Tools for improving the efficiency of durum wheat selection under Mediterranean conditions

C. Royo*, L.F. García del Moral, N. Aparicio*, D. Villegas*, J. Casadesús*** and J.L. Araus******
*Área de Conreus Extensius, Centre UdL-IRTA, Rovira Roure 177, 25198 Lleida, Spain
**Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, 18001 Granada, Spain
***Servei de Camps Experimentals, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain
****Unitat de Fisiologia Vegetal, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain

SUMMARY – Future challenges of increasing productivity and quality in durum wheat will only be met by close co-operation of multidisciplinary teams who are able to incorporate new technologies. This work briefly reviews the benefits of the use of morphophysiological traits as selection criteria in breeding programmes, and the reasons for the lack of success in their use in the past. The need for collaborative work between physiologists and plant breeders in order to define and to validate traits for indirect selection is stressed. Furthermore, the paper deals with some of the most promising morphophysiological traits that have been recommended for improving selection efficiency in empirical breeding programmes. The concern of early vigor and plant biomass on grain yield is analysed, and methodologies for selecting for these traits, such as spectral reflectance measurements, are examined. Some issues related to the usefulness of other tools such as carbon isotope discrimination, canopy temperature, chlorophyll content and chlorophyll fluorescence are also considered.

Key words: Seed size, biomass, spectral reflectance, canopy temperature, carbon isotope discrimination, chlorophyll content, chlorophyll fluorescence.

***RESUME –** "Outils pour améliorer l'efficacité de la sélection du blé dur en conditions méditérranéennes". Augmenter la productivité et améliorer la qualité du blé dur sont des enjeux qui exigent l'étroite collaboration d'équipes pluridisciplinaires, capables d'incorporer les nouvelles technologies. Cette étude examine brièvement les avantages de l'utilisation des caractères morphophysiologiques comme critères de sélection dans les programmes d'amélioration, ainsi que les causes qui expliquent le manque de résultats probants dans le passé. Elle met l'accent sur la nécessité d'une collaboration entre physiologistes et améliorateurs pour définir et valider des critères de sélection indirecte. L'étude s'intéresse ensuite à certaines caractéristiques morphophysiologiques parmi les plus prometteuses, caractéristiques qui ont été recommandées pour augmenter l'efficacité de la sélection dans les programmes d'amélioration empiriques. L'implication de la vigueur initiale et de la biomasse de la plante est également examinée au regard du rendement du grain, ainsi que les méthodologies employées dans la sélection de ces caractères, comme la réflectance spectrale. Pour terminer l'étude aborde d'autres aspects liés à l'utilité de certains outils tels que la discrimination isotopique du carbone, la température du couvert végétal, la teneur en chlorophylle et sa fluorescence.*

***Mots-clés :** Taille du grain, biomasse, réflectance spectrale, température du couvert, discrimination isotopique du carbone, teneur en chlorophylle, fluorescence de la chlorophylle.*

Introduction

In the last few decades wheat breeding has lead to striking increases in productivity in irrigated regions throughout the world. However, although increases in yields in dryland situations are evident, they have not been as spectacular. Breeding programmes are traditionally empirical, that is the selection is based on the yield *per se*, as a final integrator of all the processes occurring during the life of the plant. However, meeting future challenges of increasing productivity and quality will depend on the work of multidisciplinary teams who are ready to incorporate new technologies to complement traditional breeding programmes. Selection efficiency could be increased if specific physiological and/or morphological attributes related to yield under specific environments could be identified and used as selection criteria for complementing traditional plant breeding (Acevedo, 1991). Particularly in early generation selection, when grain yield may not be properly assessed, new tools will contribute to making a more objective screening. Moreover, this assumption implies a better understanding of the factors controlling development, growth and grain yield (Shorter *et al.,* 1991), which are addressed through close co-operation between physiological research and breeding methodologies.

In spite of the important contributions that physiological understanding may bring to the identification of target environments for selection and to the definition of traits to be used as indirect selection criteria, it is generally assumed that the impact of physiological research on breeding programs has not until now been as good as expected (Jackson *et al.,* 1996). Reviews of the traits proposed as indirect selection criteria for improving yield potential, especially under drought conditions may be found in Ludlow and Muchow (1990) and Richards (1996). However, there are only few examples where this approach has been used, and even fewer where it has been successful. The only morphophysiological traits that have been reported to be important under drought and used by breeders are: flowering time, the presence of awns, leaf pubescence, glaucousness and deeper or more extensive rooting depth (Richards, 1996). However, physiologists are convinced at present that if it can be demonstrated that the selection for a particular trait will lead to increases in grain yield, and that screening for that trait is feasible, it will be incorporated into breeding programmes (Richards, 1996). The benefit of such methodologies has been given further consideration recently, due to the availability of new apparatus for specific-trait determination that are more precise, cheaper and easy to use in field measurements.

To characterise new selection traits, it is worth understanding the reasons for the lack of success in the use of morphophysiological traits as selection criteria in the past. The causes have been related to difficulties in identifying critical traits and uncertainties in their application. They can be summarized as: (i) a lack of a real causal effect of the trait on yield; (ii) the limited number of genotypes used in physiological studies, which hinders the validation of results obtained under wide genetic backgrounds; (iii) the lack of definition of linkages between the results of the physiological studies and breeding methodologies; (iv) the lack of proper methods for evaluating the trait in a rapid routine manner; (v) the lack of genetic variability for the trait; (vi) the lack of knowledge of its inheritance; and (vii) the absence of validation studies using wide genetic backgrounds and measuring the genetic advance in segregating populations following selection.

From the point of view of the definition of traits, the first of the reasons mentioned above is basic, since the presence of phenotypical correlation between yield and a specific trait does not guarantee that selection for that trait will lead to greater improvements in grain yield than the selection for grain yield itself, because the relationship may be environment-specific (Ceccarelli *et al.,* 1991) and/or germplasm-specific (Annichiarico and Pecetti, 1995). A deep understanding of the cause-effect mechanisms involving putative traits versus grain yield, and the knowledge of the heritability of the trait and its genetic correlation with yield are essential (Jackson *et al.,* 1996). Moreover, the last step is the verification of the trait/s. The most common approaches are: (i) the use of near-isogenic lines, in which lines differing in the trait are produced and tested (an essential condition for this procedure is the availability of an easy method for the screening of the lines); and (ii) the diverging selection procedure proposed by Acevedo and Ceccarelli (1989), consisting in the cross of genotypes diverging in the trait or traits, and in the practice of divergent selection for yield and the studied traits in the progeny. The traits are considered to be valuable if they increase the selection efficiency when compared to yield alone as a selection criterion. This methodology has the advantage of testing the traits in wider genetic backgrounds.

Another important element is the definition of the appropriate environment for selection. Until now, the improvement of grain yield in dry environments has mainly been a consequence of the selection for yield under irrigated conditions (Richards, 1996), since the yield potential of a genotype is usually properly expressed under a range of environments that go from well-watered to moderate stress conditions (Sayre *et al.,* 1995), before stress is sever enough to induce a GE interaction for yield (Blum, 1996). It has been reported (Acevedo, 1991) that selection for constitutive traits (always present) could be made under optimal agronomic conditions. However, if traits are largely adaptive (present only under stress conditions), selection under stress would be mandatory. The most notable constitutive traits affecting plant productivity under drought stress are plant phenology, early plant vigour, canopy architecture, plant surface characteristics, root size and depth, root penetration capacity, stem reserve utilisation for grain filling, and potential yield (Blum, 1996).

The following pages offer a brief review of some of the most promising traits that have been recommended for selection in small grain cereals, which we are investigating in a joint project carried out by the Universities of Barcelona and Granada, and the UdL-IRTA Centre in Lleida. This project is an example of the collaboration between physiologists and breeders trying to assess the usefulness of some morphophysiological traits as selection criteria for durum wheat under Mediterranean conditions. The study includes 25 genotypes selected for their divergence in physiological attributes, and the experimental work was carried out over 3 years in four environments across Spain. The traits are analysed here individually in order to study their specific potentiality, though a combination of traits will probably be necessary to explain a high percentage of the variability found in grain yield.

Seed and embryo sizes

Rapid seedling establishment and early growth have been suggested as useful traits for improving yield under Mediterranean conditions (López-Castañeda *et al.,* 1996). Maximising the early growth of leaf area and biomass has been predicted to result in a greater yield of grain and biomass in environments where rain events are frequent immediately after sowing (Fischer, 1980). Vigorous early growth may result in high dry matter yields by anthesis and improved grain yields with no decrease in harvest index (Turner and Nicolas, 1987). The positive influence of early vigour on yield potential has been attributed to reduced evaporation from the soil surface due to greater ground cover (Fischer, 1980), to increased radiation interception (Ludlow and Muchow, 1990) and to increased transpiration and transpiration efficiency (Richards, 1996). This is likely to be particularly important in Mediterranean environments (Richards, 1996). In our field experiments, a clear relationship between the biomass of durum two-leaf seedlings and grain yield observed (Fig. 1 right). Also, early vigour was related to seed and embryo sizes in durum wheat (López-Castañeda *et al.,* 1996, and left part of Fig. 1).

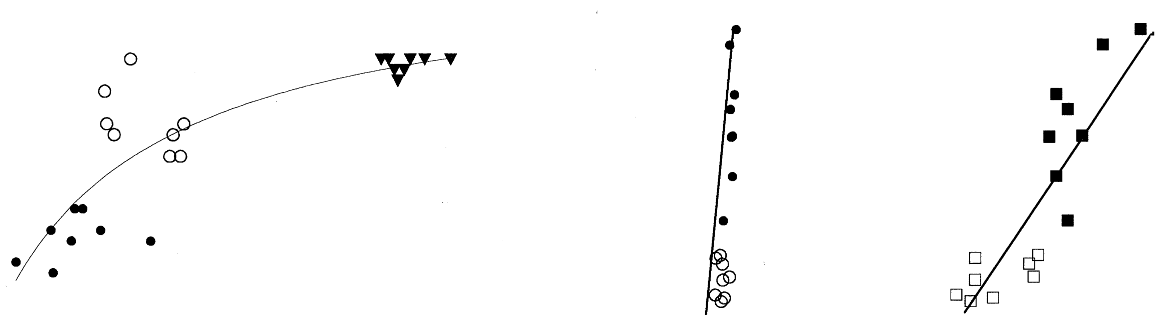

Fig. 1. Left: Relationship between the area of the embryo and the width of the first leaf in small (●), medium (○), and large seeds (▼). Points represent variety means. Right: Relationship between yield and the mass of the first leaf (circles), and the mass of two-leaf seedling (squares) under irrigated (closed symbols) and rainfed (open symbols) field trials conducted in Lleida in 1998. Data are means of eight genotypes. From Aparicio *et al.* (2000b).

Both seed size and embryo size have proved to be key factors in determining the development and growth of durum wheat seedlings until the fourth leaf-stage (Aparicio *et al.,* 2000b). Since genetic variability for early vigour seems to be present in durum wheat, in order to increase early vigour and potentially to improve yield, the identification of parents with larger seeds than existing commercial varieties, and the selection by sieving of genotypes with a high percentage of large seeds has been recommended (Aparicio *et al.,* 2000b).

Canopy temperature

Canopy temperature depends on the quantity of water transpired by the leaves, being an integrative measure of a group of mechanisms that range from the radical absorption of water to the stomatal control of transpiration. When stomates close because of reduced water status, leaf temperature rises above ambient air temperature (Ludlow and Muchow, 1990). In fact, under drought stress, those genotypes that present smaller canopy temperature will use more of the available water in the soil, thus limiting the negative effect of water stress on grain yield (Blum, 1988).

Temperature measurements are very simple using infrared thermometers. Comparison of canopy temperature depression (CTD) relative to air temperature makes it possible to detect genotypic differences related to the genetic improvement of cereals for water limited environments (Blum, 1988). The method is mainly useful under high temperature irrigated conditions, and although it is used in wheat and maize breeding programs (Acevedo, 1991), canopy temperature is highly affected by environmental conditions. Our results show that environmental effects (year and site) account for most of the variability found in canopy temperature (Table 1). Furthermore, estimations of broad sense heritabilities for canopy temperature and CTD measured at different stages during the grain filling period always gave values lower than 0.5 (Royo *et al.,* unpublished data).

Table 1. Percentage of the sum of squares of the analyses of variance for different physiological characteristics measured at grain-milk stage, explained by the main factors in the analyses. Canopy temperature was measured with an infrared thermometer; chlorophyll content was determined with the SPAD, and chlorophyll fluorescence parameters were determined from data recorded with a fluorimeter. Measurements were made in 25 durum wheat genotypes at Lleida during three years and at Granada during two years (unpublished data)

Factor	Canopy temperature	Chlorophyll content (SPAD)	Chlorophyll fluorescence†			
			Fo	Fm	Fv	Fv/Fm
Year	0-15	4-24	50	1	0	31
Environment	7-58	9	21	64	64	26
Genotype	1-2	20-35	2	2	2	4

†Only determined at Granada.

Chlorophyll content

For high irradiation levels, as is usual during grain filling in the Mediterranean basin, a high chlorophyll content is a desirable characteristic because it indicates a low degree of photoinhibition of the photosynthetic apparatus, therefore reducing carbohydrate losses for grain growth (Farquhar *et al.,*1989). A portable field unit for chlorophyll content determination (SPAD) has been extensively used in the last few years, especially to control the nitrogen nutrition in several crops (Peltonen *et al.,* 1995). Moreover, SPAD values are correlated with diverse photosynthetic parameters, such as foliar structure or Δ (Araus *et al.,* 1997), the photosynthetic rate and the absorption of photosynthetic active radiation by the canopy (Earl and Tollenaar, 1997). Broad sense heritability estimates of SPAD values in durum wheat at different stages during the first part of the grain filling period gave values near to 0.80. Also, the genotypic effects seem to account for a high percentage of the variability found in chlorophyll content (Table 1). However, we failed to find significant relationships with grain yield in specific environments (Fig. 2).

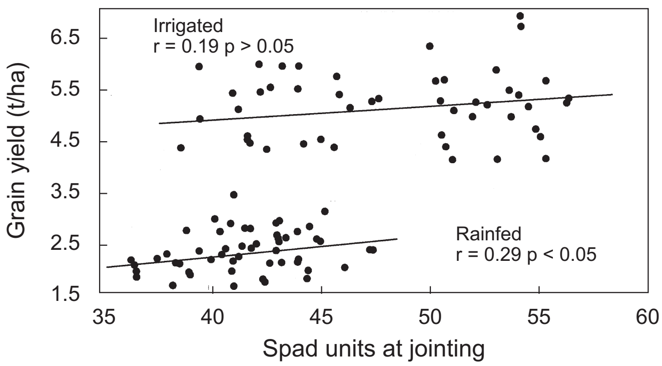

Fig. 2. Relationship between chlorophyll content at jointing, measured in spad units, and grain yield in a set of 25 durum wheat genotypes grown in Lleida under irrigated and rainfed conditions in 1997 and 1998.

Chlorophyll fluorescence

Chlorophyll fluorescence analysis may provide a sensitive indicator of stress conditions in plants. It can also be used to estimate the activity of thermal energy dissipation in photosystem II, which protects photosynthesis from the adverse effects of light and heat stress. For this reason, chlorophyll fluorescence has often been proposed as a useful tool for screening durum and bread wheat for drought (Flagella *et al.,* 1995) and high-temperature stress (Moffat *et al.,* 1990). In our study genotypic differences were found for all of the chlorophyll fluorescence parameters measured during the grain filling period, with the exception of the time of emission of Fm, which only varied significantly between environments and years. These two factors explained most of the variability found in the chlorophyll fluorescence parameters (Table 1). In this study, variations in the values of Fv (and therefore of the relationship Fv/Fm) were more associated with variations of Fm than of Fo, thus indicating the possible existence of a photoprotector mechanism in genotypes that are more productive under drought conditions. In addition, the significant relationship found between grain production and Fm, Fv and the relationship Fv/Fm suggest that these parameters could be used as easy and rapid tools for evaluating yield performance of durum wheat genotypes under Mediterranean conditions (García del Moral *et al.,* unpublished data).

Carbon isotope discrimination (Δ)

$^{13}C/^{12}C$ carbon isotope discrimination has been proposed as a useful indicator of transpiration efficiency in C_3 plants (Farquhar and Richards, 1984). The negative association between Δ and water use efficiency (WUE, measured either as net photosynthesis/transpiration or plant biomass produced/water transpired) has led to Δ being proposed as a selection criteria for WUE (Farquhar and Richards, 1984). Large genetic variation is present in durum wheat for Δ (Araus *et al.,* 1993); it is highly heritable and has a low interaction with the environment. The measurement is non-destructive and must be measured early in the plant's life (Richards, 1996).

Recent studies have reported a positive correlation between Δ and grain yield in durum wheat (Araus and Nachit, 1996). Also, a positive relationship between Δ and growth has been reported for seedlings grown under suitable water conditions (López-Castañeda and Richards, 1994). However, the assessment of genotypic variation in Δ is most effective under well-watered conditions. Thus, to be usefully applied in breeding programmes for variable environments or environments where the crop grows largely on current rainfall, Δ needs to be combined with earlier canopy cover (for example, increasing the sowing rate) (Condon and Richards, 1993). Extensive reviews of the use of Δ as selection criteria may be found in Araus (1996), Richards (1996) and Araus *et al.* (1998).

Spectral reflectance measurements as tools for the estimation of biomass and grain yield

Biomass is the most integrative parameter of plant stresses. Past achievements in breeding for wheat grain yield have been attributed to increases in harvest index, with only slight increases in biomass (Perry and D'Antuono, 1989). However, in the durum wheats derived from CIMMYT, biomass under optimal growth conditions increased 30% from 1969 to 1985 (Waddington *et al.,* 1987), and improvements in grain yield potential in modern CIMMYT durum wheats have resulted from higher biomass (Pfeiffer *et al.,* this volume). Moreover, greater yield under drought has been associated with greater above-ground dry mass at maturity (López-Castañeda and Richards, 1994). Indeed, it is generally assumed that new improvements in grain yield may be gained by increasing biomass production (Pfeiffer *et al.,* this volume) while maintaining harvest index (Austin *et al.,* 1980).

Current methods for measuring biomass production in cereal plots involve destructive sampling and excessive time and labour requirements, which is not suitable for routine use by plant breeders when large numbers of samples are to be screened. The measurement of spectral reflectance using ground-based remote sensing techniques has the potential to provide a non-destructive and less expensive estimate of plant biomass production or water stress symptoms (Peñuelas *et al.,* 1993). The method is based on the measurement of plant light reflectance in the visible and near-infrared ranges of wavelengths of light energy. Ratios of reflectance in the NIR (near-infrared) and visible range wavelengths may reliably describe crop growth or responses to stress, providing valuable information on crop status. Thus, correlations between radiometrical indices and leaf area index (LAI), green biomass, pigment concentration and crop yield have been reported for small grain cereals (Field *et al.,* 1994; Bellairs *et al.,* 1996; Peñuelas *et al.,* 1997; Aparicio *et al.,* 2000a). Four indices are most widely used for this purpose:

(i) Simple Ratio (SR) of the reflectances in the near-infrared range (IR) and red range (R), SR= R900/R680, mainly correlated with crop biomass.

(ii) Normalized Difference Vegetation Index (NDVI), defined as the near infrared minus visible reflectance divided by NIR plus visible reflectance (IR-R)/(IR+R). NDVI correlates well with canopy features such as biomass (Peñuelas *et al.,* 1997), leaf area index (LAI), absorbed photosynthetically active radiation (APAR) (Asrar *et al.,* 1984), and canopy photosynthetic capacity (Sellers, 1987). Also, it has been suggested that reflectance measurements prior to anthesis may predict grain yield response in other crops (Peñuelas *et al.,* 1997).

(iii) Water Index (WI) (the ratio between the reflectance at 970 nm and the reflectance at 900 nm, R970 nm/R900 nm), an indicator of water status, which closely tracks changes in relative water content, leaf water potential, stomatal conductance and canopy temperature depression when plant water stress is well developed (Peñuelas *et al.,* 1993).

(iv) Photochemical Reflectance Index (PRI), which is correlated with the photosynthetic radiation-use efficiency of the PAR absorbed by the canopy (Gamon *et al.,* 1997).

Our results in durum wheat show that SR (Fig. 3 left) and NDVI are good estimators of crop growth and yield. However, their usefulness for predicting durum wheat green area and grain yield is limited to environments or crop stages with LAI values lower than 3 (Aparicio *et al.,* 2000a). Also, the indirect assessment of water status provided by WI seem to be closely related, at specific plant stages, to grain yield (Fig. 3 right).

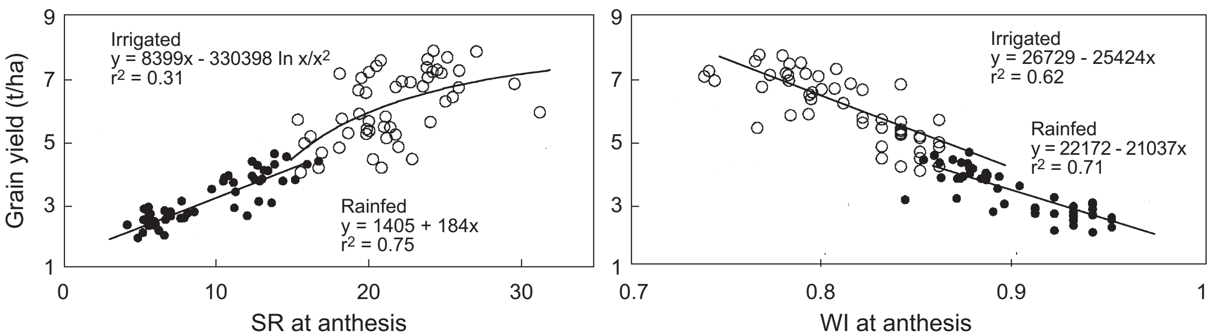

Fig. 3. Relationship between grain yield and either SR (left figure) or WI determined at anthesis. Data correspond to a set of 25 durum wheat genotypes grown in 1998 and 1999 under irrigated (○) and rainfed (●) conditions in Lleida. Spectral measurements were made with the radiometer pointed vertically (Royo *et al.,* unpublished data).

In order to extend the range of application of the results obtained, mechanicist models (based on conceptual integrative schemes) are being developed at present. In these models grain yield is expressed as a product of estimators of three factors – leaf area, photosynthetic efficiency and harvest index – and may be applied to instantaneous measurements at specific plant stages or integrated during the plant cycle from canopy reflectance indices obtained from measurements of the crop reflectance at different plant stages. Preliminary results suggest that models integrating NDVI, SIPI (structural independent pigment index) and harvest index are consistent both for instantaneous measurements or measurements integrated during different periods of the plant development, in the explanation of grain yield differences between genotypes under Mediterranean drought conditions (Royo *et al.,* unpublished data).

Acknowledgements

This study was supported by the projects CICYT AGF96-1137 and INIA SC97-039.

References

Acevedo, E. (1991). Improvement of winter cereal crops in Mediterranean environments. Use of yield, morphological and physiological traits. In: *Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments,* Montpellier, France. *Les Colloques de l'INRA,* 55.

Acevedo, R. and Ceccarelli, S. (1989). Role of physiologist-breeder in a breeding program for drought resistance conditions. In: *Drought Resistance in Cereals,* Baker, F.W.G. (ed.). CAB International, Wallingford, pp. 117-139.

Annicchiarico, P.P. and Pecetti, L. (1995). Morpho-physiological traits to complement grain yield selection under semi-arid Mediterranean conditions in each of the durum wheat types mediterraneum typicum and syriacum. *Euphytica,* 86: 191-198.

Aparicio, N., Villegas, D., Casadesus, J., Araus, J.L. and Royo, C. (2000a). Spectral vegetation indices as a non-destructive tools for determining durum wheat yield. *Agron. J.,* 91 (in press).

Aparicio, N., Villegas, D., Casadesus, J., Araus, J.L. and Royo, C. (2000b). Seed characteristics, early vigour and grain yield in durum wheat (submitted).

Araus, J.L. (1996). Integrative physiological criteria associated with yield potential. In: *Increasing Yield Potential in Wheat: Breaking the Barriers,* Reynolds, M.P., Rajaran, S. and McNab, A. (eds). CIMMYT, Mexico, D.F.

Araus, J.L., Ali Dib, T. and Nachit, M. (1998). Some insights about morphophysiological traits associated with yield increases in Mediterranean environments. In: *Durum Research Network. Proceedings of the SEWANA Durum Network Workshop,* Nachit, M., Baum, M., Porceddu, P., Monneveux, P. and Picard, E. (eds), 20-23 March 1995. ICARDA, Aleppo, Syria.

Araus, J.L., Amaro, T., Zuhair, Y. and Nachit, M. (1997). Effect of leaf structure and water status on carbon isotope discrimination in field grown-durum wheat. *Plant Cell and Environ.,* 20: 1484-1494.

Araus, J.L., Brown, H.R., Febrero, A., Bort, J. and Serret, M.D. (1993). Ear photosynthesis, carbon isotope discrimination and the contribution of respiratory CO_2 to differences in grain mass in durum. *Plant Cell and Environ.,* 16: 383-392.

Araus, J.L. and Nachit, M. (1996). *Evaluation of morphological and physiological traits related with yield on durum wheat under Mediterranean conditions.* ICARDA Ann. Report 1995, Aleppo, Syria.

Asrar, G., Fuchs, M., Kanemasu, E.T. and Hatfielf, J.L. (1984). Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. *Agron. J.*, 76: 300-306.

Austin, R.B., Bringham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L. and Taylor, M. (1980). Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. of Agric. Sci. Camb.,* 94: 675-689.

Bellairs, M., Turner, N.C., Hick, P.T. and Smith, R.C.G. (1996). Plant and soil influences on estimating biomass of wheat in plant breeding plots using spectral radiometers. *Aust. J. Agric. Res.,* 47: 1017-1034.

Blum, A. (1988). *Plant Breeding for Stress Environments.* CRC Press, Boca Raton, Florida, USA.

Blum, A. (1996). Crop responses to drought and the interpretation of adaptation. *Plant Growth Regulation,* 20: 135-148.

Ceccarelli, S., Acevedo, E. and Grando, S. (1991). Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. *Euphytica,* 56: 169-185.

Condon, A.G. and Richards, R.A. (1993). Exploiting genetic variation in transpiration efficiency in wheat: An agronomic view. In: *Stable Isotopes and Plant Carbon-Water Relations,* Ehleringer, J.R., Hall, A.E. and Farquhar, G.D. (eds). Academic Press, San Diego, pp. 435-450.

Earl, H.J. and Tollenaar, M. (1997). Maize leaf absorbance of photosynthetically active radiation and its estimation using a chlorophyll meter. *Crop Sci.,* 37: 436-440.

Farquhar, G.D. and Richards, R.A. (1984). Isotopic composition of plant carbon correlates with water-use-efficiency of wheat genotypes. *Aust. J. of Plant Physiol.,* 11: 539-552.

Farquhar, G.D., Wong, S.C., Evans, J.R. and Hubick, K.T. (1989). Photosynthesis and gas exchange. In: *Plants Under Stress,* Jones, H.G., Flowers, T.J. and Jones, M.B. (eds). Cambridge University Press, Cambridge, pp. 47-69.

Field, C.B., Gamon, J.A. and Peñuelas, J. (1994). Remote sensing of terrestrial photosynthesis. In: *Ecophysiology of Photosynthesis,* Schulze, E.D. and Caldwell, M.M. (eds). Springer-Verlag, Berlin.

Fischer, R.A. (1980). Influence of water stress on crop yield in semiarid regions. In: *Adaptation of Plants to Water and High Temperature Stress,* Turner, N.C. and Kramer, P.J. (eds). John Wiley and Sons, New York, pp. 323-339.

Flagella, Z., Pastore, D., Campanile, R.G. and Di Fonzo, N. (1995). The quantum yield of photosynthesis electron transport evaluated by chlorophyll fluorescence as an indicator of drought tolerance in durum wheat. *J. Agric. Sci., Camb.,* 125: 325-329.

Gamon, J.A., Serrano, L. and Surfus, J. (1997). The photochemical reflectance index: An optical indicator of photosynthetic radiation-use efficiency across species, functional types and nutrient levels. *Oecologia,* 112: 492-501.

Jackson, P., Robertson, M., Cooper, M. and Hammer, G. (1996). The role of physiological understanding in plant breeding; from a breeding perspective. *Field Crops Res.,* 49: 11-37.

López-Castañeda, C. and Richards, R.A. (1994). Variation in temperate cereals in rainfed environments. I. Grain yield, biomass and agronomic characteristics. *Field Crops Res.,* 37: 51-62.

López-Castañeda, C.R., Richards, R.A., Farquhar, G.D. and Williamson, R.E. (1996). Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. *Crop Sci.,* 36: 1257-1266.

Ludlow, M.M. and Muchow, R.C. (1990). A critical evaluation of traits for improving crop yields in water-limited environments. *Advances in Agronomy,* 43: 107-153.

Moffat, J.M., Sears, R.G. and Paulsen, G.N. (1990). Wheat high temperature tolerance during reproductive growth. I. Evaluation by chlorophyll fluorescence. *Crop Sci.,* 30: 881-885.

Peltonen, J., Virtanen, A. and Haggren, E. (1995). Using a chlorophyll method to optimize nitrogen fertiliser application for intensively-managed small-grain cereals. *J. Agron. Crop Sci.,* 174: 309-318.

Peñuelas, J., Filella, I., Biel, C., Serrano, L. and Savé, R. (1993). The reflectance at the 950-970 nm region as an indicator of plant water status. *Int. J. of Remote Sensing,* 14: 1887-1905.

Peñuelas, J., Isla, R., Filella, I. and Araus, J.L. (1997). Visible and near-infrared reflectance assessment of salinity effects on barley. *Crop Sci.,* 37: 198-202.

Perry, M.D. and D'Antuono, M.F. (1989). Yield improvement and associated characteristics of some Australian spring wheats introduced between 1860 and 1982. *Aust. J. of Agric. Res.,* 40: 457-472.

Richards, R.A. (1996). Defining selection criteria to improve yield under drought. *Plant Growth Regulation,* 20: 157-166.

Sayre, K.D., Acevedo, E. and Austin, R.B. (1995). Carbon isotope discrimination and grain yield for three bread wheat germplasm groups grown at different levels of water stress. *Field Crops Res.,* 41: 45-54.

Sellers, P.J. (1987). Canopy reflectance, photosynthesis, and transpiration. II. The role of Biophysics in the linearity of their interdependence. *Remote Sens. Environ.,* 21: 143-183.

Shorter, R., Lawn, R.J. and Hammer, G.L. (1991). Improving genetic adaptation of crops – A role for breeders, physiologists and modellers. *Exp. Agric.,* 27: 155-175.

Turner, N.C. and Nicolas, M.E. (1987). *Drought resistance of wheat for light-textured soils in a Mediterranean climate.* In: *Drought Tolerance in Winter Cereals,* Srivastava, P., Porceddu, E., Acevedo, E. and Varma, S. (eds). John Wiley & Sons, Chichester, pp. 203-216.

Waddington, S.R., Osmazai, M., Yoshida, M. and Ranson, J.K. (1987). The yield of durum wheats released in Mexico between 1960 and 1984. *J. Agric. Sci. Camb.,* 108: 469-477.