COMMISSIONED REVIEW

The interaction of rising CO₂ and temperatures with water use efficiency

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Abstract. Recent data concerning the impact of elevated atmospheric CO₂ upon water use efficiency (WUE) and the related measure, instantaneous transpiration efficiency (ITE), are reviewed. It is concluded from both short and long-term studies that, at the scale of the individual leaf or plant, an increase in WUE or ITE is generally observed in response to increased atmospheric CO₂ levels. However, the magnitude of this increase may decline with time. The opinion that elevated CO₂ may substantially decrease transpiration at the regional scale is discussed. The mechanisms by which elevated CO₂ may cause a change in these measures are discussed in terms of stomatal conductance, assimilation and respiration responses to elevated CO₂. Finally, recent experimental data and model outputs concerning the impact of the interaction of increased temperature with elevated CO₂ on WUE, ITE and yield are reviewed. It is concluded that substantially more data is required before reliable predictions about the regional scale response of WUE and catchment hydrology can be made.

Keywords: water use efficiency, elevated atmospheric CO₂.

Abbreviations: A, assimilation; [CO₂], atmospheric CO₂ concentration; C₅, leaf internal CO₂ concentration; Cₛ, specific heat capacity of water; D, water vapour pressure deficit; E, evaporation; G, heat flux to the leaf; g, boundary layer conductance; gₛ, stomatal conductance; ITE, instantaneous transpiration efficiency; PAR, photosynthetically active radiation; Rₛ, isothermal net radiation; Rubisco, ribulose bisphosphate carboxylase-oxygenase; WUE, water use efficiency; Δ, slope of the saturated vapour pressure against temperature curve; γₛ, psychometric constant; α, density of air; ζ, latent heat of vaporization of water; σ, Stefan Boltzmann constant; Ω, coupling factor.

Introduction

The fact that the concentration of CO₂ in the atmosphere ([CO₂]) is increasing is taken as axiomatic in this review. For a discussion of the evidence to support this view, the reader is referred to recent publications (Bolin et al., 1986; Fantechi & Ghazi, 1989). It is also taken as axiomatic that the global mean temperature will increase by approximately 2–4°C sometime during the next century. Evidence to support this contention has been extensively discussed (Bolin et al., 1986; Jones, Wigley & Wright, 1989). However, this statement should not be construed as implying that all regions of the biosphere will experience such a temperature increase. It is generally considered that the increase in temperature will be greatest at high latitudes and minimal at low latitudes. Some regions may even experience a decrease in annual mean temperature. However, since the current global circulation models of climate cannot predict future temperature changes with the resolution required to determine which regions will experience an increase in mean annual temperature and which regions will not, I shall be concerned only with the impact of a 2–4°C increase in temperature upon water use efficiency. A decrease in temperature will not be considered, whilst acknowledging that such a decrease may occur in some regions.

The impact of elevated [CO₂] upon water use efficiency (WUE) will be reviewed in this paper and the separate mechanisms by which [CO₂] may cause a change in WUE will be discussed. The interaction of additional environmental variables, such as water availability and nutrient availability, with elevated [CO₂] will also be discussed briefly in relation to WUE.

The impact of elevated [CO₂] alone (that is, without considering the influence of temperature) upon WUE will be considered first, as increased [CO₂] will occur during the next century independent of any change in regional temperature. The interaction of an increase in temperature with increased [CO₂] on WUE will then be discussed. An assessment of the influence of increased temperature alone on WUE will not be given since such an increase will not occur in the absence of an increase in [CO₂]. This is not to say that an increase in temperature is the sole result of increased [CO₂], since additional radiatively absorbent gases, such as methane, will play an increasingly important part in global warming (Fowler, 1990).

Water use efficiency: definitions

The term water use efficiency (WUE) has been used extensively for many years. However, it has been given three distinct meanings. First, hydrologists, who were concerned with the efficiency with which water available to a crop, from irrigation, rainfall and soil water already present, is used by the crop to produce yield, have defined WUE as the ratio of the volume of water used productively in transpiration, evaporation and used in growth, to the volume of water available to the crop. Second, WUE has been defined by irrigation engineers as the ratio of the increase in volume of water in the crop root zone to the total volume of water supplied by
irrigation (Bos & Nugteren, 1974, cited in Stanhill, 1986). Finally, plant physiologists and agronomists have used the term WUE in a different way. Essentially, WUE has been defined in this third sense as the ratio of the weight of dry matter produced to the amount of water transpired (Marks & Strain, 1989). Such measurements are made over the time scale of days to months. In some cases of the use of this definition, only the harvested part of the plant is considered, in other cases the entire plant is weighed. However, the instantaneous transpiration efficiency, defined as the ratio of the rate of assimilation to the rate of transpiration, has been often used as a measure of WUE. Such measurements are frequently made on individual leaves; occasionally, whole-plant gas exchange has been measured (Wong & Dunin, 1987). However, as Morison (1985) has stated, the percentage increase in instantaneous transpiration efficiency (ITE) resulting from an increase in [CO₂] is generally greater than the increase in WUE and the two measurements are not identical in the information they contain.

In this brief review, studies of both WUE, as defined by the agronomists, and ITE, as often used by physiologists, will be discussed. The term 'WUE' will be used, but some measurements discussed will actually refer to measurements of ITE. However, it may be suggested that the agronomists have a more useful definition. Thus it is difficult to state with confidence that (1) the observed changes in ITE of individual leaves will be manifested to the same degree by all the leaves of a plant, and (2) that the observed change in ITE will be maintained through time. Acclimation of assimilation during extended periods of growth under conditions of elevated [CO₂] have been documented (Eamus & Jarvis, 1989), suggesting that ITE may change with time. There appears to be very little evidence that stomatal conductance acclimates with time. Finally, an increase in ITE, expressed per unit leaf area, may occur, but the total water use per plant may increase or remain the same because of an increase in total leaf area per plant, under conditions of elevated [CO₂] (Gaudillère & Mousseau, 1989; Eamus & Jarvis, 1989). Consequently, the longer-term, larger-scale measurements of the agronomists (i.e. WUE as opposed to ITE) may provide a more realistic picture of the response of the growth and water use of a plant. However, as will be argued later, it is possible that, in attempting to predict whole crop or whole plantation forest WUE responses from measurements of individuals whole plants, we shall still encounter problems of scale, as highlighted by Eamus & Jarvis (1989) and Jarvis (1986).

**Elevated [CO₂] and WUE**

*Simple a priori considerations*

The short-term influence of [CO₂] upon assimilation rate (A) and stomatal conductance (gₛ) has been known for some years. Since the relationship between A and [CO₂] is curvilinear, in the absence of any change in gₛ, it may be predicted that a doubling of [CO₂] will increase ITE due to the increase in A, and assuming that the increase in A is reflected by an increase in growth rate, WUE may be expected to increase. Similarly, an increase in [CO₂] is most frequently associated with a decline in gₛ. Typically, gₛ is decreased by approximately 30–40% by a doubling of [CO₂] (Eamus & Jarvis, 1989; Mott, 1990). Notable exceptions have been observed, as discussed by Eamus & Jarvis (1989). However, in growth room experiments or leaf cuvette studies, when gₛ is decreased by elevated [CO₂], in the absence of any change in growth rate, WUE will increase. When A increases and gₛ decreases, in response to elevated [CO₂], WUE expressed per unit leaf area will increase even further.

It has been shown that growth under conditions of elevated [CO₂] can cause a reduction in stomatal density (Oberbauer, Strain & Fechter, 1985). Such a conclusion has also been deduced from a comparative study of leaves in an herbarium with leaves of the same species growing under ambient conditions (Woodward, 1987). Such developmental plasticity may have significant long-term ramifications for vegetation WUE responses.

Optimization theory of transpiration and assimilation has been developed for stomatal responses to VPD (Farquhar, Schulze & Kuppers, 1981; Cowan, 1981). This theory states that stomatal behaviour is optimal if minimal loss of water is sustained for a given amount of carbon assimilated over a period of time (Farquhar, Schulze & Kuppers, 1980), that is, if SE/SA is constant (Cowan, 1981). Farquhar et al. (1980) have presented data to support the view that stomatal behaviour is indeed optimal with respect to water loss and carbon gain. However, as Mott (1990) has stated, stomatal responses to C₅ have evolved to compensate for changes in C₅ which occur in response to changes in assimilation. It remains to be seen whether stomata are able to show optimal behaviour despite the rapid changes in [CO₂] that are occurring at present. Changes in ambient temperature and [CO₂] associated with climate change may have a direct impact upon the ability of stomata to maintain optimal behaviour. This point has yet to be addressed in any publications, to the author's knowledge.

**Recent results**

Much of the work published prior to 1985 has been reviewed by Morison (1982). Consequently, this discussion is confined predominantly to more recent work.

Although WUE was only explicitly measured in a few studies, changes in WUE can be inferred from measurements of transpiration (E) and assimilation (A), if WUE is defined as A/E. Table 1 lists some of the more recent reports where changes in WUE in response to elevated [CO₂] have been documented. It is clear that the overwhelming majority of data support the view that elevated [CO₂] increases WUE, on a leaf area basis, in...
controlled environmental experiments. On a whole-plant basis, however, total plant water use can remain the same despite an increase in total leaf area per plant. Thus, Morison & Gifford (1984), in a study of 16 agricultural and horticultural species, found that whilst the total leaf area per plant was increased by growth under elevated [CO₂], the time course of water use did not differ between control plants and plants grown under elevated [CO₂]. Thus, the rate of water use per plant was similar for control- and elevated-[CO₂]-grown plants. However, WUE was increased per plant. Not all of the increase in WUE was attributed to a decline in gₛ since the percentage increase in WUE exceeded the decrease in transpiration. Hence, part of the increase in WUE was attributed to an increase in A and growth in response to elevated [CO₂].

The effects of drought and elevated [CO₂] on competition between two old-field perennials have recently been studied (Marks & Strain, 1989). They observed that CO₂ enrichment significantly decreased whole plant transpiration rates (WPTR) for Andropogon virginicus in both well-watered and water-limited treatments. Leaf area was not affected by elevated [CO₂]. In contrast, WPTR of Aster pilosus was decreased by growth with elevated [CO₂] only under well-watered conditions, despite a significant increase in whole plant leaf area.

Most interestingly, an index of WUE showed that, whilst this index differed between the two species under well-watered conditions at ambient [CO₂], drought stress or growth under elevated [CO₂] resulted in there being no difference in the index of WUE (Marks & Strain, 1989). Clearly, environmental conditions can significantly alter the impact of elevated [CO₂] upon WUE and as such require further study.

Nijs, Impens & Behaeghe (1989) have shown that, whilst total water use for a canopy of Lolium perenne was unaffected by growth with elevated [CO₂], WUE was increased by 25% on a canopy basis or 87% on a leaf area basis. Canopy dark respiration rate and canopy light compensation point were increased by elevated [CO₂]. The benefit of elevated [CO₂], upon dry weight increment was greatest under high light irradiances and when the canopy was open, as opposed to a closed canopy situation, when light penetration to the lower leaves was significantly reduced. These results may suggest that seasonal patterns of WUE will change during growth with elevated [CO₂]. Such a conclusion is supported by the results of Gruix & et al. (1990), who observed that a positive carbon flux into a tussock tundra occurred 6d earlier under conditions of elevated [CO₂] and continued to have a positive carbon gain for longer at the end of the season. However, after 3 weeks
exposure to elevated \( [\text{CO}_2] \), ecosystem-level homeostatic adjustment occurred, and there was minimal difference in carbon fluxes between control and treated sites. Therefore, early and late season differences in WUE may be greater than differences in mid-season, for tussock tundra. In contrast, it may be suggested that the impact of elevated \( [\text{CO}_2] \) upon WUE was greatest for the \textit{Lolium perene} canopy before canopy closure occurred.

Elevated \( [\text{CO}_2] \) can result in an increase in WUE via three \( [\text{CO}_2] \) sensitive processes. Firstly, elevated \( [\text{CO}_2] \) can decrease transpiration due to a decline in \( g_s \), as has been the general rule (Eamus & Jarvis, 1989; Mott, 1990) although instances of 'abnormal' stomatal responses to \( [\text{CO}_2] \) have been reported (Eamus & Wilson, 1984). Secondly, elevated \( [\text{CO}_2] \) can increase \( A \). Whilst this has been the general response for short-term studies of days or weeks in duration, it is becoming apparent that the initial large increase in \( A \) observed in the early stages of the experiment is not maintained in longer-term studies, and in several such studies, \( A \) can be lower, unchangeable or only slightly greater than that for control plants (Reekie & Bazzaz, 1989; Oerbauber et al., 1985). Thus, in a study of an arctic tussock sedge community, it was shown that assimilation was enhanced by elevated \( [\text{CO}_2] \) only for the first 3 weeks of the experiment, thereafter assimilation declined back to control values (Oechel et al., 1984). Thirdly, a combination of the two can result in enhanced WUE. It is at once and to consider first, whether stomatal responses to \( [\text{CO}_2] \) are subject to modulation, and if so, what modulators are known, and second, to consider briefly the mechanism(s) by which \( \text{CO}_2 \) may exert an effect upon \( g_s \) and \( A \), and hence WUE.

\( \text{CO}_2 \) and stomata

The mechanism by which stomata sense \( [\text{CO}_2] \) remains debated. The selective advantage of stomata being able to respond to \( [\text{CO}_2] \) is also not immediately apparent (Mott, 1990). However, since leaves do experience fluctuations in \( [\text{CO}_2] \), in vivo, a means of sensing \( [\text{CO}_2] \) (or more correctly, the internal leaf air space concentration, \( C_i \)) may be beneficial by adjusting the diffusional limitations to \( A \) in response to changes in biochemical limitations on \( A \) (Mott, 1990). In addition, Mansfield, Hetherington & Atkinson (1990) have suggested that a closing response to increased \( C_i \) may be one means by which a leaf can sense increased wind speed and hence an increase in the evaporative demand on the leaf.

Stomatal sensitivity to \( C_i \) appears to be dependent upon a range of variables, and Morison (1985) has shown that the magnitude of the closing response of stomata to increasing \( C_i \) is proportional to the magnitude of the aperture prior to the increase in \( C_i \). Interestingly, there appears to be no difference between stomatal sensitivity to \( C_i \) of \( C_3 \) and \( C_4 \) species (Morison, 1985).

Stomatal sensitivity to \( C_i \) is variable. Hollinger (1987) has shown that stomatal sensitivity to \( C_i \) increased in \textit{Pinus radiata} when grown under conditions of elevated \( [\text{CO}_2] \). In contrast, sensitivity was decreased in \textit{Betula pendula} and \textit{Picea sitchensis} when grown with elevated \( [\text{CO}_2] \) (Jarvis, Sanford & Brenner, personal communication). Stomatal sensitivity to \( [\text{CO}_2] \) is also influenced by light flux density, and may increase (Morison & Gifford, 1983) or may decrease (Beadle, Jarvis & Nelson, 1979) in response to increased light levels during measurement. Morison & Jarvis (1983) observed that stomata of \textit{Commelina communis} were most sensitive to \( \text{CO}_2 \) under low light conditions.

The plant hormone abscisic acid both reduces \( g_s \) and increases stomatal sensitivity to \( C_i \) (Raschke, Pierce & Pownel, 1976). In contrast the plant hormone indole-3-yl acetic acid has been shown to reduce or eliminate the closing response of stomata to increasing \( C_i \) (Snaith & Mansfield, 1982). Cytokinins, both naturally occurring and synthetic, have also been observed to restore stomatal opening when high \( C_i \) of abscisic acid have been used to reduce stomatal opening (Mansfield et al., 1990).

Growing \textit{P. radiata} and \textit{Pinus menziesii} under conditions of elevated \( [\text{CO}_2] \) was found to decrease stomatal sensitivity to vapour pressure deficit (VPD) (Hollinger, 1987). In contrast, stomatal sensitivity to VPD of \textit{Nothofagus fusca}, grown under identical conditions as \textit{P. radiata} and \textit{P. menziesii}, was not affected by elevated \( [\text{CO}_2] \) (Hollinger, 1987). Temperature may also alter stomatal sensitivity to VPD and also possibly to elevated \( [\text{CO}_2] \) (Johnson & Ferrell, 1983).

It is clear from the above that in order to predict the magnitude, and in some cases the direction, of the stomatal response to a given variable (VPD, light flux density) under conditions of elevated \( [\text{CO}_2] \), it is not sufficient to determine the stomatal response under ambient conditions. Furthermore, the growth history of the plants also influences stomatal responses to a given variable (Eamus & Narayan, 1989; Eamus, 1987).

These facts have yet to be taken into account in growth and canopy process models, where the parameters incorporated for stomatal conductance and WUE are frequently derived from plants grown under ambient conditions.

Mechanism of action of \( \text{CO}_2 \) on guard cells

The mechanism of action of \( \text{CO}_2 \) on guard cells remains uncertain. Recent reviews of this topic include Mansfield et al. (1990) and Mott (1990). Consequently, only a brief statement of the principal hypotheses will be presented here.

An early hypothesis to explain the action of \( \text{CO}_2 \) upon stomata was proposed by Raschke (1977). Essentially, he proposed that a finite amount of \( \text{CO}_2 \) was needed for the production of malate in the guard cells. Below a critical \( [\text{CO}_2] \) (and hence \( C_i \)), insufficient malate is produced and aperture was less than maximal. Malate is
used in guard cells as a source of protons for the proton pump of the guard cell plasmalemma and as a counterion for the potassium ion taken up during stomatal opening. Malate is also an osmoticum per se. Above the critical level of [CO$_2$], (in the order of 100 μmol mol$^{-1}$), malate production exceeds demand and guard cell pH declines, allowing increased efflux of ions from guard cells with concomitant reduction in stomatal aperture. As has been highlighted by Mansfield et al. (1990), too little is known about the carbon metabolism of guard cells to fully evaluate this hypothesis. It has been suggested that the formation of malate from CO$_2$ may be central to guard cell physiology, but the manifestation of this mechanism is normally obscured by the operation of one or more additional processes.

It has been proposed that CO$_2$ acts directly upon the H$^+$ pump of the guard cell plasmalemma (Edwards & Bowling, 1985). After a detailed analysis of changes in guard cell membrane potential and conductance, Blatt (1987) concluded that such a mechanism was not operating and as an alternative he suggested that CO$_2$ exerted an effect via changes in guard cell apoplastic pH (Blatt, 1987).

Zeiger (1983) has proposed that CO$_2$ acts upon guard cells via the modulation of photophosphorylation. Whilst such a mechanism cannot operate in the dark, where stomatal opening in response to low [CO$_2$]$_a$ has been observed (Mansfield, Travis & Jarvis, 1981), it has been shown that CO$_2$ can influence the ATP levels of guard cells via an effect upon oxidative phosphorylation (Shan, Roth-Bejerano & Itai, 1989). Consequently, it could be that CO$_2$ mediates its effect via a combination of four or more interacting mechanisms, namely, malate production, oxidative and photophosphorylation, guard cell apoplastic pH and the guard cell plasmalemma proton pump. This does not preclude the existence of additional, as of yet unknown, C$_3$-sensitive processes.

CO$_2$, assimilation and whole plant carbon gain

The mechanisms by which CO$_2$ exerts a direct effect upon assimilation (independent of changes in stomatal conductance) have been well documented and only a brief description will be given here.

Carbon dioxide influences assimilation via three mechanisms. Firstly, a molecule of CO$_2$ activates the primary carboxylating enzyme of C$_3$ plants, ribulose biphosphate carboxylase oxygenase (Rubisco). Thus, increased [CO$_2$]$_a$ may increase the activation state of Rubisco. However, it has been shown that elevated [CO$_2$]$_a$ can decrease the activation state of Rubisco within minutes (Sage, Sharkey & Seemann, 1988). Secondly, CO$_2$ is a substrate of Rubisco, and thus, an effect by mass action is to be expected. Finally, photoperiod is decreased by an increase in CO$_2$.O$_2$ and so photorespiratory loss of CO$_2$ is reduced.

The response of respiration to elevated [CO$_2$]$_a$ is currently the subject of considerable research and controversy. Significant reductions in respiration have been observed at the individual plant level (Mousseau, personal communication), whilst increases (Nijs et al., 1990) and no change (Grulke et al., 1990) in canopy respiration rates have been measured. It is the balance between assimilatory carbon fixation and respiratory carbon loss that determines the magnitude and direction (positive versus negative) of net carbon flux to the plant and thus influences the impact of elevated [CO$_2$]$_a$ on WUE. The reader is referred to the relevant chapter on respiration in this issue.

Indirect effects of CO$_2$ upon whole plant carbon fixation have been less well studied. These include the possibility that [CO$_2$]$_a$ influences leaf initiation, longevity and expansion (Gaudilliere & Mousseau, 1989). Increased total plant leaf area and changes in leaf population dynamics have been documented and clearly influence whole plant carbon uptake. Feedback on the rate of assimilation via sucrose and starch accumulation and increased phosphate limitation on assimilation have also been observed (Eamus & Jarvis, 1989). These effects may be the result of either the lack of a sustained sink for carbohydrate (Downton, Grant & Loveys, 1987) leading to increased leaf accumulation of fixed carbon (Ehret & Joliffe, 1985), or may reflect the incapacity of the translocation pathway to export the excess fixed carbon. Readers are referred to the review of J. Farrar in this issue for a discussion of the response of translocation to elevated [CO$_2$]$_a$. However, it is clear that any mechanistic understanding of the impact of elevated [CO$_2$]$_a$ upon whole plant carbon gain, and hence WUE, must include an understanding of these secondary and higher-order effects of elevated [CO$_2$]$_a$ upon whole plant growth and physiology.

The interaction of elevated [CO$_2$]$_a$, temperature and WUE

The impact of the interaction of an increase in temperature with elevated [CO$_2$]$_a$ upon WUE per se has been poorly studied. The data available remain sparse and confused (Gifford, 1990). However, it is possible to tentatively infer what effect the impact may be from theoretical considerations and experimental data available concerning temperature and elevated [CO$_2$]$_a$ interactions with respect to assimilation and growth.

Idso et al. (1987) have shown that the stimulatory effect of elevated [CO$_2$]$_a$ upon the growth of Daucus carota, Raphanus sativa and Gossypium hirsutum was linearly related to air temperature. Thus, for a 3°C increase in air temperature, the average growth enhancement factor resulting from increasing [CO$_2$]$_a$ to 640 μmol mol$^{-1}$ was increased from 1.3 to 1.56. If the vapour pressure difference between leaf and air remained the same, and stomatal conductance was decreased by 30–40% (as has been generally concluded in a range of reviews (Monson, 1985; Eamus & Jarvis, 1989; Eamus, 1991), it can be concluded that WUE was substantially increased and that this increase was also temperature dependent. Interestingly, Idso et al. (1987) observed that at temperatures below 18.5°C elevated
[CO₂]ₐ reduced plant growth. In a more recent study, Idso & Kimball (1989) repeated the experiment of Idso et al. (1987) and again showed that the stimulatory effect of elevated [CO₂]ₐ was temperature dependent. Although in the later study, the temperature at which elevated [CO₂]ₐ became inhibitory for growth of Daucus carota and Raphanus sativa was 11–12°C.

Campbell, Allen & Bowes (1990) studied the response of soybean canopy photosynthesis to elevated [CO₂]ₐ and temperature. They observed that the rate of canopy assimilation was substantially increased by growth at elevated [CO₂]ₐ, but when air temperature was increased by 10°C, leaf temperature was increased by only 4°C. Furthermore, the increase in leaf temperature was not significantly different between [CO₂]ₐ treatments. Since leaf temperatures lower than air temperatures arise due to evapotranspirational cooling of the leaf, the lack of difference between [CO₂]ₐ treatments may indicate that the rate of transpiration was similar in both treatments. Therefore, it is tentatively concluded that WUE was substantially increased by elevated [CO₂]ₐ despite a significant increase in air temperature.

Grulke et al. (1990) showed that growth of tussock tundra under elevated [CO₂]ₐ resulted in the slope of the linear regression of total carbon flux against soil temperature, air temperature and the ln (light flux density, PAR) to be increased. There was a clear interaction of elevated [CO₂]ₐ with the temperature response of carbon flux at the ecosystem level. Therefore, it may be inferred (although water fluxes were not presented) that WUE was influenced by elevated [CO₂]ₐ and that there was a positive interaction of elevated [CO₂]ₐ with the three additional environmental variables of air and soil temperature and PAR.

Ziska, Drake & Chamberlain (1990) observed that the positive effect of elevated [CO₂]ₐ upon assimilation increased with increasing temperature for Scirpus olneyi. No acclimation of assimilation during the 2-year study period was observed. Furthermore, the relative impact of elevated [CO₂]ₐ upon assimilation was increased at low light flux densities. No data were presented for leaf area or transpiration rates, but if stomatal conductance was decreased and transpiration decreased or unaltered, WUE was increased substantially.

As the temperature of a leaf increases, the proportion of fixed carbon entering the photosynthetic pathway increases (Labate, Adcock & Leegood, 1990). Thus, the net increase in carbon fixation resulting from increased [CO₂]ₐ is decreased. However, there is evidence accumulating that enhanced [CO₂]ₐ results in a decrease in the rate of respiration (Mousseau, personal communication), and thus, this may more than offset the increased photosynthetic losses. It is the balance between assimilatory carbon fixation and respiratory losses that determines the net carbon flux response to elevated [CO₂]ₐ and temperature, and hence WUE.

Growth under conditions of elevated [CO₂]ₐ has been associated with an increase in thermal stability of phospho-enol-pyruvate carboxylase in C₄ weeds (Simon, Potvin & Strain, 1984). The temperature optimum for assimilation of Larrea divaricata (Pearcy & Björkman, 1983) and the thermal tolerance of Pinus ponderosa (Surano, Daley & Houpis, 1986) were increased following growth at elevated [CO₂]ₐ. These observations do suggest that with an increase in [CO₂]ₐ and temperature the enhancement of assimilation and growth (and hence WUE) will increase also. An increase in mean growth temperature may also be expected to result in an increase in the temperature optimum for assimilation.

There are too few studies that specifically address the long-term impact of the interaction of increased temperature and elevated [CO₂]ₐ on WUE of whole plants. In addition to this lack of data, controversy exists as to whether an increase in [CO₂]ₐ can act as a regional antitranspirant due to its known ability to reduce stomatal conductance. Should transpiration from entire canopies be decreased significantly, irrespective of whether assimilation increases or not, WUE would be increased. This topic is discussed below (see CO₂ as a global antitranspirant).

The interaction of elevated [CO₂]ₐ and temperature with yield

In a recent review Squire & Unsworth (1988) compared the response of a determinate crop (winter wheat) with that of an indeterminate crop (potato). Using an AFRC model of wheat yield for the UK, they showed that an increase in temperature of 1.5°C increased the number of leaves initiated but decreased the period over which each leaf expanded. If temperature was increased by a further 3°C, the increase in yield obtained by a doubling of [CO₂]ₐ was completely lost due to a decrease in the duration of grain filling. For determinate crops, they concluded that yield would decrease with an increase in temperature and that this decrease could completely negate the increase attributable to an increase in [CO₂]ₐ. If we assume that total water use per plant was unaffected or increased by elevated [CO₂]ₐ and temperature, WUE may be concluded to substantially decline.

In contrast, the indeterminate crop growth response was found to increase in response to an increase in both temperature and [CO₂]ₐ (Squire & Unsworth, 1988). If total water use per plant was unaffected or increased proportionally less than the increase in yield, WUE would be substantially increased.

Gifford (1988) has also used computer simulation of yield of wheat and concluded that the increase in yield resulting from enhanced [CO₂]ₐ can be cancelled by a 2–3°C increase in temperature. However, he suggested that, in specific cases, where summer drought occurred at the end of the growing season, the fact that grain filling was finished earlier in the season allowed the [CO₂]ₐ enrichment stimulation of yield to be expressed since the impact of drought was avoided.
If the more agronomic definition of WUE is applied, it is important to consider water loss from the soil and how this may be affected by changes in plant development, leaf area index development and transpiration, resulting from elevated \([CO_2]_a\) and temperature. With an increase in temperature, plus the possibility of a decrease in transpiration, both of which will result in increased evaporation from the soil due to increased vapour pressure deficit, it is likely that water loss due to evaporation from the soil will increase. Shuttleworth & Wallace (1985) have modelled evaporation from soils and calculated the impact of a reduction in stomatal conductance of 40%. They showed that the total evaporation (transpired through the crop and evaporated from the soil) was decreased at all values of leaf area index, but evaporation from the soil was increased. Thus, WUE is decreased since this water lost from the soil by evaporation is non-productive loss of water.

**Carbon dioxide as a global antitranspirant**

Because elevated \([CO_2]_a\) can substantially reduce \(g_s\) in growth room and leaf cuvette studies, it has been proposed that the increase in \([CO_2]_a\) will substantially reduce transpiration from canopies of vegetation. However, Jarvis & McNaughton (1986) have concluded that regional transpiration will not be significantly reduced in response to elevated \([CO_2]_a\). This is because any reduction in transpiration resulting from a decrease in stomatal aperture will be offset partially by an increase in leaf temperature (and hence an increase in leaf-to-air water vapour pressure difference) and partially by an increase in the ambient water vapour pressure deficit, which results from a decrease in transpiration. The increase in both leaf-to-air vapour pressure difference and atmospheric water vapour pressure deficit will increase transpiration from the vegetation. However, the question remains, to what extent will the decrease in transpiration due to a reduction in stomatal aperture be offset by the increase due to the two factors described above?

Monteith (1981) has derived an energy balance equation that can be used to calculate the change in evaporation for a given change in stomatal conductance:

\[
\Delta E = \frac{\Delta (R_{in} - G) + \rho C_p D g}{\Delta + \gamma (1 + g/g_s)}
\]

(1)

Symbols are defined in the table of contents. This equation highlights the fact that evaporation rate is dependent on the supply of energy to the vegetation, the vapour pressure deficit and the ratio of the conductance of the boundary layer to that of the stomata. This ratio determines the effect of a decreased stomatal conductance upon the rate of evaporation. The net radiation term must take into account the influence of leaf temperature upon net radiation. Thus:

\[
\lambda E = \frac{\Delta R_{in} + \rho C_p D g}{\Delta + k (1/g + 1/g_s)}
\]

(2)

where \(R_{in}\) = isothermal net radiation, and \(k\) is given as:

\[
k = \gamma g + rC_p/4\sigma T_e^3
\]

(3)

Symbols are defined in the table of abbreviations.

It can then be shown (see Morison, 1989) that the ratio of the rate of transpiration between two areas of vegetation that differ only in stomatal conductance, is independent of net radiation and vapour pressure deficit, but is dependent upon temperature and boundary layer conductance. Using the equations of Monteith (1981), Morison (1985) was able to show that when stomatal conductance is decreased by 40% due to elevated \([CO_2]_a\), as the ratio of stomatal conductance to boundary layer conductance increased, the percentage reduction in evaporation was substantially reduced. Furthermore, as the climate warmed and temperature and vapour pressure deficit increased, the percentage reduction in evaporation resulting from a decrease in stomatal conductance was reduced (i.e. there was a smaller percentage reduction). Consequently, despite an increase in temperature and vapour pressure deficit, WUE is increased, but the magnitude of the increase decreases with an increase in temperature and vapour pressure deficit.

Jarvis & McNaughton (1986) have derived a coupling factor (\(\Omega\); also referred to as a decoupling coefficient by McLaughlin, 1986) that is independent of temperature. The degree of coupling of the vegetation to the atmosphere determines the relative importance of net radiation, water vapour pressure deficit and stomatal conductance. When \(\Omega\) is large and the vegetation is poorly coupled to the atmosphere, evaporation is determined principally by net radiation. The degree of coupling varies according to the vegetation type. Coniferous forests are well coupled to the atmosphere (\(\Omega\) is low); deciduous forests have a larger value of \(\Omega\), and short field crops have a large \(\Omega\) (i.e. are poorly coupled). On a regional scale, as opposed to individual leaves or isolated plants, net radiation is the driving variable and the importance of changes in stomatal conductance becomes reduced. These considerations lead to three important conclusions. First, the impact of a reduction in stomatal conductance upon WUE varies according to the nature of the vegetation. Coniferous forests may be expected to show a larger reduction in transpiration than a short field crop. If the assimilation response does not differ between the vegetation types, the increase in WUE efficiency will be greater for the coniferous forest. Second, for a mixed woodland or forest with an understorey, which is less coupled to the atmosphere than the overstorey, the change in WUE for the different vegetation layers in the forest will differ. Finally, as Jarvis (1986) states, an increase in \([CO_2]_a\) will have a far lower impact upon total transpiration than was once believed and may even have no significant effect (Gifford, 1988; Jarvis, 1986). This fact is further enforced when it is noted that elevated \([CO_2]_a\) results in an increase in total plant leaf area, which has been shown in some cases to offset any increase in WUE per unit leaf area. The major assumption contained in the foregoing discussion that...
awaits testing is whether the assimilation response to elevated \( \text{CO}_2 \) of different vegetation types differs in a consistent manner. Apart from the fact that \( \text{C}_3 \) plants do not show enhanced assimilation in response to a doubling of ambient \( \text{CO}_2 \), it is too early to state whether coniferous species, deciduous trees and short field crops differ in their long-term response to elevated \( \text{CO}_2 \). Whilst there are studies of the assimilation response of different types of vegetation to elevated \( \text{CO}_2 \), the major differences in the experimental protocols employed by different workers preclude statements about substantive differences in their relative response characteristics.

Although the impact of elevated \( \text{CO}_2 \) upon regional evaporation may be minimal, an increase in WUE for whole stands is inferred from the results of models of canopy assimilation, where increased assimilation in response to elevated \( \text{CO}_2 \) are predicted (e.g. Jarvis, 1989). However, it remains to be seen whether the parameter values used in such models and obtained from juvenile plant material in short-term experiments are sufficiently close to the values eextant in the future. Jarvis (1989) has shown experimentally that \textit{Picea stichensis}, grown for 3 months in elevated \( \text{CO}_2 \), had reduced carboxylation efficiency and a reduced rate of \( \text{CO}_2 \) saturated assimilation in comparison with control trees. However, using the canopy model MAESTRO he also showed that the model predicted a significantly higher quantum efficiency and rate of light saturated assimilation for trees grown in elevated \( \text{CO}_2 \). Furthermore, he was able to show with MAESTRO that using parameter values pertaining to the present could overestimate the future canopy response to elevated \( \text{CO}_2 \) (Jarvis, 1989).

Gifford (1988) has suggested that this debate about the impact of elevated \( \text{CO}_2 \) upon regional transpiration may be circumvented or made redundant because vegetation may have overriding strategies for controlling the rate of soil water depletion (Gifford, 1986). Thus, he suggests that, for a given evaporative demand, plants have a strategy to control the rate of water loss in relation to soil water status. Consequently, irrespective of the impact of elevated \( \text{CO}_2 \) upon stomatal aperture and total leaf area, water loss per plant will be regulated with respect to soil water status. Assuming that soil water status does not change in response to elevated \( \text{CO}_2 \) (an assumption that may not be valid), it may be concluded from this model that WUE will increase per unit area only if assimilation is enhanced in response to elevated \( \text{CO}_2 \).

Conclusion

To conclude, the following may be stated. In earlier, short-term studies, large increases in WUE or ITE were observed. This response was the product of a 30-40% decrease in \( g_s \) and a substantial (but highly variable) increase in assimilation. In more recent, longer-term studies, it has been found that the large increase in assimilation observed at the start of the experiment is often not maintained, and 'ecosystem homeostasis' appears to operate (Gnulke et al., 1990). In addition, although elevated \( \text{CO}_2 \) does appear to reduce \( g_s \) in the long-term (there is no evidence of acclimation of \( g_s \) to elevated \( \text{CO}_2 \)), there is debate as to whether this decline will have a significant impact upon transpiration from entire canopies. Furthermore, it appears likely that the impact of elevated \( \text{CO}_2 \) upon regional transpiration will be dependent upon the nature of the vegetation. In view of the growing realisation that vegetation is not only influenced by climate, but that vegetation can be a major determinant of regional climate (Eamus, 1991), substantial studies of the response of canopy transpiration and WUE to elevated \( \text{CO}_2 \) appear warranted. Two approaches are needed for this. Firstly, canopy models of WUE need developing and testing by comparing model predictions for present-day conditions with water and \( \text{CO}_2 \) flux measurements to present-day vegetation assemblages. Secondly, mature tree studies need initiating, possibly by using the 'branch cuvette' technique, whereby entire branches of mature trees in a woodland/forest are subject to elevated \( \text{CO}_2 \). Finally, it appears possible that the impact of elevated \( \text{CO}_2 \) and temperature upon WUE can vary with time for a given ecosystem and that seasonal variations in the response of WUE may occur.

References


