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BRIEF COMMUNICATION

The photosynthetic response to elevated CO_2 in high altitude potato species (*Solanum curtilobum*)

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Abstract

Plants of *Solanum curtilobum* (from high altitude) and *Solanum tuberosum* (from low altitude) were grown in open-top chambers in a greenhouse at either ambient (AC, 360 μmol mol^{-1}) or *ca.* twice ambient (EC, 720 μmol mol^{-1}) CO_2 concentrations for 30 d. CO_2 treatments started at the reproductive stage of the plants. There were similar patterns in the physiological response to CO_2 enrichment in the two species. Stomatal conductance was reduced by 59 % in *S. tuberosum* and by 55 % in *S. curtilobum*, but such a reduction did not limit the net photosynthetic rate (P_N), which was increased by approximately 56 % *in S. curtilobum* and 53 % in *S. tuberosum*. The transpiration rate was reduced by 16 % in both potato species while instantaneous transpiration efficiency increased by 80 % in *S. tuberosum* and 90 % in *S. curtilobum*. Plants grown under EC showed 36 and 66 % increment in total dry biomass, whereas yields (dry mass of tubers) were increased by 40 and 85 % in *S. tuberosum* and *S. curtilobum*, respectively. EC promoted productivity by increasing P_N. Thus *S. tuberosum*, cultivated around the world at low altitudes, and *S. curtilobum*, endemic of the highland Andes, respond positively to EC during the tuberisation stage.

Additional key words: CO_2 enrichment; C_3 photosynthesis; instantaneous transpiration efficiency; *Solanum tuberosum*; stomatal conductance.

The increase in global atmospheric CO_2 concentration, and its potential impacts on climate change have been largely documented (Baker and Allen 1994). Given projected rates of fossil fuel use, the current [CO_2] (AC, about 360 μmol mol^{-1}) may double pre-industrial levels by the middle of this century (IPCC 1998). Stimulated by the global carbon cycling issue, significant amount of research has been carried out on many aspects of plant biology, including photosynthesis, respiration, nutrient uptake, and carbon partitioning (Luo *et al.* 1999). Understanding the response of crops originated from all regions of the planet to climatic variability will allow the construction of better crop growth simulation models that will assist selection and alteration of crops for specific areas (Semenov and Porter 1995).

Increasing AC may increase photosynthesis and plant growth (Griffin and Seemann 1996). The stimulatory effect of elevated atmospheric CO_2 concentration (EC) on net photosynthetic rate (P_N), which is temperature-dependent, is primarily caused by increased [CO_2] in the chloroplast. Ribulose-1,5-bisphosphate carboxylase/oxygenase is not saturated by EC, so a rise in [CO_2] increases the rate of carboxylation in C_3 plants (Drake *et al.* 1997) and reduces photorespiration rate (Long 1991). In addition, EC causes partial stomatal closure, decreasing stomatal conductance (g_s) and resulting in reduced canopy or leaf transpiration rate, *E* (Morison and Gifford 1984). Other fundamental plant processes are extremely variable in response to EC. For example, respiration rate increases or decreases depending on species during either short-term

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or long-term exposure to EC (Amthor 1997). Similarly, diverse responses of nitrogen uptake and carbon allocation (*e.g.* root/shoot ratio) to [CO_2] have also been observed (Luo *et al.* 1999)

The extent of the increase in P_N and plant growth will depend not only on the short-term stimulation of P_N but also on the long-term acclimation response of photosynthesis to EC. Short-term (min to h) increase in ambient CO_2 concentration from 350 to 700 µmol mol^{-1} typically increases P_N by 30-70 % (Luo and Mooney 1996). Many species will not maintain this stimulation of photosynthesis when grown in EC for at least a few weeks as a result of photosynthetic acclimation (Drake *et al.* 1997). This down-regulation of photosynthesis is thought to be a response to changes in cellular sugar concentrations resulting from increases in saccharide production relative to the rates of saccharide export and utilisation (Ludewig *et al.* 1998, Moore *et al.* 1998, Ghildiyal *et al.* 2001). The mechanism for down-regulation of photosynthesis at EC may involve hexokinase and sucrose cycling through invertase (Moore *et al.* 1999, Smeekens 2000).

EC and associated climate change may affect potato production in the coming decades, with consequences for world food supply (Rosenzweig and Hillel 1998). Despite the clear agronomic importance of potato, there have been only few studies on the effects of EC on the growth and photosynthetic responses of *Solanum*. Sage *et al.* (1989) observed little or no photosynthetic acclimation of *S. tuberosum* at low internal CO_2 concentration (C_i), although a positive stimulation of P_N occurred when C_i exceeded 600 µmol(CO_2) mol^{-1}. Wheeler and Tibbits (1997) reported that total biomass of plants grown at 1 000 µmol(CO_2) mol^{-1} increased but tuber dry matter yield was unaffected. Miglietta *et al.* (1998) found that tuber yield was 40 % greater at 660 µmol(CO_2) mol^{-1} compared to AC in a free-air CO_2 enrichment study. Sicher and Bunce (1999) reported that tuber dry matter yield increased by 9 and 40 %, respectively, under 530 and 700 µmol(CO_2) mol^{-1} compared to 350 µmol(CO_2) mol^{-1}. Schapendonk *et al.* (2000) found that an increase of [CO_2] from 350 to 700 µmol mol^{-1} might increase tuber dry matter yield by 27 to 49 %.

To our knowledge, no work on effects of EC in other potato species has been reported. Here we show the first characterisation of the response of *Solanum curtilobum*, a high elevation potato species of significant economic importance in the highland Andes. In the Andes, mean temperature commonly decreases by about 0.6 °C per 100 m increase in elevation. Intense insolation after sunrise can cause rapid leaf and air heating. *S. curtilobum*, a hybrid between a cultivated and a wild species, is one of the most frost hardy potato species that grows at altitudes up to 4 200 m. Indigenous cultivation of *S. curtilobum* extends principally in areas of southern Peru and northern Bolivia that can experience frosts on 300 d of the year. According to Mendoza and Estrada (1979), *S. curtilobum* can resist to –4 to –5 °C. It contains genes from *S. acaule*, a very frost resistant small wild species (National Research Council 1989). The cultivation of *S. curtilobum* long pre-dates the Inca period, and although it continues to the present, farmers grow it for its edible tubers mainly as insurance against cold weather.

Inter-species variability in the response of plants to EC may play an important role in determining productivity of ecosystems in the future climate. Depending upon species and environment, the photosynthetic enhancement occurring after short-term exposure to EC either persists or is partially or fully reversed on the long term (Sage *et al.* 1989, Greer *et al.* 1995). This variability in the long-term response of photosynthesis is often associated with inter-species differences in leaf structure and chemical composition to EC (Poorter *et al.* 1997).

In the present work the effect of exposure to AC or EC on carbon and water fluxes, water use efficiency (WUE), and yield of two potato species *S. curtilobum* and *S. tuberosum* grown in open-top chambers was studied. These potato species of different geographic origin differ in many physiological traits, especially in stress resistance. In previous studies, we determined also that *S. curtilobum* shows high salt tolerance positively related to proline content (Martinez *et al.* 1996) and that increased protection against oxidative stress induced by paraquat or water stress in *S. curtilobum* was correlated with increased superoxide dismutase activities (Martinez *et al.* 2001).

Potato plantlets of *S. curtilobum* cv. Ugro Shiri (from the germplasm bank of the International Potato Center, Lima, Peru) and *S. tuberosum* cv. Baronesa were propagated *in vitro* (Martinez *et al.* 1996) and transplanted to pots containing pre-moistened vermiculite. All pots were watered to field capacity daily with 0.5-strength Hoagland's nutrient solution. Thirty days after planting, an additional 5 cm of vermiculite was added to each pot to cover additional stem nodes to accommodate stolon growth and tuber formation. Plants were grown under glasshouse conditions until tuber initiation. At the stage of tuberisation, plants were placed into 1 m high and 0.8 m diameter open-top chambers (OTCs) with ambient, AC (≈360±15 µmol mol^{-1}) and with elevated, EC (≈720± 15 µmol mol^{-1}) CO_2 concentrations. Each chamber was continuously flushed with ambient air or ambient air enriched in CO_2. Carbon dioxide enrichment in the EC-OTC was maintained 24 h a day, for the duration of the experiment (30 d), by injecting pure CO_2 at a constant rate into the input blower, where it was mixed with ambient air before entering the chamber. The air stream reached the chamber trough a perforated lower plenum to facilitate mixing of the injected CO_2 and chamber air as described by Drake *et al.* (1989). Individual blowers made the air inside the chamber to renovate twice a minute. The concentrations of carbon dioxide in each OTC was monitored, controlled, and recorded automatically every 5 min with an infrared gas analyser (*ADC-225-MK3*, *Analytical Development Company*, Hoddesdon, UK), and a six-point gas-handling unit (*WA-161 MK3-A*, *Analytical Development Company*, Hoddesdon, UK). The IRGA was calibrated in absolute mode weekly with pressurised tank CO_2 of known concentration. The chamber transmissivity of PPFD (photosynthetic photon flux density) was about 0.95 and the air temperature within the chambers averaged 1.0 °C above ambient air.

P_N, E, and g_s were periodically measured with an open-flow infrared gas analysis system (*LCA-4*, *Analytical Development Company*, Hoddesdon, UK) on two fully expanded leaves of three plants per treatment. The centre leaflet of the measured trifoliate leaf was placed inside the portable broad leaf chamber (*PLC4B*, *Analytical Development Company*, Hoddesdon, UK) and allowed to equilibrate before recording. The leaf chamber was irradiated with a portable unit (*PLU2-002*, *Analytical Development Company*, Hoddesdon, UK). All measurements were made at a constant air temperature of 25 °C and PPFD of 1 000 $\mu mol\ m^{-2}\ s^{-1}$. Instantaneous transpiration efficiency (ITE) was expressed by the ratio P_N/E [$mmol(CO_2)\ mol^{-1}(H_2O)$] according to Nobel (1999).

P_N increased significantly in both potato species when grown at EC. Although P_N was not different between the two species when grown and measured at AC, the increase in P_N by growth at EC was more pronounced in *S. curtilobum* (56 %) than in *S. tuberosum* (53 %) (Fig. 1). E and even more g_s (Fig. 1) were reduced significantly when plants were grown at EC. The reduction in g_s by effect of EC was 59 and 55 %, the reduction in E was 15 and 17 % in *S. tuberosum* and *S. curtilobum*, respectively (Fig. 1). The ratio of intercellular to ambient [CO_2] (C_i/C_a) was not significantly affected in response to EC (Fig. 1). The significant increase in ITE induced by EC was 80 and 90 % in *S. tuberosum* and *S. curtilobum*, respectively (Fig. 1).

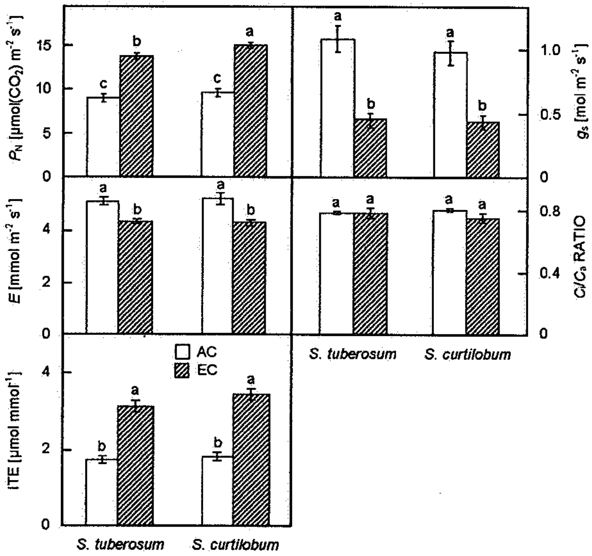

Fig. 1. Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), ratio of intercellular to ambient CO_2 concentration (C_i/C_a), and instantaneous transpiration efficiency (ITE) for two potato (*Solanum*) species in response to ambient, AC (360 $\mu mol\ mol^{-1}$) or elevated, EC (720 $\mu mol\ mol^{-1}$) CO_2 concentrations. Means±SE ($n = 3$). *Letters above vertical bars* denote significant differences at $p \leq 0.05$.

Potato plants of both species produced more total and tuber biomass under EC than under AC (Table 1): in *S. tuberosum* 36 and 40 % and in *S. curtilobum* 66 and 85 % more, respectively. Growth at EC had no effect on harvest index of *S. tuberosum*, but it increased by 13 % in *S. curtilobum* (Table 1).

Table 1. Total (DM_{total}) and tuber (DM_{tuber}) dry mass [$g\ plant^{-1}$], and harvest index (HI) of two potato species grown at ambient, AC (360 $\mu mol\ mol^{-1}$) or elevated, EC (720 $\mu mol\ mol^{-1}$) CO_2 concentrations. Significance levels from ANOVA: * $p \leq 0.05$, ** $p \leq 0.01$, NS = non-significant. Different letters within a column indicate significant differences at $p \leq 0.05$.

Species	CO_2	DM_{total}	DM_{tuber}	HI
S. tuberosum	AC	19.2 b	14.4 c	0.75 a
	EC	26.1 a	20.2 a	0.77 a
S. curtilobum	AC	14.9 b	10.2 d	0.68 b
	EC	24.7 a	18.9 b	0.77 a
Source:				
CO_2		*	*	*
Species		NS	*	NS
CO_2 × species		NS	NS	NS

The photosynthetic enhancement of *S. tuberosum* and *S. curtilobum* at EC persisted throughout the tuberisation period. The large increase (>50 %) in P_N at EC is in agreement with other results in C_3 species (Bowes 1993, Drake *et al.* 1997). Sicher and Bunce (1999) found that P_N in potato (*S. tuberosum* L. cv. Atlantic) increased 28 and 49 %, respectively, under 530 and 700 $\mu mol(CO_2)\ mol^{-1}$, compared to plants in AC. Schapendonk *et al.* (2000) found that during the first week after planting, 700 $\mu mol(CO_2)\ mol^{-1}$ stimulated the light-saturated P_N (P_{Nmax}) of two *S. tuberosum* cultivars by 80 %. However, P_{Nmax} under EC declined to the level of AC treatment in the course of growing season. In our experiment, changes in P_N in response to CO_2 treatments were proportional to increases of C_i. They support the prediction that a doubling of [CO_2] would increase P_N relative to photorespiration rate (Ogren 1984, Long 1991, Wallsgrove 1992). Increased C_i could reduce RuBP oxygenation and increase RuBP carboxylation, which in turn will increase P_N at the EC treatment (Fig. 1). Our results suggest that the suppression of photorespiration rate by EC sustained over the tuberisation period in both potato species might have contributed to increased growth and yield.

An inverse relationship between g_s and E and the [CO_2] treatment in both potato species was observed (Fig. 1). A reduction in g_s in response to CO_2 enrichment is commonly observed in terrestrial plants (Sage 1994), although the response in individual experiments can vary depending upon growth conditions (Field *et al.* 1995). In agreement with Sicher and Bunce (1999), changes of g_s and P_N in both potato species maintained C_i/C_a of *ca.* 0.78 under both CO_2 treatments. Consequently, there was no evidence for stomatal acclimation to EC. The C_i/C_a is constant for various species grown in different environments of irradiance, nitrogen, soil water availability, and CO_2 (Wong *et al.* 1985).

According to Miglietta *et al.* (1998), Sicher and Bunce (1999), and Schapendonk *et al.* (2000) double ambient [CO_2] during the tuberisation period increased tuber yield. In our experiment tubers acted as an efficient and strong sink for photosynthate that would mitigate the acclimation of P_N under EC. Ludewig *et al.* (1998) and Moore *et al.* (1999) pointed out that end product synthesis limitation of P_N could explain the progressive decline of photosynthetic enhancement in EC-grown plants. In these two potato species, active translocation of saccharides to the tubers would be necessary to keep leaf sugars at low concentrations preventing acclimation of P_N under EC. Species-specific differences in total dry matter and yield in response to EC could be attributed to interspecies differences in P_N and carbon partitioning. Körner and Diemer (1994) suggest that efficiency of CO_2 utilisation in typical high-latitude species is generally greater that in low-altitude species.

In summary, the results of this experiment confirmed the positive effects of high [CO_2] on two potato species during tuber formation under favourable water conditions.

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