Final Project Report

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Theory and Objectives:

Water use efficiency (WUE) by plants is a key determinant of productivity and survival of plants under water limiting or drought conditions. Anticipating the likely increases in temperature and frequency of drought with the coming climate change largely effected by the rising atmospheric carbon dioxide (CO₂), quantification of the potential changes in WUE is essential for the better prediction of future plant productivity and ability of plants to serve as sinks for CO₂. WUE is known to be improved under elevated CO₂. The extent of the improvement, however, varied widely from study to study in the literature. The aim of this project was to develop a mechanistic basis for predicting WUE without the prohibitive task of studying every plant species under a range of environmental conditions. A data base was to be developed for the application of a simple and newly evolved WUE framework (Hsiao, 1993) for single leaves in relation to CO₂ levels and environmental stresses. The concept was to be scaled up to the whole plant and canopy level through experimental work, and modeling and model verification. In this approach, the task was greatly simplified by using the ratio of CO₂ concentration in the leaf intercellular space (C_i) to that in the

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bulk air (C_a) as a key parameter in the quantification of CO_2 assimilation (A) rate and transpiration rate. This ratio (C_i/C_a), designated as α , has been shown by a number of previous studies to have a tendency to stay constant or to vary with environmental or plant conditions in a relatively simple manner. Making use of the conservative behavior of α , Hsiao (1993) was able to show that quite simple equations based on fundamental principles can be derived to predict the relative change in WUE of single leaves.

Methods

Experiments were conducted in growth chambers at different controlled levels of CO_2 , and in the field where CO_2 level was ambient, but highly variable diurnally. Effect of water and high temperature stress was also evaluated in the field. A water stress treatment was included while high temperature stress was studied taking advantage of the natural diurnally and day-to-day variations in temperature. Maize, cotton and soybean were grown in controlled environment chambers at the normal, 1.5x and 2x the normal CO_2 concentrations, and their biomass and water use were measured at timed intervals, along with the measurement of air and leaf temperature. Concurrently, one plant was moved at a time to the laboratory for 6 to 8 h for the characterization of its leaf photosynthesis and stomata conductance in a steady state gas exchange apparatus, yielding curves of A vs. C_i and of photosynthesis response to environmental variables such as PAR (photosynthetically active radiation), temperature, and humidity. Maize and cotton were also grown in the field in an area large enough (4 to 5 hectares) to ensure adequate fetch for the determination of evapotranspiration and canopy photosynthesis by micrometeorological methods. One half of the field was well irrigated, and the other half was subjected to water stress. The Bowen ratio/energy balance/ CO_2 gradient technique (BREB+) was used to monitor evapotranspiration, energy budget, and CO_2 flux into the canopy of each half of the field. Associated measurements included canopy temperature, canopy light interception, leaf photosynthesis and conductance, leaf area, leaf water potential, respiration of non-leaf parts of the plant, shoot biomass, and soil water balance. For model validation and verification, additional data were collected on selected days in the field. These included data on turbulent statistics measured with sonic anemometers (including three dimensional); wind, temperature, CO_2 , and humidity profiles within and above the canopy.

Highlights of Results

Extensive data were obtained indicating that the ratio (α) of intercellular CO_2 concentration (C_i) to air CO_2 concentration (C_a) remains essentially constant over a range of air CO_2 concentrations for maize, sorghum, and cotton, regardless whether grown at 360 or 720 ppm of CO_2 , and that C_i remains essentially constant over fairly wide range of PAR for cotton and maize. Small pots caused the plants to adjust photosynthesis capacity downward under high CO_2 but did not significantly affect α . The near constancy of α justifies the use of Hsiao's (1993) approach for the estimation of relative changes in WUE under elevated CO_2 . Mean biomass WUE of cotton was increased 89%, in two growth chamber experiments by increasing CO_2 from 360 to 720 ppm. The surprise was that this increase was predicted by a equation of Hsiao to within 3%, using the air humidity and leaf temperature data. Additional experiments in growth chambers verified the results. Field experiments showed biomass WUE of maize was not significantly affected by water stress, and was relatively constant when normalized for evaporative demand. Extensive data were obtained with meteorological techniques on diurnal and seasonal trends in canopy CO_2 assimilation and evapotranspiration in the field, and on photosynthetic WUE. Detailed profiles of air CO_2 concentration, humidity, and temperature within and above the canopies were also measured. These revealed that plants experience substantial fluctuations in their CO_2 environment, which are sufficiently large to impact the rate of photosynthesis and WUE. Hsiao' simple equation was also used to predict the relative changes in 5-min mean WUE of maize in the field over diurnal cycles. The predictions turned out to be surprisingly good. The equation used was developed for gas exchange of single leaves. The reason for the successful use of the equation at the whole plant (in growth chambers) and the community canopy level (field studies) is unclear, but the results do suggest that upscaling may not be a problem in the case of crop WUE. This exciting possibility of being able to predict WUE for different and changing CO_2 and environmental conditions needs additional substantiation. A coupled stomatal control and photosynthesis model was formulated and integrated with a layered canopy higher order closure model to simulate canopy response to CO_2 concentrations environmental factors. This model has been compared with some of the more conventional models for the estimation of canopy photosynthesis and water use. The extensive field data collected on canopy photosynthesis, evapotranspiration, WUE, and profiles of CO_2 and other meteorological parameters will be used to test the models further.

Gas Exchange Characteristics

Effect of growth CO₂ level on assimilation and α . A vs. C_i curves showed that cotton leaves increased photosynthesis as C_i was increased, to and beyond 400 ppm, corresponding to C_a of about 700 ppm. Similar results were obtained with soybean. In contrast, maize leaf photosynthesis responded to increases in C_i only at low levels of C_i and was essentially saturated at 120 ppm, corresponding to a C_a of about 450 to 500 ppm. Growth in 720 ppm instead of 360 ppm of CO₂ did not change the A vs. C_i curves of maize. In contrast, for cotton the curve showed a slight reduction in A at a given C_i, indicating a reduction in photosynthetic capacity when grown at 2x CO₂. The curves for soybean also appeared to be lower for the plants grown at 2x CO₂, although the difference was too small to be certain.

More important is the ratio C_i/C_a, α . For cotton (Fig. 1) and maize (Fig. 2), the ratio was essentially constant as C_a varied over a wide range. For soybean (Fig. 3), the ratio appeared to be higher at C_a < 300 ppm, but was also essentially constant as C_a varied between 300 and 700 ppm, the range of concern regarding the future rise in atmospheric CO₂. For all three species doubling of CO₂ for growth did not change the C_i/C_a ratio significantly. As expected, the ratio was much lower for the C₄ species (maize), reflecting low C_i values, than for the C₃ species. The former fell in the 0.3 range (Fig. 2) whereas the latter fell in the 0.5 to 0.7 range (Fig. 1 and 3). Constant C_i/C_a ratios would simplify the predictions and simulations of effects of elevated CO₂ and environmental stresses on WUE.

Effects of pot size. It is known that pot experiments can be complicated by the downward regulation of photosynthesis under elevated CO₂, which has been attributed to either a deficiency of mineral nutrients or a lack of sinks for photosynthetic assimilates because the space for root growth is limited. We encountered apparent downward regulation (indicated by a lower A at a given C_i) when plants were grown in small pots (2.4 liters), especially at 2x CO₂. When large pots (7.4 or 7.7 liters) were used with good fertilization, A reached the same high value under high CO₂ concentrations regardless of the growth CO₂ level, be it 360 ppm or 720 ppm, indicating the absence of downward regulation caused by high CO₂. Interestingly, although apparently downward regulated plants can show a substantial reduction in the rate of maximal photosynthesis, their C_i/C_a

ratio was similar to those of normal plants. This is additional evidence for the conservative nature of C_i/C_a .

It is not known whether the apparent downward regulation of photosynthesis is the result of nutrient deficiency or restricted rooting volume. That needs to be resolved in future studies.

Effects of CO₂ on conductance for water vapor. For all three species, total conductance for water vapor (g_w), which was mostly determined by leaf conductance because boundary layer conductance was very high in our stirred gas exchange chamber, declined with increases in C_a as expected. The decline for cotton growing in pots of adequate size was not marked whereas the decline in maize was steeper (Fig. 4). The decline in soybean (Fig. 5) appeared to be between that for cotton and maize. Doubling of the CO₂ level for growing the plants did not have any substantial effect on stomatal response to CO₂ as indicated by the conductance data (Fig. 4). On the other hand, plants growing in small pots usually had lower conductances (Fig 4 and 5), which manifested as lower assimilation rates as already mentioned. The lower g_w for the plants in small pots apparently permitted the maintenance of similar C_i/C_a ratio regardless of pot size.

Effects of PAR level on C_i of plants grown at two levels of CO₂. Assimilation was measured over a wide range of PAR and C_i calculated. For cotton, C_i remained constant over the PAR range of 500 to 2,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$, but rose somewhat as PAR decreased below 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 6). For maize, C_i remained fairly constant over a PAR range of 600 to 2,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and rose substantially as PAR decreased below 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 7). During those measurements C_a remained constant, at 360 ppm. Hence, it is clear that C_i/C_a ratio remained constant within the range of high to moderate PAR, but rose as PAR was reduced to low levels common for early mornings and very late afternoons. More importantly, doubling the growth CO₂ level had no effect on the response of C_i (hence C_i/C_a) to variations in PAR (Fig. 6 and 7). Effects of other variables, particularly temperature and leaf age (after reaching full size but before senescence) were also negligible or very small (data not shown).

Effects of Elevated CO₂ on Growth and Biomass WUE

Doubling of CO₂ in the growth chamber increased the biomass and improved the efficiency of water use of cotton, soybean, bean, and maize. The shoot dry weight of the

plant at different times as determined by sequential harvests was plotted against the cumulative amount of water used as determined by weighing the pots at each harvest. Biomass WUE (biomass produced/cumulative transpiration, abbreviated as WUE_{mt}) was calculated as the slope of the plots, which were linear. Examples of the data are given as Fig. 8 and 9, for cotton. The increase in WUE_{mt} was 84% and 93%, respectively. With soybean, another C_3 species, similar improvement in WUE_{mt} was observed. As expected, the improvement in WUE_{mt} for maize, a C_4 plant, was much less marked, only about 25%. Elevated CO_2 is known to increase the total leaf area of C_3 plants. Some studies attributed this to increases in the number of leaves but no real increase in leaf size. We found that size of the leaves on each node of cotton was increased substantially under $2x$ CO_2 (Fig. 10). In addition, after 30 to 40 d of growth, there was one more leaf on the main stem under $2x$ CO_2 , as well as more branching. Size of maize leaves was also enhanced under $2x$ CO_2 and the number of leaves at the sampling time increased by one (Fig. 10), which indicates the plant under high CO_2 was slightly more advanced in ontogeny.

Cotton plants spaced apart were compared with those spaced closely with their canopies overlapping. The response in biomass production to a doubling of CO_2 was found to be reduced substantially by the close spacing. This finding is in accordance with a theoretical prediction (Hsiao, 1993) based the first order kinetics of radiation interception by growing but incomplete canopies, and points to an important but usually unappreciated factor causing variations in the biomass response to CO_2 .

Testing of Theoretical WUE Framework with Chamber Grown Plants

The constancy of C_i/C_a ratio under most conditions regardless of the level of CO_2 under which the plants are grown is very encouraging. It should simplify the task of using the theoretical framework of Hsiao (1993) to predict changes in WUE brought about by global change, whether due to increases in atmospheric CO_2 or to environmental stresses. At the risk of pointing out the obvious, we calculated photosynthetic WUE using Eq. 9 of Hsiao for a cotton leaf over the range of C_a used to obtain the A vs. C_i curve for that leaf and plotted the results against photosynthetic WUE calculated from the measured assimilation and transpiration rate (Fig. 11). The comparison shows near coincidence (1:1 line) between the predicted and observed WUE, with the deviation of individual data points accounted for by experimental inaccuracies and slight oscillations in the values of C_i/C_a . The outcome is obvious because the calculation of the gas exchange data involves exactly the same assumptions and equations as those used to derive Eq. 9 of Hsiao (1993). That

emphasizes the fundamental nature of the equation, which may be taken as a first principle of water use efficiency as long as it is applied to individual leaves. Complications may arise, however, when scaling up to the whole plant and to canopies made up of many plants.

To test how far the simplicity of the framework equation may go, we applied it to the whole plant level by evaluated the experimental biomass WUE data obtained on cotton (Fig. 8 and 9). Leaf temperature was measured with fine wire thermocouples, and along with the air humidity record, was used to calculate the parameter ΔW (difference in water vapor concentration between the leaf interior and the bulk air) required by the framework. From the ratio of air CO_2 concentration and of ΔW for the two different CO_2 environments, the increase in photosynthetic WUE brought about by growing the plants in 720 ppm compared to 360 ppm CO_2 was predicted to be 92%. This corresponds to the measured mean increase in WUE_{mt} of 89% (84% for Fig. 8, and 93% for Fig. 9). The agreement is remarkably good when considering random errors, the complications of scaling up from single leaves to the whole plant, and night time transpiration and respiration. It is possible that many of the complicating factors had opposite effects and hence canceled out each other over time. Two other experiments with cotton gave equally close predictions, within 5% of the measured change in WUE. In addition, we conducted more complicated tests of the framework by growing plants under one level of CO_2 and humidity for 2 weeks or longer and then changed the condition to a different CO_2 and humidity. There the framework also predicted well the change in WUE_{mt} , usually within 10% of the measured values. These exciting results are being written up for publication.

Field Experiments on Various Aspects of WUE

Water use efficiency for biomass production. Two experiments were conducted on maize in the field, one in 1994 and one in 1995. One half of a large field (about 5 hectares) was well watered and served as the control and the other half was water stressed by withholding irrigation at different times after canopy establishment and had to rely on only the water stored in the soil. In 1994 water stress developed late in the season and only became substantial near the time of harvest. In 1995 water stress became relatively severe in midseason and was relieved by irrigation, and became severe again near the time of harvest. Associated with the midseason water stress was some nitrogen deficiency, due to inability of the plants to take up sufficient nitrogen from the dried out top soil where nitrogen fertilizer was applied. The water stress late in 1995 was severe enough to accelerate senescence of the leaves, reducing leaf area duration and grain yield. Biomass

consumptive water use efficiency (WUE_{me}), the ratio of dry matter produced to the amount of water evapotranspired, was determined by soil water balance and sequential harvests. When normalized for variations in the evaporative demand due to weather, WUE_{me} , determined from the slope of plots of dry matter vs. water evapotranspired (Fig. 12), was similar for the dry treatment and the control, with a tendency of the dry treatments to be lower. This is not surprising as it is consistent with the WUE framework for single leaves if C_i/C_a is not altered significantly by water stress (Hsiao, 1993).

Ear respiration. In the same experiments, respiration of maize ears (the fruiting body) was measured to determine their negative contribution to the carbon balance (and hence WUE) of the crop. Respiration rate per gram of ear dry weight was very high at the time of ear emergence, due to the dominance of fast growing tissue with high growth respiration, but declined rapidly with ear age (Fig. 13) as the proportion of growing tissue declined and mature tissue increased. The rates for the dry treatment tended to be lower than the control, probably due to slower growth. On a per ear basis, respiration rate increased with ear age due to the rapid gain in ear mass. Respiration constituted a substantial carbon drain during the grain filling. When expressed on a basis of land area (Fig. 13), respiration was equivalent to about 20% of midday net canopy photosynthesis at mid grain filling stage, and to about 30% to 40% of midday net canopy photosynthesis at late grain filling stage.

Canopy photosynthesis and evapotranspiration. During the two field seasons, daily time course of maize canopy photosynthesis and evapotranspiration were measured with the Bowen ratio/energy balance technique. An example of the data (for 5 min intervals) for the dry treatment and the control on the same date is given in Fig. 14, showing the daily pattern of ET (in terms of negative latent heat flux λE), CO_2 assimilation, PAR, air and canopy temperature, and the ratio of A to ET (, canopy photosynthetic WUE). During that late growth stage (Sept. 12, 1995), leaf area had declined substantially in the dry treatment compared to the control and intercepted less PAR. Dry treatment also had a substantially lower leaf water potential and less nitrogen in the leaves. As the consequence, ET was less for the dry treatment compared to the control and so was canopy photosynthesis. The A/ET ratio was generally also lower for the dry treatment, indicating a lower WUE. WUE was the highest in early morning because of low temperature and high relative humidity, and lowest in the afternoon because of high temperature and low relative humidity. More extensive data of similar nature were obtained on maize in 1996, and on cotton in 1997. Because of the extensiveness of the data sets, analysis of the results is still ongoing.

Micrometeorological data on profiles of temperature, CO₂, and water vapor.. To define better the conditions experienced by the crop canopies and for the validation of the higher order closure models, we have obtained 30 min mean profiles of wind, temperature, CO₂ concentration, and humidity above and within maize and cotton canopies on a number of selected days. Examples of the data for maize are given in Fig. 15. The results show that on days of strong wind, CO₂ concentrations within and above the canopy was uniform and close to ambient. In contrast, CO₂ concentrations were highly variable around the canopy on calm days, as high as >420 ppm in the morning, dropping to lows of 320 ppm early in the afternoon. The impact of these variation on canopy photosynthesis and WUE have not been taken into account in most of the current studies.

Testing of Theoretical WUE Framework in Crop Fields

The natural variation in CO₂ concentration and humidity with time in the field on calm days made it possible to test the WUE framework of Hsiao (1993). Canopy photosynthetic WUE was calculated at 5 min intervals as the ratio of measured assimilation and evapotranspiration (A/E, see Fig. 14). Taking noon time WUE as the reference point, WUE for the other times of the day was predicted using Hsiao's framework, utilizing the measured values of air humidity and CO₂ concentration, and canopy temperature. In the limited analyses carried out so far, the predicted diurnal trend in WUE matched well the measured trend in WUE. This exciting result is surprising and unexpected, since strictly speaking, the framework was applicable only to single leaves and scaling up should introduce considerable complexity, especially in the real-world situation of the field in comparison to the controlled environment chambers. The bulk of the remaining data collected over the last two seasons are still been analyzed, to verify this potentially highly important finding.

Model Development

Early in this project, in anticipation of the need to scale up mechanistically from the single leaf to the canopy level and beyond, we worked on developing and improving models for canopy function. Model development proceeded among several avenues. The first was the development of a coupled stomatal control and photosynthesis model. The second was the preliminary investigation of the implications of our hypothesis that the ratio C_i/C_a is constant on physiological responses. Lastly, the third was the modification of an existing higher-order closure model to describe the canopy-atmosphere exchange process.

The empirical stomatal control theory of Ball-Berry (Collatz et al., 1991) was coupled analytically and numerically with the von Caemmerer-Farquhar photosynthesis

model. The coupling led to a cubic solution, which had to be iterated with a quartic (4th-order polynomial) energy budget equation, to arrive at a simultaneous solution for leaf conductance, photosynthesis, leaf temperature, and leaf energy budget. This model was then used to investigate transient features of plant response to large, repeated turbulent features called 'coherent structures'. An interesting result of this simulation was that C_i was predicted to respond quickly to atmospheric turbulence.

The hypothesis that a constant C_i/C_a ratio is exhibited by plants has certain implications when combined with equations describing stomatal conductance and photosynthesis. When the assumption of a constant ratio is incorporated and combined with the von Caemmerer-Farquhar photosynthetic equation, a new equation results which shows that stomatal conductance decreases with increases in ambient CO_2 concentration, as is observed (e.g. Fig. 4). If the Ball-Berry stomatal conductance equation is used in combination with the von Caemmerer-Farquhar photosynthesis equation, C_i/C_a ratio is not strictly constant, but can be shown to vary only slightly under certain environmental conditions. These results provide interesting insights and their ramification is being explored.

A layered canopy model using higher-order closure (Paw U and Meyers, 1989) was further developed for describing the coupled energy budget and photosynthetic flux exchange between the canopy and the atmosphere. This model has 10 layers of plant canopy above one layer of soil, with another 30 layers of atmosphere above the canopy. Each canopy layer consists of 10 leaf classes, 9 representing sunlit leaves of different angles, and one shaded leaf class. For each leaf class, a full energy budget is solved, and the CO_2 flux is calculated. Inter layer exchange is described by higher-order closure principles, based on the equations of fluid motion and principles of mass and energy conservation. To provide the radiation field needed for energy budget calculations, the two-stream model of Norman (1979) was employed. Plant physiology is included by one of the two user-selected methods: the combined Ball-Berry stomatal conductance and von Caemmerer-Farquhar photosynthesis model, or a multiplicative model including the effects of leaf temperature, vapor pressure deficit, and PAR.

The higher-order closure model was run for differing values of air temperature and CO_2 concentration, to investigate how the canopy may respond to climate change in terms of CO_2 flux, canopy photosynthetic WUE (A/E), and canopy resistances. Not surprisingly, the mean CO_2 concentration is strongly dependent on physiology modeling. As expected, the canopy resistance rises with CO_2 concentration for the Ball-Berry/von Caemmerer-Farquhar model, but is unrealistically constant in the multiplicative model.

This causes the actual CO₂ fluxes to increase less for the former than for the latter model. Therefore, the increase in A/E is greater for the multiplicative model than for the Ball and Berry model. The experimental data collected are still to be used to test the different models.

The overall results (Paw U et al., 1996) show that carbon assimilation rates for different CO₂ levels are very different, depending on the difference in canopy-atmosphere model and in physiology model. Thus, it is critical that these models be tested against the experimental data already collected in the field.

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Fig. 1. Leaf photosynthesis rate (A) vs. internal CO_2 concentration (C_i), C_i vs. C_a , and C_i/C_a ratio vs. C_a , for recently matured and exposed cotton leaves grown at either $360 \mu\text{mol mol}^{-1}$ (ppm,v/v) or $720 \mu\text{mol mol}^{-1} \text{CO}_2$. Measurements were made in a steady state gas exchange chamber at 28°C and 1.5 to 1.8 kPa vapor pressure difference between leaf interior and the air (DW) under $1,400 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR. Variation in C_i was achieved by varying C_a . Each line represents one leaf of a different plant.

Fig. 2. Leaf photosynthesis rate (A) vs. internal CO_2 concentration (C_i), C_i vs. C_a , and C_i/C_a ratio vs. C_a , for recently matured and exposed maize leaves grown at either $360 \mu\text{mol mol}^{-1}$ (ppm, v/v) or $720 \mu\text{mol mol}^{-1} \text{CO}_2$. Measurements methods and conditions were as given under Fig. 1. Each line represents one leaf of a different plant.

Fig. 3. Leaf photosynthesis rate (A) vs. internal CO_2 concentration (C_i), C_i vs. C_a (air CO_2 concentration), and C_i/C_a ratio vs. C_a , for recently matured and exposed soybean leaves grown at either $360 \mu\text{mol mol}^{-1}$ (ppm, v/v) or $720 \mu\text{mol mol}^{-1} \text{CO}_2$. Measurements methods and conditions were as given under Fig. 1. Each line represents one leaf of a different plant.

Fig. 4. Total conductance for water vapor (g_w) in relation to air CO_2 concentration (C_a) for leaves of cotton and corn grown in either small or big pots at either 360 or 720 $\mu\text{mol mol}^{-1}$ (ppm, v/v) of CO_2 . Regressions were based on data from at least 4 leaves, each from a different plant. Boundary layer conductance was very large and constant so changes in g_w was the result of changes in leaf epidermal (mostly stomatal) conductance.

Fig. 5. Total conductance for water vapor (g_w) in relation to air CO_2 concentration (C_a) for leaves of soybean grown in either small or big pots at either 360 or $720 \mu\text{mol mol}^{-1}$ (ppm, v/v) of CO_2 .

Fig. 6. Effects of incident PAR on g_w , A , and C_i of leaves of cotton grown at either 360 or 720 $\mu\text{mol mol}^{-1}$ (ppm, v/v) of CO_2 . Each line represents one leaf of a different plant.

Fig. 7. Effects of incident PAR on g_w , A , and C_i of leaves of maize grown at either 360 or 720 $\mu\text{mol mol}^{-1}$ (ppm, v/v) of CO_2 . Each line represents one leaf of a different plant.

Fig. 8. Shoot dry matter of cotton planted on 8/27/1995 and growing in growth chamber at either 360 or 720 ppm CO₂ as a function of cumulative transpiration and a function of time. Dry matter was obtained by sequential harvest of 4 plants each. Transpiration was determined by adding known amounts of irrigation and weighing soil water content. Temperature was 27/20°C and relative humidity was 40/80%, for day (14h) and night periods. Transition between day and night was gradual and took 1 h each. PAR was 770 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and was increased and reduced in several steps during the transition. Biomass water use efficiency (WUE_{mt}), calculated as the slope (top figure) by linear regression ($r^2=0.999$), was 3.45 and 6.35 g kg⁻¹, for the 360 and 720 ppm plants.

Fig. 9. Shoot dry matter of cotton planted on 12/14/1995 and growing in growth chamber at either 360 ppm or 720 ppm CO₂ as a function of cumulative transpiration and as a function of time. Same conditions and methods as for Fig. 8, except that relative humidity was 45% during the day period. WUE_{mt} was calculated ($r^2=0.99$) to be 3.76 and 7.25 g kg⁻¹, respectively, for the 360 ppm and 720 ppm plants.

Fig. 10. Areas of individual leaves of cotton and maize grown in growth chamber at either 360 ppm or 720 ppm CO₂. Leaf number was in the order of emergence. Conditions were the same as Fig. 8

Fig. 11. Comparison of predicted relative change with the measured relative change in leaf photosynthetic WUE of a cotton leaf effected by changes in Ca. Relative change is given as the ratio of WUE under new Ca (WUE_n) to WUE under the original Ca (WUE_o). Prediction was made using Eq. 9 of Hsiao (1993) with DW calculated from the humidity and leaf temperature data for the determination of the A vs. C_i curve of the leaf in a gas exchange chamber. Measured WUE was calculated as the ratio of measured rate of photosynthesis to transpiration. Original Ca was $360 \mu\text{mol mol}^{-1}$.

Fig. 12. Shoot dry matter of maize produced in the field obtained by sequential harvests vs. normalized cumulative evapotranspiration as measured by soil water balance. Soil water contents at different depths were measured with a neutron probe and ET was normalized for the daily reference ET measured by a weather station nearby. Lines are calculated by linear regression ($r^2 > 0.95$) and their slopes indicate biomass water use efficiency (WUE_{me}).

Fig.13. Respiration rate of intact maize ears on plants of the dry (water stressed) and control treatment in the 1995 field experiment as a function of time, on a basis of per unit of ear dry weight (top figure) or per unit of land area (bottom figure). Respiration was measured with a special mylar chamber sealed around the ear and connected to a LiCor 6200 photosynthesis apparatus. Each measurement lasted about 1 min and was at a temperature within 2-3°C of ambient.

Fig. 14. Daily pattern of evapotranspiration (expressed in energy unit as negative λE), components of energy balance (sensible heat H , and net radiation R_n), canopy photosynthesis (A), and canopy photosynthetic water use efficiency ($WUE=A/E$) of maize of the dry treatment and control (wet) in adjacent fields on 9/12/1995. Also shown are incident PAR, air temperature, and canopy temperature measured with an infrared thermometer. Data were obtained by the Bowen ratio/energy balance/ CO_2 gradient technique. Midday leaf water potential was -1.63 MPa and -1.00 MPa, LAI was 2.2 and 4.8 and leaf nitrogen content was 1.6% and 2.2%, respectively, for the dry treatment and control.

9/12/1995

Figure 15. Samples of CO₂ diurnal variations and profiles on a windy day (9/18/1996) and a calm day (9/19/1996) for a well irrigated maize field in Davis, California. For clarity, 5 min mean CO₂ data are shown only for three heights in (a, c), and 30 min mean of profiles in (b, d). Wind speed data (i.e. U), which are the six points moving average on 5 min mean raw data, were obtained with low inertia cup anemometer at the height of 6 m. Dashed lines in (b, d) represent the canopy height. Gaps in data occurred as the result of IRGA calibration.