

Limits to Increasing the Productivity of Water in Crop Production¹

Andrew Keller and David Seckler²

The dramatic increase in world food production over the past half century has been from increased crop yields. It is generally agreed that future increases in world food production will become even more dependent on increased yields as the amount of cultivated area in the world continues to decrease. Increased yields have been accompanied by increased water productivity through a variety of factors discussed below. However, we contend that in most of the advanced agricultural areas of the world, which produce most of the world's food, the historic sources of growth in water productivity are being rapidly exhausted and there is very little of practical significance on the horizon to replace them. Thus, it is not at all clear how the increased yields are to be achieved. We shall not attempt to summarize all the various issues involved in this question here. Rather we shall concentrate on one fundamentally important question that has not received sufficient attention in our judgment. The question is: "Will increased crop yields simultaneously create increased water scarcity because of increased transpiration?"

Given the fact that transpiration³ is typically most of the total consumptive use of water by crops, this question has enormous implications for the future of irrigation and food production. It means that increased production through increased yields could create its own, formidable, constraint in terms of water scarcity. It also means that the potential for increasing water productivity through increased yields may be severely limited.

This question was posed in early 2004 by one of the present writers⁴. It stimulated an email discussion among several leading authorities in the field of irrigation and plant-water relationships. The discussion revealed wide areas of disagreement. Further research and consultation with other authorities revealed that the answer to this question depends on several factors. In this section of the paper we attempt to answer this question in relation to the various factors involved.

The first, fundamental and somewhat controversial factor to consider is the relationship between water use and crop yields. Thinking about this relationship is complicated and confused by the failure to clearly distinguish between three basic categories of plant-water relationships: transpiration, evaporation and drainage (TED). Because of the importance of getting this relationship correct, a considerable amount of space, in rather technical language, is devoted to it in the next section.

¹ This paper is an extract from a manuscript under review for publication in a special issue of *Irrigation Science*. Comments on the paper in the Forum section of Winrock Water would be appreciated.

² Brief biographies of the authors are in the Board of Editors section of Winrock Water.

³ We have attempted a brief layman's description of the process of transpiration in Appendix A.

⁴ This question mainly grew out of an earlier study of transpiration by the authors, see Seckler, 2003.

Transpiration, Evaporation, Drainage and Yields

Figure 1 shows the idealized relationship between relative crop yield (Y_{Rel}) and total available seasonal water (available soil water + rainfall + irrigation) componentized into T, E, and D. The figure begins on the left hand side with the relative yield to transpiration relationship.

The X-axis in Figure 1 is the total available water relative to the seasonal transpiration potential, T_p (water not limiting). The short-dashed curve in the figure represents the total evapotranspiration, $ET = T + E$, relative to T_p and has a maximum value of ET/T_p , which is greater than or equal to 1.0 depending on the amount of E⁵. The solid curving rightmost line represents the total available water and corresponds to the total consumed water (ET) plus drainage (D) relative to T_p . (Note that here drainage includes surface runoff as well as subsurface drainage from rainfall and irrigation.) At low levels of available water D may be zero as all available water is consumed by ET. The relative yield as a function of available water, $ET + D$, reaches a maximum of 1.0 and then begins to decline due to water logging and the leaching of nutrients as excessive amounts of water are applied⁶.

The difference between the solid line and the short-dashed ET line, drainage (D), represents the “losses” due to “inefficient” (i.e., over) irrigation and untimely rainfall. To the extent that these losses are not consumed by non-beneficial evaporation, do not flow to salt sinks, and do not cause water logging or nutrient leaching, they are inconsequential from a water conservation standpoint, since they remain somewhere in the fresh water resource; however, they may represent wasted labor and energy (see Molden, et.al., 2001).

Rainfed crop production and different irrigation technologies will have different evaporation and drainage characteristics, but the yield-T relationship will be constant for a given crop and climate. For example, subsurface drip irrigation may not have any evaporation loss after germination, in which case the ET curve would be offset from the T curve by the amount of the initial evaporation loss and parallel to it. If there were no drainage water, the ET+D curve would be coincidental with the ET curve.

Charles Burt and associates at CalPoly (2001) estimated the T and E components of ET following the FAO 56 dual crop coefficient method for various types of irrigation systems and irrigated areas of California. While the approach was more theoretical than empirical, and not highly analytical, relative comparisons are probably reasonable. The interesting conclusion is the very small difference in total ET between furrow, sprinkle, and subsurface drip irrigation (SDI). What varies more is the partitioning of ET into T and E, with SDI having the least evaporation loss of applied irrigation water (4% of seasonal ET) and sprinkle irrigation having the most (8% of ET).

⁵ The ET curve shown here assumes E increases slightly with increasing T. In actuality E may decrease at higher levels of T due to the increased shading of the ground resulting from more crop biomass associated with greater T. Indeed this is the conclusion from the analysis described in Appendix B. However, it should be noted that E is quite variable depending on the timing of irrigation and rainfall and the method of irrigation, among other factors.

⁶ Implicit here is the assumption that the water available for transpiration is more or less uniformly distributed through out the growing season such that there are no concentrated periods of extreme drought.

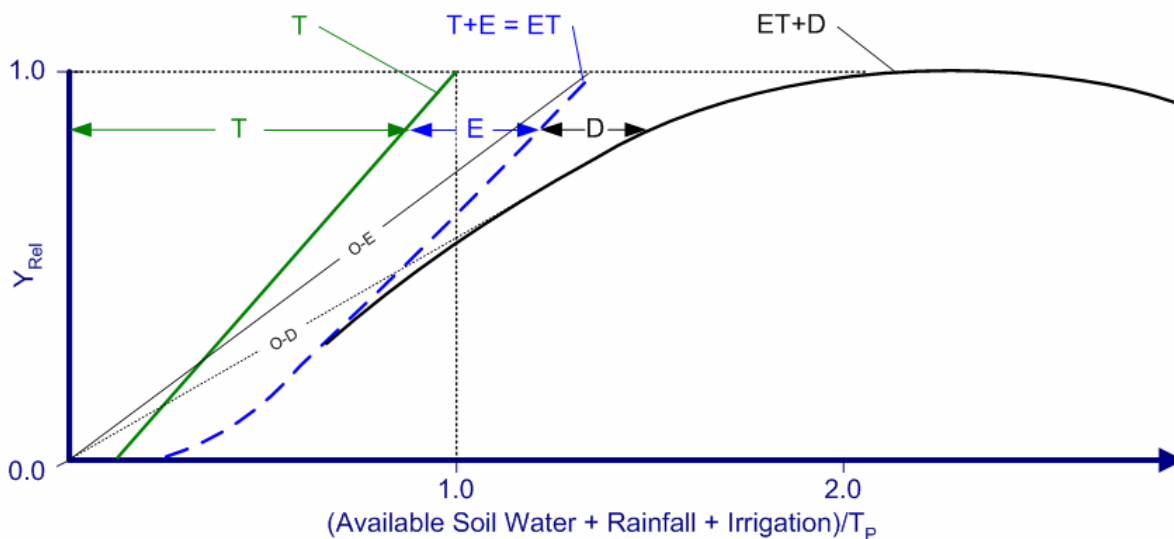


Figure 1. Relationship between relative crop yield and total available water ($T+E+D$) relative to T_p .

If the drainage water, D , is recoverable for use elsewhere, the maximum crop water productivity is obtained at the point on the ET curve that is tangent to a line running from the origin to the ET curve as depicted by the $O-E$ line in Figure 1. ET greater than this point of tangency has a declining return to consumed water⁷. Likewise, if the drainage water is not useable elsewhere, and thus is a true loss, the maximum return to water occurs at the point on the $ET+D$ curve that is tangent to a line running from the origin to the curve as depicted by the $O-D$ line in Figure 1.

From a farmer's perspective drainage water is generally a loss so the optimal position is to deficit irrigate⁸. This is particularly true with uncertain rainfall and unreliable irrigation deliveries, which motivate farmers to greatly under-irrigate. "Where a farmer has uncertain rainfall (but often less than required to mature a crop), and inadequate irrigation water to bridge the gap between rain and full ET for his holding, he will seriously under-irrigate to ensure that he captures the maximum value from the free rainfall (which is a function of area cropped)." (Perry, 2002) Thus, policies that lead to unreliable irrigation deliveries result in suboptimal return to water at the basin level even if the drainage water is reused.

⁷ Because the nature of the ET curve, maximum crop water productivity will generally occur at maximum ET .

⁸ At the farm level greater total yield can be obtained by somewhat deficiently irrigating a larger area than by fully irrigating a smaller area using the same total volume of irrigation water. However, this does not necessarily mean that the maximum economic return is at a yield point less than Y_p because the input costs associated with irrigating a large area may offset any gains in total yield. Also the risks associated with deficit irrigation are greater than those with full irrigation, so the expected value yield may actually be less.

Crop Water Productivity

Our literature review has found inconsistent use of the terms transpiration efficiency (TE) and crop water use efficiency (WUE), which has caused some confusion for us and we suspect others on this subject. Furthermore, calling these efficiency terms is misleading because doing so implies causality, i.e. crop yield is the result of water consumption. This misconception is perpetuated by plotting crop yield as the ordinate versus evapotranspiration as the abscissa and by expressing crop yield as a function of evapotranspiration.

In actuality, as explained earlier, water consumption in the form of transpiration occurs as a cost of crop growth. When a plant's stomata open to allow assimilation of CO₂, water is lost. The amount of water loss per unit biomass gain is dependent primarily on characteristics of the plant and the humidity⁹ of the plant's environment¹⁰.

We define TE as the crop aboveground (aerial) biomass (dry matter of stems, leaves, and fruit) divided by the volume of water transpired during the accumulation of that biomass. WUE is the aerial crop biomass divided by the volume of water transpired and *evaporated* in association with the production of that biomass. We have adopted the term crop water productivity (CWP) after Kinje, *et al.* (2003) and Zwart and Bastiaanssen (2004) to refer to the economic (grain, fruit, lint, etc.) yield divided by the volume of water consumed (evapotranspiration) in the production of that yield. TE, WUE, and CWP are all expressed in kg per m³.

The inclusion or exclusion of evaporation in the yield-water relationship is crucial. We contend that, when normalized for Δe , transpiration (T) and aerial biomass (aboveground dry matter yield¹¹, Y_{dm}) are essentially proportional according to a crop specific constant. In other words, TE, adjusted for Δe , is more or less constant for a crop (Eq. 1). It is the evaporation (E) component of evapotranspiration (ET) that introduces non-linearity and most variability in the yield-water relationship.

$$TE' = \frac{Y_{dm}}{T'} = \frac{Y_{P_{dm}}}{T_P} \quad \text{Eq. 1}$$

⁹ Plants and humans experience humidity differently. For humans it is the relative humidity that affects our comfort. The critical aspect of humidity from a plant's standpoint is the difference in vapor pressures inside and outside the leaf. This difference is the governing force for transpiration and is closely approximated by the vapor pressure deficit of the air outside the leaf. The vapor pressure deficit (Δe) is the difference between the saturation vapor pressure (e_s) of the air, which is temperature dependent (increasing exponentially with temperature), and the actual vapor pressure of the air (e), which is dependent on the amount of water vapor in the air and independent of temperature. Relative humidity (RH) is the ratio of e to e_s expressed as a percent: $RH=100 e/e_s$. Thus, Δe can be calculated from RH: $\Delta e=e_s (1-RH/100)$. Pressure is a force per unit area and is typically expressed in Pascals (Pa) or bars.

¹⁰ TE and WUE might be thought of as benefit-cost ratios (yield-ET) rather than efficiencies. Viewed this way we marvel at how plants optimize growth within the constraints of their environment, whereas if we look at them from an efficiency standpoint we might see them as rather inefficient. Plant scientists use the term transpiration ratio to refer to the amount of transpiration associated with biomass production, thereby avoiding the potential confusion associated with efficiency. But TE, which is essentially the reciprocal of the transpiration ratio, is also widely used by plant scientists and others. As this is a paper concerning crop water use we find ourselves generally referring to TE. Rather than inventing new terminology we have chosen to continue with TE and WUE.

¹¹ Throughout this paper we use aerial biomass and aboveground dry matter interchangeably.

TE' , T' , and T'_p in Eq. 1 are the transpiration efficiency, transpiration, and potential transpiration respectively, normalized for Δe^{12} , and Y_{dm} and $Y_{p\ dm}$ are respectively the aerial biomasses associated with T' and T'_p .

Bierhuizen and Slatyer (1965) proved that TE was linked to the vapor pressure deficit (Δe) and derived the following broadly accepted (Tanner and Sinclair, 1983; Howell, 1990a; Ehlers and Goss, 2003) relationship:

$$TE = \frac{k}{\Delta e} \quad \text{Eq. 2}$$

Expressing TE in $Mg\ ha^{-1}\ mm^{-1}$, the k factor has the units of $Mg\ ha^{-1}\ mm^{-1}\ Pa$. Since the mass of 1 ha-mm of transpired water is 10 Mg, the k factor can be expressed simply in Pa. Table 1 is adapted from Ehlers and Goss (2003) to illustrate k factors¹³ for various C₄ and C₃ crops. Although Table 1 does not show it there is some variability in k factors for a crop and an apparent slight increase with increasing Δe . (See Tanner and Sinclair, 1983; Howell, 1990a; and Ehlers and Goss, 2003 for further discussion.)

Crop	Type of CO ₂ fixation	k (Pa)
Sorghum	C ₄	13.8
Maize	C ₄	9.1
Wheat	C ₃	4.5
Barley	C ₃	4.0
Oat	C ₃	3.5
Potato	C ₃	6.2
Lucerne	C ₃	4.3
Soybean	C ₃	4.0
Pea	C ₃	3.8
Faba bean	C ₃	3.1

Using the methods of FAO Irrigation and Drainage Paper No. 56 (hereafter FAO 56), crop potential transpiration is assumed to be approximately equal to the basal crop evapotranspiration, ET_{cb} :

$$T_p \cong ET_{cb} = K_{cb} ET_o \quad \text{Eq. 3}$$

Where K_{cb} is the basal crop coefficient and ET_o is the reference evapotranspiration. K_{cb} is crop specific and varies with the leaf area of the crop relative to the ground area (leaf area index, LAI)¹⁴. The LAI is primarily a function of the crop biomass.

T is less than or equal to T_p depending primarily on the degree of water stress. The concept of crop water stress is nicely

introduced by the following from FAO 56:

Forces acting on the soil water decrease its potential energy and make it less available for plant root extraction. When the soil is wet [and salinity low], the water has a high potential energy, is relatively free to move and is easily taken up by the plant roots. In dry soils [or when enough salts are present in the soil water solution], the water has a low potential energy and is strongly bound by capillary and absorptive forces to the soil matrix, and is less

¹² T is normalized for humidity by multiplying by a reference Δe (i.e., 1 kPa) divided by the mean daytime Δe .

¹³ Note that at Δe of 1 kPa the k factor is numerically equivalent to TE expressed in $kg\ m^{-3}$.

¹⁴ Typical K_{cb} values for the initial, mid-season, and ending growth stage for maize are 0.15, 1.15, and 0.15 respectively. A typical value for cool season turf grass is 0.9.

easily extracted by the crop. When the potential energy of the soil water drops below a threshold value, the crop is said to be water stressed.¹⁵

The effects of soil water stress on transpiration are described by multiplying Eq. 3 by the water stress coefficient, K_s :

$$T = K_s T_P \cong K_s ET_{cb} = K_s K_{cb} ET_O \quad \text{Eq. 4}$$

K_s is less than 1 when there is water stress, i.e., limited availability of low salinity soil water, and equal to 1 when there is no water stress. From Eq. 1 and Eq. 4 it is apparent that the relative dry matter yield ($Y_{Rel\ dm} = Y_{dm} / Y_{P\ dm}$) equals the relative transpiration ($T_{Rel} = T / T_P$), which equals K_s .

Total crop biomass includes all dry matter in the roots, stems, leaves, and fruit (or grain) of the crop. Figure 2 shows the accumulation of total aboveground maize plant biomass (non-fruit plus fruit) by phenological stage and days since emergence (adapted from Ritchie, et.al.,1993). Once

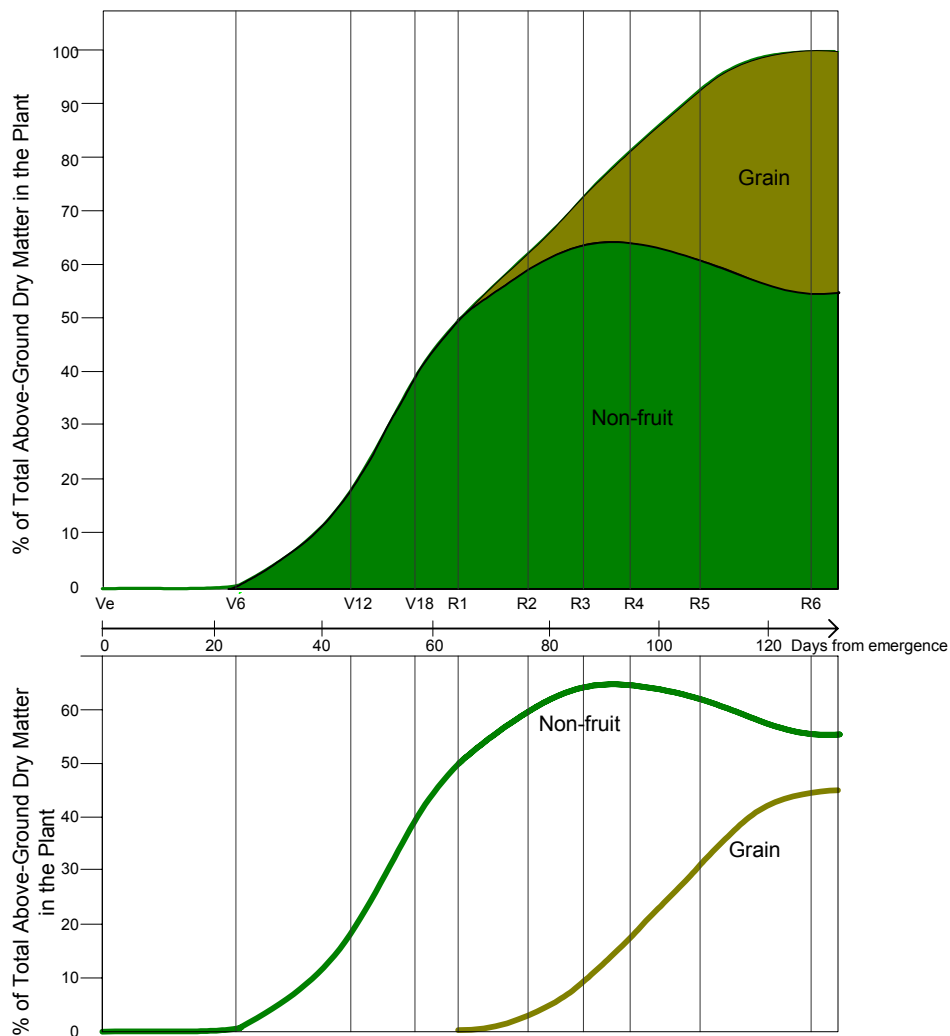


Figure 2. Total aboveground maize plant biomass (non-fruit plus fruit) by phenological stage and days since emergence.

¹⁵ FAO 56, page 161. Text between square brackets [] inserted by the us and not in the original text.

the 18-leaf (V18) stage, corresponding to early tassel and 40% of total mature plant dry matter, is reached, dry matter accumulation proceeds at a nearly constant rate. Accumulation of dry matter in the maize kernels begins at silk (R1) stage, which is about the midpoint in the growing season and total dry matter accumulation, and continues to maturity. Note that during the final reproductive stages dry matter accumulation in the grain comes, in part, from the non-grain portion of the plant.

The harvest index is typically defined as the harvested fraction of a crop at maturity. For grain crops the harvest index is the dry matter of the grain yield divided by the aboveground biomass. The lower portion of Figure 2 shows the harvest index and the non-fruit portion of the total aboveground biomass.

Howell (1990b) and others have suggested a linear relationship between grain yield, Y_{gr} , and aerial dry matter yield, Y_{dm} , as follows:

$$Y_{gr} = b(Y_{dm} - a) \quad \text{Eq. 5}$$

where a and b are crop specific constants and b can be thought of as the asymptotic harvest index and a as the dry matter required for a harvested yield. Equation 5 appears to be valid over a wide range of Y_{dm} and independent of water stress, but dependent on plant density. The relationship between grain yield, harvest index, and aerial dry matter is depicted in Figure 3 using values referenced by Howell (1990a) of 0.49 and 2.47 for b and a respectively in Eq. 5.

It is important to note that Figure 2 is for non-stressed conditions. When a plant is stressed it often enters into the reproductive stages early. But whether this changes the harvest index depends upon the timing of the stress among other factors. For our purposes here we assume that the relationship between total plant biomass and the accumulation of biomass in the fruit is similar to that shown in Figure 2, and idealized by the linear relationship of Equation 5, under both stressed and non-stressed conditions. However we recognize that with maize, particularly, stress during the V18, R1 and adjacent stages can cause disparity between the timing of tasseling and silking for some cultivars, thereby reducing pollination effectiveness and thus yield potential.

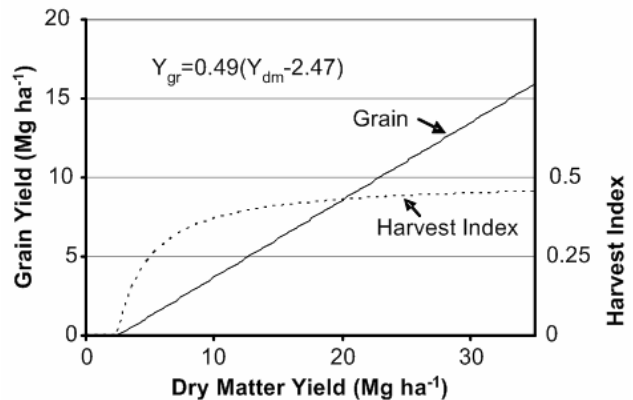


Figure 3. Relationship of grain yield, aboveground dry matter yield, and harvest index for maize.

Figure 4 shows the aerial dry matter accumulation with time, relative to the seasonal total, from Figure 2 plotted against the relative cumulative long-term (20-year) average growing season ET for Iowa¹⁶ (Shaw and Newman, undated). The linear regression line in Figure 4 demonstrates a near one to one relationship between relative biomass and relative ET.

¹⁶ The reference does not give the actual years or locations in Iowa used to compile the average or the method of measuring or estimating ET.

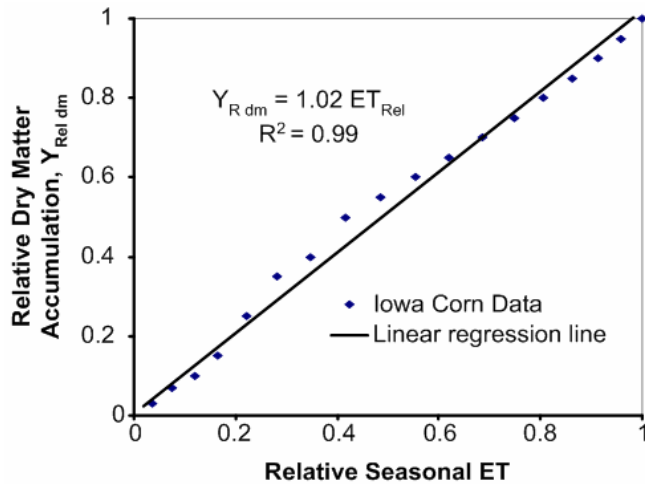


Figure 4. Relative aerial seasonal dry matter accumulation to relative seasonal ET for corn in Iowa.

Yield-ET data from multiple locations combined into a single plot have much more scatter than in Figure 4, often to the extent that they may initially appear to indicate there is little correlation between yield and ET. We contend, however, that this apparent lack of correlation is due primarily to two factors: 1) the data, coming from several different locations, likely have different associated Δe and thus TE; and 2) as stated earlier, the E part of ET is what introduces most of the noise in the yield-ET relationship once the data have been normalized for Δe . To demonstrate these points we conducted the analysis presented in Appendix B and arrived at an important and interesting

conclusion—CWP is maximized by full irrigation of a smaller area rather than by deficit irrigation of a larger area with the same volume of water. The reason is that E relative to total seasonal ET decreases as T increases. Thus, maximizing crop yield is compatible with maximizing CWP.

If the estimated E in the Appendix B analysis were reduced by half and moved to T, grain yields would increase by an average of nearly 30% with no change in total consumptive use. As long as ET is unchanged there would be no change in vapor pressure deficit around the surface of the leaves so the transpiration efficiency would remain constant and yields would increase proportional to the increase in T. However, if E were reduced without somehow shifting the reduction to T, i.e., if the total ET were reduced¹⁷, there would be a potential increase in Δe and a coincidental decrease in transpiration efficiency and crop yield. We conducted a quick analysis to evaluate this offsetting effect of reducing E and concluded that, under reference conditions, T would have to increase by up to 30% of the amount of E-reduction to obtain the same pre-E-reduction crop yield. State another way, 30% or less of E is beneficial from the standpoint of lowering Δe and thereby increasing transpiration efficiency. Accordingly, net water savings from reducing E without an equivalent increase in T are at least 70% of the E-reduction. Under windy conditions the net savings would be even greater.

Will increased yields increase water scarcity?

Now we return to the original question in the title of this section. At first blush, the answer seems straight-forward. The close linear relation between yield and transpiration demonstrated in the preceding section means that an increase in yield is *ipso facto* accompanied by a proportionate increase in transpiration. However, this does not necessarily mean that there is a proportionate increase in water consumption. There several factors to consider in the relationship between transpiration and water consumption.

¹⁷ Reducing E without a corresponding increase in T seems rather unlikely since water saved by reducing E, whether it be through mulching, weeding, or change in irrigation method, would most likely be available for T.

The first factor to consider is that the linear relationship between yield and transpiration relates to yield of total plant biomass. While nearly everyone agrees on this relationship, the situation obviously changes when yield is defined in terms of only part of the biomass—the seeds and other components of the “economic yield.” *The economic yield can be increased without increasing the total biomass* and, therefore, *without increasing transpiration*.

A substantial amount of the growth in crop yields over the past few decades has been due to plant breeders’ partitioning plant biomass toward economic yield and away from the shoots and other components of total biomass—in other words, by increasing the “harvest index” (HI). While increasing HI was done primarily to increase economic yields it simultaneously provided something of a free ride in terms of water consumption. Since the total biomass per unit area did not change, transpiration remained the same with increased economic yield.

However, the free ride provided by increasing HI may be ending. “Since about 1980, only minor increases in the harvest index have been achieved...it appears unlikely that further major yield increases in cereals can result from further major increases in HI.” (Sinclair and Gardner, 1998) This conclusion is confirmed in Zwart and Bastiaanssen (2004), whose data show that crop water productivity for wheat, rice, and maize has not changed appreciably in twenty-five years. Bennet (2003) also seems to agree with this view, giving increased HI only a moderate ranking in his survey of genetic opportunities for increasing water productivity.

A second factor to consider is the effect of increasing plant densities per unit area on water consumption. Sinclair and Gardner (1998) list this as another, perhaps the most important, source of growth in food production over the past few decades. Since increased plant densities increase total biomass per unit area, total transpiration per unit area would increase in proportion. However, as noted before, increased plant densities *also* decrease evaporation losses from the soil. Thus total evapotranspiration would not increase proportionately and some of the reduced evaporation losses would be partitioned over to transpiration.

A third factor in increasing yields is improved nutrient supply to the plant through more and better fertilizers. It is generally agreed that when there is severe nutrient scarcity to the plant but sufficient water availability, the TE of the plant decreases. Thus better fertilization will increase TE. This does not however negate the fact that total transpiration will increase along with the increased yield. Also, it is generally agreed that the effect of increased TE with better nutrient supply *occurs only with severe nutrient scarcity*—where the yield is below 40%-50% of where it would have been with adequate nutrients. Above this level, TE is constant (Tanner and Sinclair, 1983). Indeed, Euler and Goss (2003, p. 152) end their chapter on this subject by saying, “We can conclude that TE *is largely independent of the fertility status of the soil*” (their italics).

Fourth, there is the complex and presently unknown potential of crop breeding and molecular biology for increasing TE. The differences in TE between C3, C4 and CAM species discussed Appendix A. It is also known that different varieties of the same crop differ somewhat in TE and means have been devised to screen crops for the traits associated with these differences. We will not discuss this subject further here except to say that perhaps most authorities range from deep skepticism (Tanner and Sinclair, 1983) to slight optimism (Bennett, 2003) on the potential for substantial advances in this direction.

Fifth, there is one way to attain large increases in food production with lower or even substantially reduced total transpiration about which everyone does agree. This is by relocating crop production (and/or crop growth periods) to areas (and times) with lower evaporative

demand for water (see the interesting discussion of this and other alternatives in Tanner and Sinclair, 1983). By this simple expedient, TE of the relocated crops could be increased several fold. This is the underlying logic behind the concept of virtual water, discussed in Part I, and there is little question that as water scarcity becomes increasingly severe in many regions of the world, international trade will gradually reflect the comparative advantages of different regions of the world in terms of water demand and supply.

In sum, it appears to us that, barring major genetic breakthroughs and relocating crops in place and time, the major opportunities for increasing yields without increasing total water consumption lies in the three areas of: a) reducing evaporation losses; b) reducing non-beneficial transpiration losses from weeds; and c) reducing non-beneficial drainage losses. In principle, the magnitude all three of these water saving techniques can be quantitatively estimated. A possible way to make these estimations is to apply standardized TE coefficients to the yield of various crops and varieties to determine what amount of the total water applied is consumed by transpiration. Then one could estimate how much of the drainage water is beneficially used. The balance would approximate the potential water savings from E and non-beneficial drainage.

Our opinion is that in the *highly developed agricultural areas of the world*, with the exception of many flooded rice systems, the opportunities for substantial water savings by any of these techniques are rather small. Also, it should be noted that these are “once and for all” water savings, which cannot increase indefinitely, and they can be very expensive. On the other hand, in *areas of marginal agriculture*, such as most of sub-Saharan Africa and the rainfed areas of many other regions, where the need is perhaps greatest, there is large potential for such improvements.

Last, to return to the question posed at the beginning, for reasons outlined here, and given the qualifications and caveats, we conclude that under the most prevailing conditions of agriculture today, the hypothesis that increasing yields will simultaneously increase transpiration losses and therefore water scarcity is valid.

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Appendix A. The Process of Transpiration

In this appendix we attempt to briefly outline the process of transpiration in plants, as we understand, it so that the reader can see and appraise the basis from which the hypotheses in the main body of the text are derived. In this effort we have relied heavily on the clear and authoritative publications works of T. R. Sinclair and his co-authors and we advise other lay persons interested in this fascinating field to do the same¹⁸. Many other works referenced below, especially Howell (1990a) and Euler and Goss (2003) should be perused from this base. These references may compensate for an economist and an engineer trespassing on such a technical and specialized field. However, this section is written mainly for economists and engineers and other non-specialists in a way that we—and therefore, we hope they—can understand, without doing too much damage to the ear of the specialist.

Transpiration is driven by meteorological conditions, regulated by plant-soil characteristics, and constrained by available water.

The first step in understanding the process of transpiration is to regard it as part of the rather miraculous chemical manufacturing process of the leaf, the process of photosynthesis (see Sinclair and Gardner, pp. 66-69; Tanner and Sinclair, p. 13). The leaf, employing radiant energy from the sun, acquires hydrogen and oxygen by breaking down water (itself a difficult task) extracted from the soil. It acquires carbon from carbon dioxide in the atmosphere, which diffuses into the plant through small pore-like holes on the leaf, the stomata. The leaf then re-assembles these elements into a simple carbon molecule, hexose, the “photosynthate”, which is the basic building-block of the plant biomass.

Finally, the hexose needs to be converted to final product biomass in the plant. Through a careful analysis of the assimilatory pathways, Penning de Vries (1975b) estimated that from 1 g of hexose, either 0.83 g of carbohydrates, 0.40 g of protein (assuming a nitrate source of N), or 0.33 g of lipids could be produced. Therefore, in principle the conversion coefficient, b, for taking hexose to biomass could range from 0.33 to 0.83. Sinclair and de Wit (1975), examined seed production in 24 crop species and found a range for b from 0.42 in sesame to 0.75 in barley and rice. (Tanner and Sinclair, 1983, p. 13; the table for the 24 crop species is included in Sinclair and Gardner, 1998, p. 69).

The next step in understanding the process of transpiration is to see how the plant manages the very difficult problem of acquiring carbon dioxide by diffusion through the stomata at the cost of water loss by transpiration through the same process. This problem is exacerbated by the fact that the concentration of carbon dioxide in the atmosphere is quite low. For every CO₂ molecule in the atmosphere there are 100 water vapor molecules. Photosynthesis must scavenge for a trace amount of CO₂ without losing water. Animals have a much easier task with water use efficiency: There are seven, O₂ molecules (14 O molecules) for every water vapor molecule in the atmosphere, so getting oxygen without losing water is 700 times easier than getting CO₂ without losing water. (Bugbee, personal communication, cited in Seckler, 2002).

¹⁸ fn: “Transpiration,” Sinclair and Gardner (eds.) Chapters 5 and 7, and more technically in Tanner and Sinclair, 1983 (a work referred to by one authority as “the seminal paper” in the field of plant water relationships).

To manage the problem of acquiring carbon dioxide at the least cost in terms of transpiration losses, the leaf has developed a highly elaborate control system that carefully opens and closes the stomata in response to the carbon dioxide demands of the rate of photosynthesis. If the carbon dioxide concentration in the inter-cellular spaces of the leaf is too low, the stomata open wider, if the concentration is sufficient to meet photosynthetic demand the opening of the stomata becomes smaller. If water supply becomes highly constrained, the stomata are completely closed and photosynthesis stops. Howell (1990a) discusses various tests of the “optimal stomatal control theory” of the relationship between assimilation of carbon dioxide and loss of water through transpiration in plants. It is found that while there are differences among plants, they perform very close to the optimum position. A remarkable recent discovery in this field is that the stomata do not all open and close at once, or in the same degree. Instead, “patches” of stomata on one part of the leaf behave in one way, while those on other parts behave in another way. This has led to the conjecture, now being tested, that leaves are practicing a form of “distributed computing” among the stomata, a form of computing which is at the frontier of computer science and which, if proven true, would be the first such process discovered in biology (Mott, 2003).

The third step in understanding transpiration is to recognize the three different kinds of plants, which have substantially different photosynthetic pathways and, hence transpiration efficiencies under the same atmospheric and other environmental conditions (see the discussion in Howell, 1990a, pp.395-396).

The C3 plants are the most common crop plants (wheat, barley, soybeans....). Unfortunately, they are also the least efficient assimilators of carbon dioxide from the atmosphere. Therefore, they must keep their stomata open more than the other plants under the same atmospheric conditions and, hence, they have the lowest transpiration efficiency, TE (biomass per unit water transpired).

The C4 plants (maize, sorghum, sugar cane...) have developed an ingenious add-on to the basic C3 process. They have an enzyme that has twice the affinity for absorbing carbon dioxide as that in C3 plants. C3 plants also have photorespiration which occurs with photosynthesis in light and requires oxygen. This process does not occur in C4 plants. Consequently, C4 plants have 2-3 times higher TE than C3 plants.

The CAM plants (pineapple, agave ...) have the ability to assimilate CO₂ during the night and store it in the form of organic acids. During the day the stored CO₂ is available for producing carbohydrates by photosynthesis. This enables CAM plants to close their stomata during the daytime, when transpiration is highest, and open the stomata at night when it is lowest. CAM plants can attain a TE as much as 10 times that of C3 plants; however, their biomass production per unit land area is low.

Last, there are facultative plants, of which the ornamental Jade plant is one example, that can switch between the CAM and C3 processes depending on water availability (Bruce Bugbee, personal communication). Why, one may ask, if they can do CAM, would they want to do C3? The reason is that the C3 process is more energy efficient. Pineapples also seem to have this facility to some degree. Under irrigated conditions pineapples open their stomata in the daytime, but when it is dry they open them only at night (Sinclair and Bennett, 1998).

In sum, the TE of plants is determined first and foremost by meteorological conditions (saturation vapor pressure deficit). But given these conditions, TE also varies greatly among the

three major groups of plants—C3, C4, and CAM—and, within these groups, TE varies according to the crop products: carbohydrates, proteins, and lipids. All of these variations and complications are governed by the strict relations of chemical manufacturing processes combined with the elaborate control functions of the stomata. When water is limiting, the TE of biomass production is not necessarily affected, but the TE of marketable yield can vary significantly depending on the water availability at various crop stages.

Appendix B. Detailed Maize Yield-ET Analysis

Yield-ET data from multiple locations combined into a single plot may initially appear to indicate there is little correlation between yield and ET. We contend, however, that this apparent lack of correlation is due primarily to two factors: 1) the data come from several different locations with different saturation vapor pressure deficits; and 2) the E part of ET is what introduces most of the variability in the yield-ET relationship once the data have been normalized for Δe . To demonstrate these assertions we conducted the following analysis and arrived at an important and interesting conclusion—CWP is maximized by full irrigation of a smaller area rather than by deficit irrigation of a larger area with the same volume of water.

In an interesting study, Zwart and Bastiaanssen (2004) conducted an extensive literature review to develop a database of wheat, rice, and maize grain yields, and cotton seed and lint yields, versus actual ET (ET_a). For inclusion in the database ET_a had to be measured and the method of measurement reported. Figure B1 shows maize grain yields against ET_a , digitized from Figure 2d of Zwart and Bastiaanssen (2004).

Figure B2 is derived from Figure B1 by converting the grain yield to dry matter yield according to $Y_{dm} = 2.04 Y_{gr} + 2.47$. The points in Figure B2 were filtered to only include data between the 5 and 95 percentiles of the entire CWP range¹⁹ in the Zwart and Bastiaanssen (2004) database. The $Y_{p\ dm}$ curve was derived as the envelope of maximum Y_{dm} values.

The intercept of the $Y_{p\ dm}$ curve on the ET-axis in Figure B2 represents what we call the basal evaporation (E_b). For this maize data set E_b is 87 mm. To estimate the actual E and T associated with each Y_{dm} the TE associated with each data point must first be determined. If the seasonal average Δe for each point was known the Bierhuizen-Slatyer (1965) equation (Eq. 2 in the text) could be used. But since Δe was not available²⁰ we estimated TE for each data point as the average slope of two lines: one line, representing the minimum TE, being that passing through E_b on the ET-axis and the data point; and the other line, representing the probable maximum TE, being that passing through E_b on the ET-axis and $Y_{p\ dm}$ at ET_a for the data point. Once the TE is determined T is estimated as Y_{dm} divided by TE and E is ET_a minus T. The summary results for this maize data set are presented in Table B1 and appear reasonable. The Δe values summarized in Table B1 were estimated assuming a k factor of 9.1 Pa for maize in Eq. 2.

¹⁹ The entire CWP-range in the Zwart and Bastiaanssen (2004) database for maize is 0.2 to 4.0 kg m⁻³. The 5 to 95 percentile range is 1.1 to 2.7 kg m⁻³.

²⁰ Zwart and Bastiaanssen (2004) recognized and discussed the inverse relationship of Δe on CWP. Since Δe generally decreases with distance from the equator, Zwart and Bastiaanssen plotted the maximum CWP against latitude for each location and crop in their database. They found that between 30° and 40° of latitude tended to be most favorable for maximizing CWP in grain production and concluded this was likely related to Δe . We encourage Zwart and Bastiaanssen to include the associated mean growing season Δe when possible in their database.

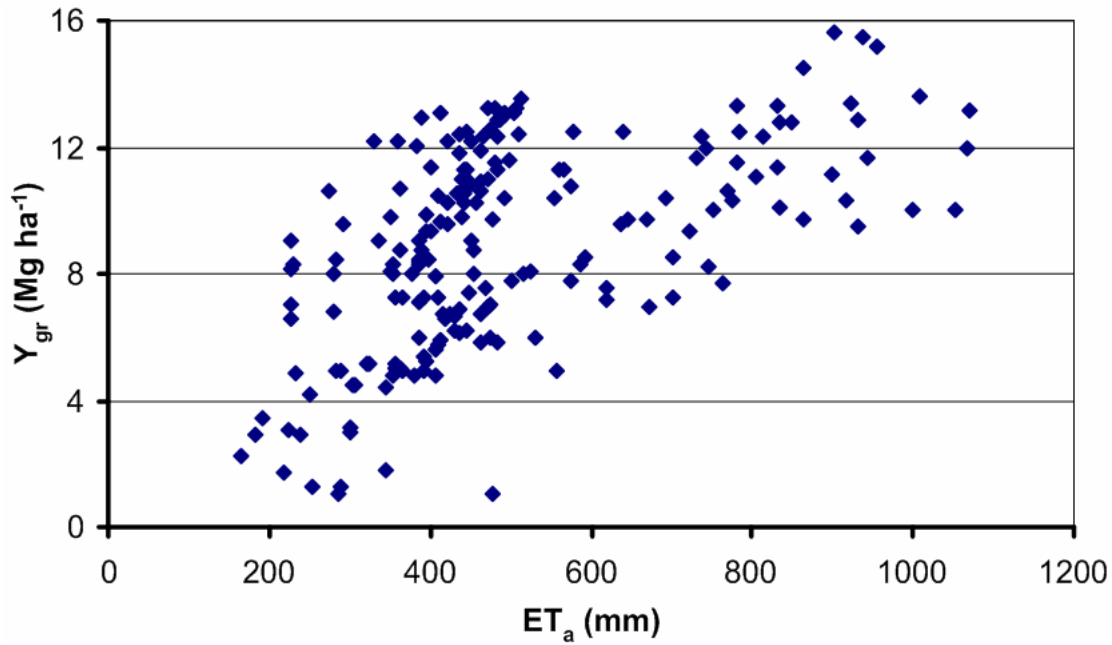


Figure B1. Maize grain yield versus actual ET digitized from Zwart and Bastiaanssen (2004).

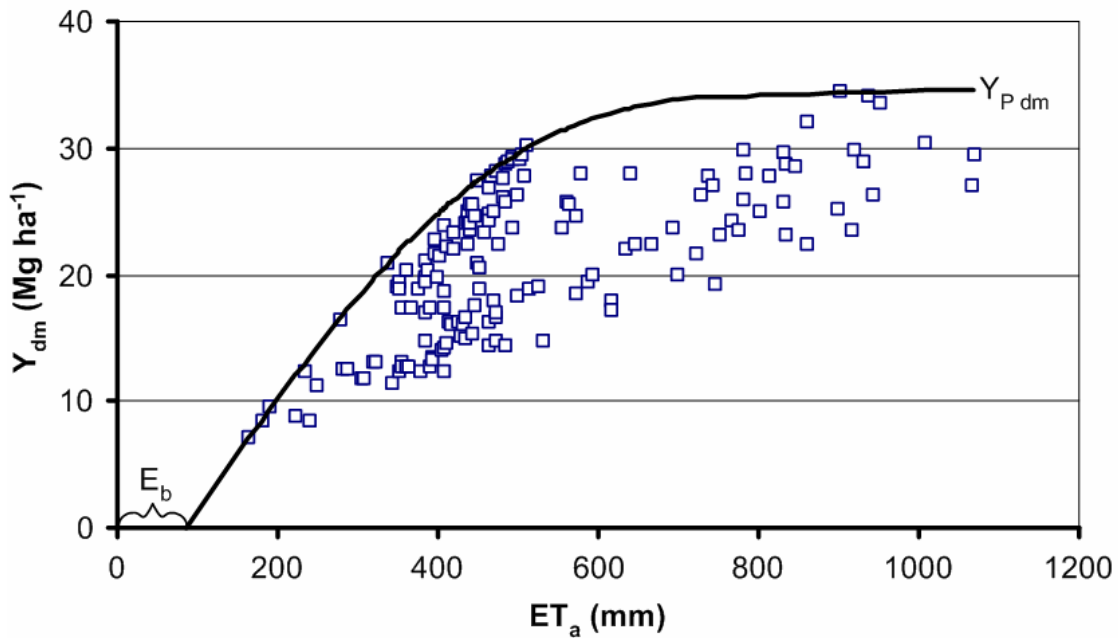


Figure B2. Maize dry matter yield versus actual ET, derived from Figure B1. Dry matter yield estimated from grain yield by $Y_{dm} = 2.04 Y_{gr} + 2.47$. Data filtered to only include points between the 5 and 95 percentiles of the entire CWP range.

Table B1. Maize yield-ET summary results from estimated TE in Figure B2. ET_a and Y_{gr} digitized from Zwart and Bastiaanssen (2004) and filtered for CWP between 1.1 and 2.7 kg m⁻³. Y_{dm} , TE, Δe , T, and E are calculated estimates.

	ET_a (mm)	Y_{gr} (Mg ha ⁻¹)	Y_{dm} (Mg ha ⁻¹)	CWP (kg m ⁻³)	WUE (kg m ⁻³)	TE (kg m ⁻³)	Δe (Pa)	T** (mm)	E** (mm)
Minimum	166	2.3	7.1	1.10	2.52	3.14	1020	79	85
Maximum	1071	15.6	34.4	2.70	6.19	8.92	2900	902	271
Average	518	9.1	20.9	1.81	4.24	6.15	1565	371	147
Median	461	9.3	21.5	1.64	3.90	6.37	1429	329	138
Std. Dev.	194	3.0	6.1	0.48	1.03	1.34	410	179	46
CV	0.37	0.37	0.37	0.26	0.24	0.22	0.26	0.48	0.31

** With the exception of the average, T and E cannot be summed to get ET_a because the summary T and E values are not necessarily for the same data points, i.e. the point with minimum T may not be the point with minimum E.

Figure B3 shows the maize grain yield versus T and ET normalized for the estimated saturation vapor pressure deficit using a reference Δe of 1 kPa. The amount of normalized evaporation is represented by the distance from the T' line to the ET' points for a specific yield. Figure B3 demonstrates that when normalized for Δe the yield and ET are strongly correlated and the variability is due to E. It should be noted, however, that this analysis out of necessity is idealized and that in reality there would be some variability in the yield-T relationship. But we doubt this variability would be significant or alter our conclusion that the Δe -normalized yield-T relationship is essentially linear and that E is the source of variability in the yield-ET relationship.

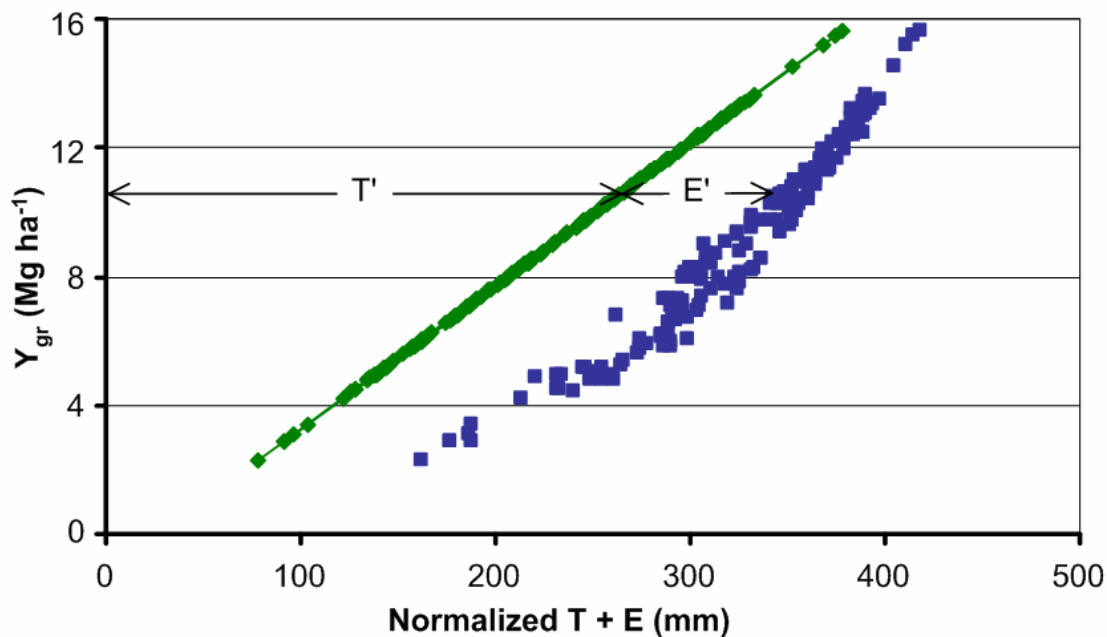


Figure B3. Maize grain yield versus T+E normalized for the estimated saturation vapor pressure deficit using a reference Δe of 1 kPa. Derived from Figure B1.

It is interesting and important to note from Figure B3 that E , which is the non-productive part of ET , decreases with increasing T particularly as a fraction of ET . This is likely due to the greater effective ground cover of crops having greater T . Thus, from the standpoint of maximizing CWP, evaporation should be minimized by maximizing T , which implies intensification of farming. Thus, in the debate of whether to spread a limited water supply over a larger area and deficit irrigate or to fully irrigate a smaller area, we conclude from this exercise that CWP is maximized by irrigating the smaller area.