

PHYSIOLOGY AND BIOTECHNOLOGY INTEGRATION FOR PLANT BREEDING

Section I Physiological basis of yield and environmental adaptation

Chapter 1

Physiology of yield and adaptation in wheat and barley breeding

José L. Araus^A, Gustavo A. Slafer^B, Matthew P. Reynolds^C, Conxita Royo^D

^AUnitat de Fisiologia Vegetal, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain; ^BDepartamento de Producción Vegetal and IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina; ^CInternational Maize and Wheat Improvement Centre (CIMMYT), Mexico; Mailing address: Apartado # 370, P.O. Box 60326, Houston, TX 77205; ^DÀrea de Conreus Extensius, Centre UdL-IRTA, Alcalde Rovira Roure 191, 25198 Lleida, Spain.

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^AUnitat de Fisiologia Vegetal, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain; ^BDepartamento de Producción Vegetal and IFEVA, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina; ^CInternational Maize and Wheat Improvement Centre (CIMMYT), Mexico; Mailing address: Apartado # 370, P.O. Box 60326, Houston, TX 77205; ^DÀrea de Conreus Extensius, Centre UdL-IRTA, Alcalde Rovira Roure 191, 25198 Lleida, Spain.

1.- Introduction

1.1.- Sources for improved production since the beginning of agriculture

Agriculture in the Old World started about 10,000 years ago, coinciding with the beginning of the Holocene. From this time up to the present, C3 cereals such as bread (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L. var. *durum*) as well as barley (*Hordeum vulgare* L.) have remained the outstanding crops in terms of area and food source (e.g. Evans, 1998). Relatively high cereal yields are suggested at the beginning of agriculture (Amir and Sinclair, 1994; Araus *et al.*, 1999; 2001b), so that the yields believed to be attained then (the equivalent to ca. 1 Mg ha⁻¹; see for instance Araus *et al.*, 2001b and references therein) were quite similar to the averaged yields attained globally at the beginning of the 20th century (Calderini and Slafer, 1998; Slafer and Satorre, 1999). This means that the increased demands produced by the growing population since the Neolithic (some 4-10 million people; Minc and Vandermeer, 1990; Evans, 1998) to 1900 (more than 1 billion people) were chiefly satisfied by the enlargement of the cultivated area. Most of the advances made in non-scientific but genuine breeding and management improvement during the 9,900 first years of agriculture allowed that average yields did not decrease despite the impressive increase in cropping area from few settlements to ca. 700 Mha of arable land worldwide, largely implying the growth of the crops under increasingly limited conditions. During the 20th century, when the Mendel's laws were rediscovered and breeding started its period of scientifically based selection, increases in average yield were still not evident until around the 1950's (Calderini and Slafer, 1998; Slafer and Satorre, 1999). There was still a large increase in growing area as a response to the increased demand during the first half of the 20th century (Slafer and Satorre, 1999). Since then, when the population was growing faster than ever and there were only negligible areas that might still be turned into agriculture, average yields increased dramatically in only a few decades. This change, known as the Green Revolution, was due to the introduction of semidwarf varieties with improved harvest index (HI) and, consequently, higher yield potential¹ (Calderini *et al.*, 1999a; Abeledo *et al.*, 2001), which in turn were more responsive to management improvement (Calderini and Slafer, 1999). It allowed the interaction between genetic and management improvement to express a relative increase in average yields even greater than that in population during the second half of the 20th century (Slafer and Satorre, 1999). Before the improvement in yield potential reached during the intermediate decades of the 20th century, responsiveness to environmental amelioration would have been limited. For instance, the increase in atmospheric CO₂ concentrations from ca. 270 ppm before the beginning of the industrial revolution to the levels observed in 1950's (ca. 350 ppm) appears to have affected only marginally the yield levels of cereals (as they remained virtually unchanged during the first 5 decades of the 20th century, Slafer and Satorre, 1999 meanwhile CO₂ concentrations increased steadily).

¹ In this paper the term yield potential is used to define the productivity of adapted, high-yielding cultivars achieved in absence of yield reductions due to either the presence of diseases, weeds and insects, or insufficient availability of water and major nutrients (see for more details, Evans and Fischer, 1999)

Therefore, the extraordinary increase in average yields (which, in fact, was not counterbalanced by a reduction in yield stability; see Smale and McBride, 1996; Calderini and Slafer 1998) obtained during the last few decades was due to the contribution of both genetic and management improvement. Although it is highly likely that the interaction between both factors may be more important than each of them separately, several analyses estimated relative breeding contributions to total yield increases obtained by farmers ranging from *ca.* 30% in Mexico (Bell *et al.*, 1995) to *ca.* 50%, in most other countries (see examples for USA, UK, and Argentina in Slafer *et al.*, 1994a), which indicates that the other 50% of the improvement arises from changes in agronomic practices (increased use of N fertilizer, P fertilizer applications, fitting of sowing density and crop phenology, use of herbicides for weed control, spread of irrigation and mechanization, etc.).

1.2.- Sources for improved production in the future

Global demand for wheat is expected to rise by approximately 1.3% per year globally (and by approximately 1.8% per year in developing countries) over the next 20 years (Rosegrant *et al.*, 1995). Meeting these demands by increasing wheat production through increased land use is not very likely. Cultivated areas of wheat in developing countries are expected to rise by only 0.14% per year through 2020 (Rosegrant *et al.*, 1995). Thus, most of the needed increase in production must come from increases in average yields. In the past contributions from management improvements have been as large as or larger than those made by genetic improvement (Slafer and Andrade, 1991; Slafer and Peltonen-Sainio, 2001). Much of the management improvements in farm yields were associated to an impressive increase in the amount of resources applied, mainly through irrigation, fertilization and pesticide application (see for instance Evans, 1997). However, both economic and environmental analyses suggest that we can only marginally depend on the contributions that improved management might make to the large increase in yield needed to keep pace with population increase. Yield gaps (potential minus actual) in high production environments are rather small: actual yields accounts for 70 to 80% of maximum yields² obtained on experiment stations (Byerlee, 1992; Pingali and Heisey, 1999), and then in those environments there is little to expect from adoption of improved management. In other, lower yielding environments, the gap between potential and actual yields is normally large, which may be taken as an indication of the potential contribution that management improvement might make in these cases. It is believed that half of the large contribution made by management improvement to raise average yields in the last decades came solely from the increase in the use of N fertilizers. However, the widespread belief that intensive agriculture should be discouraged because of its detrimental effect on the environment will lead to more sustainable agricultural systems, therefore limiting in the future the rate of resource application (*e.g.* Austin, 1999). On the other hand it is expected that a steady increase in atmospheric CO₂ concentrations will take place during the next few decades. However, although a positive effect on yields is likely in some, high-yielding conditions (*e.g.* Manderscheid and Weigel, 1995; Amthor, 2001), in many other cases (most growing regions of the world) the environmental constraints accompanying CO₂ rise may make these responses negligible or even negative (when the increased CO₂ is expected to be accompanied by warmer or drier conditions or insufficient levels of N fertilization). Even in some high yielding environments the expected increases in temperature associated with the global increase in greenhouse gases can counteract the effect of increasing atmospheric CO₂. Detrimental effects of high temperatures on both grain number per unit land area (*ca.* Fischer, 1985) and individual grain weight (*ca.* Wardlaw and Moncur, 1995) are well known.

² Also termed potential yield, the highest possible yields obtainable with ideal management and nutrient under specific soil and weather conditions

All in all, it seems that we will strongly rely on future genetic gains in yield of wheat and barley (and other cereals) as the exclusive source for the required increased production in the near future (Slafer *et al.*, 1999; Araus *et al.*, 2002).

1.3.- The importance of understanding yield physiology

The highly efficient breeding programs that collectively allowed the great increase in yield during the last five decades, must be even more efficient in the future. This time breeders have to attempt to improve yield potential starting with a crop with an already substantially improved yield potential (see reviews by Calderini *et al.*, 1999a for wheat and by Abeledo *et al.*, 2001 for barley). This relatively high yielding level of the new starting point naturally reduces the likelihood of achieving increased efficiency in improving yield potential (Araus *et al.*, 2002). In fact, further genetic increases in yield potential were becoming harder to achieve during the last decade (*e.g.* Reynolds *et al.*, 1996; Sayre, 1996; Slafer *et al.*, 1999).

It may be speculated that breeding would become more efficient in further rising yields if the characteristics at the crop level of organization conferring the ability to the plants when growing to maximize yields are identified (Araus, 1996; Richards, 1996a; 1996b; Slafer and Araus, 1998; Slafer *et al.*, 1999; Blum, 2000). To reach such an ambitious objective, our understanding of the main physiological attributes for grain yield has to be improved considerably. Once we can target a key trait underlying yield, to identify appropriate parents and efficiently select progeny would become easier (Austin, 1993). Moreover, even the potential power of biotechnology for locating gene sequences and introgressing genes is clearly demonstrated in practice for relatively simple traits of great economic value (*e.g.* some quality traits, some resistance to pests and diseases), it would also strongly depend upon our understanding of yield-determining physiological processes (Araus *et al.*, 2002). In fact there is an intrinsic complexity for identifying trustworthy QTLs for yield (Stuber *et al.*, 1999).

1.4.- Objectives

We aimed to summarize the major physiological changes that took place throughout the successful breeding process of the 20th century and review both the most promising traits to be considered in future breeding of cereals and the existence of technology that may make it possible to use these traits in realistic breeding programs. Readers interested in more basic physiological (as well as ecological and molecular) aspects of yield determination in wheat and barley may consult some of the recent books on these issues (Satorre and Slafer, 1999; Smith and Hamel, 1999; Slafer *et al.*, 2001b) as well as the renown, classic books by Evans (1975, 1993), Smith and Banta (1983), Rasmusson (1985), Heyne (1987) and Evans and Peacock (1981).

This chapter focuses mainly on analytical approaches directly linked to our ecophysiological understanding of the crop through

- (i) the classical dependence of yield (GY) on their agronomic crop components ($GY = \text{Spikes m}^{-2} \times \text{Grains/spikes} \times \text{GWt}$; the number of spikes per unit land area, grains per spike and averaged grain weight),
- (ii) the carbon-economy based relationship ($GY = RAD \times \%RI \times RUE \times HI$; the total quantity of incident solar radiation throughout the growing period [RAD], the fraction of RAD intercepted by the canopy averaged across the crop cycle [%RI], the radiation-use

efficiency [RUE], which is the overall photosynthetic efficiency of the crop, and the harvest index [HI] or fraction of the total dry matter harvested as yield),

or

- (iii) the water use based relationship ($GY = W \times WUE \times HI$; the water transpired by the crop plus direct evaporation from the soil [W], the water-use efficiency *i.e.* the ability of the crop to produce biomass per unit of water evapotranspired [WUE], and the harvest index)

2.- Physiological changes associated with genetic gains in grain yield

One popular approach to identify physiological attributes contributing to increased yield potential consists in determining the physiological bases of the differences in yield between cultivars released at different eras (*e.g.* Austin 1999; Austin *et al.*, 1980a; Feil, 1992; Loss and Siddique, 1994; Slafer *et al.*, 1994a; Calderini *et al.*, 1999a; Abeledo *et al.*, 2001).

In this section we have privileged included information from experiments growing together cultivars released at different eras. Most of these studies have been carried out under different field conditions, which seems to be adequate to produce reliable figures of genetic gains in yield and its determinants (Calderini *et al.*, 1999a). These studies have been more frequently developed on wheat (in which several reviews have been written; Slafer and Andrade, 1991; Feil, 1992; Loss and Siddique, 1994; Slafer *et al.*, 1994a; Calderini *et al.*, 1999a) than on barley (Abeledo *et al.*, 2001). Most of the traits identified in the retrospective analyses have been shown to be constitutive in nature; that is to be expressed in the absence of stress.

2.1.-Yield gains from wheat and barley breeding

In both cereals, genetic improvements in yield seemed to have been small during the first part of the 20th Century, and much faster later on (see extended discussions on this fact in reviews by Slafer *et al.*, 1994a; Calderini *et al.*, 1999a; Abeledo *et al.*, 2001). This trend resembles what has been discussed regarding actual farmer yields (see above) and provides indirect support to the idea that increasing yield potential is essential in improving the broad tolerance to mild and moderate stresses (Slafer and Araus, 1998). Although the positive interaction between genetic and management improvements on measured yield gains may overestimate the contribution frequently assigned to improvements in yield potential (see details on this discussion in Evans and Fischer, 1999) results from empirical breeding also supports the idea. For instance, the wheat program at CIMMYT focuses in rising yield potential as it appeared to be related to higher yields in realistic production environments (*e.g.* Reynolds *et al.*, 1996), and at least some high-yielding cultivars do also tolerate a number of stresses (Rajaram and van Ginkel, 1996).

Absolute gains in yield from breeding differed greatly among countries, but much of the difference was related to the environmental conditions under which the breeding process took place. In general the better the agronomic conditions the faster the rates of genetic gains, a fact that might be expected from theory (Richards, 1996b; Slafer *et al.*, 1999). For instance, genetic gains in wheat yield for a long period (from the 1860's to the 1980's) have been far larger in the UK ($23.3 \text{ kg ha}^{-1} \text{ y}^{-1}$; Austin *et al.*, 1989) than in Australia ($5.3 \text{ kg ha}^{-1} \text{ y}^{-1}$; Perry and D'Antuono, 1989), which agrees with differences between both countries in environmental growing conditions (Calderini and Slafer, 1998). But if yields of cultivars released in different eras are expressed in relative terms of the average yield of the study (as an indirect indicator of the environmental condition) yield gains are similar (Fig. 1). Thus, when considering the gains in relative terms ($\% \text{ y}^{-1}$) most differences among

breeding programs of countries contrasting in genetic gains disappeared (Calderini *et al.*, 1999a; Abeledo *et al.*, 2001).

2.2.- Physiological changes produced during genetic improvement of yield

2.2.1.-Crop phenology

Phenology largely determines the adaptability of a cereal crop to a certain range of environmental conditions and may also strongly affect yield potential (Slafer *et al.*, 2001a). However, the length of the period between seedling emergence and heading was only occasionally modified in a systematic way by breeders (Slafer *et al.*, 1994a; Abeledo *et al.*, 2001). For instance, it has been found in several studies with wheat cultivars released at different eras that time to anthesis was not (or was only slightly) modified by past breeding (*e.g.* Deckerd *et al.*, 1985; Waddington *et al.*, 1986; Hucl and Baker, 1987; Cox *et al.*, 1988; Austin *et al.*, 1989; Slafer and Andrade, 1989; Calderini *et al.*, 1997). However, developmental traits in cereals are particularly significant in water-limiting conditions of Mediterranean environments, where available water becomes increasingly scarce with time (Richards, 1991; Slafer *et al.*, 1994a; Royo *et al.*, 1995; Passioura, 1996; Bort *et al.*, 1998; González *et al.*, 1999). In this case, in which the longer the cycle of the cultivar the stronger the stress, the better adapted cultivars develop faster, reaching anthesis earlier, thus minimizing the exposure to terminal stress. Therefore, empirical selection for yield itself has naturally led to a systematic shortening of the duration from sowing to anthesis in Australian wheats (Perry and D'Antuono, 1989; Siddique *et al.*, 1989a; 1989b; Yunusa *et al.*, 1993; Loss and Siddique, 1994), as earliness is the simplest and most effective alternative to increase yield where drought during grain filling is a common event (Passioura, 1996; Slafer and Whitechurch, 2001).

In the few studies available in barley, there were no clear trends to systematic changes in developmental rates determining time to anthesis. In general, the relationship between time from seedling emergence to heading and the year of release of the cultivars was not significant (*e.g.* Wych and Rasmusson, 1983; Boukerrou and Rasmusson, 1990; Bulman *et al.*, 1993; Muñoz *et al.*, 1998), or the slope of such relationship was relatively small (Martiniello *et al.*, 1987; Riggs *et al.*, 1981; Jedel and Helm, 1994b). It is speculated that, as in wheat (Perry and D'Antuono, 1989; Siddique *et al.*, 1989a), barley breeding in these regions may have tended to systematically reduce the time to heading in order to avoid the terminal stress, characteristic of these regions (Loss and Siddique, 1994).

2.2.2.-Plant height

The stature of the stem is important in the determination of cereal productivity as it affects both yield potential and risk of yield losses due to lodging. Therefore, semidwarf wheats are able to receive higher rates of fertilizer application. There is a generalized agreement that breeding programs throughout the world consistently reduced stem height, modern cultivars being significantly shorter than the older ones, both in wheat (*e.g.* Austin *et al.*, 1980a; 1980b; Cox *et al.*, 1988; Austin *et al.*, 1989; Perry and D'Antuono, 1989; Siddique *et al.*, 1989a; Slafer and Andrade, 1989; Canevara *et al.*, 1994; Calderini *et al.*, 1995) and in barley (*e.g.* Riggs *et al.*, 1981; Jedel and Helm, 1994b; Martiniello *et al.*, 1987). While in wheat reduction in plant height has largely been a continuous process throughout the 20th century (Calderini *et al.*, 1999a), in barley the trend was less linear with stronger reductions at the beginning of the century and smaller changes thereafter (Abeledo *et al.*, 2001). In fact, barley optimum heights (in terms of productivity) were already obtained earlier than in wheat, where optimum values were only reached after the green revolution, largely produced by the introduction of *Rht* dwarfing genes.

As pointed out above lodging is an important problem in wheat and barley, often reducing yields by 30-40% (Stapper and Fischer, 1990), and improvement in lodging resistance has been an important

criterion in plant breeding programs (Abeledo *et al.*, 2001). The response of lodging is largely independent of stem length within the range of relatively short plants (stem diameter is then more critical), the risk of lodging being positively related to stem height beyond a threshold in plant height. In fact, the optimum height for yield is within the threshold between those in which lodging is insensitive to height and those directly related to lodging. It has been empirically demonstrated, in a wide range of environmental conditions, that this optimum height ranges between 70 and 100 cm (*e.g.* Fischer and Quail, 1990; Richards, 1992a; Miralles and Slafer, 1995b; Austin, 1999). Therefore, as it might be expected, breeding has tended to reduce plant height whenever the cultivars to be replaced by higher-yielding ones had been taller than the optimum values. As a consequence of all these reductions, average height of modern wheats and barleys is already within the range that optimizes yield in virtually all countries analyzed (Calderini *et al.*, 1999a; Abeledo *et al.*, 2001), implying that breeders would not further reduce plant height in the future.

2.2.3.- Dry matter production and its partitioning

In general terms, the large increase in yield produced with the release of newer cultivars was far more associated with the improved partitioning to reproductive structures than with total dry matter production. In wheat the increases in grain yield were almost entirely independent of modifications in biomass (see reviews by Slafer and Andrade, 1991; Feil, 1992; Evans, 1993; Loss and Siddique, 1994; Slafer *et al.*, 1994a; Calderini *et al.*, 1999a); although some exceptions can be found (Waddington *et al.*, 1986; Hucl and Baker, 1987). The general scenario is similar for barley, in which vegetative biomass either (i) did not show any trend with the year of release of the cultivars (Martiniello *et al.*, 1987; Bulman *et al.*, 1993; Jedel and Helm, 1994a); or (ii) was increased with the year of release of the cultivars, but at a slower pace than that for yield (Riggs *et al.*, 1981; Wych and Rasmusson, 1983; Boukerrou and Rasmusson, 1990).

The lack of systematic changes in biomass production indicates that little has been done to change the ability of the crop to either intercept more radiation or use it more efficiently (the two major components of crop growth). Although again exceptions may be found, the generalized situation is that cultivars released at different eras did not systematically differ in their leaf area indexes (Austin *et al.*, 1980a; 1980b; Deckerd *et al.*, 1985; Feil and Geisler, 1988; Canevara *et al.*, 1994; Calderini *et al.*, 1997). Consequently, neither radiation interception (Deckerd *et al.*, 1985; Slafer *et al.*, 1990; Calderini *et al.*, 1997) nor radiation use efficiency (RUE) at the canopy level have been modified substantially, whenever the length of the crop cycle has remained unmodified (Slafer *et al.*, 1990 and Calderini *et al.*, 1997). However, when breeding has increased total biomass accumulation, as in the case of some durum wheats, later maturing genotypes have been obtained (Pfeiffer *et al.*, 2000).

Lowering the level of crop organization being considered from the canopy to that of organs does not change the scenery. Thus, leaf photosynthesis seemed not to have been related to breeding progress in yield (Austin *et al.*, 1982; Austin, 1989). Although maximum photosynthesis appeared to be related with the year of release of CIMMYT's cultivars (Fischer *et al.*, 1998), mostly due to changes in stomatal conductance (Richards, 2000), these differences were not associated with increases in biomass production of similar magnitude.

Thus, apart from a few uncommon examples in which breeders may have increased crop biomass as the main way to achieve yield gains, the yield increase in wheat and barley due to breeding has been strongly dependent upon the magnitude of change achieved in biomass partitioning, reflected by higher HI at maturity (Fig. 2, see also general overviews by Evans, 1993 and Hay, 1995, besides the reviews mentioned above).

In fact, retrospective analyses show that HI has risen in the more recent genotypes not only under stress-free conditions but also under drought (Calderini *et al.*, 1999a) and low fertility (Ortiz-Monasterio *et al.*, 1997) conditions (Fig. 2). Associated with the higher HI in the modern cultivars

is a higher N use efficiency (Reynolds *et al.*, 1999) and a shorter stature (Byerlee and Moya, 1993; Austin, 1999; Slafer *et al.*, 1999). However, this last trait may have negative consequences under drought-prone environments where kernel growth may be sustained by assimilates accumulated in the upper internodes before anthesis (Loss and Siddique, 1994). This would explain the lack of (negative) relationship in durum wheat between stem length and yield under moderate-severe drought (*e.g.* Villegas *et al.*, 2000).

Due to the fact that the large genetic gains in yield achieved during the second half of the 20th century were heavily associated with improvements in partitioning of assimilates, modern cultivars in most cereal regions reached already high values of HI (Fig. 2). Thus, further genetic improvement of wheat and barley yield may strongly depend upon the development of strategies to raise biomass production (see below section on physiological avenues to increase yield potential).

2.2.4.-Yield components

It is found almost universally that yield variation of cereals is far more related to differences in number of grains per m² than in individual grain weight (see, for example, differences in yield due to locations and years, Magrin *et al.*, 1993; or to timing and doses of fertilizer application, Fischer, 1993a). Breeding higher-yielding cultivars has also affected more markedly number of grains per unit land area than the average individual grain weight in both wheat (Feil, 1992; Loss and Siddique, 1994; Slafer *et al.*, 1994a; Calderini *et al.*, 1999a) and barley (Abeledo *et al.*, 2001), though few exceptions may be found. In wheat some studies analyzed the fate of the florets to determine how breeding improved the ability of the plants to set more grains. Modern cultivars exhibited a superior ability to sustain the development of floret primordia just before anthesis allowing a higher survival to take place, thereby increasing the number of fertile florets at anthesis (Siddique *et al.*, 1989b; Slafer and Andrade, 1993; Slafer *et al.*, 1994b). Moreover, the greater number of florets per spike at anthesis in semi-dwarf than in standard height genotypes has been attributed to the reduced mortality of floret primordia between flag leaf appearance and anthesis rather than to differences in the maximum number of floret primordia initiated (Kirby 1988). An example may be given for durum wheat changes through time in Spanish genotypes, since the number of spikelets per main spike has been reduced a 3% comparing old genotypes (from the 20's) and recently released varieties, whereas the number of grains per spike has increased more than a 30% (Royo *et al.* unpublished data). This change is critical, as only a minor proportion of the florets initiated in each spike is able to produce fertile florets at anthesis (Kirby, 1988), and was the result of an improved growth of the spikes immediately before anthesis in association with a reduction in stem height (Siddique *et al.*, 1989b; Slafer and Andrade, 1993). The clearest example comes from the impact of the introgression of major dwarfing genes in the wheat genome. *Rht 1* and *Rht 2* genes, which reduce cell size in most above-ground organs, also inhibit the elongation of the internodes releasing thus a relatively large amount of resources that would have been used in stem growth otherwise (Miralles *et al.*, 1998). These resources are then available to the growing spikes. This, in turn, results in an increased spike growth improving floret fertility (Fischer and Stockman, 1980; Brooking and Kirby, 1981; Slafer and Miralles, 1993; Richards, 1996b), because of a remarkable reduction in floret abortion (Youssefian *et al.*, 1992; Miralles and Slafer, 1995b).

The fact that cereal breeding tended to increase more substantially the number of grains per m² than the individual grain weight is also consistent with results from studies aimed to determine the main yield limitations. When both wheat and barley crops are subjected to a shading, thinning, degreening or defoliations after the grain set phase (a week or so after anthesis), the growth of the grains is not, or is only slightly, affected (*e.g.* Martinez-Carrasco and Thorne, 1979; Borghi *et al.*, 1986; Koshkin and Tatarina, 1989; Savin and Slafer, 1991; Slafer and Miralles, 1992; Bulman and Smith, 1993; Nicolas and Turner, 1993; Slafer and Savin, 1994; Dreccer *et al.*, 1997; Kruk *et al.*, 1997).

Even within semi-dwarf germplasm, which already had a plant height within the optimum ranges, progress in yield of irrigated wheat has been most strongly associated with improved HI and grain number (Kulshrestha and Jain, 1982; Waddington *et al.*, 1986, 1987; Calderini *et al.*, 1995; Sayre *et al.*, 1997; Calderini and Slafer, 1998). It is well known that semidwarf genotypes have greater tillering rates than normal genotypes (see references in McMaster, 1997) and that the recessive gene *Tin* (Richards, 1988) inhibits tillering in wheat. In old cultivars only 35% of tillers survive to produce grain (Siddique *et al.*, 1989a). Reduced tillering may contribute to a higher HI both in the presence and absence of drought (Richards *et al.*, 2002). Tillering capacity is a major determinant of grain yield in barley, has been associated to yield stability (Simmons *et al.*, 1982), and is a critical trait for the crop recovery from early season drought (Blum *et al.*, 1990a; El Hafid *et al.*, 1998).

2.3.- Genetic basis of yield improvement

CIMMYT's Wheat Improvement Program has expanded the genetic base of modern wheat lines using conventional breeding as well as cytogenetic approaches (Table 1, see also Evans and Fischer 1999). The Veery lines of bread wheat produced in the early 1980s (Rajaram *et al.*, 1990), resulted from a cross to a winter wheat parent containing the 1B/R translocation from rye. The Veery's show outstanding yield potential as well as wide adaptation and other physiological characteristics. The variety Seri 82, for example, shows high leaf photosynthetic rate, stomatal conductance, and leaf greenness relative to a set of hallmark varieties developed both before and after its release (Fischer *et al.*, 1998). Broad adaptation and superior performance may also be related to increased stress tolerance (Villareal *et al.*, 1997a; Slafer and Araus, 1998).

The development of synthetic hexaploid wheat, the product of wide crossing between durum wheat and wild (D genome) diploids, has enabled new genetic diversity to be introduced into the bread wheat genepool. Although initial objectives centered on improved disease resistance (Villareal, 1995; CIMMYT, 1996), many synthetic lines also have good yield characteristics (Villareal *et al.*, 1997b; Calderini and Reynolds, 2000; Calderini *et al.*, 2001). Synthetic hexaploid lines are now used in approximately 15% of all crosses made by CIMMYT's wheat improvement program.

Recently, a chromosome translocation containing the *Lr19* gene from *Agropyron elongatum* has been shown to be associated with a significant increase in yield and biomass when introduced into already high yielding backgrounds (Singh *et al.*, 1998; Reynolds *et al.*, 2001a).

The semidwarf photoperiod insensitive variety Jori 69, developed by the Durum Program at CIMMYT, was bred primarily for irrigated subtropical areas. With Jori 69 and other early semidwarfs, the project internationalized and globalized with varieties such as Cocorit 71, Mexicali 75 and Yavaros 79. All varieties were developed for irrigated conditions but showed some adaptation to moisture stress situations. Particularly Yavaros 79 showed high additional adaptation to high rainfall conditions in addition to a more dramatic increase in yield potential (Pfeifer *et al.*, 2000). After that, Altar 84 and Aconchi 89 were obtained from ideotype breeding for erectophile leaf canopy. Later on more emphasis was put in the development of varieties with higher yield potential, which allowed the recent release of Atil 2000, a high water-use and input efficiency variety (Pfeiffer *et al.*, 2001).

2.4.- Some pointers for the future

The theoretical limit to HI was estimated by Austin *et al.*, (1980a) to be 60%, and even empirically a figure closer to 0.50 looks more realistic. Because this value is not much higher than that of modern cultivars in many cereal regions worldwide (*e.g.* Fig. 2), and evidence suggests that optimal plant heights have already been achieved (Richards, 1992a; Miralles and Slafer, 1995a; Austin, 1989), it would seem that continued increase in yield potential must come about in the future by

exploiting different physiological traits from those very successfully used in the past. It is clear that future yield gains will far more strongly depend upon biomass increases (as perhaps per above CIMMYT examples cited in the previous section) than on further increase in HI, which might only be marginally increased in most temperate areas (Austin *et al.*, 1980a; 1980b; Loss and Siddique, 1994; Slafer *et al.*, 1994a; Austin, 1999; Slafer *et al.*, 1999; Reynolds *et al.*, 2000). Regarding yield components, further increases in number of grains per unit land area would be required, as the negative relationship between average grain weight and grain number per unit land area seldom reflects competition between grains during grain filling (Slafer and Savin, 1994; Miralles and Slafer, 1995b). In fact a stronger sink- than source-limitation for yield during grain filling in both wheat and barley have been usually reported (Slafer and Savin, 1994; Miralles and Slafer, 1995b; Miralles *et al.*, 1996; Richards, 1996b; Dreccer *et al.*, 1997; Kruk *et al.*, 1997). 1

However recent results raise again the dilemma of sink versus source limitation. In the case of six high biomass lines from CIMMYT containing chromosome substitution associated with the *Lr19* gene, improved yield (average 13%) and biomass (average 10%) was shown to be associated with an improved source-sink balance manifested by increased investment of biomass in spike at anthesis and up to 25% higher rates of flag leaf photosynthesis during grain filling (Reynolds *et al.*, 2001a). Moreover these data from CIMMYT provides empirical evidence that genetic increases in biomass can be achieved, as the most recently bred cultivars exhibit improvements in yield associated with biomass improvement (Table 2).

Nevertheless lines with high yield associated with improved biomass do not exhibit a single physiological strategy or plant type, as can be seen when comparing, for example, yield components and other characteristics of recent CIMMYT lines (Table 2). Comparing the same three lines, semi-erect leaves are apparent only in Bacanora-88, while Seri-82 has high chlorophyll and stay-green characteristics, and Baviacora-92 is a tall robust looking plant type with large kernel size. There are apparently different potential strategies to advance yield. Nonetheless, the idea initially proposed by Donald (1968) that yield potential could be achieved by improving adaptation to high plant density is supported by data from CIMMYT wheat lines (Reynolds *et al.*, 1994a) as well as in modern maize hybrids (Duvick, 1992; and several chapters in Otegui and Slafer, 2000). It has been shown that selection for yield potential in early generations can be enhanced by reducing interplant competition between genotypes in both bread (Lungu *et al.*, 1987) and durum wheat (Mitchell *et al.*, 1982).

3.- Physiological avenues to increase yield potential

3.1.- Biomass increase

When considering avenues for increasing yield it is worthwhile establishing what the biological limitations may be for a given environment based on solar radiation. Theoretical wheat yield potential has been calculated for the Yaqui Valley, NW Mexico (Reynolds *et al.*, 2000) based on the potential range of RUE for wheat estimated by Loomis and Amthor (1996). Accumulated solar radiation for this environment averages 2250 MJ m⁻² for the cycle, however, after allowing for light not intercepted by the canopy, active absorption was estimated at 1750 MJ m⁻². At quantum requirements ranging from 15-24 mol_[photons] mol_[CO₂]⁻¹ fixed as CH₂O (Fischer, 1983; McCree, 1971) RUE varies from 1.5 to 2.6g CH₂O MJ⁻¹ solar radiation (Loomis and Amthor, 1996). Using the value of 1750 MJ m⁻² of absorbed radiation, biomass would vary between 2,600 and 4,550 g m⁻². Irrigated wheat in this environment currently approaches an aboveground biomass of 2100 g m⁻² (Reynolds *et al.*, 1999), so assuming that the cost of root growth and maintenance under irrigated conditions is not substantially higher than previously estimated (*i.e.* 10% of aboveground biomass, Weir *et al.*, 1984) there would seem to be room for improving wheat biomass and therefore yield potential.

An increase in biomass must be achieved avoiding that the trait used to reach the objective brings about other characteristics reducing yield potential (*e.g.* increases in biomass compensated by reductions in HI) or increasing yield losses (*e.g.* increases in biomass resulting in lodging-prone cultivars). Both provisions prevent the possibility of selecting for taller plants (Slafer *et al.*, 1999). However, it has been demonstrated that the semidwarf wheats carrying the alleles *Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*) are insensitive to GA and they produce smaller leaf areas and plant dry weights early in the season than the wheats GA-sensitive (Richards, 1992b). Although the benefits for biomass production may be found in increasing the length of the stems (it would improve light distribution within the canopy, and then RUE) it would most likely reduce rather than increase cereal yields due to both reductions in HI expected from an increased stem growth (Siddique *et al.*, 1989b; Slafer and Andrade, 1993), and increased lodging. Thus, although high biomass lines may be taller than the modern cultivars of barley (Hanson *et al.*, 1985), the highest yield is achieved in a range of optimum plant height balancing biomass production, with increase in HI and minimizing lodging. This optimum range in cereals includes the height of most modern cultivars (see above). Therefore, biomass must be increased, while maintaining the height within the optimum range, by increasing the amount of radiation intercepted and/or the efficiency of the photosynthetic tissues to use the intercepted radiation. This may be achieved through modifications in photosynthetic metabolism, canopy architecture, and source–sink balance.

3.1.1.- Radiation interception

It has been long recognized that biomass is largely linearly related to the amount of accumulated intercepted (actually absorbed) photosynthetically-active radiation (*e.g.* Puckridge and Donald, 1967; Sibma, 1970; Monteith, 1977; Biscoe and Gallagher, 1978; Fischer, 1983). More intercepted radiation may be accumulated by the crop by (i) increasing the length of the growing cycle, so that the canopy is exposed by a longer time duration larger to incoming radiation, or (ii) increasing total daily interception by the canopy.

Although lengthening the cycle of the crop would be easily manipulated genetically, through searching for the appropriated combination of photoperiod and vernalization genes (Slafer and Rawson, 1994; Snape, 1996; 2001; Slafer and Whitechurch, 2001), this is mostly unlikely to be a successful proposal in practice. In fact, time to anthesis is the primary trait improved when the crop is bred for a new region, as it determines the adaptation of the crop to the growing conditions, and has therefore been optimized in most regions making unlikely any further change, in traditional cereal areas at least (Slafer *et al.*, 1996).

Alternatively, increasing the ability of the crop to intercept incoming radiation may be proposed. The yield of cereals is quite dependent to the rate of growth of the crop (Figure 3), specially during the period of stem elongation (*e.g.* Fischer, 1985; Thorne and Wood, 1987; Savin and Slafer, 1991), and where the growing cycle is not markedly short, cereal crops normally achieve maximum radiation interception before the onset of stem elongation. In these conditions it may be only possible to increase the ability of the canopy to increase interception during early phases of development when the crop yield is not responsive and therefore mostly meaningless. However, for environments with very short growing seasons or subjected to moderate-severe water stresses, and because the short crop cycle required, fast early coverage of the soil may be instrumental to guarantee maximum interception at the start of the critical stem elongation phase. In these environments vigorous genotypes are likely to yield more grain and biomass than less vigorous types (Richards *et al.*, 2002). The same reasoning is valid for some regions with poor interception related to deficiencies in soil resources (Richards, 1996a; 1996b). Therefore, genetic variation in early vigour is important when the target environments are characterised by conditions preventing full coverage by the onset of stem elongation, frequently where the season is markedly short, like in Nordic

countries, or under severe stress conditions (Richards, 2000). Rapid canopy establishment may be beneficial for increasing radiation interception and reducing evaporation of soil moisture if conditions are favorable in the early part of the cycle (Richards, 1996a) or for water-limited environments where most water comes as rain on the crop. Traits contributing to early vigor include minimizing the time from sowing to seedling emergence, likely due to different sensitivities to temperature (Slafer and Rawson, 1994), thin leaves (with large leaf area to weight ratio) or presence of coleoptile tillers (Liang and Richards, 1994; Richards, 1996a).

However, except for growing conditions involving very short seasons and/or severe stress it is unlikely to improve yield through improvements of radiation interception (as it has been already maximized during the critical stem elongation phase; Slafer *et al.*, 1999). The realistic alternative for breeding to improve biomass may be then to attempt increasing RUE, particularly during the critical period of stem elongation.

3.1.2.- Radiation-use efficiency

This is a rather complex character that has received little changes during the breeding process carried out along the 20th century (Siddique *et al.*, 1989b; Slafer *et al.*, 1990; Calderini *et al.*, 1997). However, the values recorded in these and other studies with modern cereals leave room for at least some substantial improvements: in fact the values frequently reported (*ca.* 1.2 g MJ⁻¹ on a solar radiation basis; Calderini *et al.*, 1999a) are quite low, less than one half of the potential RUE calculated for C3 cereals (Loomis and Amthor, 1996). Such expectation is particularly evident for an improvement in post-anthesis when estimations show RUE to often be even lower, that may be brought about as a consequence of the increased demand of a larger sink (Calderini *et al.*, 1997; Miralles and Slafer, 1997). A larger sink strength during post-anthesis may be associated with either a further improved number of grains per m² or an increased potential size of the individual grains (see below). Apart from altering the source-sink balance other potential alternatives to increase RUE include the manipulation of leaf photosynthesis, photorespiration and radiation distribution.

Leaf photosynthesis. - The relationship between grain yield and leaf photosynthetic rate per unit leaf area at light saturation (photosynthetic capacity, A_{max}) is complicated. Firstly, yield differences in wheat are generally better associated with HI than with RUE (Slafer *et al.*, 1994a; Calderini *et al.*, 1995, 1999a). Even when yield is source limited, an association between A_{max} and yield cannot necessarily be anticipated. In addition, instantaneous readings of leaf A_{max} cannot be extrapolated to predict canopy photosynthesis throughout the day or the crop cycle. Moreover leaf thickness or nitrogen content per unit leaf area (leaf characteristics determining A_{max}) use to be negatively related with total leaf blade area (see references in Araus *et al.*, 1989). As a consequence no, or even negative, relationships between leaf photosynthesis and yield have been usually reported for wheat (Evans and Dunstone, 1970; Austin *et al.*, 1982; Johnson *et al.*, 1987; Carver *et al.*, 1989; Evans, 1993), so that selection for higher photosynthesis failed in producing yield gains (Austin, 1989) and *vice-versa*. However, in a recent study under hot irrigated conditions, where yield increases of cultivars were related to greater biomass, association between A_{max} , biomass and yield was reported (Reynolds *et al.*, 1994b; Gutiérrez-Rodríguez *et al.*, 2000). The latter study demonstrated genetic gains of yield in response to selection for flag leaf photosynthetic rate and stomatal conductance in F₅ sister lines (Table 3).

Other recent work has reported an association between yield and photosynthetic rate under temperate conditions (Fischer *et al.*, 1998). In these studies at CIMMYT the increases in A_{max} were associated with larger stomatal conductance (g_s), and in fact this was the photosynthetic trait most strongly related to yield progress, even when mesophyll conductance also seemed to increase (Fischer *et al.*, 1998; see also Richards, 2000). This relationship across different wheat

genotypes between stomatal conductance and yield has already been observed for the emerging “green revolution” semi-dwarf wheat cultivars (Shimshi and Ephrat, 1975). A higher g_s may reflect decreased stomatal sensitivity to VPD or to subtle water stress, extra leaf cooling particularly at warmer temperatures, or increased sink strength (Reynolds *et al.*, 1994b; Fischer *et al.*, 1998; Richards, 2000).

Alternatively the concentration of nitrogen in the leaves may also affect A_{max} (Evans, 1983; Araus and Tapia 1987; Evans, 1989; Sinclair and Horie, 1989; Dreccer *et al.*, 2000) and thus RUE (*e.g.* Sinclair and Muchow, 1999). An improved distribution of the absorbed nitrogen within the canopy, with more N being partitioned to the top layer of leaves and less N remaining in the darker layers, would benefit by maximizing photosynthetic rates in the more illuminated leaves (Field, 1983; Hirose and Werger, 1987, Dreccer *et al.*, 1997).

Reducing photorespiration.- Another way to increase RUE might be to reduce photorespiration, perhaps by increasing the affinity of Rubisco for CO₂, thereby decreasing its oxygenase activity. Modest variation for CO₂ specificity has been found in land plants (Parry *et al.*, 1989; Delgado *et al.*, 1995), with wheat having among the highest values for crop species. However, much higher values are reported in marine algae (Read and Tabita, 1994). Molecular techniques may offer the possibility of genetically transforming wheat Rubisco from its current specificity of 95 to potentially values of 195, corresponding to thermophilic alga *Galderia partita*. However, Rubisco also plays a protective role in dissipating excess energy, with O₂ uptake in the light playing a significant role in preventing chronic photoinhibition under field conditions (Osmond and Grace, 1995). In which case it may not make sense to alter Rubisco’s oxygenase specificity especially in crops subjected to abiotic (such as drought or temperature) stresses.

Distribution of the incoming radiation.- Plant height does alter the distribution of radiation within the canopy, but it has been already discussed that there is little, if any, margin to manipulate stem length in most situations. Alternatively, at a higher level of crop organization, a direct way to improve RUE may lie in improving the distribution of the incoming radiation through the crop by changing the optical properties of the canopy, mainly reducing its coefficient of light attenuation (Slafer *et al.*, 1999 and references cited therein). Given the difficulties associated with measuring or accurately simulating canopy photosynthesis, traits which could potentially modify RUE at the canopy level must be tested empirically by measuring their effect in near isogenic material. Simulation is however a good way to test leaf size and angle effects on canopy photosynthesis as a function of latitude, date, and cloudiness. Several lines of evidence suggest that more erectophile canopies may have higher RUE (Duncan, 1971; Angus *et al.*, 1972; Innes and Blackwell, 1983). Moreover genetic manipulation of leaf angle is not complex, probably involving only two to three genes (Carvalho and Qualset, 1978). However more erect leaves may prove to be inefficient in improving yields perhaps due to the pleiotropic negative effects not only on flag leaf area, but more important, on yield components such as the number of kernels per spike (Araus *et al.*, 1993). Nevertheless more erect leaf canopy types are characteristic of many of CIMMYT’s best yielding wheat lines of the seventies and eighties (Fischer, 1996). In fact, smaller and more erect upper-culm leaves may allow the incoming radiation to be more evenly distributed through the canopy (Richards, 1996b).

Source-sink balance.- Slafer and Savin (1994) in their analysis of data from 15 studies where source-sink balance was manipulated at or after anthesis showed that while source and sink can both limit yield, sinks are generally more limiting during grain filling. Increased wheat yield and biomass at CIMMYT has been shown in one case to be associated with a chromosomal translocation containing the *Lr19* gene from *A. elongatum* (Singh *et al.*, 1998). In a study with 6 near isogenic pairs, improved source-sink balance was shown to be associated with increased biomass (Reynolds *et al.*, 2001a). This was reflected by a higher partitioning of assimilates to the developing spike at anthesis in some backgrounds, indicating that higher photosynthetic rates

observed during grain filling in these lines were a response to increased sink strength. However, in other backgrounds larger spike size was associated with more total biomass at flowering as well as higher photosynthetic rates in grain filling (Reynolds, unpublished data). The isogenic lines were compared with respect to their phenology, and in particular duration of spike growth phase since it has been suggested that this may influence source-sink balance (Slafer *et al.*, 1996). However, in the case of *Lr19*, although source-sink balance was improved, it was not associated with changes in the relative duration of spike growth phase or any other phenological stage (Reynolds *et al.*, 2001a).

3.2.-Opportunities to increase number of grains and final grain weight

The number of grains per m² is the final result of a process in which a huge number of primordia are firstly generated during the initial phases of development followed by an abortion of most of these structures (Fischer, 1983; Kirby, 1988; Miralles *et al.*, 1998). This major yield component, which is the combination of number of spikes per m² plus the number of grains per spike, is thus formed throughout the whole period from sowing to anthesis (Slafer and Rawson, 1994). On what concern the number of grains per spike, clearly the phase coinciding with the mortality (or survival) of floret primordia is far more important for yield formation than the initiation phase (*e.g.* Fischer, 1985; Thorne and Wood, 1987; Kirby 1988; Savin and Slafer, 1991; Slafer and Savin, 1994). This is why yield is generally better related to the growth of the spikes during stem elongation (Fischer, 1985; Siddique *et al.*, 1989b; Slafer and Andrade, 1993; Slafer, 1995; Miralles *et al.*, 1998). To increase the number of grains per m² the requirement will be then to produce more growth of the spikes during the spike growth period (approximately the last half of the stem elongation phase) occurring normally during the 2-3 weeks immediately before anthesis (Kirby, 1988; Siddique *et al.*, 1989b; Slafer and Andrade, 1993). In fact, this has been the avenue explored by wheat breeding in the past: the main reason for the increase in yield was the achievement of a higher number of grains per m², in response to a larger amount of dry-matter allocated into spikes as the stem growth was progressively inhibited by dwarfing genes (Siddique *et al.*, 1989b; Slafer and Andrade, 1993). Due to the limit in HI, in the future there seems to be little room for further improvements in biomass partitioning (*e.g.* Slafer *et al.*, 1999 and references therein) through the genetic manipulation of phasic development (Miralles *et al.*, 2000), carpel size (Calderini *et al.*, 1999c), sterile tiller reduction (Richards, 1988), and grain set (Fischer *et al.*, 1998). Thus, the possibility of raising the growth of the spikes is rather restricted to increasing the growth of the whole canopy, while maintaining the actual, high values of biomass partitioning. This might be attained by increasing RUE during this phase (see above) or by lengthening the phase of spike growth, so that growth during the critical phase is larger (*e.g.* Slafer *et al.*, 2001a).

The length of the critical period for the determination of grain number per m² may be extended by manipulations of genes responsible for the sensitivity to photoperiod or for earliness *per se* (Snape *et al.*, 2001), provided the sensitivity to photoperiod during this late reproductive phase (Slafer and Rawson, 1997, Miralles and Richards, 2000) and the variability for earliness *per se* are large (Slafer, 1996). For instance, the stem elongation (and spike growth) phase of both wheat and barley was lengthened when exposed to shorter photoperiods and *vice-versa* (Miralles and Richards, 2000; Miralles *et al.*, 2000; Slafer *et al.*, 2001a). The extra time for spike growth would result in larger spikes with more fertile florets, due to reduced abortion, and more grains (Slafer *et al.*, 2001a), though photoperiodic effects beyond those mediated through an extended duration of spike growth may not be discarded (Gonzalez, Slafer and Miralles, unpublished).

In addition, the grain-setting efficiency (*i.e.* the number of grains set per unit of spike dry matter) of the cultivars may also be an alternative avenue for a role in determining the number of grains per unit land area. Abbate *et al.* (1998) have identified genetic variation in this efficiency, which might be related to the dry matter partitioning within the spike between the spikelets and the rachis (Slafer and Andrade, 1993).

The other major yield component, the averaged weight of the grains, might be also improved. It has been demonstrated that under cool conditions durum wheat kernel weight is the main determinant of yield, whereas the number of spikes m^{-2} plays a major role in yield formation in warmer environments (García del Moral *et al.*, 2003). As many of the source-sink studies during grain filling mentioned above have shown, grain growth is hardly affected by the source strength. In other words, the photosynthetic capacity of the crop during grain filling, together with the accumulated reserves in vegetative organs translocable to grains, are in most situations adequate or in excess compared with the requirements of the grains to be completely filled (Savin and Slafer, 1991; Slafer and Miralles, 1992; Richards, 1996b). In this context, any increase in the potential size of the grains may be translated into higher yields (Slafer *et al.*, 1999). However, we need to learn first which are the physiological determinants of the potential size of the grains. As it seems that the vascular system would unlikely be responsible of the final weight of the grains (Evans, 1993), candidates are structural features imposing a limit to the grains for further growth. For instance, Calderini *et al.* (1999b) and Calderini and Reynolds (2000) convincingly showed that the growth of the carpels immediately before anthesis is critical in the determination of an upper limit to grain growth, suggesting that the improved growth of the carpels may lead to greater average grain weight by raising the final weight of the smaller grains of the spikes (Calderini *et al.*, 2001), which would also be beneficial for the industrial quality of the grain, particularly so in malting barley.

3.3.- Water use and its efficiency

Improved crop performance in environmental conditions characterized by water shortages may be achieved through improvements in water use, water-use efficiency (WUE) and HI (Passioura, 1977; 1996). Increasing water use is relevant when there is still soil water available at maturity or when deep-rooted genotypes access water not normally available (deep in the soil profile). The other two factors become more significant when all available water is normally used up by the end of the crop cycle. Up to now the single most important attribute determining performance under water stress has been phenology (but mainly in Mediterranean type conditions), matching crop development and seasonal rainfall pattern (see references in Richards, 1996a; Slafer and Araus, 1998; Villegas *et al.*, 2000). In fact, this attribute may affect either water use, or WUE, or HI. Early sowings may drastically increase WUE and biomass, but the final grain yield is often unchanged due to the low harvest-index of early-sown crops (Gomez-Macpherson and Richards, 1995). However, varieties with modified dry matter partition and allocation should be developed to overcome this problem (Richards *et al.*, 2002). Other developmental traits, such as deeper root systems and early vigor, may also help the crop to use more water. Moreover, these two traits may be particularly significant in the water-limiting conditions of the Mediterranean environment (Slafer *et al.*, 1994a; Royo *et al.*, 1995, 1999; Bort *et al.*, 1998; González *et al.*, 1999). Thus, greater early vigor and/or faster phenological development (*e.g.* earlier date of anthesis or maturity) reduces the evaporative loss of water from the soil surface on the one hand, while also ensuring that more growth and transpiration occur when the vapor pressure deficit is small. However, the suitability of greater early vigor and even more phenological adjustment (earliness) as breeding traits will strongly rely on the nature of the water stress since a high early water use may lead to a lower harvest index when terminal drought is present and the genotype is late flowering.

If water is a major limitation, then maximized growth coinciding with periods of cool weather and relatively low vapor pressure deficits will raise WUE and biomass production (Richards, 1991; Gomez-MacPherson and Richards, 1995). Manipulation of major genes responsible for sensitivity/insensitivity to photoperiod and vernalization enable temperate cereals to be grown with a very wide range of duration (Richards, 2000). Therefore increasing the relative duration of the spike growth phase, discussed above as a strategy to further raise the number of grains per unit

land area in potential conditions, might also contribute to increase WUE, as an increased proportion of the transpired water would be used during the critical period for yield determination.

It must be taken into account, before defining a selection strategy for increased water use or WUE, that both characteristics are not independent. Actually they are frequently negatively related as the greater the amount of water captured and transpired by the crop the greater will be the g_s and consequently the lower the WUE. One practical consequence of selecting for increased discrimination against ^{13}C would likely result in lines with increased water use but decreased water use efficiency.

3.4.- Target environments and breeding strategy

The design of a breeding program depends on its target environment. The fact that a uniform criteria cannot be easily applied is clearly illustrated by the controversy between breeding strategies of CIMMYT and IRRI, on the one hand, and ICARDA, on the other hand. CIMMYT coined the term “megaenvironment”, postulating for wheat to select under stress-free conditions (Reynolds *et al.*, 1996) with an idea of further increasing yield in a wide range of environmental conditions, ranging from stress-free to mild and moderate stress environments. The same can be said for IRRI on rice. ICARDA breeding efforts on barley are more devoted to improving performance under severe stress and, thus, yield stability is privileged over yield potential by selecting in drought-prone, poor environments characterized by yields frequently below 1.0 Mg ha^{-1} of small cereals, mostly barley and durum wheat (Ceccarelli and Grando, 1996). However, the above controversy appears fictitious in the sense that it is based on the premise that the goals to achieve both strategies for selection are correct. These two strategies fit well with the model of Finlay and Wilkinson (1963) whereby the response of yield of particular genotypes is related to the environmental index, understood as the average yield of all participating genotypes. If the range of environmental (E) index and genotype (G) variation is large enough, there would virtually always appear a kind of negative G x E interaction, represented by a crossover in the yield of the genotypes of high and low yield potential (see Araus *et al.*, 2002 for details). In other words, the genotypes selected for low yield conditions will probably perform better than those released for high-yielding environments when grown under very poor environments. Thus, crop selection performed in nurseries with good growing conditions is frequently translated to cultivars with higher water use and larger productivity in a wide range of growing conditions (considered as a whole as a megaenvironment), from non-limiting (*e.g.* with yields beyond 7.0 Mg ha^{-1}), to mild stress (*ca.* $4.5\text{-}7.0 \text{ Mg ha}^{-1}$) and moderate stress (*ca.* $2.0\text{-}4.5 \text{ Mg ha}^{-1}$) environments. However, in more stressed environments the situation may reverse, with the genotypes selected in good environments performing worse than those selected under the poor conditions of the target environment. Normally, such crossover is placed at low yield levels and appears to be slightly higher for barley ($2.0\text{-}2.5 \text{ Mg ha}^{-1}$; Ceccarelli and Grando, 1991) than for wheat ($1.0\text{-}1.5 \text{ Mg ha}^{-1}$; Laing and Fischer, 1977; Fischer, 1993b).

One of the most difficult problems that have to be faced by breeders is the large genotype x environment (both site and/or year) interactions that usually occur when the performance of elite lines is evaluated in a range of target environments. These interactions mask the expression of the differences between genotypes and slow genetic advance.

From an ecophysiological perspective, traits associated with abiotic stresses such as drought may be divided into two distinct categories: those conferring the ability to survive under extreme stress, and those permitting agronomically acceptable levels of productivity under a relatively large range of less stressful conditions (by avoiding stress). The expression of the former may have penalties in yield under less-severe conditions, due to the fact these traits conferring stress tolerance (and usually related with a low growth) are constitutive and expressed independently of the degree of stress. By contrast the latter tend to be facultative in their response (*e.g.* deeper rooting under

drought or evaporative cooling under heat stress) which confer broader adaptation. The fact that selection for higher yielding performance has frequently resulted in higher yields in a wide range of environments (see examples in Calderini and Slafer, 1999; Araus *et al.*, 2002) is probably largely a consequence of facultative stress avoidance traits. In these examples, modern cultivars have consistently outyielded older cultivars even in the lowest-yielding conditions of each particular study (Austin *et al.*, 1980a; Perry and D'Antuono, 1989; Slafer and Andrade, 1989, 1993; Calderini *et al.*, 1995). Shorter crop duration is the most conspicuous strategy of drought escape. It is a constitutive trait which confers genotypes better performance (in terms of yield and stability) in severe to moderate drought environments (particularly when the drought is terminal, like in Mediterranean regions (Loss and Siddique, 1994). However, this trait may also have negative implications in yield potential if the reduction in cycle compromises light interception during the critical phase of stem.

4.- Using physiological tools to complement empirical selection: a hypothesis

By combining information on the physiological basis of yield limitation with new physiological selection tools, the probability of accelerating the rate of genetic progress through plant breeding should be significantly increased. Parents can be selected for improved physiological traits and crossed to high-yielding agronomically elite materials. Further, identification of the progeny phenotypes with the favorable interactions among genes permitting the expression of higher yield can be enhanced by: (i) eliminating inferior agronomic phenotypes visually in early generations; (ii) selecting superior physiological phenotypes using rapid detection techniques in intermediate generations; and (iii) selecting for higher performance in yield trials in advanced generations (Reynolds *et al.*, 2000). Actually, matching phenology, photoperiod and vernalization responses or plant height, are analytical or indirect (physiological in nature) selection criteria used for decades in empirical programs. Other examples of physiological approaches that have been used in wheat breeding and that have had impact over the years are the introgression of more erect leaf angle (Fischer 1996), carbon isotope discrimination in Australia (Richards *et al.*, 2002; Condon *et al.*, 2002) or canopy temperature depression for selection in drought and heat nurseries at CIMMYT.

However, in the past the use of yield-related physiological selection traits (as distinct from morphological or visual ones) in cereal breeding has fallen short of expectations. Many possible reasons have been stated to explain this lack of success. One is the great integrating power of empirical selection for characteristics influenced by many processes and genes as yield potential and yield stability (Evans, 1993). Another is the difficulty of understanding - in spite of the enormous amount of information that has been accumulated about physiological processes - what causes low grain yields, and how putative traits may enhance drought resistance and contribute to grain yield in water-limited environments (Ludlow and Muchow, 1990). Other causes are related to the inadequate methodology used in the investigations, which sometimes lead to incorrect conclusions, or the differences in the approaches to dealing with genotype by environment interactions in the disciplines of crop physiology and plant breeding (Jackson *et al.*, 1996). In spite of this, most scientists agree at present that the contribution of crop physiology to breeding is expected to be larger in the next years.

From a breeding perspective there are, of course, specific requirements that any indirect or physiological trait should fulfill before being included in a breeding program. Namely, it must exhibit enough genetic variability, a high genetic correlation with yield and a higher heritability than yield itself in genetic populations representative of those being evaluated (Jackson *et al.*, 1996). Moreover, evaluation of these traits must be fast, easy and cheap (Araus, 1996; Slafer and Araus, 1998; Araus *et al.*, 2001a; 2002).

Any trait to be considered must be directly related to yield. The literature is filled with proposed traits dealing with the lower levels of organization (*i.e.* molecular, biochemical), which frequently show only poor and inconsistent relationships with crop yield in the field (Richards, 1996a; Araus *et al.*, 2001a; 2002). In this category we can include metabolic traits such as enzyme activities (*e.g.* rubisco or nitrate reductase), levels of substrates (*e.g.* proline or sugars), and growth regulators such as ABA (an updated review on these mechanisms for barley is provided in Araus, 2001). As illustrated before in this chapter yield is by nature a very integrative trait: through the plant cycle, it takes in many levels of plant organization, from molecular level to the canopy. Therefore, any trait consistently related to yield should also be integrative, either in time (by being determined through part, if not all, of the crop cycle), or in level of organization (by representing a level close, if not identical, to that of yield); or both (Araus, 1996; Slafer and Araus, 1998; Araus *et al.*, 2001a; 2002). In fact even yield per plant is not usually a trait well related with crop yield. Given that wheat yield progress has been shown to be strongly associated with adaptation to density (Reynolds *et al.*, 1994a) it is not surprising that individual plant yield is not well associated with plot/canopy based yields. Besides the difficulty of finding physiological traits simpler than yield itself, but unequivocally linked to it, a major obstacle in practice has frequently been the unlikely chances that these physiological traits might be used in realistic breeding programs. Many of them which are easily performed in an experiment with several plots (and may be used for screening a small number of genotypes for use as parents) are extremely time-consuming for a breeding program with several thousands plots. The last decade has been quite prolific in identifying surrogates that may be used instead of the physiological traits themselves with a reasonable degree of confidence, being both faster and cheaper than the proposed traits. A comprehensive description can be found in Araus (1996), Slafer *et al.* (1999), Reynolds *et al.*, (2001b) and Araus *et al.*, (2002). In what follows we will focus on some of the promising techniques for evaluating secondary traits addressed to improving yield in the right side of the G x E interaction, that is, under favourable down to moderate stress situations (as covered in 3.4). These techniques may be grouped into those remotely sensing either the composition of the radiation reflected by the plots (i), or the temperature of the canopies (ii), and those measuring the relative contribution of different stable isotopes in the biomass produced (iii). This is not intended to be an exhaustive list and probably in the near future new technical approaches will emerge.

4.1.- Spectroradiometrical indices

Assessments based in remote sensing of the spectral reflectance of the canopy are extremely useful for estimating the structure of the canopy in a fast way. Due to the differential absorption and reflection of particular regions of the spectral irradiance by the soil and plant organs, estimates of for example leaf area index, radiation interception, canopy chlorophyll content, among others, can be made in few seconds and without sampling plants or any component of the plots (Field *et al.*, 1994), though accepting some assumptions based on proper calibration and validation. As the reflectance between the near-infrared and red is quite similar in soils but contrasting in leaves, the proportion of red wavelength is (i) reduced with increasing the fraction of radiation intercepted by the canopy, and (ii) increased with increasing the fraction of radiation intercepted by the soil. The most widely used indexes are the normalized difference vegetation index, NDVI, and the simple ratio, SR (see references in Araus, 1996; Araus *et al.*, 2001a). As the relationship between light interception and leaf area index is curvilinear, *i.e.* increases in leaf area index determine proportional increases in radiation interception at relatively low values, the accuracy of the estimates for discriminating among genotypes in a breeding program should be maximum during early developmental phases. The advantages in time-efficiency and low cost make the use of spectroradiometry well-suited for screening purposes in realistic breeding programs (see further discussion in Elliott and Regan, 1993; Bellairs *et al.*, 1996; Peñuelas *et al.*, 1997; Peñuelas and

Filella, 1998; Aparicio *et al.*, 2000; Araus *et al.*, 2001a). Besides the usefulness of spectroradiometry in assessing canopy structure and thus biomass, there is the possibility of estimates RUE as well. The useful wavelengths are others (530 vs. 570 nm), and would reflect the activity of the xanthophyll cycle which is negatively associated with RUE (Filella *et al.*, 1996), and the proposed index is the photochemical reflectance index, PRI (Araus *et al.*, 2001a).

4.2. Using stomatal aperture related traits to select for yield

Leaf photosynthesis cannot be measured rapidly in the field and hence the trait does not lend itself to large scale screening of segregants in a breeding program. However certain traits that are related to photosynthesis, namely stomatal conductance (g_s) and transpiration-driven canopy temperature depression (CTD) can be measured within a few seconds on a leaf and plot basis, respectively (Blum *et al.*, 1982; Rebetzke *et al.*, 1996; Amani *et al.*, 1996). Both traits, g_s and CTD have been shown to be associated with performance of irrigated wheat under high radiation levels (Araus *et al.*, 1993; Reynolds *et al.*, 1994b; 1999; Fischer *et al.*, 1998). In the same way, stable carbon isotope discrimination ($\Delta^{13}C$) has also proved itself a potentially powerful approach for wheat and barley (Farquhar and Richards, 1984; Acevedo, 1993; Araus *et al.*, 1998) with the advantage of integrating not only the functioning of the crop at its highest level of organization (the canopy level, as CTD does) but also through at least part of the plant growing cycle. For a fast assessment of g_s on single leaves it has been proposed the utilisation of viscous air-flow porometers, that measures resistance to mass flow through the leaf. However the utilization of this device is worth only on irrigated plants and takes between 10-20 seconds to do a single measurement (Richards *et al.* 2001).

The interest of evaluating g_s either directly at the leaf level or by means of more integrative approaches (CTD, $\Delta^{13}C$) is highlighted by studies that suggested g_s seems to be a better indicator of the plant water status effect on photosynthesis than for, example, the water potential or the relative water content, with changes in the photosynthetic metabolism during progressive drought being very well tracked by g_s (Sharkey, 1990; Flexas *et al.*, 2000).

4.2.1.- Canopy temperature

A major function of transpiration in plants is leaf cooling. When plant water status is reduced and stomata close leaf temperature rises due to the lack of transpirational cooling. Hence, canopy temperature can serve as an indirect probe of plant transpiration and plant water status. This probe has been widely developed and used in agronomy and plant breeding with the development of the infrared thermometer that can sense canopy temperature remotely and speedily. Thus canopy temperature has been used to develop a crop water stress index (CWSI) in wheat and other crops (see http://www.plantstress.com/articles/drought_i/drought_i_files/CWSI_phoenix.pdf) leading to its use in irrigation scheduling.

Canopy temperature is also being used as a screening tool for drought resistance (avoidance). On a relative basis, genotypes having lower canopy temperature at midday have relatively better water status and are taken as drought avoidant (Blum *et al.*, 1982; Garrity and O'Toole 1995). A significant positive relationship was found across a large number of wheat breeding materials between midday canopy temperature under stress and yield stability under stress (Blum *et al.*, 1990b), even when less supportive reports have been also published (see for example Villegas *et al.*, 2000; Royo *et al.*, 2002 for durum wheat). The main consideration in using canopy temperature for the selection for drought avoidance in wheat is that plants must be under adequate stress, typically around -2.0 to -2.5 MPa of leaf water potential at midday, and a full soil covering by the canopy. Additional guidelines for using the method are given at http://www.plantstress.com/admin/files/IRT_protocol.htm. However, the relationship between canopy temperature depression (canopy minus air temperature (CTD) and yield is best expressed

under well-watered conditions and high evaporative demand. High evaporative demand develops under high air temperature and high vapor pressure deficit. It was shown that under such conditions CTD can be used to select for high yield potential wheat materials (Reynolds *et al.*, 1994b, 1998; Amani *et al.*, 1996).

The potential for using aerial IR imagery for screening purposes has also been demonstrated; a positive association was found between yield of recombinant bread wheat inbred lines and their plot temperatures when sensed from a height of 800m (Reynolds *et al.*, 1999).

4.2.2.- Carbon isotope discrimination

The techniques of remote sensing (spectroradiometry and CTD) discussed above need a canopy structure and then are not useful for selection with isolate plants (e.g. in early generations). Moreover these techniques provide instantaneous readings, and consequently to reflect a time-integrative behavior a plot must be measured at different stages. By contrast the proportion of different stable isotopes in the dry-matter compared with the natural proportion of them in the environmental source, though requiring the sampling and analyses of part of the material, may in many cases integrate the behavior of the genotype during at least part of the growing season and allows the estimation to be made in early generations. As the abundance of ^{13}C in C3 plants (including small grain cereals) is commonly less than that in air CO_2 to be photosynthesized, plants like wheat and barley discriminate against ^{13}C in the photosynthetic process (Farquhar *et al.*, 1982; 1989a; Hall, 1990). When measured in dry matter the carbon isotope discrimination ($\Delta^{13}\text{C}$) indicates the reduction in the proportion of ^{13}C relative to ^{12}C (both stable isotopes of C in the air) experimented during plant growth. Whereas the main discrimination against ^{13}C takes place during carboxylation (Farquhar *et al.*, 1989a), $\Delta^{13}\text{C}$ is associated with the ratio of the intracellular to air concentrations of CO_2 ($\text{C}_i:\text{C}_a$ ratio; e.g. Hall, 1990; Farquhar *et al.*, 1989b), and then $\Delta^{13}\text{C}$ increases as C_i remains high. Therefore, and providing water pressure deficit is steady, it can be assumed that a higher $\Delta^{13}\text{C}$ is an indicator of a lower photosynthesis/transpiration ratio (namely water-use efficiency). Plants discriminating heavily against ^{13}C , and thus having a low water use efficiency, are those able to keep a relatively high C_i , either due to a higher g_s or, less commonly, a low internal photosynthetic capacity, or both together (Richards, 2000). There is abundant literature supporting a positive correlation between grain yield and $\Delta^{13}\text{C}$ for bread wheat (e.g. Condon *et al.*, 1987; Araus *et al.*, 1993; Sayre *et al.*, 1995; 1997; Fischer *et al.*, 1998), durum wheat (Araus *et al.*, 1998; Villegas *et al.*, 2000; Royo *et al.*, 2002) and barley (Romagosa and Araus, 1991; Araus *et al.*, 1999; Voltas *et al.*, 1999) among other C3 crops. These positive relationships are found particularly in the range of moderately drought-stressed to full irrigated environments. Providing not differences in phenology exist among genotypes, the positive correlation between $\Delta^{13}\text{C}$ and yield may be explained by the fact that plants with higher $\Delta^{13}\text{C}$ are those having either better status during crop cycle and thus probably maintaining higher g_s (Richards 1996a; Condon *et al.*, 2002; Araus *et al.*, 2003) or exhibiting a constitutive higher g_s (Farquhar and Richards, 1984; Fischer *et al.*, 1998). Therefore high values of $\Delta^{13}\text{C}$ are frequently indicating lines with higher efficiency for converting the intercepted radiation into new dry-matter (Slafer *et al.*, 1999). However, the relationship between $\Delta^{13}\text{C}$ and yield tend to shift to negative when the environmental conditions are characterized by a relatively severe drought and then reduced g_s is related to higher WUE and yield (see discussion in Farquhar and Richards, 1984; Hubick and Farquhar, 1989; Acevedo, 1993; Slafer and Araus, 1998). Negative relationships between $\Delta^{13}\text{C}$ and yield have been also reported for cereals in water limited environments where crop growth is more dependent on soil moisture stored from rain that falls outside the main crop growth phase (Richards *et al.*, 2002).

To conclude it has been reported a large degree of variation among cereals genotypes in $\Delta^{13}\text{C}$ and this trait seemed to be highly heritable (Farquhar *et al.*, 1989a; Condon *et al.*, 1990; Richards and

Condon, 1993; Sayre *et al.*, 1995; Araus *et al.* 1998), evidencing the likelihood of using $\Delta^{13}\text{C}$ in realistic breeding programs for selecting for improved either ability to capture more water (and then keep transpiration flux less restricted) or water use efficiency (Richards, 2000; Araus *et al.*, 2003).

5.- Potential use of biotechnology to raise cereal yields

The above discussion has stressed the need to look for ways to complement conventional breeding for yield *per se*. Integration of novel techniques and methodologies into conventional programs is needed to facilitate the identification, characterization and manipulation of genetic variation for continued and accelerated progress (Sorrells and Wilson, 1997). In fact before a substantial body of tangible evidence is available we shall need a better understanding of the genetic basis of complex physiological traits so that we can manipulate them more reliably (it was relatively easy for genetically simple traits such as reduced height and sensitivity to photoperiod).

Biotechnology offers two new ways for improving wheat and barley: one through the development and application of molecular markers and the other through genetic engineering. However, the different size of wheat (16×10^9 bp for bread wheat, *Triticum aestivum*, 10×10^9 bp for durum wheat *T. turgidum* L. var *durum*) and barley (5×10^9 bp) genomes, and their different structure (genomes ABD in bread wheat, AB in durum wheat, but only H in barley) makes much more complex the use of molecular markers for breeding and selection in wheat than in barley. Moreover, bread and durum wheat have a lower level of polymorphism than barley or other cereals (Chao *et al.*, 1989; Devos *et al.*, 1995), and the level of polymorphism is not consistent across genomes or crosses (Langridge *et al.*, 2001).

Molecular markers technology offers a series of novel approaches to improve the efficiency of selection strategies. Marker-mediated genetical analyses are useful in the prediction and tracking of valuable alleles, the analysis of the genetic control of specific traits and the analysis of the whole genome. Molecular markers have become a critical tool in studies of diversity in cereals since they offer an easily quantifiable measure of genetic variation within a given species. Their use is enlarging the variability available for breeding programs and allowing the detection of the origin of specific alleles introduced on recent varieties.

The development of comprehensive genetic maps based on molecular markers has enormously improved the power of genetical analysis (Snape *et al.*, 2001). In addition, the use of marker assisted selection (MAS) will enhance selection efficiency not only for Mendelian traits, for which individual phenotypes provide large information about the underlying genotypes, but also for most of the complex traits with agronomic interest, for which phenotypes are less informative about the underlying genotypes (McCouch, 2001; Tuberosa *et al.*, 2002). The detection and location of quantitative trait loci (QTLs) enables the use of MAS for attributes difficult to manage by conventional breeding approaches, leading to a potentially more reliable, quick and efficient selection. Traits that in the past were recalcitrant to analysis, such as abiotic stress responses, are now amenable, and individual major genes and QTL mediating the variation can be identified (Snape *et al.*, 2001).

Molecular markers linked to traits of economic importance have been identified in wheat (see examples in Langridge *et al.*, 2001 and a broad catalogue in <http://wheat.pw.usda.gov>), and barley (Barr *et al.*, 2000). This has allowed the development of strategies for stress amelioration changing the phenology of genotypes or introducing genes that enable the plant to tolerate stress (Snape *et al.*, 2001). For instance, genes for vernalization response and cold tolerance have been located in chromosomes of homeologous Group 5 of wheat (Snape *et al.*, 2001). It is likely to tailor wheat varieties with different cycle length and thus, changed yield potential by adjusting the allele at the

Vrn-A1 locus, one of the five loci that control vernalization requirements in wheat (Snape *et al.*, 2001). The Group 5 carries also genes controlling a range of stress responses such as tolerance of freezing temperatures, drought, osmotic stress and high temperatures (Snape *et al.*, 2001).

While some workers report that they have identified QTLs for yield, WUE, and other complex quantitative characteristics (examples in Slinkard 1998 and Yin *et al.*, 1999), QTL identification is much more complex than for simple traits, and the G x E interactions on the expression of these QTLs are frequently large (*e.g.* Kjaer and Jensen, 1996). In this scenario, what appears indispensable is better understanding of the causes underlying that G x E interaction through a collaboration between crop physiologists, plant breeders and molecular biologists. In fact, until now the impact of marker-based QTL analysis on the development of new varieties with enhanced quantitative traits has been less than expected, partially due to the disconnection between QTL studies and variety development (Tanksley and Nelson, 1996). Nevertheless, their impact on breeding and selection will be much more higher than that of the markers for single or few genes. QTL analyses have been recently carried out for some yield-related traits, such as grain weight (Varshney *et al.*, 2000), ear compactness (Sourdille *et al.*, 2000b), lodging resistance (Keller *et al.*, 1999), heading time (Sourdille *et al.*, 2000a) or abiotic stresses such as responses to drought (Quarrie *et al.*, 1995), salt tolerance (Mano and Takeda, 1997) or manganese efficiency (Pallotta *et al.*, 2000). However, many of them are poorly understood at the physiological or biochemical level (Langridge *et al.*, 2001). Physiological markers are likely to be more useful at least until denser molecular maps can be developed. These promising techniques may then be put to wider use to increase yield potential and tolerance to complex and largely unpredictable stresses (Slafer and Otegui, 2000). The role of markers in screening breeding populations for yield and adaptation will increase when these complex traits will be tagged with molecular markers (Langridge *et al.*, 2001).

The ability to use genetic transformation technology opens up opportunities to raise cereal yields using molecular biology. Apart from the direct interest of the inclusion of specific foreign genes in a cereal genome, transformation techniques open the possibility of drastically increase the genetic variability available for plant breeding. There are two approaches to the transformation of cereals. One consists in modifying and reinserting native genes or promoters or suppressors back into the same species in order to increase the expression of these genes, modify their products or to switch them off. The second approach consists in generating novel germplasm through the introduction of genes from alien sources, such as virus, bacteria, plants or animals (Snape, 1998). Progress in transformation cereals have been faster in rice and maize (*e.g.* Lazzeri and Shewry, 1993; Tanksley and McCouch, 1997; Sheehy *et al.*, 2000) than in wheat and barley (Barceló *et al.*, 1998), but the system is now turning attention to what can be achieved by the modification of cereals for agronomic characteristics.

Wheat or barley genetic modified varieties are not cultivated at present in part due to the obstacles derived from ethical, environmental and political aspects. Moreover, the reluctance of the industry and consumers to accept transgenic varieties will restrict the application of the technology. However, the expectation is that many genes will be amenable to manipulation via genetic engineering. Field trials of genetically engineered wheat (Langridge *et al.*, 2001) and barley (Lörz *et al.*, 2000) are now well advanced in many countries. A major difficulty at present in transformation is derived from the restricted number of genotypes which can be handled and regenerated successfully *in vitro*, but other problems that have to be addressed relate to the efficiency of transformation, the number of integrated transgenes, the unpredictable variation in regenerated plants and progeny and the stability of transgene expression (Lörz *et al.*, 2000).

At present the work is focused in the acquisition of genes that code for agronomically and qualitatively interesting characteristics. Traits such as photoperiod and dwarfing genes, that contributed significantly to increase yields in the past, are often considered to be useful for future gains in yield potential (Worland *et al.*, 1998; Sears, 1998; Slafer *et al.*, 2001a), but interest should

be also focused on producing cultivars with faster growth rates and greater biomass during grain filling (Austin, 1999; Villegas *et al.*, 2001) even when these are traits much more complexes. Transgenic wheat plants with higher water use efficiency and improved total biomass, root and shoot dry weights have been obtained introducing the ABA-responsive barley gene *HVA1* (Sivamani *et al.*, 2000). Increased yield in transgenic varieties may be also accomplished indirectly through the introduction of resistance to herbicides, resistance to viral and some fungal pathogens that are the main targets considered so far (Langridge *et al.*, 2001). However, the expectation is that many genes will be amenable to manipulation via genetic engineering.

In theory, new approaches such as functional genomics will make it possible to reveal the genetic basis of any given phenotypic response to the environment and hence open up the possibility for genetic transformation. However, as outlined above adaptation to stress at the whole plant level involves the interaction of many genes which are expressed at multiple levels (*i.e.* environmental condition, different plant tissue, phenological stage, time of day, dosage etc.). The techniques involved in genomics are now being applied to specific biological issues including abiotic stress. At present there is a massive database resource to explore (e.g. <http://wheat.pw.usda.gov/genome>). The challenge now is to sift through these databases to identify genes associated with QTLs for drought and other stress tolerances (Forster *et al.*, 2000b). Considerable investment will be required before genetic engineering as a means of improving cereal cultivars for different target environments becomes routine. Furthermore, on what concerns to, for example, with water stress, much of the research being conducted at the molecular level considers processes related to dehydration tolerance and recovery (Cushman and Bohnert, 2000) more than focusing on drought avoidance strategies. In fact crop productivity depends to a large degree on strategies for avoiding stress through deep rooting, and the timing of developmental events such that WUE is optimized with respect to grain formation (Richards *et al.*, 2001). For example, late-embryogenesis-abundant (LEA) proteins appear when drying initiates in developing seeds and disappear after imbibition (Roberts *et al.*, 1993). The genes are similar to those expressed in drought stressed vegetative tissue of wheat (Curry *et al.*, 1991), and ABA can induce expression of these proteins. Sugar synthesis also seems to play a role in drought providing compatible solutes for osmotic adjustment (Bohnert *et al.*, 1995) or through various protective roles including protection of membranes (Crowe *et al.*, 1992). Antioxidants such as superoxide dismutase and ascorbate peroxidase increase in response to drought stress (Mittler and Zilinskas, 1994) and probably play a role in tolerance since excess radiation and increased photorespiration associated with stress can results in accumulation of active oxygen species. Some other relatively simple biochemical processes involved in drought which may lend themselves to genetic transformation include osmotic adjustment, repair and degradation of proteins, and structural adjustment for example of the cell wall (Ingram and Bartels, 1996). Examples of drought-related traits studied by QTL analysis include leaf ABA content in wheat (Quarrie *et al.*, 1994), and water status, water-soluble carbohydrate, osmotic adjustment, plant architecture, growth habit and chlorophyll content in barley (Teulat *et al.*, 1997, 1998, 2000, 2001). A problem highlighted by QTL analysis is the association of abiotic stress traits with genetic loci of agronomic importance (Forster *et al.*, 2000b). For instance, genetic linkage between salt tolerance at germination and ABA response has been found from QTL mapping in barley (Mano and Takeda, 1997). Important genes for adaptation to target environments such as genes responsive to vernalization and photoperiod, and semi dwarf genes frequently show pleiotropic effects on stress tolerance. In addition QTLs for stress responses can coincide with yield and quality QTLs or other important genomic regions (Forster *et al.*, 2000a).

The marker-mediated genetical analyses are revealing detailed information about the genetical control of adaptation and stress responses, and the influence of specific genes of yield performance in different environments. When this genetical information will be translate into selection tools to be used by breeders on an efficient and low cost basis, it will enable the pyramiding of desirable genes.

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Table 1. Examples of the successful application of wide crossing to introduce alien genes into the hexaploid wheat genome (Adapted from Reynolds *et al.*, 1999).

Alien genes	Effect	Reference
1B/R translocation from rye	Present in >300 cultivars	Rajaram <i>et al.</i> , 1990
1B/R translocation	Increased stress tolerance	Villareal <i>et al.</i> , 1997a
<i>T. tauschii</i> x <i>T. turgidum</i>	Good yield characteristics	Villareal <i>et al.</i> , 1997b
Synthetic hexaploids	Used in approximately 15% of all	van Ginkel, 1997,
		pers.
	CIMMYT bread wheat crosses	communication.
<i>Lr19</i> (<i>A. elongatum</i>)	Significant increase in yield	Singh <i>et al.</i> , 1998 and
	and biomass over check lines	Reynolds <i>et al.</i> ,
2001		

Table 2. Performance recent CIMMYT bread wheat lines in Obregon, NW Mexico, 1997-1998 (Adapted from Reynolds *et al.*, 1999).

Cultivars	Yield (Mg ha ⁻¹)	Biomass at maturity (M ha ⁻¹)	Harvest index	Grain number (m ⁻²)	Grain weight (mg)	Days to maturity (d)	Plant height (cm)
Seri-82	9.2	18.7	0.43	18,250	44.5	132	95
Bacanora-88	9.4	20.8	0.40	24,000	34.3	129	90
Baviacora-92	9.8	20.2	0.43	17,200	50.0	132	110
LSD (0.05)	664	2,030	0.426	1804	2.4	5.1	6

Table 3. Correlation between photosynthetic traits measured of 16 individual F₅ plants and performance in F_{5:7} yield plots, 1995-1996 (Adapted from Gutiérrez-Rodríguez *et al.*, 2000).

Individual F ₅ Plants (Grain filling)	F _{5:7} Yield Plots		
	Yield	Biomass	A _{max}
A _{max}	0.66**	0.67**	0.68**
Stomatal conductance	0.65**	0.68**	0.68**

** denotes statistical significance at the 1% probability level

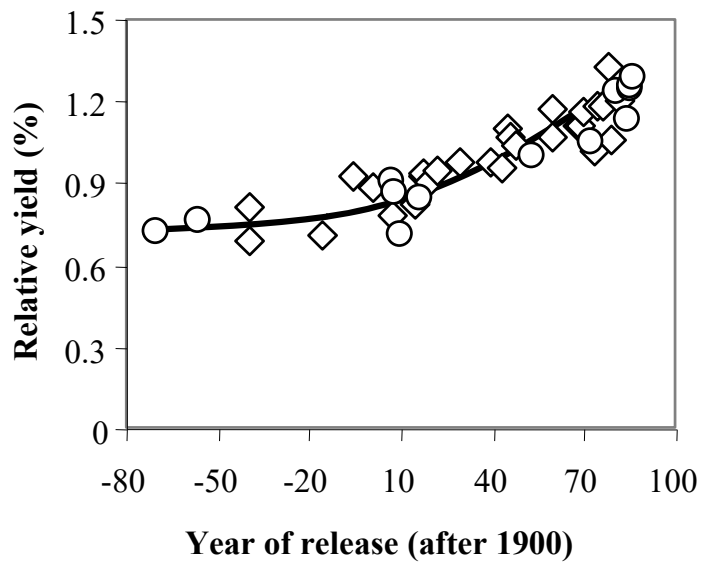


Figure 1. Grain yield of cultivars released at different eras when grown simultaneously in the field in favorable (UK, circles) and stressed (Australia, rhombs) conditions. Yields are given in relative values (the yield of each cultivar as a percentage of the average yield of the corresponding experiment). Adapted from Calderini and Slafer (1999) and Araus *et al.* (2001b).

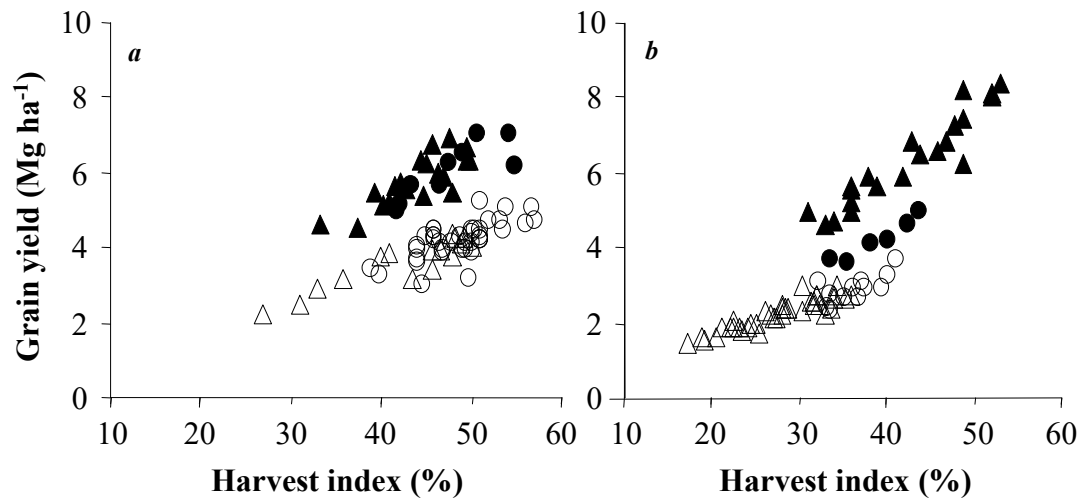


Figure 2. Yield barley (a) and wheat (b) cultivars released at different eras in each country vs. harvest index. Countries in this example (United Kingdom, $\blacktriangle$; Italy, $\bullet$; United States, $\triangle$, and Canada $\circ$) are characterized by substantially different environmental conditions for cereal growing (responsible for the large differences in average yield among them). Original data from Wych and Rasmusson, 1983; Boukerrou and Rasmusson, 1990; Martiniello *et al.*, 1987; Bulman *et al.*, 1993; Jedel and Helm, 1994a. Adapted from Abeledo *et al.* (2001).

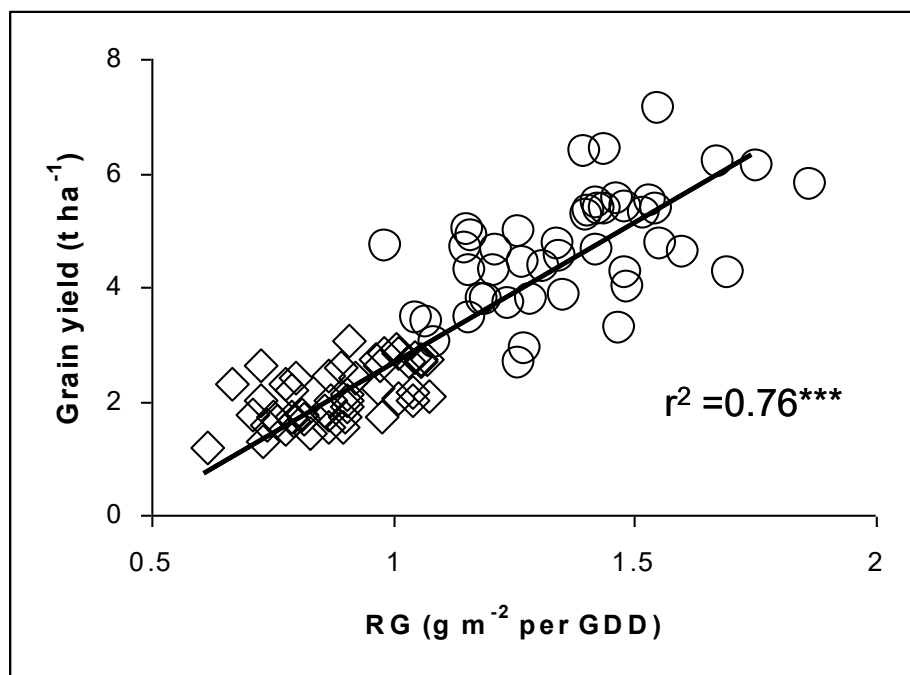


Figure 3. Relationship between the mean rate of growth and grain yield of 25 durum wheat genotypes grown under irrigated (O) and rainfed (□) environments during two crop seasons. Adapted from Villegas *et al.* 2001. Determination coefficients for the relationships across the 25 genotypes within rainfed and irrigated environments were 0.33 and 0.32 ($P < 0.001$), respectively.