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Some remarks on ecophysiological traits for breeding

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SUMMARY – This work discusses, from an ecophysiological perspective, how to select the trait or set of traits able to characterize in durum wheat genotype differences in yield performance under Mediterranean conditions. After a brief introduction justifying the potential contribution of ecophysiological assessment to breeding programs we discuss some practical aspects concerning evaluation of traits. In this context the advantages of evaluating integrative traits during the late stages of the crop cycle are stressed as well as the importance of the growing environment when defining the best trait or set of traits to assess. All these general recommendations are illustrated with examples of durum wheat grown in field conditions. In such context different promising tools for trait evaluation are presented.

Key words: Durum wheat, yield, breeding, drought, phenology, carbon isotope discrimination, spectroradiometry.

RESUME – *"Quelques remarques sur des caractères écophysiologiques pour l'amélioration". Ces travaux discutent, sous une perspective écophysiologique, comment déterminer ou sélectionner les traits qui nous permettent de caractériser dans le cas du blé dur les différences génotypiques de rendement sous des conditions méditerranéennes. Après une brève introduction justifiant la grande contribution potentielle des évaluations écophysiologiques concernant l'amélioration, on a discuté certains aspects pratiques concernant l'évaluation des caractères. Dans ce contexte, les avantages de l'évaluation des caractères intégratifs durant les derniers stades du cycle de culture sont soulignés, ainsi que l'importance des conditions environnementales lorsqu'on définit le meilleur caractère ou lorsqu'on détermine le caractère à évaluer. L'ensemble de ces recommandations générales et les différents instruments utilisés pour l'évaluation des caractères sont illustrés avec des exemples sur le blé dur en conditions de champs.*

Mots-clés : *Blé dur, rendement, amélioration, sécheresse, phénologie, discrimination isotopique du carbone, spectroradiométrie.*

Introduction

Why use ecophysiological assessment?

Conventional (i.e. empirical) breeding for higher yield is based on the use of yield itself as the main selecting trait. Whereas this approach requires extensive multitrial assays the genetic gain attained is frequently modest, particularly when breeding is performed in harsh environments (Passioura, 1996; Slafer and Araus, 1998). Indeed yield is a quantitative trait that is strongly affected by the environment and thus characterised by low heritability.

Plant ecophysiology may help us to identify traits or set of traits that maximize yield and its stability in either non-stressed or stressed conditions. The development of varieties that grow effectively with inadequate supplies of water and nutrients is particularly important in less developed countries, which often lack the economic and infrastructure resources to support high-intensity agriculture. Although molecular biology and traditional breeding programs provide the tools to develop new combinations of traits in plants, ecophysiology is perhaps the field that is best suited to determine the cost, benefits, and consequences of changes in these traits, as whole plants (indeed the whole plant community or the canopy) interact in a complex manner with the environment (Lambers *et al.,* 1998; Araus *et al.,* 1998a, 1999; Slafer *et al.,* 1999). The potential contribution of the physiological approach to plant selection, as well as its inherent limitations and requirements have already been reviewed from a purely breeding perspective (see, Jackson *et al.,* 1996). The theoretical framework to define the ecophysiological determinants of yield, which are the obvious candidates to be evaluated have also been reasonably well established (Slafer *et al.,* 1993; Araus, 1996; Passioura, 1996; Richards, 1996), and different selection traits (and methods for trait evaluation), based on such framework have been proposed for bread and durum wheat (Richards, 1996; Araus *et al.,* 1998a, 1999; Slafer and Araus 1998; Slafer *et al.,* 1999). In this paper we will discuss from a purely ecophysiological perspective (i.e. using phenotypical correlations as an experimental approach) some recommendations concerning the evaluation of these traits and the most suitable way to perform it. All the examples presented will refer to evaluations of durum wheat under field conditions. Durum wheat is an important winter cereal crop in the Mediterranean region, where drought stress (i.e. water stress combined with high temperature and irradiance) during the second half of the crop cycle is the main environmental constraint on grain yield.

What to evaluate

Instantaneous versus integrative traits?

Within the term “instantaneous” we can include all those traits which provide an instantaneous or short-term picture of how a plant part, usually a leaf, is affected (e.g. in terms of photosynthetic gas exchange or chlorophyll fluorescence) by the stress. In the same category of instantaneous traits we can also consider those based on measurements at low levels of plant organization. In this category we can include metabolic traits such as enzyme activities (e.g. rubisco or nitrate reductase) or levels of substrates (e.g. proline or sugars) and growth regulators (e.g. ABA). These traits have frequently been proposed as selection criteria but, in general, without success (Richards, 1996; Slafer and Araus, 1998; Araus *et al.,* 1999). In contrast “integrative” traits are those which integrate in time (e.g. water status measured as Δ in dry matter) or at the highest level of organization (e.g. total green biomass or leaf area index) the functioning of the crop. They are much closer to the yield which is indeed the highest integrative trait.

These temporal and spatial scaling-up principles when choosing a selection trait can be adequately illustrated with the photosynthetic rate. Thus, for example, what we cannot derive from measurements on photosynthesis of single leaves is what the rate of photosynthesis of an entire canopy will be, neither the growth rates (Lambers *et al.,* 1998). It is also quite clear that short-term measurements on gas-exchange do not reflect the overall situation in the long term of the crop. In such a context tools able to evaluate “integrative” traits are necessary. Among these tools is worth mentioning remote sensing techniques addressed to the evaluation of traits at the whole canopy; that is at the highest level of plant organization. We can include in this section from infrared thermometry (see Reynolds *et al.,* 1994) evaluations, to the long array of indices derived from single spectroradiometrical measurements (Araus *et al.,* 1999; Aparicio *et al.,* 2000a). Since these indices predict for example total canopy green biomass (Aparicio *et al.,* 2000a) or crop phenology (Fig. 1), they can also be used properly to predict genotype differences in yield.

Of course, the particular conditions of cereals under Mediterranean conditions where the harvestable yield depends to a large extent on the activity and duration of few photosynthetic organs during the grain filling (a time when the main abiotic stresses, such as drought and heat, are present) make this scenario more simple. Indeed physiological evaluations performed just either in the penultimate or the flag leaf or in the spike can become reliable predictors of genotypical differences in yield (Araus *et al.,* 1997, 1998b). This can be extended even to the utilization of instantaneous traits such as chlorophyll fluorescence (Araus *et al.,* 1998c).

A trait or a set of traits?

Usually there is not a unique (i.e. “superb”) trait but frequently alternative and complementary traits. The same can be said regarding the tools for trait evaluation. Therefore the usual scenario can involve the evaluation of a set of different traits. Nevertheless this set of traits may change depending on the target environment where breeding should be addressed (Villegas *et al.,* 2000). For moderately stressed environments larger yields of durum wheat were associated with shorter plants and higher carbon isotope discrimination (Δ) of grains, and to a less extent with higher early vigour and lower canopy temperature, whereas phenological traits made no contribution to genotype differences in yield. In contrast, for the genotypes cultivated under less favourable conditions, higher yields were related with an earlier heading date or alternatively to a higher chlorophyll content during grain filling. A higher Δ in mature kernels also seems to be a positive trait (Villegas *et al.,* 2000). In addition the kind of environment where the morphophysiological traits are evaluated may affect the performance of these traits as yield predictors. The combination of significant traits measured in good environments performs better than when measured under more stressed conditions.

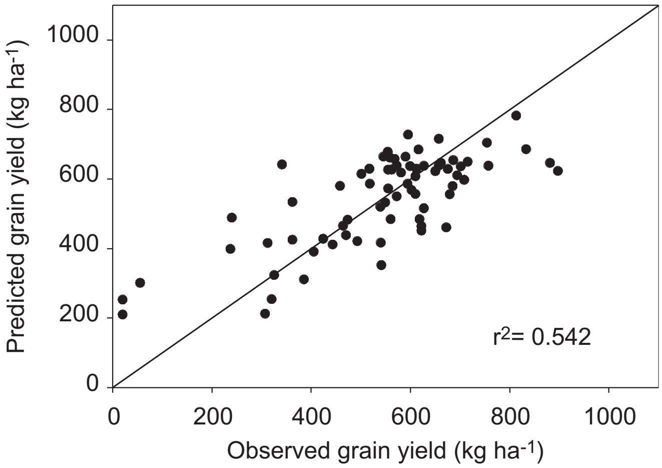

Fig.1. Prediction of grain yield based in the combination of three different spectroradiometrical indices calculated from the spectra reflected by the canopy. Measurement was done (on early June 1998) at mid grain filling in a set of 74 genotypes of durum wheat corresponding to the WANADIN collection developed by the CIMMYT/ICARDA breeding program. The three canopy reflectance indices used were SAVI = (R900-R680)/(R900+R680+L) x (1+L) with L = 0.5 for most crops (Huete, 1988), SIPI = (R800-R435)/(R415+R435) (Peñuelas *et al.,* 1995a), and NPQI = (R415-R435)/(R415+R435) (Peñuelas *et al.,* 1995b). The function of prediction was grain yield = 3616 – 4297SAVI – 1370SIPI – 3240NPQI. Its performance seems to be based in the differences across genotypes in the date of maturity. Plants were grown at Tel-Hadya (headquarters of ICARDA), North-West Syria (Casadesús, Araus, and Nachit, unpublished results).

Table 1. Mean and standard deviation of grain yield (kg ha^{-1}) of a set of 140 genotypes of the Durum Core Collection grown during the 1996-1997 season at Tel-Hadya (headquarters of ICARDA), North-West Syria. Three different growing conditions were assayed: the two first were winter plantings under irrigated and rainfed conditions and the third a late planting trial. The correlation coefficient of the relationship between grain yield and number of days from planting to heading are shown for each growing condition (Bort, Araus, Asbati and Nachit, in preparation)

	Irrigated	Rainfed	Late planting
Mean yield	4096	2410	1579
Standard deviation	773	468	564
Correlation coefficient	-0.15	-0.43	-0.77
Significance	n.s.	***	***

n.s.: not significant; ***significant at α = 0.001.

In general terms, as the yield constraint imposed by the stress increases, the combination of traits significantly explaining genotypical differences in yield decreases (Villegas *et al.,* 2000). Under extreme environments one physiological trait (usually related with phenology) alone may explain a high portion (even the majority) of genotypic differences in yield. Thus for example under high temperature rainfed environments, phenological adjustment are by far the best trait, with those varieties of shorter duration (i.e. exhibiting an evading strategy) being the most productive (Table 1). For high temperature irrigated-conditions the maintenance of transpiration, evaluated at the canopy level by infrared temperature, also explains more than half the variability in yield (Reynolds *et al.,* 1994). For intermediate scenarios such as high temperatures and support irrigation the combination of two traits, providing information on water status (Δ) and phenology (chlorophyll content) traits can be an option (Table 2).

Table 2. Percentage of variation in grain yield across durum wheat genotypes as explained by the progressive addition of several independent traits: carbon isotope discrimination (D) of mature kernels, the total chlorophyll content on leaf area basis measured in the flag leaf blade with a portable device (SPAD) either around anthesis and at mid grain filling (1st or 2nd sampling dates, respectively), and the initial chlorophyll fluorescence (F_0) parameter measured in the ear around anthesis. Two sets combined, of 24 genotypes each, corresponding to the regional durum yielding trials for temperate and continental areas, from the CIMMYT/ICARDA breeding program, were assayed. Genotypes were cultivated during 1995 in a late planting trial at Tel-Hadya (headquarters of ICARDA), North-West Syria (Araus, Amaro, Asbaty and Nachit, unpublished results)

Δ kernels	40%
Δ kernels + SPAD-2nd flag leaf	45%
Δ kernels + SPAD-2nd flag leaf + F_0 ear	46%
Δ kernels	40%
Δ kernels + SPAD-1st flag leaf	42%
Δ kernels + SPAD-1st flag leaf + SPAD-2nd flag leaf	47%
Δ kernels + SPAD-1st flag leaf + SPAD-2nd flag leaf + F_0 ear	47%

When to evaluate: early or late in the plant cycle?

Rapid seedling establishment has been proposed for different cereals (Acevedo *et al.,* 1991; López-Castañeda *et al.,* 1996) including durum wheat (Aparicio *et al.,* 2000b) as a useful trait to improve yield under Mediterranean conditions. Indeed early vigour may reduce evaporation from the soil surface due to a greater ground cover (Richards, 1987), while increasing radiation interception and transpiration efficiency (Ludlow and Muchow, 1990), and there is genetic variability in temperate cereals (Regan *et al.,* 1992; Richards, 1987, 1996; Aparicio *et al.,* 2000b).

Nevertheless, the relationship between early dry matter production and grain yield has not always been found (Regan *et al.,* 1992; Richards, 1996; Bort *et al.,* 1998) and even for durum wheat there are contradictory results. Thus there are reports of a positive relationship across genotypes between grain yield and development of the seedling at the two leaf stage correlation is not significant when seedlings of 4 to 6 leaves are considered (Aparicio *et al.,* 2000b). Similarly, a recent study performed with a large collection of durum wheat genotypes grown at ICARDA headquarters (Aleppo, Syria) failed to find significant relationships between grain yield and either dry mass or area of seedlings, at the stage of 4 to 6 leaves or width of the first leaf (Araus, Villegas, Asbati and Nachit, unpublished results). In addition, in disagreement with earlier reports in bread wheat (see Richards, 1996) early vigour was not related in this case with the width of the first leaf (Fig. 2), a trait that seems to integrate both embryo size and the ratio of leaf area to leaf weight. Different aspects can be involved in the lack of effect of a higher early vigour increasing final yield. At the early stages of the crop a different sensitivity to low temperatures (i.e. freezing) can be involved (Bort *et al.,* 1998), with those genotypes more developed being the more susceptible. Alternatively inter-plant competition after the seedling stage can also be involved in this lack of relationship (Bremner *et al.,* 1963). Additionally, in those environments (typically Mediterranean) where the faster development of leaf area may result in the premature exhaustion of soil water, a greater early vigour, by itself, can be a negative attribute (Richards, 1996). Indeed vigorous early growth may be particularly appropriate as a good trait when combined with early flowering, which may greatly contribute to a greater water-use efficiency over the crop cycle.

As pointed out above, drought is the main environmental constraint limiting yield under Mediterranean conditions and it develops progressively during the last part of the crop cycle. In these circumstances the same trait evaluated late in the crop cycle can exhibit better performance assessing differences among genotypes in yield (Acevedo 1991; Araus *et al.,* 1998b, 1999). This is valid for crop development, where for example crop biomass at anthesis is generally much better correlated with final yield than early vigour is. This is also the case for example of the carbon isotope discrimination an indicator which integrates the water status under which the crop is developing (Araus *et al.,* 1998b). The performance of Δ as a yield predictor improves progressively as $^{13}C/^{12}C$ analyses are performed plant parts developed later on the crop cycle (Table 3).

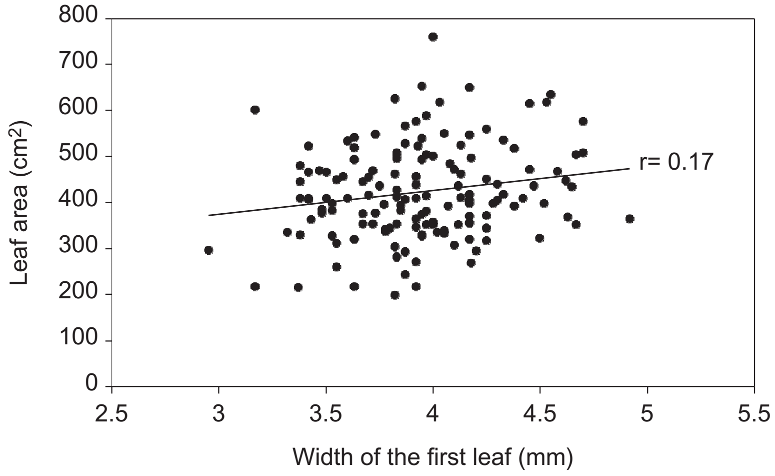

Fig. 2. Relationship between the width of the first emerged leaf and the early vigour, measured as the total leaf area of the seedlings sampled in 1-meter length row (p = 0.066). Measurements were performed during January 1998 and correspond to the 144 genotypes of the durum wheat population Jennah Khetifa/Cham-1 developed by the CIMMYT/ICARDA breeding program. Plants were cultivated at Tel Hadya (headquarters of ICARDA), North-West Syria (Villegas, Araus, Asbati and Nachit, unpublished results).

Table 3. Relationship between grain yield and carbon isotope discrimination measured in dry matter of seedlings, in the penultimate leaf and in mature kernels for a set of 144 durum wheat genotypes of the Durum Core Collection grown under rainfed conditions at Tel-Hadya (headquarters of ICARDA), North-West Syria (Araus *et al.,* 1998b, 1999)

	Seedlings	Penultimate leaf	Mature kernel
Correlation coefficient	-0.14	+0.29	+0.50
Significance	n.s.	***	***

n.s.: not significant; ***significant at α = 0.001.

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