Desiccation-Tolerant Plants under Elevated Air CO_2: A Review

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This article summarises present knowledge of the ecophysiological responses to elevated atmospheric CO_2 of desiccation tolerant (DT) plants. It deals primarily with lichens and bryophytes, as the most prominent groups of DT photosynthetic organisms, but includes some comment on algae and vascular DT plants. Results of research on DT plants are compared with those on desiccation sensitive vascular C_3 plants, the most widely investigated group in the field of global change. Both DT and non-DT plants show an immediate positive response of photosynthesis to elevated CO_2, but in both groups the longer term effect is generally reduced (or even reversed) by down-regulation or feedback inhibition of photosynthesis, or other limitations on production and growth. In bryophytes and lichens, enhanced short-term photosynthesis may or may not be reflected in increased production; bryophytes have limited source-sink differentiation, and lichens invest excess photosynthate in secondary metabolites. DT plants may gain some advantage from elevated CO_2 at both low and excessive water contents. Neither theoretical considerations nor experimental results suggest that elevated atmospheric CO_2 will lead to any substantial shift in the balance of advantage between DT and non-DT plants.

Introduction

The concentration of CO_2 in the atmosphere has been increasing in the two last centuries from about 280 ppm to a present value of 360 ppm, and is expected to reach more than twice the pre-industrial concentration in the next century (Houghton *et al.*, 1990). The increasing concentrations CO_2 might be expected to have substantial impacts on plants and vegetation through changes caused to photosynthesis and other physiological processes (Drake *et al.*, 1997). Variations in atmospheric CO_2 concentration are nothing new. Evidence from air trapped in polar ice shows that CO_2 concentration fell to 180–200 ppm during the Pleistocene glaciations, rising to around 280 ppm during the interglacials (Barnola *et al.*, 1987), and CO_2 concentrations were higher during some earlier geological periods (Berner, 1998). What is new is that the present increase appears to be driven by human activity through burning of fossil fuels and clearance of forest, that it is faster than most changes that have taken place in the geologically recent past, that it has already reached levels hitherto unknown in Pleistocene and recent times, and

that our own and immediately succeeding generations will have to cope with whatever consequences it may bring.

Over the last few years an enormous body of experimental data has become available on the responses of non-DT plants to elevated concentrations of CO_2 (see recently published comprehensive reviews and books, e.g. Körner and Bazzaz, 1996; Drake *et al.*, 1997; Raschi *et al.*, 1997 and references cited). Reports on the changes in non-DT plant responses (physiology, growth, production and ecology) have shown various patterns. The responses of plants growing under elevated CO_2 largely depend on the type and degree of physiological acclimation to the high CO_2 environment. Elevated tropospheric CO_2 level affects photosynthesis most directly, therefore studies generally concentrate on photosynthesis and its acclimation.

The most extreme tolerance of water loss occurs in the desiccation-tolerant (DT) or 'resurrection' plants (Gaff, 1989), which can survive the loss of 80–95% or more of their cell water content, so that the plants appear completely dry and no liquid phase remains in their cells. After a shorter

or longer period in the desiccated state, they revive and resume normal metabolism on remoistening (Oliver and Bewley, 1997; Proctor, 1981). This is a qualitatively different phenomenon from drought tolerance as ordinarily understood in higher-plant physiology. Physiologically, DT plants function in ways that are significantly different from vascular plants. DT plants have in general evolved physiological adaptions to intermittent supply of water, rather than structural adaptions for maintaining a constant water supply (Proctor, 1981, 1982; Tuba *et al.*, 1998a). The DT plants are metabolically active when water is available, and when water is lacking their life is suspended.

DT plants span a wide range of adaptation. Poikilochlorophyllous DT (PDT) species lose most or all of their chlorophylls when dry (Gaff, 1989; Tuba *et al.*, 1998a), and the photosynthetic apparatus is resynthesised *de novo* on rehydration (see Tuba *et al.*, 1998a and their references cited in it). By contrast, in homoiochlorophyllous DT (HDT) plants (which are the majority) the photosynthetic apparatus is preserved during desiccation in a state from which it can recover quickly and fully on rehydration (Gaff, 1989; Tuba *et al.*, 1998a.). HDT and PDT plants represent the extremes of a range of strategies to solve variations of the same ecological problem (Tuba *et al.*, 1998a). Desiccation-tolerance occurs widely in the plant kingdom. The *potential* for it is perhaps universal (most spores and seeds are desiccation tolerant); Oliver and Bewley (1997) consider that it has arisen independently in vegetative tissues on at least twelve occasions. Within the vascular plants, desiccation tolerance is currently known in 18 genera of ferns, 23 genera of monocotyledons and ten genera of dicotyledons (Gaff, 1989). It is commonplace in lichens and bryophytes (Kappen, 1973; Proctor, 1981). These small cryptogamic DT plants are important, characteristic and sometimes dominant constituents of many vegetation types from the tropics to the polar regions (Kappen, 1973; Smith, 1982). Their importance lies not only in their biomass production but also in their ability to modify their environment in terms of microclimate, water economy, soil characteristics and decomposition rate (Oechel and Lawrence, 1985). The DT plants tend to increase in abundance and significance under unfavorable climate conditions, where non-DT plants maintain much of their biomass below ground, or are unable to establish (Tenhunen *et al.*, 1992; Kappen, 1973; Porembski *et al.*, 1994). Since large pools of nutrients and carbon can be found in the DT plants of these extreme vegetation-types, significant aspects of ecosystem function depend on their physiological responses, production and turnover pattern.

Studying the effects of rising CO_2 concentration on natural vegetation of the Earth without considering the responses of the DT plants leaves a large (and sometimes crucial) lacuna in our understanding. Despite this, and the volume of research on the physiology of desiccation tolerance (Oliver and Bewley, 1997; Ingram and Bartels, 1996; Farrant, 1998), the potential effects of elevated air CO_2 on DT plants have received much less attention than effects on normal vascular plants (e.g. Körner and Bazzaz, 1996; Drake *et al.*, 1997). Because the water relations and organisation of the photosynthetic tissues are often so different, and because the desiccation–rehydration cycle itself causes profound changes in the photosynthetic activity of the DT plants (Tuba *et al.*, 1998a), the effects of increased atmospheric CO_2 concentration on their carbon balance and growth need not necessarily parallel those of non-DT plants.

Desiccation-tolerant plants under elevated CO_2 – is there a question?

Some have cast doubt upon the relevance of this question. They argue that DT (and non-DT) bryophytes already take advantage of locally elevated CO_2 from soil respiration (Sveinbjörnsson and Oechel, 1992), so increased CO_2 level in the open atmosphere may be of little consequence to them. Thus soil respiration of the taiga reaches about 450 mg CO_2 m^{-2} h^{-1} on a daily average (Gordon *et al.*, 1987). Bazzaz and Williams (1991) confirmed the buildup of high CO_2 concentration on the bryophyte level in a deciduous forest as well. The CO_2 originating from bark respiration must penetrate through epiphytic moss cushions and lichen thalli. However, as global change brings elevated temperature too, soil and plant respiration are likely to increase resulting in an even richer CO_2 supply to these cryptogams (Peterson and Billings, 1975). A possible counter-effect of elevated CO_2 in depressing soil respiration could not been verified by Oberbauer *et al.* (1986). In fact,

DT plants occupy exposed habitats (Porembski *et al.*, 1994), where wind and poor soil or an impermeable substrate do not permit CO_2 accumulation, and these are exposed to ambient atmospheric CO_2. The available $\delta^{13}C$ values for bryophytes show clear evidence of uptake of respired CO_2 only in a limited range of aquatic species (Raven *et al.*, 1985, Proctor *et al.*, 1992 and the relevant references cited by them). A simplistic assumption sometimes made is that, because they lack stomata, bryophytes should have lower diffusion resistances and respond more simply and directly to variations in atmospheric CO_2 than vascular plants. The $\delta^{13}C$ data suggest that the relation between diffusion and carboxylation resistances in bryophytes (-lichens) and C_3 vascular plants is broadly similar, so immediate responses to elevated CO_2 in the two groups are not likely to be very different (Proctor *et al.*, 1992; Williams and Flanagan, 1996); in lichens the carbon-concentrating mechanisms of many of the photobionts complicate the picture, but lichens seem unlikely to be favoured relative to vascular plants by rising CO_2 (see below).

Immediate responses to elevated CO_2

In general, the present ambient CO_2 concentration is suboptimal for bryophytes and lichens, so short-term laboratory experiments show a positive response to elevated CO_2. This interacts with effects of water status, which can vary widely in these poikilohydric plants. At less than full turgor photosynthesis depends on water content in much the same way as in non-DT vascular plants (Tuba *et al.*, 1996). Above this point, an increasing proportion of the water associated with a moist, actively-metabolising bryophyte or lichen is external or intercellular (Dilks and Proctor 1979; Beckett, 1997). While the capillary structure of the plants generally ensures that there is a broad optimum range over which gas exchange can proceed relatively freely, at high water contents CO_2 uptake is limited by increasing diffusion resistance (Dilks and Proctor, 1979). At low levels of hydration the thallus of the lichen *Ramalina maciformis* presents only a small diffusion resistance to CO_2, but above the optimum water content net CO_2 assimilation becomes severely depressed (Lange and Tenhunen, 1981). At a water content of 200% dry weight (DW) and ambient CO_2 more than two-thirds of the diffusion resistance in the lichens studied by Cowan *et al.* (1992) was attributable to the water. However, this depression diminished at 800 ppm CO_2 and disappeared completely at 1600 ppm CO_2. A similar effect of high CO_2 was recorded by Silvola (1985) in *Sphagnum*. This effect is purely physical, due to the raised partial pressure of CO_2 around the photosynthesizing cells (Jauhiainen *et al.*, 1998).

In non-DT homoihydric plants, elevated atmospheric CO_2 may facilitate net photosynthesis more at higher temperatures, but the result of this interaction is highly species-specific (Tremmel and Patterson, 1993). The synergy between increasing CO_2 and temperature has been established for various bryophytes as well (Silvola, 1985) and will be favourable if elevated CO_2 is accompanied by higher temperatures. The immediate effect of exposure to high CO_2 levels is to increase net photosynthesis of mosses dramatically, and this may more than compensate for low photosynthetically active radiation (Silvola, 1985). It also lowers light compensation point (Sonesson *et al.*, 1996). Bearing in mind, that bryophytes rarely encounter bright sunlight in an active, hydrated state for only limited periods (Proctor, 1990) and global warming might bring increased cloud cover and denser forest canopies, this CO_2 effect looks promising for them (Sveinbjörnsson and Oechel, 1992).

Medium-term effects of elevated CO_2

When exposure to elevated CO_2 lasts for a prolonged time (20–40 days), the primary advantageous effects start to decline (Jauhiainen and Silvola, 1996) and signs of negative (downward) acclimation of the photosynthetic system in non-DT plants appear (Drake *et al.*, 1997). In lichens it is characterized by the fall of the photosynthetic capacity (i.e. Rubisco content, carboxylation efficiency, quantum yield of CO_2 assimilation, CO_2 assimilation in saturating light) (Balaguer *et al.*, 1996). In lichens, there is no sign of any changes in photosystem II yield under short-term elevated CO_2 (Sonesson *et al.*, 1995). The decrease in light compensation point induced by immediate CO_2 enrichment disappears during continuing exposure (Grulke *et al.*, 1990). The temporariness of the stimulation caused by elevated CO_2 levels has several possible causes.

Cyanobacterial symbionts, and photobionts with a pyrenoid (e.g. *Trebouxia*) in the chloroplast, possess a photosynthetic CO_2-concentrating mechanism (CCM). This maintains a higher concentration of dissolved inorganic carbon inside the chloroplast as compared with the environment (Badger *et al.*, 1993). Although its capacity is sufficient neither to saturate Rubisco activity at present CO_2 level nor to overcome the diffusion resistance caused by excess water, the CCM is repressed under elevated CO_2 (Badger *et al.*, 1993). A decreased ratio of pyrenoidal Rubisco seems to confirm the inactivation of the CCM in response to high CO_2 (Borkhsenious *et al.*, 1998). This might also contribute to the downward acclimation of some lichen species.

In *Lobaria pulmonaria*, a lichen with a nitrogen-fixing *Nostoc* cyanobacterium, nitrogenase activity doubled in response to short-term high-CO_2 exposure (Norby and Signal, 1989). In lichens without the ability to fix N_2, nitrogen is a limiting factor in nutrient-poor environments (Crittenden *et al.*, 1994). Increased carbon assimilation resulting from elevated atmospheric CO_2 causes relative N-deficiency (Drake *et al.*, 1997). For lichens this situation may be even worse, because they also have to invest N into the chitin-containing fungal cell-wall (Palmqvist *et al.*, 1998). The decrease in Rubisco concentration is an adaptive regulation of photosynthesis, cutting luxury investment of N into the photosynthetic system in non-DT plants (Drake *et al.*, 1997); it appears markedly in the lichen *Parmelia sulcata* after one month of exposure to 700 ppm CO_2 (Balaguer *et al.*, 1996). Decrease in Rubisco was not associated with contraction of pyrenoid volume in green-algal (Balaguer *et al.*, 1996), as Miyachi *et al.* (1986) found for free-living algae.

Higher nutrient availability tends to increase the responsiveness of non-DT vascular plants to elevated CO_2 (Drake *et al.*, 1997). The mineral demand of most mosses is relatively modest and moss production is commonly not nutrient limited (Oechel and Svejnbjörnsson, 1978). Despite this, N addition was the only controlling factor in the biomass production of various *Sphagna* in the experiments of Jauhiainen *et al.* (1998), while simultaneous exposure to elevated CO_2 had a negligible effect. There was only one instance when the synergism between nutrient addition and high CO_2

concentration commonly found in non-DT plants, was detected in bryophytes. It was reported by Baker and Boatman (1990), who investigated *Sphagnum cuspidatum* and applied P and K in addition to N. This is not surprising, as Overdieck (1993) described phosphorus as the main limiting nutrient for non-DT plants under elevated CO_2. In his view, plants can tolerate some decrease in the concentrations of all minerals but phosphorus. More P is required to enable increased flux of carbon through the photosynthetic carbon reduction cycle. *Sphagna* generally receive their nutrients from atmospheric sources, and they failed to respond positively to extra N (Jauhiainen *et al.*, 1998), therefore it would be worth to put to the test other, more minerotrophic bryophyte species.

Decrease in Rubisco content as a response to CO_2 enrichment can explain well the fall of the light-saturated rate of photosynthesis. Under limiting light, however, half of the Rubisco can be removed without impairing carbon assimilation in non-DT homoihydric plants (Quick *et al.*, 1991). Consequently, there must be processes behind the downward regulation of photosynthesis other than the decrease in Rubisco content. There is growing evidence, at least in vascular plants, that negative feedback exerted by excess photosynthates and lack of sufficient sink strength are among the main causes of downward acclimation (Drake *et al.*, 1997). This might apply for lichens as well, because Balaguer *et al.* (1996) found significant increment in cytosolic lipid content in *Parmelia* photobiont. As to the bryophytes, there was no correlation between photosynthesis and growth responses in the experiments of Jauhiainen *et al.* (1998). The increased amount of photosynthates enlarged the non-structural carbohydrate pool in *Sphagnum papillosum* and *S. balticum* at elevated CO_2 concentration. This phenomenon is a well-established indication of insufficient sink strength (Drake *et al.*, 1997). Bryophytes can be characterized by little assimilate translocation and little sink differentation. However, the control by end-product or sink-demand cannot be generalized to all bryophytes as Svejnbjörnsson and Oechel (1992) found positive correlation between total non-structural carbohydrate pool and maximum photosynthetic rates in mosses in Alaska.

From the data presented above it can be inferred that the investigated DT lichens and bryo-

phytes have a limited inherent capability to increase production significantly under short-term CO_2 enrichment. In both groups excess photosynthates emerged and downward acclimation appeared.

Long-term effects of elevated CO_2

Evidences obtained using artificial CO_2 fumigation techniques

In the long run, photosynthetic apparatus seems to be even more influenced by elevated CO_2. The first DT moss put to test in a high-CO_2 experiment was *Polytrichum formosum*, which was exposed to four different CO_2 levels for eleven months in open top chambers (Csintalan *et al.*, 1995). In this case, even photochemical activity, as reflected by relative fluorescence decrease ratio, Rfd, was negatively affected by the two highest CO_2 concentrations (700 and 683 ppm). The higher CO_2 concentration was applied, the higher decrease in Chl_{a+b} content was indicated by the fluorescence ratio parameter, F690/F730. Obviously, the more common signs of downward regulation could also be detected: lowered Rubisco capacity and elevated levels of soluble sugars and starch. Since moss gametophytes lack stomata, these results suggest that stomata probably play a less important role in the acclimation of photosynthesis in non-DT plants (Drake *et al.*, 1997).

Most surprisingly, the highly DT, ectohydric moss *Tortula ruralis* and the foliose *Trebouxia* ascolichen, *Cladonia convoluta* did not display any signs of acclimation in their photosynthesis after four months of exposure to 700 ppm CO_2. In addition to this, elevated CO_2 level resulted in a slightly, but significantly higher net photosynthesis rate from the 15th minute of the rehydration period in *T. ruralis*. *C. convoluta* reached the CO_2 compensation point in less than half the time taken at present CO_2 and its net carbon assimilation raised, too (Csintalan *et al.*, 1997). The difference between the responses of *P. formosum* and the responses of *T. ruralis* and *C. convoluta* is difficult to explain, but may be related to the more elaborate morphology of the *Polytrichum*. The lack of acclimation in the latter two species be a consequence of the intermittent acclimation periods. 'Short' and 'long-term' are relative. Probably the time spent dry and inactive should be

subtracted from the exposure period to obtain the time available for acclimation; a CO_2 fumigation experiment longer than 40 days may still be 'short-term' to the plant. This discrepancy between the behaviour of *P. formosum* and that of *T. ruralis* and *C. convoluta* is a warning against uncritically treating all bryophytes (still less bryophytes and lichens) as a uniform group.

Elevated CO_2 level proved to be beneficial also at the drying-out end of the dehydration-rehydration cycle in *T. ruralis* and *C. convoluta*: not only did the high CO_2 exposure increase the overall carbon gain by about one third but also prolonged net photosynthesis without influencing the rate of water loss (Tuba *et al.*, 1998b). Carboxylating enzymes are only inactivated but not degraded on desiccation and bryophytes are able to fix CO_2 at quite low water potentials (Dilks and Proctor, 1979). Most likely, in DT plants CO_2 is a limiting factor for carboxylation even at this low hydration level (Tuba *et al.*, 1998).

A natural laboratory: in the neighbourhood of CO_2 springs

Balaguer and Barnes (1999) investigated *Parmelia caperata*, an indigenous *Trebouxia*-ascolichen in the vicinity of an uncontaminated natural CO_2 spring. Surprisingly, they did not find symptoms of downward acclimation of photosynthesis except for decreased Rubisco content in the algae from the thallus rim. The latter was attributed to the N-starvation of these photobiont cells induced by the mycobiont in order to limit algal multiplication (Crittenden *et al.*, 1994). In spite of the preserved photosynthetic capacity, there was no sign of increased primary productivity. Instead of non-structural carbohydrates, assimilated carbon was allocated to extracellular phenolic secondary metabolites to avoid negative feedback on photosynthesis. For non-acclimating non-DT plants, the protein competition model (Jones and Hartley, 1998) predicts no change or even a decrease in phenolics content. Empirical data for higher plants show small but variable changes in non-acclimated or nutrient-limited plants. It is a speciality of the lichens, that some of them can accumulate phenolics up to 20% DW (Lawrey, 1995). Phenolics protect lichens against parasitic fungi, bacteria and even slugs

(Lawrey, 1995). They also render the thallus opaque in the desiccated state and thus they offer some photoprotection. Phenolics are thought to inhibit algal cell division and their increase might affect the balance of photobiont and mycobiont in the lichen (Honegger, 1993). On the whole, long-term elevated CO_2 seems to be beneficial for the green-algal lichens. However the competitive advantage is not exerted by increased biomass but by improved protection.

Desiccation-tolerant vascular plants at elevated CO_2 concentration

Only two experiments have dealt with the long-term responses of desiccation tolerant vascular plants to CO_2 enrichment (Csintalan *et al.*, 1997; Tuba *et al.*, 1998a). On desiccation, elevated CO_2 level (700 ppm) did not affect the drying time of the monocotyledonous desiccation tolerant shrub *Xerophyta scabrida* (Tuba *et al.*, 1998a). It did not have an influence on the loss of photochemical activity nor on the breakdown pattern of the chlorophylls and carotenoids. However, the length of positive net photosynthesis was extended by 300%. The reason for this may be the ability of carboxylating enzymes to function at low water contents and the higher intercellular CO_2 concentration within the leaves. Dark respiration was not altered by elevated CO_2 concentration at all. Nevertheless, elevated CO_2 does not have the same beneficial effect on the carbon balance during and after rehydration (Csintalan *et al.*, 1997). While it did not influence the reconstruction of the photosynthetic apparatus as measured by the chlorophyll fluorescence parameter Rfd, it enhanced respiratory activity and delayed the onset of positive net carbon assimilation. After the reconstruction of the photosynthetic apparatus, the net CO_2 assimilation rate was higher in the high CO_2 leaves; however, it rapidly declined to a level lower than in the ambient-CO_2 plants. This acclimation was accompanied by a decrease in photosynthetic pigments and stomatal conductance. A decrease in Rubisco capacity could also be shown (Csintalan *et al.*, 1996). Based on these experiments, the benefits from the elevated CO_2 concentration for *X. scabrida* will offset losses if climate change includes an increase in the intermittency of drought.

Conclusions

It is not possible to draw parallels between the responses to CO_2 enrichment of DT and non-DT plants without caution and qualifications. There are some similarities. In both groups photosynthesis shows an immediate positive response to elevated CO_2, but in the longer term this tends to be negated to varying degrees by downward acclimation of photosynthesis or other limitations on production and growth. Most lichens and mosses live in nutrient-poor habitats and this exerts some limitation on their photosynthetic and production responses to elevated atmospheric CO_2. Of the moss species studied, *Polytrichum formosum* comes closest to the non-DT homoihydric plant pattern. In general, mosses have limited source-sink differentiation, while lichens invest their extra carbon into secondary substances, which has parallels in non-DT higher plants (Cipollini *et al.*, 1993). Lichens and bryophytes are poikilohydric and evergreen. This means that they often have to face suboptimal environmental factors and to react immediately to intermittent favourable periods. There are indications that elevated CO_2 favours DT bryophytes and lichens most when their water content is too low or too high for positive net carbon assimilation at present CO_2. There are also indications that DT plants may generally (but not always) cope better with heavy metal pollution and other stresses at higher CO_2 (Takács *et al.*, 1999). Increases in extracellular phenolics in lichens under long-term elevated CO_2 concentration may mean better defence against herbivores and pathogenes. DT vascular plants also experience a down-regulation of photosynthesis but CO_2 enrichment seems to be beneficial for them during drying out. The responses of DT plants are thus likely to interact in quite complex ways with other climatic factors. No simple predictions can be made. Broad biogeochemical considerations predict that rising atmospheric CO_2 should result in faster net (photosynthetic) transfer of carbon from atmosphere to biosphere (Schlesinger, 1997), but this has yet to be unequivocally demonstrated even for non-DT vascular plants, far less quantified. Much more experimental evidence from long-term experiments would be needed to make a confident forecast of the re-

sponses of desiccation tolerant plants to the global environmental changes that may be expected in the next century.

Acknowledgements

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