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REVIEW PAPER

Maize reproductive development and kernel set under limited plant growth environments

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Abstract

Maize grain yield is highly related to the number of kernels that are established during the flowering period. Kernel number depends on the accumulation of ear biomass and the efficiency of using this biomass for kernel set. Ear biomass depends on the rate of plant biomass accumulation and the proportion of this biomass that is allocated to the ear. In contrast to other major crops, the proportion of plant biomass that is allocated to the ear is not constant in maize, being almost zero under stress conditions. Fortunately, there is wide native genetic variability for this trait, with major practical implications for crop management and plant breeding. Conditions that inhibit plant growth commonly delay silk appearance relative to male anthesis. Time to silking and silk extrusion, which is a tissue expansion process, is dependent on water turgor and ear biomass accumulation, and the magnitude of this delay is used as a marker to phenotype for stress susceptibility. Ear biomass accumulation can also be used for predicting the number of silks that have been extruded if genotype-specific parameters are known. Here, several mechanistic plant and canopy traits are described, together with their implications for better understanding maize yield determination under limited plant growth environments. An ideal genotype sustains growth in environments with limited water or nutrients, has uniform canopies, has increased biomass partitioning to the ear at reduced plant growth, reaches silking with minimum ear biomass, and has rapid silk extrusion for minimizing developmental delays between competing structures within the ear. All these traits help maximize kernel set and yield at limited plant growth, and most have been indirectly selected by breeders when increasing yield.

Keywords: Breeding, crop yield, kernel number, maize, reproductive development, silk number.

General framework to understand kernel set in maize

Yield in major field crops is determined by the harvested kernel number per unit land area and average kernel weight. Both traits vary across genotypes and environments in maize, but kernel number is responsible for most yield variation (Early *et al.*, 1967; Otegui, 1995; Chapman and Edmeades, 1999). Understanding and predicting the number of kernels per plant or per unit land area is critical for guiding maize breeding and crop management for yield improvement.

Kernel number has traditionally been described as a function of biomass accumulation at the reproductive structure bearing kernels and the reproductive efficiency by which this biomass is used for setting the kernels (Fischer, 1985). Charles-Edwards (1984) generated a mechanistic model for

describing genotype and environmental effects over kernel number within this framework:

$$KN = (CGR \times PR) / AG \quad (1)$$

where KN is the number of kernels set per unit land area, CGR is the crop growth rate around the period when kernel number is determined (for maize ~15 d pre-anthesis to 15 d post-anthesis; Fischer and Palmer, 1984; Otegui and Bonhomme, 1998; Andrade *et al.*, 1999), PR is the proportion of crop growth that is partitioned to reproductive organs during this period, and AG is the minimum assimilate flux required by an individual flower primordium to continue development and establish a kernel. Because of the difficulty in measuring AG, its inverse (kernel set efficiency, EG) is commonly used (Vega *et al.*, 2001). Kernel set efficiency is estimated as the number of kernels set per unit of accumulated reproductive biomass during kernel set (Vega *et al.*, 2001; Slafer *et al.*, 2015). The model described in Eq. 1 helped consolidate the concept that harvested kernel number depends on the biomass accumulated at the reproductive structure bearing kernels during the flowering period, and on the efficiency of plants for using this biomass for setting kernels not only in maize but in other crops as well (Fischer, 1985; Van Oosterom and Hammer, 2008; Rotundo *et al.*, 2009).

The proportion of plant growth that is partitioned to maize ear during flowering (PR, Eq. 1) presents large genotypic differences, affecting ear growth for similar plant growth. This genetic variability is evident when comparing older *vs* newer genotypes (Echarte *et al.*, 2004), when studying hybrids with contrasting stand density responses (Hernández *et al.*, 2014), and when using recombinant inbred line (RIL) populations (Messina *et al.*, 2011; Amelong *et al.*, 2015). Maize genotypes also show ample genetic variability in CGR during the flowering period (Luque *et al.*, 2006; Hernández *et al.*, 2014; Amelong *et al.*, 2015) and in kernel set efficiency per unit accumulated ear biomass (Echarte *et al.*, 2004; D'Andrea *et al.*, 2008).

Similar kernel number can be attained by optimizing different trait combinations, especially when considering that all traits show ample genetic diversity in maize. Figure 1 shows how traits described in Eq. 1 correlate with kernel number for a set of current commercial maize genotypes from Argentina (redrawn from Tamagno *et al.*, 2015 by using 24 dented GMO hybrids; Fig. 1A) and for a set of RILs developed from the B73 × Mo17 cross (Fig. 1B, from Amelong *et al.*, 2015). For the commercial genotypes described in Fig. 1A, higher kernel numbers were related to higher seed set efficiency, with almost no correlation with PGR or PR. Contrarily, for the RIL population higher kernel numbers were correlated with higher PR, and mostly not correlated with PGR or EG (Fig. 1B). Evidently, there is a need to understand the specific trait from Eq. 1 that helps explain genotypic differences in kernel number for the available germplasm. Because all traits show considerable genetic diversity, different combinations can explain differences in harvested kernel number.

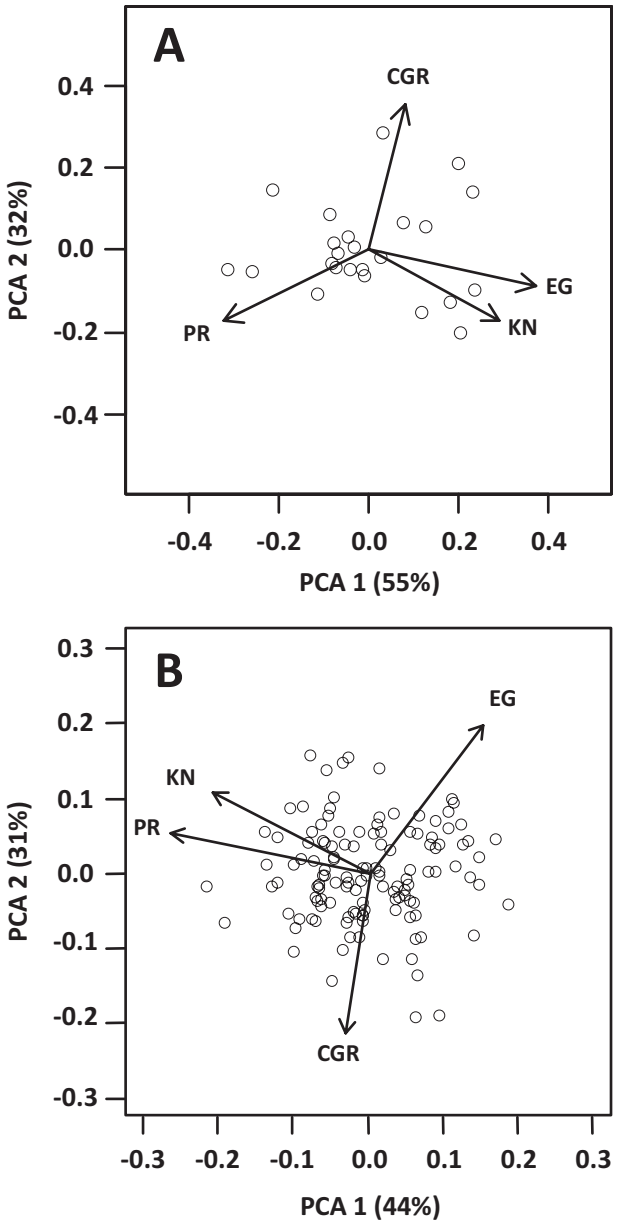

Fig. 1. Biplot describing genotype arrangements for harvested kernel number per square meter (KN), crop growth rate around flowering (CGR), biomass partitioning to the reproductive structure (PR) and kernel set efficiency per unit of accumulated ear biomass during flowering (EG) for 24 commercial genotypes grown under two environments (A) and 125 RILs from the IBM Syn4 (B73 × Mo17) population also grown under two environments (B). Data for (A) were re-analysed from Tamagno *et al.* (2015) using only dented GMO genotypes, and for (B) were re-analysed from Amelong *et al.* (2015).

Physiological determinants of contrasting genotypic responses at limited plant growth environments

Models of maize yield response to stress

In maize there is substantial native genetic variation in tolerance to abiotic stress generating reductions in plant growth. The studies by Duvick *et al.* (2004) have described no yield changes with breeding for yield improvement when considering isolated plants (no stress, large plant growth), but

large differences in crop yield when plants are grown under high stand densities (a stressful environment, reduced plant growth). This is also evident when comparing current commercial genotypes grown at contrasting stand densities. For genotype yield, differences are minimal at low stand densities while very large at high stand densities, where plant-to-plant competition for resources is high (Hernández *et al.*, 2014).

Three different hypotheses can explain genotypic differential plant yield reductions under reduced plant growth resulting from increased stand density or reduced water availability (Fig. 2A). These hypotheses consider the relationship between plant growth (PGR) and biomass partitioning (PR) to the reproductive structure bearing kernels during the flowering period. Although it is clear from Fig. 1 that differences in kernel set efficiency (EG) do play a significant role, here we will focus on kernel set differences due to PGR or PR.

The first hypothesis, and most obvious, assumes a genotype that reduces plant growth under stressful situations more than others (Fig. 2B). This can be related to reduced radiation use efficiency (Tollenaar and Aguilera, 1992; Lindquist *et al.*, 2005) or reduced water use efficiency (Reyes *et al.*, 2015).

The second hypothesis, also commonly recognized and referenced, is related to genotypic differences in plant biomass partitioning during flowering (Fig. 2C). This is usually described when comparing new *vs* old genotypes. In maize the reproductive structure where kernels are set is an axillary ear, located at the middle of the plant. This structure is not a dominant one, and has poor biomass allocation at reduced plant growth. Whenever plant growth is reduced by limited water or nutrients, ear growth is reduced not only because the entire plant is accumulating less biomass, but also because the proportion of the total biomass that is effectively allocated at the ear level is further reduced. Data from Andrade *et al.* (1999) showed that the proportion of plant growth that was allocated to the ear in a particular commercial hybrid was about one-sixth when plants grew more than 3 g per plant per day during the flowering period, but was reduced to 1/18 at growth values of 2 g per plant per day and reached zero at plant growth values lower than 1 g per plant per day. This non-constant biomass partitioning to the ear during the seed set period is unique to maize, as other crops, such as wheat, sorghum, and soybean, show

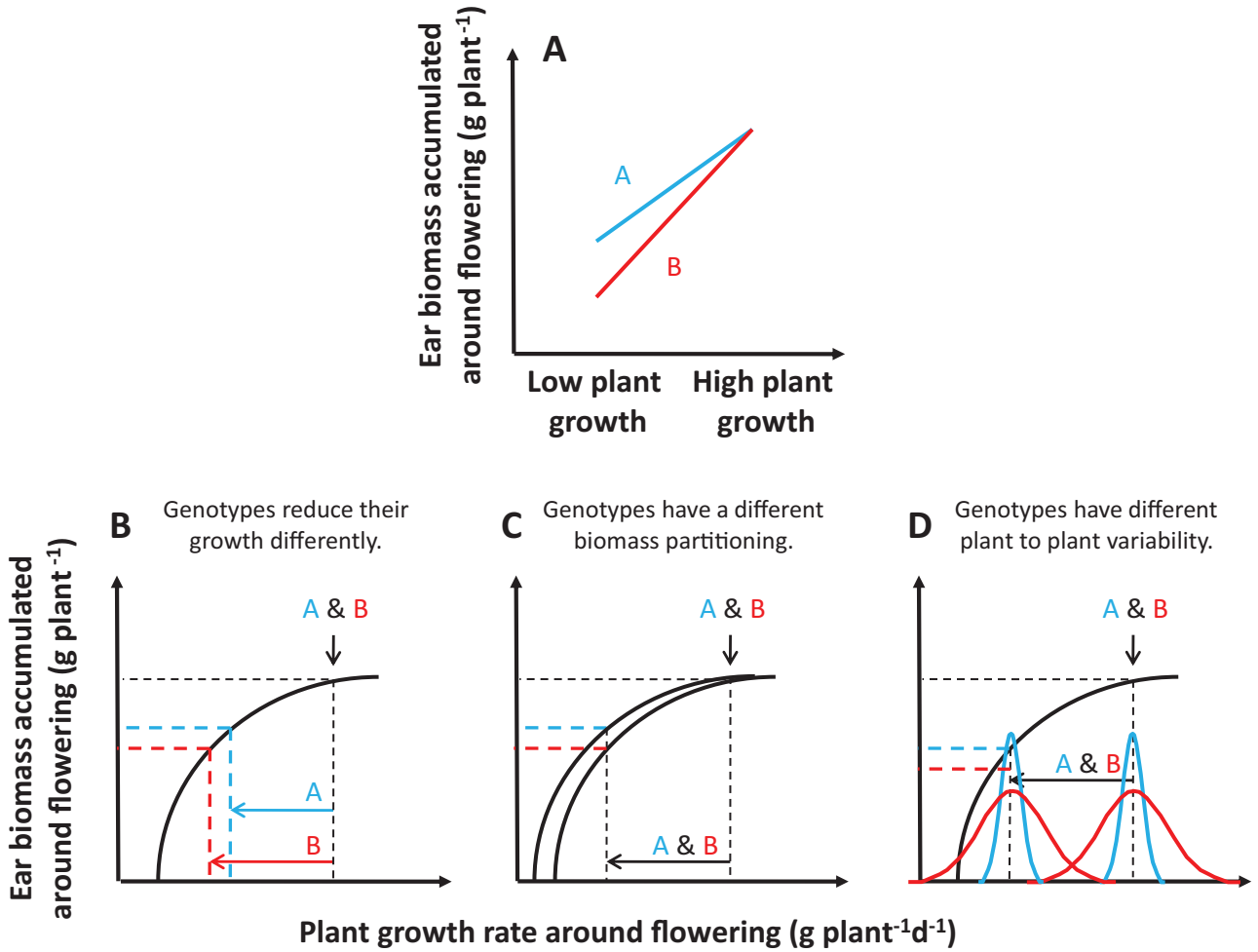

Fig. 2. Description of possible genotypic differences in ear biomass accumulation per plant response to reductions in plant growth rate during the flowering period. Genotype A represents a plant with lower ear biomass accumulation reductions whenever plant growth is reduced when compared with genotype B under stressful environments that limit plant growth (A). (B–D) Three possible mechanisms explaining the contrasting stress tolerance of these hypothetical genotypes. In the first case one genotype reduces its growth more than the other (B), in the second case genotypes differ in how plant biomass is partitioned to the ear (C), and in the third case genotypes differ in their plant-to-plant variability (D). (This figure is available in color at *JXB* online.)

relatively constant values (Miralles and Slafer, 1998; Van Oosterom and Hammer, 2008; Rotundo *et al.*, 2009).

Hormonal plant growth regulators affecting plant biomass distribution (Cicchino *et al.*, 2013) or male sterility genes affecting tassel growth (Loussaert *et al.*, 2017) can also be effective in reducing competition between developing reproductive organs and improving ear growth and kernel set under limited plant growth environments (Fig. 2C).

A third, and rarely considered, hypothesis is related to genotypic differences in plant-to-plant variability (Fig. 2D). The non-constant curvilinear nature of maize plant biomass allocation at the ear level during flowering has important consequences, especially when coupled with the normally observed plant-to-plant growth differences within canopies.

Implication of plant-to-plant variability in coping with conditions of limited plant growth

The first evident effect of reduced availability of water or any other nutrient is reduced canopy growth. Plant growth is an integrative response, and is commonly well captured by crop simulation models through its effect on canopy leaf expansion and light capture, or water capture and use. The framework depicted in Eq. 1 has been helpful for understanding large genotypic and environmental differences in grain yield. Evidence has shown that changes in biomass partitioning to the ear, plant growth rate, and kernel set efficiency have been critical for yield improvements (Echarte *et al.*, 2004; Campos *et al.*, 2004; Luque *et al.*, 2006). However, there is a need to realize that maize canopies are intrinsically composed of plants having different growth rates. This concept is useful for further understanding maize kernel number and yield changes across environments.

Plants within canopies have different growth rates, and commercial maize genotypes have a plant-to-plant growth variability that is not minor. Individual plants within canopies grow at different rates, and this variability is driven by genetic, environmental, management, and possible interaction effects (Rossini *et al.*, 2011). Plants within canopies respond to their neighbors, and this response has a genetic component in maize and other crops (Maddonni *et al.*, 2002; Crepy and Casal, 2015; Lopez Pereyra *et al.*, 2017). Common plant-to-plant growth variability around the flowering period for a maize commercial stand is around 20–35%, and differs when commercial genotypes are compared (Hernández *et al.*, 2014). At stressful growing conditions average plant growth is reduced, and plant-to-plant variability increases, making canopies even less uniform (Glenn and Daynard, 1974; Maddonni and Otegui, 2004; Rossini *et al.*, 2011). The relative growth difference between dominant and dominated plants within canopies increases under stressful situations.

Stand uniformity has very different effects depending on the growth environment, especially in a crop where the proportion of plant biomass that is allocated at the structure bearing the kernels is not constant. The nature of the non-constant curvilinear relationship between ear biomass accumulation and plant growth around flowering has important consequences. At high plant growth the penalty for having non-uniform canopies is minor when compared with the evident effect in reduced growth environments. In Fig. 2D the blue and red parabolas represent genotypes with different individual plant-to-plant growth variability but a similar average plant growth. In low plant growth environments, non-uniform canopies tend to have a large proportion of barren plants when compared with more uniform ones. And yield reductions in dominated barren plants are never fully compensated by dominant plants having above average growth. Ford and Hicks (1992) and Tollenaar and Wu (1999) showed that the yield penalty for having non-uniform canopies is larger at high stand densities, but minimal at lower stand densities where individual plant growth is higher. This concept is not fully captured by Eq. 1.

In brief, plant-to-plant growth variability in maize canopies shows clear genotypic differences (Hernández *et al.*, 2014; Amelong *et al.*, 2015), and can also help explain genotype × environment interactions for kernel number. This hypothesis is almost never considered when describing genotypic differences in abiotic stress tolerance, and common crop growth models do not have any description of within-canopy variability.

Indirect breeding effects on reproductive attributes leading to increased abiotic stress tolerance

Ear growth and the anthesis–silking interval

Pollination in maize occurs when airborne pollen shed by the staminate florets on the tassel is captured by the stigmatic tissue (silks) of pistillate florets located at the ear. Because the durations of pollen shed and silk receptivity are limited, close synchrony between tassel and ear development is required for optimum kernel set in maize crops.

Time to anthesis is determined by developmental mechanisms governed by genotype, temperature, and photoperiod response effects, and not affected by plant growth (Yao *et al.*, 1991). Ultimately, maize time to anthesis depends on differentiated leaf number in the apical plant meristem and phylocron. Contrary to this, time to silk appearance is strongly dependent on plant growth, and is a function of ear biomass accumulation (Borrás *et al.*, 2007). Environmental conditions that reduce plant growth, such as drought or low nitrogen availability, delay silk emergence relative to pollen shed (protandry) and generally decrease kernel number per ear (Herrero and Johnson, 1981; Hall *et al.*, 1981; Edmeades *et al.*, 1993). Drought stress environments have shown to reduce the number of pollen grains per tassel but not pollen viability (Herrero and Johnson, 1981; Hall *et al.*, 1981). However, they do reduce silk receptivity (Bassetti and Westgate, 1993).

Silking at the individual plant level depends on the specific timing when an ear reaches a critical biomass. At the canopy level, however, the proportion of plants reaching silking will depend on the time that the different fractions of plants within the canopy reach this minimum ear biomass. Because canopies are composed of plants growing at different rates,

each canopy fraction will reach silking differently, the fastest growing plants being the earliest ones (Borrás *et al.*, 2007; Pagano *et al.*, 2007). The timing of plant-to-plant first silk appearance in a maize stand is never normally distributed, even though plant-to-plant growth during flowering is commonly normally distributed (Borrás *et al.*, 2009). This is because the proportion of plant growth that is partitioned to the ear is not constant, but lower at reduced plant growth.

The anthesis to silking interval (ASI) has received considerable attention by maize breeders and physiologists. It is a simple visual observation that correlates with kernel number determination and yield in stressful conditions (Bolaños and Edmeades, 1993; Edmeades *et al.*, 1993; Campos *et al.*, 2004). Kernel set and the capacity for an ear to reach silking are both a consequence of adequate assimilate supply and expansion growth at the ear level (Oury *et al.*, 2016*a*). The earliest studies describing negative correlations between ASI and yield in stressful situations identified lack of pollen for late appearing silks as the cause of reduced kernel numbers (Hall *et al.*, 1981). The concept that silk receptivity is reduced under water stress also helped in concluding that inadequate pollen and silking synchrony are major determinants of reduced kernel set. Consequently, authors hypothesized about the benefits of including a proportion of plants from a different genotype (i.e. a mix or blend of hybrids) of longer cycle for obtaining adequate pollination. However, later studies adding fresh pollen to late appearing silks showed pollen density and inadequate synchrony were not the main limitation (Otegui *et al.*, 1995). Inadequate assimilate supply for supporting embryo development emerged as a major cause of reduced kernel set under these environments (Zinselmeier *et al.*, 1995; Schussler and Westgate, 1995; Andrade *et al.*, 1999). As a consequence of the difficulty in separating water transport and energy flux (Fricke, 2017), assimilate supply and tissue water status are both currently considered limiting factors for silk appearance, flower development, and kernel set (Oury *et al.*, 2016*a*,*b*).

In brief, differences in ASI due to genotypes or environmental conditions around the flowering period are a direct consequence of PGR or PR differences (Borrás *et al.*, 2009), both affecting ear biomass accumulation.

Ear growth and silk number

Silk appearance has traditionally been described as a function of time (Bassetti and Westgate, 1993, 1994; Cárcova *et al.*, 2000; Cárcova *et al.*, 2003). However, a recent alternative

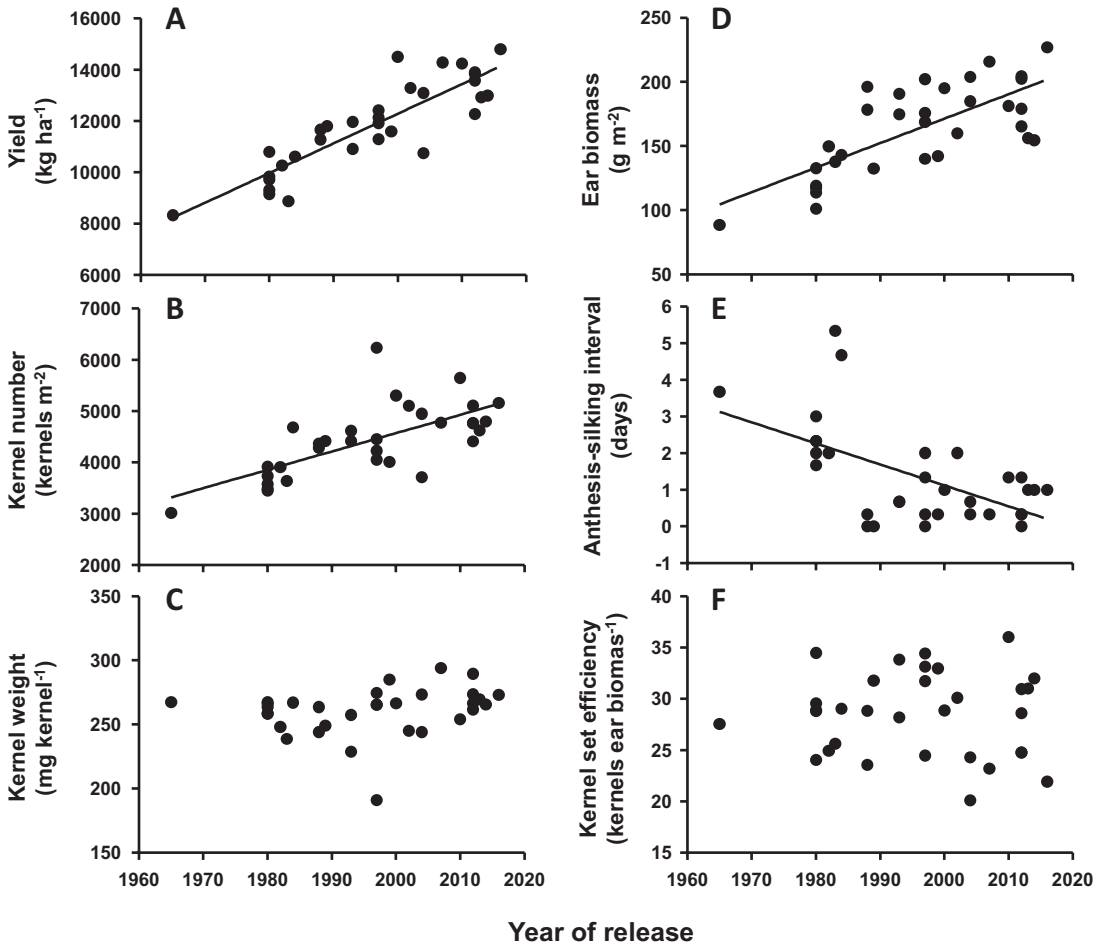

Fig. 3. Description of yield (A), kernel number per plant (B), individual kernel weight (C), ear biomass at 14 days after 50% anthesis (D), anthesis to silking interval (E), and kernel number per unit of accumulated ear biomass during flowering (E) for a set of 32 genotypes released in Argentina from 1965 to 2016 by Dekalb. All genotypes were grown at a uniform stand density of 10 plants m^{-2}, and the average of three randomized field repetitions is presented. Additional information is available as Supplementary Table S1.

describes not only time to silking but also silk appearance rate as a function of ear biomass accumulation. Cooper *et al.* (2014) introduced the concept that each genotype has a unique relationship between ear biomass accumulation and silk appearance, and that this relationship differs when comparing drought-tolerant *vs* susceptible genotypes. The drought-tolerant genotype needed less ear biomass to reach silking than the susceptible one, and also had more rapid silk appearance per unit of accumulated ear biomass.

We tested this concept by describing genotypic differences in the relationship between ear biomass and silk appearance using commercial hybrids released to the Argentinean market from 1965 to 2016 by the Dekalb-Monsanto breeding program. Previous evidence showed that yield increases in Argentina improved both the rate of ear biomass accumulation around flowering and kernel set efficiency (Echarte *et al.*, 2004; Luque *et al.*, 2006; D'Andrea *et al.*, 2008). We hypothesized that contrasting silk number *vs* ear biomass accumulation patterns could help explain breeding changes in ASI mediated by variations in the minimum ear biomass to reach silking.

Figure 3 describes changes in yield and other relevant traits for 32 genotypes released from 1965 to 2016 grown at a high stand density. A high stand density was specifically used for testing genotypes in conditions of limited individual plant growth. Yield increased at a rate of 113 kg ha^{-1} year^{-1}, and this increase was related to kernel number increases and not kernel weight changes. Ear biomass accumulation during

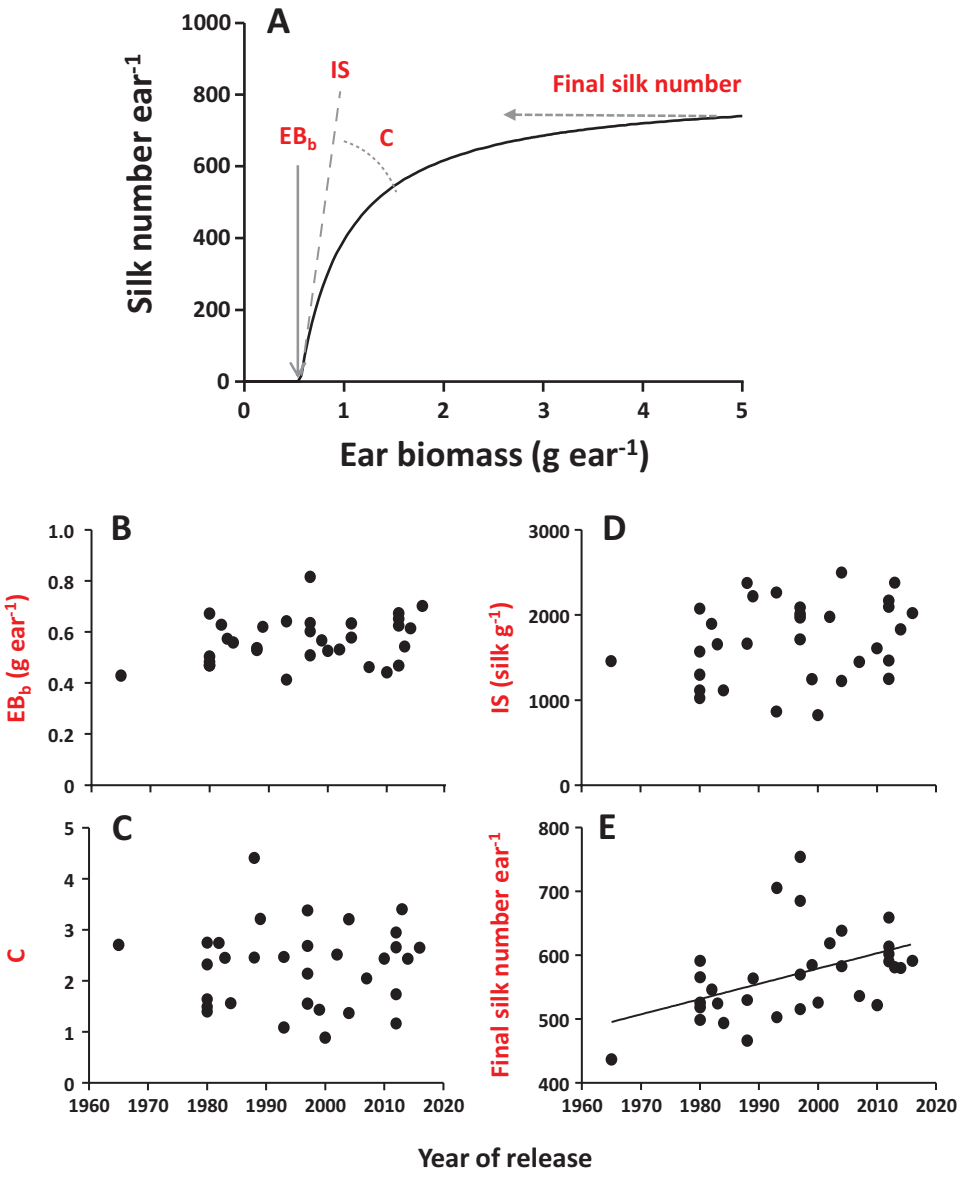

Fig. 4. Conceptual framework describing silk appearance as a function of ear biomass accumulation (A), and how the different traits describing this relationship were indirectly affected by breeding selection for yield from 1965 to 2016 in genotypes released to the Argentinean marked by Dekalb (B–E). (B) Minimum ear biomass for reaching silking (EB_b); (C) curvature (C); (D) initial slope (IS); (E) final silk number per ear. Final silk number is not a parameter determining the curve described in (A) but the combination of different curvatures (C) and initial slopes (IS). The 32 genotypes were grown at a uniform stand density of 10 plants m^{-2}, and samples of silk number and ear biomass were collected around flowering in each genotype replicate. The average of three randomized field repetitions is presented. Additional information is available as Supplementary Table S1. (This figure is available in color at *JXB* online.)

flowering increased, ASI decreased, and kernel set efficiency remained constant (Fig. 3). Except for kernel set efficiency remaining constant and not showing an increase, all traits showed the expected trends (Tollenaar and Wu, 1999; Duvick *et al.*, 2004; Luque *et al.*, 2006).

We sampled ears throughout the flowering period to describe genotypic differences in silk appearance as a function of ear biomass accumulation (Fig. 4). Results showed that breeding selection for yield had minimum effects on function parameters. No specific parameter describing the relationship between silk extrusion and ear biomass accumulation showed any clear trend towards being modified by breeding. Only final silk numbers per ear showed a slight increase with market release year. As such, for this particular germplasm breeding reduced ASI by increasing ear biomass accumulation during the flowering period, and not by affecting the efficiency for extruding silks per unit of ear biomass, as could be expected (Cooper *et al.*, 2014). There was no breeding effect on the minimum ear biomass needed to reach silking, but there was an indirect effect on the time to reach this minimum biomass, evident in modern hybrids having higher biomass accumulation rates than the older ones.

As a consequence of enhanced ear biomass accumulation in modern commercial genotypes, the ASI reduction was accompanied by an increased number of exposed silks at any given time around anthesis. Figure 5 describes the number of silks per plant as a function of the genotype release year from 3 d before anthesis to 5 d after. Modern genotypes reach silking earlier and have more extruded silks at any time point around anthesis. This is a direct consequence of accumulating more ear biomass around the flowering period. Even if the parameters describing silk appearance as a function of ear biomass accumulation presented no changes when breeding is based exclusively on yield (Fig. 4), a faster ear biomass accumulation is enough for generating a faster silk appearance in modern genotypes.

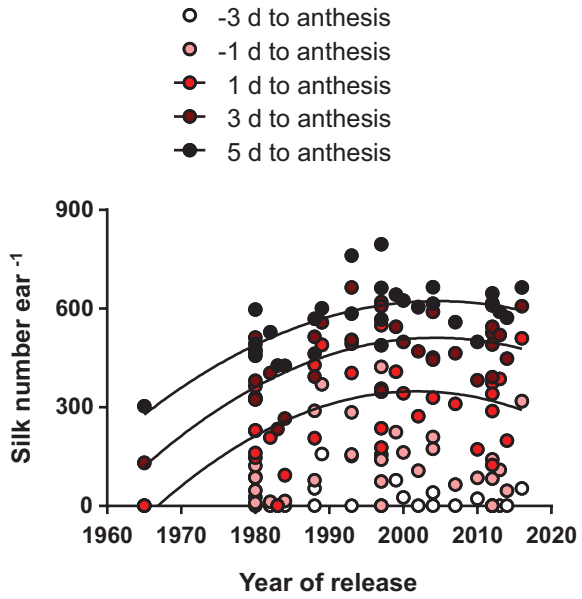

Fig. 5. Number of silks that had appeared per ear for 32 genotypes released to the Argentinean market from 1965 to 2016 at 3 d before anthesis, at 1 d before anthesis, at 1 d after anthesis, at 3 d after anthesis, and at 5 d after anthesis. All genotypes were grown at a uniform stand density of 10 plants m^{-2}, and the average of three randomized field repetitions is presented. Additional information is available as Supplementary Table S1.

Developmental effects over kernel number determination

Kernel number has not only been described as a function of ear biomass accumulation, it has also been linked to specific developmental processes. In maize the timing of silk appearance and pollination follow a sequential pattern depending on the position along the ear (Bassetti and Westgate, 1993; Fuad-Hassan *et al.*, 2008). The basal ones appear first, and silks from the same ear normally extrude during a time period of 4–9 d. Under field conditions silks are pollinated as they appear, so the pollination of the different ovaries from the same ear is distributed in time.

Evidence has shown that the development of younger apical pollinated ovaries can stop as a consequence of competitive interactions with earlier established sinks. The first descriptions of this effect were the studies by Freier *et al.* (1984) and Sarquís *et al.* (1998). Latter, this was directly tested and corroborated

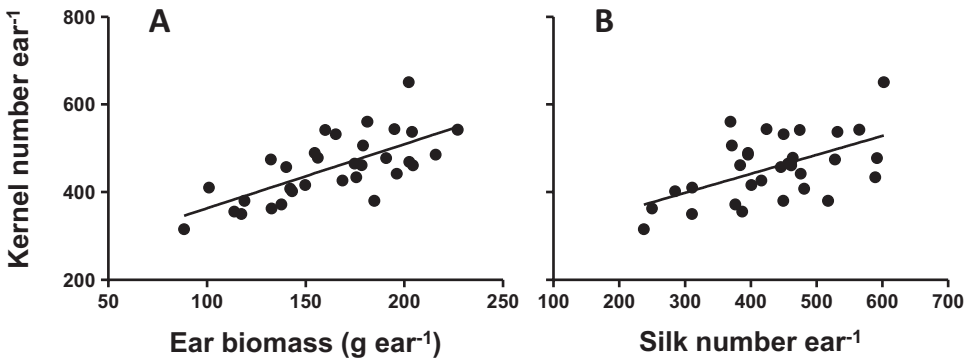

Fig. 6. Kernel number per plant as a function of ear biomass accumulated at 14 d after 50% anthesis (A), and kernel number per plant as a function of number of silks that had appeared at 3 d after the first extruded silk was pollinated (B), for a set of 32 genotypes released to the Argentinean market from 1965 to 2016 by Dekalb. All genotypes were grown at a uniform stand density of 10 plants m^{-2}, and the average of three randomized field repetitions is presented. Additional information is available as Supplementary Table S1.

by Cárcova *et al.* (2000) with synchronous pollination treatments. Briefly, results have shown there is a time window of 2–4 d when competing flowers have a chance to set kernels. After this time window has elapsed, established reproductive structures dominate any later pollinated ovaries, reducing their chances to continue development into viable kernels.

We further tested this concept using the set of genotypes described in Fig. 3. Yield changes after breeding selection has indirectly selected for more kernels, and these kernels are a consequence of more silks exposed per ear during a 3 d time period from first silk appearance (Fig. 6). Modern genotypes have a more synchronous silk appearance, and this is related not to changes in extruded silks per unit of accumulated ear biomass but to more rapid ear biomass accumulation. As such, breeding changes in kernel number can be described as a consequence of more ear biomass accumulation (Fig. 6A) and/or more silks extruded within a specific time period (Fig. 6B). Both traits can be considered relevant ones for cultivar improvement.

Conclusions

An ideal genotype sustains growth in environments with limited water or nutrients, has uniform canopies, has increased biomass partitioning to the ear at reduced plant growth, reaches silking with minimum ear biomass, and has rapid silk extrusion for minimizing developmental delays between competing structures within the ear. All these traits help maximize kernel set and yield at limited plant growth, and most have been indirectly selected by breeders when increasing yield. Studying these traits in elite germplasm will help determine the ones that provide breeding opportunities for further optimization. Stand uniformity in maize crops has received considerably less attention when compared with the other traits, but has important consequences for improving maize yields in environmental conditions that reduce canopy growth.

The anthesis to silking interval is a simple visual marker that helps select for most of these traits, and is the reason why breeders and physiologists have used this trait for describing and selecting genotype susceptibility to drought environments.

Supplementary data

Supplementary data are available at *JXB* online.

Table S1. Description of the 32 genotypes released by Dekalb in Argentina from 1965 to 2016 and tested in the present study (release year, yield, kernel number, kernel weight, ear biomass at 15 d post-anthesis, ASI, kernel set efficiency, EB_b, curvature, initial slope, final silk number, kernel per ear, silks 3 d after initial pollination, silk number at −3, −1, 1, 3, and 5 d after anthesis).

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