Water-Use Efficiency in Crop Production

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Plant biomass accumulation, and consequently yield, was shown to be inextricably linked to transpiration. The ratio of plant productivity to water loss, water-use efficiency, was very conservative. Only a few variables are available for manipulating water-use efficiency, and these have already been exploited to a large degree. (Accepted for publication 10 June 1983)

A prime concern in cultivating crops has always been water availability. The earliest crops may have been seeded about 18,000 years ago on the high dunes area of the Nile floodplain immediately after the flood waters receded (Wendorf et al. 1982). This practice assured adequate moisture for plants to grow and produce grain. Plant water-use efficiency was a topic for early scientific study (Briggs and Shantz 1913, Lawes 1850, Woodward 1699). Knowledge of the factors influencing crop water-use efficiency and a hope to improve the efficiency has continued to be an objective in many modern investigations. Wittwer (1975) identified water as the second-most limiting factor, behind land area, to increasing food production. He argued that a high research priority should be an improvement in the efficiency of water use by plants.

Considerable research has been done on crop water-use efficiency during the past century, but much work resulted in empirical conclusions that seemed confusing or contradictory. However, recent developments in the understanding of the physical and physiological processes regulating crop growth and water loss allow crop water-use efficiency to be analyzed in quantitative, mechanistic terms.

One of the greatest confusions appears to remain in the use of the phrase *water-use efficiency*. It has been used to describe a range of observations covering a diversity of time and process scales.

Water-use efficiency has been used interchangeably to refer to observations ranging from gas exchange by individual leaves for a few minutes, to grain yield response to irrigation treatments through an entire season. Clear distinctions must be made between these observations, so the significant variables that are common and different among experiments can be resolved.

In this paper we delineate the mechanisms that influence water-use efficiency for each scale of observation. First, we examine the processes regulating leaf gas exchange. Additional processes and relations are assembled to analyze water-use efficiency in crop biomass and grain production, then in evapotranspirational water-use efficiency expressed on the basis of total water input to the system. This analysis clarifies the important variables and the opportunities available for further improvements in water-use efficiencies.

Water-use efficiency (WUE) is defined as a ratio of biomass accumulation, expressed as carbon dioxide assimilation (A), total crop biomass (B), or crop grain yield (G), to water consumed, expressed as transpiration (T), evapotranspiration (ET), or total water input to the system (I). The time-scale for defining water-use efficiency can be instantaneous (i), daily (d), or seasonal (s). Water-use efficiency is written symbolically as a function of these three variables. For example, we use WUE(A, T, i) to refer to water-use efficiency expressed as the ratio of carbon dioxide assimilation to transpiration for an instantaneous observation.

LEAF TRANSPIRATIONAL WATER-USE EFFICIENCY

The major function of leaves is to transform the energy of sunlight to chemical energy via the fixation of carbon dioxide (CO_2). Stomata on leaf epiderma are the valves that allow CO_2 to enter the leaf and to be available for photosynthesis. However, having stomata open for CO_2 entry simultaneously provides a pathway for water vapor diffusion out of the leaf to the atmosphere. Consequently, in the process of CO_2 fixation there is potential for water to evaporate from leaves. The rate of water loss, or transpiration rate, is proportional to the vapor pressure difference between the bulk atmosphere and the inside of the leaf, which is essentially the saturated vapor pressure at the leaf temperature.

The ratio of CO_2 assimilation (A) and transpiration (T), or leaf transpirational water-use efficiency, $WUE(A, T, i)_L$, was initially examined by Bierhuizen and Slatyer (1965). They considered the fact that each process was driven by a concentration gradient and modulated by the resistances to diffusion resulting from stomata (r_s), leaf aerodynamic boundary layer (r_a), and leaf mesophyll resistance. An expression equivalent to the one they developed is:

$$WUE(A, T, i)_L = \frac{M_C}{M_W} \frac{(P_a - P_i)}{(e^*_L - e)} \frac{(r_a + r_s)}{(r'_a + r'_s)} \quad (1)$$

where M_C = mole weight of CO_2 (44 g), M_W = mole weight of water (18 g), P_a = partial pressure of CO_2 in the atmosphere, P_i = partial pressure of CO_2 inside the leaf air spaces, e^*_L = saturation vapor pressure at leaf temperature, and e = vapor pressure of the atmosphere. The prime notations on the resistance terms in the denominator signify that these resistances are for CO_2 rather than water vapor. The differences between these resistances are well defined by gas diffusion laws, and the total of the resistances for CO_2 are approximately 50% greater than the total for water vapor. Equation (1) can be simplified by evaluating M_C and M_W, and by expressing the resistances to CO_2 in terms of water vapor resistances, and then cancelling the resistance terms. That is,

$$WUE(A, T, i)_L = 1.6 \frac{P_a - P_i}{e^*_L - e} \quad (2)$$

Recently, evidence has been accumulating that suggests a further simplification is possible in expressing the CO_2 concentration difference. For a range of growing conditions and environments

the ratio of P_i/P_a is approximately constant (Goudriaan and van Laar 1978, Wong et al. 1979). The value of the ratio is essentially constant across species fixing CO_2 directly by the C_3 pathway and constant with a differing value for those species initially fixing CO_2 through the C_4 pathway. For mathematical convenience we define this apparent constant as $c = (1-P_i/P_a)$. The value of c for C_3 crops is approximately 0.3 and for C_4 crops approximately 0.7. Equation (2) becomes

$$WUE(A, T, i)_L = 1.6c \frac{P_a}{(e^*_L - e)} \quad (3)$$

The data of Bierhuizen and Slatyer (1965) confirmed the constant relationships between $WUE(A, T, i)_L$ and $(e^*_L - e)$ as predicted by equation (3).

Equation 3 shows that there are very limited options for improving $WUE(A, T, i)_L$. Certainly an increase in the value of c would lead directly to an improvement in $WUE(A, T, i)_L$. Cultivar selections that result in an increased c would be an approach for increasing water-use efficiency. However, there may be some important restrictions on this approach. It seems unlikely that the value of c can be improved a great deal in C_4 species, since it is already high. The opportunities for increasing c in C_3 species are seemingly greater. Two approaches to increasing c would be to improve carboxylation and to alter stomatal resistance. While some improvement in carboxylation may be possible, major adjustments in leaf biochemistry and morphology must be accomplished to allow C_3 species to become as efficient as C_4 species.

Proposed improvements in stomatal resistance may necessitate a trade-off between water conservation and high CO_2 assimilation. That is to lower P_i, stomatal resistance may have to be increased and consequently the overall CO_2 assimilation rate reduced.

The best opportunity to increase $WUE(A, T, i)_L$ is for leaves to exchange gas only when $(e^*_L - e)$ is small. Some species native to arid and semiarid environments employ this strategy by closing their stomata at midday when $(e^*_L - e)$ is greatest (Fischer and Turner 1978). This reduces the gas exchange during that period and minimizes the effect of the high $(e^*_L - e)$ on daily water-use efficiency. In fact, Cowan and Farquhar (1977) argued from control theory that the optimum stomatal behavior would be one that allowed $\delta A/\delta T$ to remain con-

stant with changing environment. Some plants seem to use this strategy (Farquhar et al. 1980). The penalty, of course, for midday stomatal closure is a reduction in the opportunity for CO_2 assimilation.

Another approach to increasing WUE (A, T, i) by reducing $(e^*_L - e)$ is to simply grow crops in more humid climates. Since political and social constraints limit geographical solutions, a temporal solution may be more practical. Water-use efficiency can be increased by growing crops during times of the year when $(e^*_L - e)$ is lowest. Such a solution generally means that a greater fraction of the cropping season would be shifted to cooler periods of the year. For cereals, Fischer (1981) has argued that cultivars and management practices allowing for more of the growth cycle to take place during early spring would be a good approach to increasing water-use efficiency. The difficulties are that crop growth is usually slow in cool temperatures, and the plants may need to develop defense mechanisms, which may be very costly in terms of energy requirement, to survive cool or even freezing temperatures.

CROP TRANSPIRATION WATER-USE EFFICIENCY

The extrapolation of knowledge about leaf gas exchange to the performance of a leaf canopy is difficult. For example, Bierhuizen and Slatyer (1965) assumed that WUE(B, T, s) must also depend greatly on $(e^*_L - e)$, as found for individual leaves. In an evaluation of the early water requirement data Bierhuizen and Slatyer determined empirically the coefficient relating the two variables. Previously, deWit (1958) had done a similar empirical analysis to show very strong linear relations between WUE(B, T, s) and pan evaporation.

Recently Tanner and Sinclair (1983) derived an expression explicitly identifying the variables defining water-use efficiency on a daily basis for an entire crop canopy, WUE(B, T, d). They employed a number of simplifying assumptions including a leaf area index greater than 3, a separation of leaves into only two groups of irradiance exposure, and shaded leaf temperatures equal to air temperature. Other considerations were the maintenance respiration rate and the conversion coefficient of hexose to plant biomass (b). Their solution for daily, crop transpirational water-use efficiency in producing biomass was

$$WUE(B, T, d) = \frac{k_d}{(e^*_a - e)} \quad (4)$$

where e^*_a = saturation vapor pressure at air temperature and the term $\overline{(e^*_a - e)}$ is a daily mean, weighted only for the periods of transpiration. The constant, k_d, was defined as

$$k_d = 1.6 \, abc \, P_a \frac{L_D}{L_T} \quad (5)$$

where a = molecular weight ratio of (CH_2O) to CO_2 (0.68), L_D = leaf area index exposed to direct beam radiation ($\sim$1.4), and L_T = leaf area index equivalent for area of "fully transpiring leaves." Numerically L_T is approximately 2.2 in many situations, but will vary with more extreme environmental conditions and can be explicitly evaluated in accordance with the derivation of Tanner and Sinclair (1983).

The value of k_d is essentially constant except for species differences in c and b. The difference in c between C_3 and C_4 species was discussed in the previous section. The value of b depends on the fraction of carbohydrates, protein, and lipids in the plant biomass produced. Evaluating equation (5) for k_d of soybean, wheat, and maize, this constant is predicted to be 4×10^3 Pa, 5×10^3 Pa, and 12×10^3 Pa, respectively. Tanner and Sinclair (1983) found good agreement between theoretical estimates of k_d and those obtained from analysis of published data for soybean, alfalfa, potato, sorghum, and maize.

Tanner and Sinclair (1983) obtained an expression for seasonal water-use efficiency by integrating equation (4).

$$WUE(B, T, s) = \int k_d T/\overline{(e^*_a - e)}/\int T \quad (6)$$

It was necessary to keep T in the numerator of the integral because of the correlation between daily T and $\overline{(e^*_a - e)}$.

Equations (4) and (6) are completely consistent with the monumental work and original conclusion of Briggs and Shantz (1917) that water-use efficiency is inversely proportional to the evaporation rate from a free water surface. Evaporation rate would, of course, be related to $\overline{(e^*_a - e)}$. Furthermore, equations (4) and (6) offer little hope for increasing crop water-use efficiency beyond that discussed for individual leaves.

Many studies of water-use efficiency focus only on the production of marketable grain yield. Equation (6) can be extended to obtain a water-use efficiency

based on marketable crop yield, by multiplying the constant, k_d, by the ratio of marketable grain yield to total crop biomass. This ratio is called harvest index (H) and has been found to be relatively stable for a particular cultivar over a fairly wide range of conditions (Donald and Hamblin 1976).

$$WUE(G, T, s) = H \int k_d \; T/\overline{(e^*_a - e)}/\int T \tag{7}$$

The inclusion of harvest index in the expression of water-use efficiency introduces a very important variable for characterizing crop productivity. Evans (1980) suggested that one of the main variables for yield increases seen to date has been increases in harvest index. Consequently, parallel increases in water-use efficiency would be achieved when expressed on a marketable yield basis. Evans (1980) further suggested that additional large increases in harvest indices are unlikely. Therefore, further increases in water-use efficiency based on marketable yield are not likely from increases in the harvest index.

An important exception to the potential contribution of increased harvest index to improved water-use efficiency is for water-limited environments. Passioura (1977) and Fischer (1979) have argued that obtaining high harvest indexes under water-limited conditions is especially important in obtaining high water-use efficiencies. They proposed strategies for conserving water during vegetative growth so that there is an adequate water supply for reproductive growth. As discussed previously, Fischer (1979) proposed that the vegetative period of growth for cereals be shifted to cooler parts of the season. The value of $(e^*_a - e)$ would be lower during this period, allowing more water to be conserved for reproductive growth. Passioura (1977) proposed that cereals for water-limited environments be developed with roots with restricted water uptake rates. Again, such an alteration would, in principle, conserve water during vegetative growth leaving more soil water for extraction during grain development. The key aspect of both strategies is that sustained reproductive growth is essential for a high harvest index.

CROP EVAPOTRANSPIRATION WATER-USE EFFICIENCY

In the previous section water-use efficiency was expressed in terms of transpi-

ration. However, crop transpiration is difficult to determine accurately under field conditions, and much research has not attempted to discriminate between water loss by transpiration and soil evaporation (E). Water-use efficiency is thus frequently expressed on the basis of evapotranspiration (ET), which combines these two processes of water loss.

$$ET = T + E \tag{8}$$

The expression of water-use efficiency based on evapotranspiration is curious, because it includes a term to which plant growth is closely linked, T, and a term which has no direct bearing on plant growth, E. Consequently E could vary among treatments independently of a stability in plant productivity and transpirational water-use efficiency, yet evapotranspiration water-use would be quite variable. Nevertheless, equation (7) can be easily modified to obtain an expression for evapotranspirational water-use efficiency,

$$WUE(G, ET, s) =$$

$$H[\int k_d \; ET/\overline{(e^*_a - e)} - \int k_d E/\overline{(e^*_a - e)}] \int ET \tag{9}$$

Equation (9) is comprehended more readily by assuming a season of reasonably constant conditions. Then the integrals in equation (9) may be eliminated,

$$WUE(G, ET, s) =$$

$$(1 - E/ET) \; H \; k_d/\overline{(e^*_a - e)} \tag{10}$$

The importance of soil evaporation in determining evapotranspirational water-use efficiency is clearly illustrated in equation (10). The fraction of the total ET committed to E influences the magnitude of WUE(G, ET, s). A large fraction of soil evaporation results in low WUE (G, ET, s). As the relative size of E is reduced, the value of WUE(G, ET, s) asymptotically approaches WUE(G, T, s). Therefore, the fraction of soil evaporation determines the proximity to which WUE(G, ET, s) actually achieves the limit defined by WUE(G, T, s).

In fact, for modern agriculture, most management practices tend to minimize the ratio E/ET. For a fully developed leaf canopy (leaf area index greater than 4), E/ET is generally in the range of 0.15 to 0.25. However, possibilities may exist for decreasing seasonal E/ET by reducing E prior to the development of a full canopy. Rapid growth of leaves early in the season would reduce the amount of time the soil is exposed to high levels of

solar radiation and would thereby minimize E.

Equations (9) and (10) are consistent with much data obtained on crop water-use efficiency. Graphs of experimental data commonly show a linear relation between crop yield and total evapotranspiration. Recently such data have been presented for sorghum (Faci and Fereres 1980, Garrity et al. 1982b), soybeans (Lawn 1982), sunflower (Stegman and Lemert 1981), cowpea (Turk and Hall 1980), and maize (Musick and Dusek 1980, Stegman 1982). Hanks (1983) has, in fact, used the stability of the relationship between yield and ET to construct yield models. The significance of these experimental observations is best visualized by assuming constant conditions and rearranging equation (10). That is,

$$G = (ET - E) \; H \; k_d/\overline{(e^*_a - e)} \tag{11}$$

Therefore, the slopes of the graphs of crop yield plotted against ET are transpirational water-use efficiency, WUE (G,T,s), and the intercept on the evapotranspiration axis is soil evaporation, E. It is important to note that deviations from linearity are introduced into this graphical analysis when the assumptions of constant $\overline{(e^*_a - e)}$ and E among treatments are violated. Nevertheless, a remarkable consistency exists between the experimental observations and predicted responses in water-use efficiency.

INPUT WATER-USE EFFICIENCY

One additional expression of water-use efficiency is based on the total water input. This expression includes consideration of water losses due to surface runoff and deep percolation. An important, special case is the efficiency for water input from irrigation. In the case of irrigation, losses between the water source and the field might also be considered.

An equation for defining input water-use efficiency could be developed using arguments similar to those presented in the previous section dealing with soil evaporation. Each of the inputs and losses of water would be included in the equation. By accounting for the inputs and these additional losses and assuming reasonably constant conditions, an expression similar to equation (11) could be derived. Consequently, a plot of crop yield versus total water input would also generally produce a linear relationship with the slope equal to WUE(G,T,s) and the intercept on the abscisa equal to the total nontranspired water loss. Furthermore, under many circumstances a plot

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using only a portion of the input water, that is, irrigation water, is likely to produce a linearity for moderate irrigation levels. Such linear relationships between crop yield and irrigation amounts have been observed in sorghum (Garrity et al. 1982a), and in soybeans, peanuts, and maize (Hammond et al. 1981). Again, deviations from a linear graph are to be expected if the assumptions of equal $(e^*_a - e)$ and equal amounts of nontranspired water loss among treatments are violated.

One approach to increasing the water-use efficiency of the total available water is the development of crops with better root systems. Greater rooting density and deeper rooting depths would increase the amount of soil water available for extraction (Taylor 1983). Water reserves previously unavailable to the transpiring plant could be made available with an improved rooting system. Both the total amount of available water and potential storage capacity of the soil would be improved with the extraction of soil water from deeper depths.

However, a deeper and more extensive rooting system may have drawbacks. A greater root biomass would almost surely result in lowered harvest index. Carbohydrates would be diverted for the construction and maintenance of a larger root mass. In a prolonged drought, rapid and more efficient use of stored soil water may be deleterious. A less effective, slow-growing root system may leave some water reserves that would be partially available for surviving a drought.

CONCLUSIONS: IMPROVING CROP WATER-USE EFFICIENCY

From this analysis five options for improving water-use efficiency seem possible. Unfortunately, most of these alternatives have important limitations or drawbacks.

Biochemical alterations. Either improved photosynthetic efficiencies (a) or altered composition of plant products (b), would lead directly to increased water-use efficiency. Opportunities for improving c in C_4 species seem quite limited because its value is already very high. Although greater opportunities to improve c seemingly exist in C_3 species, important problems must be considered. Improvement in the biochemistry of C_3 photosynthesis will require significant technological breakthroughs. Cultivar selection is a more direct method for obtaining higher c values, but this ap-

proach may achieve increased c values at the expense of CO_2 assimilation rate. Alteration in the biochemical composition of the plant products is technically a much more feasible option. The difficulty in this approach is that current levels of protein, lipids, and carbohydrates in the marketable fraction are a major reason for initially selecting a species for crop production. To improve soybean water-use efficiency by decreasing oil and protein content of the seed would defeat the purpose for which soybeans are grown. Therefore, it is unlikely that improvements in water-use efficiency will be achieved by altering the b coefficient.

Stomatal physiology. Stomatal sensitivity for preventing high transpiration rates could be important for improving water-use efficiency. In particular, midday closure of stomata during periods of high $(e^*_a - e)$ would be a very useful strategy for increasing water-use efficiency. Certainly, for some horticultural crops, midday stomatal closure may be highly desirable to improve water-use efficiency and to minimize any midday water stress that may damage the crop. However, in many field crops the desirability of having midday stomatal closure is less clear. To compensate for the periods of lost CO_2 assimilation, the growing season would have to be extended and, thus, further increase the potential for major crop losses from pests and environmental stresses.

Alteration of the cropping environment. Crop growth under conditions when $(e^*_a - e)$ is minimal, would improve water-use efficiency directly. A geographical solution would be to place greatest emphasis in crop production on those regions with the more humid climates. The more humid climates inherently have the greater water-use efficiency because of lower $(e^*_a - e)$. An alternative solution is to shift the cropping season to periods of lower $(e^*_a - e)$. In general, this would mean developing crops and cropping systems in which maximum growth is achieved during the cooler periods of the year. It has been suggested greater growth of cereals during early spring should be of high priority in water-limited environments (Fischer 1981). The search for improved water-use efficiency among breeding lines then becomes a search for tolerance and good performance under cool temperatures. A drawback may be that, to achieve hardiness in cool weather, special morphological or biochemical alterations are required that consume plant energy and/or lower harvest index potential.

Improved harvest index. As illustrated in equations (7) and (9) improvements in harvest index result directly in increased water-use efficiency. The difficulty is that for many crops it appears that further substantial improvements in harvest index are unlikely. An exception may be under conditions of limited water where drought stress, particularly during reproductive growth, can lead to greatly reduced harvest indexes. Proposals to alter plant growth for the conservation of water for later extraction during reproductive growth are being researched. Shorter season cultivars that complete their life-cycles and produce a high harvest index before the available water supply is exhausted is another approach. Cowpea yields have been increased in a water-limited environment by developing lines with shorter growing seasons (Turk et al. 1980). Of course, irrigation schedules that assure adequate water during reproductive growth are a direct approach to maintaining high harvest indexes.

Increased proportion of transpired water. Methods that allow more of the input water to be made available for transpiration would improve overall water-use efficiencies. Certainly, all management practices that minimize surface runoff, soil evaporation, and deep percolation would be beneficial. Greater rooting depths would generally make more soil water available for transpiration, but this advantage is somewhat offset by potentially lowering harvest index and the possibility of more rapid exhaustion of soil water. The basic definition of water-use efficiency expressed in terms of transpiration (equation 7) defines the limit for improving water-use efficiency through these conservation approaches.

In conclusion, the inescapable fact is that crop production is inextricably linked to crop transpiration. To increase crop biomass production, more water must be used in transpiration. The climate has a great influence on the magnitude of this linkage, expressed as water-use efficiency, through the vapor pressure deficit term $(e^*_a - e)$. Although opportunities exist for some improvement in water use efficiencies, a considerable fraction of these opportunities have already been exploited in high-yield, high-technology agriculture. For water-limited environments, a greater potential apparently exists for improving water-use efficiency. But the reality remains that without additional water, these areas cannot be expected to become regions of high crop yields. Irriga-

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tion and full exploitation of humid climates are seemingly of highest priority in attempting to increase food production in view of the conservative nature of crop water-use efficiency.

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