Crop Productivity, Water Use Efficiency, and Drought Adaptation under Elevated Atmospheric CO_2[1]

Theodore C. Hsiao

ABSTACT

Biomass water use efficiency of a given crop is usually a near constant at the given ambient CO_2 concentration when normalized for the evaporative demand of the environment, regardless of the extent of water stress. This conservative behavior is rooted in two basic tenets of plant productivity, the capture of radiation and assimilation of CO_2 in exchange for water lost. The dominant factor is probably radiation capture, which supplies the energy for transpiration and for photosynthesis. Radiation capture depends on the extent of canopy cover, and hence, on leaf growth, a process most sensitive to water stress.

If canopy cover is complete, water stress, when severe enough, would reduce photosynthesis and stomatal opening. The intercellular CO_2 concentration (C_i), however, remains constant in many instances, or would decrease in others. Using the equations for CO_2 transport only in the gaseous phase and the equation for transpiration, and taking into account energy balance, it is shown that photosynthetic WUE of single leaves would decrease in the case of constant C_i, and may remain about the same or increase in the case of decreased C_i, depending on the magnitude of the change in C_i and in leaf temperature.

Elevated levels of CO_2 reduce stomatal aperture, steepen the CO_2 gradient for assimilation, and accelerate the development of leaf area particularly for C_3 plants. The first effect lowers transpiration per unit effective leaf area. The reduction, however, may not be large due to energy balance requirements, and especially for closed canopies under low wind conditions. The second effect raises C_i sufficiently in spite of the lower stomatal conductance to effect a net gain in photosynthesis per unit of effective leaf area. The combined impact of the

---

[1] Modified from: Hsiao, T. C. (1993) Effects of drought and elevated CO on plant water use efficiency and productivity. *In* Jackson, M. B., and Black, C. R. (eds.) Interacting Stresses on Plant in a Changing Climate. NATO Advanced Research Workshop series. Springer-Verlag, Berlin. (In press).

first two effects on WUE, again evaluated using the equations for assimilation and transpiration, is that the percentage increase in photosynthetic WUE due to elevated CO_2 is nearly proportional to the ratio of the new to the original concentration of CO_2, in agreement with some published data. The third effect of enhancing leaf development would lead to increases in both transpiration and photosynthesis per unit land area prior to the completion of canopy cover, but has little effect on photosynthetic WUE. The compounding effect with time of elevated CO_2 when canopy is incomplete provides an explanation for the phenomenon of a disproportionally larger enhancement of biomass compared to the enhancement in photosynthesis per unit leaf area effected by elevated CO_2. Effects of water stress on photosynthetic WUE under high CO_2 should be minimal and similar to that under normal CO_2.

The conceptual framework based on the aforementioned equations provides a rational basis for the systematic evaluation of WUE, although application at the canopy level remains to be tested.

INTRODUCTION

Atmospheric CO_2 is going to rise continuously for decades or centuries to come. Whether this rise will result in a hotter and drier climate is not yet totally certain, although the dominant opinion points to that direction. Regardless of the resultant change in climate, elevated CO_2 will have a direct impact on plant productivity and water use, by enhancing photosynthesis and by effecting partial stomatal closure. Numerous studies, although nearly all under conditions different from that of the open field, have shown that plant growth (Kimball, 1983; Lawlor & Mitchell, 1991) and water use efficiency (Kimball & Idso, 1983; Morison, 1985; Eamus, 1991) are enhanced under elevated levels of CO_2. The extent of enhancement, however, is highly variable. For the same species, one study could show little response to elevated CO_2 whereas another would show a marked response. Some of the discrepancies could be attributed to the different growth conditions, or to factors other than CO_2, such as mineral nutrients, being limiting. Many discrepancies, however, could not be easily evaluated without a more systematic framework. The beginning of a framework is proposed in this paper, which highlights some of the key parameters often ignored but should be measured in studies of plant productivity and water use efficiency under elevated CO_2 and accentuated stresses.

CROP PRODUCTIVITY IN RELATION TO LIGHT CAPTURE AND CO_2 ASSIMILATION

The basic framework for productivity is the carbon economy of the plant—the acquisition and expenditure of carbon as photosynthetic assimilates, and the partition of the carbon gained to different organs. The acquisition of carbon in turn depends on the the capture and use of solar radiation for photosynthesis.

For crop species, the desired product or the yield consists of the carbon-based products in the harvested part of the plant. The accretion of this product is intimately tied to CO_2 assimilation and the partition of the assimilates over the growing season, and can be summarized in equation form as:

$$Y = HI \cdot c \left\{ \int_e^h A\,dt - \int_e^h R\,dt \right\} \tag{1}$$

where Y is the yield per plant or per unit area of land at harvest; and the proportion of the biomass in the harvested part of the plant is represented by the harvest index, HI. The rate of net CO_2 assimilation per plant or per unit of land area, A, is for daytime only and is integrated over the period from plant emergence time e to harvest time h. The loss of carbon during the night is represented by the rate of night respiration R, also integrated from the time of emergence to harvest. The factor c accounts for the difference in mass per mole of carbon between the total biomass and the assimilated CO_2 (Penning de Vries, 1975). The inclusion of day time respiration in the net assimilation term and the assignment of a separation term for night time respiration are arbitrary, for the convenience of considering water use efficiency and interpreting experimental data. Although written for crop species, this equation is also useful when applied to many wild plants. The only change in view point is that Y should be taken to represent reproductive organs such as seeds or tubers, on which the survival and succession of the species depend.

Eq. 1 expresses the total carbon gained as an integral of time. Implicit is the need to integrate over space to account for variations in the photosynthetic ability of the leaves making up the foliage canopy, as well as variations in local environment of the leaves. Fortunately a simpler approach is available by considering canopy CO_2 assimilation or biomass accumulation in terms of the amount of photosynthetically active radiation (PAR) intercepted by the canopy and the efficiency of use of the intercepted PAR for CO_2 assimilation or biomass production. The efficiency of the use of intercepted PAR for canopy photosynthesis is fundamental but data are limited. Many more studies have been conducted on biomass production in relation to radiation interception by the canopy. The amount of biomass produced per unit of PAR intercepted—here termed the radiation use efficiciency (RUE)—is a reflection of PAR use efficiency for photosynthesis, for a given pattern of respiration and chemical composition of the biomass. It turned out that for the life cycle of a given herbaceous crop, RUE averaged over a number of days is relatively constant when other factors are not limiting, up to the beginning of the maturation and senescence phase (Williams et al., 1965; Monteith, 1977; Gallagher & Biscoe, 1978; Fischer, 1983). Thus, the major variable determining how much CO_2 is assimilated and how much biomass is produced by a crop is the cumulative amount of PAR intercepted by its canopy. Surprisingly, RUE appears to be even similar between C_3 and C_4 species, at least in the limited comparisons available (Charles-Edwards et al., 1986, p. 29; Held & Hsiao, in preparation).

The near constancy of RUE, or the close to linear relationship between biomass produced and PAR intercepted, has the basis in the following facts: (1) Canopy photosynthesis responds to increasing levels of PAR up to the level encountered at noon on clear summer days (2.0 mmol m^{-2} s^{-1} or higher), either in a linear (Hesketh & Baker, 1967; Sale, 1977) or curvilinear (Puckridge, 1971; Sale, 1977; Connor et al., 1985; Campbell et al., 1990) fashion. (2) Photosynthesis of a canopy is proportional to its PAR interception, with a near constant light use efficiency for different growth stages prior to maturation and senescence (Hesketh and Baker, 1967; Puckridge & Ratkowsky, 1971; Puech-Suanzes et al., 1989). (3) After the canopy is complete and intercepts most of the radiation, the rate of canopy photosynthesis on sunny days at midday varies only slightly over a period of several weeks when other factors are not limiting.(Puckridge, 1971; Jones et al., 1985; Puech-Suanzes et al, 1989) (4) Photosynthesis (Björkman, 1981), particularly that of canopies (Sale, 1977), is relatively insensitive to temperature within the normal temperature range for the growth of the plant. (5) Short-term fluctuations in RUE tends to average out over longer time intervals.

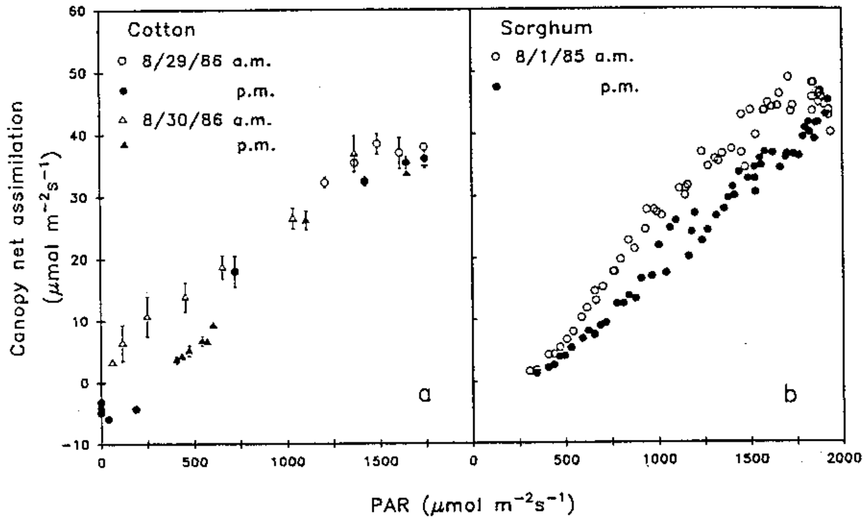
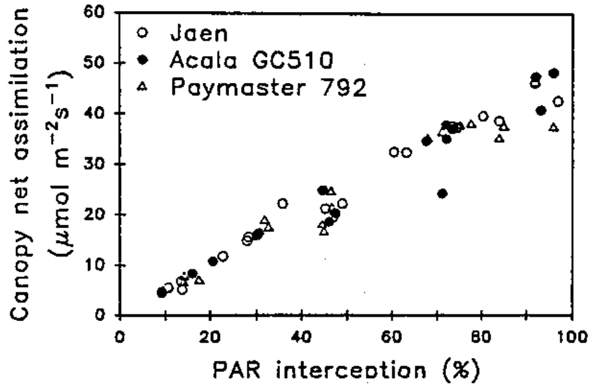


Fig. 1. Net photosynthesis per unit land area of complete canopy of cotton (a) and sorghum (b) in the field in relation to incident PAR flux. Variations in PAR flux was the result of daily change in solar angle, with the associated changes in temparature. The data for cotton (Puech-Suanzes et. al, 1989) were taken with a canopy chamber with soil covered to exclude soil and root respiration. The data for sorghum (Held & Hsiao, 1993) were taken with the micrometeorological method of Bowen ratio/energy balance/CO_2 gradient (Held et al., 1990) and were not corrected for soil and root respiration, which was estimated to be in the order of 2 to 3 μmol m^{-2} s^{-1}.

Examples of the near linear light response over a daily time course are given in Fig. 1, for the canopy of cotton, a C_3 crop, and sorghum, a C_4 crop. The lower rate of assimilation at a given PAR in the afternoon than in the morning shown in Fig. 1 has been frequently reported (e.g., Sale, 1977; Connor et al, 1985, Puech-Suanzes et al., 1989) and is attributed to various causes such as saturation of sinks by assimilates, water stress, or high temperature. In Fig.2, an example is given of canopy photosynthesis being linearly related to radiation interception when data collected at different times and different canopy size were plotted together. The corollary is that biomass accumulation rate is maximal and relatively constant during the period just after canopy closure and before senescence, in agreement with experimental observations (Gallagher & Biscoe 1978; Fischer, 1983).

Fig. 2. Canopy net photosynthesis per unit land area of three cultivars of cotton at midday in relation to the percentage of incident PAR intercepted by the canopy. Data were taken over the major part of the season as the canopy developed. (from Puech-Suanzes et. al., 1989)



Radiation use efficiency does decline under stresses of various kinds which are sufficiently severe. For example, it is known that sufficient water stress lowers photosynthetic light use efficiency of canopies (Jones et al, 1986; Puech-Suanzes et al., 1989). Other stresses can also be inhibitory (Fischer, 1983). Indications are, however, that the reductions in RUE are often minor to negligible and RUE is much more resistant to stresses than are leaf area per plant and canopy size. This point will be elaborated on below.

With RUE being a fairly conservative parameter, the net carbon gain of a plant over the season is readily affected by the amount of PAR the plant captures. In this analysis, the growing season may be divided into three phases (Hsiao, 1982) as depicted in Fig. 3. Early in the season, canopy is small or sparse and much of the incident radiation is missed by the canopy. So the major limiting factor for productivity is the degree of canopy cover. Any enhancing or retarding effect on leaf growth will be amplified with time (Hsiao, 1982; Bradford & Hsiao, 1982) as the production of additional photosynthetic area is a function of existing area. As the canopy enlarges and reaches full size or canopy closure, the effective radiation capture surface reaches a maximum and the amount of radiation captured would depend only on the level of insolation. Late in the season, senescence sets in and the light capturing surface declines. More importantly, there is also a decline in RUE through the decline in photosynthetic capacity of the old and senescing leaves.

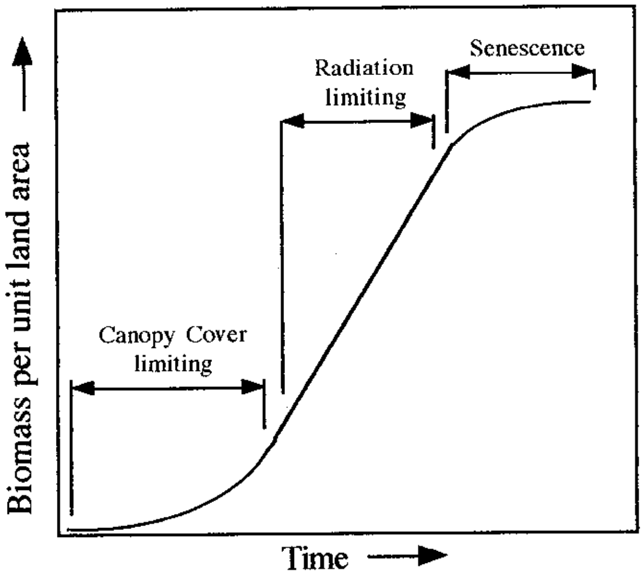


Fig. 3. Conceptual depiction of seasonal pattern of biomass accumulation for annual crops in the absence of significant stress periods. The early phase is approximately exponential and when the canopy is incomplete and PAR interception is determined by canopy size. The middle phase is approximately linear and when canopy is complete and intercepts nearly all the incident PAR. The last phase covers the period of maturation and leaf senescence when net assimilation declines and finally becomes zero.

The expansive growth of leaves making up the canopy is highly sensitive to environmental variables, including water supply, salinity, temperature, and nutritional status. So in the canopy-cover limiting phase, even mild stresses can slow the development of light capturing surface and leads to slower biomass accumulation. This aspect will be elaborated on further in a later section. Once the canopy is full, mild stresses sufficient to reduce leaf expansive growth probably would not be sufficient to inhibit photosynthesis per leaf area or per unit of absorbed PAR. In that case biomass accumulation would not be affected. During the maturation and senescence phase, sufficient stress will accelerate the senescence of older leaves and reduce their photosynthetic capacity. The loss of green leaf area is quantified in the literature as reduced green leaf area duration (green leaf area index integrated over time). Grain yield is often well correlated with green leaf area duration because most of the assimilates for filling the grain come from photosynthesis late in the season.

The negative side of carbon balance is respiration. For the purpose of evaluating productivity, respiration is often divided, somewhat simplistically, into that for growth and that for the maintenance of existing tissue (McKree, 1970). The more active the growth, the higher the rate of respiration, which supplies the energy and building blocks necessary for the syntheses associated with growth. Maintenance respiration, on the other hand, is more proportional to the size of the plant. Over the life cycle of a crop, growth respiration constitutes a major portion of the total respiration in the early stage. Maintenance respiration becomes a larger and larger portion as the plant gains biomass, until the time of senescence when it becomes the dominant component of total respiration. In crops grown for grain or fruits, respiration by the fruiting bodies can be a major component (Bolaños and Hsiao, 1991). Respiration over the plant life cycle is highly important, consuming one fourth to two thirds of the total assimilates, according to highly variable estimates summarized by Amthor (1989, Table 6.1). A major uncertainty is the lack of good quantitative data on daily canopy photosynthesis and nightly respiration spanning the season.

Environmental conditions can also affect yield by altering the proportion of biomass allocated to the harvestable organs. Severe water deficiency at anthesis time can prevent pollination in grain crops. The reduction in the number of potential grains limits the amount of assimilates in the harvestable organ and HI is lowered. Hence, the reduction in yield would be more than being proportional to the reduction in biomass. Heat stress at the time of microspore formation can cause the pollens formed in cereal crops to be largely sterile. Again HI and grain number are reduced although there may be only very minor effects on the amount of total biomass produced. Less dramatic is the change in partition of carbon to roots. It is well known that root growth is favored over that of the shoot by mild to moderate water stress (Sharp & Davies, 1979). This change, though of adaptive advantage (Bradford and Hsiao, 1982), would reduce HI slightly.

EVAPOTRANSPIRATION IN RELATION TO ENERGY SUPPLY

It is also necessary to outline the basic aspects of the evapotranspiration (ET) process before considering water use efficiency. ET is the sum of evaporation from the soil (E) and transpiration from the plant (T). Water used by ET is referred to as consumptive use. The pivotal consideration is energy supply, as ET can only be sustained by the continuous input of energy corresponding to the rate of ET in terms of latent heat of vaporization. The energy comes from the sun as net absorbed radiation (net radiation flux) of any wavelength, and additionally can be from the surrounding air when the foliage or soil is cooler and hence there is a net transfer of sensible heat to the leaves or the soil surface. Not all the net radiation is necessarily used to evaporate water, part of it can also be dissipated as sensible heat, when temperature of the leaves or soil surface is hotter than that of the surrounding air. The part of the net radiation used for photosynthesis is very small (less than 3 or 4%) and usually considered as negligible.

As a generalization, net radiation of the plant canopy can be considered to be dominant in determining transpiration rates, as long as stomata are substantially open. In many situations, the daily rate of transpiration, when expressed in energy units as latent heat flux, is closely approximated by the net radiation flux of the plant canopy. Deviation is caused by significant sensible heat flux. Sensible heat flux supplies significant amount of energy for transpiration when the canopy is sparse and the exposed soil surface is relatively dry. The warmer soil surface, the consequence of radiative heating, then warms the air and enhances sensible heat transfer to the canopy. In dry areas, extra energy supply for the canopy, regardless whether it is sparse or complete, also comes from large scale advections (horizonal flow of energy and associated materials, in this case, as warm and relatively dry air), especially in crop fields surrounded by fallow areas under windy conditions. In areas of high humidity, leaf temperature is often higher than air temperature and transpiration in energy equivalent tends to be less than net radiation due to sensible heat flux away from the foliage. Sensible heat also dissipates considerable portion of the energy from net radiation if stomata are substantially closed by stresses or senescence of the leaves, restriciting water vapor passage and transpirational cooling.

In the field it is nearly impossible to separate out transpiration from soil evaporation experimentally without altering the natural energy supply for T or for E. Hence, it is often necessary to consider the consumptive use of water instead of transpirational use in calculating water use efficiency. In general soil evaporation follows the same principles as transpiration, except there is no stomatal control. Instead, water vapor concentration at the soil surface is reduced by soil drying. The main source of energy for E is also net radiation, for the soil. E from exposed soil is much higher than from soil shaded by plants at the same wetness of the soil surface. When soil is wetted frequently, E constitutes the major part of ET early in the season when canopy is sparse, but declines with time as more and more of the soil is shaded by the developing canopy. When the canopy is complete, E is only a small fraction of the ET even when the soil surface is wet (Ritchie and Burnett, 1971).

DEFINITIONS OF WATER USE EFFICIENCY

The above descriptions of plant productivity and ET serve as a basis for the considerations of the efficiency of water use by plants. Water use efficiency (WUE) can be viewed in a number of ways (Fischer & Turner, 1978). The most basic is in terms of the carbon gained through photosynthesis relative to the water lost through transpiration. The ratio of net assimilation to transpiration, sometimes known as transpiration ratio in the literature, is here termed photosynthetic WUE. Photosynthetic WUE can be used to describe the behavior of a single leaf, of a plant, or of a canopy made up of a population of plants. It can refer to the near instantaneous behavior (A/T), or to the overall outcome with the rates of A and T integrated over periods of minutes to a day or longer ($\int Adt / \int Tdt$). When referring to the whole plant, the respiration of the non-photosynthetic parts must be accounted for in arriving at values for A. Unfortunately, much of the data reported so far in the literature have been of the near instant or short term nature, and usually only for individual leaves, and are of very limited value in deducing WUE in the field over time intervals of significant duration. For long spans of weeks and months, because of the paucity of data due to the difficulties in the continuous operation of instruments to monitor A, it is usually necessary to consider instead biomass transpirational WUE, the amount of biomass produced per unit of water transpired, or biomass consumptive WUE, which includes the water evaporated from the soil in addition to that transpired. Biomass consumptive WUE is closely linked to photosynthetic WUE, but differs from the latter by the factor c of Eq. 1, by the night respiration integral, and by soil evaporation E, as follows:

$$\textbf{Biomass consumptiveWUE} = \frac{c\left\{\int A\,dt - \int R\,dt\right\}}{\int ET\,dt} \qquad (2)$$

Most of the data in the literature on long term WUE are based on consumptive use. a few studies are based on transpiration by covering the soil (which increases sensible heat flux from the covered soil to the leaves) or by deducting E estimated by various methods.

The overall WUE of a crop at harvest may bear little relation to the photosynthetic WUE at a particular time in the life of the crop or even to its biomass transpirational WUE. Yield water use efficiency (harvested yield per unit of water used) would be of more concern. In addition to being a function of biomass WUE integrated over the life time of the crop, yield WUE is also dependent on the partition of carbon among plant organs, i. e., on HI, such that

$$\text{Yield WUE} = \text{HI (biomass WUE)} \qquad (3)$$

Eq. 3 is applicable to either consumptive or transpirational water use. Yield WUE of most crops have been greatly improved with the development of modern high yielding cultivars as the inadvertent result of aiming for higher yields, which led to higher HI. Although important in the context of the effects of stresses (Fischer & Turner, 1978) and of high CO_2 (Lawlor & Mitchell, 1991), yield WUE is not considered further here due to a space limitation.

VARIATIONS AND CONSTANCY IN WATER USE EFFICIENCY

At the ambient CO_2 concentration, the instantaneous photosynthetic WUE varies markedly with time of the day, as exemplified by some data collected at Davis, California (Fig. 4). The main cause of the variations lies in the discordance between the daily pattern of PAR flux and canopy temperature. The air and hence the canopy temperature are lower in the morning than in the afternoon. As the consequence, water vapor concentration in the interior of the leaf is higher in the afternoon than in the morning at the same PAR. Thus, T is higher in the afternoon while A remains similar, resulting in lower photosynthetic WUE. Biomass WUE, a time integral, however, tends to fall within a narrow range of values for a given species, prob-

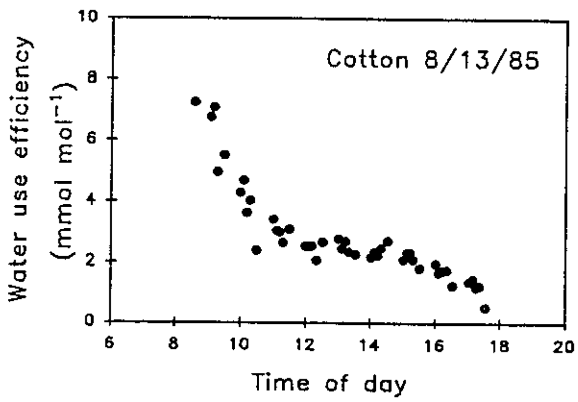


Fig. 4. Diurnal time course of photosynthetic water use efficiency of a full cotton canopy in the open field. The day was basically sunny with 1.79 mmol m^{-2} s^{-1} of incident PAR and 2.44 kPa of vapor saturation deficit at midday. Measurements were made with the micrometeorological method of Fig. 1 and no correction was made for soil and root respiration (see Fig. 1) or soil evaporation, which should be minimal due to the canopy cover. (from Held & Hsiao, 1993)

ably because the diurnal trends in weather are similar for most days and the variations in weather from day to day tend to average out over periods of weeks. In fact, when normalized for the evaporative demand of the atmosphere (de Wit, 1958; Arkley, 1963; Tanner and Sinclair, 1983), biomass WUE at the ambient CO_2 concentration has been found to be nearly constant for many crop species under different weather and regimes of water supply, i.e., the relationship between biomass produced and water consumed is linear. At least several hundreds of such near linear relationships can be found in the literature (e.g., Hanks, 1983).

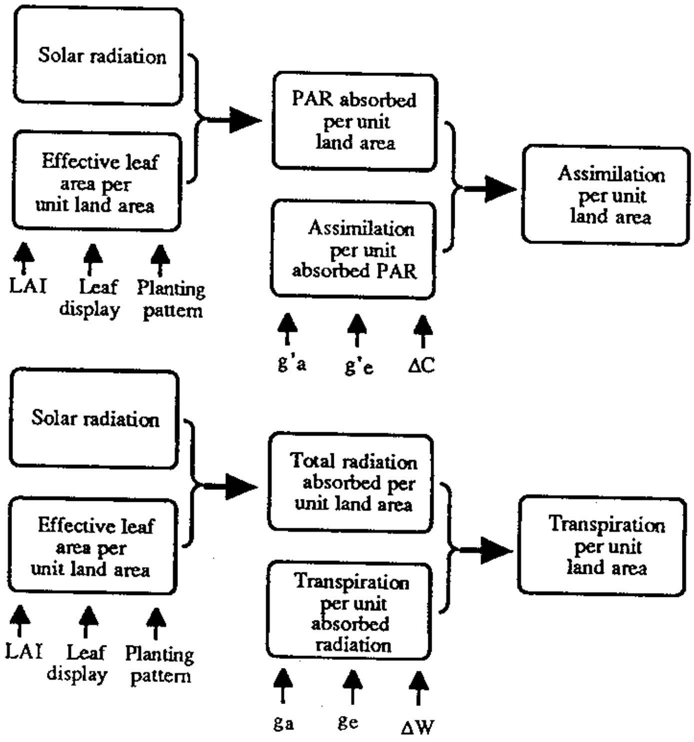


Fig. 5. Similarities and differences in factors affecting assimilation and transpiration per unit land area. Arrows indicate causal relations. Leaf area index = LAI; g'_a and g'_e represents respectively conductance of the air boundary layer and of the leaf epidermis to CO_2; g_a and g_c have analogous meaning but are for water vapor; ΔC and ΔW is respectively the difference in CO_2 and in water vapor concentration between the bulk air and the leaf intercellular space. (Modified from Hsiao & Bradford, 1983)

What are the reasons for this conservative behavior of biomass WUE? Although not widely discussed in the literature, it appears that the behavior is rooted in two basic tenets of plant productivity—the role of intercepted radiation in both A and T, and the sharing of transport pathway by CO_2 and water vapor in their passage between the atmosphere and the intercellular space of leaves. The dominant factor is probably radiation capture. As shown in Fig. 5, the extent of radiation capture depends on the effective leaf area or foliage canopy size, which in turn is dependent on the actual leaf area (or leaf area index) as modulated by leaf distribution and geometry. Plant distribution over the land area and factors which are highly species specific, such as leaf distribution and foliage angles within the canopy, are important determinants. A and T share mostly the same source of captured energy. One difference is that sensible heat flux can either supply additional energy for transpiration or dissipate a part of the absorbed radiactive energy which otherwise would be used for transpiration, as discussed earlier. The other difference is that assimilation utilizes only radiation in the photosynthetically active band (approx. 350 to 750 nm, see McCree, 1981) whereas transpiration uses radiation of any wavelength. At the same time, PAR is a fairly constant portion of the incident solar radiation (Varlet-Grancher et al., 1989), and the ratio of absorptance for PAR and non-PAR is relatively constant for many leaves. Consequently, any change in the amount of radiation captured by the canopy, whether the result of changes in weather or in effective leaf surface area, would affect A (or biomass production) and T very similarly and WUE is kept nearly constant. This commonality (Hsiao and Bradford, 1983) has not been emphasized in the literature, which often attributed the tight relationship between biomass produced and water consumed to the shared pathway for CO_2 and water vapor transport (Kanemasu, 1983; Tanner and Sinclair, 1983), shown in the central portion of Fig. 5.

The shared pathway between CO_2 and water vapor for single leaves can be formalized with two simple transport equations, one for assimilation and one for transpiration. By assuming steady state conditions, the rate of assimilation can be equated to the rate of CO_2 transport from the bulk air to the intercellular space, making it possible to consider assimilation in terms of CO_2 transport only in the gaseous phase. The resultant equation is, along with the equation for transpiration:

$$A = \frac{1}{r'_a + r'_e}\left(C_a - C_i\right) \tag{4a}$$

$$T = \frac{1}{r_a + r_e}\left(W_i - W_a\right) \tag{4b}$$

where the resistance to gas transport of air boundary layer and leaf epidermis are denoted respectively by r_a and r_e, with r_e being the resistance made up by two parallel resistances, one of the stomata and the other of the cuticle. The resistances for CO_2 are indicated by a prime in contrast to the resistances for water vapor without the prime. Due to its heavier molecular mass, CO_2 diffuses slower than water vapor and $r' = 1.6\,r$, or $r = 0.625\,r'$, for both boundary layer and epidermal parts of the pathway (Farquhar & Sharkey, 1982). The driving force for CO_2 and water vapor transport are, respectively, the difference in the concentration of CO_2 (ΔC) between the bulk air (C_a) and the intercellular space (C_i), and the difference in the water vapor concentration (ΔW) between the intercellular space (W_i) and the bulk air (W_a). The advantage of not going beyond the gaseous phase for CO_2 is that complex metabolic changes in the liquid phase associated with changes in environmental conditions need not be dealt with directly. Instead, they are reflected in the absolute value of C_i and the relative value of C_i to C_a. Since only physical processes are involved in the gaseous phase, all terms in the equation for A are well defined and can be experimentally determined.

Returning now to Fig. 5, it shows that for a given amount of radiation absorbed, A and T are dependent additionally on their respective resistances r'_a and r'_e, and r_a and r_e. Since resistances for CO_2 and for water vapor differ by a constant factor, any change in resistance of either the boundary layer or of the stomata would have similar impact on A and on T. On the other hand, Fig. 5 and Eq. 4a and 4b also highlight the fact that the driving force for A (ΔC) and T (ΔW) are totally different and could lead to changes in photosynthetic WUE upon changes in certain conditions. The most obvious is the increase in the ΔC under elevated CO_2, leading to increased WUE, as will be discussed later. Also obvious is why WUE of a given species differ under different climates unless the quantity of water consumed is normalized for the evaporative demand of the atmosphere. Often the normalization takes the form of dividing the total ET by the mean vapor pressure deficit of the air (Tanner and Sinclair, 1983). The latter is an approximation of the mean ΔW, as ΔW is vapor pressure deficit of the air in the appropriate units if leaf temperature is identical to air temperature.

Based on Eq. 4a and 4b, and recognizing that $r = 0.625\,r'$, photosynthetic WUE (hereon referred to simply as WUE unless otherwise stated) of single leaves can be written (Farquhar et al., 1989) as

$$WUE = \frac{(r_a + r_e)}{(r'_a + r'_e)} \frac{\Delta C}{\Delta W} = 0.625 \frac{\Delta C}{\Delta W} \qquad (5)$$

regardless whether the plant is well watered and growing under optimal conditions or is affected by stresses. The equation highlights the importance of knowing ΔC and ΔW in evaluating WUE.

Eq. 4 and 5 are written for single leaves but provide a conceptual basis for the examination of canopy WUE. The problems of scaling up from processes at the leaf level to those at the canopy are complex and receiving much current attention (e.g., Kim & Verma, 1991). On the other hand, indications are that the "big leaf" model for canopy ET (Penman-Monteith combination equation, Monteith, 1973) and for canopy A are reasonably valid for short canopies such as those of most herbaceous crops which are fully or close to fully covering the ground (Jarvis & McNaughton, 1986; McNaughton & Jarvis, 1991). Applications to canopies of trees and forests require much more caution (Jarvis, et al., 1976). In any event, the basic elements in many scaling-up models are single leaves or their equivalent. Therefore information developed in terms of the concept represented by Eq. 4 and 5 and their derivatives would be valuable.

FURTHER CONSIDERATIONS OF STRESS EFFECTS ON WATER USE EFFICIENCY

Detailed discussion of WUE as affected by water supply needs to take into account the time of water stress relative to the time of plant growth stages and the severity of water stress. Only the first two stages of the life cycle of an annual crop as depicted in Fig. 4 are considered here because of space limitation.

Mild Water Stress. Of all the known plant processes, expansive growth of leaves is the most sensitive to water stress and is the first process inhibited as water stress develops (Boyer, 1970; Acevedo et al., 1971; Hsiao, 1973; Bradford and Hsiao, 1982). When canopy cover is incomplete and the capture of incident radiation only partial (first phase of Fig. 3), continued enlargement of the canopy is crucial for the plants to reach their maximal rate of radiation capture and biomass production. Even mild water stress would reduce the rate of leaf area development, leading to less PAR captured by the canopy. As pointed out earlier (Hsiao, 1982; Bradford and Hsiao, 1982), this effect compounds with time and a small percentage

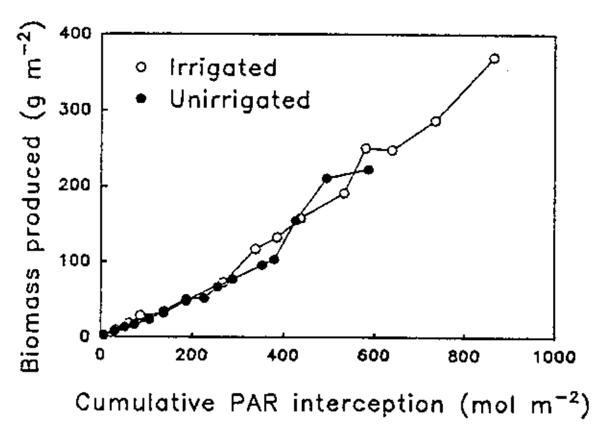


Fig. 6. Above-ground biomass production in relation to cumulative PAR interception by irrigated and unirrigated bean (*Phaseolus vulgaris*) in the field. Same crop and treatments as in Fig. 6. Biomass were sampled at regular intervals shortly after plant emergence. Daily time course of PAR interception was measured at regular intervals and interpolated for days in between, then summed to the appropriate date. (Unpublished data of F. Arruda and T. C. Hsiao)

reduction in the daily leaf growth rate can result in much larger reductions in biomass or radiation intercepting canopy area. In a number of experiments we carried out in California, the main or only effect of mild to moderate water stress in the field was a reduction a canopy size and radiation capture. For example, in an experiment with beans, when the above ground biomass sampled at different times was plotted against the cumulative intercepted PAR, the data for the irrigated and unirrigated treatment fell on the same line (Fig. 6). That is, for any sampling date, the biomass produced by the unirrigated treatment was lower, proportional to its smaller quantity of intercepted PAR. These results indicate that RUE was not altered by the mild water stress and that canopy size and PAR interception accounted for all the difference in biomass production.

With assimilation and transpiration both dependent on radiation capture, when biomass is reduced only by restricted canopy development, biomass and transpirational water use are reduced in a closely linked way, leading to very little change in biomass transpirational WUE during this stage. The possible small change is a slight decrease due to a small increase in leaf temperature resulting from sensible heat flux from a less shaded and hence hotter soil surface if that surface is often dry.

Biomass consumptive WUE could be reduced more. If the soil is frequently wetted by rain or irrigation, because of the slower canopy development, more soil would remain unshaded and there would be more E. The reduction in WUE, however, is not likely to be marked, as E constitutes only a minor part of the ET integral under most situations. The exception is when canopy is sparse for most of the season and the soil is frequently wetted.

If the plant canopy covers the ground completely and is already intercepting nearly all the incident radiation (phase 2 of Fig. 3), or when the vegetative growth is complete, mild water stress should have minimal or no effect on productivity and WUE since leaf area is already sufficient and stomata and photosynthesis are less sensitive to water stress than expansive growth (Boyer, 1970; Acevedo et al., 1971; Hsiao, 1973).

This discussion has been on effects of water stress. Indications are, however, that leaf growth is also very sensitive to other environmental stresses such as salinity and cold temperature, and what has been discussed should apply to those stresses as well.

Moderate to Severe Water Stress. Under more severe water stress, in addition to the inhibition of leaf growth, CO_2 assimilation and stomatal opening would be reduced, frequently along with photosynthetic capacity of the leaf, and WUE during any of the three phases (Fig. 3) may change either due to changes in ΔC or in Δw. Designating WUE for well watered plants as WUE_O and for water stressed plants as WUE_S and utilizing Eq. 5, the ratio of WUE under stress to that under well watered conditions would be

$$\frac{WUE_S}{WUE_O} = \frac{\Delta C_S \, \Delta W_O}{\Delta C_O \, \Delta W_S} \tag{6}$$

It turns out that for many species C_i has a tendency to remain constant under a range of environmental conditions, including water stress (Wong et al, 1979; review by Morrison, 1987), as long as CO_2 concentration in the air remains the same. Available data indicate near constancy in C_i even as temperature varied within a 15° range of the optimal temperature for photosynthesis (Björkman, 1981). In some cases C_i remains constant under water stress; in other cases C_i is reduced. In plants with stomata which responds to ΔW, C_i tends to decrease linearly with increases in ΔW (Ball & Berry, 1982; Morison, 1987). Examples of constancy and changes in C_i are given in Fig. 8, for tomato leaves. C_i of these leaves remained almost constant over a range of PAR flux and increased only when PAR dropped to a low level. Of the three leaves shown in Fig. 8b, C_i for two remained essentially constant as water potential decreased over the range tested, while C_i of the third showed some decline.

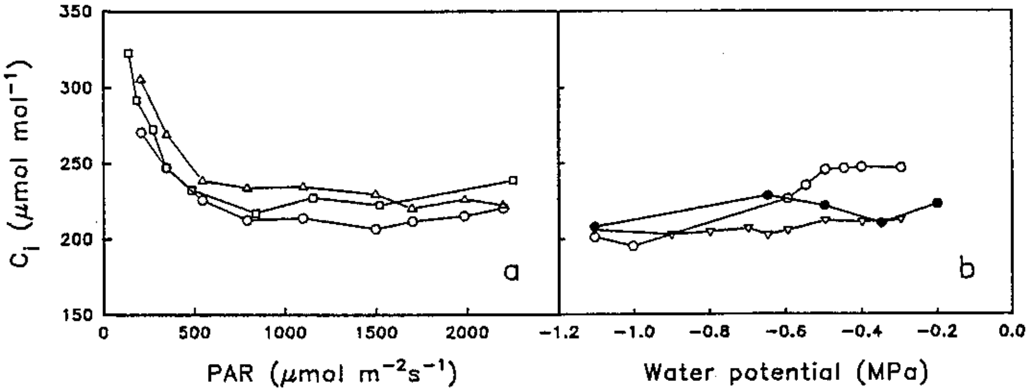


Fig. 7. Intercellular CO_2 concentration (C_i) of the youngest, fully expanded and fully exposed field grown tomato leaves in relationship to (a) PAR flux and (b) leaf water potential. Each line represents a leaf from a different plant. Air CO_2 concentration (C_a) was ambient. For (b), PAR was at approximately 2 mmol m^{-2} s^{-1}. The apical leaflet of a leaf was monitored in a gas exchange chamber with the remaining leaflets covered by plastic film and aluminum foil to stop transpiration. One covered leaflet each was excised at intervals for the measurement of leaf water potential in a pressure chamber as the plant dried out. The measure water potential was assumed to be that of the exposed and assimilating leaflet. [Data in (a) are from Bolaños and Hsiao (1991), and in (b), are unpublished results of the same authors.]

For the case where C_i remains the same, ΔC would remain the same as long as C_a does not change. Hence, according to Eq. 6 the ratio of WUE with and without stress would simply be $\Delta W_o/\Delta W_s$. For the same atmospheric humidity (same W_a), ΔW would depend on W_i, which in turn is determined by leaf temperature as the intercellular space is virtually saturated with water vapor and saturation vapor concentration is a function of temperature. Stomata are less open and transpiration is reduced under many stresses. Leaf temperature then rises as dictated by the principle of energy balance, leading to a higher W_i. Consequently $\Delta W_o/\Delta W_s <$

1 and $WUE_s < WUE_o$ as long as C_i remains the same. Exactly how much WUE is reduced would depend on the degree of stomatal closure, the thermal and radiation environment, air humidity, and boundary layer conditions affecting sensible heat transfer. The impact of these factors show up in the ratio of ΔW. Other things being equal, the more severe the stress and the greater the stomatal closure, the more WUE would be reduced. It should be pointed out that the situations described are not those occurring in the typical gas exchange chambers used to determine WUE of single leaves. There, by keeping the chamber or leaf temperature constant, the principle of energy balance as it operates in the open field is circumvented and W_i is kept constant. Hence, WUE would remain the same as long as C_i remains the same. An interesting point made clear by Eq. 6 is that the impact on WUE of a given increase in leaf temperature effected by water stress would be greater at higher air relative humidities. This is significant when comparing estimates of changes in WUE made in the field to those in controlled environments, where relative humidity is often higher.

The conclusion that WUE is reduced by stresses which cause stomatal closure in plants whose C_i remains constant is not surprising, except for the case of water stress. The tendency is to view the plant as a well adapted organism with capabilities to improve efficiency of utilization of the resource that is the most limiting. In the case of water stress this appears to be not true, for the plants which maintain their C_i nearly constant. For the plants which exhibit reduced C_i, either directly due to the stress or indirectly induced by the increase in ΔW, the direction and extent of change in WUE would depend on the increase in ΔC due to the reduction in C_i relative to the increase in ΔW. In any event, if the linear relationship between biomass production and crop water use is any indication, it would be unusual for WUE to be changed markedly by water stress. What is probable is that in many cases the main limiting factor for the production of most of the biomass is a lack of adequate leaf area and radiation interception, which would be associated with an essentially constant transpirational biomass WUE. The remaining portion of the biomass is produced when water stress is severe enough to cause stomatal closure and possibly altering C_i, with the consequent changes in WUE. The overall biomass WUE, however, would be nearly constant because it reflects more the WUE of the major portion of the biomass produced.

IMPACT OF HIGH CO_2 ON WATER USE EFFICIENCY

It is well known that under high CO_2 assimilation is increased, especially for C_3 species. Stomata in most cases close partly under high CO_2, leading to some reductions in transpiration. Morison (1987) concluded from reviewing 80 observations in the literature on 25 species that stomatal conductance at a CO_2 concentration twice of the present ambiance is approximately 60% of the conductance under the ambient CO_2, regardless whether the species is C_3 or C_4. With the increase in A and reduction in T, WUE is generally enhanced, but to a highly variable degree. Although WUE as affected by elevated CO_2 has been reviewed and evaluated a number of times (Kimball & Idso, 1983; Morison, 1985; Eamus, 1991), there is still no reference framework to analyze and reconcile these highly variable results. It is hoped that the proposed analysis below, though simplistic to a certain degree, will serve such a purpose.

Using an approach similar to that used for water stress effects and denoting the new (whether higher or lower) CO_2 level with a subscript n, the ratio of WUE under new CO_2 to that under present day CO_2 without water stress can be expressed as:

$$\frac{WUE_N}{WUE_O} = \frac{\left(C_{e,N} - C_{i,N}\right)\Delta W_{ei,O}}{\left(C_{e,O} - C_{i,O}\right)\Delta W_{ei,N}} \tag{7}$$

Eq. 7 is based on transport over the epidermal path segment ei, between the air immediately adjacent to the leaf epidermis, denoted by subscript e for its location, and the intercellular space i. ΔW_{ei} is the differnce in W between the two locations. For steady state transport, rates of A or of T are the same for the epidermal and the boundary layer segment as they are connected in series; hence, Eq 7 is an expression of the ratio of the new to the original WUE.

A major question is how C_i is affected by C_a or C_e. Starting with the work of Wong et al (1979), analyses (Ball & Berry, 1982; Morison, 1987) show that the ratio of C_i to C_e, designated by α ($\alpha = C_i/C_e$), at various C_e is generally a conservative quantity, but decreases linearly with increases in ΔW. Substituting αC_e for C_i in Eq. 7, the expression becomes

$$\frac{\boldsymbol{WUE_N}}{\boldsymbol{WUE_O}} = \frac{\left(1-\alpha_N\right)}{\left(1-\alpha_O\right)}\frac{\boldsymbol{C_{e,N}}}{\boldsymbol{C_{e,O}}}\frac{\boldsymbol{\Delta W_{ei,O}}}{\boldsymbol{\Delta W_{ei,N}}} \tag{8a}$$

For situations where the air is highly turbulent or when stomata are only narrowly open, $C_a \cong C_e$ and $\Delta W \cong \Delta W_{ei}$, the ratio of WUE can then be approximated as

$$\frac{\boldsymbol{WUE_N}}{\boldsymbol{WUE_O}} \cong \frac{\left(1-\alpha_N\right)}{\left(1-\alpha_O\right)}\frac{\boldsymbol{C_{a,N}}}{\boldsymbol{C_{a,O}}}\frac{\boldsymbol{\Delta W_O}}{\boldsymbol{\Delta W_N}} \tag{8b}$$

α is conservative in that it generally remains nearly constant as air CO_2 concentration varies or as PAR flux varies for short periods (Ball & Berry, 1982; Morison, 1987). Very little data are available on the long-term effects of different concentrations of CO_2 on α. If α remains essentially unchanged when grown under high CO_2 (Radoglou et al., 1992; Ryle et al., 1992) then $\alpha_n = \alpha_o$ and Eq. 8b becomes

$$\frac{WUE_N}{WUE_O} \cong \frac{C_{a,N}}{C_{a,O}} \frac{\Delta W_O}{\Delta W_N} \tag{9}$$

Accordingly, as the first approximation, the change in WUE would be somewhat less than being proportional to the change in CO_2 concentration, regardless whether the species is C_3 or C_4. How much less is determined by the ratio of ΔW_o to ΔW_n, which in turn is determined by how much leaf temperature is increased in the high CO_2 environment due to partial stomatal closure. In apparent agreement with the prediction of Eq. 9, the data of Allen and coworkers (Allen, 1990) showed that WUE of soybean was increased 120 to 130 % when CO_2 concentration at which the plants were grown was increased from 330 to 800 μmol mol^{-1}, an increase of 142%. Some studies have shown that WUE increased linearly with increases in CO_2 (Eamus & Jarvis, 1989).

Returning to the question of constancy of α, given the likelihood that the climate is going to be hotter under elevated CO_2 (larger ΔW), α may decline slightly. On the other hand, for plants grown over a long time under high CO_2, α may increase slightly at a given ΔW due to the often observed reduction in photosynthetic capacity of the leaf of plants grown for a long time in high CO_2. These counteracting effects may hold changes in α to a minimum. In that case, the increase in WUE would be somewhat less than being proportional to the CO_2 increase, as pointed out above. As for yield WUE, in many cases HI of plants grown in elevated CO_2 did not change significantly, although there were more harvestable assimilate sinks per plant (Lawlor & Mitchell, 1991). Hence, improvement in yield WUE would be the sole result of improvement in photosynthetic and biomass WUE. On the other hand, HI of some root crops was found to be increased under high CO_2 (Idso et al., 1988).

The elevated CO_2 level in the future world is likely to be accompanied by more atmospheric droughts. Plants, especially C_4 species, however, may not necessarily experience more water stress because of the improvement in WUE under high CO_2. In any event, the combined effect of water stress and high CO_2 can be examined using the same approach. Denoting the situation of water stress under high CO_2 by the subscript N+S, $\Delta C_{N+S}/\Delta C_N = 1$ if C_i is not altered by the stress. Utilizing Eq. 6 and 9,

$$\frac{WUE_{N+S}}{WUE_O} = \frac{WUE_{N+S}}{WUE_N} \frac{WUE_N}{WUE_O} \cong \frac{C_{a,N}}{C_{a,O}} \frac{\Delta W_O}{\Delta W_{N+S}} \tag{10}$$

Note Eq. 10 is basically the same as Eq. 9, except that ΔW is to be evaluated for the stressed treatment under the new level of CO_2.

IMPACT OF HIGH CO_2 ON PRODUCTIVITY

The literature indicates that the response in biomass production to increases in atmospheric CO_2 is also highly variable, depending not only on species, but apparently also on the particular study (Kimball & Idso, 1983). Here too a conceptual framework would be helpful in the analysis of the contridicting results and providing explanations for the different responses. Using also the single leaf approach, the ratio of assimilation rates under the original and under the high CO_2 concentration, denoted by A_N and A_O respectively, can be expressed as

$$\frac{A_N}{A_O} \cong \frac{\left(r'_{a,O} + r'_{e,O}\right)}{\left(r'_{a,N} + r'_{e,N}\right)} \frac{\left(1 - \alpha_N\right)}{\left(1 - \alpha_O\right)} \frac{C_{a,N}}{C_{a,O}} = \frac{g'_{ae,N}}{g'_{ae,O}} \frac{\left(1 - \alpha_N\right)}{\left(1 - \alpha_O\right)} \frac{C_{a,N}}{C_{a,O}} \tag{11}$$

It is convenient to express the path transmission characteristics in terms of conductances g', with the subscript ae denoting the overall conductance for the boundary layer and the epidermis segments. For the simplest case of constant α and low boundary layer resistance, the equation shows that the enhancing effect of higher C_a on assimilation and primary productivity is reduced in proportion to the reduction in gaseous phase conductance caused by stomatal closure. For example, if C_a is doubled but gaseous phase conductance is reduced by 25%, then the new assimilation rate would be 50% higher than the original. Again, information on the constancy or variability of α is crucial to evaluate the applicability of this relationship. Eq. 11 is consistent with published results on cotton and maize (Wong, 1979), giving good estimates of the observed difference in A between leaves on plants grown at normal and two times normal CO_2 with good nitrogen supply. Differences in biomass productivity under different levels of CO_2 must be traceable to differences in integrated assimilation and respiration, or in the chemical composition of the biomass. The advantage of Eq. 11 is that the myriad of variables underlying assimilation are reduced to a small number which can be easily evaluated with modern instrumentation.

The enhanced rate of assimilation per unit leaf area under high CO_2 may have variably effect on biomass production, depending on the growth phase. The higher assimilation under high CO_2 usually leads to faster leaf area development (Cure et al., 1989). In the canopy cover limiting phase (Fig. 3), this effect compounds with time, resulting in a larger percentage increase in biomass than the percentage increase in assimilation per unit leaf area. That is consistent with the results of Wong (1979). Photosynthetic rate of cotton leaves was enhanced 50% under high CO_2, but biomass was doubled. On the other hand, during the radiation limiting phase leaf area is already adequate and there would not be a compounding effect by adding leaf area. The increase in biomass production would then be more proportional to the increase in photosynthetic rate. In fact, excessive leaf area can be an respiratory drain on the carbon pool in that case. There is much conflict in the literature on the extent of the enhancing effect of high CO_2 on biomass production for the same plant species. Possibly much of the difference could be explained had a distinction been made between the canopy limiting and the radiation limiting phase.

ADAPTATION TO DROUGHT UNDER HIGH CO_2

It has been frequently postulated that the future world under higher CO_2 would be warmer with more areas subjected to climatic drought. On the other hand, the effects of high CO_2 on the plant are such that the impacts of climatic drought should be ameliorated substantially. To start off, WUE of both C_3 and C_4 species are enhance under high CO_2. In the case of complete canopy cover or a lack of stimulation of leaf growth, a given amount of soil water would provide for the need of the plant for a longer period. In the case of incomplete canopy cover and stimulated leaf growth, the same amount of soil water would support a higher rate of biomass production. With more assimilates available under high CO_2, osmotic adjustment should be more readily achieved and the plant can extract soil water to a lower water potential and tolerate a lower tissue water potential before serious damage occurs. Further, the additional assimilates may make it possible to grow more roots, enhancing the volume of soil explored for water. These facets are only beginning to be investigated and analysis in terms of resource economics of the plant is sorely needed.

ACKNOWLEDGMENT

This work was partly supported by USDA Competitive Grant 88-37/30-3849 and by Regional Research Project W-154.

LITERATURE CITED

Acevedo E, Hsiao TC, Henderson DW (1971) Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiology 48:631-636

Allen LH Jr. (1990) Plant responses to rising carbon dioxide and potential interactions with air pollutants. Journal of Environmental Quality 19:15-34

Amthor JS (1989) Respiration and crop productivity. Springer, New York., Berlin Heidelberg London Paris Tokyo

Arkley RJ (1963) Relationships between plant growth and transpiration. Hilgardia 34:559-584

Ball JT, Berry JA (1982) The C_i/C_s ratio: a basis for predicting stomatal control of photosynthesis. Carnegie Institution of Washington Yearbook 1981:88-92

Bradford KJ, Hsiao TC (1982) Physiological responses to moderate water stress. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II Water relations and carbon assimilation. Springer, Berlin Heidelberg New York, pp 263-324 (Encyclopedia of plant physiology, n.s., vol 12B)

Bolaños JA, Hsiao TC (1991) Photosynthesis and respiratory characterization of field grown tomato. Photosynthesis Research 28:21-32

Boyer JS (1970) Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiology 46:233-235

Campbell WJ, Allen LH Jr, Bowes G (1990) Response of soybean canopy photosynthesis to CO_2 concentration, light, and termperature. Journal of Experimental Botany 41:427-433

Charles-Edwards DA, Doley D, Rimmington GM (1986) Modelling plant growth and development. Academic Press, Sidney Orlando San Diego New York Austin London Montreal Tokyo Toronto

Connor DJ, Palta JA, Jones TR (1985) Response of sunflower to strategies of irrigation. II. Crop photosynthesis and transpiration. Field Crop Research 12:281-293

Cure JD, Rufty TW Jr, Israel DW (1989) Alterations in soybean leaf development and photosynthesis in a CO_2-enriched atmosphere. Botanical Gazette 150:337-345

de Wit CT (1958) Transpiration and crop yields. Versl. Landbouwk. Onderz. 64.6. Institute of Biological and Chemical Research on Field Crops and Herbage, Wageningen

Demetriades-Shah TH, Fuchs M, Kanemasu ET, Flitcroft I (1992) A note of caution concerning the relationship between cumulated intercepted solar radiation and crop growth. Agricultural and Forest Meteorology 58:93-207

Eamus D (1991) The interaction of rising CO_2 and temperatures with water use efficiency. Plant, Cell, and Environment 14:843-852

Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Advances in Ecological Research 19:1-55

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annual Review Plant Physiology and Plant Molecular Biology 40:503-537

Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. Annual Review of Plant Physiology 33:317-345

Fischer RA (1983) Wheat. In: Productivity of field crops. International Institute of Rice Research, Los Baños, Philippines, pp129-154

Fischer RA Turner NC (1978) Plant productivity in the arid and semiarid zones. Annual Review of Plant Physiology 29:277-317

Gallagher JN, Biscoe PV (1978) Radiation absorption, growth and yield of cereals. Journal of Agricultural Science Cambridge 91:47-60

Hanks JR (1983) Yield and water-use relationships: an overview. In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitations to efficient water use in crop production. Agronomy Society of America, Madison, Wisconsin, pp 393-411

Held AA, Hsiao TC (1993) Canopy assimilation and evapotranspiration of well watered crops in the field: I. Closed canopies and role of stomata (in preparation)

Held AA, Steduto P, Orgaz F, Matista A, Hsiao TC (1990) Bowen ratio/energy balance technique for estimating crop net CO_2 assimilation, and comparison with a canopy chamber. Theoretical and Applied Climatology 42:203-213

Hesketh J, Baker D (1967) Light and carbon assimilation by plant communities. Crop Science 7:285-293

Hsiao TC (1973) Plant responses to water stress. Annual Review of Plant Physiology 24:519-570

Hsiao TC (1982) The soil-plant-atmosphere continuum in relation to drought and crop production. In: Drought resistance in crops, with emphasis on rice. International Rice Research Institute, Los Baños, Philippines, pp 39-52

Hsiao TC, Bradford KJ (1983) Physiological consequences of cellular water deficits. In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitations to efficient water use in crop production. Agronomy Society of America, Madison, Wisconsin, pp 227-265

Idso SB, Kimball BA, Mauney JR (1988) Effects of atmospheric CO_2 enrichment on root:shoot ratios of carrot, radish, cotton and soybean. Agriculture, Ecosystems and Environment 21:293-299

Jarvis PG, James GB, Landsberg JJ (1976) Coniferous forest. In: Monteith JL (ed) Vegetation and the atmosphere. Case studies. Volume 2. Academis Press, London, pp 171-240

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. Advances in Ecological Research 15:1-49

Jones JW, Zur B, Bennett JM (1986) Interactive effects of water and nitrogen stresses on carbon and water vapor exchange of corn canopies. Agricultural and Forest Meteorology 38: 113-126

Jones P, Jones JW, Allen LH (1985) Seasonal carbon and water balances of soybeans grown under stress treatments in sunlit chambers. Transaction of American Society of Agricultural Engineers 28:2021-2028

Kanemasu ET (1983) Yield and water-use relationships: Some problems of relating grain yield to transpiration. In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitations to efficient water use in crop production. Agronomy Society of America, Madison, Wisconsin, pp 413-417

Kim J, Verma SB (1991) Modeling canopy photosynthesis: scaling up from a leaf to canopy in a temperate grassland ecosystem. Agricultural and Forest Meteorology 57:187-208

Kimball BA, Idso SB (1983) Increasing atmospheric CO_2: effects on crop yield, water use and climate. Agricultural Water Management 7:55-72

Lawlor DW, Mitchell RAC (1991) The effects of increasing CO_2 on crop photosynthesis and productivity: a review of field studies. Plant, Cell and Environment 14:807-818

McKree KJ (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. In: Setlik I (ed) Prediction and measurement of photosynthetic productivity. Centre for Agricultural Publishing and Documentation, Wageningen, pp 221-229

McKree KJ (1981) Photosynthetically active radiation. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology I, responses to the physical environment. Springer, Berlin Heidelberg New York, pp 41-55 (Encyclopedia of plant physiology, n.s., vol 12A)

McNaughton KG, Jarvis PG (1991) Effects of spatial scale on stomatal control of transpiration. Agriculatural and Forest Meteorology 54:279-301

Monteith JL (1977) Climate and the efficiency of crop production in Britain. Philosophical Transactions Royal Society London B 281:277-294

Monteith JL (ed)(1973) Principles of environmental physics. Edward Arnold, London

Morison JIL (1985) Sensitivity of stomata and water use efficiency to high CO_2. Plant, Cell, and Environment 8:467-474

Morison JIL (1987) Intercellular CO_2 concentration and stomatal response to $CO._2$ In: Zeiger E, Farquhar GD, Cowan IR (eds) Stomatal function. Stanford University Press, Stanford, California, pp 229-251

Penning de Vries FWT (1975) Use of assmililates in higher plants. In: Cooper JP (ed) Photosynthesis and productivity in different environments. Cambridge University Press, Cambridge, pp 459-480

Puckridge DW, Ratkowsky DA (1971) Photosynthesis of wheat under field conditions. IV The influence of density of leaf area index on the response to radiation. Australian Journal of Agricultural Research 22:11-20

Puech-Suanzes I, Hsiao TC, Fereres E, Henderson DW (1989) Water stress effects on the carbon exchange rates of three upland cotton (*Gossipium hirsutum*) cultivars in the field. Field Crop Research 21:239-255

Radoglou KM, Aphalo P, Jarvis PG (1992) Response of photosynthesis, stomatal conductance and water use efficiency to elevated CO_2 and nutrient supply in acclimated seedlings of Phaseolus vulgaris L. Annals of Botany 70:257-264

Ritchie JT, Burnett E (1971) Dryland evaporative flux in a subhumid climate. II. Plant influences. Agronomy Journal 63:56-62

Ryle GJA, Woledge J, Tewson V, Powell CE (1992) Influence of elevated CO_2 and temperature on the photosynthesis and respiration of white clover dependent on N_2 fixation. Annals of Botany 70:213-220

Sale PJM (1977) Net carbon exhchange rates of field-grown crops in relation to irradiance and dry weight accumulation. Australian Journal of Plant Physiology 4:555-569.

Sharp RE, Davies WJ (1979) Solute regulation and growth by roots and shoots of water-stressed maize plants. Planta:146:319-326

Tanner CB, Sinclair TR (1983) Efficient water use in crop production: research or re-search? In: Taylor HM, Jordan WR, Sinclair TR (eds) Limitations to efficient water use in crop production. Agronomy Society of America, Madison, Wisconsin, pp 1-27

Varlet-Grancher C, Gosse G, Chartier M, Sinoquet H, Bonhomme R, Allirand JM (1989) Mise au point: rayonnement solaire absorbé ou intercepté par un couvert végétal. Agronomie 9:419-439

Williams WA, Loomis RS, Lepley CR (1965) Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiation. Crop Science 5:211-215

Wong SC (1979) Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44:68-74

Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282:424-426