Carbon gains by desiccation-tolerant plants at elevated CO₂

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Summary

1. There have been no reports of the long-term responses of the desiccation-tolerant (DT) plants to elevated CO₂. *Xerophyta scabrida* is a DT woody shrub, which loses chlorophylls and thylakoids during desiccation: a so-called poikilochlorophyllous desiccation-tolerant species (PDT). When the leaves of *X. scabrida* are allowed to desiccate, the species shows many of the normal features of (P)DT plants.

2. However, the duration of photosynthesis in *X. scabrida* is prolonged by 300% when the measurements are made at 700 as opposed to 350 p.p.m. CO₂. The implication is that the carboxylating enzymes must still have been active at this time to enable appreciable photosynthetic activity. This response could have far-reaching implications for the success of such species in a future climate.

3. Lichens and mosses, representing the homoiochlorophyllous DTs (HDT), retain their chlorophyll content and photosynthetic apparatus during desiccation. We show the desiccation responses of two common HDT species (*Cladonia convoluta* and *Tortula ruralis*) to elevated CO₂ for comparison. Both HDT species showed increased net CO₂ uptake in the material grown at high CO₂ by more than 30% in moss and by more than 50% in lichen. It is concluded that desiccation-tolerant plants will be among the main beneficiaries of a high CO₂ future.

Key-words: Desiccation tolerance, elevated CO₂

Introduction

Future increases in atmospheric CO₂ concentration (Houghton, Jenkins & Ephramus 1990) will have a direct effect on the productivity of plants through changes in the functioning of the photosynthetic apparatus (Long 1991). Plant responses to drought may be superimposed on this in unexpected and indirect ways, and favour one group of plants against another (Field *et al.* 1992). Although considerable data are available on short-term and long-term responses of plants to elevated CO₂ (Ceulemans & Mousseau 1994) there have been no reports of the long-term responses of an important functional group, the desiccation-tolerant (DT) plants (Gaff 1977, 1989; Bewley 1979). Of the DT plants, the so-called poikilochlorophyllous (PDT) species (Hambler 1961) are of special interest because they lose their chlorophylls and thylakoids during desiccation (Gaff, Zee & O’Brien 1976; Hallam & Luff 1980; Hetherington & Smillie 1982) and resynthesize them on rehydration (Tuba, Lichtenthaler *et al.* 1994). Thus, the impact of elevated CO₂ on carbon balance over the desiccation cycle is of considerable interest. Here we show the response of a typical PDT species to elevated CO₂ during desiccation. *Xerophyta scabrida* (Pax) Th. Dur. et Schinz is a woody shrub which occurs in arid regions of east Africa (Pócs 1976; Dahlgren, Clifford & Yeo 1985). Desiccation tolerance is also well developed in lichens (Kappen 1973) and mosses (Proctor 1981), representing the homoiochlorophyllous DTs (HDT), which retain their chlorophyll content and photosynthetic apparatus during desiccation (Bewley 1979; Gaff 1989). We show some responses of a common HDT lichen and moss species to elevated CO₂ for comparison.

Materials and methods

*Xerophyta scabrida*, a member of the Velloziaceae, Velloziales, relates to the Bromeliales (Dahlgren *et al.* 1985), is a C₃ photosynthesis type (stable carbon isotope ratio δ¹³C = −27.3‰) pseudoshrub of 0.4–0.9 m in height and with perennial leaves (Tuba, Lichtenthaler, Csintalan & Pócs 1993). On the top of cliffs it forms semi-desert-like bush vegetation on biotite migmatite and hornblende gneiss rocks, in regions with a dry season lasting 5–6 months (Pócs 1976).
Detached and desiccated leaves were rehydrated and regreened at their respective CO$_2$ concentrations (350 and 700 p.p.m.) until their photosynthetic apparatus and activity were fully reconstituted (Tuba, Lichtenthaler et al. 1994; Csintalan et al. 1996).

These leaves were then desiccated slowly in an atmosphere of 350 or 700 p.p.m. CO$_2$ on racks over water in square glass containers kept in Plexiglas chambers at controlled photon flux density (800 μmol m$^{-2}$ s$^{-1}$), temperature (23°C) and relative air humidity (90%).

The lichen thalli of Cladonia convoluta (Lam.) Valin. and moss cushions of Tortula ruralis (Hedw.) Gaertn. ssp. ruralis were transplanted with their original soil substrate from a temperate dry sand grassland dominated by Festuca vaginata (Fekete, Tuba & Melkó 1988) (Fülöpháza, Hungary, 19° 14’ E; 47° 30’ N, at 130 m a.s.l.) into open-top chambers (Tuba, Szente et al. 1994) where they were exposed to elevated (700 p.p.m.) and ambient (350 p.p.m.) CO$_2$ concentrations, respectively, for 5 months. Prior to desiccation the species were rehydrated for 12 h which resulted in full photosynthetic activity. Immediately before the start of the desiccation procedure they were oversaturated by the addition of distilled water. Air humidity (70% r.h.), temperature (23°C) and photon irradiance (400 μmol photons m$^{-2}$ s$^{-1}$) were set to simulate the length of the desiccation period in natural conditions.

Tissue water content was measured by a direct thermogravimetric method (Catsky 1974). Plants were dried to constant weight at 90°C.

The photosynthetic pigments [chlorophylls $a$ and $b$ as well as total carotenoids: xanthophylls + carotenes ($x + c$)] were determined (in 100% acetone extract) by spectrophotometry (Lichtenthaler 1987).

The variable fluorescence decrease ratios (Rfd 690) were calculated from the chlorophyll fluorescence induction kinetics measured in the 690 nm region (i.e. the fluorescence maximum of the chlorophyll fluorescence emission spectrum) by means of the He/Ne laser-equipped chlorophyll fluorometer (Lichtenthaler & Rinderle 1988).

Dark respiration ($R_D$) and light-saturated net photosynthesis rates ($A$) were measured using a gas analysis system (LCA2, ADC Co. Ltd, Hoddesdon, UK) operated in differential mode at ambient and/or elevated CO$_2$ concentrations of 350 and 700 p.p.m. produced by a gas diluter (GD 600, ADC Co. Ltd, Hoddesdon, UK) (Tuba, Lichtenthaler et al. 1994; Tube, Szente et al. 1994). Photon flux density during the measurement of X. scabrida was controlled at 800 μmol photons m$^{-2}$ s$^{-1}$ and leaf temperature was 20 ± 0.5°C.

Internal CO$_2$ concentrations ($c_i$) were calculated from the CO$_2$ exchange measurements (von Caemmerer & Farquhar 1981). Stomatal conductance ($g_s$) was measured with a mass flow porometer (AP4 Delta-T Devices, Cambridge, UK).

CO$_2$ exchange of C. convoluta and T. ruralis (both are $C_3$ photosynthesis type) was measured using special chambers with a volume of 150 ml and 300 ml min$^{-1}$ flow rate through the chamber. The CO$_2$
exchange measurements were made at a constant tissue temperature of 23.0 ± 0.5 °C at 350 and 700 p.p.m. CO₂ concentration as before by illuminating the plants at a photon irradiance of 300 μmol photons m⁻² s⁻¹ for net photosynthesis.

Results

Elevated CO₂ did not affect the drying time in the PDT X. scabrida (Fig. 1a). During desiccation, the mesophyll between the parallel leaf veins contracted (Gaff 1977), substantially reducing the specific leaf area (Fig. 1b) and contributing to the reduction in the rate of water loss (Fig. 1a). During the course of desiccation 85% of the chlorophyll a + b content was lost at normal and elevated CO₂ concentrations (Fig. 1c). The leaves lost about 60% of their carotenoids (Fig. 1c). The process was unaffected by the CO₂ concentrations to which the plants were exposed. The functioning of the thylakoid membranes, judged by slow chlorophyll fluorescence probe, declined rapidly in parallel with the water content and was also unaffected by the CO₂ concentration during desiccation (Fig. 1d).

Prior to desiccation, CO₂ uptake by illuminated leaves grown at present-day CO₂ concentrations was enhanced by 30–35% when the measurements were made at elevated CO₂ (Fig. 2a). A similar pattern was obtained for the plants grown at elevated CO₂ but the rates were all somewhat lower (by 15–20%). However, the most important observation was that plants measured at elevated CO₂ maintained their ability to assimilate carbon for a much longer period during desiccation, 1.5 days instead of 0.5 days (Fig. 2a), irrespective of their growing and desiccating conditions. This brought about a substantial improvement in carbon balance over the entire period of the drying curve: the elevated CO₂ plants gained 75 mmol m⁻² whereas the present CO₂ plants gained only 7 mmol m⁻² (these values are obtained by numerical integration of the data in Fig. 2a). Dark respiration declined in parallel with the tissue water content and was only slightly affected by the CO₂ concentration during desiccation (Fig. 2b).

The persistence of photosynthesis at high CO₂ was associated with a much higher internal CO₂ concentration over the desiccation period (Fig. 3a, b). The stomatal conductance declined steadily over the period but the stomata were still appreciably open after 1 day, when the leaf water content had already fallen from 2.5 to less than 1.0 mg g⁻¹ (Fig. 3c).

The situation in the HDT foliose lichen C. convoluta, which has a green-algal phycobiont, and the HDT ectohydric moss T. ruralis is rather different (Fig. 4). Their tissues (being poikilohydric and less bulky) dried more rapidly (Fig. 4a) and during desiccation from the fully wetted state, net photosynthesis increased at first (Fig. 4b), because their capillary system is filled with water (Proctor 1979; Lange & Tenhunen 1981), which constitutes a substantial resistance to gas diffusion (Dilks & Proctor 1979; Lange & Tenhunen 1981). Maximum assimilation was achieved at a tissue water content of about 60% and thereafter the assimilation fell to zero after 140 min (at present CO₂) or 160 min (at elevated CO₂) (Fig. 4a). The rate of assimilation at elevated CO₂ was 25–35% enhanced at 60% water content and during the whole period the assimilation was increased by elevated CO₂ from 83 to 140 mmol kg⁻¹ dry mass in the case of T. ruralis and from 94 to 143 mmol kg⁻¹ in the case of C. convoluta.

Discussion

The pattern of water loss, the changes in SLA, photosynthetic pigment content and potential thylakoid activity in the water-saturated, photosynthetically fully active leaves of the PDT X. scabrida over the desiccation period was similar to that described previously (Tuba et al. 1996).

Elevated CO₂ concentration had no effect on the rate of water loss, nor on the breakdown pattern of the chlorophylls and carotenoids or the loss of photochemical activity in the desiccating X. scabrida

![Fig. 2. CO₂ exchange in light (a) and dark respiration (b) of X. scabrida during a cycle of drying at 350 and 700 p.p.m. CO₂ concentration.](image-url)
leaves. The decrease of SLA was also unaffected by CO₂ concentration. The elevated CO₂ did not protect the loss of photosynthetic pigments and thylakoid activity which progressed as expected from earlier studies on PDT species (Hetherington & Smillie 1982; Tuba et al. 1996). Carotenoids x+ c were lost to a lesser extent than chlorophylls, as found in earlier works on PDT plants (Gaff 1989; Tuba, Lichtenthaler, Csintalan & Pócs 1993; Tuba et al. 1996) which preserve these pigments in osmiophilic plastoglobuli within the remains of chloroplasts (Tuba, Lichtenthaler, Maróti & Csintalan 1993).

However, the duration of photosynthesis in the desiccating X. scabrida leaves is prolonged by 300% when the measurements are made at 700 as opposed to 350 p.p.m. CO₂. The implication is that the carboxylating enzymes must still have been active at this time to enable appreciable photosynthetic activity. The data do not permit the construction of a full net CO₂ assimilation (A) vs internal CO₂ concentration (c_i) response curve, but a two-point plot of A vs c_i suggests rather similar carboxylating activity in the two desiccation CO₂ conditions, declining rapidly after 0.5 days. Therefore it is likely that carboxylating enzymes in the DT plants are only inactivated but not degraded, because these enzymes are able to fix CO₂ even at extremely low (–38 and –22 MPa) osmotic potentials (Dilks & Proctor 1979; Nash et al. 1990), even in the desiccation-intolerant mesophytes (Kaiser et al. 1981). Enzymes involved in respiration also retain their activity at extremely low water potentials (Dilks & Proctor 1979; Nash et al. 1990). This may explain why the PDT and two HDT plants respired until complete desiccation was achieved at both CO₂ concentrations. It can be concluded that at present-day CO₂ concentration the CO₂ assimilation in the desiccating DT plants is rather limited by their low internal CO₂ concentration. The above can also be applied to the HDT lichen and moss. Both HDT species showed increased net CO₂ uptake in the material grown at high CO₂, by more than 30% in T. ruralis and by more than 50% in C. convoluta.

In desiccation-intolerant plants the influence of elevated CO₂ on the improve of carbon balance has been found to vary considerably but does not usually exceed 25% (Körner 1993). In desiccation-tolerant plants, it appears that the overall effect assessed over the drying cycle may be very much larger and in the case of vascular DTs perhaps several-fold. Within the vascular plants, desiccation tolerance is currently exhibited in 18 genera of ferns, 23 genera of monocotyledons and 10 genera of dicotyledons (Gaff 1989). It is widespread in lichens and mosses (Kappen 1973; Proctor 1981), which are important, characteristic and sometimes dominant in several climatic regions of the Earth (Smith 1982; Hawksworth & Ritchie 1993). These plants are likely to be among the beneficiaries of elevated CO₂, especially if climate change includes an increase in the intermittency of drought (Houghton et al. 1990; Ceulemans & Mousseau 1994).

Acknowledgements

We thank Professor T. Pócs for the X. scabrida material. This work was supported by Ecocraft Environment R&D Programme (Brussels) and by the Hungarian Scientific Research Foundation. Additional support by PHARE/ACCORD and Soros Foundation (Budapest) is also acknowledged.

Fig. 3. Internal CO₂ concentration c_i (a and b) and stomatal conductance g_s in X. scabrida (c) during the drying cycle. The treatments are as before (cf. Fig. 2).
Fig. 4. Drying pattern (a) and CO₂ exchange in light (b) of a DT lichen Cladonia convoluta and a common DT moss Tortula ruralis at two CO₂ concentrations.

References


Received 16 September 1996; revised 1 April 1997; accepted 2 April 1997