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REVIEW

# Development of water stress under increased atmospheric $CO_2$ concentration

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## Abstract

The increase in water use efficiency (the ratio of photosynthetic to transpiration rates) is likely to be the commonest positive effect of long-term elevation in $CO_2$ concentration (CE). This may not necessarily lead to decrease in long-term water use owing to increased leaf area. However, some plant species seem to cope better with drought stress under CE, because increased production of photosynthates might enhance osmotic adjustment and decreased stomatal conductance and transpiration rate under CE enable plants to maintain a higher leaf water potential during drought. In addition, at the same stomatal conductance, internal $CO_2$ concentration might be higher under CE which results in higher photosynthetic rate. Therefore plants under CE of the future atmosphere will probably survive eventual higher drought stress and some species may even be able to extend their biotope into less favourable sites.

*Additional key words:* global climate change, net photosynthetic rate, stomatal conductance, transpiration rate, water potential, water transport, water use efficiency.

## Introduction

Environmental stresses hinder plants growing in agricultural ecosystems from expressing their full genetic potential for production. One of the environmental stresses that is crucial for productivity is drought and the risk of its occurrence will probably increase in some areas in the future.

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*Abbreviations:* CA - ambient $CO_2$ concentration; CE - elevated $CO_2$ concentration; E - transpiration rate; $g_s$ - stomatal conductance; $P_N$ - net photosynthetic rate; RWC - relative water content, WUE - water use efficiency; $WUE_m$ - biomass accumulation per water consumption: $\psi_w$ - leaf water potential; $\psi_p$ - pressure potential; $\psi_s$ - osmotic potential.

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Different mechanisms developed during plant evolution that led to avoidance of dangerous water deficit, and to tolerance to mild water deficit. Shoot desiccation is prevented mainly by the cuticle and by stomatal regulation of transpiration rate. With the decrease of bulk water potential below a threshold value, the stomata close, even if other environmental conditions are optimal. In addition, stomata close in response to increasing rates of peristomatal transpiration induced by decreasing air humidity, or in response to decreasing soil moisture and rate of water absorption by roots. Abscisic acid (ABA) is the main signal messenger in regulating stomatal closure. Some plant species acclimate to water deficit by a shift in the relationship between water and pressure potentials, reached by a decrease in osmotic potential due to accumulation of osmotically active substances (osmotic adjustment), increased cell wall elasticity, increased apoplastic water fraction, and/or increased hydraulic conductivity. A number of genes that respond to drought at the transcriptional level have been described and stress-induced proteins identified.

Since yield and dry matter accumulation are usually highly related, considerable effort has been expended to gain a better understanding of carbon metabolism in response to water stress. In many cases, water deficit reduces growth, leaf area expansion and life-span. Stomatal closure which decreases the water efflux also decreases the $CO_2$ influx, usually limiting photosynthesis under mild water stress. Under high irradiance restricted $CO_2$ influx may cause photoinhibition. The severe water stress also directly affects the photosynthetic capacity of the mesophyll, causing decrease in carboxylation as well as electron transport chain activities, and/or ultrastructural changes in chloroplasts.

Carbon dioxide concentration is expected almost to double within the next century. The increase is occurring because global $CO_2$ consumption in photosynthesis and other absorption does not keep pace with $CO_2$ released from all sources (see, *e.g.*, Murray 1997).

Plant species differ in their responses to $CO_2$ and these differences can be very large, even among co-occurring species in a community. Physiological responses to CE are usually more evident in $C_3$ than in $C_4$ plants. For plant species, they are different at leaf, plant, and stand scale. They depend on $CO_2$ concentration (double, triple, or supraoptimal) and duration of CE treatment (lasting for weeks, months or years). The range of effects of individual physiological parameters by long-term CE is further dependent on other environmental factors. In addition, CE affects not only absolute values of physiological parameters, but also modifies the responses of plants to other environmental factors (Kellomäki and Wang 1997a, Wang and Kellomäki 1997).

The upward trend in atmospheric $CO_2$ concentration has probably already enhanced the photosynthesis of many plants, especially $C_3$ species, and potentially will continue to do so. In spite of thousands of papers on $P_N$ responses to CE, the central question–whether long-term exposure of plants to CE results in a down-regulation of photosynthesis, *i.e.*, that $P_N$ under CE is lower than it would be expected based on short-term assessment of photosynthetic rates as a function of $CO_2$ concentration–is still not satisfactorily explained (for reviews see, *e.g.*, Mott 1990, Bowes 1993, Allen 1994, Reining 1994, Sage 1994, Sage and Reid 1994, Sharkey

1994). In addition, increased $P_N$ under CE seems to be maintained only if the acquisition of other resources is sufficient as it usually is in agrosystems but not in natural ecosystems.

The global climate change includes not only an increase in $CO_2$ concentration but also increases in temperature and drought probability in some areas. The aim of this review is to illustrate whether elevated $CO_2$ concentration might *1*) slowdown the development of water stress, *2*) increase the efficiency of water use, and *3*) ameliorate the negative effects of water stress on carbon metabolism. From a voluminous literature only important up-to-date references have been selected.

## Stomatal conductance and transpiration rate

Water stress in plants usually develops in consequence of insufficient water supply and/or high evaporative demand of the atmosphere. Increased $CO_2$ concentration can affect the development of water stress mostly by its effects on stomatal conductance and transpiration rate.

Long-term CE often leads to a decrease in stomatal conductance ($g_s$) (for reviews see, *e.g.*, Morison 1987, Bowes 1993, Beerling 1994, Field *et al.* 1995, Jones and Jongen 1996, Drake *et al.* 1997, Pospíšilová and Čatský 1999) which results in decreased transpiration rate (E) per unit leaf area (for review see, *e.g.*, Jarvis 1993, Jones and Jongen 1996, Saralabai *et al.* 1997). However, no response or even an increase in $g_s$ and E to CE was also found (see Table 1).

Besides contraction of the size of stomatal pores, lower stomatal density is usually observed under CE (*e.g.* Woodward and Kelly 1995). However, a larger reduction in $g_s$ than in stomatal frequency may indicate that stomatal closure predominates (Ceulemans and Mousseau 1994, Clifford *et al.* 1995). Persistent decrease in $g_s$ of many plant species grown near a natural $CO_2$ source was not associated with changes in stomatal density (Bettarini *et al.* 1998). Also increased epicuticular wax deposition under CE (*e.g.* Murray 1997, Paoletti *et al.* 1998) may lead to decreased E.

The effect of CE is dependent on $CO_2$ concentration during measurements: *e.g.*, in *Trifolium repens*, the highest $g_s$ was found when plants were grown and measured at ambient $CO_2$ concentration (CA), followed by that in plants grown under CE and measured at CA or grown at CA and measured under CE, and the lowest when plants were grown and measured under CE (Ryle *et al.* 1992). In *Eucalyptus tetrodonta* (Berryman *et al.* 1994), *Ginkgo biloba* (Beerling *et al.* 1998), and *Maranthes corymbosa* (Berryman *et al.* 1994), the CE-induced decrease in $g_s$ was only observed when it was measured at CA. The lower E of CE-grown than of CA-grown *Festuca rupicola* and *Dactylis glomerata* plants was found at all internal $CO_2$ concentrations; however, in *Filipendula vulgaris* slightly higher E under CE-grown than at CA-grown plants was observed at low internal $CO_2$ concentration and in *Salvia nemorosa* at high internal $CO_2$ concentration (Tuba *et al.* 1996).

The situation is complicated because the magnitude of $g_s$ decline induced by CE is often affected by other environmental factors, such as irradiance, temperature, and vapour pressure deficit (Wilson and Bunce 1997, Wang and Kellomäki 1997, Seneweera *et al.* 1998), and may be different in adaxial and abaxial surface (*e.g.* in *Rumex obtusifolius* - Pearson *et al.* 1995). A greater reduction in $g_s$ was usually observed under sufficient water supply than under water stress (Grant *et al.* 1995, Tschaplinski *et al.* 1995, Groninger *et al.* 1996, Knapp *et al.* 1996, Faria *et al.* 1997, Goodfellow *et al.* 1997, Lauber and Körner 1997, Ferris *et al.* 1998, Rabha and Uprety 1998). In *Quercus ilex* and *Q. pubescens*, CE induced much higher decrease in $g_s$ in the morning than in the afternoon (Tognetti *et al.* 1998a). On the other hand, in *Triticum aestivum*, the CE induced decrease in $g_s$ was more pronounced at midday than in the morning or afternoon but did not change during the season (Garcia *et al.* 1998). In *Fragaria* × *ananassa* grown under CE, $g_s$ and E were reduced in old leaves but increased in young leaves (Chen *et al.* 1997a).

In addition, CE also affects the response of stomata to other environmental factors. In *Maranthes corymbosa* and *Picea abies*, but not in *Eucalyptus tetrodonta* and *Picea rubens*, $g_s$ was more sensitive to leaf water status under CE, which may decrease the risk of water stress (Berryman *et al.* 1994, Samuelson and Seiler 1994, Dixon *et al.* 1995). On the other hand, the $g_s$ of *Glycine max* (Ferris *et al.* 1998) or *Alnus firma* (Liang and Maruyama 1995), which was lower under CE, decreased less during a period of water stress than that at CA. Similarly, the closing response of *Fagus sylvatica* stomata to drought was delayed in CE but only when plants were grown with low nutrient supply (Heath and Kerstiens 1997a). CE-grown *Quercus suber* seedlings were less responsive in terms of $g_s$ to high temperature (Faria *et al.* 1996) than those grown at CA. On the other hand, no interactions between CE and growth temperature were found in *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus* (Tjoelker *et al.* 1998). Similarly, the response of $g_s$ in *Acer pseudoplatanus* to air humidity was not affected by $CO_2$ concentration (Woodward 1987), but in *Pinus sylvestris* the sensitivity of $g_s$ to low air humidity was increased in trees grown under CE (Kellomäki and Wang 1997b). On the other hand, in CE-grown *Quercus ilex*, the response of $g_s$ to decreasing air humidity was less steep than in CA-grown trees (Tognetti *et al.* 1998b). In addition, in *Andropogon gerardii*, more rapid stomatal responses to sun/shade transitions were observed under CE (Owensby *et al.* 1997). Conversely, $g_s$ of CE- and CA-grown *Cercis canadensis*, *Quercus rubra*, *Populus deltoides* × *P. nigra*, and *Pinus taeda* seedlings were similar and responded in the same manner to $CO_2$ concentration, irradiance and humidity during measurements (Will and Teskey 1997).

Under CE, leaf area per plant is often increased. This may be the reason why E per plant may not necessarily decline. Decreased $g_s$ and no differences in E per plant due to larger leaf area were found, *e.g.*, in *Glycine max* (Jones *et al.* 1985a, Baker and Allen 1993) and *Acacia smallii* (Polley *et al.* 1997a). Similarly, due to the leaf area increase a small effect was found of CE on evapotranspiration in grassland ecosystems (Jones and Jongen 1996, Lauber and Körner 1997) and in a *Lolium perenne* stand (Schapendonk *et al.* 1997). Canopy conductances were lower by as much as 20 % in *Medicago sativa* and by 60 % in *Dactylis glomerata*, but the evapotranspiration rate never differed by more than 3 % in the former or by 8 % in the latter (Bunce *et al.* 1997). The lower magnitude of response of canopy evapotranspiration to CE is also a result of less effective cooling of leaves due to lower E. CE affects leaf energy balance by reducing latent heat flux and increasing sensible heat flux (Ham *et al.* 1995). Increased leaf temperature and decreased humidity in the boundary layer could increase the gradient of water vapour concentration between leaf and its surroundings, and so it might increase E. Therefore evapotranspiration under CE is a result of increased driving force and decreased $g_s$ (Eamus 1991, Lawlor and Mitchell 1991, Jarvis 1993, Morison 1993, Allen 1994, Jones and Jongen 1996, Boote *et al.* 1997).

## Water uptake and transport to leaves

Reduced E can improve leaf water potential by decreasing water loss from leaves, although it might be accompanied by reduced rate of water transport to them (Table 1). Reduced sap flow under CE was found, *e.g.*, in *Andropogon gerardii* (Bremer *et al.* 1996), *Quercus ilex* (Tognetti *et al.* 1998b), *Pinus sylvestris* (Kellomäki and Wang 1998), *Sorghastrum nutans* (Bremer *et al.* 1996) and *Vernonia baldwini* (Bremer *et al.* 1996). Small differences in sap flow were found in *Triticum aestivum* (Senock *et al.* 1996) and *Fagus sylvatica* (Heath *et al.* 1997), but no effect was found in *Gossypium hirsutum* (Dugas *et al.* 1994). Hydraulic conductance increased under CE in *Quercus ilex, Q. robur*, and *Prunus avium* × *P. pseudocerasus* (Atkinson and Taylor 1996, 1997) but decreased in *Abutilon theophrasti*, *Amaranthus hypochondriacus*, *Glycine max*, *Medicago sativa*, and *Zea mays* (Bunce 1996, Bunce and Ziska 1998). In *Quercus ilex*, hydraulic conductance was similar under sufficient water supply but decreased less during water stress in CE-grown trees (Tognetti *et al.* 1998b). Increased hydraulic conductance in *Q. ilex* was connected with increased number of vessels per stem and total vessel lumen cross-sectional area per stem (Atkinson and Taylor 1996).

The root/shoot ratio under CE is usually altered in favour of roots (for review see, *e.g.*, Bowes 1993, Morison 1993, Stulen and den Hertog 1993, Tyree and Alexander 1993, Polley 1996, Saralabai *et al.* 1997), which might increase water uptake. However, no changes in root/shoot ratio in *Betula pendula* and *Picea abies* were observed (Mortensen 1994). In addition, in *Bouteloua gracilis* the vesicular-arbuscular mycorrhiza and thus water uptake was promoted under CE (Morgan *et al.* 1994). Increased water uptake was observed in *Solanum tuberosum* (Mackowiak and Wheeler 1996), whereas decreased water uptake and water consumption were recorded in *Chrysanthemum* × *morifolium* (Gislerod and Nelson 1989).

The total amount of water used during growth was reduced in *Arrhenatherum elatius*, *Calluna vulgaris*, *Danthonia richardsonii*, *Erica tetralix*, *Molinia caerulea*, *Oryza sativa*, *Rumex obtusifolius*, and *Vaccinium myrtillus* grown under CE (Lutze and Gifford 1995, Baker *et al.* 1997a,b, Arp *et al.* 1998). CE-grown *Triticum aestivum* plants used less water per day during the first 30 d of soil drying, but more water per day during a further 10 d (Samarakoon *et al.* 1995). Similarly, under high irrigation a slight reduction in seasonal water use by *Triticum aestivum* was observed, but under low irrigation the water use even slightly increased (Grant *et al.* 1995). However, if the leaf area increases we may expect even higher water use per plant and so water stress may develop more rapidly (Jones and Jongen 1996, Samarakoon and Gifford 1996b). Thus whole-plant water consumption increased under CE in *Fagus sylvatica* (Heath and Kerstiens 1997) and *Gossypium hirsutum* under sufficient soil moisture (Samarakoon and Gifford 1995). In CE-grown *Fragaria* × *ananasa* daily water consumption also increased despite decreased $g_s$ and E per leaf area unit, and increased water use efficiency (WUE) (Chen and Lenz 1997, Chen *et al.* 1997b). Similarly, CE in well-watered *Quercus petraea* and *Pinus pinaster* increased water consumption, but decreased it under water stress (Guehl *et al.* 1994). However, in young *Castanea sativa*, *Fagus sylvatica*, and *Quercus robur* trees grown under CE, stomata failed to close in response to increased evaporative demand of atmosphere; hence additional carbon gain in CE was made at the expense of water economy (Heath 1998).

## Water potential and its components

Many studies have shown that plants under CE tend to dry more slowly as water is withheld, consistently with their lower $g_s$ and E (for review see Tyree and Alexander 1993). In *Lotus corniculatus* relative water content in droughted plants was higher under CE than at CA (Carter *et al.* 1997). In many water-stressed plants higher leaf water potential ($\psi_w$) was reported when grown under CE (see Table 1), but in *Lolium perenne* (Ferris *et al.* 1996), *Picea abies* (Dixon *et al.* 1995), *Quercus ilex* (Tognetti *et al.* 1998a,b), and *Zea mays* (Rozema 1993) no difference in $\psi_l$ was found. In *Lolium perenne*, pressure potential ($\psi_p$) increased at elevated $CO_2$ in spring and remained similar in summer, and osmotic potential ($\psi_s$) decreased in spring and increased in summer (Ferris *et al.* 1996). Decrease of $\psi_w$ and $\psi_s$ in *Lotus*, *Sanguisorba*, *Plantago* and *Anthyllis* occurred under CE, while $\psi_p$ increased (Ferris and Taylor 1994, 1995). In *Phaseolus vulgaris*, $\psi_w$ and $\psi_s$ increased and $\psi_p$ was not affected by CE (Ranasinghe and Taylor 1996). Increased $\psi_s$ at zero $\psi_p$ was determined in *Acer saccharum* but not in *Platanus occidentalis* and *Liquidambar styraciflua* (Tschaplinski *et al.* 1995a). $\psi_s$ was not affected by $CO_2$ treatment in *Prosopis glandulosa* (Polley *et al.* 1996b). Sunlit leaves of *Glycine max* plants grown under CE had higher $\psi_p$ and lower $\psi_s$ than those of plants grown under CA, whereas $\psi_w$ was similar. On the other hand, under water stress $\psi_w$ remained higher under CE than under CA, but zero $\psi_p$ was reached at the same $\psi_w$ (Allen *et al.* 1998).

Both drought and CE resulted in osmotic adjustment in *Helianthus annuus* (Conroy *et al.* 1988), *Betula populifolia* (Morse *et al.* 1993), and *Quercus robur* (Picon *et al.* 1997). Drought had a greater effect than $CO_2$, and their interaction was positive. On the contrary, no indication of enhanced osmotic adjustment was found under CE in *Pinus taeda* (Tschaplinski *et al.* 1993). In leaves of *Quercus robur*, a water stress induced osmotic adjustment was found only under CE, in roots under both CA and CE (Vivin *et al.* 1996). Under CE, decreased $\psi_s$ and symplast water fraction, and increased modulus of elasticity, were found in *Quercus pubescens* and *Q. ilex* (Tognetti *et al.* 1996).

Table 1. Long-term effects of elevated $CO_2$ concentration [μmol mol$^{-1}$] on stomatal conductance ($g_s$), transpiration rate (E), water use efficiency (WUE = $P_N$/E), biomass production per water use ($WUE_m$), sap flow rate (T), total water consumption ($W_t$), leaf water potential ($\psi_w$), net photosynthetic rate ($P_N$) and growth (biomass accumulation, growth analysis, *etc.*) in different plant species. Only the most important recent papers were selected; review papers were not included.

*Additional abbreviations*: ⇓ - decrease; ⇑ - increase; ⇔ - no significant change; ❖ - further parameters of water relations studied; CELSS - controlled ecological life support system; Ci - internal $CO_2$ concentration; CSTR - continuous stirred tank reactor; DRO - drought; FACE - free-air $CO_2$ enrichment; GC - controlled-environment cabinet, growth chamber; GH - controlled-environment glasshouse; LY - lysimeter; N - nature (field, forest); OTC - open-top chamber; PGH - plastic covered greenhouse; PHY - phytotron (glasshouse); PT - plastic tent tunnel; SACC - screen aided $CO_2$ control; SOC - semi-open chamber in field; VHGH - SOLARDOME, strongly ventilated hemispherical greenhouse; VPD - vapour pressure deficit.

| Plant species, cultivation | $CO_2$ concentration; duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\psi_w$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Abies fraseri* GC | 374/713; 1 year | ↓ |  | ⇔ | – | – | – | – | ↓ | ⇑ | – | Samuelson and Seiler 1992 |
| *Acacia smallii* GH | 335/690/980; 13 months | ↓ | ↓ | ⇑ | ⇑ | – | – | – | ⇑ | ⇑ | – | Polley *et al.* 1997a |
| *Acer rubrum* GH/CST | 401/798; 2 cycles, 10 months each | – | – | – | – | – | – | – | ⇑* | ⇑* | *irrespective of water supply | Groninger *et al.* 1996 |
| *Acer saccharum* OTC | 343/652; season | ↓ | – | ⇑ | – | – | – | ⇑ | ⇑ | ↑ | ❖ DRO | Tschaplinski *et al.* 1995a |
| *Acer saccharum* OTC | amb./amb.+300 | – | – | – | – | – | – | – | – | – | ❖ DRO, osmotic adjustment | Tschaplinski *et al.* 1995b |
| *Alnus firma* GC | 350/600-900; 3 months | ↓* | ↑↓* | ⇑ | – | – | ⇔ | – | ⇑ | – | *depends on DRO | Liang and Maruyama 1995 |
| *Andropogon gerardii* OTC | ambient/2× ambient; | ↓ | ⇓ | – | – | ⇓ | – | – | – | ↑⇓ | – | Bremer *et al.* 1996 |
| *Andropogon gerardii* OTC | 330/660; 2 seasons | ↑* | – | – | – | – | – | ⇑ | ⇑* | – | *depends on temperature | Knapp *et al.* 1993 |
| *Andropogon gerardii* OTC | 330/660; 2 seasons | ↓⇔ | – | – | – | – | – | ⇑ | – | – | – | Knapp *et al.* 1996 |
| *Andropogon gerardii* OTC | ambient/2× ambient; 34 d | ⇓ | – | – | – | ↑ | – | – | ↑*⇔♦ | – | season: *early, ♦end | Ham *et al.* 1995 |
| *Andropogon gerardii* OTC | 350/700; 60 d | ↓↑* | – | – | – | – | ⇑ | – | ⇔↑* | – | *DRO | Hamerlynck *et al.* 1997 |
| *Andropogon gerardii* OTC | ambient/2× ambient; 7 seasons | ⇓ | ⇓ | – | – | ↓ | ⇓ | ⇑ | – | ⇑ | – | Owensby *et al.* 1997 |
| *Anthyllis vulneraria* GC | 350/590; 45 d | ↓ | ⇓ | – | ⇑ | – | – | ↓ | ↑ | ↑ | – | Ferris and Taylor 1995 |
| *Anthyllis vulneraria* GC | 350/590; 35 d | – | – | – | – | – | – | ⇓ | – | ⇑* | *roots | Ferris and Taylor 1994 |

(*continued*)

| Plant species, cultivation | $CO_2$ concentration; duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\psi_W$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Anthyllis vulneraria* FACE | amb./600: 14 months | ↓ | ↓ | – | – | – | – | – | ⇔*⇑◆ | – | *pre-cut; ◆post-cut | Bryant *et al.* 1998 |
| *Arachis hypogaea* GH | 350/700: full season | – | – | – | – | – | ⇑ | – | ↑ | ⇑ | – | Clifford *et al.* 1993 |
| *Arachis hypogaea* GH | 375/700: in summer | ⇔*⇓⁺ | – | – | – | – | – | – | ⇑ | – | *35 d, ⁺114 d old | Clifford *et al.* 1995 |
| *Arrhenatherum elatius* GH | 350/560: full season | – | – | – | ⇑ | – | ↓ | – | – | ⇑* | *only in high N | Arp *et al.* 1998 |
| *Atriplex canescens* GH PT | 200/350/700/1000: season | ↓ | – | ⇑ | ↑ | – | – | – | ↑ | – | ❖ subambient $CO_2$ | Polley *et al.* 1996a |
| *Betula papyrifera* GC | 370/580: 91 d | ↓ | – | ⇑ | – | – | – | – | ⇔* | ⇑ | *on mass basis | Tjoelker *et al.* 1998 |
| *Betula pendula* GC | 350/700: 35-45 d | – | ⇓ | – | – | – | – | ↑ | ⇑ | ⇑ | – | Mortensen 1994 |
| *Betula pendula* OTC | 350/700: 4 seasons | ↓ | – | – | – | – | – | – | ⇑ | – | – | Rey and Jarvis 1998 |
| *Bouteloua gracilis* LY GC | 350/700: 11 weeks | – | – | – | ⇑ | – | – | ↑ | – | ⇑ | – | Morgan *et al.* 1994 |
| *Bouteloua gracilis* GC | 350/700: 2 months | – | ⇑ | ↑ | ⇑ | – | – | ↑ | ⇑ | ⇑ | – | Morgan *et al.* 1998 |
| *Brassica juncea* OTC | ambient/600: 70 d | ↓ | ⇓ | – | – | – | – | ⇑ | ⇑ | ↑* | *root; ❖ DRO | Rabha and Uprety 1998 |
| *Bromopsis erecta* FACE | amb./600: 14 months | ↓ | ⇑*⇓** | – | – | – | – | – | ⇑ | – | * pre-cut; ** post-cut | Bryant *et al.* 1998 |
| *Bromus erectus* SACC | ambient/600: season | ↓ | – | – | – | – | – | – | – | ⇔ | no change under DRO | Lauber and Körner 1997 |
| *Calluna vulgaris* CH | 350/560: full season | – | – | – | ↑ | – | ⇓ | – | – | ↑* | *only in high N | Arp *et al.* 1998 |
| *Carex flacca* SACC | ambient/600: season | ⇔ | – | – | – | – | – | – | – | ↑ | no change under DRO | Lauber and Körner 1997 |
| *Castanea sativa* VHGH | amb./amb.+250: *ca.* 3 months | ↓*⇔ | – | – | – | – | – | – | ↑ | – | *low leaf-to-air VPD | Heath 1998 |
| *Chenopodium album* GC | 350/700: 2 years | ↓* | – | ↑ | – | – | – | – | ↓* | – | *on Ci basis | Šantrůček and Sage 1996 |
| *Chrysanthemum* × *morifolium* SACC | 340/940: 6 weeks | ↓ | – | – | – | – | ⇓ | – | – | ⇑ | – | Gislerød and Nelson 1989 |
| *Dactylis glomerata* SOC | 350/700: several years | ↓ | – | – | – | – | – | – | – | – | ❖ also canopy conductance | Bunce *et al.* 1997 |
| *Dactylis glomerata* OTC | 350/700: 231 d | ↓ | ⇔ | ↑ | – | – | – | – | ⇑ | – | – | Szente *et al.* 1998 |
| *Dactylis glomarata* OTC | 350/700: 11 month | – | ⇓ | ↑*↓◆ | – | – | – | – | ↑ | – | measured at *700, ◆350 | Tuba *et al.* 1996 |
| *Danthonia richardsonii* PHY | 357/712: 1 year | – | – | – | ⇑ | – | ⇓ | – | – | ↑ | – | Lutze and Gifford 1995 |
| *Erica tetralic* GH | 350/560: full season | – | – | – | ⇑ | – | ↓ | – | – | ⇑* | *only in high N | Arp *et al.* 1998 |
| *Eucalyptus macrorhyncha* GH | 350/700: 60 d | ↓ | – | – | – | – | – | ⇑ | ⇓↑* | ↑ | *DRO<br>❖ heat and water stresses | Roden and Ball 1996 |

**(continued)**

| Plant species, cultivation | $CO_2$ concentration: duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\Psi_w$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eucalyptus tetradonta* PT | 355/700: 10 months | ⇓*↑◆ | .. | – | – | – | – | – | – | – | measured in *355 ◆560 | Berryman *et al.* 1994 |
| *Eucalyptus rossii* GH | 350/700: 60 d | ⇓ | – | – | – | – | – | ⇑ | ↓↑* | ⇑ | *DRO<br>❖ heat and water stresses | Roden and Ball 1996 |
| *Fagus sylvatica* VHGH | amb./amb.−250: 2 seasons | ↓*⇔ | – | – | – | – | ⇑ | – | ↑ | ⇑ | *cloudy days. ❖ DRO | Heath and Kerstiens 1997 |
| *Fagus sylvatica* VHGH | amb./600: 2 seasons | ⇔* | – | – | – | – | – | – | – | – | *sunny days<br>❖ hydraulic conductance | Heath *et al.* 1997 |
| *Fagus sylvatica* VHGH | amb./amb.−250: *ca.* 3 months | ↓*⇔ | – | – | – | – | – | – | ↑ | – | *low leaf-to-air VPD | Heath 1998 |
| *Festuca rupicola* OTC | 350/700: 231 d | ↑ | ⇑ | ⇑ | – | – | – | – | ↑ | – | – | Szente *et al.* 1998 |
| *Festuca rupicola* OTC | 350/700: 11 month | – | ⇓ | ↑ | – | – | – | – | ⇑ | – | *in dependence on Ci | Tuba *et al.* 1996 |
| *Filipendula vulgaris* OTC | 350/700: 11 month | – | ↓ | ⇑ | – | – | – | – | ⇑ | – | – | Tuba *et al.* 1996 |
| *Filipendula vulgaris* OTC | 350/700: 231 d | ↑ | ⇑ | ⇑ | – | – | – | – | ↑ | – | – | Szente *et al.* 1998 |
| *Fragaria* × *ananassa* GS | 300/450/600/750/900: 50 d | ↑*⇓** | ↑*⇓** | ⇑ | – | – | – | – | ⇑* | ↑ | leaves: *young, **old | Chen *et al.* 1997a |
| *Fragaria* × *ananassa* GS | 300/450/600/750/900: 50 d | – | – | – | ⇑ | – | ⇑ | – | – | ⇑ | | Chen *et al.* 1997b |
| *Fragaria* × *ananassa* GS | 340/680: 1 month | ⇓* | ↓* | ↑⇓** | – | – | ↑ | ⇑* | ↑ | – | *young-old leaves<br>**P deficiency | Chen and Lenz 1997 |
| *Gingko biloba* GH | 350/560: 3 years | ↓*↑** | – | ↑ | – | – | – | – | ⇑ | – | measured in *355 **560 | Beerling *et al.* 1998 |
| *Glycine max* GC | 330/660: 11 d | ↓ | ↓ | ↑ | – | – | – | ↑ | ⇑ | – | – | Allen *et al.* 1994 |
| *Glycine max* GH | 360/700: season | ↓ | ↓ | ↑ | – | – | – | ⇓ | ⇑ | – | – | Ferris *et al.* 1998 |
| *Glycine max* OTC | 360/700: season | ↓ | – | – | – | – | – | – | – | ↑ | – | Fiscus *et al.* 1997 |
| *Glycine max* GC | 320/640: 18 d | – | – | ↑ | – | – | ⇓ | – | ⇑ | ↑ | – | Jones *et al.* 1985b |
| *Glycine max* CELLS | 500/1000/2000/5000: 90 d | ↓⇑ | – | – | ⇑⇓* | – | ⇓ | – | – | ↑⇔ | *supraoptimal [$CO_2$] | Wheeler *et al.* 1993 |
| *Glycine max* GC | 330/450/660/800: upto 77 d | ↓ | ⇓ | – | – | – | – | ⇓ | – | – | ❖ DRO | Allen *et al.* 1998 |
| *Glycine max* GC | 330/800: season | ↓ | – | ⇑ | – | – | ⇓ | – | ⇑ | ⇑ | ❖ short- and long-term $CO_2$ application | Jones *et al.* 1985a |

***(continued)***

| Plant species, cultivation | $CO_2$ concentration: duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\Psi_w$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Glycine max* GC | 350/700: 21 d | ↓ | ⇓ | – | – | – | – | ↓ | ↑ | – | – | Bunce 1996 |
| *Gossypium hirsutum* N, FACE | 370/550: 5 months | – | – | – | – | ⇔ | – | – | – | – | – | Dugas *et al.* 1994 |
| *Gossypium hirsutum* PHY | amb./2 × amb.: ± 50 d | ↓⇔ | ⇓ | – | ↑ | – | ↓⇑ | – | – | ⇑ | ❖ DRO | Samarakoon and Gifford 1995 |
| *Gossypium hirsutum* PHY | 352/710: ± 50 d | – | ⇓ | – | ⇑ | – | ↑ | – | – | ⇑ | ❖ DRO | Samarakoon and Gifford 1996b |
| *Helianthus annuus* GC | 340/660: several weeks | ⇑ | – | – | – | – | – | – | – | – | – | Conroy *et al.* 1988 |
| *Hordeum vulgare* GC | 330/680: ± 18 d | ⇓ | – | – | – | – | – | – | ⇓ | – | premature senescence at 680 | Sicher 1998a |
| *Hordeum vulgare* GC | 330/680: 3 weeks | ↓ | – | – | – | – | – | – | ⇓ | – | – | Sicher 1998b |
| *Larix laricina* GC | 370/580: 91 d | ↓ | – | ⇑ | – | – | – | – | ↑ | ⇑ | – | Tjoelker *et al.* 1998 |
| *Larrea tridentata* GH*, FACE** | 360, 550, 700: 1 year*<br>360/550: 6 months** | – | – | – | – | – | – | ⇓** | ⇓+ | – | +well-watered; ❖ DRO | Huxman *et al.* 1998 |
| *Liquidambar styraciflua* OTC | 343/652; season | ↓ | – | ⇑ | – | – | – | ⇑ | ⇑ | ⇑ | ❖ DRO | Tschaplinski *et al.* 1995a |
| *Lolium perenne* PT | 350/700: 2 years | – | – | – | ↑ | – | – | – | – | ⇑ | – | Casella *et al.* 1996 |
| *Lolium perenne* OTC/PGHT | 360/700: season | – | – | – |  | – | – | ↑↓* | – | ↑* | *depends on season | Ferris *et al.* 1996 |
| *Lolium perenne* N and enclosures | 360/700: 2 years | – | ⇔ | ⇑ | – | – | – | – | ⇑ | ↑ | – | Schapendonck *et al.* 1997 |
| *Lotus corniculatus* GH | 350/700: season | – | – | – | ↑ | – | – | – | – | ⇑ | – | Carter *et al.* 1997 |
| *Lotus corniculatus* GC | 350/590: 35 d | – | – | – | – | – | – | ↓ | – | ↑* | *roots | Ferris and Taylor 1994 |
| *Mangifera indica* GC | amb./700: season | ↓ | – | – | – | – | – | – | ⇑ | ⇑ | – | Goodfellow *et al.* 1997 |
| *Medicago sativa* SOC | 350/700: several years | ↓* | – | – | – | – | – | – | – | – | *also canopy conductance | Bunce *et al.* 1997 |
| *Medicago sativa* GC | 350/700: 21 d | ↓ | ⇓ | – | – | – | – | – | ⇓ | – | – | Bunce 1996 |
| *Medicago sativa* OTC | 340/600: ± 30 d | – | – | – | – | – | – | ⇔* | – | – | *lower decrease under water stress | Sgherri *et al.* 1998 |
| *Molinia coerulea* GH | 350/560: full season | – | – | – | ⇑ | – | ⇓ | – | – | ↑* | *only in high N | Arp *et al.* 1998 |
| *Oryza sativa* GC, LY | 350/700: season | – | – | – | – | – | – | – | – | ↑ | ❖ DRO | Baker *et al.* 1997a |
| *Oryza sativa* GC | 330/700: season | – | – | ↑ |  | – | – | – | ↑↓* | ↑⇓* | *DRO | Vu *et al.* 1998 |

*(continued)*

| Plant species, cultivation | $CO_2$ concentration; duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $U_W$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oryza sativa* GC, LY | 350/700; season | – | – | ↑ | – | – | ⇓ | – | ⇑ | – | ❖ DRO | Baker *et al.* 1997b |
| *Panicum coloratum* GC | 350/1000; 35 d | – | ↓ | ↑ | – | – | ⇓ | ↑ | – | ↑ | ❖ DRO | Seneweera *et al.* 1998 |
| *Pascopyrum smithii* GC | 350/700; 2 months | – | ⇑ | ↑ | ⇑ | – | – | ⇑ | ↑ | ↑ | – | Morgan *et al.* 1998 |
| *Phaseolus vulgaris* GH, OTC | 200/700; 17 d | ↓* | – | ↑* | – | – | – | – | ⇑* | – | *measured at 5 $CO_2$ conc. | Radoglou *et al.* 1992 |
| *Picea abies* OTC | 350/700; 150 d | ⇔ | | ↑ | | – | | ⇔ | ⇑ | ↑ | – | Dixon *et al.* 1995 |
| *Picea abies* OTC | 350/700; 3 seasons | ⇓ | – | ↑* | – | – | – | ↓ | ⇑** | – | *less under DRO;<br>**depends on day time | Le Thiec and Dixon 1996 |
| *Picea abies* GC | 350/700; 35-45 d | – | ⇓ | – | – | – | – | ↑ | ⇑ | ⇑ | – | Mortensen 1994 |
| *Picea mariana* GC | 370/580; 91 d | ⇓ | – | ↑ | – | – | – | – | ⇑ | ⇑ | – | Tjoelker *et al.* 1998 |
| *Picea rubens* GC | 374/713; 2 seasons | ↑*⇓ | – | – | – | – | – | – | ⇑* | – | *in young seedlings<br>❖ water stress | Samuelson and Seiler 1994 |
| *Picea sitchensis* VHGH | 350/600; 6 months | ⇓ | – | ↑ | – | – | – | – | ⇑ | ⇑ | ❖ DRO | Townend 1993 |
| *Picea sitchensis* VHGH | 350/600; 2 years | – | – | – | – | – | – | – | – | ⇑ | ❖ DRO | Townend 1995 |
| *Pinus banksiana* GC | 370/580; 91 d | ↓ | – | ⇑ | – | – | – | – | ⇑ | ⇑ | – | Tjoelker *et al.* 1998 |
| *Pinus pinaster* GH | 350/700; season | – | – | – | ⇑ | ⇔⇑* | ↑*↓◆ | – | – | ⇑ | *well watered, ◆water stress | Guehl *et al.* 1994 |
| *Pinus pinaster* GHPT | 350/700; season | ⇔ | – | ⇑ | – | – | – | – | ⇑ | ↑* | ❖ DRO | Picon *et al.* 1996 |
| *Pinus sylvestris* branch bag | 350/700; 2-3 seasons | ↓ | – | – | – | – | – | – | ⇑ | – | – | Kellomäki and Wang 1997 |
| *Pinus sylvestris* OTC | 350/700; 2 seasons | ↓ | – | – | – | – | – | – | ↑ | – | – | Kellomäki and Wang 1997 |
| *Pinus sylvestris* OTC | 330-480/670-730; 1 year | ↓* | ↓* | – | – | ↓ | – | – | – | ⇑ | *in other papers | Kellomäki and Wang 1998 |
| *Pinus sylvestris* OTC | amb./550-600; 4 years | ↓ | ↓ | – | ⇑ | – | – | – | – | ⇔ | ❖ water stress | Wang and Kellomäki 1997 |
| *Pinus tæda* PHY | 350/650; 4 years | ⇓ | – | ⇑* | – | – | – | – | ↑ | ⇑ | *$P_N/g_s$ | Tissue *et al.* 1997 |
| *Pinus tæda* GH/CST | 401/798; 2 cycles 10 months each | – | – | – | – | – | – | – | ↑* | ⇑* | *irrespective of water supply | Groninger *et al.* 1996 |
| *Pinus tæda* GC | 350/700; 4 months | | | | | | | | | ⇑ | ❖ water supply, osmotic adjustment | Tschaplinski *et al.* 1993 |

***(continued)***

| Plant species, cultivation | $CO_2$ concentration: duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\Psi_w$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Plantago media* GC | 350/590; 35 d | – | – | – | – | – | – | ↓ | – | ⇑* | *roots | Ferris and Taylor 1994 |
| *Platanus occidentalis* OTC | 343/652: season | ↓ | – | ⇑ | – | – | – | ↑ | ⇑ | ⇑ | ❖ DRO | Tschaplinski *et al.* 1995a |
| *Populus tremuloides* GC | 370/580; 91 d | ↓ | – | ⇑ | – | – | – | – | ⇔* | ⇑ | *mass-based | Tjoelker *et al.* 1998 |
| *Prosopis glandulosa* | 370/710/1050: season | ↓ | ⇓ | – | – | – | – | – | – | ⇑ | – | Polley *et al.* 1996 |
| *Prunus avium* × *pseudocerasus* GH | 350/700: 19 months | ↓ | ⇓ | ⇓ | ⇓ | – | – | – | ⇑* | ⇑ | *PAR saturated | Atkinson *et al.* 1997 |
| *Pseudotsuga menziesii* GC | 350/750; 14 months | – | – | ⇑⇔* | – | – | – | – | ⇑ | ⇑ | *long-term treatment | Gorissen *et al.* 1995 |
| *Quercus ilex* OTC | amb./amb.+350: 3 years | – | – | – | – | – | – | ↓ | ⇑ | – | ❖ DRO | Scarascia-Mugnozza 1996 |
| *Quercus ilex* N | amb./500 to 1000*: 2 months | ⇔ | ⇓ | – | – | ⇑ | – | ⇔ | – | – | *near natural spring of $CO_2$ | Tognetti *et al.* 1996 |
| *Quercus ilex* N | 350/500 to 1000*: 2 months | ↓ | ⇓ | – | ⇑ | ⇑ | – | ⇔ | ⇑ | – | *near natural spring of $CO_2$ | Tognetti *et al.* 1998a |
| *Quercus ilex* N | 350/500 to 1000*: 2 months | ↓ | ⇓ | – | – | ⇓ | – | ⇑⇔ |  | – | *near natural spring of $CO_2$<br>❖ hydraulic resistance, DRO | Tognetti *et al.* 1998b |
| *Quercus petraea* GH | 350/700: season | – | – | – | ⇑ | ⇓*⇑◆ | – | – | – | ⇑ | *well watered, ◆water stress | Guehl *et al.* 1994 |
| *Quercus petraea* GH PT | 350/700: season | ↓ | – | ⇑ | – | – | – | – | ⇔ | – | *DRO | Picon *et al.* 1996b |
| *Quercus pubescens* N | 350/500 to 1000*: 2 months | ⇓ | ↓ | – | ↑ | ⇑ | – | ⇔ | ⇑ | – | *near natural spring of $CO_2$ | Tognetti *et al.* 1998a |
| *Quercus pubescens* N | amb./500 to 1000*: 2 months | ⇓ | ⇓ | – | – | ↑ | – | ↑ | – | – | *near natural spring of $CO_2$ | Tognetti *et al.* 1996 |
| *Quercus robur* GH | 350/700: 19 months | ↓ | ⇓ | ⇑ | ⇓ | – | – | – | ↑* | ⇑** | *PAR saturated, **only shoot | Atkinson *et al.* 1997 |
| *Quercus robur* VHGH | ambient/ambient+250: 2 seasons | ↓ | – | – | – | – | – | – | ⇑ | ⇑ | ❖ DRO | Heath and Kerstiens 1997 |
| *Quercus robur* VHGH | ambient/600: 2 seasons | ↓ | – | – | – | – | – | – | – | – | ❖ hydraulic conductance | Heath *et al.* 1997 |
| *Quercus robur* GH PT | 350/700: season | – | ↓ | – | ⇑ | – | ⇔ | ⇑↓* | – | ⇑ | *DRO | Picon *et al.* 1996a |
| *Quercus robur* GH PT | 350/700: 22 weeks | – | ⇓↑* | – | – | – | – | ↑↓* | – | ⇑ | *DRO | Vivin and Guehl 1997 |
| *Quercus robur* GH PT | 350/700: season | – | – | – | – | – | ↓⇑* | ⇔ | ⇑⇓* | ⇔⇑** | *DRO; ** end of season; | Vivin *et al.* 1996 |
| *Quercus robur* GH | 350/700: season | ↓⇔* | – | ⇑ | – | – | – | – | ⇑ | ⇑* | *DRO | Picon *et al.* 1997 |

***(continued)***

| Plant species, cultivation | $CO_2$ concentration: duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\Psi_W$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Quercus robur* GC | amb./1100: 15 weeks | – | – | – | – | – | – | ↓⇑* | – | ⇑ | *DRO+mycorrhiza | Schulte *et al.* 1998 |
| *Quercus robur* VHGH | amb./amb.+250: *ca.* 3 months | ↓*⇔ | – | – | – | – | – | – | ⇑ | – | *low leaf-to-air VPD | Heath 1998 |
| *Quercus rubra* OTC | 350/700: 3 seasons | ↓ | – | ⇑* | – | – | – | ⇓ | ⇑** | – | *less under DRO<br>**depends on day time | Le Thiec and Dixon 1996 |
| *Quercus suber* GH | 350/700: 14 months | ↓* | – | – | – | – | – | – | ⇑↓* | – | *depends on temperature | Faria *et al.* 1996 |
| *Rhizophora apiculata* GH | 340/700: 3 months | ↓ | ⇑↓ | – | ⇑ | – | – | – | – | ⇔*⇑** | limitation by *salinity, **humidity | Ball *et al.* 1997 |
| *Rhizophora stylosa* GH | 340/700: 3 months | ⇓ | ↑⇓ | – | ⇑ | – | – | – | – | ⇔*⇑** | limitation by *salinity, **humidity | Ball *et al.* 1997 |
| *Rumex obtusifolius* GH | 350/560: full season | – | – | – | ↑ | – | ⇓ | – | – | ⇑* | *only in high N | Arp *et al.* 1998 |
| *Rumex obtusifolius* FACE | 350/600: 2 seasons | ↓ | ↓ | – | – | – | – | – | ⇑ | ⇑ | abax./adax. $g_s$ | Pearson *et al.* 1995 |
| *Salvia nemorosa* OTC | 350/700: 231 d | ⇔ | ⇔ | ⇑ | – | – | – | – | ↑ | – | – | Szente *et al.* 1998 |
| *Salvia nemorosa* OTC | 350/700: 11 months | ↓ | ↓ | ⇑ | – | – | – | – | ↑ | – | – | Tuba *et al.* 1996 |
| *Salvia pitcheri* OTC | 350/700: 60 d | ↓↑* | – | – | - | – | ⇔ | – | ↑ | - | *DRO | Hamerlynck *et al.* 1997 |
| *Salvia pitcheri* OTC | ambient/2× ambient: 7 seasons | ⇓ | ⇓ | – | – | ↓ | ⇓ | ⇑ | – | ⇑ | – | Owensby *et al.* 1997 |
| *Sanguisorba minor* GC | 350/590: 45 d | ⇓ | ↓ | – | ⇑ | – | – | ↓ | ⇑ | ↑ | – | Ferris and Taylor 1995 |
| *Sanguisorba minor* FACE | amb./600: 14 months | ⇑*↓** | ⇑ | – | – | – | – | – | ⇑ | – | *pre-cut, **post-cu | Bryant *et al.* 1998 |
| *Schizachyrium scoparium* GH, PT | 200/350/700/1000: season | ↓ | – | ↑ | ↑ | – | – | – | ⇑ | – | – | Polley *et al.* 1996a |
| *Sinapis alba* glass-top chambers | 350/700: 2 months | ↓ | – | – | ⇑ | – | – | – | – | ⇑ | – | Retuerto and Woodward 1993 |
| *Solanum tuberosum* GC | 50/100/500/1000: 105 d | ⇑ | – | – | ↓ | – | –⇑ | – | – | ↑⇔ | – | Mackowiak and Wheeler 1996 |
| *Sorghastrum nutans* OTC | ambient / 2× ambient | ⇓ | ↓ | – | – | ↓ | – | – | – | ⇑↓ | – | Bremer *et al.* 1996 |
| *Sorghastrum nutans* OTC | ambient / 2× ambient: 34 d | ↓* |  | – | – | – | – | – | ↑*♦⇔• | – | *canopy, ♦earlier growth stages; •end of season | Ham *et al.* 1995 |
| *Sorghastrum nutans* OTC | 330/660: 2 seasons | ↓⇔ | – | – | – | – | – | ⇑ | – | – | – | Knapp *et al.* 1996 |

***(continued)***

| Plant species, cultivation | $CO_2$ concentration: duration | $g_s$ | E | WUE | $WUE_m$ | T | $W_t$ | $\psi_w$ | $P_N$ | Growth | Remarks | Author(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Symphoricarpus orbiculatus* OTC | 350/700: 60 d | ↓↑* | – | – | – | – | ⇑ | – | ↑ | – | *DRO | Hamerlynck *et al.* 1997 |
| *Trifolium repens* GC | 340/680: 3-4 weeks | ↓ | ↓ | ⇑ | – | – | – | – | ↑⇔* | ⇑ | *measured at 340 | Ryle *et al.* 1992 |
| *Triticum aestivum* FACE | 370/550: 3 months | ↓⇔* | – | – | – | – | – | – | ↑ | ⇑ | *during season | Garcia *et al.* 1998 |
| *Triticum aestivum* FACE | 370/550: season | ↓⇔* | ⇑⇓* | – | – | – | ↓ | ⇑ | ⇑ | ⇑ | *full irrigation | Grant *et al.* 1995 |
| *Triticum aestivum* FACE | 370/550; 2 seasons | – | – | – | ↑- | – | – | – | – | ⇑ | – | Hunsaker *et al.* 1996 |
| *Triticum aestivum* PHY | amb./2 × amb.: ± 50 d | ↓ | ⇓ | – | ⇑ | – | ⇓ | – | – | ⇑ | ❖ DRO | Samarakoon and Gifford 1995 |
| *Triticum aestivum* PHY | 350/700: ± 50 d | ↓ | ⇓ | – | ⇑ | – | ↑⇔ | – | – | ⇑ | ❖ DRO | Samarakoon *et al.* 1995 |
| *Triticum aestivum* FACE | 370/550: 30 d | – | – | – | ⇑ | – | – | – | – | ⇑ | – | Hunsaker *et al.* 1996 |
| *Triticum aestivum* GC | 350/700: 116 d | – | – | – | – | – | ↓ | – | – | ⇑ | – | van Vuuren *et al.* 1997 |
| *Vaccinium myrtillus* GH | 350/560: full season | – | – | – | – | ↓ | ⇓ | – | – | – | – | Senock *et al.* 1996 |
| *Vernonia baldwini* var. *interior* OTC | 2× ambient | ↓ | ↓ | – | – | ↓ | – | – | – | ↑ | – | Bremer *et al.* 1996 |
| *Zea mays* GH | 350/700: season | ⇓ | ⇓ | ↑ | – | – | – | – | ⇑ | – | – | Bethenod *et al.* 1995 |
| *Zea mays* GH, PT | 200/350/700/1000: season | ↓ | – | ⇑ | ↑ | – | – | – | ⇑ | – | – | Polley *et al.* 1996a |
| *Zea mays* PHY | amb./2× amb.: ± 50 d | ⇔ | ⇔⇓ | – | ⇑ | – | ↓ | – | – | ⇔⇑* | *DRO | Samarakoon and Gifford 1995 |
| *Zea mays* PHY | 362/717: ± 50 d | – | ⇓ | – | ⇑ | – | ↓ | – | – | ⇔ | ❖ DRO | Samarakoon and Gifford 1996a |

From plant species mentioned in this table increased WUE or $WUE_m$ was observed in more than 90 % of CE plants mostly due to increased $P_N$ *in situ*, found in about 85 % of CE plants. Decreased $g_s$ and E was found in about 75 % of CE plants; in more than 50 % of CE plants total water uptake was decreased and development of water stress was slowed-down in terms of less negative $\psi_w$.

## Effect of elevated $CO_2$ concentration on water use efficiency

WUE usually means ratio of net photosynthetic rate ($P_N$) to E, sometimes also biomass production per amount of water used. The response of $P_N$ and E to some environmental factors may be different and all these factors affect the $P_N/E$ ratio. In addition, every change in $g_s$ brings about the change in $P_N/E$ ratio, because the effect of $g_s$ on E is usually more marked than that on $P_N$, due to differences in the transport pathways of water vapour and $CO_2$. Thus the $P_N/E$ ratio is usually higher at lower $g_s$ than at a higher one.

Under long-term CE the increase in WUE is the most common positive effect. Increased $P_N/E$ ratio was observed not only in plants with increased $P_N$ but also in plants where down-regulation of $P_N$ was observed, because in these plants a decrease in $P_N$ was usually accompanied with decrease in $g_s$. The range of increase in WUE induced by CE depends on plant species and other environmental factors, especially water stress (Table 1; for review see, *e.g.*, Bazzaz 1990, Hogan *et al.* 1991, Morison 1993, Ceulemans and Mousseau 1994, Pospíšilová and Čatský 1999).

WUE was increased under CE under both well-watered and drought treatments, *e.g.*, in *Glycine max* (Allen *et al.* 1994) and *Picea sitchensis* (Townend 1993). In *Alnus firma* (Liang and Maruyama 1995) and *Anthyllis vulneraria, Panicum coloratum*, and *Sanguisorba minor* (Ferris and Taylor 1995, Seneweera *et al.* 1998) this usually occurred with a higher average increase under water stress. On the other hand, the relative enhancement in WUE under CE was reduced in *Quercus rubra* or even disappeared in *Picea abies* (Le Thiec and Dixon 1996) when the trees were subjected to drought. In *Rhizophora apiculata* and *R. stylosa*, WUE was increased under CE combined with high or low air humidity and high or low salinity, even if $g_s$ in *R. apiculata* grown under CE and low humidity was increased (Ball *et al.* 1997). In *Phaseolus vulgaris* CE doubled the WUE at high nutrient supply and tripled it at low nutrient supply (Radoglou *et al.* 1992).

WUE in *Chenopodium album* more than doubled after a short-term doubling of $CO_2$ concentration. However, WUE of plants grown and measured under CE was only about one and a half times that of plants transiently exposed to CE, due to stomatal acclimation (Šantrůček and Sage 1996). Similarly, in *Trifolium repens* the increase in WUE was much more dependent on $CO_2$ concentration, irradiance, and leaf temperature during the measurement than on $CO_2$ concentration during growth (Ryle *et al.* 1992).

However, WUE was not increased under CE in *Abies fraseri* (due to strong down-regulation of $P_N$ - Samuelson and Seiler 1992), and in *Quercus robur* (Atkinson *et al.* 1997), and even decreased in *Prunus avium* (Atkinson *et al.* 1997). In grassland, changes in WUE depended on the period of the year (Fredeen *et al.* 1998).

CE also increased biomass accumulation per water consumption ($WUE_m$, Table 1), or grain production per water consumption in *Triticum aestivum* (Hunsaker *et al.* 1996). In *Gossypium hirsutum, Triticum aestivum*, and *Zea mays*, $WUE_m$ increased under CE for both wet and dry conditions. Similarly in *Lolium perenne* $WUE_m$ increased under CE with no significant interaction with soil moisture or N supply (Casella *et al.* 1996). Under supraoptimal $CO_2$ concentration, $WUE_m$ was decreased in *Glycine max* (Wheeler *et al.* 1993) and *Solanum tuberosum* (Mackowiak and Wheeler 1996).

Analysis of carbon isotope composition ($\delta^{13}C$) in tree rings (*e.g.* Duquesnay *et al.* 1998) or in herbarium leaves (Beerling 1994) also showed increased WUE with increased $CO_2$ concentration during the past century. Similarly, $\delta^{13}C$ decreased in needles of *Pinus sylvestris* grown under CE for 3 years (Beerling 1997).

## Amelioration of the negative effects of water stress on carbon metabolism

In most plant species and under most circumstances, $g_s$ is the main limiting factor to $P_N$ under mild water deficit. and elevated $CO_2$ concentration may compensate for decreased $g_s$ by an increased gradient of $CO_2$ concentration between the exterior and interior of the leaf (for review see, *e.g.*, Chaves and Pereira 1992). In connection with this, increased $P_N/g_s$ ratio was found in *Quercus ilex*, *Q. pubescens* (Tognetti *et al.* 1998), *Q. petraea* (Picon *et al.* 1996b), *Q. rubra* (Dixon *et al.* 1995), *Picea abies* (Dixon *et al.* 1995), *Pinus pinaster* (Picon *et al.* 1996b) and *Pinus taeda* (Tissue *et al.* 1997) grown under CE, but not in *Zea mays* (Bethenod *et al.* 1995). In *Quercus robur* the stimulating effect of CE on the $P_N/g_s$ ratio was observed in well-watered seedlings, maintained under moderate drought, but it disappered with severe drought (Picon *et al.* 1997). Similarly, in *Betula pendula* (Rey and Jarvis 1998) and *Glycine max* (Fiscus *et al.* 1997) stomatal limitation of photosynthesis was less under CE than at CA.

However, another possible consequence of CE and water stress might be the change in susceptibility to photoinhibition. The probability of photoinhibition might be increased due to reduction of photorespiration or decreased by better supply of $CO_2$ (for review see Chaves and Pereira 1992). Increased photoinhibition and premature senescence under CE was found in *Hordeum vulgare* (Sicher 1998).

Increased $\psi_w$ under CE could stimulate leaf expansion and carbon dioxide fixation, and thereby contribute to the stimulation of growth (Bunce 1996, Polley *et al.* 1996a). In *Larrea tridentata*, increased $\psi_w$ under CE ameliorate negative effect of drought on maximum $P_N$, carboxylation efficiency, variable to maximum fluorescence ratio and photochemical quenching (Huxman *et al.* 1998). In *Oryza sativa*, reduction of evapotranspiration and enhancements in both $P_N$ and WUE under CE helped to delay the adverse effects of severe drought and allowed the stressed plants to continue photosynthesis for further one or two days (Baker *et al.* 1997, Vu *et al.* 1998). In CE-grown *Bauhinia multinervia*, *Quercus ilex*, *Q. robur*, and *Spatiphylum cannifolium* maximum $P_N$ during the day and daily plant carbon uptake were less responsive to decreasing $\psi_l$ than in CA-grown plants (Scarascia-Mugnoza *et al.* 1996, Vivin and Guehl 1997, Fernández *et al.* 1998). Decreased water use, observed, *e.g.*, for *Oryza sativa* (Baker *et al.* 1997a), *Triticum aestivum* (Van Vuuren *et al.* 1997), or for grassland (Field 1995) allowed photosynthesis or growth to continue for some days longer during drought under CE compared to CA. CE stimulates tallgrass prairie productivity during dry periods (Hamerlynck *et al.* 1997). In many plant species, CE alleviates the negative effect of drought on plant growth, *e.g.*, in *Oryza sativa* (Baker *et al.* 1997) and *Panicum odoratum* (Seneweera *et al.* 1998), or on starch and sugar content of leaves, *e.g.*, in *Brassica juncea* (Uprety and Rabha 1999).

*Glycine max* photosynthesis recovered fully after a period of water stress only under CE but not at CA (Ferris *et al.* 1998). On the other hand, CE had no effect on the rate of rehydration, nor on the *de novo* photosynthesis in desiccated *Xerophyta scabrida* (Csintalan *et al.* 1996).

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