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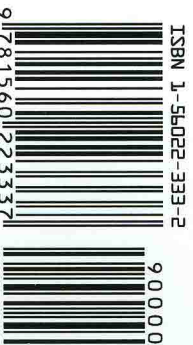
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— Pirjo Peltonen-Sainio, PhD,
Professor, Plant Production Research,
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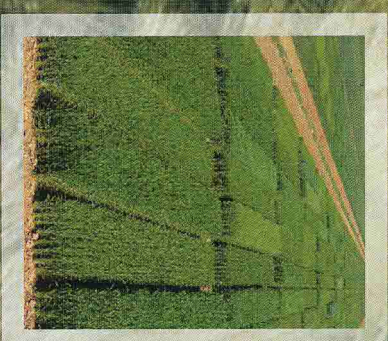
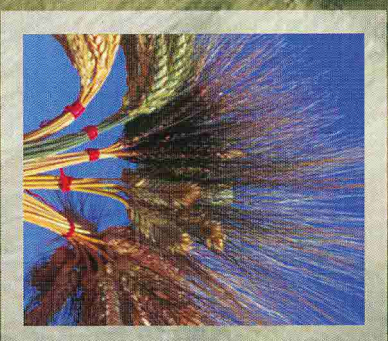


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Durum Wheat Breeding

Current Approaches and Future Strategies

Volume 1



**Conxita Royo • Miloudi M. Nachit
Natale Di Fonzo • José Luis Araus
Wolfgang H. Pfeiffer • Gustavo A. Slafer
Editors**

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Chapter 13

Genetic Improvement Effects on Durum Wheat Yield Physiology

Luis F. García del Moral
Conxita Royo
Gustavo A. Slafer

INTRODUCTION

Genetic improvement of yield has been the result of empirical, trial-and-error selection based on the choice of parents and selection of the progeny mainly for yield per se in most major crops, including durum wheat. This empirical approach has been quite successful in substantially boosting yield potential of many grain crops during the twentieth century (see examples in Slafer, 1994), particularly in wheat (Rajaram, 2001).

However, it appears that breeders will be expected to be even more efficient in the future than in the past (see Chapter 3). In this context, the use of physiological attributes of the crop, both to choose the progenitors of a breeding program oriented to augmenting yield (beyond other objectives), as well as to select the progeny, is increasingly likely in bread wheat (Shorter, Lawn, and Hammer, 1991; Reynolds, Rajaram, and Sayre, 1999; Reynolds, van Ginkel, and Ribaut, 2000; Slafer, Araus, and Richards, 1999), and some evidence suggests that an analytical breeding approach might also be more efficient in durum wheat (Annicchiarico and Pecetti, 1998). In fact, the use of physiological approaches to breed for further increasing yields is likely to be more important for drought-prone than for high-yielding target environments (e.g., Richards, 1982, 1996; Braun, Pfeiffer, and Pollmer, 1992). Approximately three-quarters of the worldwide area cultivated with durum wheat is concentrated in the Mediterranean region (Srivastava, 1984; Belaid, 2000), which is characterized by frequent and intense terminal drought for temperate cereals (Lloss and Siddique, 1994).

Thanks to the Spanish Ministry of Science and Technology for financing the research projects included in this chapter.

Improving performance under mild and moderate stress brings about improvements in adaptation as well (Blum, 1996; Slafer and Araus, 1998; Pfeiffer, Sayre, and Reynolds, 2000; Araus et al., 2002). Thus, identifying putative traits for improving yield potential is a major goal for crop physiologists, as the correct identification of relatively simple traits that underlie yield would allow faster breeding progress (Austin, 1993). Part of the failure of properly identifying useful physiological traits in the past has been due to the suggestion of traits well apart from the yield level of organization and therefore not mechanistically related to it (see Chapter 19). Therefore, as has recently been pointed out (Slafer, Araus, and Richards, 1999), trustworthy traits to be proposed should be causally related to greater yields (Richards, 1996; Slafer, Calderini, and Miralles, 1996), highly heritable, and easily (and cheaply) measured or estimated in a realistic screening process of a commercial breeding program (Araus, 1996; Araus, Casadesús, and Bort, 2001; Richards, 1996; Richards et al., 2002).

Different approaches are used to identify the most promising morpho-physiological characteristics for future breeding, either directly, by formulating a selection index (e.g., Annicchiarico and Pecetti, 1998) or by building up an ideotype (Donald, 1968), as exemplified in Chapter 14. One enlightening approach has been the use of cultivars released in different periods (historical series) to identify attributes that have been altered while improving yield of cultivars. Such studies have proliferated in most major crops (see several examples in the reviews by Feil, 1992; Evans, 1993; Loss and Siddique, 1994; Slafer, Satorre, and Andrade, 1994; Calderini, Reynolds, and Slafer, 1999; Olegui and Slafer, 2000; Abeledo, Calderini, and Slafer, 2002).

Durum wheat, perhaps due to its similarity to bread wheat (by far the most widely cultivated and investigated hexaploid relative), has received less attention, and only scattered results are available for this tetraploid form of wheat. In this chapter, we seek to bring together the results of these disparate efforts in an attempt to devise general patterns for identifying physiological traits that might be useful in future durum wheat breeding. With this aim, we have analyzed the yield progress attributed to breeding in this cereal. Identification of the major traits related to these improvements (mechanistic relationships of these attributes with yield) are discussed in Chapters 15 and 16.

YIELD GAINS ACHIEVED BY BREEDING IN THE TWENTIETH CENTURY

Numerous advances have been made in bread wheat yield during the twentieth century, including cases under contrasting environmental/agro-

nomie conditions (e.g., Austin et al., 1980; Sinha et al., 1981; Kulshrestha and Jain, 1982; Deckerd, Busch, and Kofoid, 1985; Hucl and Baker, 1987; Cox et al., 1988; Ledent and Stoy, 1988; Austin, Ford, and Morgan, 1989; Feil and Geisler, 1988; Perry and D'Antonio, 1989; Siddique et al., 1989; Siddique, Kirby, and Perry, 1989; Slafer and Andrade, 1989, 1993; Camarava et al., 1994; Calderini, Dreccer, and Slafer, 1995; Ortiz-Monasterio et al., 1997; Sayre, Rajaram, and Fischer, 1997). In general, genetically based yield improvements in bread wheat amounted to ca. 50 percent under most conditions worldwide (see several references in Slafer, Satorre, and Andrade, 1994), though some estimates are lower (e.g., 30 percent Bell et al., 1995). Similarly, breeding advances have contributed roughly 30 to 40 percent of the increases in barley yields under different conditions (Silvey, 1986; Strand, 1994; Abeledo, Claderini, and Slafer, 2003). Durum wheat has been analyzed in only a few cases. The two published cases available, which compare a series of cultivars released from breeding programs, concern genetic improvements in Canada (McCaig and Clarke, 1995, partly reassessed by Dexter and Marchylo, 1996), and in CIMMYT-Mexico (Waddington et al., 1987; Pfeiffer, Sayre, and Reynolds, 2000). Studies have not been found providing data for series of historical cultivars grown together in Mediterranean conditions, where most durum wheat has been grown. In this chapter we report preliminary data (Royo and García del Moral, unpublished) of this type for cultivars released both in Spain as well as in Italy from the 1900s to the 1990s and grown under two different Mediterranean conditions. We will compare this with the Canadian and Mexican information. Additional information on retrospective studies may be found in Chapter 14.

In the three cases (Mediterranean, Canadian, and Mexican conditions), a positive relationship can be drawn between cultivar yield and year of release or registration (see Figure 13.1). In Canada, the relationship is clearly bilinear with no increases until the end of the 1950s and linearly increased yields thereafter (see Figure 13.1a). Meanwhile, in Mexico (see Figure 13.1b) and southern Europe (see Figure 13.1c), this relationship is strongly linear along all the range of time studied. The different performance in Canada may be partially attributable to the fact that the first variety of the Canadian program was released in 1963, whereas, prior to that, durum wheat production was based on varieties introduced from the United States (see Chapter 30).

The yield gain achieved by durum wheat breeding in Canada and southern Europe appears to be far smaller than in Mexico. This may be a result of different breeding periods, the contrasting environmental conditions under which breeding programs were conducted, and the diverse intensity of breeding efforts made in CIMMYT and in national programs. In bread

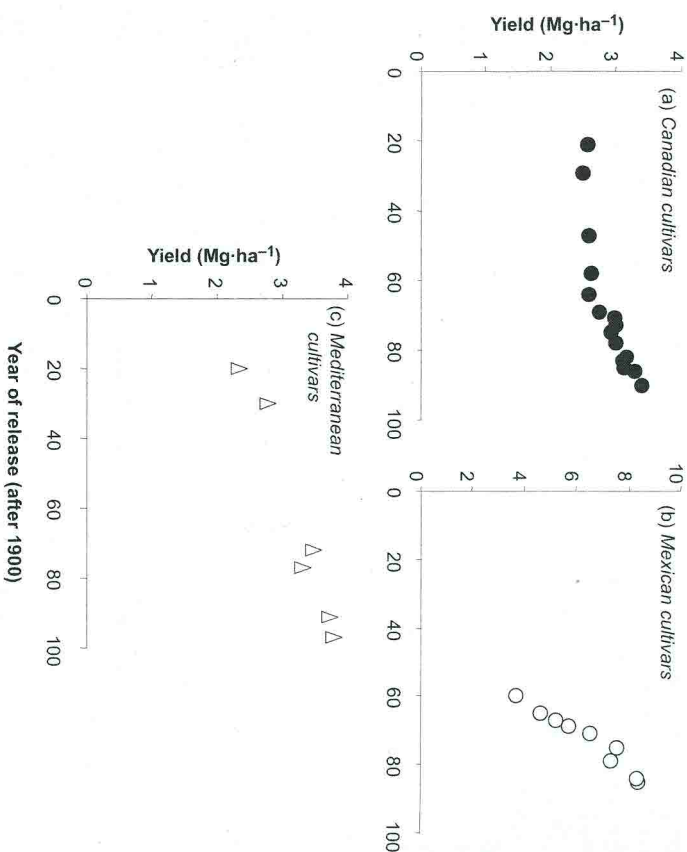


FIGURE 13.1. Yield of durum wheat cultivars versus their year of release in Canada (a), Mexico (b), and Italy and Spain (c). Data on Canadian wheat adapted from Dexter and Marchylo (1996) were based on original data published by McCaig and Clarke (1995). Mexican data correspond to CIMMYT germplasm (consequently data start only in 1960) and are averages of two experiments (Waddington et al., 1987). Data for Italy and Spain are the average of four old, intermediate, and modern cultivars for each country in experiments conducted for two years in two environments (from Royo and García del Moral, unpublished).

wheat, it has been clearly established that, during the first half of the twentieth century, yield potential increased more slowly than that during the second half (see several examples in Slafer, Sattore, and Andrade, 1994). A similar scenario has also been depicted by Riggs et al. (1981) for barley in the United Kingdom (genetic gains in yield were three times higher in the second half than in the first half of the century). Curvilinear relationships are also common for barley in other regions when the period analyzed includes data for the 1900–1950 period (Abelido, Calderini, and Slafer, 2002). On the other hand, Waddington et al. (1987) tested the durum wheat

under nonstress conditions at CIMMYT, where genotypes could express their yield potential, whereas trials conducted in Canada and in southern Europe were carried out in moderately stressed environments. Actually, a positive relationship between the genetic gain estimated and the average yield of the experiment has been reported for cases in which the same set of cultivars was analyzed under many different environmental conditions (e.g., Perry and D'Antuono, 1989; and the reappraisal published by Calderini and Slafer, 1999). This is clearly shown by Figure 13.2, which displays yield increases for Spanish and Italian durum wheat cultivars evaluated in two contrasting environments within Spain (Catalonia in the north and Andalusia in the south). The better the environmental conditions (Catalonia versus Andalusia) the greater the estimated genetic gains in yield for the same set of cultivars.

Thus, a more realistic comparison may be based on the relative genetic gain in yield (e.g., Slafer and Andrade, 1991). Considering the linear phase of the curves (i.e., from 1960 onward) shown in Figure 13.1, we find that the Canadian and the southern European cases exhibited a still smaller figure (Figure 13.3) for the same analysis period as used in the Mexican case: 0.9 percent y^{-1} for the former two cases and almost 3 percent y^{-1} for the latter (see also Chapter 15).

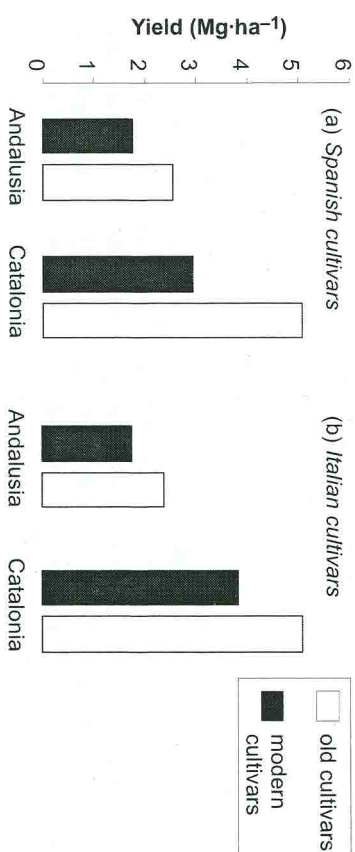


FIGURE 13.2. Average yield of four old (released before 1930) and four modern (released after 1980) cultivars of durum wheat bred in Spain (a) and in Italy (b). Spanish and Italian cultivars were grown for two years under two distinct Mediterranean conditions: the moderately stressed conditions of Catalonia (Royo et al., unpublished) and the highly stressed, lower-yielding conditions of Andalusia (García del Moral et al., unpublished).

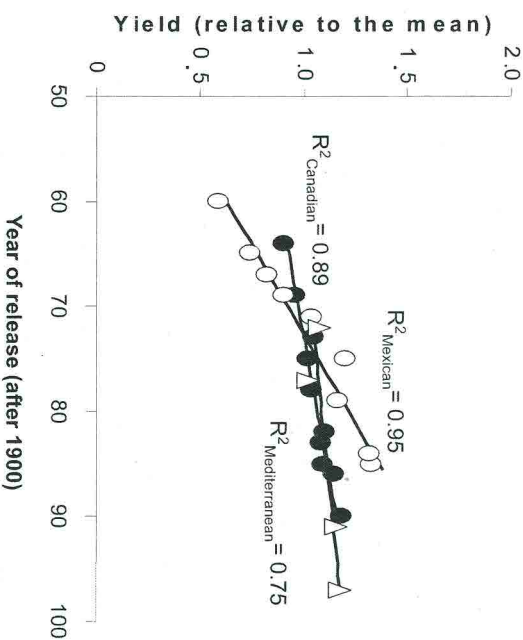


FIGURE 13.3. Yield of cultivars expressed as a relative value of the average yield in each experiment regressed against their year of release for Canada (McCaig and Clarke, 1995; black circles), restricting the analysis to the cultivars released after 1960), Mexico (Waddington et al., 1987; white circles), and southern Europe (Italian and Spanish groups of intermediate and modern cultivars, Royo and García del Moral, unpublished; triangles).

The difference may simply reflect the results of a large breeding investment (both in financial and in human resources) of an international center such as CIMMYT rather than a poor performance of Canadian, Spanish, and Italian breeders. In fact, the values of relative genetic gains for durum wheat in these countries are similar to the value 0.4–0.6 percent- y^{-1} reported for many cases of bread wheat (see examples in Calderini, Reynolds, and Slafer, 1999). Also in the case of bread wheat, the relative genetic gains reported for CIMMYT during the second half of the twentieth century are higher than those reported for most other, frequently commercial or national, programs (which are in fact subjected to greater financial, human, and political restrictions). Despite the fact that breeding is conducted under stress conditions, the progress achieved in both Spain (Figure 13.2a) and Italy (Figure 13.2b) is clear. The relative genetic gain in yield broadly estimated from these figures is about 0.8 and 0.6 percent- y^{-1} for Spanish and Italian cultivars, respectively. Thus the efficiency of durum wheat breeders in the two countries proved comparable to that of many bread wheat programs (Calderini, Reynolds, and Slafer, 1999).

PHYSIOLOGICAL DETERMINANTS OF THE YIELD GAINS BY DURUM WHEAT BREEDING

Two complementary approaches have been frequently used to analyze the physiological factors governing genetic gains in crop yield. As breeding has been mostly based on an empirical trial-and-error process during the twentieth century (Loss and Siddique, 1994), these approaches allow determination of the physiological and agronomical attributes which were altered, mostly unintentionally, while improving crop yield. These approaches include, first, the classical yield division in numerical components and, second, the determination of dry-matter accumulation and partitioning. The former is relatively simpler than the latter, but the frequent negative association between components makes the approach difficult to use in prospective analyses (Fischer, 1984). The two major constituents of the numerical-components approach are the number of grains per unit of land area and the average grain weight, with the number of grains often being divided into number of spikes per square meter and number of grains per spike (and these may be further subdivided). The other approach is based on the amount of biomass produced and the fraction of total dry matter allocated to grains, or harvest index (Fischer, 1984, and see Chapter 19).

The information on these attributes has been exhaustively analyzed in bread wheat (e.g., Calderini, Reynolds, and Slafer, 1999, and references therein), but the specific studies dealing with historical series of durum wheat cultivars has, up to now, provided only limited opportunities to delve into the detailed physiological changes engendered by the breeding of this crop.

CHANGES IN YIELD COMPONENTS

In the three studies available, the changes in the number of grains per unit of land area produced by breeding throughout the period analyzed mirrored those produced in yield. In the case of Canada (where data were only available in relative terms, assuming a 100 percent value for cv. Hercules, widely cultivated for decades; McCaig and Clarke, 1995), the number of grains remained virtually unchanged during the initial decades, when genotypes were introduced from the United States, and then consistently increased as newer, higher-yielding cultivars developed in the Canadian breeding program were released (Figure 13.4a). No clear trends were discerned for changes in the other major yield component (Figure 13.4a, inset). Similarly, the number of grains rose sharply with the successive release of cultivars from 1960 onward in the case of the CIMMYT program (Figure

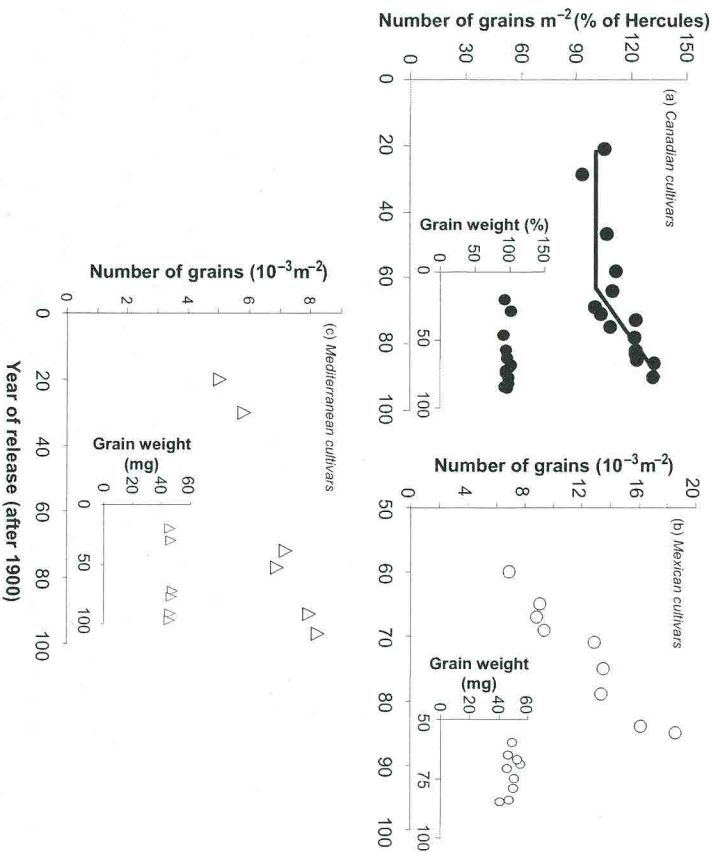


FIGURE 13.4. Number of grains per unit of land area (main panels) and mean grain weight (insets) of cultivars released during different periods in Canada (a), Mexico (b), and southern Europe (Italy and Spain) (c) plotted against their year of release (references as in Figure 13.1). Canadian data expressed as a relative value of the cultivar Hercules.

13.4b), while no major trends were noticeable for the mean individual grain weight (Figure 13.4b, inset). This trend has continued during the period following the one analyzed in Figure 13.4b (see Pfeiffer, Sayre, and Reynolds, 2000). The situation is similar for varieties released in Italy and Spain over a longer period of time (Figure 13.4c). Consequently, the difference between old and modern cultivars of durum wheat in the three regions studied were dependent exclusively upon their differential abilities to set grains.

These findings parallel what has been firmly established for bread wheat (see reviews by Loss and Siddique, 1994; Slafer, Sartore, and Andrade, 1994; Calderini, Reynolds, and Slafer, 1999 and several individual references quoted therein), in which breeding has increased almost exclusively

the number of grains per unit of land area, and, in some examples, grain weight was even reduced by genetically improved wheat yield (e.g., Slafer and Andrade, 1989; Loss et al., 1989). A higher number of grains per square meter was also the most frequent effect of barley breeding in different regions (Riggs et al., 1981; Wych and Rasmusson, 1983; Jedel and Helm, 1994). Therefore, although exceptions may be found in which breeders have enlarged the average size of the grains while selecting for higher yielding ability (Cox et al., 1988; Boukerrou and Rasmusson, 1990), an overwhelming number of cases from many regions of the world reflect that most of the yield gains achieved by breeding in different cereals were associated with a higher number of grains per unit of land area (see recent reviews by Calderini, Reynolds, and Slafer, 1999, for bread wheat; Abeledo et al., 2002, for barley; and Figure 13.5 for durum wheat). This increase could mainly be attributed to the fact that modern varieties possessed more fertile florets per spikelet as a consequence of a higher assimilate partitioning to the spike during the preflowering critical period (Fischer, 1984), as found both for bread (Calderini, Dreccer, and Slafer, 1995) and recently for durum wheat (Miralles et al., 2002).

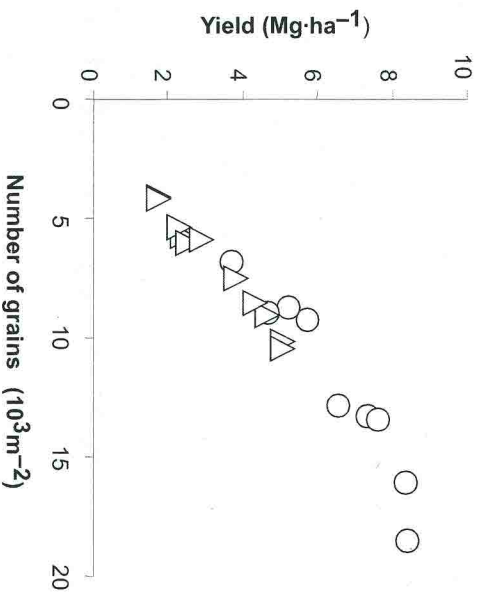


FIGURE 13.5. Relationship between yield and number of grains per unit land area for Mexican (circles) and Mediterranean (Spanish and Italian; triangles) cultivars released during different periods. Mexican data adapted from Wadlington et al. (1987), Mediterranean data from Royo and García del Moral (unpublished).

Thus, it seems valid to extrapolate to durum wheat what has been widely demonstrated for bread wheat under many different conditions: that yield is far more frequently limited by the size of the sink than by the strength of the source during grain filling (e.g., Slafer and Savin, 1994; see also Chapter 14). Hence, future improvements in the number of grains per unit of land area and per spike might further improve yield (Slafer, Araus, and Richards, 1999; Araus et al., 2002). The apparent lack of restrictions in the ability of the vascular system to allow the filling of extra grains, as demonstrated by various studies with sink-source manipulations during grain filling (Martinez-Carrasco and Thorne, 1979; Jedel and Hunt, 1990; Slafer and Savin, 1994; Kruk, Calderini, and Slafer, 1997), is consistent with the fact that breeding appeared not to have systematically altered the size of the vascular tissues in the peduncle of durum wheat improved in the Mediterranean region (Figure 13.6). In other words, yield increased without changing the size of either the phloem or metaxylem areas of the peduncle, implying that the old cultivars (with lower number of grains per spike) had a larger vascular system than required for adequate grain filling (López-Garrido et al., 2001).

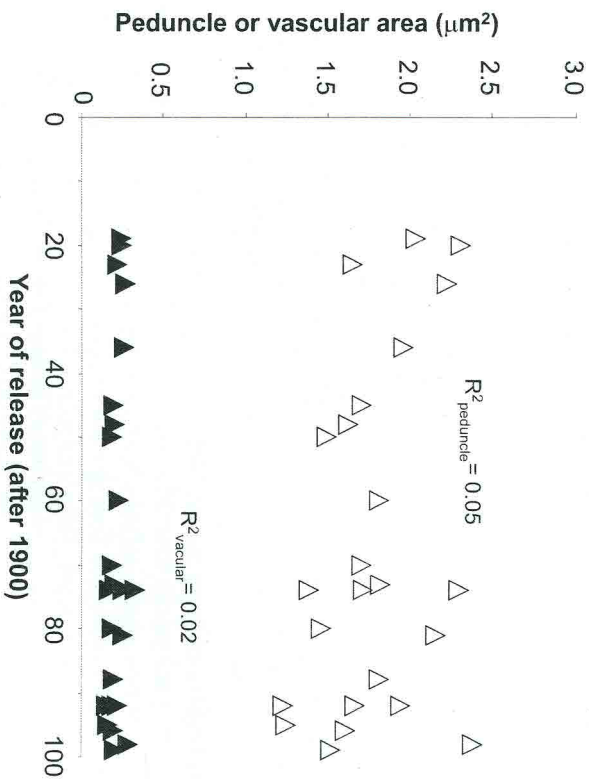


FIGURE 13.6. Relationship between the cross-sectional size (area) of the peduncle (open triangles), and vascular system inside it (dark triangles) and the year of release of the cultivars. Data for cultivars released by Mediterranean programs (Spanish and Italian) were adapted from López-Garrido et al. (2001).

CHANGES IN DRY-MATTER PRODUCTION AND PARTITIONING

Unfortunately, the Canadian study (McCaig and Clarke, 1995) did not report on changes in dry-matter economy, and the analysis was necessarily restricted to the Mexican study (Waddington et al., 1987) and to the preliminary results for the Mediterranean experiments in Catalonia and Andalusia (Royo and García del Moral, unpublished).

Overall, breeding for yield potential at CIMMYT slightly augmented biomass during the three decades analyzed, but changes in biomass production were clear only in the mid-1980s (Figure 13.7a). Conversely, the harvest index almost doubled in the first two decades, with no further gains in the last decade analyzed (Figure 13.7b; see also Pfeiffer, Sayre, and Reynolds, 2000 for a more recent comparison following this trend). Preliminary results of four experiments in Spain also showed that modern and old cultivars which were improved in the Mediterranean region differed in both biomass and harvest index. Although both attributes contributed to the yield advantages of modern Mediterranean cultivars over their predecessors, the harvest index was quantitatively more important than biomass, as in the Mexican study, but it also tended to reach a plateau in the newest varieties released.

Consequently, in the cultivars representing successful breeding efforts both at CIMMYT and in European Mediterranean regions, yield was closely related to the harvest index, though the slope was slightly steeper than for isobiomass (Figure 13.7c).

These findings coincide partially with the results of most studies focused on bread wheat and barley, in which breeding efforts achieved an increase yield negligibly or only partially related to increases in vegetative biomass (see several references and a synthesis in reviews by Calderini, Reynolds, and Slafer 1999; Abeledo et al., 2002, for bread wheat and malting barley, respectively). Much of the biomass gain seems to have been achieved when no further increases in harvest index were obtained, once the released cultivars had reached harvest indexes close to 50 percent (Figure 13.7b and Pfeiffer, Sayre, and Reynolds., 2000). Harvest index in temperate cereals has an upper threshold (due to both physiological and agronomic reasons) of around 60 percent (Austin et al., 1980), and, as the current values approach the upper threshold, further increases will become more elusive.

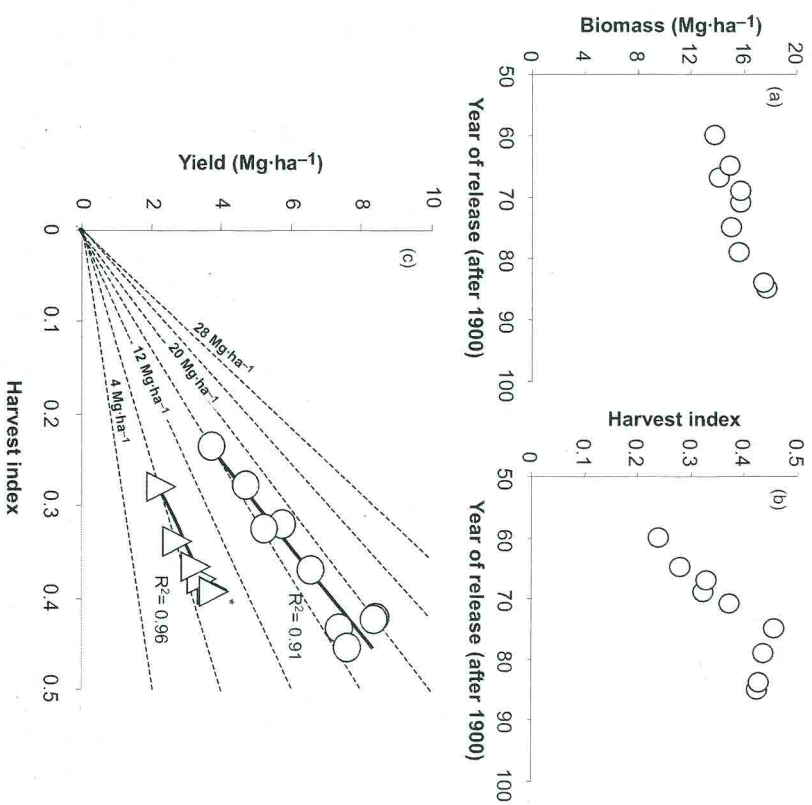


FIGURE 13.7. Biomass at maturity (a) and harvest index (b) of cultivars released during different periods in Mexico, and the relationship between yield of these cultivars and harvest index (c) for these data (circles) as well as those from the Mediterranean environment (triangles). In panel c, dotted lines reflect different levels of biomass production, increasing counterclockwise (adapted from Wadlington et al., 1987, averaging two experimental years, and unpublished data from Rojo and García del Moral). The asterisk indicates that there are two overlapped data points.

CONCLUSION

In this chapter, we have described the magnitude of the genetic gains attained by durum wheat breeding and we have identified the major physiological and agronomical changes associated with breeding progress in this crop. Faced with a paucity of published data specifically for durum wheat,

we have also used preliminary data from an ongoing project, comparing the findings with those reported for breeding effects in related species, for which much more information is available (mainly bread wheat and barley).

Durum wheat achieved genetic gains in yield potential during the past few decades at a rate comparable to that of bread wheat, both under high-yield and stressful conditions, but with higher genetic gains in the former than in the latter situation. These gains were attained by consistently boosting the number of grains per unit area (as well as the number of grains per spike), while the mean weight of the grains remained virtually unchanged. This suggests that, as in bread wheat, durum wheat yield is more restricted by the size of the sink than by the strength of the source after anthesis. Such restriction may be interpreted as an indication that future breeding should continue to enlarge the size of the sink, for which the physiological attributes favoring the formation and set of grains under high-yield potential and stressful conditions must be identified (see Chapters 15 and 16). Practical tools to be used in breeding to improve these attributes should be designed (see Chapter 19).

Regarding the dry-matter economy of the crop, yield was augmented primarily due to a higher harvest index and also due to improved biomass production, particularly after high harvest-index values had been reached. As a result, modern cultivars reflect relatively high indices of dry-matter partitioning to grains, and therefore, under many conditions, improved biomass production is required for continued increases in yield. In this sense, genetic variability for biomass production in durum wheat has to be detected and exploited, the physiological bases of biomass production must be identified, and tools to allow breeders to select for key traits should be developed. Opportunities for genetic manipulation of biomass and its components are examined in Chapters 15 and 19.

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