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Grain Yield Determination and Resource Use Efficiency in Maize Hybrids Released in Different Decades

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Additional information is available at the end of the chapter

1. Introduction

Maize (Zea mays L.) grain yield have increased during the last decades. A recent review [1] indicated genetic grain yield gains of 74 to 123 kg ha^{-1} year^{-1} for different time periods between 1930 and 2001, in the US corn belt, Argentina and Brazil [2-6]. Current reviews on the physiological processes associated with those yield increments have been focused on US corn belt hybrids and maize hybrids of Ontario, Canada [e.g. 1; 7; 8]. As such, grain yield increments were associated mainly with an increased kernel number, a consistently improved stay green, and a longer period of grain fill. Those reviews agreed on that harvest index (HI; i.e. the relationship between grain yield and final shoot biomass) did not consistently change over time; in contrast, HI of Argentinean maize hybrids have increased during the 1960-1990 period [9; 10]. This review will be focused on the ecophysiological mechanisms contributing to the greater yield in modern than in older maize hybrids; with particular interest in Argentinean maize hybrids because they have shown a distinctive trait change over the years (i.e. HI increment).

Grain yield

Grain yield can be expressed as the product between shoot biomass and harvest index. In Argentina, harvest index was increased while shoot biomass was not consistently increased over the years during the period 1965-1993 [11]. As such, HI increased from 0.41 to 0.52 in maize crops growing under optimal conditions [9]. The increased harvest index was associated mainly to a greater increase in grain yield numerical components (i.e. kernel number and/or kernel weight) than in shoot biomass. On the contrary, shoot biomass has increased while harvest index have remained constant in maize hybrids released in Canada

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and the US in different decades [1; 12]. Most of the shoot biomass accumulation increments in those hybrids, occurred during the grain-filling period [13; 14]; and they were mainly associated with an increased capacity of maintaining higher leaf photosynthetic rate of green leaf area (i.e., functional "stay green") during the grain-filling period [15-17]. The next sections will review the main processes influencing grain yield numerical components determination (i.e. kernel number and kernel weight) and their changes in Argentinean maize hybrids released in different decades. Implications on stress tolerance and resource use efficiency will be also discussed.

Kernel number

Kernel number is the main yield component accounting for grain yield increments over the years [18; 19]. Figure 1 illustrates a conceptual framework of the main processes contributing to kernel number determination in maize.
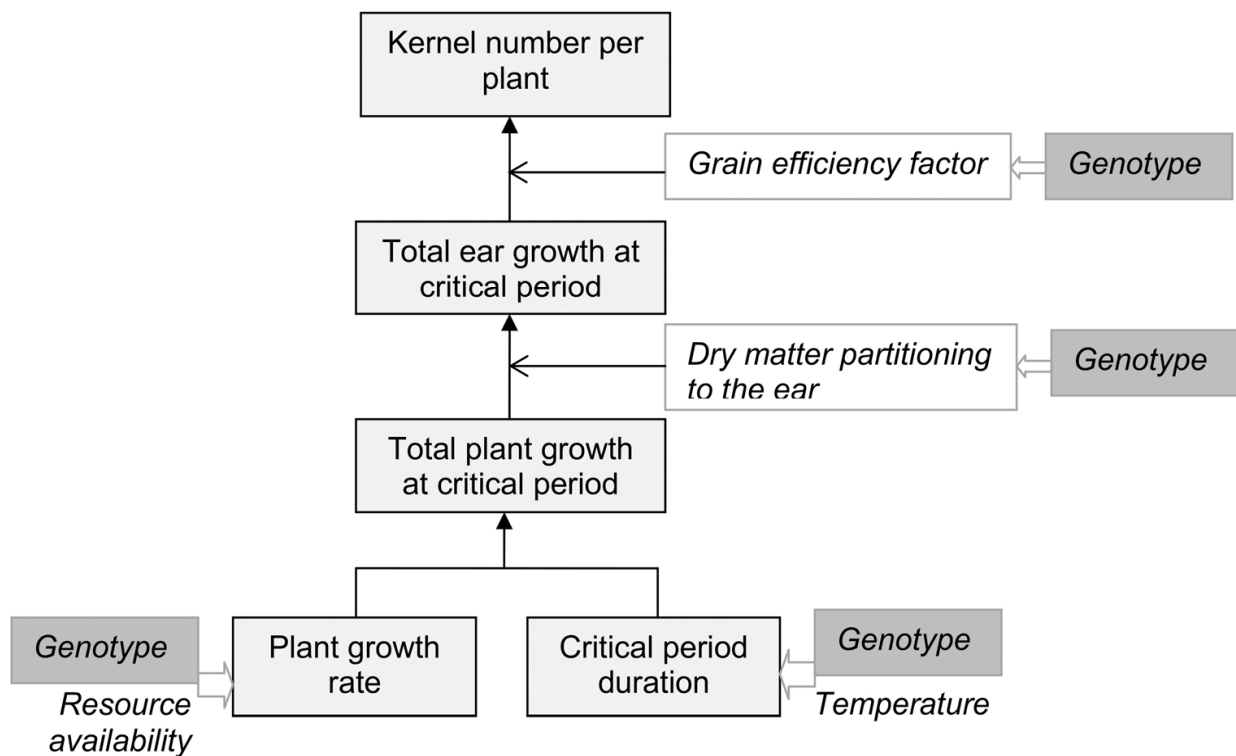

Figure 1. General model for kernel number determination in maize (Adapted from Andrade et al. (20)).

Kernel number per plant is a function of the physiological condition of the crop or plant at a period of 15 days bracketing silking (i.e. critical period for kernel number determination; 21-26) or between -227 and 100°C day from silking [27]. As such, kernel number is a function of photosynthesis at silking [22] and it is closely related with plant growth rate during the critical period for kernel set [18; 28]. The relationship between kernel number per plant (KNP) and plant growth rate during the critical period for kernel set (PGRs) was described by two successive curves to account for the first and second ear in prolific hybrids, or a single curve in non-prolific hybrids [18; 28; 29]. A particular feature of the KNP-PGRs relationship is the significant PGRs threshold for kernel set that results in abrupt reductions

in kernel number at low resource availability per plant [29]; which might reflect a strong apical dominance [24; 30]. Using contrasting plant densities along with individuals instead of plot means provide a wide range of values for PGRs and KNP; and it is possible to obtain more precise estimations of the threshold PGRs for kernel set [28; 29]. Allometric models are fitted to the relationship between shoot biomass and morphometric measurements (i.e. stem diameter, ear length, ear diameter) and are used to estimate the growth during the critical period for kernel set of individuals that remains in the field from sowing to physiological maturity (i.e. individual plant methodology, 29). The regression between estimated shoot biomass using allometric models and the actual shoot biomass of plants before silking is depicted in Figure 2 and it shows an example of the reliability of the individual plant methodology.
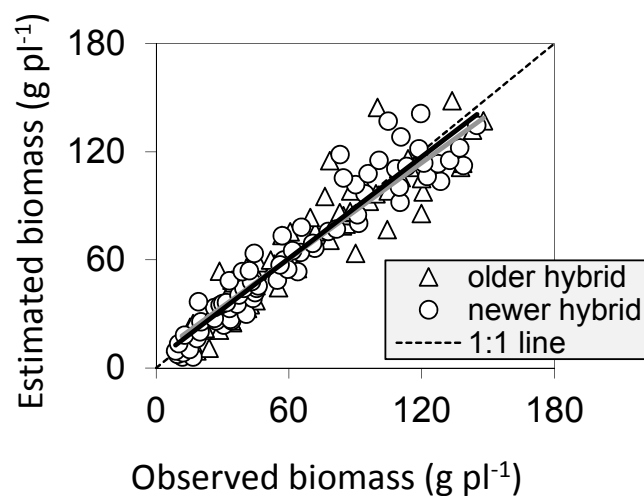

Figure 2. Relationship between estimated and actual shoot biomass at the beginning of the critical period for kernel set, for an older (DKF880) and a newer (DK752) maize hybrid. Shoot biomass was estimated using allometric models. The dotted line shows the 1:1 ratio and the solid lines show the fitted model for the older (gray) and the newer (black) maize hybrids. Fitted linear equations were y = 0.89 x + 7.1, R^2 = 0.87, n=71 for the older hybrid, and y = 0.94 x + 4.2, R^2 = 0.91, n=72 for the newer hybrid (Adapted from Echarte et al. (10)).

A comparison of the KNP-PGRs relationship among 5 Argentinean hybrids released between 1965 and 1993 established that newer hybrids set more kernels per unit PGRs than older hybrids as was indicated by (i) the lower threshold PGRs for kernel set and (ii) the greater potential kernel number at high availability of resources per plant, for newer than for older hybrids (10; Figure 3). Plant growth rate during the critical period for kernel set at each plant density did not show a clear trend with the year of release. The lower threshold PGRs for kernel set contributed to reduce the number of sterile plants in modern than in older maize hybrids and thus to a higher kernel number per plant as resource availability per plant decreases. Other authors also found less % of barren plants in newer than in older hybrids [31; 32; 18]. The lower threshold PGRs for kernel set could have probably resulted from indirect selection of genotypes under progressively higher plant densities and from a wide testing area that includes low-yield environments [33-38]. The determination of the

thresholds of plant growth rate for kernel set were recently suggested as a phenotyping trait in breeding programs (39). However, the individual plant methodology [29; 10] seems more suitable for a reliable estimation of PGRs thresholds for kernel set than the mean PGRs per plot calculated in other works [18; 40]. At high resource availability per plant, the greater potential kernel number in the topmost ear contributed to a high KNP [9; 10]. Although differences were found among hybrids, there was not a clear trend with the year of hybrid release in threshold PGRs for prolificacy, nor in percentage of prolific plants beyond that threshold [9]. Also, no significant changes in ears per plant for US maize genotypes released between 1930 and 1980 were evident [32]. However, an increase in prolificacy with the year of hybrid release was reported in other works [3; 18].
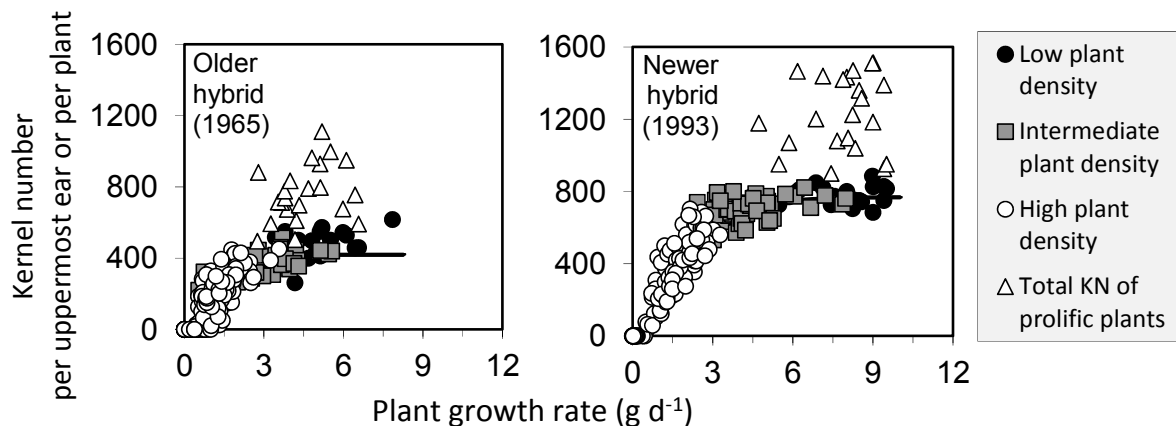

Figure 3. Relationship between kernel number per uppermost ear or per plant and plant growth rate during a period bracketing silking (PGRs) in an older (DKF880) and a newer (DK752) maize hybrid released in Argentina in different decades (year of release between brackets). Triangles represent kernel number of prolific plants (kernel number of the topmost plus the second ear). Other symbols represent KN of the topmost ear at low (2-4 plants m^{-2}; solid circles); intermediate (8 plants m^{-2}; squares), and high plant densities (16-30 plants m^{-2}; white circles). Adapted from Echarte et al. (10).

A greater dry matter partitioning to the ear (i.e. ear growth rate per unit PGRs) and/or a greater grain efficiency factor (i.e. kernel set per unit of ear growth rate during the critical period for kernel set) are physiological processes contributing to a greater KNP per unit PGRs (41; Figure 1). It has been stated that kernel set improvements with the year of the hybrid release were attributable to (i) increased partitioning of dry matter to the ear during the critical period for kernel set at low and intermediate resource availability per plant; and to (ii) greater kernel set per unit of ear growth rate at high resource availability per plant (10; Figure 4). Previous works have shown dry matter partitioning to the ear increments as a result of a reduction in tassel size or tassel removal [24; 42; 43]. Greater dry matter partitioning to the ear in newer compared with older maize hybrids is in agreement with the declined tassel size of US hybrids from the 1930s to the 1990s [15]. Tassel branch number and dry weight were reduced over the years in US hybrids [2; 3]. At high resource availability, the greater kernel set per unit ear growth rate was mainly attributable to the greater potential kernel number per ear [10]. Other processes contributing to elucidate differences among hybrids in grain efficiency factor, like a lower assimilate requirement per

kernel [21; 40; 42] or a more synchronous fertilization of florets within the ear [44;45], did not show a clear trend with the year of the hybrid release [10]. The inherent greater stand uniformity of the single-cross modern than in double-cross older hybrids was not an additional factor influencing kernel set per unit PGRs; since, plant size variability at the critical period for kernel set was similar among hybrids of different decades [9].
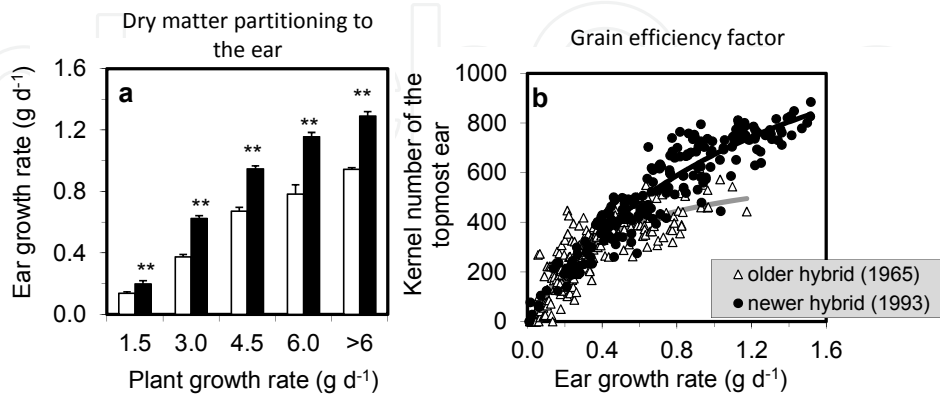

Figure 4. Dry matter partitioning to the ear (a) and grain efficiency factor (b), for an older (DKF880) and a newer (DK752) maize hybrid released in Argentina in different decades (year of release between brackets). Bars indicate standard error. ** indicates significant differences between hybrids at P< 0.05. Adapted from Echarte et al. [10].

The modifications to the features of the relationship between KNP and PGRs (i.e. lower threshold PGRs for kernel set and greater potential kernel number) were associated with a more uniform HI across resource availabilities in newer than in older maize hybrids (Figure 5; 9). At low resource availability, decreases in HI were sharper in older hybrids. At high resource availability per plant, decreases in HI of non-prolific plants were less pronounced in newer than in older hybrids (Figure 5; 9);
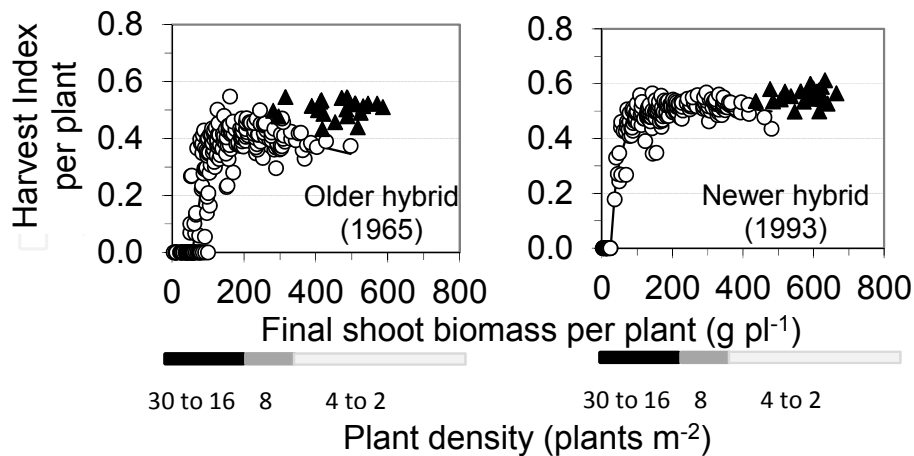

Figure 5. Relationship between harvest index per plant and final shoot biomass per plant in an older (DKF880) and a newer (DK752) maize hybrid released in Argentina in different decades (year of release between brackets). Triangles represent harvest index of prolific plants. Bottom bars represent the plant densities used to obtain the corresponding ranges of shoot biomass per plant. Adapted from Echarte and Andrade (9).

The lower threshold PGRs for kernel set was associated also with an improved tolerance to high plant density in newer maize hybrids [10]. Greater tolerance to high plant density was reported for hybrids released during different decades in the US, Canada and Argentina [3; 18; 32; 36; 40; 46]. The response of grain yield to plant density was curvilinear in Argentinean maize hybrids released between 1965 and 1993 [19] and between 1965 and 1997 [40], in agreement with the generally reported grain yield response to plant density for maize [47; 48]. Grain yield response to plant density was mostly associated with number of kernels per unit area [19], in accordance with other works [18; 47; 49]. In general, differences in kernel number m^{-2} among hybrids released in different decades increased with plant density [19]. Figure 6 shows that kernel number m^{-2} of a hybrid released in 1965 increased with plant density up to 8 pl m^{-2}; whereas, kernel number of a newer hybrid released in 1993 increased with plant density up to 14.5 plants m^{-2}. A recent study demonstrated that kernel number of current Argentinean maize hybrids (i.e. released in 2010) is consistently higher than that of an hybrid released in 1993 at high plant densities [50]. Greater tolerance to other stresses like weed competition (51), low night temperatures [16; 52], low soil nitrogen [17; 53; 54] and drought [55] were reported for hybrids released during different decades in the US and Canada. It was demonstrated that the nature of the environmental stress (e.g., plant density, nitrogen, water) causing variations in PGRs did not influence the KNP-PGRs relationship [56; 57]. Therefore, it is likely that a lower threshold PGRs is the underlying feature contributing to explain the greater general stress tolerance in newer than in older maize hybrids.

The greater kernel number at low plant density in newer compared with older maize hybrids (Figure 6) is another distinctive trait improved in Argentinean maize hybrids; since no grain yield improvement at very low plant densities was reported for US and Canadian hybrids [3; 37]. Moreover, although newer Argentinean hybrids released in 2010 yielded more than hybrids released in 1993 in a range of plant densities between 5 to 14.5 plants m^{-2}, the greatest grain yield improvement during the 1993-2010 period occurred at the lowest plant density (i.e. 5 plants m^{-2}; 49).
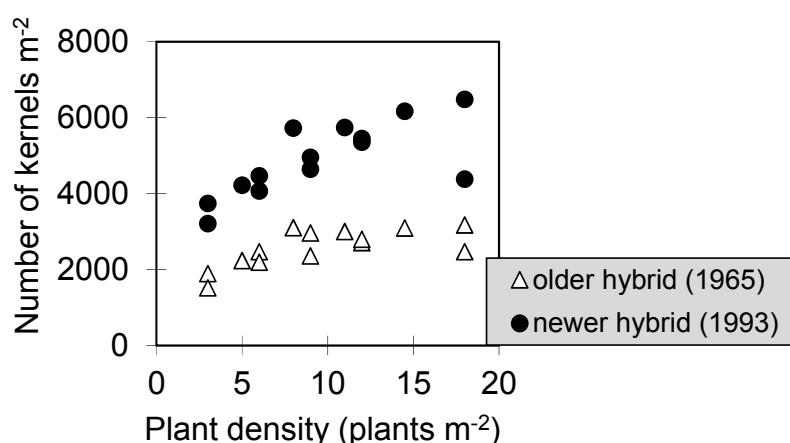

Figure 6. Number of kernels m^{-2} as a function of plant density for an older (DKF880) and a newer (DK752) maize hybrid released in Argentina (year of release between brackets). Adapted from Echarte et al. (19).

Kernel weight and chemical quality

A general model for kernel weight determination in maize is shown in Figure 7. Although kernel weight differed among hybrids it did not show a clear trend with the year of hybrid release [60].
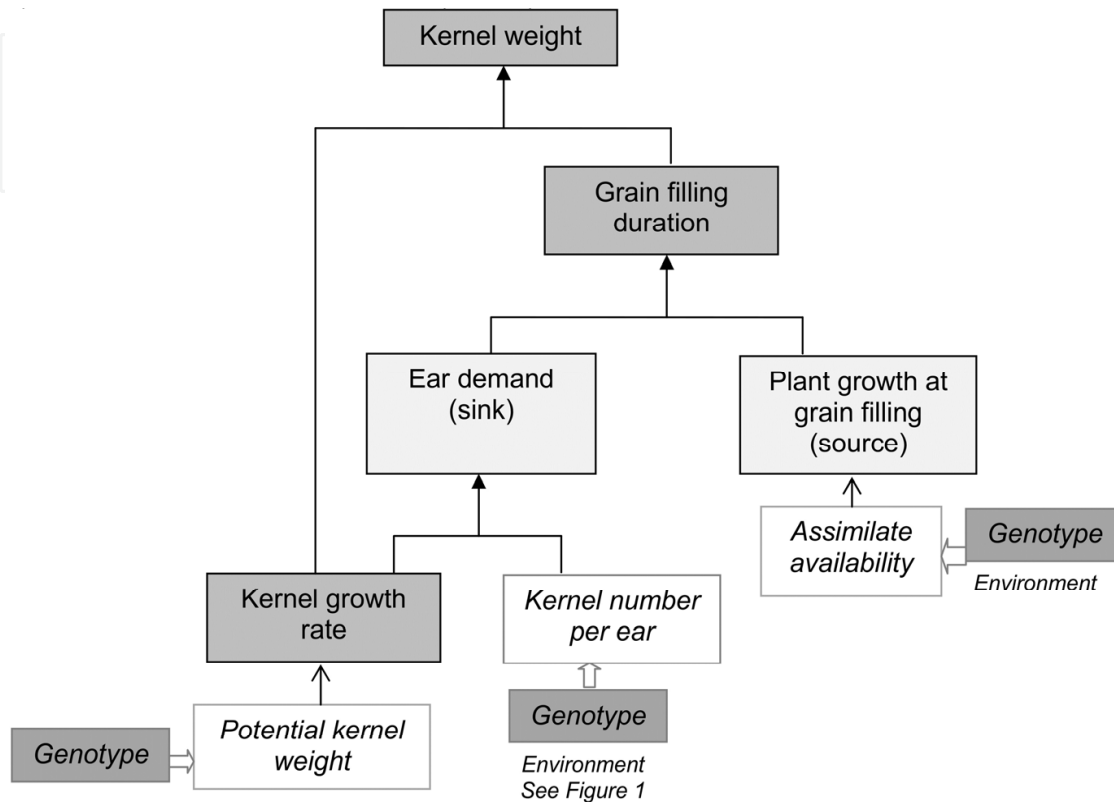

Figure 7. General model for kernel weight determination in maize.

Biomass accumulation in kernels begins shortly after fertilisation and it can be represented by a sigmoidal pattern in which a lag and a linear growth phase can be distinguished [58; 59]. Of the two components that determine final kernel weight (i.e. the kernel growth rate during the linear phase or effective grain filling period and the effective grain filling duration; Figure 7), kernel growth rate was the main component contributing to explain differences in kernel weight among hybrids released in different decades up to 1993 [60]. Kernel growth rate is strongly correlated with number of endospermatic cells and starch granules, which in turn determine the potential kernel size [61-63]. This contention suggests underlying differences among hybrids in potential kernel weight.

Duration of the grain filling period, and in turn kernel weight, is affected by the ratio between assimilate availability (source) and the potential capacity of the ear to use the available assimilates (i.e. ear demand, sink) during the grain filling period (Figure 7; 29; 65; 67-71). Since under optimal growing conditions, hybrids differ in kernel number per plant but also in kernel growth rate or potential kernel weight [60]; the ear demand (i.e. sink) was better described by both, the number of kernels per ear and their potential kernel weight (i.e., ear demand = KNP x kernel growth rate) rather than by KNP alone as in previous

works [64-68]. As such, ear demand was greater in newer than in older hybrids by means of a greater kernel number per plant or a large potential kernel weight [60].There was not a clear trend with the year of the hybrid release in source-sink ratio in non-limiting environments (i.e. optimum resources availability; 59). An enhanced source-sink ratio (i.e. calculating the sink as kernel number alone) has been indicated for Argentinean maize hybrids released between 1965 and 1997 [40]. However, kernel weight reductions in response to source reductions due to defoliation during grain filling were greater in newer than in older hybrids (Figure 8a; 60). This response was associated with the greater ear demand relative to the source capacity in newer Argentinean maize hybrids (Figure 8b). Thus, if breeding for high yield potential continue increasing the ear demand without a proportional increment in total source capacity, kernel weight would be source limited and it will be more affected by source variations during the grain filling period in the newer maize hybrids. In agreement, ear demand of current Argentinean maize hybrids (i.e. released in 2010) was greater than that of maize hybrids released in 1993 [72]. As such, ear demand increased at a rate of 1.13% year^{-1} during the last 45 years in Argentina; and kernel number was the main component influencing this increment rather than kernel growth rate [72]. In contrast, source-sink ratios were greater for newer than for older Ontario maize hybrids for the 1959-2007 period [8]. The increased functional "stay green" (i.e. capacity of a leaf to retain its photosynthetic rate during the grain filling period; 8) was the main factor underlying the larger source during the grain filling period in newer maize hybrids of the US corn belt and Ontario, Canada [1; 8; 17].
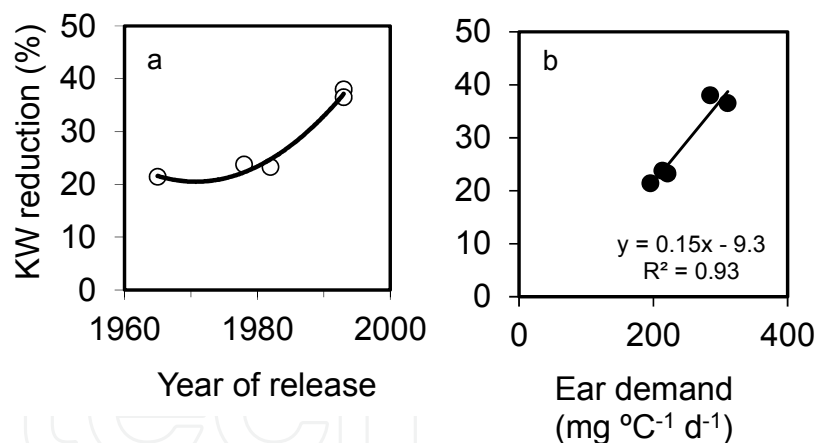

Figure 8. Kernel weight reduction (%) due to full defoliation during the grain filling period as a function of (a) year of hybrid release and (b) ear demand (mg ºC^{-1} d^{-1}) for 5 hybrids released in Argentina from 1965 to 1993. Adapted from Echarte et al. [60].

The greater ear demand along with the genotypes used in the Argentinean maize breeding programs influenced the grain chemical quality of hybrids released in different decades [11]. Protein concentration decreased with the year of the hybrid release in an environment without nitrogen (N) fertilization but it was not modified when N was applied (Table 1); soil N-NO₃ level at V6 stage in this experiment was higher than the minimum required for maximum yield achievement (i.e. 27 ppm in this experiment versus a threshold of 24 ppm

N-NO$_3$ for maximum yield; 73). Protein concentration was negatively correlated with grain yield (r=-0.79, p=0.06) in agreement with previous findings [74-76]. The decline in protein concentration in kernels might have been the result of non-proportional increments of N and carbon fluxes to the kernels over the years. In addition, lower protein concentration in kernels were associated with low source-sink ratios [65; 77]. Similar trends in protein concentration over the years were reported for other crops [78; 79] and for US maize hybrids released during the period 1930-1991 [3]. On the contrary, protein concentration in kernels increased in Canadian hybrids released in different decades [80]. The increment in both, grain yield and protein concentration, might be associated with the increased source-sink ratio in Canadian maize hybrids [54]. As well, similar protein concentration under high N availability in Argentinean maize hybrids released in different decades might have been related to N luxury consumption [81; 82]. Oil kernel concentration was stable in hybrids released between 1965 and 1984; but it was reduced in hybrids released in 1993 (r^2=0.84, p<0.05, Figure 9). Oil is mainly located in the embryo [83; 84] and it is probable that the embryo-endosperm ratio has decreased with the year of the hybrid release. In agreement, embryo-endosperm ratio was greater in US hybrids selected for high oil concentration [85].

Hybrid	Year of release	Protein (g kg^{-1})	
		No N fertilized	N fertilized
DKF880	1965	95.0 a	98.7 a
M400	1978	93.0 ab	95.7 a
DK4F36	1982	81.0 bc	86.7 a
DK4F37	1985	77.7 c	88.3 a
DK664	1993	78.0 c	86.7 a
DK752	1993	79.7 c	93.0 a
SE within columns		4.04	
SE within rows		3.85	

Table 1. Protein concentration (g kg^{-1}) in grains of Argentinean maize hybrids released between 1965 and 1993 under two nitrogen treatments (i.e. N fertilized and no N fertilized). From Echarte [11].

Figure 9. Oil concentration (g kg^{-1}) in grains of Argentinean maize hybrids released between 1965 and 1993 under two nitrogen treatments (i.e. N fertilized and no N-fertilized). From Echarte [11].
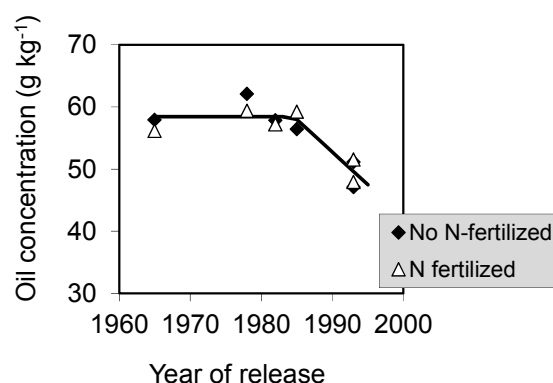
Resource capture and resource use efficiency

Greater grain yields of newer maize hybrids might have resulted in a concomitant increase in resource capture and/or resource use efficiency.

In non-limiting environments, grain yield can be expressed as the result of intercepted radiation, radiation use efficiency for shoot biomass production and harvest index [86]. Intercepted radiation did not consistently change in Argentinean maize hybrids released between 1965 and 1993 [11], in accordance with the lack of a consistent trend with the year of the hybrid release for shoot biomass. On the contrary, another study [40] reported accumulated intercepted radiation increments for Argentinean maize hybrids released between 1965 and 1997; which were attributed mainly to greater interception during the grain filling period. Contrasting results between works could be related to period under study and/or interaction between genotype and environment [87]. Nevertheless, grain yield increments were attributed to a large extent to greater radiation use efficiency for grain yield in both studies [11; 40]. The improved radiation use efficiency was not related to an improved light distribution within the canopy, as a lower extinction coefficient was not evident with the year of the hybrid release [40]. These results are in contrast to the more upright leaf habit with the year of the hybrid release reported for US hybrids [31]. A greater radiation use efficiency was also the main mechanism contributing to explain the greater shoot biomass of newer Canadian maize hybrids [88]. A smaller decline in maximum leaf photosynthetic rate from silking to maturity was the underlying process contributing to explain the greater radiation use efficiency in newer Canadian maize hybrids [16;17; 89]. Maximum leaf photosynthetic rates at silking, however, were similar among hybrids released in different decades [17].

In water and/or nitrogen limited environments, greater grain yields associated with resource capture increments might have exposed current maize hybrids to more frequent nutrient or water stresses. Nevertheless, as it was previously discussed, newer genotypes are more tolerant to stresses than older hybrids. Grain yields of newer maize hybrids were greater than those of older hybrids across **N levels** [31; 53; 90; 91]. Nitrogen use efficiency (the ratio of grain production to soil available N) can be expressed as the result of nitrogen recovery efficiency (NRE, the ratio of N uptake to soil available N) and nitrogen internal efficiency (NIE, the ratio of grain yield to whole plant N uptake at physiological maturity). Nitrogen use efficiency increased with the year of the hybrid release in Argentina during the 1965 – 2010 period [91; 92]. Nitrogen internal efficiency rather than greater N uptake largely explained the greater N-use efficiency of newer maize hybrids than older hybrids [92; 93]. These results are in agreement with findings in Canada and US [94]. The greater N-use efficiency in a newer than in an older Canadian maize hybrid was associated with a lower rate of decline of leaf photosynthesis towards physiological maturity, under both high and low N availability [17].

Water stress is one of the main limitations to crop grain yield worldwide; and it may reduce maize grain yield by 12-15% in temperate regions [95, 96]. Grain yield of newer maize hybrids was greater than that of older hybrids across **water regimes** during the grain filling period [97]. Preliminary results of our group indicate that grain yield improvements in

Argentinean maize hybrids released between 1980 and 2004 has been associated with increased water use efficiency for grain production and not with water uptake, which has remained relatively stable [98]. This is in contrast with previous reports suggesting that water capture increased with the year of the hybrid release in US hybrids [99]. However, the consistently increased total shoot biomass with the year of the hybrid release in US hybrids and not in Argentinean maize hybrids may contribute to explain discrepancies between works. Although seasonal water uptake was similar among Argentinean maize hybrids released in different decades, soil water uptake during the critical period for kernel set was greater in newer than in older maize hybrids when soil available water was low [100]. In agreement, a modern Canadian hybrid was able to maintain higher leaf photosynthesis and transpiration during short periods of low water availability at silking than an older hybrid in a greenhouse study [55]. Water use efficiency for grain production was consistently higher in a newer than in an older Argentinean maize hybrid, and differences were greater at low water availability [101].

2. Conclusions

Greater grain yield of newer Argentinean maize hybrids was mainly related to an increased harvest index; whereas shoot biomass did not consistently increased with the year of the hybrid release. Kernel number was the main yield numerical component contributing to explain grain yield increments. Processes influencing kernel number determination in hybrids released in different decades were analyzed using as a framework the relationship between kernel number per plant (KNP) and plant growth rate during the critical period for kernel set (PGRs); and it was evident that features of the relationship were changed through the years. As such, threshold PGRs for kernel set was lower and maximum kernel number per plant was higher in newer than in older hybrids. The lower threshold PGRs for kernel set contributed to explain the greater tolerance of newer hybrids to high plant densities, and it probably contributed to a greater tolerance to other stresses like low water availability or low soil N. The lower threshold PGRs for kernel set was associated with a greater assimilate partitioning to the ear at low resource availability per plant; which was probably related to a lower apical dominance in newer than in older maize hybrids. The higher maximum kernel number per plant at high resource availability was associated with morphogenetic changes leading to a greater potential kernel number per ear; whereas prolificacy was not consistently improved. This response of kernel number to an increased resource availability contributed to explain the greater grain yield of newer hybrids at low plant densities. As such, harvest index of newer maize hybrids was not only greater but it was also more stable at different resource availability than that of older maize hybrids.

Kernel weight did not show a clear trend with the year of the hybrid release; but it was evident that kernel weight of newer hybrids was more susceptible to stresses during the grain filling period than that of the older hybrids. Kernel weight response to resource availability during the grain filling period was analyzed in terms of the source-sink ratio. The sink or the ear demand for assimilates during the grain filling period was greatly increased in newer maize hybrids; as a result of either a greater kernel number and/or a

greater kernel growth rate. Kernel growth rate has been shown to be closely associated with the potential kernel weight. However, the ear demand was increased to a greater extent than the source (i.e. plant growth during the grain filling period), and stresses during the grain filling period reduced kernel weight of newer hybrids more than that of the older hybrids. Thus, future breeding efforts for yield improvement would need to focus also on an increase in source capacity during the grain filling period. Kernel chemical quality was also modified with the year of the hybrid release; as such, protein concentration in kernels was lower in newer hybrids at moderate soil N availability. This change was attributed to both, the genotypes used in the selection programs as well as the increased carbon fluxes to the kernels without proportional increments in the flux of nitrogen. When N luxury consumption occurred, protein concentration in kernels was similar among hybrids released in different decades. Oil concentration also decreased in newer hybrids released in 1993.

Resource use efficiency increments, rather than greater resource capture, concomitantly increased with grain yield of Argentinean maize hybrids released in different decades. In non-limiting environments, radiation use efficiency for grain production (i.e. grain yield per unit of intercepted radiation) was a consistently increased mechanism contributing to explain the greater grain yield of newer maize hybrids. This was associated mainly with the greater partitioning of assimilates to the ear and/or a greater potential kernel number per ear that allowed for an increased harvest index. An improved light distribution within the canopy was not evident. In soil N-limited environments, greater yield of newer maize hybrids were associated with greater nitrogen use efficiency for grain production; which was largely explained by a greater nitrogen internal efficiency (i.e. the ratio of grain yield to whole plant N uptake at physiological maturity). Similarly, in water limited environments, water use efficiency for grain production was greater in a newer than in an older maize hybrid. The lower thresholds PGRs for kernel set in newer compared with older maize hybrids might have resulted in a lower frequency of barren plants or with low number of kernels and thus in a greater kernel number at low N or low water availability. Resource capture was not consistently increased with the year of the hybrid release indicating that stressful conditions are not more frequent in current maize hybrids than before.

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