

# THE PHYSIOLOGY OF COTTON WATER USE EFFICIENCY

T. J. GERIK<sup>1</sup>, J. A. LANDIVAR<sup>2</sup>, AND K. L. FAVER<sup>1</sup>

1 - Texas Agricultural Experiment Station, Blackland Research Centre, 808E. Blackland Road, Temple TX 76502, USA

2 - Texas Agricultural Research Centre, HWY 44 West, Rt. 2, Box 589, Corpus Christi, TX 78406-9704, USA

## Abstract

Availability of water causes major variation in cotton yield. Water use efficiency confers meanings of water conservation (i.e., savings of water and/or costs of water application) and transpiration efficiency (i.e., increasing productivity per unit of water transpired). Because of the commonality in the pathways shared between transpiration and CO<sub>2</sub> assimilation, there is a strong link between crop growth and transpiration. This paper briefly reviews the circumstances leading to water use efficiency of cotton through water conservation, but fully explores our knowledge and water use as it relates to the transpiration efficiency and productivity of the cotton plant. Emphasis is placed on our understanding of carbon isotope discrimination as it relates to transpiration efficiency and productivity.

## Introduction

There is little question that water causes major variation in cotton yield. It is understandable why we place so much importance on improving our knowledge on the factors controlling crop water use and the limitations of water stress on crop development and productivity in our effort to improve the efficiency of crop water use. However, the term "water use efficiency", is ambiguous. It may confer a meaning of water conservation (i.e., savings of water and/or costs of water application from a given supply or infer increasing productivity per liter of water applied) or it can infer transpiration efficiency (e.g., increasing productivity per unit of water transpired). Both meanings are important in the production of cotton. In this paper we briefly discuss circumstances leading to water use efficiency through conservation, and more fully explore our knowledge of water use as it is related to transpiration efficiency.

## Water Conservation

When water is freely available and crops have large LAI, most water is consumed by transpiration. Yet, a significant quantity of water is lost directly by evaporation from the soil surface. The crop's water use efficiency (WUE<sub>c</sub>) is often illustrated as follows:

$$WUE_c = Y / (ET) \quad (1)$$

where, Y is the crop yield and ET is the evapotranspiration (sum of water losses from evaporation and transpiration), discounting losses from percolation below the root zone and runoff. Data from Ritchie (1983) shows that when the soil surface is dry and LAI approaches 3.0, transpiration is the dominant component of crop water use and evaporation is negligible (Fig. 1). Yet, when the soil surface is dry and LAI < 3.0 or when the soil surface is wet, evaporative water loss is a significant component of total water loss and accounts for more than 15% of the total water use. Clearly, practices and plant attributes that reduce the exposure of soil to incoming radiation lowers evaporation and conserve water for transpiration and plant growth.

A number of management strategies enhance water conservation. These include: a) optimizing plant density, narrow row spacing and maintaining proper fertility, b) shifting growing seasons or maturity period to best utilize rainfall and the annual climate, c) controlling disease and

insects, d) eliminating needless transpiration from weeds, e) using crop residue as water vapor barriers, and f) adopting water conserving irrigation technologies (i.e., Low Energy Precision Application, micro-catchments, trickle irrigation, etc.). Water conservation strategies adopted are dependent on the climate, soils and water resources available to the farmer and must be designed within the constraints of the farm unit.

## Transpiration Efficiency

### *Direct measurements of transpiration efficiency*

There is a strong link between crop growth and transpiration because of the commonality in processes and pathways shared between transpiration and CO<sub>2</sub> assimilation. This linkage is not unique to cotton and has been described for numerous crops by de Wit (1958), Arkley (1963) and Tanner and Sinclair (1983). Similarly, there is a strong link between crop growth and ET because dry matter accumulation and maximum ET are so tightly coupled with solar radiation (Ritchie, 1983). Using data from Gerard *et al.* (1980), Grimes *et al.* (1969) and Jordan (1982) illustrates the tight coupling between cotton fiber yield and total water use (Fig. 2).

When water supplies become limited, plants react by slowing expansive growth, closing stomates and restricting water vapor and CO<sub>2</sub> exchange, shifting hormone levels within the plant, and slowing translocation. Frequent reactions of cotton to water deficit are illustrated in Table 1 and typify those observed by many C<sub>3</sub> plants. Because water vapor and CO<sub>2</sub> share common transport pathways, much research on cotton's response to water deficits and water use efficiency has focused on transpiration and CO<sub>2</sub> assimilation processes. Although cell growth and leaf expansion are the most sensitive growth processes affected by water stress (Hsiao *et al.*, 1976), suppression of leaf gas exchange and CO<sub>2</sub> assimilation is not far behind (Figs. 3, 4). Hutmacher and Krieger (1983) suggested that the nonlinearity in CO<sub>2</sub> assimilation observed at high leaf conductance (Fig. 4) when external CO<sub>2</sub> concentrations were high, resulted from limitations of photosynthetic processes in the leaf mesophyll and/or chloroplast. It is important to remember that the plant's CO<sub>2</sub> assimilation capacity is the product of the photosynthetic rate per unit leaf area and leaf area of the plant. Because transpiration and photosynthesis both depend on radiation capture and leaf growth is reduced with water stress, the photosynthetic capacity of cotton is irreparably harmed if water deficits occur during the important expansive growth stage, from first square appearance to flowering (Jackson and Gerik, 1990; Gerik *et al.*, 1994a).

Theoretically, crop yield in water-limited environments can be improved by increasing the ratio of dry matter or yield per plant, "Y", to water loss or transpiration per plant, "T". Transpiration efficiency may be estimated on a leaf (TE<sub>L</sub>), whole plant (TE<sub>p</sub>), or canopy (TE<sub>c</sub>) basis. On a gas exchange basis transpiration efficiency may be expressed as  $A/g_h$  where "A" is the assimilation of CO<sub>2</sub> by the leaf and "g<sub>h</sub>" is leaf conductance of water vapor. On a whole plant or canopy basis, transpiration efficiency may be estimated gravimetrically and expressed as g accumulated dry matter per liter water transpired.

Plant characteristics affecting the transpiration efficiency of cotton are listed in Table 2. Variability exists among cultivated cottons for most of these characteristics. Yet, correlations between dry matter accumulation or yield and transpiration efficiency are complicated by interrelationships among many of these plant characteristics. Quisenberry and McMichael (1991) studied the transpiration efficiency (whole plants) of cultivated and primitive race stocks of *G. hirsutum* L. and *G. barbadense* L. and race stocks of *G. herbaceum* L. and were unable to find any appreciable differences in the amount of water used, but they did observe differences in dry matter production and days to permanent wilting among the genotypes tested. Furthermore, there was no significant interaction between genotypes and the different environments used in the study regarding total water used, dry matter produced, or water use efficiency. Yet, among all genotypes studied they found that the difference in transpiration efficiency of whole plants (the total dry matter accumulated per liter of water) was as about 28%, however, they found that the transpiration

efficiency of primitive race stocks of *G. hirsutum* L. was 14% higher than the best cultivar.

Because the primitive race stocks were more efficient in water use as a group than the cultivated genotypes, Quisenberry and McMichael implied that cotton geneticists and breeders have inadvertently selected against transpiration efficiency in developing modern, high yielding cultivars. However, examining the cultivated genotypes only Quisenberry and McMichael's reported a high correlation between cumulative dry weight and water use efficiency (Fig. 5). Therefore, identification of cotton genotypes with high water use efficiency (dry matter/water transpired) could have a direct link to dry matter production and yield when water supplies are limited.

Selection of genotypes for improved transpiration efficiency with conventional methods is time consuming and imprecise because the estimates of transpiration efficiency from leaf gas exchange and gravimetric methods is quite variable. This variability typically arises from rapidly changing atmospheric conditions during measurements and cumbersome methodology that prevents sufficient plant sampling to reduce large plant to plant variation observed in plant growth and leaf gas exchange.

### *Indirect measurement of transpiration efficiency*

#### Theory of carbon isotope discrimination ( $\Delta$ )

Findings that carbon isotope discrimination ( $\Delta$ ), the difference in C isotope composition between the plant and the CO<sub>2</sub> in air in which it is grown, can provide an indirect measure of transpiration efficiency (Farquhar *et al.*, 1982; Farquhar and Richards, 1984) has renewed interest in introducing transpiration efficiency as a selection criterion in plant breeding programs. Using  $\Delta$  as an indirect measure of transpiration efficiency is based on the fact that ribulose 1,5-bisphosphate carboxylase, the primary carboxylating enzyme in C<sub>3</sub> plants, discriminates against heavy carbon isotopes, like <sup>13</sup>CO<sub>2</sub>, and favors the lighter and more abundant isotope <sup>12</sup>CO<sub>2</sub>. Mathematically,  $\Delta$  can be explained on a leaf level by the following equation:

$$\Delta = a + (b - a)(c_i/c_a) - d \quad (2)$$

where  $c_a$  and  $c_i$  are the volumetric CO<sub>2</sub> concentrations in the external air and internal air in the leaf, respectively, and  $a$ ,  $b$ , and  $d$  are parameters for isotope effects on discrimination caused by diffusion in air ( $a$ ), carboxylation ( $b$ ), and respiration and other processes ( $d$ ). Steady-state studies of  $\Delta$  suggest that isotopic fractionation due to  $a$ ,  $b$ , and  $d$  are 4, 27, and 3‰ (i.e., air and products generated by carboxylation and respiration are depleted in <sup>13</sup>CO<sub>2</sub> by these amounts) (Brugnoli *et al.*, 1988). Greater detail concerning the theory of  $\Delta$  is given by Farquhar and Lloyd (1993).

The transpiration efficiency of a leaf is defined as the ratio of the rates of photosynthetic uptake of CO<sub>2</sub> ( $A$ ) to the transpiration of water from the leaf ( $T$ ) and can be described as follows:

$$TE = A/T = g_c(c_a - c_i) / g_h(H_i - H_a) \quad (3)$$

OR

$$TE = A/T = 0.62 g_c (1 - c_i/c_a) / (H_i - H_a)$$

where  $A/T$  is the transpiration efficiency (TE) of the leaf, 0.62 is the ratio of the leaf diffusive conductance to CO<sub>2</sub> ( $g_c$ ), water vapor ( $g_h$ ), and  $H_i$  and  $H_a$  are the volumetric concentrations of water vapor within the leaf and in the external air, respectively. It should be noted that Equation 2 still retains stomata effects (as they influence  $g_c$  and  $g_h$ ) in that  $c_i/c_a$  is influenced by the balance between the factors influencing the supply of CO<sub>2</sub> to the leaf and those influencing the mesophyll demand for CO<sub>2</sub> by photosynthesis.

From Equations 2 and 3, it is apparent that  $\Delta$  and transpiration efficiency are independently related to  $c_i/c_a$ . Instantaneous values of  $\Delta$  and transpiration efficiency should exhibit a negative, linear association providing  $c_a$  and  $H_i - H_a$  are similar for different treatments and parameters  $a$ ,  $b$ ,

and  $d$  are constant. Parameter "a" may vary slightly depending upon the relative size of the boundary layer and leaf diffusive conductance (Farquhar and Lloyd, 1993). Parameter "b" could vary depending upon the extent of  $\text{CO}_2$  fixation by Ribulose 1,5-bisphosphate carboxylase, but to date, substantial differences in "b" have not been detected in  $\text{C}_3$  crops. The theoretical basis for "d" is complex and is discussed by Farquhar and Lloyd (1993).

When  $\Delta$  is measured from carbon of a leaf, it provides a temporally- and spatially-integrated estimate of leaf transpiration efficiency or more precisely  $A/g_c$ . The  $\Delta$  value is assimilation-weighted because photosynthetic rates influence the total size of the carbon pool (Hall *et al.*, 1994). Periods when photosynthesis is high have more influence on  $\Delta$  than when photosynthesis is low. Moreover, the assimilation-weighted aspect of  $\Delta$  is useful, because it is equivalent to measuring accumulated carbon via photosynthesis over a period per unit of water transpired.

### Field results and $\Delta$

The validity of theory for transpiration efficiency at the leaf level, as illustrated in Equation 3, is well established. A positive, linear relationship between  $\Delta$  and  $c_i/c_a$  (Fig. 6) and a negative, linear relationship between  $\Delta$  and leaf transpiration efficiency (Fig. 7) have been verified for several  $\text{C}_3$  crops. Studies of barley, bean, cotton, cowpea, peanuts, and wheat confirm a negative, linear relationship between  $\Delta$  and whole plant transpiration efficiency (Farquhar and Richards, 1984; Evans *et al.*, 1986; Hubick *et al.*, 1986; Hubick and Farquhar, 1988; Ehleringer *et al.*, 1991; Ismail and Hall, 1992). It is important to remember that the relationships between  $\Delta$  and instantaneous measurements of  $A/g_c$  or  $c_i/c_a$  may be complex. For example, when the water vapor gradients between the leaf and air ( $H_i - H_a$ ) are high and strongly influence transpiration, leaf temperature will increase and alter photosynthesis and  $c_i/c_a$  (Hall *et al.*, 1994).

While the negative relationship between  $\Delta$  and leaf and/or whole plant transpiration efficiency is well established, positive relationships between  $\Delta$  and productivity were recently established in bean (White, 1993), barley (Acevedo, 1993), and wheat (Condon *et al.*, 1987; Ehdai *et al.*, 1991; Condon and Richards, 1993; and Morgan *et al.*, 1993) (Fig. 8). Similarly, Gerik *et al.* (1994b) found a positive, linear relationship ( $r^2 = 0.80$ ) between  $\Delta$  of young cotton leaves (i.e., at appearance of first squares) and lint yield in Texas. These reports suggest that stomatal conductance is positively associated with crop yield. Hutmacher and Krieger (1983) reported differences in stomatal conductance among Upland Cotton (*G. hirsutum* L.) varieties and Cornish *et al.* (1991) attributed genetic advances in yield of Pima cotton varieties (*G. barbadense* L.) to selection of plants with higher stomatal conductance. Therefore, plants with high  $\Delta$  values may have higher stomatal conductance and higher potential yield capabilities than plants with low  $\Delta$ .

### Inconsistencies in $\Delta$ relationships

Situations have occurred when the relationship between  $\Delta$  and transpiration efficiency and  $\Delta$  and productivity do not conform to theory. Negative association between  $\Delta$  and productivity and positive association between  $\Delta$  and transpiration efficiency have been reported (Acevedo, 1993; Morgan *et al.*, 1993). Hall *et al.* (1994) point out that these inconsistencies arise from complexities in making the assessments. Inconsistency with theory may arise from the following factors:

- Sampling time - genotypic effects on transpiration efficiency are greatest early in the morning when  $\text{CO}_2$  assimilation and conductance is greatest, whereas drought effects on assimilation and transpiration frequently occurs in the afternoon;
- Tissue sampling - carbon is assimilated and translocated to different organs at different times. The isotopic composition is most influenced by discrimination at the time when the carbon is assimilated. This is especially true of tissue obtained from grain or fruit of indeterminate plants. Therefore, isotopic

Growth stage -	composition of grain or fruit tissue may not accurately reflect the $\Delta$ during grain or fruit development; the reproductive load may exert considerable differences in assimilation, respiration and carbon partitioning, therefore $\Delta$ may differ between vegetative and reproductive growth stages;
Plant morphology -	differences in leaf orientation, leaf shape, or leaf size may change leaf temperature and change transpiration, and photosynthesis. These changes may affect the $c_i/c_a$ ratio and $\Delta$ ;
Edaphic influence -	extreme nutrient deficiencies can decrease transpiration to a greater extent than photosynthesis; high soil strength reduces root development, plant available soil water and decreases $\Delta$ , partial stomatal closure and increases in transpiration efficiency and alters species differences to soil water limitations; salinity decreases $\Delta$ , stomatal conductance and increases photosynthetic capacity; rooting volume (i.e., influenced by the size of container, rooting depth, and root density) changes $\Delta$ through effects on drought; mechanical impedance and drought can increase the total plant weight/leaf area ratio and may increase respiration as a proportion of total carbon gain; and
Atmospheric factors -	temperature, vapor pressure, and wind speed can affect assimilation and stomatal conductance and alter the relationship between transpiration efficiency and $\Delta$ . When $\Delta$ is used to assess genotypic or edaphic effects on transpiration efficiency, similar atmospheric conditions should be used. Also, large diurnal changes in temperature, vapor pressure, and wind speed can complicate comparisons between $\Delta$ and gas exchange measurements.

Knowledge of these factors is important in reducing the influence of confound factors on  $\Delta$  and with the relationship between  $\Delta$  and transpiration efficiency and between  $\Delta$  and productivity.

### Transpiration efficiency and yield considerations

The inverse relationship between  $\Delta$  and transpiration efficiency and between  $\Delta$  and yield (i.e., high photosynthetic capacity) is not surprising. Most work on  $\Delta$  has focused on its role in improving crop transpiration efficiency. Yet, evidence is growing that suggests it may aid in identifying plants with high yield and productivity. However, it is unlikely  $\Delta$  can serve these two roles simultaneously, since  $\Delta$  theory is based on the  $\text{CO}_2$  gradient between the air and the substomatal cavity and because  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor exchange between the leaf and air use similar pathways, but move in opposite direction.

The questions then arise, "Do you improve crop transpiration efficiency and use varieties with low  $\Delta$  values?" or "Do you maximize crop productivity and use varieties with high  $\Delta$  values?". We believe the answer to these questions lie in the environment and climatic conditions where the crop will grow. If the crop is heavily dependent on stored soil water, as in a Mediterranean climate, then varieties with high transpiration efficiency and low  $\Delta$  would produce the highest yield. If, however, the crop is irrigated or heavily dependent on precipitation during the growing season, then varieties with high  $\Delta$  values which maximize  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor exchange would have the highest potential yield.

### Using $\Delta$ to improve transpiration efficiency and productivity

For  $\Delta$  to be a useful in manipulating  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor exchange, it's genetic expression must be consistent over environments. Generally,  $\Delta$  values have been stable over locations and environmental conditions for varieties of a number of crops including, peanut (Wright, 1993),

barley (Craufurd *et al.*, 1991), cowpea (Hall, 1992), and wheat (Condon and Richards, 1992) and cotton (Gerik *et al.*, 1994b). Yet, differences in rooting depth (i.e., plant available soil water), pot size, or large differences in vapor pressure deficit have produced inconsistent rankings in  $\Delta$  for cowpea (Hall *et al.*, 1992, Hall *et al.*, 1993), wheat (Richards and Condon, 1993), and common bean (White, 1993).

The dependability of  $\Delta$  as a genetic trait for improving transpiration efficiency and/or yield depends on its heritability and inheritance. Because heritability assessments are heavily dependent on sampling procedures, experimental error must be minimized. For  $\Delta$  studies, it is important to obtain carbon that is assimilated during similar growth stages and time of season. This minimizes the effect of factors which give rise to inconsistencies with  $\Delta$  theory (see previous discussion). For example, Hall *et al.* (1990) found that the broad-sense heritability of  $\Delta$  from seed of cowpea was one-half the value obtained from leaves, but the estimates were similar under both well watered and water stressed conditions. Condon and Richards (1992) observed that sampling vegetative tissue from young wheat was more effective in identifying high and low  $\Delta$  varieties than other plant parts, but they acknowledge that early sampling may not accurately assess transpiration efficiency in the middle and late growth stages, when drought often occurs. Therefore, it is important that sampling procedures for  $\Delta$  are standardized using tissue of similar type (i.e., leaf blades) of the similar age (i.e., nodal position), and collected during a same growth stage and time of day (i.e., to minimize differences in starch accumulation in leaves).

The inheritance characteristics of the  $\Delta$ , must be known to successfully select and maintain the trait in succeeding generations. Traits with high broad-sense heritability (i.e., 0.80) are easily passed to following generations, while traits with high narrow-sense heritability are easily lost if selection occurs in early generations of selection. Estimates of broad- and narrow- sense heritability of cotton are not known, but broad-sense heritabilities of  $\Delta$  for wheat ranged from 0.78 to 0.94 (Condon and Richards, 1992) and the broad-sense heritability of two cowpea crosses were 0.58 and 0.27 (Hall *et al.*, 1994). Narrow-sense heritability of  $\Delta$  (obtained from  $F_2$  to  $F_3$  regression) was moderate (0.25 and 0.31) for two crosses of cowpea (Hall *et al.*, 1994). Therefore, early selection for  $\Delta$  may be possible for wheat, but is questionable for cowpea.

Work is underway to understand the heritability of  $\Delta$  in a number of crops, including wheat, cowpea, and peanut (Hall *et al.*, 1994). The number of genes involved in the inheritance of  $\Delta$ , and dominance relations, depend upon the species and parents selected. Selection for  $\Delta$  in the  $F_3$  generation of wheat in southern Australia was more effective than selection from  $F_2$  lines (Hall *et al.*, 1994). The advantage in delaying selection one generation was attributed to a reduction in the error variance in a pooled sample of several plants from an  $F_3$  line compared to a sample from a single  $F_2$  plant.

#### Importance between transpiration efficiency and agronomic characteristics

Researchers should keep in mind that the traits influencing  $\Delta$ , yield, and water use efficiency are heavily influenced by edaphic constraints and agronomic traits of the crop. For example, root systems can explore and extract water from the soil may cause some hybrids to differ  $\Delta$ , yield, and water use efficiency more strongly than the parents (Hall *et al.*, 1994). In water limited environments, crop yield (Y) can be explained as follows:

$$Y = \sum_{i=0}^{i=n} E_i \times W_i \times (T_i/E_i) \times HI_i \quad (4)$$

where 'i' is an approximation in days from zero (which may correspond to emergence or anthesis) to 'n' (which may correspond to maturity), 'E<sub>i</sub>' is the quantity of plant available water and depends on rainfall, soil physical characteristics and rooting depth, 'T<sub>i</sub>' is transpiration and is influenced by the evaporative demand, canopy coverage, and leaf conductance, 'W<sub>i</sub>' is the

transpiration efficiency per day and 'HI<sub>i</sub>' is the harvest index or partitioning of carbohydrate to yield (Hall *et al.*, 1994). Yet, some interactions between these components and agronomic traits could occur where: deeper rooting could increase  $E_i$  and  $T_i/E_i$ , higher stomatal conductance would increase  $T_i$  and, therefore,  $E_i$ , but decrease  $W_i$ , higher photosynthetic capacity would increase  $W_i$ , but decrease  $T_i/E_i$  if associated with smaller leaves and less ground cover (Hall *et al.*, 1994).

The effect on yield by selecting for higher transpiration efficiency (i.e., by indirectly selecting for lower  $\Delta$ ) depends on the genetic associations between earliness, harvest index, rooting depth, and the rate of leaf area development. Genotypic differences in flowering and maturity have a big effect on all parameters in Equation 4 (Hall *et al.*, 1994). Because plant breeders typically select genotypes with optimal flowering and reproductive periods for the prevailing climate therefore, the confounding influences of phenology on  $\Delta$  is usually small. Ideally, the components in Equation 4 should be independent so that increases in any of them results in higher yield. Genetic associations between  $\Delta$  and these agronomic traits vary and depend on the crop studied. With common bean, cowpea, wheat, and barley, early flowering was associated with high leaf  $\Delta$  (White, 1993; Ehdaie *et al.*, 1991, Richards and Condon, 1993; and Hall *et al.*, 1993). Richards and Condon (1993) point out that this association may have arisen from the unconscious selection by breeders for cultivars with faster growth, higher stomatal conductance, and shorter vegetative periods.

Positive associations between  $\Delta$  and harvest index have been observed for peanut (Wright *et al.*, 1993) and cowpea (Hall *et al.*, 1993). However, association between  $\Delta$  and harvest index should be carefully examined with cultivars of similar phenology because late flowering genotypes usually have lower harvest index. Early canopy growth and  $\Delta$  were positively associated for wheat grown under well watered conditions (Richards and Condon, 1993). Finally, White (1993) reported a positive association between rooting extent and  $\Delta$  when common beans were grown under water limited conditions.

### Summary

Relatively little progress has been made in increasing productivity of cotton or other major crops per unit of water or solar radiation, even though dryland and irrigated yields have increased. These yield increases have arisen mainly from changes in carbohydrate partitioning favoring fruit production (Gifford *et al.*, 1984), although recent work suggest that genetic advances in yield of Pima cotton varieties (*G. barbadense* L.) resulted, in part, from selection of plants with higher stomatal conductance and photosynthesis (Cornish *et al.*, 1991). Nevertheless, selection for photosynthesis and stomatal conductance, per se, has not been used in improving yield of cotton and other field crops. Measurements of photosynthesis and stomatal conductance with conventional gas exchange techniques are too variable, measuring plant performance over a brief period time. Integrated over the season small changes in leaf gas exchange can result in large differences in total carbon uptake or water use. Errors associated with direct gas exchange measurements may be too large to detect small gains in gas exchange efficiency. In contrast,  $\Delta$  appears to be more effective than conventional gas exchange measurements in detecting genotypic differences in transpiration efficiency and productivity for several important crops (Hall *et al.*, 1992).

The crucial role of water in production of cotton will not change. Industrial, municipal, environmental, and recreational demands for water will intensify. Cotton farmers must continually examine and adopt sound water conservation practices. At the same time scientists must continue to improve our understanding of crop water use and productivity. We believe carbon isotope discrimination provides us with a new tool to improve the transpiration efficiency and productivity of field crops. Whether carbon isotope discrimination can be use to improve water use efficiency of cotton remains to be answered.

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Table 1. Effects of water deficits on plant characteristics of cotton (Jordan, 1986; Krieg and Sung, 1986).

Plant character	Response under water deficit †
Leaf area	
- whole plant	----
- single blade	----
Leaf number	----
Total nodes	----
Total fruiting branches	----
Daily photosynthesis	--
Daily assimilate retained by leaf	++
Squares shed	----
Bolls per plant	
- Total	----
- At first position	----
Bolls per dm <sup>2</sup> leaf area	++
Bolls retained	++
Boll weight (g lint/boll)	-
Lint yield	----
Harvest Index	
- (yield: total dry matter)	--

† The symbols, + and -, signify positive and negative plant responses to water stress. The number of consecutive symbols (i.e., one to four) represent the magnitude of the response from slight to highly responsive.

Table 2. Phenological, physiological, morphological, and agronomic characteristics which affect transpiration efficiency of cotton.

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Plant character	
Phenological	Time to flowering
	Time of flowering
	Leaf appearance rate
Physiological	Stomatal response
	Membrane stability
	Enzyme stability
	Osmoregulation
	ABA, growth regulator regulation
	Leaf expansion
	Fruit retention
Morphological	Leaf thickness
	Leaf area/shape
	Root architecture & length
Anatomical	Stomatal density
	Cuticle waxiness
	Root/Stele diameter
	Xylem diameter

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- Figure 1. The relationship between leaf area index (LAI) and the ratio of transpiration (T) to maximum evapotranspiration ( $ET_{max}$ ) for cotton when soil surfaces are wet and dry (redrawn from Ritchie, 1983).
- Figure 2. The relationship between the total water use and lint yield of cotton (redrawn from Jordan, 1982).
- Figure 3. The relationship between leaf water potential and photosynthesis of field grown cotton (unpublished data, K.L. Faver and T.J. Gerik, Blackland Research Center, Temple, TX, USA).
- Figure 4. The relationship between gross photosynthesis on leaf conductance of water vapor for cotton (redrawn from Hutmacher and Krieg, 1983).
- Figure 5. Relationship between cumulative dry weight and transpiration efficiency (g dry matter / g water used) for seven cotton cultivars in two glasshouse experiments (from Quisenberry and McMichael, 1991).
- Figure 6. The correlation between on-line measurements of carbon isotope discrimination ( $\Delta$ ) in ‰ as a function of the ratio of intercellular to ambient  $CO_2$  concentrations ( $c_i/c_a$ ). The line represents the theoretically expected relationship using Equation 2 (redrawn from Ehleringer *et al.*, 1991).
- Figure 7. Transpiration efficiency of 65 day old cotton plants from six cultivars versus carbon isotope discrimination ( $\Delta$ ) of the youngest leaves of the plants (redrawn from Hubick and Farquhar, 1988).
- Figure 8. Relationships between carbon isotope discrimination ( $\Delta$ ) and grain yield (A) and above-ground dry matter productivity (B) for irrigated and nonirrigated wheat genotypes in 1989 (redrawn from Morgan *et al.*, 1993).