Vegetatio **104/105**: 47–62, 1993.
J. Rozema, H. Lambers, S.C. van de Geijn and M.L. Cambridge (eds). CO_2 and Biosphere

Plant water relations and the effects of elevated CO_2: a review and suggestions for future research

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Keywords: Carbon dioxide, Water relations, Water use efficiency, Water potential, Transpiration, Stomatal movement, Growth

Abstract

Increased ambient carbon dioxide (CO_2) has been found to ameliorate water stress in the majority of species studied. The results of many studies indicate that lower evaporative flux density is associated with high CO_2-induced stomatal closure. As a result of decreases in evaporative flux density and increases in net photosynthesis, also found to occur in high CO_2 environments, plants have often been shown to maintain higher water use efficiencies when grown at high CO_2 than when grown in normal, ambient air. Plants grown at high CO_2 have also been found to maintain higher total water potentials, to increase biomass production, have larger root-to-shoot ratios, and to be generally more drought resistant (through avoidance mechanisms) than those grown at ambient CO_2 levels. High CO_2-induced changes in plant structure (i.e., vessel or tracheid anatomy, leaf specific conductivity) may be associated with changes in vulnerability to xylem cavitation or in environmental conditions in which runaway embolism is likely to occur. Further study is needed to resolve these important issues. Methodology and other CO_2 effects on plant water relations are discussed.

Abbreviations: A = net photosynthesis; C_a = ambient $[CO_2]$; C_i = internal $[CO_2]$; E = evaporative flux density; g_l = leaf conductance; g_s = stomatal conductance; LSC = leaf specific conductivity; IRGA = infrared gas analyzer; LAI = leaf area index; PAR = photosynthetically active radiation; Ψ = total plant water potential; Ψ_{soil} = soil water potential; Ψ_s = solute potential; Ψ_{pt} = turgor pressure potential; Ψ_{px} = xylem pressure potential; RH = relative humidity; R:S = root to shoot ratio; RWC = relative water content; SLA = specific leaf area; SLW = specific leaf weight; SPAC = soil-plant-atmosphere-continuum; SWC = soil water content; VPD = vapor pressure deficit; WUE = water use efficiency.

Introduction

In recent years, much attention has been focused on anthropogenic increases in atmospheric concentrations of various 'greenhouse' gasses, so called due to their ability to trap terrestrial radiation and so warm the atmosphere. Carbon dioxide (CO_2) is one such gas that has been of interest due to its importance in both the theory of global warming and the photosynthetic production of vegetation. The global average atmospheric CO_2 concentration is currently thought to be around 350 μmol mol^{-1}, an increase of *circa* 70 μmol mol^{-1} since the mid 1800's (Leadley *et al.* 1987; Arnone & Gordon 1990; Conroy *et al.* 1990), and may nearly double by the mid-21st century (Tolley & Strain 1984a; Leadley *et al.* 1987). It has been hypothesized that this increase

will impact plant growth (Higginbotham *et al.* 1985; Idso 1988), competition (Carlson & Bazzaz 1980; Marks & Strain 1989), and water relations (Sionit *et al.* 1981; Rogers *et al.* 1984; Barr *et al.* 1990). Aside from sun light, the one factor most basic to the continuance of plant metabolic processes and survival is water. The relationship between atmospheric carbon dioxide concentration (C_a) and plant water relations, therefore, is a vital area of interest and, as such, is the subject of the current review. In this paper, we summarize work done on the effects of elevated CO_2 on various aspects of plant water relations, including gas exchange, morphology, and internal water stress, and the methods used to carry out this work.

Methods

Plant material

Species most commonly used in these investigations are those considered to be agriculturally important. Among the variety of plants studied are soybean (*Glycine max* (L.) Merr.), wheat (*Triticum aestivum* L.), cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), and sunflower (*Helianthus annuus* L.). Also studied have been temperate tree species such as Monterey pine (*Pinus radiata* D. Don), loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.) and white oak (*Quercus alba* L.). Several tropical tree species, such as *Ochroma lagopus* Swartz, *Pentaclethra macroloba* Willd., *Cecropia obtusifolia*, *Piper auritum*, and *Garcinia mangostana* L., have also been studied, as has the CAM plant *Agave vilmoriniana* Berger. These species have been the focus of the majority of research on increased C_a and water relations, and represent all three carbon pathway plant types (C_3, C_4, and CAM). In general, cultivated seedlings of the study species have been used due to logistical constraints.

Plant culture

Plant material for these studies has been grown most often in open-topped chambers in which C_a can be monitored with an infrared gas analyzer (IRGA) and maintained at desired levels by adding bottled CO_2. These chambers can be placed outdoors to take advantage of natural light and temperature regimes (Jones *et al.* 1984; Rogers *et al.* 1984; Idso *et al.* 1987; Szarek *et al.* 1987), or closed chambers placed in greenhouses, where environmental factors are more readily controlled (Khan & Madsen 1986; Reekie & Bazzaz 1989; Arnone & Gordon 1990). Controlled environment rooms are frequently used to grow seedlings at enhanced C_a (e.g., Higginbotham 1985; Wray & Strain 1986). Growing conditions generally span normal terrestrial light and temperature ranges, but include C_a's ranging from 350 to 675 μmol mol^{-1} (Oberbauer *et al.* 1985; Idso 1988; Marks & Strain 1989; Nijs *et al.* 1989a), with some studies involving CO_2 treatments of 800 to 1,000 μmol mol^{-1} (Tolley & Strain 1984a; Del Castillo *et al.* 1989), and still others as high as 2000 μmol mol^{-1} (Higginbotham *et al.* 1985) and 4,000 μmol mol^{-1} (Pallas 1965).

The potting medium in which seedlings have most often been grown has been a 1:1 mix of sand or gravel and vermiculite (Oberbauer *et al.* 1985; Sionit & Patterson 1985; Hollinger 1987), or a variation including commercial potting soil (Sionit *et al.* 1981; Tolley & Strain 1984b; Arnone & Gordon 1990). In some cases in which drought stress was the focus, excised branches of mature trees have been placed in, and then removed from, a water bath as a means of imposing short-term water stress (Beadle *et al.* 1979)

In studies in which environmental conditions other than C_a were controlled, light intensity, or photosynthetically active radiation (PAR), was commonly maintained at moderate levels of 450 to 750 $\mu E\ m^{-2}\ s^{-1}$ (Sionit *et al.* 1981; Conroy *et al.* 1988a; Sasek & Strain 1989). Some workers, however, grew plants at low light levels of less than 150 $\mu E\ m^{-2}\ s^{-1}$ (Khan & Madsen 1986) and some at high light levels between 1000 and 2000 $\mu E\ m^{-2}\ s^{-1}$ (Rogers 1983; Tolley & Strain 1984a; Reekie & Bazzaz 1989), depending on plant material and objectives. Light sources were either fluorescent and incandescent bulbs (Sasek & Strain 1989), high intensity discharge lamps (Tol-

ley & Strain 1984a), natural sun light (Rogers 1983; Reekie & Bazzaz 1989), or some combination of these sources (Khan & Madsen 1986). Most workers used growing temperatures between 20 and 30 °C (Sionit *et al.* 1981; Rogers 1983; Reekie & Bazzaz 1989; Sasek & Strain 1989).

The interactive effects of elevated C_a and water stress on plant water relations have been investigated by several workers. In these studies, soil water potential (Ψ_{soil}) has been allowed to decrease to between *circa* -1.5 MPa (Sionit *et al.* 1981; Rogers *et al.* 1984; Sionit & Patterson 1985; Conroy *et al.* 1988b) and *circa* -2.5 MPa (Beadle *et al.* 1979; Tolley & Strain 1984b; Frederick *et al.* 1990). In general, soil water status was gauged by observed predawn Ψ (Rogers *et al.* 1984; Tolley & Strain 1984b;), expressed gravimetrically as soil water content (SWC) (Conroy *et al.* 1988a; Barr *et al.* 1990), or judged by 'time since last watered' (Sionit & Patterson 1985; Idso 1988). Among the papers we found reporting C_a and plant water relations, nobody has measured Ψ_{soil} directly, such as with a soil thermocouple psychrometer (Kramer 1983). In situ soil psychrometers should be used in conjunction with measurements of predawn Ψ of leaves to get the best estimate of soil water potential.

Plant water potential

The two most widely used tools for measuring Ψ, the Scholander pressure bomb (or pressure chamber) and the thermocouple psychrometer, have received fairly equal use by researchers in this field. Both methods can be reliable if used with knowledge and caution, but serious errors can result when inappropriately used. The pressure bomb method has been used by a number of researchers studying effects of CO_2 on plant water relations (Beadle *et al.* 1979; Tolley & Strain, 1984b; Higginbotham *et al.* 1985; Teskey *et al.* 1986; Sasek & Strain 1989; Frederick *et al.* 1990). Readers are referred to Tyree and Jarvis (1982) for an account of how this analysis is done and examples of possible sources of error (Cheung *et al.* 1976; Tyree *et al.* 1976; Tyree & Richter 1981 & 1982).

The Spanner thermocouple psychrometer method of measuring Ψ (or variations to it) has also been used by many workers (Sionit *et al.* 1981; Sionit & Patterson 1985; Szarek *et al.* 1987; Conroy *et al.* 1988b) and may, like the pressure bomb, be used on either the stem or foliage. On stems a temperature corrected psychrometer is strongly recommended (Dixon and Tyree 1984). A thermocouple junction is placed near to the plant material, and both are sealed in a small chamber to allow the water vapor pressure to equilibrate between the surface of the plant and the air in the chamber. Peltier cooling (Kramer 1983) is then used to condense a small drop of water on the thermocouple junction. As water evaporates from the junction the temperature of the junction falls a few hundredths of a degree below the air temperature. This temperature change is measured and is found to be proportional to the Ψ of the sample (or calibration standard).

It is possible to measure the dehydration isotherm of samples using a psychrometer and from that calculate the components of tissue water potential as commonly done with the pressure bomb. But the usual method is to measure the solute potential (Ψ_s) by freezing and thawing leaf disks, thus rupturing the cells and releasing solutes into the sap. With Ψ_{pt} now equal to zero, Ψ is equal to Ψ_s, so a remeasurement of Ψ after a freeze thaw cycle will yield Ψ_s. Knowing the initial Ψ and Ψ_s, Ψ_{pt} can be calculated by subtracting Ψ_s from Ψ. This method however has some inherent errors caused by the dilution of solute in the cell sap by water in the apoplast after the freeze-thaw cycle. This tends to make Ψ_s less negative and thus Ψ_{pt} too low or even negative (Tyree 1976). So this method, while fast, should be used with caution. For example, exposure to high C_a can change leaf anatomy and thus the amount of apoplastic water relative to symplastic water, which could cause a bigger underestimate of Ψ_s in plants grown in high C_a than in low C_a.

Stomatal/Transpirational response

The most widely used method for measuring the response of evaporative flux density (E), and thus leaf conductance (g_l), to increased C_a appears to be steady state porometry (Rogers *et al.* 1984; Sionit & Patterson 1985; Khan & Madsen 1986; Teskey *et al.* 1986). In the steady state porometer, a given foliar area is placed into a cuvette, or chamber. As plant water loss proceeds, the flow rate of dry air pumped into the chamber is adjusted automatically to maintain RH at the ambient level, and E can be calculated given flow rate, leaf area, RH and temperature. Open systems in which changes in RH of ingoing and outgoing air can be monitored have also been commonly used to measure E (Beadle *et al.* 1979; Wong 1979; Morison & Gifford 1983), from which g_l can be calculated (Barr *et al.* 1990). Still others have estimated E gravimetrically, by changes in plant and pot weight (Conroy *et al.* 1988a; Barr *et al.* 1990). Most cuvette systems alter the energy budget of leaves and thus change E. Many have felt that the measurement of g_l by steady state porometry is accurate if done quickly even with altered energy budgets. However, it is now clear (Tyree & Wilmot 1990) that leaf temperatures are incorrectly measured in many steady state porometers and thus the calculated g_l is also wrong. Caution is recommended in interpreting results.

Developmental responses of stomata to CO_2 have also been investigated. Woodward (1987) and Peñuelas and Matamala (1990) used microscopic techniques to determine changes in stomatal density. Subjects were herbarium specimens of several species collected over the past 200 years, and plants grown from seed at elevated C_a.

Results and discussion

Stomatal response

The effect of increasing C_a on stomatal movement is an issue central to the present review. Most studies have shown that, all else equal, elevated C_a brings about a decrease in g_s, and thus in E. This response has been observed in studies involving both short term exposure to elevated C_a (Pallas 1965; Akita & Moss 1972; [contrast: Beadle *et al.* 1979;]) and long term exposure starting at or soon after germination (Sionit *et al.* 1981; Wray & Strain 1986; Barr *et al.* 1990; [contrast: Nijs *et al.* 1988]). It has been hypothesized that this negative relationship between C_a and g_s is due to the effects of C_a on internal [CO_2] (C_i), and that it is an increase in C_i that is the direct cause of stomatal closure (Rosenberg 1981; Morison & Gifford 1983; Oechel & Strain 1985). There does seem to be some question as to whether whole plant water use decreases with increasing C_a, considering that although E (generally expressed on a per-unit-leaf area basis) has been seen to decrease, total evaporative leaf surface increases. Idso *et al.* (1987) obtained some contradictory water loss results in their study of *Gossypium hirsutum* in which leaf area increased with increasing C_a, observed over a treatment period of 3 years. The results of several studies do indicate a variety of stomatal responses to changes in C_a. Beadle *et al.* (1979) observed that stomatal response to short term increases in C_a depended on the degree of existing water stress (see below). Higginbotham *et al.* (1985) observed no CO_2 related change in g_s of *Pinus contorta* foliage grown at C_a's as high as 2,000 μmol mol^{-1}, while Nijs *et al.* (1988) report that in *L. perenne* grown at elevated C_a, E, and presumably g_s, increased with increasing C_a.

Many studies focusing on the impact of increased C_a on plant water relations have examined the interactive effects of other environmental factors. In general, it has been found that the greatest benefit to plant water conservation due to elevated C_a is attained under various forms of stress (Morison 1985). The most common stress factor studied with regard to C_a has been drought. Drought is defined here as any period of time when water extraction from soils exceeds the rate of water input for a protracted period. It has often been seen that increased C_a significantly reduces transpirational water loss, and that these reduc-

tions are greatest under conditions of drought (Dahlman *et al.* 1985). Idso (1988) noted that water stressed plants of the C_3, C_4, and CAM groups are able to remain turgid and functional under drought conditions for a longer period of time at a C_a of 640 μmol mol^{-1} than at normal, ambient CO_2 levels. The notion that plants can endure drought better when exposed to high C_a has also been put forth by Conroy *et al.* (1988b), who found similar results in their study of sunflower leaves grown in enhanced C_a. Conroy *et al.* attributed this drought resistance at high C_a to a combination of osmotic adjustments in the chloroplasts and stomatal closure. Similarly, Tolley & Strain (1984b) found that water-stressed seedlings of *L. styraciflua* and *P. taeda* were able to maintain higher Ψ when grown at higher-than-ambient C_a. The Ψ_{leaf} increased and g_s decreased in drought-exposed *T. aestivum* plants grown at an elevated C_a of 1,000 μmol mol^{-1} (Sionit *et al.* 1981), as was found for *L. perenne* and *Trifolium repens* L. (Nijs *et al.* 1989a). Contrary to the above findings, Beadle *et al.* (1979) observed only a slight negative relationship between g_s and C_i in needles of Sitka spruce (*Picea sitchensis* Bong. (Carr.)) grown at ambient C_a under well-watered conditions, and a minor positive relationship under water stress. The workers attributed the lack of pronounced response of g_s to the relative insensitivity of conifer stomata to C_a.

In their study of C_a, vapor pressure deficit (VPD), and soil water content (SWC) in C_4 plants, Barr *et al.* (1990) also found that E and leaf conductance (g_l) of *Z. mays* plants decreased with increasing C_a, but, in contrast to the works cited above, this effect was most pronounced at low VPD and high SWC (i.e., under low water stress). Barr *et al.* (1990) attributed this contrasting observation to a growth strategy that prioritizes carbon uptake over water loss and thus a greater benefit from elevated C_a growing conditions. Oechel & Strain (1985) have suggested that stomata are more sensitive to changes in C_a at higher VPD. Given the findings of many workers that elevated C_a tends to ease the effects of drought, this hypothesis is not unreasonable. However, Morison & Gifford (1983), like Barr *et al.* (1990), found that stomata of several grasses grown at ambient C_a were least sensitive to C_a at high VPD, as also reported by Hollinger (1987) for two coniferous and one broad-leaved tree species.

Effects of C_a on Ψ

An important aspect of drought tolerance in plants growing in an elevated C_a is the maintenance of high Ψ. In *G. max* plants exposed to drought conditions, Rogers *et al.* (1984) observed that retention of high Ψ was positively associated with C_a, and that plants growing in the high C_a treatment wilted less and incurred less drought related damage than did plants in the ambient C_a treatment. Sionit *et al.* (1981) obtained similar results with *T. aestivum*. Tolley & Strain (1984b) also found that Ψ in drought-stressed seedlings of *P. taeda* and *L. styraciflua* remained higher at high C_a, as was observed by Wray & Strain (1986) on *Aster pilosus* and *Andropogon virginicus* and by Sionit and Patterson (1985) for several C_3 and C_4 grasses.

As mentioned earlier, Conroy *et al.* (1988b) found that Ψ and solute potential (Ψ_s) in cells of drought-stressed *H. annuus* leaves were maintained at lower levels (more negative) in plants grown and monitored in high C_a than those exposed to ambient C_a. Osmotic adjustments in leaves of plants in above-ambient CO_2 treatments were credited with the maintenance of higher relative water content (RWC) and turgor pressure (Ψ_{pt}), and prevention of full stomatal closure, allowing net photosynthesis (A) to proceed. This differential osmotic response creates a differential response in Ψ_{pt} (Kramer 1983), and thus greater calculated turgor in plants exposed to equal water stress but higher C_a (Thomas & Harvey 1983). The occurrence of similar osmotic adjustments in kudzu (*Pueraria lobata* (Willd.) Ohwi) leaves was reported by Sasek & Strain (1989). In contrast, Reekie & Bazzaz (1989) found no correlation between C_a and Ψ and only a slight negative relationship between C_a and g_s in several tropical tree species. This lack of obvious CO_2 effects was

attributed to the well-watered condition of the study plants.

Water use efficiency

Water use efficiency (WUE), defined as the ratio of the amount of carbon fixed photosynthetically (A) to the amount of water lost due to evaporative flux density (E), is a parameter that interests many workers owing to its usefulness as an index of productivity vs. moisture requirements. Water use efficiency has often been observed to increase with increasing C_a. Many workers have ascribed these increases in WUE to greater A associated with greater CO_2 availability, lower E resulting from decreased g_s, or a combination of the two. Rosenberg (1981) and Kramer (1981) suggest that it is the combination of factors that produces increased WUE, especially in that lower g_s is more limiting to E than to A. Similar results have been obtained by several other workers for both C_3 and C_4 species (Wong 1979; Carlson & Bazzaz 1980; Morison & Gifford 1983; Jones *et al.* 1984; Norby & O'Neill 1989; Rozema *et al.* 1991A&B). Rogers (1983) and Rogers *et al.* (1983) have found this phenomenon to hold true for most species studied in their work, with the exception of *Z. mays*, which exhibited no increases in A at elevated C_a. The observed increase in WUE was thus solely attributed to decreases in E.

Nijs *et al.* (1989b) indicate that increased WUE of *L. perenne* subjected to high C_a was due to the enhancement of A alone, without a concurrent decrease in E. In contrast, the same workers found that WUE of *L. perenne* decreased by an average of 9 % with increasing C_a from ambient to 600 μmol mol^{-1} (Nijs *et al.* 1988). This contrary finding was said to have resulted from a negative response of A to increasing C_a, which may have been the result of greater self-shading due to increased leaf area. The effects of CO_2-induced changes in leaf area and other anatomical features on plant water relations will be discussed in the following section.

Effects of increased atmospheric CO_2 on growth

Two of the most crucial metabolic functions in determining the magnitude of plant growth are carbon assimilation and water use. Because of the observed impact of increased C_a on these functions, many studies have been undertaken to determine the relationship between C_a and plant growth, a relationship most often described as a positive one.

Changes in the capacity of a plant to produce biomass may affect several aspects of plant water relations: Ontogeny, which can change the ability of a plant to take advantage of higher spring moisture regimes, and thus be less negatively impacted by dryer summer growing conditions (Oechel & Strain 1985); Foliage anatomy and display, which contribute to the regulation of transpirational water loss; growth of ground and conductive tissue in the shoot, changes in which will affect both foliar display and resistance to water flow, and thus stem conductivity and Ψ; Root-to-shoot ratio (R:S), which determines the patterns of water supply and demand within the plant. The ultimate impact of growth changes on plant water relations can best be integrated by an analysis of the effects of C_a on hydraulic architecture of plants. While changes in some components of hydraulic architecture have been documented, the total impact of these changes has not been evaluated quantitatively and, until that is done, a major gap in our knowledge will persist.

Foliage growth

Early and rapid development of leaves and leaf area under elevated C_a has been observed in several studies (Wulff & Strain 1982; Goudriaan & de Ruiter 1983; Dahlman *et al.* 1985; Higginbotham *et al.* 1985; Nijs *et al.* 1988; Downton *et al.* 1990; Rozema *et al.* 1991A). It has generally been found that increased C_a results in increased leaf area index (LAI) or leaf area per plant (Wong 1979; Goudriaan & de Ruiter 1983; Jones *et al.* 1984; Sasek & Strain 1989). Several workers have attributed this increase in leaf area to an increase

in the total number of leaves (Goudriaan & de Ruiter 1983; Conroy *et al.* 1986; Downton *et al.* 1990) or shoots (Rozema *et al.* 1991B), while others have found that it is leaf size, and not number, that results in increased total leaf area (Jones *et al.* 1984). Jones *et al.* (1984) observed a 30 % increase in LAI of *G. max* grown at high C_a. This increase was linked to an increase in WUE that resulted from enhanced A and a decrease in E. The increased growth rate of foliage treated with high C_a is most likely due to increased carbon gain (Rogers *et al.* 1984; Tolley & Strain 1984; Norby *et al.* 1986), providing more building material for leaf tissue and increased cell Ψ_{pt} (Sionit *et al.* 1981; Norby *et al.* 1986; Sasek & Strain 1989), allowing a higher rate of cell expansion over a longer duration. Wulff & Strain (1982) reported increases of 20 % in leaf area and specific leaf weight (SLW-leaf weight per unit leaf surface area) in *Desmodium paniculatum* (a leguminous perrenial herb) grown at a C_a of 1,000 μmol mol^{-1}. Norby *et al.* (1986), however, reported no response of leaf area to C_a in *Q. alba*, due to the determinant growth strategy of the species, while Oechel & Strain (1985) reported a decrease in leaf area of *Ledum palustre* L. (an arctic evergreen shrub), possibly the result of photoinhibition.

Some researchers who have observed that increases in C_a cause increases in SLW (Oberbauer *et al.* 1985; Reekie & Bazzaz 1989) have noted that these experimental responses are mirrored by historical changes in stomatal density and specific leaf area (SLA) in plants over the past 200 years of atmospheric change (Peñuelas & Matamala 1990). Leaf thickness has been shown to increase in a number of species (Wulff & Strain 1982; Rogers 1983; Goudriaan & de Ruiter 1983). Workers have cited increased amounts of vascular and transfusion tissues (Thomas & Harvey 1983; Conroy *et al.* 1986; Leadley *et al.* 1987), in addition to an increased number of palisade layers (Thomas & Harvey 1983), as the reason for this observed foliar thickening. This addition of mesophyll layers may increase the absorption of PAR and contribute to observed increases in A.

Woodward (1987) studied herbarium specimens of several temperate hardwoods, and found that stomatal densities in species such as plane tree maple (*Acer pseudoplatanus* L.) and European beech (*Fagus sylvatica* L.) have decreased by 40 %, on average, in the past 200 years. Woodward concluded that modern individuals of species such as *A. pseudoplatanus* have greater WUE than their preindustrial ancestors. In a similar study, Peñuelas & Matamala (1990) calculated a 21 % decrease in stomatal density of several coniferous and deciduous species over the past two centuries, and drew similar conclusions to those of Woodward (1987). Water use efficiency may be enhanced by lower stomatal density in that the number of open pathways to water vapor diffusion is decreased. This is consistent with the view that most water evaporates from parastomatal regions (a hypothesis totally consistent with Fick's Law of diffusion, Tyree & Yianoulis 1980; Yianoulis & Tyree 1984). Evaporative flux density should decrease with stomatal density (all else being constant) whereas A is less sensitive to stomatal density since the main diffusional resistance to CO_2 uptake by chloroplasts probably resides in the liquid and membrane diffusion pathways. This is probably the best mechanistic explanation for the increase of WUE with increasing C_a, and thus corresponding increases in both the rate and magnitude of foliar development.

Total biomass production

In terms of above ground dry matter production, Nijs *et al.* (1988) found a 43 % increase in *L. perenne* plants grown at 600 μmol mol^{-1} over those grown at normal, ambient C_a. This increased biomass production was the result of a 77 % increase in A and in spite of a small decrease in WUE. In a later study, Nijs *et al.* (1989b) found a 19 % increase in shoot growth at 600 μmol mol^{-1} C_a, with a 25 % increase in WUE, attributed solely to increases in A. Results obtained by Sionit *et al.* (1985) indicate a 56 % enhancement in growth of *P. taeda* seedlings grown at a C_a of 500 μmol mol^{-1}, and there was

an increase in total dry matter production of nearly 100 % in *D. paniculatum* grown at a C_a of 1,000 μmol mol^{-1} (Wulff & Strain 1982). Although these plants demonstrated increases in leaf area and SLW (see above section on foliage), no gain in photosynthetic capacity was observed (when measured on a leaf area basis at 350 μmol mol^{-1} C_a, Wulff & Strain 1981). The authors suggest that this lack of response in A may have been the result of damaged thylakoid membranes due to high C_a-induced starch accumulation. Oberbauer *et al.* (1985) reported similar results from their study of tropical pioneer and climax tree species. Many other workers have observed increased biomass production in various species, including a variety of tropical species (Downton *et al.* 1990; Ziska *et al.* in press), temperate trees (Luxmoore *et al.* 1986; Norby *et al.* 1986; Hollinger 1987; Arnone and Gordon 1990), agricultural crop species (Wong 1979; Imai & Coleman 1983; Rogers 1983; Del Castillo *et al.* 1989), a vine (Sasek & Strain 1989) and a succulent CAM species (Idso *et al.* 1986; Szarek *et al.* 1987).

In contrast to these observations of marked growth enhancement due to elevated CO_2, Tolley & Strain (1984a) reported no significant enhancement in growth of *P. taeda* seedlings. Reekie & Bazzaz (1989) recorded lower biomass production in seedlings of the tropical tree *Cecropia obtusifolia* grown at 525 μmol mol^{-1} than in those grown at ambient C_a, which they attributed to a lack of response in photosynthetic capacity to changes in C_a. The authors suggest that this lack of response may have been due to a negative feedback, such as that suggested by Wulff & Strain (1982), and the inability of the plant to efficiently translocate an excess of accumulated carbohydrates.

Stem morphology

Changes in wood characteristics in association with increases in C_a are of interest to physiologists and agronomists alike. Increases in wood dimensions have been reported for several temperate tree species, including stem height of *P. taeda* (Rogers *et al.* 1983; Sionit *et al.* 1985), stem diameter at the expense of apical growth in *P. radiata* (Conroy *et al.* 1990), and wood density in *Pinus ponderosa* Dougl. ex. Laws. (Tinus 1972 – reported in Conroy *et al.* 1986) and *P. radiata* (Conroy *et al.* 1990). Increasing C_a has also been observed to increase stem height, diameter, and wood density in *L. styraciflua* (Rogers *et al.* 1983; Sionit *et al.* 1985). Conroy *et al.* (1990) ascribed the increase in wood density to a 44 % increase in tracheid wall thickness and a slight decrease in lumen diameter, resulting from increased photosynthate translocation from the foliage. These changes in plant morphology are important in that decreases in water conduit diameter *within a species* may lessen vulnerability to cavitation (Tyree & Sperry 1989), an adaptation that could be of great importance in plants producing greater leaf areas and thus greater potential tranpirational demand (see below for more discussion).

Root growth

The uptake of water by a plant is dependent on a number of factors, not the least of which is the degree of soil exploration by the roots. As with other plant parts, the growth of roots is thought to be enhanced by elevated C_a as demonstrated by studies on Virginia pine (*Pinus virginiana* Mill. Luxmoore *et al.* 1986) and *G. max* (Del Castillo *et al.* 1989). In the latter more detailed study, the enhanced soil exploration was attributed to more root tips per soybean plant without an increase in elongation rate of root tips. Goudriaan & de Ruiter (1983) have indicated that elevated C_a can either increase or suppress root growth, depending on existing soil moisture and nutrient availability. They observed that root growth of *L. perenne* was increased by high C_a under conditions of nitrogen deficiency, but decreased in *Z. mays* and lucerne (*Mediago sativa* L.). Rooting depth was slightly increased and root mass was increased (but mostly in the upper 10 cm of soil) in winter wheat but all this occurred without a change in R:S with or without water stress (Chaudhuri *et al.* 1990).

Root-to-shoot ratio

Root to shoot ratio, important in the balance of carbohydrate allocation in and water use by plants, is also known to be effected by elevated C_a. The fact that, as discussed previously, increased C_a has the dual effect of increasing A (and thus carbohydrate production) and diminishing g_s (thus lessening water stress in the plant and soil) indicates that increased C_a could result in increased biomass both above and below ground. The questions facing researchers, then, are: Is it the root or the shoot that is favored by increased C_a, or are they equally benefited, and how? The answer is mixed; sometimes the R:S is enhanced but sometimes only when stimulated by water stress (Tolley & Strain 1984b). In other cases R:S is decreased or experiences no change in response to increased C_a. Some of the mechanism that could lead to these differences are discussed in other papers in this volume (Rozema 1992; den Hertog *et al.* 1992).

Variations in the response of R:S to increasing C_a have been interpreted in several ways. Dahlman *et al.* (1985) suggested that species which respond to increased C_a with an increase in R:S do so because of the greater photosynthetic surface area that occurs under high C_a. The resulting increase in carbohydrate production allows greater translocation to the roots which, coupled with greater relative transpirational demand, causes an increase in growth of roots relative to the above ground biomass. Sionit *et al.* (1985) attributed differences in response of *L. styraciflua* and *P. taeda* to species-specific metabolic function and translocation priorities, as did Tolley & Strain (1984b), who added that intraspecific differences in self shading may have had some impact on the variation in R:S response of *P. taeda*. Tolley & Strain (1984b) attributed the increased R:S of *L. styraciflua* under water stress to increased priority of photosynthate allocation to the roots at the expense of the leaves. We assume that the low R:S at high SWC and C_a was associated with increased leaf production and lesser carbohydrate requirements of the roots.

The report by Norby *et al.* (1986) of increased R:S in nutrient deficient *Q. alba* is in agreement with Kramer's (1983) observation that nutrient deficiency favors root growth. Additionally, the fact that elevated C_a further increased R:S was attributed by Norby *et al.* to the determinant growth of the species. These authors reported increased root biomass that resulted from increased A and decreased leaf abscission in oak seedlings exposed to high C_a resulted in the observed increase in R:S. But it is not clear to us why greater leaf retention, which should increase shoot biomass would necessarily cause more root than shoot growth. Nijs *et al.* (1989b) give a similar explanation of increased R:S in *L. perenne*, although in this case decreases in shoot growth were said to be due to the effects of aging on shoots of this perennial grass, rather than determinance. Wulff & Strain's (1982) finding that C_a had no effect on R:S of *D. paniculatum* may have been linked with their observation that C_a had no effect on g_s and a negative impact on A due to starch accumulation, thus eliminating the driving force for an increase in R:S.

Summary and suggestions for future research

The usual impact of increased C_a on plant water relations causes g_s to decline, and, if all else is equal, then E decreases and Ψ_{leaf} increases. The reason for this effect is best understood in terms of the hydraulic architecture of plants and the soil-plant-atmosphere-continuum (SPAC). Water flux through the various parts of the SPAC can be treated as a catena process, analogous to the current in an electrical circuit composed of a series of conductances (or resistances = inverse conductance). Realistically a branched plant should be treated as a branched catena but a simple unbranched catena model is shown in Figure 1. In the Ohm's law analogy the flux of water through a discrete region from A to B, T_{AB} (kg s^{-1}), is proportional to the product of the hydraulic conductance (G_{AB}, kg s^{-1} MPa^{-1}) of that region and the water potential drop across the structure (Ψ_A-Ψ_B, MPa). In the SPAC model of Figure 1 the driving force on vapor phase

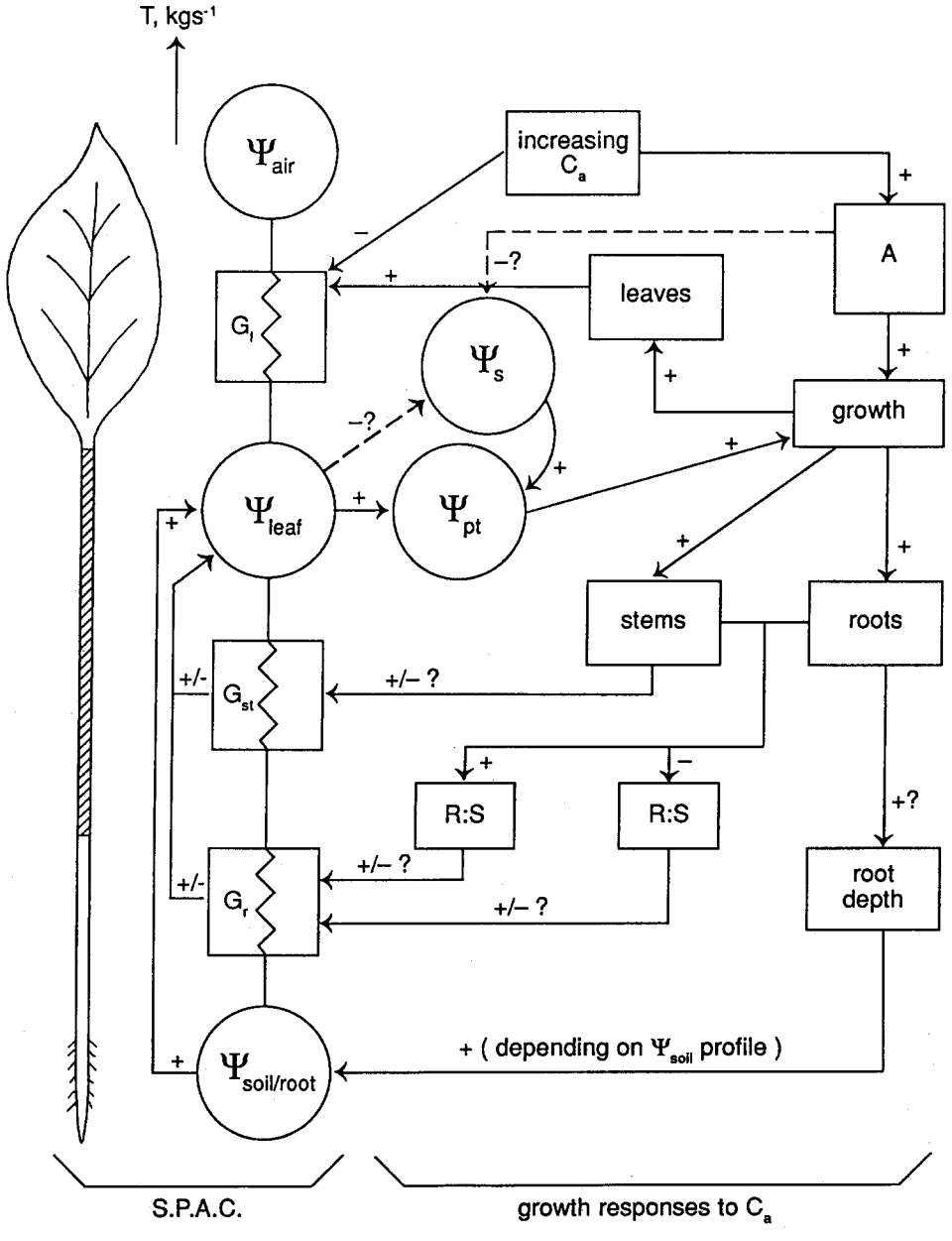

Fig. 1. Soil-Plant-Atmosphere-Continuum (S.P.A.C.) for a 'linear' plant or unbranched catena and control mechanisms affecting S.P.A.C. after exposure to increasing C_a. The elements of the S.P.A.C. are from base to apex: $\Psi_{soil/root}$ = water potential at soil/root interface, G_r = root hydraulic conductance, G_{st} = stem hydraulic conductance, Ψ_{leaf} = leaf water potential, G_l = leaf conductance (including any diffusive and convective boundary layers), Ψ_{air} = water potential of water vapor in the air. The growth responses indicated are: Ψ_{pt} = turgor pressure potential, Ψ_s = solute potential, A = photosynthetic assimilation rate, GROWTH = total biomass increase, LEAVES, STEMS, ROOTS indicates biomass increase in each organ, R:S = root to shoot biomass ratio. See text for more details.

transport is expressed in MPa units. All G's in Figure 1 are expressed on a whole plant basis. This means that G_{leaf} is not in the same units as g_s and is in fact a non-linear function of g_s times the total leaf area per plant. G_{leaf} is the smallest conductance element (= highest resistance ele-

ment) in the catena so the flux of water through the SPAC is controlled mostly by G_{leaf}, i.e.,

$$T = G_{leaf}(\Psi_{leaf} - \Psi_{air}) \approx G_{leaf}\Psi_{air} . \quad (1)$$

So applying this rule to every conductance element in the plant and solving for Ψ_{leaf} yields

$$\Psi_{leaf} = -T(1/G_{root} + 1/G_{stem}) + \Psi_{soil} . \quad (2)$$

Since T is controlled by G_{leaf} and by air dryness (Ψ_{air}) it follows that plant water stress (measured in terms of Ψ_{leaf}) will be higher if T is lower because g_s (or G_{leaf} is lower), all else being equal. It is usefull to combine Eqs (1 & 2) to get

$$\Psi_{leaf} = \Psi_{soil/root} + G_{leaf}\Psi_{air}(1/G_{root} + 1/G_{stem}) . \quad (3)$$

From this it is easy to see the immediate feedback between drought (that lowers $\Psi_{root/soil}$) and Ψ_{leaf}. Also the immediate impact of G_{leaf} is obvious as well as the opposite impact of G_{root} and G_{stem}.

Plant stress at any moment is a function of a more-or-less static (slowly changing) stress due to soil dryness (Ψ_{soil}) and a dynamic stress due to frictional drops in Ψ as water passes through the various conductances as in the soil-plant continuum. At times of high Ψ_{soil} and high T the dynamic term dominates whereas in dry soils (low Ψ_{soil}) when T ought to be low because g_s is low then the static term (second term) dominates (Fig. 2 and Eq. 2).

What is not clear is whether the reduced plant stress (measured as Ψ) is all due to a decline in T or whether plant conductances actually increase to reduce the dynamic term or decrease, partly countering the effect of reduced T. The nature of the growth feedback to enhanced C_a and its ultimate effects on G_{stem} and G_{root} are unclear. In a linear plant with one root, one stem and one leaf all in series, it is easy to see that flow through each linear element will be the same (neglecting water movement to and from storage along the path). But in a branched plant where water is divided into separate streams as it moves up the plant into

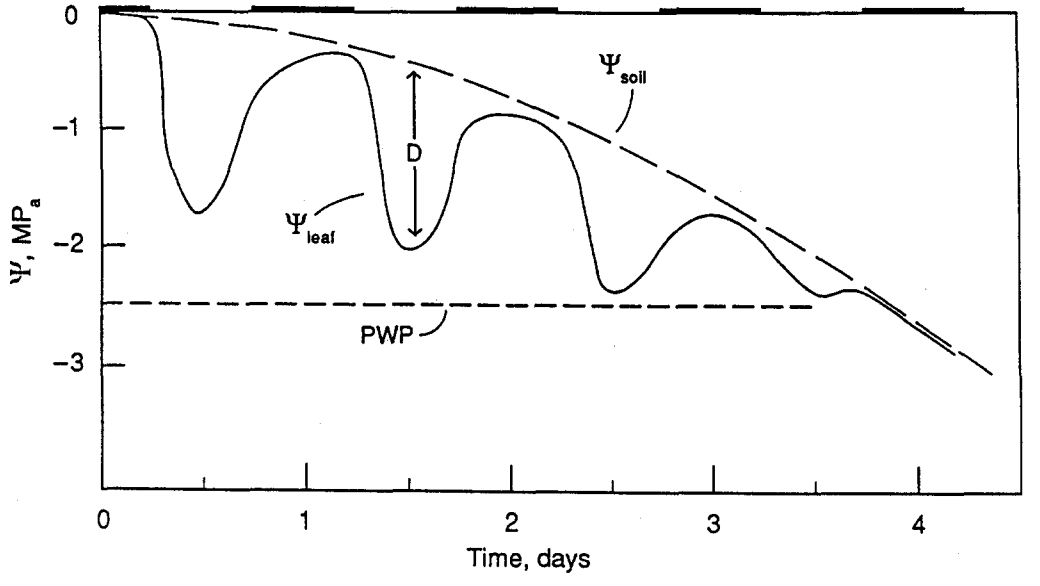

Fig. 2. Soil and leaf water potential changes during a drought period. D = dynamic component of water potential (given by first term in Equation 2); this component is dynamic in the sense that it disappears whenever T stops, e.g., at night. The soil water potential is the static component in the sense that it remains to influence leaf water potential even after T falls to zero. Bars above the graph indicate night periods. PWP indicates water potential for permanent loss of turgor potential.

branches and into leaves coming off the same branch and in a plant where branch dimension and leaf area changes in response to increasing C_a, it is not possible to say what is happening in terms of Equations 2 and 3.

For shoots a useful approach would be to measure changing hydraulic architecture of branches grown in high and low C_a. Hydraulic architectures of woody plants have been studied for the past 15 years (Tyree & Ewers 1991), but few similar comprehensive studies have been done on crop plants. However, many of the parameters measured in trees can also be documented in herbaceous plants. One parameter of particular interest would be to measure the Leaf Specific Conductivity (LSC) of branches of herbs (or tree seedlings) growing in high and low C_a. LSC is the proportionality constant between E of leaves downstream from a branch segment and the pressure gradient (dP/dx) needed in the branch to supply water to the leaves; $E = LSC \times dP/dx$. Knowing how C_a effects LSC is the equivalent to knowing whether G_{stem} in an unbranched catena increases or decreases (Equation 2). Measurements of hydraulic maps of crop plants will permit a full analysis of the influence of C_a on the dynamic component of water flow in shoots and this ought to be a much simpler analysis than in large trees (Tyree 1988 & 1989) because there are far fewer branches to map and use in models of dynamic water flow.

A similar analysis of root architecture might be useful, but perhaps not as informative because the main resistance to water flow in roots is often thought to reside in the radial path from the soil to the xylem vessels in the fine roots. Many studies have reported an increase in R:S biomass ratio in response to increased C_a, but it is not clear by what mechanism this provides an improved water supply to the shoot. An improved R:S biomass ratio does not necessarily mean that there is an improved ratio of absorbing root area per unit leaf area. If root exploration is confined to the same soil horizons in both control and high C_a grown plants, then improved surface area ratios are more important than improved biomass ratios. If root exploration extends into lower soil horizons with high Ψ_{soil} then the water balance of plants might be improved in spite of the decreased hydraulic conductance of the longer root system. It should be possible to design experiments to find out if either scenario is at play. This could be done with cleverly designed experiments using soil and stem psychrometers on plants to measure the driving force on water flow through root systems. Pot size could be used to moderate exploration , in that roots could be confined to narrow horizons in shallow pots or allowed to explore to deep horizons in deep pots. Water flow through the root systems can be estimated by gravimetic change in pot + plant weight, which in combination with Ψ_{soil} and Ψ_{stem} measurements would yield estimates of overall root conductances. If root conductances are expressed on a per unit leaf area basis then one can evaluate how they change with changes in R:S biomass ratio induced by changes in C_a.

Another area that needs to be explored is the effect of high C_a on the vulnerability of plants to xylem dysfunction by cavitation events. Cavitation events occur in plants because water is transported in xylem at negative pressures typically -1 to -2 MPa, and sometimes as low as -10 MPa. Liquid water at this pressure is in a metastable state. While in this state cavitations in xylem conduits result in a primarily water-vapor filled conduit that eventually fills with air. A conduit in this air-filled state is embolized and is not available for water conduction. Loss of conduits by this type of xylem dysfunction makes plants more prone to large dynamic stresses because partly embolized stems have lower hydraulic conductances.

The occurrence and mechanism of cavitations has been studied in woody plants for the past 10 years (Tyree & Sperry 1989), but little comparable work has been done on crop plants in spite of the high probability that it will prove to be an important phenomenon in crops (Byrne, Begg & Hansen 1977; Tyree, Fiscus, Wullschleger & Dixon 1986). The vulnerability of xylem conduits rapidly grown under well watered conditions appears to be more than later conduits grown under water stress (Tyree & Dixon 1986; Dixon, Butt

Murr, Tsujita 1988). The vulnerability of vessels is known to be due to the porosity of pit membranes (Sperry & Tyree 1988; Sperry, Tyree & Donnelly 1988) and in tracheids cavitations occur when the tori of bordered pits are displaced (Sperry & Tyree 1990). The observed effects of C_a on plant growth rate and on stem anatomy are of the type that could change vulnerability to cavitation. Several reasons why growth changes could increase as well as decrease vulnerability to cavitation could be proposed. How these predictions are argued is unimportant, but experiments to find out the consequences of changing C_a on vulnerability of plants to cavitation should be designed. For example the early leaf senescence of *Aster pilosus* causing a reduction in leaf area in high C_a treatments relative to controls (Wray & Strain 1986) might be the consequence of increased vulnerability to cavitation in leaves growing rapidly under high C_a and low water stress. Predicted elevations in C_a are bound to have corresponding effects on weather and rainfall patterns. One realistic fear is that increased growth rate caused by high C_a in spring when water resources could be adequate could make plants more vulnerable to cavitation and thus less likely to survive static drought stresses due to soil dryness in the late growth seasons. This could have a dramatic impact on survival and species distribution in woody perennials but could be equally important to annuals.

Cavitations in leaves and stems will block water flow and could be the first step leading to leaf damage or death of the whole plant. It has been well established that plants grown in high C_a delay reaching low Ψ for longer times during periods when irrigation is withheld than plants grown at low C_a, but experiments are usually terminated when the plants grown in low C_a are showing damage (e.g. Rogers *et al.* 1984 and others cited above); we know of only two studies in which water was withheld until either plant or soil Ψ reached similar values in both high and low C_a treatments (Conroy *et al.* 1988b; Tolley & Strain 1984b). Since cavitation events are threshold effects that occur when Ψ gets low enough, it is not known whether plants grown in high C_a are more (or less) vulnerable to cavitation than others because these plants usually are not allowed to dehydrate enough. In many agricultural and all natural situations plants do not receive irrigation. Plants that avoid low Ψ for longer periods of time will not necessarily tolerate lower, cavitation-inducing Ψ. Experiments to check the influence of high C_a on vulnerability to cavitation should be done. Methods for detecting cavitations (Tyree & Sperry 1989b) and for measuring their impact on water relations have been developed on woody plants (see for example, Tyree & Sperry 1988; Tyree, Snyderman, Wilmot & Machado 1991) and should be usable on herbs with only minor modifications.

The biggest problem with trying to design experiments to study the water relations consequences of increasing C_a is that it is still not understood what physiological parameter (or collection of parameters) confers increased drought resistance to plants. A number of possibly important parameters are recognized and can show that some correlate with anecdotal perceptions of drought tolerance. Among these properties are (1) low Ψ_s, (2) adjustments to Ψ_s in response to drought stress because this permits maintenance of high turgor pressure, (3) differences in cell wall elastic modulus, (4) humidity sensitivity of stomates, (5) water storage capacity, and other characteristics. But few people have demonstrated quantitatively how much any or a combination of these properties actually improve performance of plants under water stress. A unifying concept is needed that will demonstrate quantitatively why these properties are important. One such concept is contained in the hypothesis that the ultimate aim in drought tolerance and drought avoidance is the need of the plant to prevent cavitation events. Studies of the hydraulic architecture of plants and of the vulnerability of plants together with models of the dynamics of water flow through plants will allow a better understanding at a quantitative and mechanistic level how plants respond to water stress.

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