$). During the 3-week period between the first and final harvest in 1995, the late cultivar lost 24% of its green leaves at low CO_2, but 57% at elevated CO_2. These results are in agreement with the decrease in ground cover of the late cultivar, especially in 1995 (Fig. 1). Senescence of the early cultivar did not respond to CO_2 concentration (Table 1).

Specific leaf area (SLA) was significantly decreased by elevated CO_2 in both years and for both cultivars (Table 2). This than compensated for the small CO_2 stimulation in leaf weight, so LAI was not increased.

In summary, the results show that light interception is not affected much by elevated CO_2, but that the underlying dynamics of leaf growth and senescence vary strongly with environmental conditions and cultivar. There are no effects of CO_2 on LAI until canopy closure but a faster decline of LAI was observed at elevated CO_2 under warm conditions.

Other components of crop biomass

Elevated CO_2 had similar effects on stem biomass as on leaves. Biomass allocation between above-ground plant parts

Table 1. Data from destructive harvests in OTCs

Statistical significance of the effects of cultivar, CO_2 and the interaction of cultivar CO_2 are indicated as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$) or n.s. (not significant)

		Harvest yield (g dry mass m^{-2})				Statistical significance			CO_2 effect (%)	
Year	Variable	Elles, 350	Elles, 700	Gloria, 350	Gloria, 700	cv.	CO_2	cv. × CO_2	Elles	Gloria
1995	*First harvest (24 July)*									
	Leaves + stems + tubers	1054	1235	848	1023	*	*	n.s.	17	21
	Green leaves	155	141	62	74	***	n.s.	*	–9	19
	Dead leaves	19	16	25	23	n.s.	n.s.	n.s.	–16	–8
	Stem	82	70	22	20	***	n.s.	n.s.	–15	–9
	Tubers	797	1008	739	907	n.s.	*	n.s.	26	23
	Final harvest (14 August)									
	Leaves + stems + tubers	1279	1539	1118	1357	*	**	n.s.	20	21
	Green leaves	158	81	21	27	***	**	**	–49	29
	Dead leaves	37	76	85	83	n.s.	n.s.	n.s.	105	–2
	Stem	78	67	21	20	**	n.s.	n.s.	–14	–5
	Tubers	1007	1316	992	1227	n.s.	***	n.s.	31	24
	Roots	55	73	24	30	**	n.s.	n.s.	32	27
	Change from first to final harvest (i.e. in 3 weeks)									
	Leaves + stems + tubers	276	304	271	333	n.s.	n.s.	n.s.		
	Green leaves	2	–61	–42	–47	n.s.	**	**		
	Dead leaves	17	59	60	61	n.s.	n.s.	n.s.		
	Stem	–4	–3	0	–1	n.s.	n.s.	n.s.		
	Tubers	210	308	252	320	n.s.	n.s.	n.s.		
1996	*First harvest (22 July)*									
	Leaves + stems + tubers	850	1098	803	803	*	n.s.	n.s.	29	0
	Green leaves	208	242	112	102	***	n.s.	n.s.	16	–9
	Dead leaves	6	18	1	4	**	*	n.s.	200	300
	Stem	140	170	18	13	***	n.s.	n.s.	21	–28
	Tubers	497	669	671	685	n.s.	n.s.	n.s.	35	2
	Final harvest (12 August)									
	Leaves + stems + tubers	1373	1899	1153	1130	**	n.s.	*	38	–2
	Green leaves	170	195	61	38	***	n.s.	n.s.	15	–38
	Dead leaves	57	76	48	57	n.s.	n.s.	n.s.	33	19
	Stem	148	141	18	15	**	n.s.	n.s.	–5	–17
	Tubers	999	1487	1025	1021	n.s.	*	*	49	0
	Change from first to final harvest (i.e. in 3 weeks)									
	Leaves + stems + tubers	523	801	350	327	***	*	*		
	Green leaves	–38	–46	–51	–64	n.s.	n.s.	n.s.		
	Dead leaves	51	59	47	53	n.s.	n.s.	n.s.		
	Stem	9	–29	0	2	n.s.	n.s.	n.s.		
	Tubers	502	818	354	336	**	*	*		

Table 2. Leaf area and specific leaf area

Data determined in OTCs at first harvests (24 July 1995 and 22 July 1996). Statistical significance of the effects of cultivar, CO_2 and the interaction of cultivar × CO_2 are indicated as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$) or n.s. (not significant). LAI given as m^2 leaf m^{-2} ground. SLA given as m^2 leaf kg^{-1} leaf dry matter

						Statistical significance			CO_2 effect (%)	
Year	Variable	Elles, 350	Elles, 700	Gloria, 350	Gloria, 700	cv.	CO_2	cv. × CO_2	Elles	Gloria
1995	LAI	3.72	3.15	1.71	1.72	***	n.s.	n.s.	–15	1
	SLA	30.9	28.3	31.9	27.0	n.s.	*	n.s.	–8	–15
1996	LAI	6.01	6.17	2.72	1.78	***	n.s.	n.s.	3	–35
	SLA	37.7	32.2	27.3	19.1	***	**	n.s.	–15	–30

was not affected. Tuber weight, however, was increased by elevated CO_2 in both cultivars (Table 1). No significant CO_2–cultivar interaction was observed. In the temperate year 1996, the percentage increase by CO_2 was higher than in the warm year 1995. For the late cultivar, the CO_2 effect on tuber yield increased during the 3 weeks between the two harvests from 26 to 32% in 1995, and from 35 to 49% in 1996. These strong increases in tuber yield by elevated CO_2 contrast with the small effect of CO_2 on above-ground biomass. We observed not only a stimulation of total CO_2 assimilation under elevated CO_2, but also noticed that assimilates were preferentially exported to the tubers.

Roots were only assessed at the final harvest in 1995, and showed a similar stimulation by elevated CO_2 as the tubers (Table 1). The late cultivar had significantly more roots than the early cultivar.

Leaf photosynthesis and fluorescence

In both years, elevated CO_2 initially increased A_{max} of both cultivars by more than 80% (Figs 3*a*, 4*a*, 5*a*). In contrast, we did not find an effect of elevated CO_2 on the efficiency of electron transport (Φ_{PC}) until senescence (Fig. 6). After the initial stimulation of A_{max} for both cultivars, we observed a gradual decrease of the CO_2 effect until the values of A_{max} under elevated CO_2 were equal to those at low CO_2. Marked differences in the rates of decline were observed between years and cultivars (Figs 3*a*, 4*a*, 5*a*). The dynamics of the weather conditions in the experimental years were completely different. In 1995, temperature and irradiance increased sharply to high values from day 165 onwards and remained high until the end of the experiment (Fig. 2). The period of increased irradiance and temperature coincided with strong photosynthetic acclimation. In 1996, radiation and temperature declined between days 160 and 175, and photosynthetic acclimation was delayed and less pronounced than in 1995. These results show that photosynthetic acclimation is correlated with high irradiance and high temperature. In 1995 with the strongest acclimation, the positive effect of CO_2 on accumulated biomass between the first harvest and the final harvest was 28 compared to 278 g m^{-2} in 1996.

Carbohydrate response to elevated CO_2

Potato leaves can store high amounts of starch. In microscopically examined leaf cross sections, we observed large starch grains in the mesophyll cells in elevated-CO_2 plants but not in the low-CO_2 treatment. We measured the starch content in the same leaves as those used for the photosynthesis measurements. The amount of accumulated starch was always lower in the low-CO_2 treatment (Figs 3*b*, 4*b*, 5*b*). Starch concentration increased 5-fold in young leaves between planting and the time that full light interception was reached. In the elevated-CO_2 treatments, the starch was clearly visible as large granules in the chloroplasts in microscopic cross sections of the leaves (not shown). Starch accumulation coincided with a strong increase in irradiance. In the late cultivar, a peak accumulation of starch only occurred at elevated CO_2. In agreement with the idea that the accumulation of starch was related to irradiance, we observed that the peak accumulation of starch was almost absent in 1996 because, contrary to the conditions in 1995, irradiance decreased in the corresponding period of the year (Fig. 2). In the early cultivar, carbohydrate concentrations, especially starch, peaked not only at elevated CO_2, but also at low CO_2. Similarly to the starch content of the leaves, sucrose levels were higher at elevated CO_2. The time patterns, however, were less variable, and the differences between the treatments were smaller than for starch (Figs 3*c*, 4*c*, 5*c*). Sucrose is present only in small amounts compared to the vast amounts of starch. The start of photosynthetic acclimation and the increase of carbohydrate accumulation coincide, but in contrast to carbohydrate accumulation, the acclimation effect was not reversible. The obvious decline of the carbohydrate content following a decline in irradiance levels did not reverse acclimation of A_{max}.

Rubisco response to elevated CO_2

The Rubisco content of leaves under elevated CO_2 is consistently lower than in leaves grown under low-CO_2 conditions (Figs 3*d*, 4*d*, 5*d*). It was clear from these independently obtained samples in time that the Rubisco content of leaves over the season is declining over the season (1995), or stable

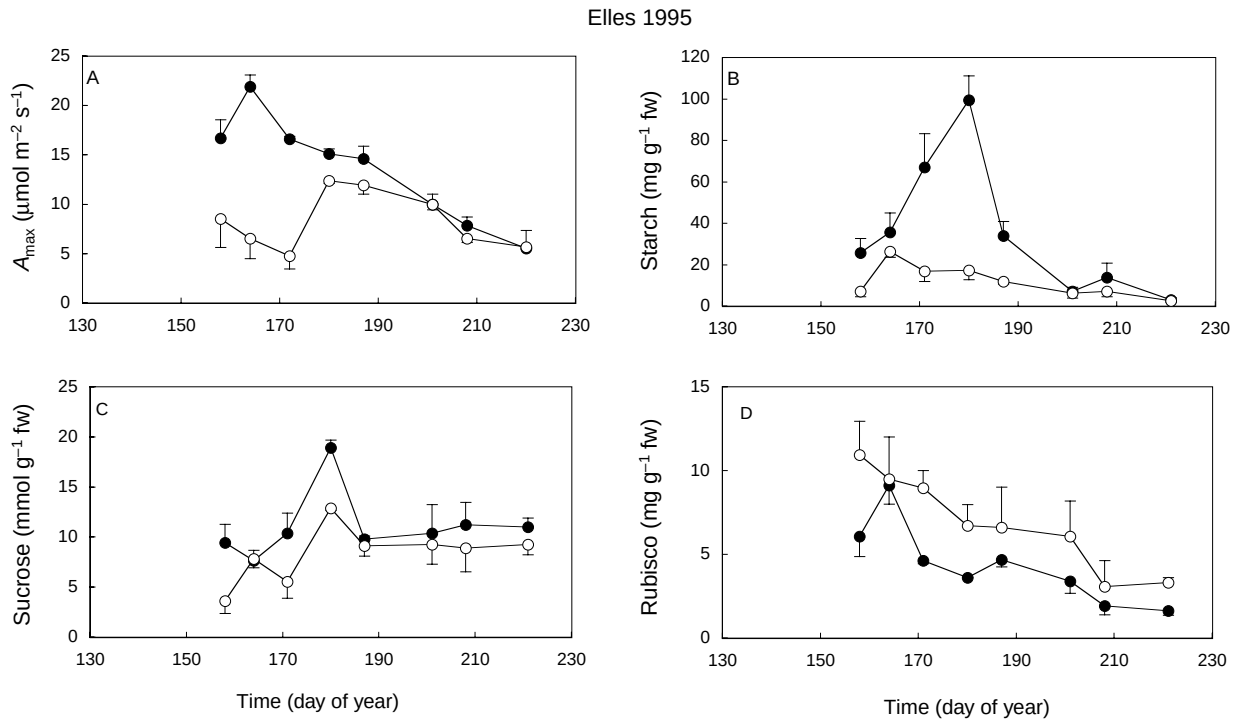

Fig. 3. Seasonal course of physiological parameters, measured in 1995 on young fully expanded leaves of the late maturing cultivar Elles, grown and measured at either 350 or 700 µL CO_2 L^{-1}. (*A*) Photosynthetic rate at 1200 µmol PAR m^{-2} s^{-1}. (*B*) Starch concentration. (*C*) Sucrose concentration. (*D*) Rubisco concentration. ● = high CO_2; ○ = low CO_2. Vertical bars indicate standard errors (n = 3).

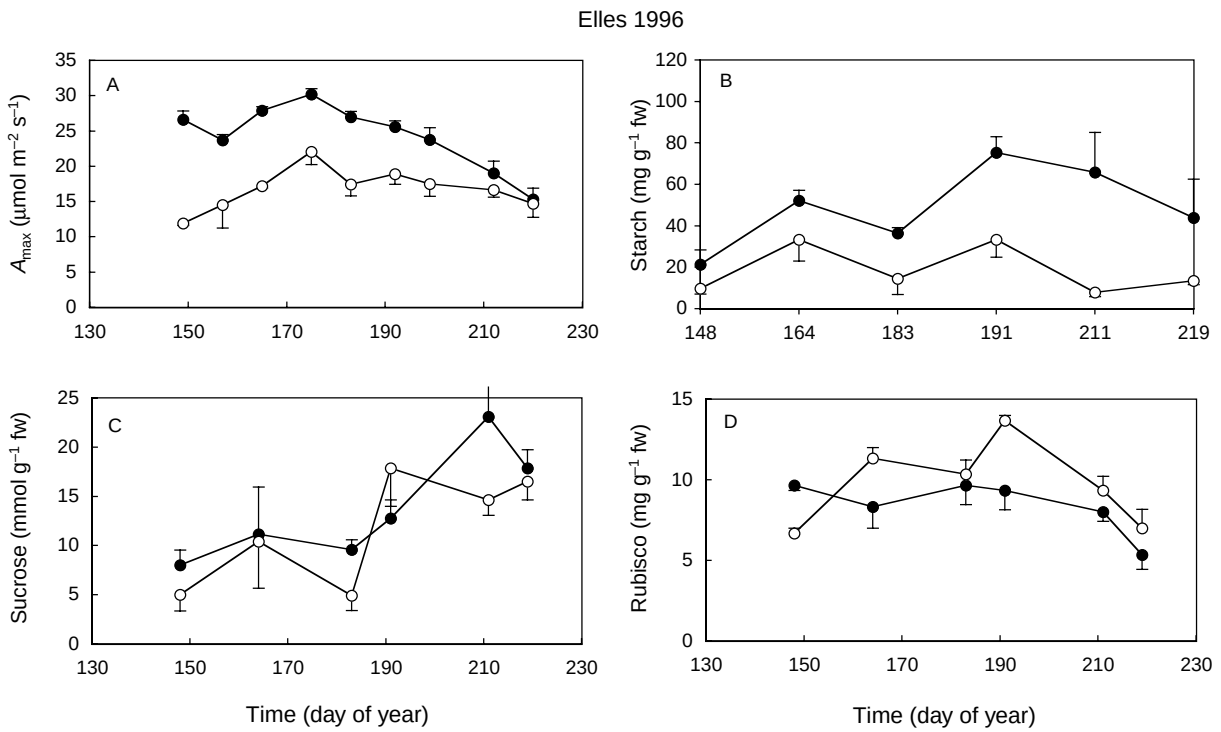

Fig. 4. Seasonal course of physiological parameters, measured in 1996 on young fully expanded leaves of the late maturing cultivar Elles, grown and measured at either 350 or 700 µL CO_2 L^{-1}. (*A*) Photosynthetic rate at 1200 µmol PAR m^{-2} s^{-1}. (*B*) Starch concentration. (*C*) Sucrose concentration. (*D*) Rubisco concentration. ● = high CO_2; ○ = low CO_2. Vertical bars indicate standard errors (n = 3).

until day 200 and declining afterwards in the senescence stage (1996). The differences between the CO_2 treatments persisted until the end of the season.

Evaluation of photosynthetic acclimation by means of modelling

What was the effect of photosynthetic acclimation on tuber yield? To answer that question, we ran a simulation model with measured A_{max} values as input to drive the photosynthetic subroutine (Fig. 7). The results show that the simulated yield responses to elevated CO_2 were in good agreement with the measured yield at the final harvest, with a slight underestimation for the late cultivar and overestimation for the first harvests of the early cultivar (Fig. 7). The next step was to remove the acclimated A_{max} values, for the elevated CO_2 treatment measured at elevated CO_2, and substitute them with the non-acclimated A_{max} values of the low-CO_2 treatment, measured at elevated CO_2. The results indicate that CO_2 would have increased total dry matter production by about 36% in the absence of acclimation instead of the simulated 19% and observed 21% with acclimated photosynthetic rates. This shows that acclimation of leaf photosynthesis under elevated CO_2 is responsible for a major reduction of the CO_2 effect on potato productivity.

Comparison with ambient plots

There was a strong negative effect of the OTCs themselves on all yield components (Table 3). Total biomass declined in the range 21–42%. This is the result of a decrease in irradiance (–20%), an increased temperature (+2.1°C) due to heat dissipation in the OTCs by the ventilators, a reduced relative air humidity (–10%) and an overall change in the microclimatological conditions of the leaves due to artificial air movement patterns.

Discussion

The response of potato to elevated CO_2 concentrations was within the range reported for other crops (Kimball 1983; Lawlor and Mitchell 1991). The CO_2 effect on potato production in the present study ranged from 23% for the early variety to 49% for the late variety (Table 1), in agreement with the findings of Miglietta *et al.* (1998). Leaf area was hardly affected by CO_2 concentration. From previously made simulation studies it was predicted that doubling CO_2 concentration would stimulate potato yield, ranging from 20% for the late varieties to 30% for the early varieties (Schapendonk and Goudriaan 1995). These predictions were based on the expectation that a higher CO_2 concentration would increase light interception by the formation of more leaf area. This would be more beneficial to the early cultivar with its lower LAI than to the late cultivar with a predominantly high LAI.

In addition, the average irradiance at the leaf surface will be higher in the early cultivar because there is less internal shading. Since the response of A_{max} to elevated CO_2 will increase with increasing irradiance, this also would stimulate photosynthesis of the early variety more than the late variety. None of the above assumptions, however, appeared to be true and therefore the 'source-part' of our hypothesis for CO_2 effects on potato cultivars, which stated that the early cultivar in particular would profit from elevated CO_2 through faster leaf formation, less vulnerability to senescence and a higher light interception, must be rejected. Elevated CO_2 had no effect on light interception during early spring, and hardly any effect on total leaf formation in general. The only effect was on senescence of leaves, which was accelerated by a combination of elevated CO_2 and high irradiance/high temperature, especially in the late cultivar. Thus, the amount of intercepted light remained equal, and it is therefore concluded that photosynthesis on a leaf area basis is the most important attribute to explain the observed yield increases.

The second, sink-strength related part of our hypothesis, concerning CO_2 effects on potato cultivars, stated that stimulation of photosynthesis by elevated CO_2 would be maintained longer in late cultivars, which have greater sink activity than early cultivars because of their prolonged tubering capacity. This was investigated by comparing the responses in cultivars that were known to differ significantly with respect to tuber growth rates and by investigating the interaction with light intensity and temperature. The very high starch content under elevated CO_2 indicates that the export to the tubers is either limited by an export blockage or that tuber growth in potato is more sink-limited than we would expect from the large sink potential of the growing tubers. Wheeler *et al.* (1991) demonstrated that doubling the CO_2 concentration increased tuber dry matter by 32% under 12-h photoperiods but had no effect under a 24-h photoperiod regime. This difference was attributed to faster tuberization under the shorter photoperiod, providing a greater sink for assimilates.

Sink limitation or carbon export blockage may even cause irreversible damage of the chloroplasts due to starch accumulation (Goudriaan and de Ruiter 1983). The negative feedback mechanism that down-regulates the photosynthetic rate was apparently not sufficient to prevent starch accumulation. In agreement with these results, we found that the chloroplasts of leaves from the elevated CO_2 treatments contained much larger starch granules than leaves from the low-CO_2 treatments. Even though starch was reduced in the newly formed leaves later in the tuber-filling stage, this was not accompanied by a recovery of the photosynthetic rates (Figs 3*a*, *b*, 5*a*, *b*) or the Rubisco content. It is therefore doubtful that starch has a signaling function. By leaf-specific antisense repression of the key enzyme of starch synthesis (ADPglucose pyrophosphorylase), it was shown by Ludewig *et al.* (1998) that the accumulated starch itself does not cause down-regulation, but on the contrary they assumed that the starch pool was necessary as a kind of overflow to allow a constant rate of CO_2 assimilation.

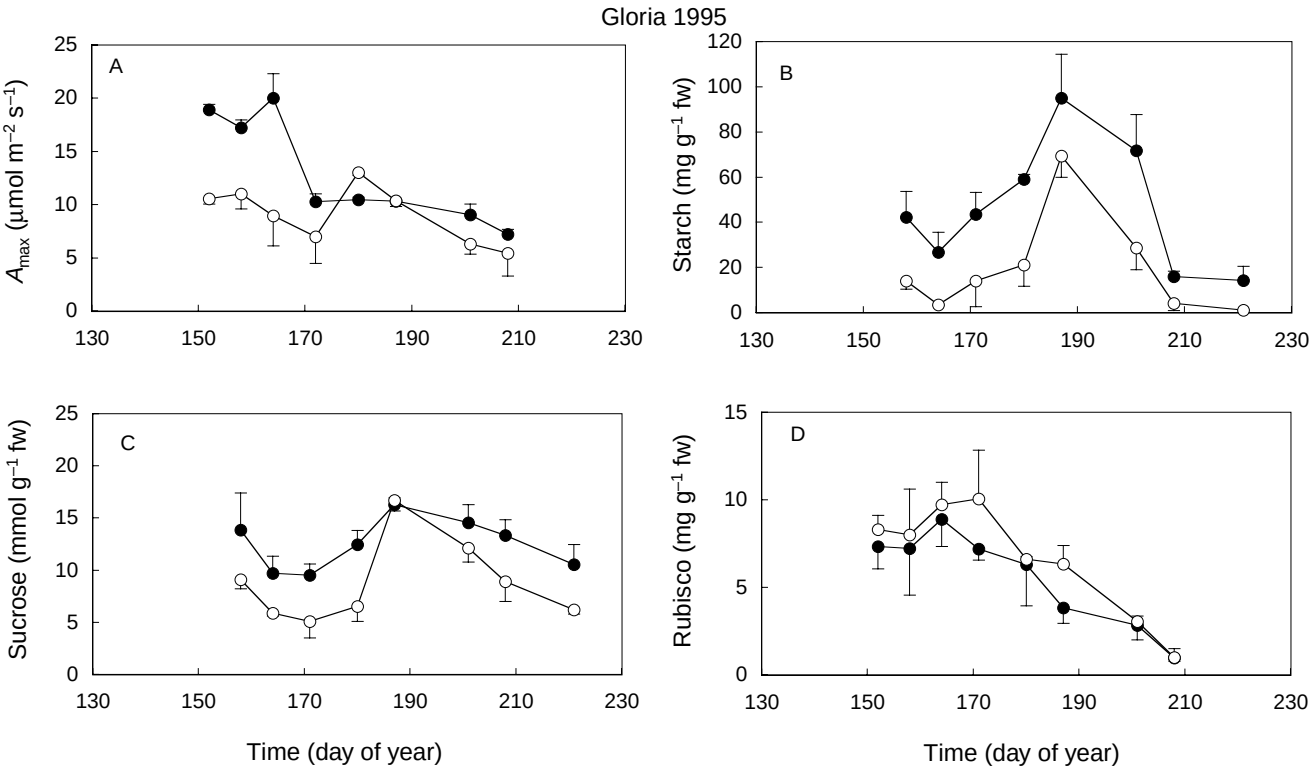

Fig. 5. Seasonal course of physiological parameters, measured in 1995 on young fully expanded leaves of the cultivar Gloria, grown and measured at either 350 or 700 µL CO_2 L^{-1}. (*A*) Photosynthetic rate at 1200 µmol PAR m^{-2} s^{-1}. (*B*) Starch concentration. (*C*) Sucrose concentration. (*D*) Rubisco concentration. ● = high CO_2; ○ = low CO_2. Vertical bars indicate standard errors (n = 3).

It is more likely that carbohydrate regulation of photosynthetic gene expression is mediated by pathways intermediate to starch synthesis. Sucrose repression of several photosynthetic genes including the genes that code for Rubisco may be involved in hexose metabolism via hexokinase or directly as a signal metabolite (Moore *et al.* 1999). It has been argued that the Rubisco content, in general, remains in excess of that required to support the measured photosynthetic rates, also at elevated CO_2, and that acclimation would be caused by other limiting factors such as the regeneration of orthophosphate in the chloroplasts (Sage *et al.* 1989). However, it is difficult to debate on this topic in general terms, because acclimation can only be assessed indirectly by studying processes and enzymes that are strictly regulated by the internal energy balance of plants, which depends on temperature and absorbed irradiance. Our results show that transients of temperature–irradiance combinations have a big impact on acclimation of photosynthetic enhancement. In addition, it is clear that apparent acclimation and senescence are difficult to separate and that both are often linked to the same phenomenology (Miglietta *et al.* 1998).

In a recent study, it was concluded that the Rubisco content was unaffected by elevated CO_2, and that this would eliminate the possibility that major leaf proteins were responsible for photosynthetic acclimation in *Solanum*

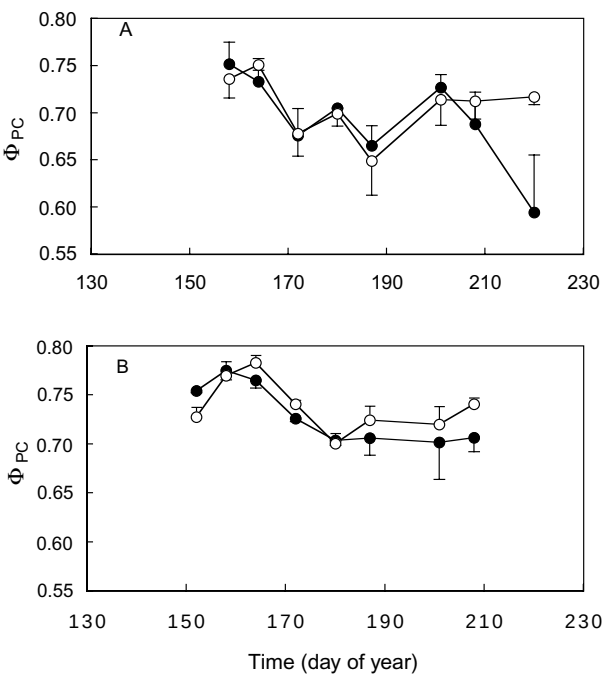

Fig. 6. Seasonal course of the efficiency of energy transfer to open photosystem II reaction centres Φ_{PC} in Elles (*A*) and Gloria (*B*). ● = high CO_2; ○ = low CO_2. Vertical bars indicate standard errors (n = 3).

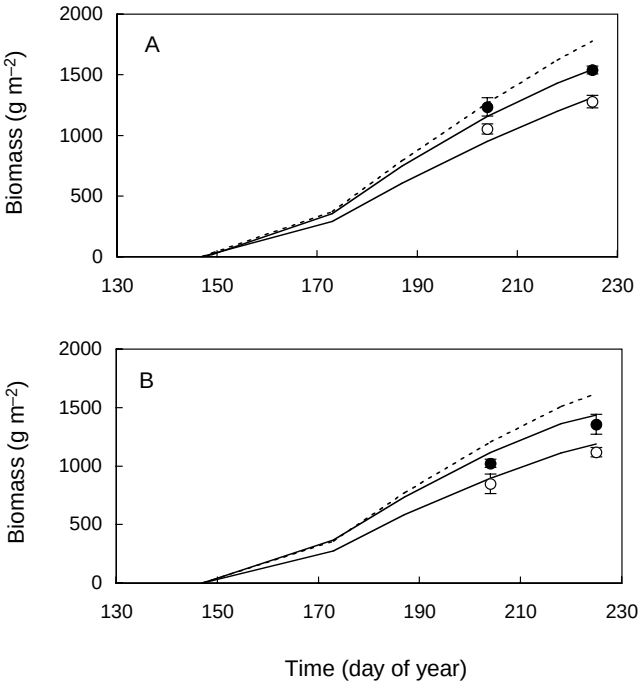

Fig. 7. Observed and simulated growth for 1995. The points represent observed total crop dry matter at low CO_2 (open symbols) and elevated CO_2 (closed symbols). Vertical bars indicate standard errors ($n = 3$). The lines represent simulated time courses of dry matter production for low CO_2 (lowest lines) and elevated CO_2 with (middle lines) or without acclimation (dotted lines).

tuberosum (Sicher and Bunce 1999). This led to the conclusion that the observed progressive decline of the photosynthetic enhancement were attributed to inhibitory effects of as yet unknown compounds on Rubisco activity. Our results, however, show a clear coherence between the temporal variation of A_{max} and the temporal variation of the Rubisco content, which declines over the season and more so at elevated CO_2. However, a direct proof that the correlation is a causal one can not be given yet, for the obvious reason that the observed effects are the result of complex mechanisms, with negative feedback of sink–source balance induced by high temperature and high irradiance levels.

Late varieties have greater sink capacities than early varieties. This is illustrated by the low amount of starch accumulation in the low-CO_2 treatment of the late variety and the strong starch accumulation in the early variety in 1995, during the period in which irradiance increased sharply (Figs 3*b*, 5*b*). When the environmental conditions are such that sink limitations are eliminated, the CO_2 effect on yield might increase, and this trend will be more positive for late than for early cultivars. Interestingly, we observed a preferential allocation of carbon to roots and tubers under elevated CO_2, especially in the late maturing cultivar Elles. Preferential allocation of carbon to below-ground parts has also been commonly observed in other crops. For potato, it means that the sink function of the tuber itself is stimulated by elevated CO_2. However, it is evident that this increase in sink strength was not enough to prevent acclimation.

Interaction with environment

The source–sink balance is strongly influenced by the environment (Long 1991; Grashoff *et al*. 1995). In that sense, it was a coincidence that the two experimental years were contrasting for irradiance and temperature during the critical periods that acclimation occurred. This created the opportunity to get a good impression of the environmentally induced variability on acclimation and the time course of A_{max}.

We observed a stimulation of A_{max} in the beginning of the growth season. This might be due an acceleration of the physiological development of the leaves under elevated CO_2, leading to a faster gain of maximum photosynthetic capacity. A shift in the timing of the normal photosynthetic stages of leaf ontogeny would also result in an earlier onset of the photosynthetic decline (Miller *et al.* 1997). Our results are partly consistent with this suggestion. However, we did not observe any ontogenetic shift due to elevated CO_2 on reaction centre efficiency, because the time courses of Φ_{pc} were equal until senescence, and it is unlikely that this would have been the case if development had been affected. A_{max} was higher at elevated CO_2, but the effect diminished in time. Limitations in the capacity to export the assimilated carbon could be the reason for that. Because the differences in photosynthetic capacity existed only during the 4–8 weeks after planting, this seems to be the critical period for the CO_2 effect.

General implications for OTC experiments

The observed interactions with the environment also have implications for OTC experiments in general. The average higher temperature in the OTCs and the lower irradiance will have had an influence on the observed CO_2 responses. The aspect of higher temperatures in OTCs compared with ambient temperatures was assessed by Van Oijen *et al.* (1999). They found that for wheat, cooling of the OTC mainly extended the period before leaf senescence, but that light use efficiency was not affected. The cooling decreased the magnitude of the CO_2 effect. It would be too speculative to try to estimate the separate effects of irradiance and temperature from our experimental results. However, we think that because the climatic variation between the two years is large, it covers a major part of the bandwidth of irradiance and temperatures, including the offset caused by the OTCs. Nevertheless, it cannot be excluded that OTC experiments will slightly overestimate the CO_2 effect (Van Oijen *et al.* 1999).

Table 3. Data from destructive harvests in ambient plots

OTC effect given as the percentage by which measurements in OTCs at 350 ppm CO_2 (given in Table 1) differ from those in ambient plots (this Table). Statistical significance of the OTC effect is indicated as *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$) or n.s. (not significant)

Year	Variable	Harvest yield (g dry mass m^{-2})		OTC effect (%)		Statistical significance
		Elles, ambient plots	Gloria, ambient plots	Elles	Gloria	of the OTC effect
1995	*First harvest (24 July)*					
	Leaves + stems + tubers	1814	1358	–42	–38	***
	Green leaves	270	157	–43	–61	***
	Dead leaves	14	18	35	37	n.s.
	Stem	169	31	–51	–30	**
	Tubers	1361	1152	–41	–36	*
	Final harvest (14 August)					
	Leaves + stems + tubers	2287	1531	–46	–27	***
	Green leaves	252	46	–37	–54	**
	Dead leaves	32	78	13	9	n.s.
	Stem	184	20	–58	7	*
	Tubers	1819	1388	–45	–29	***
	Roots	67	29	–18	–19	n.s.
1996	*First harvest (22 July)*					
	Leaves + stems + tubers	1291	1089	–34	–26	***
	Green leaves	344	161	–40	–30	**
	Dead leaves	20	6	–69	–83	**
	Stem	217	23	–36	–22	*
	Tubers	710	899	–30	–25	**
	Final harvest (12 August)					
	Leaves + stems + tubers	1878	1465	–27	–21	***
	Green leaves	286	69	–41	–12	***
	Dead leaves	68	83	–16	–41	*
	Stem	109	22	36	–19	n.s.
	Tubers	1414	1291	–29	–21	***

Conclusions

Maximum leaf area and total light interception are not affected much by elevated CO_2. Therefore, we reject the hypothesis that early cultivars with a low LAI will profit more than late cultivars.

Under elevated CO_2, the allocation of assimilates becomes more directed to the tubers, but not enough to prevent acclimation due to sink limitation.

Photosynthesis acclimated under elevated CO_2, especially under high radiation and temperature. Acclimation was accompanied by a decrease in the Rubisco content and an accumulation of starch and sucrose, more so in the early than in the late variety. This resulted in a lower stimulation of yield and total biomass.

Model calculations showed that the acclimation of photosynthesis under elevated CO_2 reduced the response to CO_2 concentration by 50% compared to a hypothetical situation where this acclimation did not occur. If photosynthetic acclimation can be decreased through breeding or management, potato, especially late varieties, could profit more from an increase in the atmospheric CO_2 concentration than indeterminate crops such as cereals.

Acknowledgments

We thank J. van Kleef and H. E. Peeters for their help in the OTC experiments. We are indebted to J. A. Bakker for assistance with the starch analyses.

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Manuscript received 16 December 1999, accepted 11 September 2000