39

Transpiration Efficiency: Avenues for Genetic Improvement

G. V. Subbarao, Chris Johansen, and R. C. Nageswara Rao
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India

Graeme C. Wright
Queensland Department of Primary Industries, Kingaroy, Queensland, Australia

I. INTRODUCTION

In view of the increasing demand for water for nonagricultural uses (such as for urban and industrial uses), and to rationally redeploy available water resources for more areas of crop production, it is important to optimize the use of water for crop production. Agricultural research has a major responsibility to develop and use techniques and practices that will result in more effective use of water in farming systems. This involves improvement of *water use efficiency* (WUE), defined here as aerial dry matter production of a crop per unit of evapotranspiration (ET). *Transpiration efficiency* (TE) is a component of WUE, being aerial dry matter production per unit of water transpired by the crop. The difference between WUE and TE is important, as suppression of soil evaporation and transpiration by weeds can improve WUE without improving TE, which is a direct measure of the crop species performance. Plant attributes (such as canopy structure, rate of canopy development, etc.) and management means (such as manipulating plant population, optimizing planting dates, fertilizer management, etc.) can modify soil evaporative losses (E_s) relative to transpiration (T), and can therefore affect WUE to a greater extent than can TE.

Generally, any means (either genetic or management) that promotes early canopy development and radiation interception will reduce E_s and increase T (as evaporational losses would be negligible once the canopy closes), often with little or no increase in total ET [1,2]. For example, in Syria, erect chickpea lines intercept less solar radiation, thus permitting greater evaporative water losses during early growth, and consequently, they had a lower WUE value than that of chickpea lines with a prostrate habit [3]. Similarly, leafless pea had a lower WUE value than that of either semileafless or conventionally leafed types [4]. Leafless pea intercepts less radiation than semileafless or conventionally leafed pea, and therefore the crop suffers greater E_s losses. Fertilizer application can increase WUE [5], as it promotes greater leaf area development and reduces E_s relative to T. In many legumes, a basal dose of nitrogen and phosphorus promotes early growth rate and thus minimizes E_s [2]. Other management options,

such as improving water delivery systems, nutrient management approaches, and improved cultural practices, could enhance WUE by minimizing E_s.

Also, vapor pressure deficits (vpd) during the growing season play a major role in determining the WUE. When other factors are nonlimiting, the cost of producing dry matter (in terms of water) would be much higher under high vpd (i.e., results in low WUE) compared to low vpd (i.e., results in high WUE) conditions. For instance, in Mediterranean environments, the seasonal WUE varies from 8.5 g/kg (grams of dry matter produced per kilogram of water evaporated or transpired) in midwinter to only 2.5 g/kg in midsummer [6]. Thus management (by early planting, optimizing the plant population and fertility requirements, etc.) and genetic means (such as early vigor, rapid canopy development, cold tolerance, and tolerance to diseases such as *Ascochyta*) that would permit full canopy development, and rapid dry matter accumulation during periods when the vpd is low, would maximize WUE for the growing season. Early planting (i.e., winter planting) in Mediterranean climates usually allows rapid canopy development and dry matter production when the vpd is low and thus results in higher WUE of both dry matter production and grain yield [2,7].

However, once options for minimizing E_s relative to T are exhausted, further improvements in WUE are possible for a given crop only by genetically improving the TE value of that crop. Under water-limited environments, yield is a function of T, TE, and harvest index (HI) [8]. Increased production may result from increased TE if other components (i.e., T and HI) are independent [9] and not affected. By reducing T or by allowing more efficient use of transpirational water in photosynthesis, available soil moisture could be better rationed during the cropping period, which should increase productivity [8].

Plants lose water as they fix carbon dioxide (CO_2) from the air. The loss is inevitable because it is necessary for CO_2 to dissolve in water in order to become available for photosynthesis [10]. This would lead to evaporation as the wet cell surface inside the leaf is exposed to the atmosphere. CO_2 diffuses down a concentration gradient to the leaf interior and water diffuses outward along a decreasing humidity gradient [10]. The lower the external humidity, the higher will be the evaporation, when all the other factors are constant. This two-way diffusion of CO_2 and water forms the basis of improving TE [10]. Cultivars with improved TE are those with inherent characteristics that will allow increased production of dry matter per unit of water transpired [11]. This chapter focuses on exploring the opportunities for genetic improvement of the various morphological, physiological, and biochemical factors that determine TE in C3 crop plants and assesses the scope for exploiting this trait in plant breeding programs.

II. FACTORS AFFECTING TE

Transpiration efficiency is a function of both environmental and plant attributes related to resistances to CO_2 fixation by leaves. Under some circumstances, the environment can have a significant influence on TE. Variation in humidity and temperature can influence TE [12]. TE is governed by three factors: (a) the vpd between air and leaf, (b) the CO_2 gradient from the air to the leaf, and (c) the diffusion resistances for both CO_2 and water [13]. The first factor is mainly abiotic, although the surface temperature of the leaf will actually respond to the atmosphere (e.g., radiation and vpd). The last two factors are largely plant-controlled factors. Also, incident irradiance has an important effect on TE [14]. There is an optimum irradiance for maximum efficiency of water use which is usually less than the irradiance incident on a leaf [15] (see Section II.C for further discussion on this aspect).

A variety of morphological, anatomical, physiological, phenological, and biochemical

processes enable crop plants to regulate and ration water for production of dry matter and yield in a given agroecological production system. These are discussed below.

A. Stomatal Behavior

Stomata may exert relatively greater control on water loss than that exerted by CO_2 uptake. This is because the rate of biochemical reactions involved in CO_2 assimilation (A) influences removal of CO_2 from cell solutions and thereby affects CO_2 gradients [16]. This is in addition to resistances faced by CO_2 in its transport, with stomatal resistance perhaps being a smaller component of the total resistance for CO_2 than for water [16]. Stomatal aperture plays a key role in maintaining the balance between taking up CO_2 and losing water [17]. Stomatal movements are the most rapid means by which plants can adjust to changes in the environment [17]. In particular, stomata respond directly to ambient humidity [18], thereby strongly influencing plant TE.

For C3 crop plants, optimization of TE normally requires midday stomatal closure [12]. Such behavior has been observed frequently and is at least partly attributable to the effect of water deficit [19] or is a direct stomatal response to vpd [20]. If diurnal variation in a natural environment were regular and predictable, optimization would require only an appropriate circadian rhythm for stomatal movement [17]. However, this is usually not the case, and therefore optimization requires that the plant respond directly to the changing environment [17]. This demands that stomata respond to changes in external environmental conditions, which in turn influences rates of T and A. Thus stomata should be capable of controlling gas exchange by a feedforward process, making it possible for T to decrease when environmental changes tend to enhance the rate of T (e.g., under high vpd), or for intercellular partial pressure of CO_2 (P_i) to increase when environmental changes would tend to enhance A [21].

Reduced stomatal aperture increases TE because the rate of A is reduced proportionately less than that of T [22–24]. This often happens when plants are subjected to moderate levels of water stress. Factors such as osmotic adjustment (OA) can significantly influence stomatal aperture and thus determine TE under moisture stress. For example, the critical leaf water potential for stomatal closure varies with the level of OA [25,26]. Crop plants show genetic variation for stomatal characteristics such as stomatal density, aperture size, opening patterns, and sensitivity to changes in internal plant water status and soil water status [27–30]. This, in turn, affects their ability to regulate and optimize water use [31,32]. The existence of genetic variation in stomatal characteristics suggests that it may be possible to develop cultivars that utilize water more efficiently, thus contributing to their adaptation to moisture-limiting environments [33,34].

B. Canopy Structure

The aerodynamic resistance of a crop can play a role in determining the relative importance of stomatal conductance (g_s) to TE. If the canopy resistance to heat and water vapor diffusion is large, an increase in g_s would tend to cool and humidify the air in the boundary layer, thus lowering the leaf-air vpd; TE would then increase [35,36]. Thus cultivars with greater g_s could assimilate more at the same level of TE [21,37]. Under field conditions, the boundary layer that forms over crop canopies could cause gas exchange to be less dependent on g_s, and is thus one of the important factors affecting TE [38].

A plant with high TE may be able to decrease the aerodynamic conductance of its canopy boundary layer through greater rigidity of the canopy, while maintaining a high g_s value [39]. This provides it with ready access to CO_2 within the canopy, which is not depleted compared to the bulk atmosphere, while retaining water vapor within the canopy. Boundary layer resistance

is a function of the thickness of the unstirred air boundary layer adjacent to the leaf, which in turn is determined by the leaf size [40]. Smaller leaves have a thinner unstirred boundary layer [40]. Thus boundary layer resistance at the canopy level depends on canopy architecture, which is determined by leaf size, leaf arrangement, growth habit (i.e., prostrate versus erect), and height of the canopy. With a low canopy conductance, leaf water equilibrates with an adjacent airspace of higher humidity than the bulk atmosphere [39]. However, such a canopy structure may create sufficiently high levels of humidity within the canopy to be conducive to fungal disease development, thus negating the positive effects of higher TE on biomass production or yield. For instance, in chickpea the closed canopy types, which have greater WUE than that of open canopy types [3], also provide a conducive microenvironment for the development of *Botrytis* and *Ascochyta* blight diseases [41]. Thus the positive effects of such closed canopies on improving the TE of a crop and its production would depend on the availability of sources of resistance to such diseases, which could be incorporated into cultivars forming closed canopies if they lack disease resistance.

C. Leaf Movements and Surface Reflectance

Incident radiation is completely absorbed by the canopy once 100% ground cover is achieved and the incident energy is partitioned between T and A [10]. The proportional allocation differs between species and climates and from year to year [42]. The optimum irradiance for maximum TE is usually less than the irradiance incident upon a leaf oriented normal to the sun's rays [15,43,44]. This is primarily because T normally shows a positive relationship (linear or curvilinear) with increasing irradiance (due to rising leaf temperature and falling stomatal resistance), while A shows a downward curvilinearity with increased irradiance [6]. Leaf movements and surface reflectance provide a means of optimizing this radiation load on the leaf for the maximization of TE. This can be particularly advantageous in water-deficit environments, to dissipate the energy as latent heat, to minimize heat damage, and to optimize TE and radiation use efficiency (RUE) [45–48]. The main advantage of leaf movements is that they would allow maximum exposure of leaf area to direct radiation when evaporative demand is low and thus improve TE. Almost all crop plants show some degree of leaf movement in response to radiation, soil, and plant water status. However, the degree of leaf movement, and the threshold soil and plant water status that triggers these movements, varies among and within crop species, which could contribute partially to their growth performance in water-limited environments [31,49–51].

Leaf pubescence and surface reflectance can provide additional means of controlling leaf temperature and water balance, apart from stomatal control and leaf movement [52–54]. In near isogenic lines of soybean it was shown that lines with pubescent leaves had significantly lower T than either normal or glabrous isolines [52,55]. Leaf pubescence in *Encelia farinosa* reduced absorbance of irradiance as much as 56% compared with the nonpubescent plant *E. californica* [56]. This reduced absorbance can result in lower leaf temperatures and lower T [57]. However, leaf hairs can reflect radiation, which may reduce A. Nevertheless, it appears that in climates with high irradiance and temperatures, beneficial effects of reduced leaf temperature would more than counterbalance the effect of decreased light on A [58]. Other morphological features, such as cuticle thickness and wax deposits on the leaf surface, can to some extent control evaporational losses from the leaf surface [59–62]. There is genetic variability in a number of crop species for leaf surface wax levels and cuticle thickness [60–62].

D. Specific Leaf Area

Variation in TE in crop plants can result from changes in water vapor flux through stomata or by changes in photosynthetic capacity [28,63]. In wheat, variation in TE is caused by stomatal

mechanisms [28,64], while in groundnut it appears to be caused by variation in photosynthetic capacity [63,65]. Genotypic variation in photosynthetic capacity on a unit leaf area basis has been observed in many crops [66,67], and a significant negative correlation has been shown between photosynthetic capacity and specific leaf area [68]. This evidence suggests indirectly that the basis of variation in TE through specific leaf area (i.e., leaf thickness) may result from differences in photosynthetic capacity on a unit leaf area basis (see Section V.B for more discussion of this).

Root Systems

Root distribution, density, and resistance can influence water use in space and time. Thus WUE can be affected by the rate of growth and spread of roots, particularly during early stages of crop growth. Under receding residual moisture situations, profligate water use during early crop growth might lead to water-deficit conditions during reproductive growth stages. In such circumstances, induction of a large resistance within the plant to the flow of water through selection for smaller metaxylem vessel diameters in the seminal roots should change the pattern of water use for different growth phases [69]. Thus the same amount of water can be transpired to produce more grain yield. Selection for increased root resistance has been shown to be amenable to genetic manipulation in cereals [70,71]. Differences in root radial resistance to water flux have been suggested to occur among groundnut genotypes [72].

III. ASSESSMENT OF GENOTYPIC DIFFERENCES IN TE

Measurement of T in the field is quite complex [73]. Even the field measurement of ET is difficult in many situations where drainage from the root zone, water uptake from saturated zones, and runon and runoff from the area are difficult to measure both temporally and spatially. Transpiration is usually estimated from evapotranspiration measurements such as by (a) subtraction of an estimate of soil evaporation (E_s), which is often a seasonal constant, from the measured seasonal ET [74,75]; (b) daily water balance simulation using empirical functions to calculate T separately from daily calculations of ET, using measured plant parameters such as leaf area index (LAI) or ground cover [75,76]; or (c) measuring E_s and subtracting it from measurements of ET [77]. All of these measurement techniques, however, result in indirect estimates of T. Direct long-term estimates of TE require accurate measurements of the water used. Rates of water movement through plants can be measured using heat-pulse velocity techniques [78], but difficulties in volume calibrations have limited the accurate estimation of transpiration flux. However, recent improvements in heat-pulse instrumentation have reduced the calibration problems [79,80]. Technical problems related to data collection limit the number of plants that can be measured using this technique. This limits its use in genetic improvement programs where large numbers of plants and genotypes need to be characterized. Pot experiments can give reliable estimations of TE, as they allow accurate measurement of T and dry matter production, including roots. However, these experiments are extremely laborious and are not realistically applicable to screening germ plasm or to genetic studies associated with cultivar improvement [81].

Assessment of genetic variation in TE has often been made based on instantaneous measurements of CO_2 fixation and T from single leaves [82]. However, both of these processes vary markedly during the day and according to leaf and plant age. Thus these instantaneous measurements do not integrate performance throughout the life of the plant. Also these instantaneous measurements of TE cannot assess the impact of morphological or physiological adaptations to drought that may influence season-long TE and plant performance under

water-limited conditions [83,84]. Further, these measurements have large coefficients of variation and are thus usually not suitable for screening and selection studies [85]. It is therefore apparent that breeding for improved TE has been constrained by difficulties in measuring TE on a large number of plants under field conditions [86]. Selection criteria and methods are therefore needed that are efficient and can be used at least indirectly to select genotypes with high TE from large populations in the field.

IV. CARBON ISOTOPE DISCRIMINATION AND ITS RELATION TO TE

A. Theoretical Background

Carbon occurs naturally as two stable isotopes, ^{12}C and ^{13}C. Most carbon is ^{12}C (98.9%), with 1.1% being ^{13}C. As the ^{12}C isotope is lighter than ^{13}C, $^{12}CO_2$ diffuses faster than $^{13}CO_2$. Ribulose 1,5-biphosphate carboxylase (Rubisco) fixes the lighter isotope faster, thus discriminating against the heavier isotope ^{13}C [87]; these two effects cause the $^{13}C/^{12}C$ ratio to be lower in plants than in the ambient atmosphere. The link between TE and $^{13}C/^{12}C$ discrimination (Δ) is *via* the gas-exchange characteristics of the leaves [88]. Since the isotopes are stable, the information inherent in the ratio of abundance of carbon isotope ($^{13}C/^{12}C$) is invariant [88]. The extent of discrimination against the naturally occurring stable isotope ^{13}C during photosynthetic CO_2 fixation in C_3 plants is determined largely by the ratio of intercellular to atmospheric partial pressure (P_i/P_a) of CO_2 [81,88]. As Rubisco actively discriminates against $^{13}CO_2$ [35], $^{13}CO_2$ is concentrated relative to $^{12}CO_2$ in the intercellular spaces as P_i decreases. This concentrating effect results in Rubisco fixing an increased proportion of ^{13}C relative to ^{12}C, and Δ decreases. This is reflected in the carbon isotope ratio of C3 plants, which shows a ^{13}C value of around −25‰ [37]. Therefore, Δ normally correlates positively with P_i/P_a in C3 plants and not in C4 plants (Figure 1), where Rubisco plays a relatively minor role in overall CO_2 fixation. Thus according to theory, in C3 plants a lower ^{13}C discrimination is associated with a higher TE. Variation exists among C3 crop species in their photosynthetic rates (A). This leads to variation in P_i/P_a and is reflected in ^{13}C discrimination values ranging from −22 to −40‰, depending on the crop species [89]. For C4 crops, which have a higher TE than that of C3 crops, ^{13}C discrimination values range from −9 to −19‰; however, these lower values are due mainly to the alternative pathways of CO_2 fixation in C4 crops, such as PEP carboxylase, which does not discriminate between C_{13} and C_{12} [89].

The carbon isotope ratio ($\delta^{13}C$) can be calculated by comparing the ^{13}C to ^{12}C composition of a sample (R_{sample}) relative to the Pee–Dee–Belemnite (PDB) standard (R_{PDB}).

$$\delta^{13}C_{sample} = \left(\frac{R_{sample}}{RPDB} - 1\right) \times 1000$$

These $\delta^{13}C$ values can be used to calculate isotope discrimination (Δ), as described by Farquhar and Richards [28] and Hubick et al. [63]:

$$\Delta = \frac{\delta^{13}C_{air} - \delta^{13}C_{sample}}{1 + \delta^{13}C_{sample}\ 1000}$$

The absolute isotopic composition of a sample is not easy to measure directly; the mass spectrometer measures the deviation of the isotopic composition of the material from the standard.

$$\delta P = \frac{R_p - R_s}{R_s} = \frac{R_p}{R_s} - 1$$

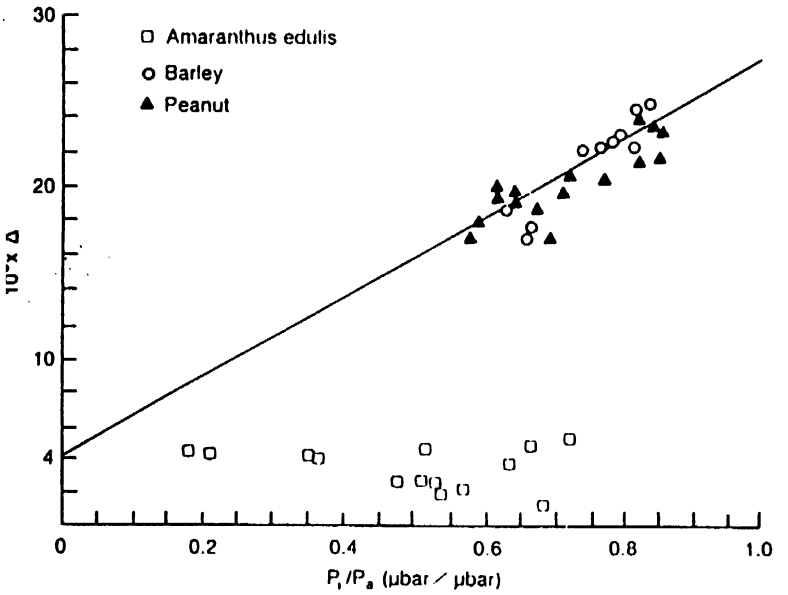


Figure 1 Carbon isotope discrimination, Δ, versus the ratio of intercellular and ambient partial pressures of CO_2 (P_i/P_a), when both are measured simultaneously in a gas-exchange system. Peanut and barley are C3 species and *A. edulis* is a C4 species. (From Ref. 37.)

$$\delta a = \frac{R_a - R_s}{R_s} = \frac{R_a}{R_s} - 1 \tag{4}$$

where δP is the carbon isotope composition of the plant sample, δa the carbon isotope composition of air, R_s the molar abundance ratio of $^{13}C/^{12}C$ of the standard, and R_p and R_a the molar abundance ratio of $^{13}C/^{12}C$ of the plant sample and air, respectively.

The reference material in determinations of carbon isotope ratios has traditionally been in CO_2 generated from a fossil PDB. The carbon isotope composition (δ) is standardized against PDB; atmospheric CO_2 has a value of $-8‰$ relative to PDB [90].

The carbon isotopic technique can also be used to quantify internal CO_2 levels of leaves on a long-term basis. Internal CO_2 levels (C_i) represent a balance between A and T. The existence of variation in C_i confirms the existence of genotypic differences in TE. Carbon isotope discrimination and TE are related through independent relationships with P_i/P_a [9]. This depends to different extents on the way in which plants coordinate leaf conductance to water vapor with the capacity for photosynthetic CO_2 uptake. Variation in coordination of leaf g_s and A can give rise to variation in P_i/P_a [9]. This, in turn, results in variation in TE and carbon isotope discrimination. It has been stated that if plant breeding is to affect detectable changes in TE of dry matter production, ($1-P_i/P_a$) needs to be modified substantially [91]. In theory, greater TE will be associated with low Δ if the leaf-to-air vpd remains constant [9].

Farquhar et al. [88] have suggested that Δ can be expressed based on gas exchange, as follows:

$$\Delta = a\frac{P_a - P_i}{P_a} + b\frac{P_i}{P_a} = a + (b - a)\frac{P_i}{P_a} \tag{5}$$

where a is the fractionation occurring due to diffusion in air, which is about –4.4‰ [92], b the net fractionation caused by carboxylation, which is about –27‰ [28], and P_a and P_i the ambient and intercellular partial pressures of CO_2, respectively.

The significance of b in equation (5) is that when g_s is small in relation to CO_2 fixation, P_i is small and Δ tends toward a (–4.4‰); when conductance is comparatively large, P_i approaches P_a, and Δ approaches b (–27 to –30‰; i.e., becomes more negative) [88]. Thus ^{13}C discrimination measurements should be useful in studying the genetic control of g_s in relation to A. Measurements of Δ in C3 crops may contribute to selection for TE. Theory [88] and supporting empirical evidence have shown that differences in intrinsic TE were associated with Δ in a range of crops [9,28,63,65,84,93,94].

The instantaneous ratio of CO_2 assimilation rate of a leaf (A) to its T is given approximately by

$$\frac{A}{T} = \frac{P_a - P_i}{1.6v} \tag{6}$$

where v is the difference in partial pressure of water vapor between the intercellular spaces and the surrounding air. The factor 1.6 is the ratio of the diffusivity of water vapor and CO_2 in air [35].

Farquhar et al. [35] suggested that equation (6) may be rewritten as

$$\frac{A}{T} = \frac{P_a(1 - P_i/P_a)}{1.6v} \tag{7}$$

Equation (7) emphasizes that a small value of P_i/P_a would result in an increase in TE for a constant vpd. Selecting for lower P_i/P_a thus should equate with selecting for greater TE [35]. Therefore, carbon isotope composition ($^{13}C/^{12}C$) of C3 plant tissues provides a long-term integrated measure of photosynthetic capacity [95].

To account for losses of carbon and water due to metabolic and physical processes, Farquhar et al. [35] modified equation (7) to describe the molar ratio, W, of carbon gain by a plant-to-water loss:

$$W = \frac{P_a(1 - P_i/P_a)(1 - \phi c)}{1.6v(1 + \phi w)} \tag{8}$$

where ϕc is the proportion of carbon lost due to respiration, and ϕw is the proportion of water lost other than through stomata (i.e., cuticular transpiration, etc.).

The presence of vpd (v) in equation (8) suggests that TE is affected by environment as well as by physiological responses of the plant [37]. Thus v can vary because of alterations in canopy interception and absorption of radiation via changing leaf angle and surface reflection properties (see Section II.C for more details) and increases or decreases in their coupling to ambient temperature by decreasing or increasing leaf size respectively.

Equation (8) also explains that TE is likely than Δ to be more affected by processes independent of those resulting in variation in P_i/P_a [9]. For example, genetic differences in respiratory losses of carbon, and nonstomatal water losses such as cuticular transpiration, may affect TE independent of P_i/P_a [9]. Thus equations (8) and (5) can be combined to show that Δ is largely dependent on P_i and vpd. Plants with higher TE values will therefore show less negative ^{13}C values or lower Δ values, giving a negative correlation between TE and Δ [35]. This theoretical relationship between Δ and TE in plants with a C3 photosynthetic pathway has been confirmed for several crops in pot [9,28,63,65,81,96–98] and field experiments [72,94,99] (Figure 2).

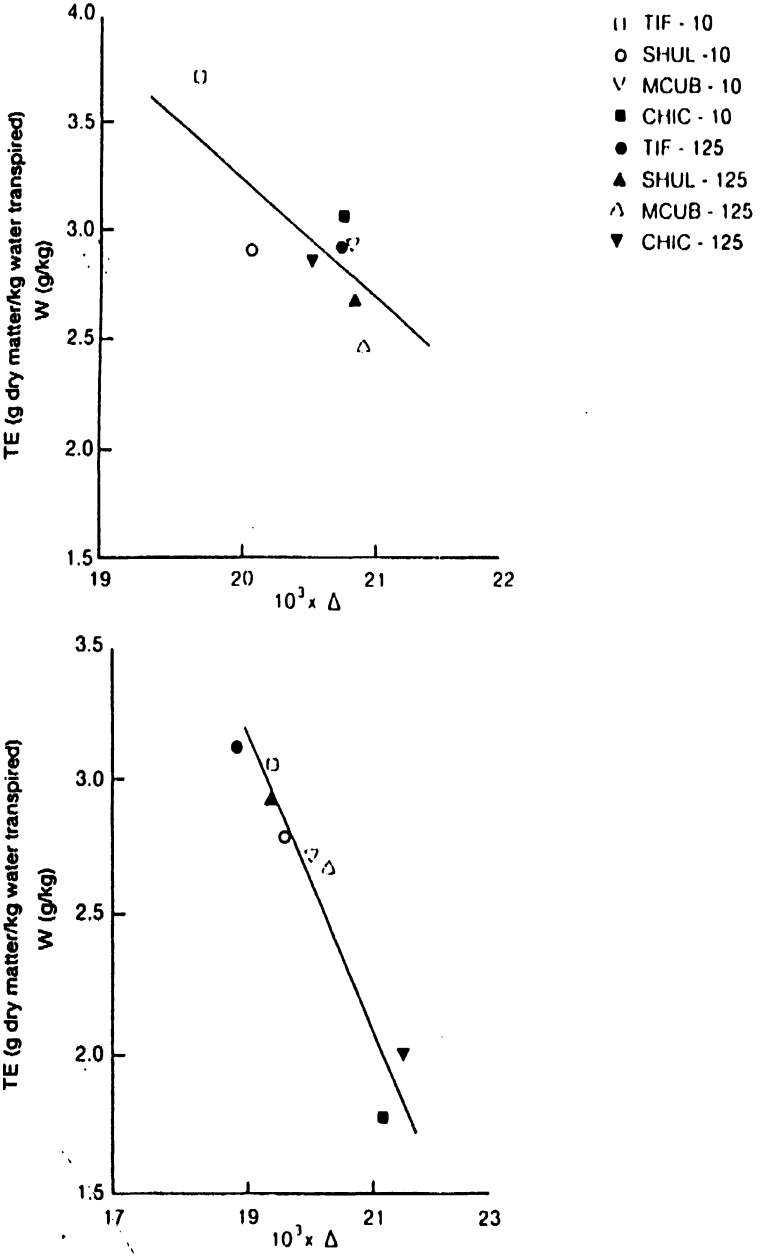


Figure 2 Relationship between transpiration efficiency (grams of dry matter per kilogram of water transpired) and carbon isotope discrimination (Δ) under well-watered and moisture-deficient conditions for a range of peanut cultivars grown under field conditions. (From Ref. 72.)

B. Water Deficit and TE

The degree of stomatal closure induced by water stress depends on the level of stress and the ability of the crop to meet evapotranspirational demands [100]. Direct measurement of TE using whole plant carbon and water balances have shown that moderate drought can cause an increase in TE of up to 100%, while extreme drought could substantially decrease TE [101]. A common response to water stress is a simultaneous decrease in A and T and an increase in leaf temperature [102]. If T decreases faster than A, then P_i will decrease [23,103]. This response results in water savings to the plant and a subsequent increase in TE. As Rubisco discriminates against $^{13}CO_2$, the proportion of $^{13}CO_2$ to $^{12}CO_2$ also increases within the leaf. Thus $^{13}CO_2$ discrimination decreases as stress becomes more pronounced [104]. In long-term observations in both growth chamber and field conditions, plants under water deficit had lower P_i, as indicated by ^{13}C discrimination analysis [28,105–108]. Several studies with a number of crop species have shown that moderate water stress leads to an increase in TE as indicated by the level of ^{13}C discrimination (Δ) [86,96,109,110]. Water stress resulted in about 2‰ lower Δ than that in well-irrigated plants of chickpea [105]. Similarly, for cowpea (*Vigna unguiculata*), it was shown that leaves sampled from field-grown plants in a dry environment had about a 1.5‰ lower Δ than that of plants from irrigated conditions [111].

Under severe water deficit, TE is reported to decrease [101]. This is because leaves become less efficient with respect to water and CO_2 exchange; water can still be lost through the cuticle, but CO_2 entry through stomata is severely restricted, causing reduced TE [17]. In groundnut, the relation between Δ and TE can break down under severe drought conditions, which could be related to increased respiratory losses of carbon [72]. A similar response has been reported for sunflower [98]. Respiratory losses of carbon can be as much as 40% under severe drought conditions [101].

C. Influence of Crop Canopy on Δ and TE

The negative relationship between Δ and TE might hold with individual plants in pots [63], or for small plots in the field [65,72] or field-grown crops [94], but might become inconsistent when results are extended to a large area, depending on the crop and microclimate [35]. First, the microclimate in field canopies is usually different than that of isolated plants in pots. This could lead to potential differences in stomatal control of T as influenced by environmental factors, and thus to a breakdown in the relationship between TE and Δ. This emphasizes the problem in the field, where the aerodynamic resistance of the crop has to be taken into account if the canopy and leaf boundary layer resistances to energy flux are very large [37,72]. Because of this it is possible that under high atmospheric evaporative demands, plants can have a high g_s, and thus a high Δ, but also high TE, due to complete closure of the canopy [112]. However, this is less likely to occur when crops have small LAIs, as would be the case under conditions where stress occurs early in the cropping season, because under these conditions the crop is more closely coupled to the atmosphere [38,112]. However, if the source of variation in Δ is the capacity for photosynthesis, the effects of boundary layers are unimportant [112], as seems to be the case for groundnut [9,72]. Therefore, at the crop level, identification of the causes underlying differences in Δ may become important.

Second, the nonstomatal loss of water (i.e., cuticular transpiration, soil evaporation) (ϕw) could vary with leaf area development and the level of wax deposition on the cuticle, and thus is not an independent fixed proportion of transpiration. This could influence Δ, as ϕw is an important component of WUE [equation (8)]. Also, since vpd is an important component of equation (8), any fluctuation in vpd during the growing season and the growth rate of a given variety during the growing season could influence TE. For example, those genotypes that grow

faster when vpd is small because of their adaptation to low temperatures could show a greater TE for the same Δ.

V. SCOPE FOR GENETIC IMPROVEMENT OF TE IN C3 CROP PLANTS

A. Relation Between Transpiration and Photosynthesis

Since the stomatal diffusion pathway is the same for both water vapor and CO_2 exchange, water is inevitably lost when stomata open and CO_2 is absorbed. Stomatal conductance is believed to adjust according to the assimilatory capacity of the mesophyll tissue [113]. That is, other factors being similar (i.e., nonlimiting), stomata open to the extent required to provide CO_2 at rates sufficient to meet the CO_2 fixation requirements of the metabolic pathway [114]. Close coupling between A and T is expected since CO_2 and H_2O move simultaneously through the stomata [115]. The diffusive conductance of the stomatal opening imposes a major control on the rates of both processes, although C_i concentration and the external water vapor concentration determine the magnitude of the respective gradients [115]. However, changes in g_s may not necessarily affect T and A similarly [23].

There is a strong correlation between A and g_s over a wide variety of plant species and under a diversity of environmental conditions [114,116]. This implies some level of regulation between CO_2 demand by chloroplasts and CO_2 supply, via stomatal control. Generally, leaf conductance and photosynthesis are correlated at low conductance levels but are uncoupled at high conductance levels [117]. If there is no deviation from the slope of photosynthesis versus conductance relationships, and if the intercept is zero (as is assumed initially), the P_i values of all crop plants should be constant, depending only on the photosynthetic pathway [83]. Although many studies have shown a significant tendency for photosynthesis and conductance to be correlated [114], many of these data sets exhibit some deviation from a linear relationship or nonzero intercept [118,119].

Genotypic variation in TE can result from variation in g_s but with the genotypes having the same level of photosynthetic capacity [56]. The slopes of the regression line of g_{max} (stomatal conductance maximum) versus A_{max} vary substantially among C3 plants [56,120]. For high evaporative environments, it has been shown that genotypic differences in P_i, based on long-term gas-exchange studies, as well as on ^{13}C discrimination analysis offer the possibility of genetically modifying TE [56]. However, for low evaporative environments, it appears that A is highly dependent on leaf g_s suggesting little possibility of improvement of TE [56].

B. Mechanisms by Which Genotypes Differ in TE

Any factor that influences genetic variation in either g_s or A in a disproportionate manner would influence Δ and thus TE [37]. If variation in A was the only cause of variation in P_i, increasing photosynthetic capacity should lower P_i/P_a and therefore lower Δ. In this situation, TE would increase and the relationship between Δ and plant biomass should be negative [121]. In groundnut, differences in A are reported to be largely responsible for TE variation, as dry matter production is negatively correlated with Δ in pots [9,72] and at the canopy level [65,94]. Significant variation in A per unit leaf area have been reported in groundnut genotypes and there is also heterosis for this trait [67,122–124]. Similarly, in cowpea, genotypic means for TE were positively correlated with A but only weakly correlated with g_s, indicating that genotypic differences in TE were due primarily to differences in A [110].

A strong positive correlation has been observed between Δ and specific leaf area (SLA) among groundnut genotypes [99]. This is consistent with the foregoing hypothesis that high TE genotypes have higher A. Indeed, the genotypes with thicker leaves (low SLA) had significantly

higher leaf nitrogen contents, again indicative of higher photosynthetic capacity. The significant application of these observations is that breeders could use the inexpensively measured SLA, in lieu of Δ, to screen for high TE among groundnut genotypes within specific environments [72].

However, if g_s is the main source of variation in P_i/P_a, greater g_s should increase P_i/P_a and therefore increase Δ. In adequately irrigated coffee, higher TE values of some of the genotypes tested was associated with reduced stomatal aperture rather than increased A at a given g_s [97]. This suggests that high TE may restrict yield when water supply is not limiting. Thus in this case, as in wheat, selection for higher Δ could lead to increased biomass production but with decreased TE [125]. For example, in crested wheatgrass, greater TE in low Δ clones resulted from a proportionately greater decline in g_s than in A [104]. Similar results were reported for chickpea [105]. However, variation in P_i/P_a among wheat genotypes is approximately equal to variation in leaf g_s and in A [64,126–128]. In wheat, it was reported that g_s covaried with A, with the change in g_s being relatively greater [128]. This means that there could be a positive correlation between A and P_i/P_a. The effect of this on growth may be compounded if genotypes with large P_i/P_a partition more carbon into shoots [129].

Cultivar differences in Δ may also result indirectly from genetic variation in root characteristics affecting the level of water stress experienced by the canopy [96,130]. Differences in root growth affect the degree of dehydration postponement, and this could prolong gas-exchange activity and the maintenance of relatively high P_i and thus Δ [130].

C. Genetic Variation and Genetics of TE and Δ

Genetic variation in TE and Δ has been reported in wheat [64,121,125,131], barley [93], tomato [84], sunflower [98], chickpea [105], groundnut [63,65,72], cowpea [86], and coffee [97]. In wheat, variation in Δ among genotypes is typically in the range 2×10^{-3} [131]. This is equivalent to a variation in TE of 59% [131]. In groundnut, genotypic variation in TE is estimated as about 65% [63]. Based on extreme cases of genotypes which differ in TE, it was reported that cowpea genotypes such as vita 7 and 8049 had nearly 67% higher TE values than those of other genotypes tested [109]. Also, earliness is generally associated with low TE in cowpea; however, significant genotypic differences were noted within any given maturity group, suggesting that these two traits are not necessarily linked [109]. Similarly, tall landrace genotypes of wheat, which are also late maturing, had higher TE values than did the modern dwarf and semidwarf genotypes [121]. However, among Australian wheats, low values of Δ and thus high TE have been found to be strongly associated with the WW15 genetic background, which was introduced into Australia from CIMMYT as a major source of the dwarfing gene in Australian wheats.

The utility of a trait for selection in plant breeding programs is strongly enhanced by the consistency of genotypic ranking across environments [110]. Based on studies with wheat, cowpea, crested wheat grass, groundnut, and beans, it was found that genotypic ranking for Δ across environments is consistent [36,37,99,107,109,110,125,131,132]. For crops such as groundnut, it was shown that genotypic ranking for Δ was maintained during ontogeny [72] (Figure 3). However, in crops such as wheat, genotypic ranking could change between the early vegetative stage and the heading and grain filling stages [131]. This could be due to a number of factors, including hormonal imbalance, causing loss of stomatal control on water loss after heading. Also, the plant material used for Δ analysis could determine the level of heritability [131]. It was shown in a number of crops that the Δ value of leaf material is a better indicator of differences in TE than that of grains [9,36,63,107,109,121]. One of the main reasons could be genotypic differences in the ability to translocate preanthesis-stored carbohydrate reserves for grain filling [133].

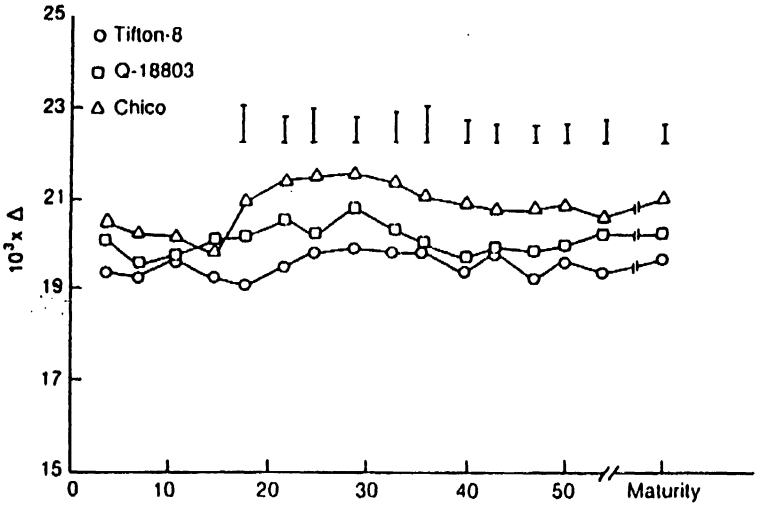


Figure 3 Change in carbon isotope discrimination in leaves and error variation versus time for well-watered groundnut cultivars of Tifton-8, Q 18803, and Chico grown in a greenhouse. (From Ref. 72.)

The effectiveness of indirect selection for TE using Δ will depend partly on the magnitude of the heritabilities for TE and Δ and the genotypic correlation between these characters [134]. Broad-sense heritability, which is the proportion of total phenotypic variance that is attributable to genotypic differences, is a measure of the repeatability of the expression of those genotypic differences [131]. In many crops, heritabilities for Δ are above 80% [9,37, 107,109,121,131].

D. Advantages of Using Δ for TE Evaluations

Breeding for improved TE has been limited by the lack of screening tools for identifying desirable genotypes under field conditions [110]. The ^{13}C discrimination technique makes it possible to survey a large number of plants with a simple, albeit expensive analysis of the leaf tissue [10]. As Δ provides an integrated estimate of TE, it has been suggested that measurement of Δ may better differentiate among genotypes than most instantaneous physiological assays [121]. Genotypic ranking based on Δ is much more consistent than that based on gas-exchange measurements [110], and thus should be easier to select for in breeding programs. Also, as Δ remains reasonably constant throughout crop ontogeny, selection could be made during crop development [72].

Further, Δ is faster and easier to measure than total growth relative to total water use [28]. It is readily determined on field-grown plants because it does not require the plant to be sheltered from rain, or that any other special experimental treatment be maintained. Measurements can be made on small plant samples collected at maturity with minimal problems of storage and handling. The material can be either leaf, stem, or grain. Leaves and stems are easier to grind, and use of vegetative material has the potential advantage that selection can be made early in the crop growth cycle and thus could assist in improving selection efficiency and reducing the time and maintenance costs [28,131].

E. Limitations of Using Δ to Select for TE

Carbon partitioning and Δ would not be expected to be stable across all environments and with changes in plant hormonal balance. For example, cytokinins and ABA can affect both leaf gas exchange and carbon allocation [104]. Also, there are some problems of assessment of TE through carbon isotope estimations: (a) it is a "ratio" and not correlated directly with yield or productivity; (b) the small sample size may introduce subsampling errors and careful grinding is required; and (c) the technique requires considerable capital investment in equipment and technical expertise [104].

Also, there are a number of potential sources of nongenetic variability in the measurement of Δ. Some can be readily overcome by technical or sampling precautions, as they are associated with the composition of plant dry matter [135] and the size and storage of the dry matter sample used in the measurement [37]. Other sources of variation in Δ among plant organs result from temporal variation in the growth environment. Increased salinity [136,137], decreased soil water availability [28,65,106], soil compaction [129], and a decrease in vpd [138] could all result in lower values of Δ.

Genotypic variation for Δ measured under field conditions could be complicated by inherent differences in root growth [130]. This would affect the degree of dehydration postponement that could allow prolonged maintenance of relatively large g_s, thus decreasing TE but increasing growth and yield. Positive correlations between root length density and Δ have been reported in crops such as beans [130,139] (Figure 4), and thus selection for low Δ (high TE) may lead to selection of genotypes with poor root attributes, such as shallow rooting and low root densities. Bean genotypes that had a deeper root system had high Δ values compared to the shallow-rooted genotypes [130]. Thus leaf physiology (as measured by Δ) is not independent of root activity, and it seems that there is a close correlation between gas exchange under water-deficit environments and root attributes [130]. One way to overcome this problem of differences in root attributes is to evaluate germ plasm lines under irrigated conditions, where differences in root growth do not affect the leaf gas-exchange characteristics, and thus Δ. In many crop species, variation in P_i/P_a and Δ has been reported among genotypes under irrigated conditions, indicating the existence of genetic variation in the "baseline C_i" that is expressed under nonstress conditions [130].

In crops such as groundnut, there is a moderately positive correlation ($r = 0.55$) between Δ and HI, and thus selecting for low Δ (high TE) could lead to selection of genotypes with low partitioning [9,65,94]. This indicates that selection for high TE and HI, and thus yield potential, could be difficult because of this negative association. However, the possibility of combining high HI and high TE requires further research [9,94]. This highlights the need for physiologists and breeders to be aware of the potential for negative associations between traits such as TE, partitioning of biomass, and root water uptake attributes of roots.

As several factors can alter plant dry weight independently of Δ, there may not always be a direct association between Δ and productivity [35]. However in many crops, the general trend in relationship between Δ and dry matter productivity is negative; that is, higher productivity under optimum conditions (e.g., irrigated) is associated with lower Δ [132]. Thus in crops where there is a positive association between Δ and dry matter production, it may be that high HI and potential for dry matter productivity are incompatible. For crops such as wheat, barley, and beans, where differences in TE are due mainly to differences in g_s, there appears to be a positive correlation between Δ and dry matter production [125]. This indicates that selection for low Δ could lead to selection of genotypes with low dry matter accumulation capability and thus potential productivity. It was suggested that selection for low Δ will improve adaptation to drought [28], whereas selection for high Δ should improve yield potential [125]. However, it should still be possible to identify genotypes that do not comply with this general relationship.

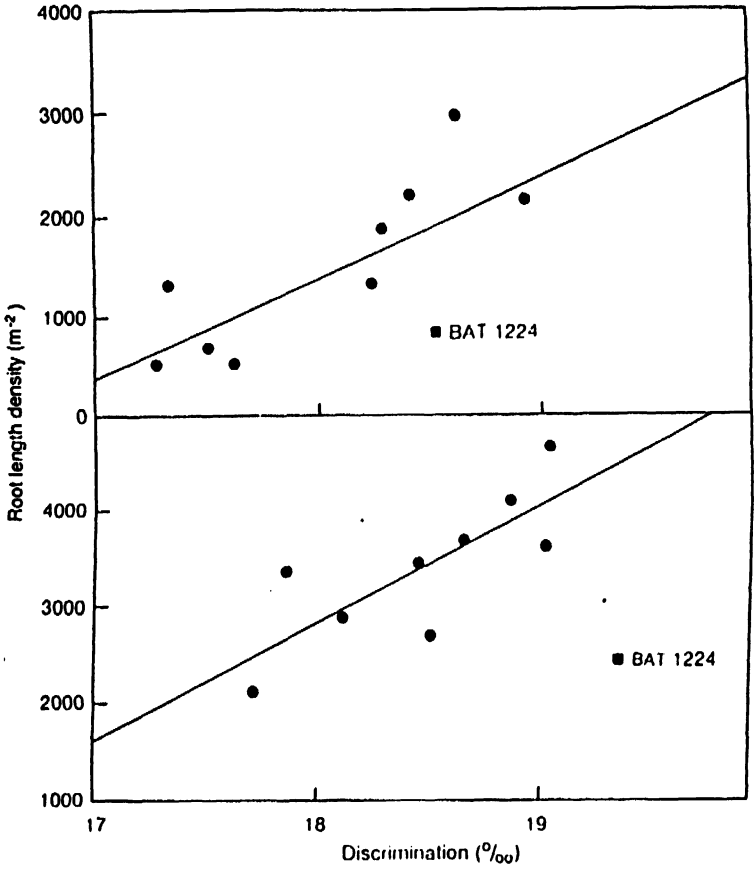


Figure 4 Relations between leaf carbon isotope discrimination and root length density for rain-fed bean genotypes at two locations: Palmira (upper graph) and Quilichao (lower graph). (From Ref. 130.)

For example, in barley, although there is generally a negative relationship between TE and dry matter accumulation among the genotypes tested, certain genotypes deviate from this relationship (Figure 5) [140].

For crops such as groundnut, and in cool-season grasses, where photosynthetic rates are the main source of variation in TE, selection for low Δ should lead to genotypes with high dry matter production capabilities [9,36,65,132]. Thus it is interesting to note that the usefulness of Δ in selection for high TE could vary depending on the crop species and the target environment; in one case it could lead to improving productivity, and in other cases it could be detrimental to productivity.

F. Role of TE in Improving Drought Resistance of Crops

Crop plants have evolved a variety of strategies to cope with water-deficit conditions [141]. The seasonal progression of temperature, the distributrion and intensity of rainfall, and the

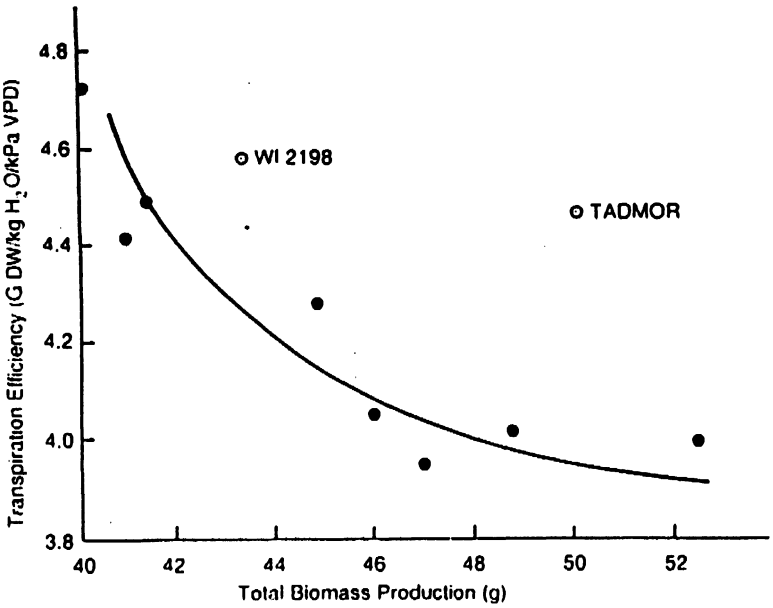


Figure 5 Transpiration efficiency and total biomass production in barley genotypes grown in greenhouse. (From Ref. 140.)

availability of soil moisture will largely determine the plant attributes that need to be altered beneficially to improve the efficiency of water use [142]. Transpiration efficiency is one of the components involved in adaptation to drought by potentially extending the period of soil moisture availability, and is thus expected to contribute to improving adaptation to drought-prone environments. This is particularly so if the crop is raised on finite amounts of stored moisture. A drought-resistant groundnut genotype (drought resistance defined here as relative total dry matter production under drought conditions), Tifton-8, was found to be very efficient in its water use compared to a sensitive *A. villosa* [143]. Chico, a short-season groundnut variety, had a lower TE value than those of long-season groundnut varieties [96], which are also found to be more drought resistant than the short-season varieties. In wheat, barley, cowpea, and groundnut, TE is positively correlated with days to heading, which indicates that selection for early maturity might result in decreased TE values [63,94,109,121,125,144]. However, in groundnut, there is still considerable variation in TE/Δ within similar maturity groups, indicating that the variation in TE could be located in any given maturity group [63,94]. Thus simultaneous selection for TE and phenological characteristics should be practiced to improve TE within an optimum maturity group. Tall landrace wheat genotypes had greater total dry matter and TE, but were later in maturity than the modern dwarf and semidwarf genotypes [121].

In many cropping systems where irrigation water is not readily available, yield stability can be affected by intermittent droughts [9]. Ideally, maximum growth with the water available is a goal. One possibility for improving productivity in low-rainfall and drought-prone areas is to select and breed plants that require less water for growth without losing their yield potential (i.e., to improve their TE value). However, there is a distinction between TE and drought resistance as a whole, and it needs to be recognized that the development and use of

drought-resistant plants can lead to the effective use of limited soil water that would otherwise be unavailable. In effect, WUE would be increased for the entire land area even if the drought-resistant crops grown actually transpire more water per unit of dry matter than do nonresistant crops.

In rain-fed environments, TE alone may not play a key role in determining the level of drought resistance of a given cultivar. The negative correlations between reduced Δ, biomass, yield, and LAI indicate that greatest growth under rain-fed conditions would occur in cultivars best able to postpone desiccation and maintain relatively large stomatal conductance (i.e., mostly to deal with the efficiency with which the water is extracted rather than utilized), thus showing less reduction in C_i than that occurs in irrigated treatments [130]. However, high levels of TE and efficient root systems (deep root system, uniform root length distribution through the soil profile, efficient water uptake from low soil water potentials, etc.) are independent attributes of a plant; therefore, they need not be incompatible. Thus one could improve the TE of a given variety through breeding even if it is found to have a more efficient root system but a low TE. In groundnut, some of the genotypes that have deep rooting attributes and are more efficient in water uptake also had higher levels of TE than those of genotypes poor in both attributes [145].

Assuming that the traits contributing to drought resistance are independent attributes, it would be necessary to develop ideotypes to suit the requirements of specific target production environments [146,147]. Then genetic improvement would depend largely on the local variety that needs to be improved, which can be guided by using the ideotype as a basis for the evaluation of traits that need to be incorporated [146]. Thus genetic improvement for better adaptation to moisture-deficit environments could be focused on a few selected traits rather than considering adaptation as a single component of improvement. This would assist in quantifying progress and devising appropriate strategies for further improvement, apart from being able to use genetic stocks developed during the process in related breeding programs in other production environments.

VI. FUTURE OUTLOOK

Large sums of money have been spent to develop irrigated cropping systems throughout the world, but relatively little attention has been paid to research on improving WUE, let alone genetically improving the TE values of crop species [148]. Although differences among and within crop species in their TE values (thus in their total water requirements to produce a given amount of yield) were demonstrated 80 years ago [149], very little progress has been made since in initiating breeding programs specifically targeted at improving TE values in any crop species. This is due mainly to the lack of appropriate means of characterizing and quantifying genotypic variation in TE and the inability to handle the large number of samples required in a breeding program. The recent finding that TE is negatively related to ^{13}C discrimination (Δ) has led to a renewed interest in TE as a potentially exploitable trait, and thus Δ has been proposed as a selection criterion for improving TE in plant breeding programs [28]. It has now been shown that genetic variation in TE exists for many crop species under both well-watered and moisture-deficit environments. The high levels of heritability for Δ have further strengthened the argument that Δ is amenable to genetic improvement. This opens the way for developing crop varieties that require less water to produce the same amount of yield according to their present potential. This also provides scope for much more rational deployment of irrigation water.

However, ^{13}C discrimination analysis of plant samples requires mass-spectrometer facilities, and it is beyond the ability of many breeding programs to acquire and maintain such expensive

and sensitive equipment. This is particularly so in developing countries, which are located mostly in semiarid regions, where improving crop TE could play a crucial role in improving and stabilizing crop production. Thus this would presently be the limiting factor for the use of this technology in breeding programs focused specifically toward genetic improvement of TE. Nevertheless, it could still be handled by having centralized facilities in selected institutes where analyses could be done. Also, once the equipment is installed and maintained, the actual analysis costs may be within the capability of many breeding programs. Correlated traits such as specific leaf area, which has been shown to be related with Δ, could thus be used as a surrogate to ^{13}C discrimination analysis. Measuring specific leaf area could be relatively inexpensive and requires no special equipment. However, it needs to be proved that selection programs based on specific leaf area could lead to genetic enhancement of TE and its heritability needs to be established clearly before proposing this as surrogate to Δ in a selection program. There are indications in groundnut that it could be used effectively as an alternative to Δ in selecting for TE [99], but this needs to be proved convincingly. It will therefore be interesting to observe the extent to which this new tool (i.e., Δ) is put into use in developing varieties that are better adapted to moisture-deficit environments without a loss in yield potential.

ACKNOWLEDGMENT

We wish to acknowledge editorial assistance from the ICRISAT Editorial Committee in improving the structure and presentation of this manuscript.

REFERENCES

1. P. J. M. Cooper, J. D. H. Keatinge, and G. Hughes, *Field Crops Res.*, *7*: 299 (1983).
2. P. J. M. Cooper, G. S. Campbell, M. C. Heath, and P. D. Hebblethwaite, in *World Crops: Cool Season Food Legumes* (R. J. Summerfield, ed.). Kluwer Academic Publishers, London, pp. 813–829 (1988).
3. G. Hughes, J. D. H. Keatinge, P. J. M. Cooper, and N. F. Dee, *J. Agric. Sci., (Camb.), 108*: 419 (1987).
4. M. C. Heath and P. D. Hebblethwaite, *Ann. Appl. Biol., 107*: 309 (1985):
5. F. G. Viets, Jr., *Adv. Agron., 14*: 223 (1962).
6. R. A. Fischer and N. C. Turner, *Annu. Rev. Plant Physiol., 29*: 277 (1978).
7. M. C. Saxena, in *The Chickpea* (M. C. Saxena, and K. B. Singh, eds.), CAB International Wallingford, Berkshire, England, pp. 207–232 (1987).
8. J. B. Passioura, *J. Aust. Inst. Agric. Sci., 43*: 117 (1977).
9. K. T. Hubick, R. Shorter, and G. D. Farquhar, *Aust. J. Plant Physiol., 15*: 799 (1988).
10. J. S. Boyer, in *Plant Breeding in the 1990s* (H. T. Stalker, and J. P. Murphy, eds.), CAB International, Wallingford, Berkshire, England, pp. 181–200 (1992).
11. D. K. Barnes, in *Limitations to Efficient Water Use in Crop Plants* (H. M. Taylor, W. R. Jordan and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis., pp. 127–136 (1983).
12. W. J. Davies, in *Plant Physiology: A Treatise*, Vol. IX, *Water and Solutes in Plants* (F. C. Steward J. F. Sutcliffe, and J. E. Dale, eds.). Academic Press, New York, pp. 49–154 (1986).
13. D. Hillel, in *Irrigation of Agricultural Crops* (B. A. Stewart, and D. R. Nielson, eds.), American Society of Agronomy, Madison, Wis., pp. 5–30 (1990).
14. S. M. A. Faiz and P. E. Weatherley, *New Phytol., 81*: 19 (1978).
15. H. G. Jones, *J. Appl. Ecol., 13*: 605 (1976).
16. D. N. Moss, J. T. Wooley, and J. F. Stone, *Agric. Meteorol., 14*: 311 (1974).
17. W. Wenkert, in *Limitations to Efficient Water Use in Crop Plants* (H. M. Taylor, W. R. Jordan and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis., pp. 137–172 (1983).
18. G. D. Farquhar, *Aust. J. Plant Physiol., 5*: 787 (1978).

19. H. Meidner and T. A. Mansfield, *Physiology of Stomata*, McGraw-Hill, London (1968).
20. E. D. Schulze, O. L. Lange, M. Evenari, L. Kappen, and M. Evenari, *Oecologia*, *17*: 159 (1974).
21. I. R. Cowan and G. D. Farquhar, in *Integration of Activity in the Higher Plants* (D. H. Jennings, ed.), Cambridge University Press, Cambridge, pp. 471–505 (1977).
22. K. J. Bradford, T. D. Sharkey, and G. D. Farquhar, *Plant Physiol.*, *72*: 245 (1983).
23. I. R. Cowan and J. H. Troughton, *Planta*, *97*: 323 (1971).
24. J. I. L. Morison, *Plant Cell Environ.*, *8*: 467 (1985).
25. K. W. Brown, W. R. Jordan, and J. C. Thomas, *Physiol. Plant.*, *37*: 1 (1976).
26. E. Fereres, E. Acevedo, D. Henderson, and T. C. Hsiao, *Planta*, *44*: 261 (1978).
27. M. M. Ludlow, in *Adaptations of Plants to Water and High Temperature Stress* (N. C. Turner and P. J. Kramer, eds.), Wiley, New York, pp. 123–138 (1980).
28. G. D. Farquhar and R. A. Richards, *Aust. J. Plant Physiol.*, *11*: 539 (1984).
29. A. H. Markhart, *Plant Physiol.*, *77*: 113 (1985).
30. D. Vignes, A. Djekoun, and C. Planchan, *Can. J. Plant Sci.*, *66*: 247 (1986).
31. R. J. Lawn, *Aust. J. Agric. Res.*, *33*: 481 (1982).
32. R. G. Henzell, K. J. McCree, C. H. M. van Bavel, and K. F. Schertz, *Crop Sci.*, *16*: 660 (1976).
33. L. Riccardi and P. Steduto, *FABIS Newsl.*, *20*: 21 (1988).
34. M. J. Hattendert, D. W. Evans, and R. N. Peaden, *Agron. J.*, *82*: 873 (1990).
35. G. D. Farquhar, J. R. Ehleringer, and K. T. Hubick, *Annu. Rev. Plant Physiol.*, *40*: 503 (1989).
36. J. J. Read, R. C. Johnson, B. F. Carver, and S. A. Quarrie, *Crop Sci.*, *31*: 139 (1991).
37. G. D. Farquhar, K. T. Hubick, A. G. Condon, and R. A. Richards, in *Stable Isotopes in Ecological Research* (J. R. Ehleringer and K. A. Nagy, eds.), Ecological Studies, Vol. 68, Springer-Verlag, New York, pp. 21–40 (1988).
38. P. G. Jarvis and K. G. McNaughton, *Adv. Ecol. Res.*, *15*: 1 (1986).
39. C. D. Walker and R. C. N. Lance, *Aust. J. Plant Physiol.*, *18*: 411 (1991).
40. D. F. Parkhurst and O. L. Loucks, *J. Ecol.*, *60*: 505 (1972).
41. C. Johansen, B. Baldev, J. B. Brouwer, W. Erskine, W. A. Jermyn, Lang Li-Juan, B. A. Malik, A. Ahad Miah, and S. N. Silim, "Biotic and Abiotic Stresses Constraining Productivity of Cool Season Food Legumes in Asia, Africa and Oceania," *Proceedings of the International Food Legume Research Conference II*, Apr. 12–16, 1992, Cairo (F. J. Muehlbauer and W. J. Kaiser, eds.), Kluwer, Dordrecht, The Netherlands (in press).
42. R. J. Hanks, in *Limitations to Efficient Water Use in Crop Production* (H. Taylor, W. R. Jordan, and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis. pp. 393–411 (1983).
43. J. F. Beerhuizen and R. O. Slatyer, *Agric. Meteorol.*, *2*: 259 (1965).
44. R. W. Downes, *Aust. J. Biol. Sci.*, *23*: 775 (1970).
45. K. A. Shackel and A. E. Hall, *Aust. J. Plant Physiol.*, *6*: 265 (1979).
46. M. M. Ludlow and O. Bjorkman, *Planta*, *161*: 505 (1984).
47. I. N. Forseth and A. H. Teramura, *Ecology*, *67*: 564 (1986).
48. V. S. Berg and S. Heuchelin, *Crop Sci.*, *30*: 631 (1990).
49. R. C. Muchow, *Field Crops Res.*, *11*: 309 (1985).
50. G. R. Squire, *The Physiology of Tropical Crop Production*, CAB International, Wallingford, Berkshire, England (1990).
51. R. B. Matthews, D. Harris, J. H. Williams, and R. C. Nageswara Rao, *Exp. Agric.*, *24*: 203 (1988).
52. S. R. Ghorashy, J. W. Pendleton, and M. E. Bernard, *Crop Sci.*, *11*: 426 (1971).
53. J. Ehleringer, in *Adaptation of Plants to Water and Temperature Stress* (N. C. Turner and P. J. Kramer, eds.), Wiley-Interscience, New York, pp. 295–308 (1980).
54. M. Ashraf and F. Karim, *Trop. Agric. (Trinidad)*, *68*: 57 (1991).
55. D. D. Baldocchi, S. B. Verma, and N. J. Rosenberg, *Agric. For. Meteorol.*, *34*: 53 (1985).
56. E. D. Schulze and A. E. Hall, in *Physiological Plant Ecology II: Water Relations and Carbon Assimilation* (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), Springer-Verlag, New York, pp. 181–230 (1982).
57. J. R. Ehleringer, O. Bjorkman, and H. A. Mooney, *Science*, *192*: 376 (1976).
58. J. R. Ehleringer and H. A. Mooney, *Oecologia*, *37*: 183 (1978).

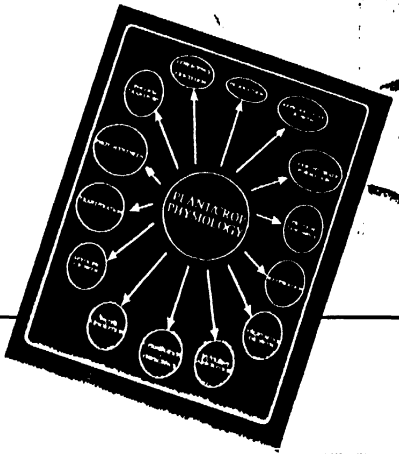
59. J. M. Clarke and R. A. Richards, *Can. J. Plant Sci.*, *68*: 975 (1988).
60. M. C. M. Paje, M. M. Ludlow, and R. J. Lawn, *Aust. J. Agric. Res.*, *39*: 363 (1988).
61. J. M. Clarke, I. Ramagosa, S. Jana, J. P. Srivastava, and T. N. McCaig, *Can. J. Plant Sci.*, 1075 (1989).
62. Y. Castonguay and A. H. Markhart, *Crop Sci.*, *31*: 1605 (1991).
63. K. T. Hubick, G. D. Farquhar, and R. Shorter, *Aust. J. Plant Physiol.*, *13*: 803 (1986).
64. A. G. Condon, G. D. Farquhar, and R. A. Richards, *Aust. J. Plant Physiol.*, *17*: 9 (1990).
65. G. C. Wright, K. T. Hubick, and G. D. Farquhar, *Aust. J. Plant Physiol.*, *15*: 815 (1988).
66. D. H. Wallace, J. L. Ozbun, and H. M. Munger, *Adv. Agron.*, *24*: 97 (1972).
67. A. S. Bhagsari and R. H. Brown, *Peanut Sci.*, *3*: 1 (1976).
68. G. M. Dornhoff and R. M. Shibles, *Crop Sci.*, *16*: 377 (1976).
69. J. B. Passioura, *Aust. J. Agric. Res.*, *23*: 745 (1972).
70. R. A. Richards and J. B. Passioura, *Crop Sci.*, *21*: 249 (1981).
71. R. A. Richards and J. B. Passioura, *Crop Sci.*, *21*: 253 (1981).
72. G. C. Wright, K. T. Hubick, G. D. Farquhar, and R. C. Nageswara Rao, in *Stable Isotopes and Plant Carbon–Water Relations* (J. E. Ehleringer, A. E. Hall, and G. D. Farquhar, eds.), Academic Press, New York, pp. 247–267 (1993).
73. N. L. Klocke, D. F. Heermann, and H. R. Duke, *Trans. ASAE*, *28*: 183 (1985).
74. R. J. Hanks, H. R. Gardner, and R. L. Florian, *Agron. J.*, *61*: 30 (1969).
75. T. A. Howell, K. R. Davis, R. L. McCormick, H. Yamada, V. T. Walhood, and D. W. Meek, *Irrig. Sci.*, *5*: 195 (1984).
76. R. J. Hanks, in *Advances in Evapotranspiration*, ASAE, St. Joseph, Mich., pp. 431–438 (1985).
77. R. J. Lascano, C. H. M. van Bavel, J. L. Hatfield, and D. R. Upchurch, *Soil Sci. Am. J.*, *51*: 113 (1987).
78. M. E. Bloodworth, J. B. Page, and W. R. Cowley, *Soil Sci. Soc. Am. Proc.*, *19*: 411 (1955).
79. T. Sakuratini, *Agric. Meteorol.*, *40*: 273 (1984).
80. J. M. Baker and C. H. M. van Bavel, *Plant Cell Environ.*, *10*: 779 (1987).
81. J. R. Evans, T. D. Sharkey, J. A. Berry, and G. D. Farquhar, *Aust. J. Plant Physiol.*, *13*: 281 (1986).
82. A. B. Frank, R. E. Barker, and J. D. Berdahl, *Agron J.*, *79*: 541 (1987).
83. T. R. Sinclair, C. B. Tanner, and J. M. Bennett, *Bioscience*, *34*: 36 (1983).
84. B. Martin and Y. R. Thorstenson, *Plant Physiol.*, *88*: 213 (1988).
85. H. G. Jones, in *Stomatal Function* (E. Ziegler, G. D. Farquhar and I. R. Cowan, eds.), Stanford University Press, Stanford, Calif. (1984) (cited in Ref. 24).
86. A. M. Ismail and A. E. Hall, *Crop Sci.*, *32*: 7 (1992).
87. R. D. Guy, M. F. Fogel, J. A. Berry, and T. C. Hoering, in *Progress in Photosynthetic Research III* (J. Biggins, ed.), Martinus Nijhoff, Dordrecht, The Netherlands, pp. 597–600 (1987).
88. G. D. Farquhar, M. H. O'Leary, and J. A. Berry, *Aust. J. Plant Physiol.*, *9*: 121 (1982).
89. J. H. Troughton, in *Photosynthesis II: Photosynthetic Carbon Metabolism and Related Processes* (M. Gibbs and E. Latzko, eds.), Springer-Verlag, Berlin, pp. 140–149 (1979).
90. W. G. Mook, M. Koopmans, A. F. Carter, and C. D. Keeling, *J. Geophys. Res.*, *88*: 10915 (1983).
91. C. B. Tanner and T. R. Sinclair, in *Limitations to Efficient Water Use in Crop Production* (H. Taylor, W. R. Jordan, and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis., pp. 1–28 (1983).
92. H. Craig, *J. Geol.*, *62*: 115 (1954).
93. K. T. Hubick and G. D. Farquhar, *Plant Cell Environ.*, *12*: 795 (1989).
94. R. C. Nageswara Rao, J. H. Williams, K. D. R. Wadia, K. T. Hubick, and G. D. Farquhar, *Ann. Appl. Biol.*, *122*: 357 (1993).
95. W. S. F. Schuster, S. L. Philips, D. R. Sandquist, and J. R. Ehleringer, *Am. J. Bot.*, *79*: 216 (1992).
96. G. C. Wright, T. A. Sarwanto, A. Rahmianna, and D. Syarefuddin, in *Peanut Improvement: A Case Study in Indonesia* (G. C. Wright and K. J. Middleton, eds.), ACIAR Proc. No. 40, Canberra, Australia, pp. 74–84 (1993).

97. F. C. Meinzer, G. Goldstein, and D. A. Grantz, *Plant Physiol.*, *92*: 130 (1990).
98. ,J. M. Virgona, K. T. Hubick, H. M. Rawson, G. D. Farquhar, and R. W. Downes, *Aust. J. Plant Physiol.*, *17*: 207 (1990).
99. R. C. Nageswara Rao and G. C. Wright, *Crop Sci.*, *34*(1) (in press) (1993).
100. R. D. Guy, P. G. Warne, and D. M. Reid, in *Ecological Studies 68: Stable Isotopes in Ecological Research* (P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, eds.), Springer-Verlag, Berlin, pp. 55–75 (1988).
101. K. J. McCree and S. G. Richardson, *Crop Sci.*, *27*: 543 (1987).
102. G. D. Farquhar and T. D. Sharkey, *Annu. Rev. Plant Physiol.*, *33*: 317 (1982).
103. I. R. Cowan, in *Physiological Plant Ecology II: Water Relations and Carbon Assimilation* (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), Encyclopedia of Plant Physiology, New Series, Vol. 12B, Springer-Verlag, Berlin, pp. 589–613 (1982).
104. D. A. Johnson, K. H. Assay, L. L. Tieszen, J. R. Ehleringer, and P. G. Jefferson, *Crop Sci.*, *30*: 338 (1990).
105. K. Winter, *Z. Pflanzenphysiol.*, *101*: 421 (1981).
106. K. T. Hubick and G. D. Farquhar, *Aust. Cotton Grow.*, *8*: 66 (1987).
107. J. R. Ehleringer, in *Research on Drought Tolerance in Common Bean* (J. W. White, G. Hoogenboom, F. Ibarra, and S. P. Singh, eds.), Working Document 41, CIAT, Cali, Colombia, pp. 165–191 (1988).
108. J. R. Ehleringer and T. A. Cooper, *Oecologia*, *76*: 562 (1988).
109. A. E. Hall, R. G. Mutters, K. T. Hubick, and G. D. Farquhar, *Crop Sci.*, *30*: 300 (1990).
110. A. E. Hall, R. G. Mutters, and G. D. Farquhar, *Crop Sci.*, *32*: 1 (1992).
111. W. R. Kirchhoff, A. E. Hall, and W. W. Thomson, *Crop Sci.*, *29*: 109 (1989).
112. I. R. Cowan, in *Flow and Transport in the Natural Environment: Advances and Applications* (O. T. Denmead, ed.), Springer-Verlag, New York, pp. 160–172 (1988).
113. C. B. Osmond, K. Winter, and H. Ziegler, in *Physiological Plant Ecology II: Water Relations and Carbon Assimilation* (O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds.), Encyclopedia of Plant Physiology, New Series, Vol. 12B, Springer-Verlag, Berlin, pp. 479–547 (1982).
114. S. C. Wong, I. R. Cowan, and G. D. Farquhar, *Nature*, *282*: 424 (1979).
115. T. A. Howell, in *Irrigation of Agricultural Crops* (B. A. Stewart and D. R. Nielson, eds.), American Society of Agronomy, Madison, Wis., pp. 391–434 (1990).
116. J. Goudriaan and H. H. van Laar, *Photosynthetica*, *12*: 241 (1978).
117. D. R. Krieg, in *Limitations to Efficient Water Use in Crop Production* (H. M. Taylor, W. R. Jordan, and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis., pp. 319–330 (1983).
118. C. Ramos and A. E. Hall, *Photosynthetica*, *16*: 343 (1982).
119. M. H. O'Leary, I. Treichel, and M. Rooney, *Plant Physiol.*, *80*: 578 (1986).
120. S. D. Wullschleger, *J. Exp. Bot.*, *44*: 907 (1993).
121. B. Ehdaie, A. E. Hall, G. D. Farquhar, H. T. Nguyen, and J. G. Waines, *Crop Sci.*, *31*: 1282 (1991).
122. J. E. Pallas, Jr., and Y. B. Samish, *Crop Sci.*, *14*: 478 (1974).
123. J. E. Pallas, Jr., *Peanut Sci.*, 9: 14 (1982).
124. W. D. Branch and J. E. Pallas, Jr., *Peanut Sci.*, *11*: 56 (1984).
125. A. G. Condon, R. A. Richards, and G. D. Farquhar, *Crop Sci.*, *27*: 996 (1987).
126. D. Shimshi and J. Ephrat, *Agron. J.*, *67*: 326 (1975).
127. R. C. Johnson, H. Kebede, D. W. Mornhinweg, B. F. Carver, A. Lanerayburn, and H. T. Nguyen, *Crop Sci.*, *27*: 1046 (1987).
128. R. L. Dunstone, R. M. Gifford, and L. T. Evans, *Aust. J. Biol. Sci.*, *26*: 295 (1973).
129. J. Masle and G. D. Farquhar, *Plant Physiol.*, *86*: 32 (1988).
130. J. W. White, J. A. Castillo, and J. Ehleringer, *Aust. J. Plant Physiol.*, *17*: 189 (1990).
131. A. G. Condon and R. A. Richards, *Aust. J. Agric. Res.*, *43*: 921 (1992).
132. R. C. Johnson and L. M. Bassett, *Crop Sci.*, *31*: 157 (1991).
133. P. C. Pheloung and K. H. M. Siddique, *Aust. J. Plant Physiol.*, *18*: 53 (1991).

134. D. S. Falconer, *Introduction to Quantitative Genetics*, Longman Group, New York (1981).
135. M. H. O'Leary, *Phytochemistry*, *20*: 553 (1981).
136. W. J. S. Downton, W. J. R. Grant, and S. P. Robinson, *Plant Physiol.*, *78*: 85 (1985).
137. R. D. Guy and D. M. Reid, *Plant Cell Environ.*, *9*: 65 (1986).
138. K. Winter, J. A. M. Holtum, G. E. Edwards, and M. H. O'Leary, *J. Exp. Bot.*, *33*: 88 (198
139. B. N. Sponchiado, J. W. White, J. A. Castillo, and P. G. Jones, *Exp. Agric.*, *25*: 249 (198
140. E. Acevedo, in *Physiology: Breeding of Winter Cereals for Stressed Mediterranean Environm* (E. Acevedo, A. P. Conesa, P. Monneveux, and J. P. Srivastava, eds.), INRA, Paris (1991).
141. T. C. Hsiao and E. Acevedo, *Agric. Meteorol.*, *14*: 59 (1974).
142. G. H. Heichel, in *Limitations to Efficient Water Use in Crop Production* (H. M. Taylor, W. Jordan, and T. R. Sinclair, eds.), American Society of Agronomy, Madison, Wis., pp. 375–(1983).
143. T. A. Coffelt, R. O. Hammons, W. D. Branch, P. M. Mozingo, P. M. Phipps, J. C. Smith, E. Lynch, C. S. Kvien, D. L. Ketring, D. M. Porter, and A. C. Misen, *Crop Sci.*, *25*: 203 (19
144. P. Q. Craufurd and A. B. Austin, *Annual Report of the Agriculture and Food Research Cou* Institute of Plant Science Research and John Innes Institute, John Catt Ltd., England, pp. 12 (1987).
145. G. C. Wright, R. C. Nageswara Rao, and H. B. So, "Variation in Root Characteristics and T Association with Water Uptake and Drought Tolerance in Four Peanut Cultivars," paper prese at the *Australian Agronomy Conference*, Sept. 19–24, The University of Adelaide, Adelaide, S Australia (1993).
146. G. V. Subbarao, C. Johansen, A. E. Slinkard, R. C. Nageswara Rao, N. P. Saxena, and Y Chauhan, *CRC Crit. Rev. Plant Sci.* (in preparation).
147. S. Ceccarelli, E. Acevedo, and S. Grando, *Euphytica*, *56*: 169 (1991).
148. M. N. Christiansen, in *Breeding Plants for Less Favorable Environments* (M. N. Christiansen C. F. Lewis, eds.), Wiley, New York, pp. 1–11 (1982).
149. L. J. Briggs and H. L. Shantz, *USDA-Bur. Plant Ind. Bull.*, *285*: 1 (1913).

HANDBOOK OF PLANT AND CROP PHYSIOLOGY

edited by
MOHAMMAD PESSARAKLI



about the book . . .

This comprehensive, single-source reference provides up-to-date, in-depth coverage of plant physiological stages and processes *from* seed germination *to* senescence and abscission under both normal and stress conditions—examining every important aspect of the field, including plant genetics and crop production.

Organized into eight self-contained sections to facilitate access to specific information, ***Handbook of Plant and Crop Physiology*** addresses nutrient uptake, plant-water relationships, and the role of temperature in the physiology of crop plants . . . discusses growth promotor and growth inhibitor hormones . . . illustrates the physiological responses of plants and crops to stress with detailed empirical investigations . . . introduces developmental genetics in both higher and lower plants . . . presents information on transpiration efficiency and the physiological mechanisms relevant to the genetic improvement of salinity tolerance in crop plants . . . shows how whole-system research functions as a complement to reductive research . . . elucidates the effects of species, growth conditions, and physiological development on the fractionation products of plants . . . and much more.

With over 4700 literature citations and some 360 photographs, drawings, tables, and equations, ***Handbook of Plant and Crop Physiology*** is an indispensable resource for plant and crop physiologists; plant, crop, soil, and environmental scientists; botanists; agronomists; agriculturalists; horticulturists; biochemists; foresters; plant growers; and upper-level undergraduate and graduate students in these disciplines.

about the editor . . .

MOHAMMAD PESSARAKLI is a Research Specialist, Senior, at the College of Agriculture, the University of Arizona, Tucson. The editor of the *Handbook of Plant and Crop Stress* (Marcel Dekker, Inc.) and the author or coauthor of more than 30 journal articles, he is a member of the Agronomy Society of America, the Soil Science Society of America, the International Society of Soil Science, and the American Association of University Professors, among other organizations. A Certified Professional Agronomist, Certified Professional Soil Specialist, and Certified Professional Soil Scientist as designated by the American Registry of Certified Professionals in Agronomy, Crop Science, and Soil Science, Dr. Pessarakli received the B.S. degree (1977) in environmental resources in agriculture and the M.S. degree (1978) in agriculture from Arizona State University, Tempe, and the Ph.D. degree (1981) in soil and water science from the University of Arizona, Tucson.

Printed in the United States of America ISBN: 0—8247—9250—5

marcel dekker, inc./new york · basel · hong kong