

Increasing cereal yield potential by modifying developmental traits

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Abstract

On-farm grain yield of most grain crops has paralleled the improvement in grain yield potential, which has been mainly associated with an increase in the number of harvestable grains. A reduction in plant height (most cereal species) and tassel size (maize), with the concomitant improvement in assimilate availability for the growing spike, have been key traits for enhancing kernel number. The benefits of these traits, however, seem no longer useful for improving grain yield, and new molecular technologies are still far from giving a good explanation of the causal relationships between genes and the phenotype of complex traits like grain yield. In this paper we briefly reviewed (i) the importance of improving yield potential for further increasing actual yields in a range of conditions, and (ii) the significance of considering physiological attributes for achieving this goal. We finally discuss recent research on two developmental traits as tools for further raising yield potential in cereals. These are the particular extent of the stem elongation phase in wheat and the synchrony in the emergence of silks within ears in maize.

Media summary

Genotypic differences in duration of the stem elongation phase in wheat and in the synchrony of silk emergence in maize can help improve grain yield.

Key Words

Cereals, yield potential, physiology, development, breeding.

Introduction

Cereals are at the top of the list of human nutritional needs, with wheat and maize especially important in the food of Western cultures while rice dominates Asian meals. The primary use of wheat and maize grains after harvest, however, is very different: the former has a more direct inclusion in our diets through diverse products, among which bread is by far the dominant, whereas the main use of maize is for animal feeding. Another distinctive trait of these two cereals is their position in current cropping systems which is linked to the growing requirements of each species but also to the profitability determined by grain price, production cost and its value in the rotation. Thus, in rainfed regions where both crops can be widely grown and no economic pressure (e.g. subsidies) helps buffer market trends, land area cropped to each cereal can shift substantially. This phenomenon has been evident in the Argentine *Pampas* region, where a third crop, soybeans, won acreage steadily during the last decade. Historically, wheat in the *Pampas* occupied a larger part of the agricultural land than maize, mainly due to the lower production costs per hectare of the former and its better performance in areas where summer droughts always represent a high risk for profitable maize crops. Nowadays, a similar analysis applies with respect to soybeans, boosted by the high international prices of the oil crop. The result of these trends has been a concentration of maize in the most productive areas of the *Pampas*, and a significant proportion of wheat production coming from double crop wheat-soybeans, in which soybean is sown immediately after wheat harvest. In this scenario, the insertion of cereal crops in the rotation is highly dependent upon their yield and the need of preserving a minimum frequency of large-residue crops in order to keep soil organic matter, and consequently soil properties, at levels compatible with the sustainability of the system.

Grain yield of most cereals, but particularly of wheat and maize, exhibited a sustained increase during the second half of the last century. Evidence from the last decade, however, suggests a softening in this trend for most of these crops (Calderini and Slafer 1998; Slafer and Otegui 2000). This change in trend turns gloomier in view of the expected global demand of these staples. While world demand for wheat has been increasing at a rate of 3% per year, the rate of increase in yield potential of this cereal has been of 0.8% per year (McWilliam 1989). In this context, future cereal breeding needs to be even more efficient than in

the past, when yield potential increased dramatically. On the other hand, traditional breeding may benefit today by the contribution from molecular biology (Araus et al. 2002), which is likely to help in this field. Initially promising perspectives from new molecular technologies, however, have not yet yielded the expected results for improving complex traits related to crop productivity (Slafer 2003). Remarkable progress has been made with the discovery and transfer of major genes, almost exclusively linked to the control of biotic constraints, like the Bt for insect control and the glyphosate resistance for weed management. Molecular tools are still far from giving a good explanation of the causal relationships between genes and the phenotype of complex traits linked to productivity under field conditions, the initial step for their subsequent manipulation. This is particularly evident in the case of yield, which is formed continually from sowing to harvest and with virtually all genes contributing directly or indirectly to its determination in a quantitative manner. In this context, there is good consensus at present among breeders about the importance of an adequate phenotyping as the first task for the identification of genes responsible for a given trait. The second task is the detailed characterization of the target environment, generally neglected by breeders and physiologists (Acevedo and Fereres 1993). Both aspects, i.e. improved phenotype and environment data collection, will enhance the analysis and comprehension of the genetic bases of yield determination with respect to statistical approaches most currently used in breeding. This is a key step for the correct application of many identified QTLs and genes.

In this paper we will briefly discuss the importance of improving yield potential for further increasing actual yields in a range of conditions, and will then focus on the significance of considering physiological attributes for achieving this goal. A range of traits may be considered (see for instances reviews in Otegui and Slafer 2000, and Reynolds et al. 2001), mostly based in growth attributes. Developmental traits, on the other hand, have been mostly regarded only as characters conferring adaptation (Slafer and Whitechurch 2001). However, recent advances in this field provide initial evidence suggesting that fine-tuning developmental patterns may further raise yield potential of cereals. To illustrate this issue we will concentrate on two examples of newly proposed alternatives for further improving yield potential through manipulation of developmental traits, one for wheat and another for maize.

Relevance of further raising cereal yield potential

There is on-going discussion as to whether it is relatively more important to further improve yield potential genetically, with the concomitant increase of actual grain yield in the field, or agronomically, reducing the gap between this potential yield of modern cultivars and actual yields achieved by farmers. The relative importance of these two viewpoints would, at first sight, depend upon the magnitude of the gap between potential and actual yields. If the gap is small, little can be expected from improved management, and future improvements in actual yields may largely depend on further raising yield potential. This is the case in many irrigated high production regions of the world, like major rice-producing provinces of China, wheat production in the Yaqui Valley of Mexico, and maize contest-winners of the US corn-belt, where actual yields are reaching the 80% yield potential threshold that marks the start of on-farm yield stagnation (Cassman et al. 2003).

The issue is rather more complex for the environments in which actual yields represent only a rather small proportion of potential levels, which is the case for most cereal growing regions of the world. In these environments, the magnitude of the gap between potential and actual yields is frequently interpreted as an indication of the potential contribution that management improvement might make. However, the alternative view suggests that, independently of the magnitude of the gap, increases in yield potential are critical even in these circumstances. This view is based on the parallelism between improvement in yield potential and responsiveness to management improvement (Cassman et al. 2003). For instance Kirigwi et al. (2004) have shown that it is feasible to retain genes for relatively high yield under stress from selection carried out under stress-free conditions in wheat, and similar conclusions apply to other cereal crops like barley (Abeledo et al. 2003) and maize (Duvick 1992).

The fact that (i) there has been little or no increase in actual yields until there was a consistent increase in potential yield of cultivars released by breeders in different crops (e.g., Evans 1993), and (ii) cultivars released by breeding with higher yield potential outyielded their predecessors in a wide range of environmental conditions (e.g. Russell 1991; Calderini and Slafer 1999; Tollenaar and Lee 2002) support this view. Thus, it may be expected that future genetic progress in yield potential (yield in favorable

environments) should continue contributing to increases in actual yields in less favorable growing environments (see reviews in Reynolds et al. 2001).

Determination of cereal yield potential

In order to increase yield potential, the traditional approach has been selecting for yield *per se*. It seems that in the future, the traditional approaches may benefit from complementation with analytical tools. These analytical tools need to consider determinants of yield potential that must be functionally related to yield so that they may be reliably used in breeding or pre-breeding. The initially most popular approach of dividing yield into its numerical components, though apparently logical and simple, is unfortunately of little use due to the negative relationship expected among them under agronomic conditions (Fischer 1984).

A more functional approach has been the analysis of the timing when yield is chiefly being determined. In all crops yield is the end result of growth and development, determined by the genotype, the environment and their interaction. Yield can be affected at any time from sowing to maturity: at any stage of development one or more components of yield are being determined, either through their generation or their degeneration/death (Slafer and Rawson 1994). However, only a relatively small fraction of the whole growing period is actually critical to the determination of yield in most grain crops. This is, in general, the period when the number of grains per unit land area is largely determined in response to the growing/partitioning conditions of the crop. This is so, in turn, because grain yield is much more related to the number of grains per unit land area than to the average weight of the grains. The latter is far less responsive to changes in availability of assimilates, although here there are differences among crops (Borrás et al. 2004).

This critical period is always concentrated around the flowering stage, with specific differences likely dependent upon the floral biology and mating system. For instance in wheat, a cleistogamous species (pollination occurs before the opening of the flowers), most of the floret primordia that reach the stage of fertile floret become grains after anthesis. The critical period is when a proportion of the large number of floret primordia becomes fertile florets. This period is during stem elongation, a few weeks prior to anthesis (e.g. Fischer 1985; Kirby 1988). In maize, a monoecious crop (grains are set in the axillary, female inflorescences fertilized with pollen from the apical inflorescence, mostly from other plants in the population due to protandry), the critical period includes the periods immediately before and immediately after anthesis/silking, but grain set rather than the determination of the number of fertile florets is the relevant process (for a review on this topic see Otegui and Andrade 2000, and Westgate et al. 2004).

By improving either crop growth or partitioning to reproductive structures during their respective critical periods, the number of grains per unit land area (and yield) would be concomitantly improved both in wheat (e.g., Fischer 1985) and maize (Andrade et al. 2002). Consequently, various traits presumably associated with improved growth of harvestable organs during the critical period (e.g. reduced plant height, reduced tassel size) have been included in breeding programs, in order to identify prospective parents or to directly select the progeny (e.g., various chapters in Otegui and Slafer 2000, and Reynolds et al. 2001).

Developmental patterns have received far less consideration as potential traits to improve yield potential. Developmental attributes have mostly been studied in terms of their effects on anthesis time, strongly related to adaptation but not clearly related to yield potential. For instance, wheat breeding that increased crop yields noticeably during the second half of the 20th century worldwide (Calderini et al. 1999), only generated systematic changes in developmental patterns in countries with large areas of the crop under Mediterranean conditions of terminal drought, in which shortening the cycle improved stress avoidance (such as in Western Australia). In regions where mid-season stress or stresses occur irregularly during the season, improved yields have not consistently followed changes in developmental patterns of the crop (see Araus et al. 2002, for an extended discussion of this issue). However, in the last decade or so, several cases have emerged in which manipulation of particular developmental attributes (beyond general changes in time to anthesis) seemingly influences crop yield. These developmental attributes might be potential candidates for breeding for further increasing yield, with virtually no effect on adaptation. In the last sections of this paper we will concentrate on the likelihood of using particular developmental

attributes in wheat and maize as tools to actually improve yield potential. They are the duration of the stem elongation phase in wheat and the synchrony in the emergence of silks within ears in maize.

Duration of late reproductive phases in wheat as an alternative to improve its yield potential

Brief hypothetical framework

It has been proven that (i) number of grains per unit land area in wheat is strongly associated with the dry matter accumulated in the spikes at anthesis (see references above), a relationship that holds for a wide range of growing conditions, and (ii) spike dry-matter accumulation takes place only during a brief period within the phase of stem elongation (Kirby 1988; González et al. 2003b) in strong competition with the growing internodes (e.g., Fischer 1995).

Most breeding success in the past has been associated with improvements in the partitioning of dry matter to the growing spikes (as recently reviewed by Calderini et al. 1999), and most of this achievement has been accomplished by the introgression of major *Rht* genes for reduced stem growth, increasing thus the availability of assimilates for the developing spikes. As modern wheats have already reached an optimum height (Miralles and Slafer 1995), further reductions in height are likely counterproductive, and then the trait most successfully altered in the recent past seems no longer useful for further increases in yield potential (Slafer et al. 1999).

Increasing crop growth rate during the critical phase of stem elongation is likely the universal mechanism by which most management practices impact on grain yield of many annual crops (e.g., Fischer 1993; Andrade et al. 2002). Consequently, a lot of public and private research effort is aimed to improving knowledge of the developmental pattern of each cultivar in each environment (e.g., days or thermal time to anthesis), a key issue for matching the critical period with the best growing conditions. In the main wheat producing areas of Argentina, for instance, spring type cultivars predominate and sowing date is scheduled in order to place the anthesis of the crop as soon as late frosts do not represent a serious risk of spike damage. Spring types avoid the extra water uptake of longer cycles early in winter, which can be particularly disadvantageous in some areas (Savin et al. 1995), and early anthesis dates exploit mild temperatures during grain filling. The combined effect of cycle duration and planting date also lead to cereal harvest as soon as possible in December for the early sowing of second-planted soybeans, the yield of which is significantly reduced for each day delay in planting (Calviño et al. 2003). In this cropping scenario there is little room for significant changes in wheat cycle duration, and it seems likely that increasing crop growth rate genetically by improving either radiation interception or radiation use efficiency during the critical phase of stem elongation may be required to keep on increasing yield potential (Slafer et al. 1999).

It has been only relatively recently hypothesized that lengthening the stem elongation phase (independently of the previous phases) would bring about improvements in both spike dry weight at anthesis and number of grains to be filled from then on (Slafer et al. 2001). This hypothesis would potentially work in any condition in which wheat yield is clearly sink-limited during grain filling, and then increasing the number of grains per m² would result in actual increases in yield. This situation is seemingly generalized over many different growing conditions and cultivars (Borrás et al. 2004). Thus, if differences among genotypes in the length of the phase of stem elongation (due to either sensitivity to photoperiod or intrinsic earliness for the specific phase) may be found independently of the photoperiod sensitivity or the intrinsic earliness ranking of previous phases, the developmental pattern of a genotype might be tailored. In other words, for a specific length of the total phase to anthesis (critical for adaptation, and thus already optimized in most regions) a combination of different lengths of developmental phases occurring before and after the onset of stem elongation may be hypothetically arranged. The fact that developmental rates of different phases seem to be, at least partially, independently modulated by photoperiod (e.g., Slafer and Rawson, 1996; Miralles et al. 2000) and intrinsic earliness (Slafer 1996), supports the hypothesis.

Empirical evidence of genotypic variation in partitioning of total time to anthesis among phases occurring before and after the onset of stem elongation

We conducted a detailed study to try to uncover any variability existent within modern wheats cultivated in Argentina for the duration of the stem elongation phase (from the onset of stem elongation to anthesis)

within commercial cultivars released in recent years and of similar time to anthesis when sown in their recommended dates (Whitechurch, Slafer and Miralles, unpublished). We preferred to test variation within modern cultivars as they are the core material used to pyramid yield increases.

Sixty-four cultivars grouped into subsets of similar emergence-anthesis durations were sown in field experiments and screened for their phenology. We found some clear examples of pairs of cultivars with similar times to anthesis combined with contrasting distribution of that time between phases elapsed before and after the onset of stem elongation (Fig. 1). This variability is in agreement with that observable in barley when a screening is made with several cultivars (Kernich et al. 1997). In addition, there was variation among genotypes regarding the stage of the stem elongation period responsible of the observed variability, being sometimes from the onset of stem elongation to flag leaf emergence and in other times from then on (data not shown). A detailed understanding of the response may be relevant when considering possible effects on traits influencing canopy survival and/or photosynthetic activity after anthesis. For instance, lengthening the first stages of stem elongation may enhance rooting and access to N sources after anthesis, while lengthening the late stages of this period may act more directly on floret primordia survival. Testing the effects of these phenological changes on biomass partitioning and kernel set requires more than the simple comparison of cultivars, as discuss in the next section.

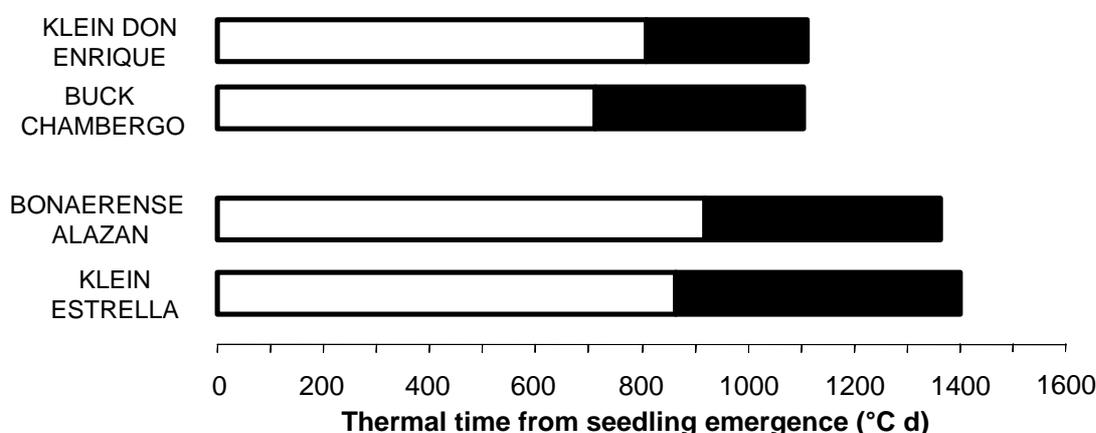


Figure 1. Examples in which a pair of wheat varieties with relatively short (top pair) or long (bottom pair) periods to flowering exhibited different durations of the phases from seedling emergence to the onset of stem elongation (open bars) and from then to flowering (closed bars) (Whitechurch, Slafer and Miralles, unpublished).

Responses of grain number to changes in duration of stem elongation

Even before exploring the existence of genetic variation in length of the stem elongation phase, independently of variation in duration of previous phases, we searched for the actual sensitivity of this late reproductive phase to photoperiod. A summary of those experiences has been reviewed in Slafer et al (2001). To recap briefly, we firstly dealt with the generalized assumption that only relatively early developmental phases are responsive to photoperiod. However a reappraisal of the literature data from studies in which photoperiod treatments were imposed directly rather than by changes in sowing dates clearly suggested that the late reproductive phase of stem elongation was highly sensitive to photoperiod (Slafer and Rawson 1994), and in addition quite variable in terms of intrinsic earliness (Slafer 1996). The suggestion of the strong responsiveness of the stem elongation phase to photoperiod was significantly supported by experiments specifically designed, both in controlled conditions (Slafer and Rawson 1996) and in the field (González et al. 2002), in which plants were exposed to different photoperiods throughout their development but the responses of different phases analyzed independently. In later studies we exposed the late reproductive phase to different photoperiods independently of the photoperiod experienced in the previous phases, in order to test direct responses (and sensitivity) of this critical phase. Both in controlled conditions (Miralles et al. 2000) and in the field (González et al. 2003a; Slafer and Abeledo, unpublished) the stem elongation phase responded to photoperiod regimes imposed exclusively at that stage, lengthening the phase as photoperiod decreased. It seems then that sensitivity to photoperiod may actually be used as a tool to further increase wheat yields, by specifically manipulating the sensitivity to photoperiod during the stem elongation phase. As direct phenotypic selection for this trait seems unrealistic, it is crucial to identify genetic bases for the sensitivity to photoperiod during the stem

elongation phase. Only initial efforts have been made (and these only with the three major *Ppd* alleles) in this field so far, (Whitechurch and Slafer 2001, 2002) and this must be strengthened in the near future.

In all studies (under controlled or field conditions; with photoperiod regimes imposed throughout or only during the stem elongation phase), only changes in duration of the stem elongation phase were reflected in changes of the number of fertile florets or grains produced by the crop (Slafer et al. 2001; Fig. 2). In the phytotron study, plants of a photoperiod-responsive spring wheat (UQ189), grown in a naturally lit phytotron at constant (9, 13 and 19 h) and reciprocally interchanged photoperiods at the onset of stem elongation. The stem elongation phase was actually lengthened under shorter photoperiods and *vice-versa*, irrespective of the length (and photoperiod condition) of the previous phases; and these changes in duration of stem elongation translated into changes in the number of fertile florets (Fig. 2a) through parallel changes in spike dry matter at anthesis (Miralles et al. 2000). In the field study, plants of different degrees of sensitivity to photoperiod x vernalization were grown under natural photoperiod until the onset of stem elongation, and from then to anthesis either maintained in that condition or exposed to a longer photoperiod in the field. Focusing on the cultivar that was insensitive to vernalization (to avoid the interaction here), there was a clear change in duration of the stem elongation phase due to exposure to different photoperiods during the stem elongation phase, and this change resulted in changes in number of fertile florets (Fig. 2b); once again mediated through changes in spike dry weight at anthesis (González et al. 2003a).

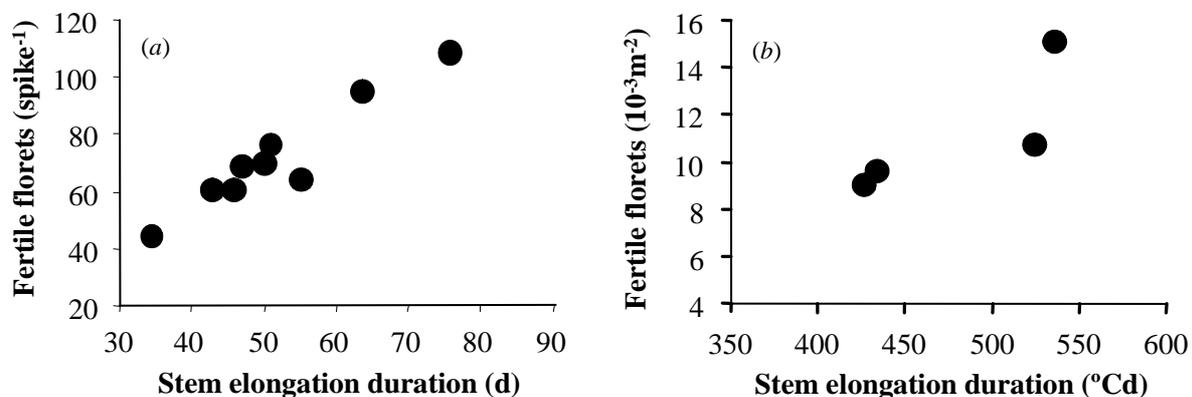


Figure 2. Number of fertile florets in response to changes in duration of stem elongation (in degree days, °Cd) in wheat independently of changes in previous phases as a consequence of exposure to different photoperiods only during the stem elongation phase in controlled (a) and field conditions (b). Data taken (a) or adapted (b) from Miralles et al. (2000) and González et al. (2003a), respectively. For details see text.

Synchrony in the emergence of silks within ears of maize as an alternative to improve its potential grain yield

Yield potential improvement in maize: controversies and needs.

From recent publications that included the analysis of trends in maize yield potential (Tollenaar and Lee 2002; Cassman et al. 2003) it can be concluded that there has been no real improvement in this trait during the last 30 years, because on-farm grain yields as high as 19.7 Mg ha⁻¹ have been reported as early as in the 1970s. Neither recent grain yield contests for irrigated systems (Cassman et al. 2003) nor results from small-plot trials (Otegui et al. 1996) indicate an improvement in yield potential with respect to the 1970's records, which are close to the estimate of 25 Mg ha⁻¹ computed by Tollenaar (1983) for the conditions of central North America. On the other hand, results from breeding studies indicate a sustained genetic gain in average on-farm grain yields, with no clear signs of having reached a plateau (Slafer and Otegui 2000). In other words, this contrast in trends between potential and actual maize grain yields is clear evidence of the main objective pursued by breeders during the recent decades and the approach they used for successfully achieving it: search for improved stress tolerance in order to obtain improved grain yield stability, based on a large number of testing sites that included those currently encountered by most commercial maize crops in a given region (Tollenaar and Lee 2002). This strategy is still successful because most average on-farm grain yields are yet far from the potential, especially in the developing world. Problems related to lack of improvement in grain yield potential could be expected in some

irrigated systems, like those already quoted for some US corn-belt farmers (Cassman et al. 2003) or maize production in some high-yielding Mediterranean environments (e.g., Chile).

5.2 Grain yield and reproductive development in maize

One aspect has been consistent from most studies on grain yield improvement in maize: grain yield increases have been mostly related to an improved number of harvestable kernels per unit land area, indicative of a predominant sink limitation to crop yield (Borrás et al 2004). This fact led to increased attention to attributes that control final kernel number. The main features of reproductive differentiation in maize have been thoroughly studied (Bonnett 1966), both for the apical meristem that gives place to the tassel (botanically a panicle) responsible for pollen production, and for the axillary buds that produce the ears (modified spikes), which bear the grains. This diclinous monoecious characteristic of the species is the trait that most strongly conditions its reproductive success, because harvestable organs (i.e., the ears) start differentiation and growth after the tassels do, and remain under the dominance of the male structure until pollen is shed. Any growth restriction, therefore, will have a larger negative effect on the progress of the ears than on the evolution of the tassels.

Under stress conditions, silk emergence is delayed relative to pollen shed, which can result in lack of pollen for late-appearing silks on apical ears, reduced silk emergence from sub-apical ears, failure in ovary fertilization, and ultimately, reduced kernel set (for more on this topic refer to Otegui and Andrade 2000, and Westgate et al. 2004). Moreover, this unfavorable reproductive pattern is not offset by other phenotypic traits that usually add plasticity to a species adaptation to the environment, like tillering or branching. Commercial maize vegetative phenotype can be described as very *rigid* in this aspect. Consequently, close synchrony between pollen shed (i.e., anthesis) and silk emergence (i.e., silking, when the first silks emerge from the husks) is required for high kernel set in maize (Bolaños and Edmeades 1993), and a negative relationship exists between final kernel number and the extent of the anthesis-silking interval ($ASI = \text{date of silking} - \text{date of anthesis}$). Hall et al. (1982) hypothesized that the lack of pollen for late-appearing silks was among the causes of kernel number reduction under water stress conditions in maize, but their own results and subsequent research on kernel number determination demonstrated that kernel abortion still occurred when fresh pollen was added to late-exposed silks (Otegui et al. 1995). Therefore, factors other than greater pollen availability must be involved in improving final kernel number in response to a shorter ASI.

Under natural conditions, the delay in silk growth among ovaries along the ear, together with the position-dependent length the silk must attain to emerge (Bonnett 1966; Cárcova et al. 2003), determines a time lag between the first-appearing silks (from the lower half of the inflorescence) and the late-appearing ones (from the tip of it). This feature, together with the male-female asynchrony described above, results in pollination asynchrony among ovaries along the ear, and the natural embryo abortion of those ovaries located at the tip of the ear usually observed in most maize crops. The rate of kernel abortion is strongly dependent on plant growth rate around silking (Andrade et al. 1999, 2002), and this abortion can be partially overcome by increasing assimilate supply of plants during this critical period. Nevertheless, evidence indicates that assimilate availability per fertile floret seems not to be the only factor controlling kernel set when water and nutrients are not limiting growth. It is well known that kernel set in the subapical ear depends on synchronous silking and pollination of both ear shoots. Considering pollination synchrony within the ear, a significant reduction in kernel set has been observed when the pollination interval between early- and late-appearing silks in the apical ear was artificially increased (Cárcova and Otegui 2001). On the other hand, maize kernel set can be improved significantly (8–31%) through synchronous hand pollination, both between ears at low plant population and within the apical ear at high stand densities (Cárcova et al. 2000). The benefits of synchronous pollination on final kernel set have been thoroughly assessed (Cárcova 2003), with studies including several hybrids (two Americans and two Argentines, and among the latter their normal and male-sterile versions), environments (cool-temperate at 48°N in MN, USA, and temperate at 34°S in Argentina and for the latter, in four growing seasons), and plant populations (from almost isolated plants at 3 plants m⁻² to a high density of 9 plants m⁻²). On the other hand, uncertainty remains with respect to the translation of this increment in kernel number to an increase in grain yield. A thorough analysis of seed weight response to the post-flowering source-sink ratio in different species (Borrás et al. 2004) showed that maize kernel weight is particularly sensitive to reductions in this ratio. In other words, a further increase in the numbers of kernels in this crop will turn into an improved grain yield only if it is accompanied by an enhanced production of biomass after

flowering. Up to present, improvements in post-silking biomass have been possible because of selection for enhanced green leaf area persistence (*stay-green*), a trait strongly related to grain yield in maize (Russell 1991; Duvick 1992) and in other source-responsive crops like sunflower (de la Vega and Hall 2002).

Promising traits to be considered when breeding for improved pollination synchrony among ovaries within the ear

Improved kernel set obtained with artificially forced synchrony in pollination timing, suggested that the rates of silk emergence and pollination might explain part of the genotypic differences observed in final kernel number. Thus, a better knowledge of the pattern of ear development and growth would help identify traits that integrate the effects of several basic processes related to kernel set. Lafitte and Edmeades (1995) observed that selection for improved performance under water or N stress brought about a reduction in the number of florets along the ear (i.e., shorter ears) and an increased biomass per floret, which apparently promoted greater kernel number per ear (i.e., increased kernel set) and prolificacy. They postulated that, because final kernel number per plant is always smaller than the potential number of fertile florets per ear (i.e., kernel set <1) in most maize crops, breeding for synchronous pollination should be focused on the selection of short ears, which usually exhibit synchronous exposure of most silks in a short period of time. They hypothesized that this trend, however, can not be extended indefinitely, due to eventual yield restrictions under favorable growing conditions. In these circumstances, prolificacy could not compensate for the reduced potential kernel number attainable with the apical ear (Andrade et al. 1999). An analysis of the evolution of potential ear size (i.e., spikelets per ear) performed on widely used commercial hybrids representative of different breeding eras in Argentina, revealed exactly the opposite trend to that suggested by Lafitte and Edmeades (1995) (Table 1). Grain yield improvement for this environment has been related to increased kernel number (Luque 2000), and this trend has been matched by an increase in potential ear size (Matthiess et al. 1999; Luque 2000), both in the number of spikelets per ear row and in the number of spikelet rows per ear. We hypothesized that the increased number of spikelet rows determines a large number of silks exposed synchronously in a few days after silking of each plant, and that the enhanced number of florets along the ear gives the genotype a better chance for increasing kernel number in good years than the alternative, an increase in prolificacy (Table 1).

Recently, Cárcova et al (2003) studied in detail the female developmental characteristics of two hybrids with very contrasting ear types, the short-eared DEA from France and the long-eared DK696 from Argentina. They observed that these hybrids had similar trends with respect to (i) the proportion of final ear size reached at silking, (ii) the dynamics of spikelet and silk initiation, and (iii) the pattern of silk elongation, which was similar among ovaries along the ear but acropetally delayed in time. Genotypes, however, displayed a different rate of ear and silk elongation, and convergence in silking among spikelets along the ear was attained (i) by synchronous silk initiation along the ear and a similar pattern of silk elongation among florets in the short-eared DEA, or (ii) by an increased silk elongation rate from the base to the tip of the ear in the large-eared DK696. The former is a development-based response pattern while the latter is a growth-related one, and consequently maybe more dependent on environmental conditions that control growth (e.g. water, light). Future studies should determine if synchronous silk initiation is always related to short ears or can be selected independently of ear size.

Table 1. Reproductive traits of a set of hybrids released at different eras in Argentina (adapted from Matthiess et al. 1999).

Stand Density	Hybrid	Year of release	Silked ears per plant	Florets per ear	Kernel rows per ear	Florets per kernel row	Grained ears per plant	Kernels per plant
3 plants m ⁻²	DKF880	1965	1.90 a*	636 c	14 c	44 b	1.60 b	660 c
	M400	1978	1.65 b	678 c	14 c	47 b	1.45 b	718 c
	DK752	1993	2.00 a	973 a	19 a	51 a	1.85 ab	954 a
	DK757	1997	2.00 a	1012 a	20 a	51 a	1.50 b	925 ab
9 plants m ⁻²	DKF880	1965	1.35 b	543 d	14 c	38 c	0.90 a	339 e
	M400	1978	1.30 b	609 c	14 c	44 b	1.00 a	450 d
	DK752	1993	1.81 a	949 a	19 a	51 a	1.00 a	690 b
	DK757	1997	1.90 a	972 a	20 a	51 a	1.05 a	743 a

* Different letters within a column and stand density indicate significant differences ($P < 0.05$) among hybrids.

Finally, studies performed by Luque (2000) gave some clues of the degree of genotypic variability for traits related to ear growth and development. For a set of seven hybrids, that included among others those described in Table 1, and stand densities between 3 and 18 plants m⁻², he determined that (i) short ears do not necessarily confer improved biomass per floret, because there is variability for biomass partitioning to the ear, and (ii) improved kernel number obtained with new, large-eared hybrids, is not always related to an improved ASI. Apparently, the increased number of silks exposed soon after silking from large ears could compensate, at least partially, the negative effect on kernel set of a longer ASI. In his study, final kernel set was modulated by the ASI, the potential ear size (i.e., spikelets per ear) and the biomass achieved per floret. All these traits varied among genotypes, and no constant link was detected among them.

Concluding remarks

For most grain crops, grain yield improvement during the last few decades has been mainly related to increases in grain yield potential, associated with an enhanced number of harvestable grains, and in the use of agrochemical inputs. It seems likely that future increases in actual yields would depend more strongly upon further improvements in yield potential, due to the global demand for the adoption of more sustainable agricultural practices. In many species, but particularly in small-seeded cereals, past genetic gains in yield potential were largely achieved by a reduction in plant height that reduced the competition for assimilates between the spike and the growing internodes soon before anthesis. In maize, this trend was accompanied by a reduction in the anthesis-silking interval, evidence of a decline in apical dominance obtained through the selection for small tassels and the concomitant enhanced biomass partitioning to the ear. These traits (i.e. reduction in plant height and tassel size), together with improved agronomic practices like selecting the best sowing date for an optimum setting of the critical period in relation to the growing conditions of each environment, have been currently exploited to their maximum in most cropping systems, and seem no longer useful for further increasing potential and actual grain yields. Consequently, future gains in grain yield appear to depend upon a more detailed knowledge of the responses of each species to the environment and a precise description of the genotypic variability in promising traits like those analyzed in this work (i.e., a fine-tuned phenotyping for developmental attributes), which are particularly attractive because they seem of value for any cropping system (e.g. irrigated or rainfed). These promising traits must be, sooner or later, unquestionably related to increases in biomass. For instance, the hypothesis of improving the number of grains in wheat through lengthening of the stem elongation phase would concomitantly increase the growth accumulated in that phase, when both the canopy and root growths are at their maximum rates.

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