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Physiological differences in yield related traits between flint and dent Argentinean commercial maize genotypes

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ABSTRACT

Argentina is the worldwide single maize (*Zea mays* L.) exporter of non-GMO flint maize, also called plata maize. This grain is known for high dry-milling yields, the production of large endosperm grits and specific cooking functional properties. But, this special maize has lower yields at farmer fields when compared to regular dent germplasm, and studies describing the physiological characteristics behind this are scarce. Our objective was to understand differences in yield determination mechanisms between flint and dent commercial germplasm for the temperate area. We characterized 31 genotypes (24 dent and 7 flint) growing at five different environments for describing their yield differences, and also described specific physiological traits to unravel the mechanisms behind these yield differences.

Grain yield, KNP, KW, plant growth rate and biomass partitioning around flowering, kernel set efficiency per unit of accumulated ear biomass at flowering and assimilate availability per kernel during flowering all showed significant kernel type (flints vs. dents) effects ($p < 0.05$). And significant genotype differences within each kernel type were evident for all traits ($p < 0.01$). Flint kernel type showed lower yields (ca. 80% of dents) due to reduced KNP and KW. This lower KNP in flints was mostly related to a lower plant growth rate around flowering, although they also showed a reduced biomass partitioning to the ear during this period. Flint genotypes, however, showed higher kernel set efficiency per unit of accumulated ear biomass when compared to dents ($p < 0.01$). Lower KW in flints was related to a reduced assimilate availability per kernel around flowering ($p < 0.01$), both kernel types showed similar assimilate availability per kernel during grain filling ($p > 0.05$). This indicated flint and dent kernel types had the same amount of assimilates to fulfill their early established potential KW. Our results emphasize the importance of the flowering period for understanding yield differences between flints and dents, and biomass accumulation rate during this period was identified as a key trait for increasing flint yields.

1. Introduction

Argentina is a historically consistent maize exporter, and one of the five largest producers of maize worldwide. It is also the single maize exporter of non-GMO flint maize, also called plata maize. Argentine flint maize is well known for high dry-milling yields and the particular quality that provides to a wide range of end-products, like breakfast cereals, snacks, and other textured ingredients (Rooney and Serna-Saldivar, 2003). Flint kernels possess a major proportion of high density vitreous endosperm, associated with kernel hardness. Kernel hardness prevents grain damage during mechanical harvesting, manipulation and storage, and is specially appreciated for the production of large endosperm grits (Paulsen and Hill, 1985). The European Union has a special import permit for hard endosperm maize (Commission Regulation, 1997) that has traditionally been sourced only by flint maize from Argentina. During the last two decades Argentina has exported to the European Union around 350.000 metric tons per year of this special grain (SENASA, 2012).

In the last decades the introduction of dent germplasm has contributed to large increases in yield potential of Argentinean commercial genotypes (Brun and Dudley, 1989). The higher yield of GMO dent maize at production fields has led to a massive use of dent and semi-dent genotypes by farmers. Flint non-GMO production fields are currently conducted under contract, and farmers are paid a premium for this special product. Studies describing crop management options and physiological characteristics of flint hybrids

Abbreviations: KNP, kernel number per plant; KW, kernel weight.

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are scarce. Cirilo et al. (2011) described many traits related to yield performance of several flint genotypes grown under different agronomic practices. They did not, however, determined the traits that are behind yield differences among flint and dent germplasm. Most research using Argentinean genotypes are focused on dent germplasm (Gambín et al., 2006; Hernández et al., 2014). When dents are compared to other kernel types, like popcorn, it is evident there are specific differences in crop physiological traits that are behind yield and environmental responses (Severini et al., 2011).

Maize yield is determined by the number of harvested kernels and their individual weight (Otegui, 1995; Chapman and Edmeades, 1999). Kernel number is commonly considered the main yield component, highly correlated with final grain yield (Andrade et al., 1999). Kernel number determination is specifically related to three physiological processes, (i) the rate of plant biomass accumulation around flowering, (ii) the proportion of the plant biomass that is partitioned to the reproductive structure bearing the kernels (ear) during this period, and (iii) the kernel set efficiency per unit of accumulated biomass at the ear level during the flowering period (Vega et al., 2000). These three traits determine different physiological strategies for kernel set determination (e.g., high kernel set efficiency, plant growth rate or biomass partitioning). It is known that current commercial maize genotypes in Argentina vary for all these traits (Hernández et al., 2014). It is not known, however, if there are consistent kernel type differences in these yield determination traits when flint and dent germplasm is compared.

Although most yield variations are related to differences in kernel number determination, genotype and environmental variations in kernel weight (KW) can also affect grain yield. Genotypic differences in KW among Argentinean commercial genotypes are common (Borrás and Gambín, 2010). Differences in KW can be related to changes in the potential weight established early after flowering, or in the capacity of the crop to fulfill this potential. Working with a reduced set of genotypes Cirilo et al. (2011) have shown that kernel hardness is correlated with post-flowering assimilate availability per kernel, supporting the hypothesis that flint genotypes should have higher values when compared to dents. Differences in KW among dent and popcorn genotypes, however, are mostly related to changes in potential KW established at flowering, and these differences are related to the assimilate availability per kernel during the flowering period, when kernels are being set (Severini et al., 2011). This is also the mechanism behind most genotypic KW differences among dent commercial genotypes (Gambín et al., 2006).

Our general objective was to understand differences in yield determination between flint and dent commercial genotypes. In this particular study we first characterized a large number of flint and dent genotypes growing at different environments for describing their yield differences. We latter described specific physiological parameters to further understand the mechanisms behind these yield differences.

2. Materials and methods

2.1. Sites and crop management

Thirty one commercial genotypes were tested in five environments. Locations were Venado Tuerto (33°45′S 61°58′W), Franck (31°35′S 60°56′W), Laguna Larga (31°77′S 63°80′W), and Zavalla (33°1′S, 60°53′W). All trials were planted early during the growing season, between 15 September and 17 October, during the 2012/2013 growing season except at Zavalla were two seasons were tested (2011/2012 and 2012/2013). Plots were four rows 5.5 m long with 0.52 m row spacing. They were over planted and hand-thinned at V3 (Abendroth et al., 2011) to a uniform stand density of 8 pl m^{-2}. All measurements were done using the two central rows. The crops were all fertilized with 100 kg N ha^{-1} as urea (46-0-0 N-P-K) at V4 and 16 kg N ha^{-1} as monoammonium phosphate (10-50-00) at planting. Weeds and pests were controlled with common agronomic practices. Insect pressure was specifically monitored and controlled throughout the season for minimizing any possible effect.

Genotypes represented the most common commercial hybrids used by farmers in the temperate Argentinean central region, and were sourced from different companies. Twenty four genotypes were regular GMO dent (or semi-dent) kernel type. Seven genotypes were non-GMO flint kernel type. These seven flint genotypes are widely used by both local dry-milling industry and exporters.

2.2. Phenotypic measurements

Yield was analyzed by harvesting the two central rows from each plot. Additionally, in the two trials conducted in Zavalla several plant biomass measurements during the flowering and grain filling periods were done.

In both experiments at Zavalla fifteen consecutive plants were selected from the central rows and tagged 20 days (d) before flowering. A non-destructive alometric method for biomass estimations was used for measuring plant growth rate and plant biomass partitioning. The method based on allometric relations provides an accurate measure of plant biomass corresponding to tagged plants that remain in the field until harvest. We use this model to quantify total plant biomass at the individual plant level at the pre- and post-flowering stages (Vega et al., 2000; Borrás et al., 2009) for all 15 plants per replicate. Allometric models were developed from three additional tagged plants per replicate, which were immediately harvested after being measured. Shoot biomass was obtained after cutting plants in small pieces and drying them in a forced-air oven at 65 °C for at least 7 d. The pre-flowering models were based on the linear regression between shoot biomass (15 d before 50% anthesis; DBA) and stem volume. Stem volume was calculated from plant height (ground level up to the uppermost leaf collar) and stem diameter at the base of the plant. The post-flowering biomass sample was taken 15 d after 50% anthesis (DAA), and the allometric models utilized stem volume and maximum apical ear diameter with husks. A unique allometric model was made for each genotype at each growing season.

At physiological maturity (defined as 75% milk line; Hunter et al., 1991) all tagged plants were harvested and used to measure kernel number per plant (KNP), average KW per plant, and grain yield per plant. The above-ground weight of five consecutive plants per plot was measured after drying in a forced-air oven at 65 °C.

Plant growth rate around flowering (mg $plant^{-1}$ °Cd^{-1}) was calculated as the difference between the post-flowering and the pre-flowering biomass divided by the accumulated thermal time between sample dates (base temperature of 8 °C; Eq. (1)).

$$\text{PGR (mg plant}^{-1}\text{°Cd}^{-1}\text{)} = \frac{\text{Estimated biomass (mg plant}^{-1}\text{)}_{\text{DAA}} - \text{Estimated biomass (mg plant}^{-1}\text{)}_{\text{DBA}}}{\text{thermal time between samples}} \quad (1)$$

Ear biomass at 15 days after 50% anthesis was used to determine the partitioning coefficient of total above-ground plant biomass to reproductive structures, and calculated as the ratio between the ear biomass per plant (g $plant^{-1}$) and the total above-ground biomass (g $plant^{-1}$), both measured at 15 days after 50% anthesis (Eq. (2)).

$$\text{Partitioning Coefficient (\%)} = \frac{\text{Estimated ear biomass (g plant}^{-1}\text{)}_{\text{15DAA}}}{\text{Estimated biomass (g plant}^{-1}\text{)15DAA}} \quad (2)$$

Kernel set efficiency was calculated as the ratio between kernel number per plant and ear biomass 15 days after 50% anthesis (Eq.

(3)).

$$\text{Kernel Set Efficiency (kernel g}^{-1}\text{)} = \frac{\text{Kernel plant}^{-1}}{\text{Estimated ear biomass (g plant}^{-1}\text{)}_{15DAA}} \quad (3)$$

Assimilates available per kernel around flowering (mg °C^{-1} kernel^{-1}) was determined as the ratio between plant growth rate during this period and the kernel number per plant counted at harvest. Assimilates available per kernel during grain filling (mg °C^{-1} kernel^{-1}) was calculated as the ratio between plant growth rate during this period and final kernel number per plant.

Thermal time to flowering was calculated as the thermal sum (°Cd) using a base temperature of 8 °C from planting to anthesis. Grain-filling duration was calculated as the thermal sum using a base temperature of 0 °C (Muchow, 1990; Borrás et al., 2009) from anthesis to physiological maturity.

2.3. Statistical analysis

For analyzing kernel type, genotype, location and all possible interactions we did an ANOVA fitting a general linear model with genotype nested inside kernel type using the GLM procedure (SAS Institute, 1999). Field experiments had completely randomized plots with three replications per genotype.

In order to have a visual ordination of the different genotypes and its multiple trait relationships a Genotype-Trait (GT) bi-plot was done using R software (R Core Team, 2013). The results of the ordination analysis were presented in three different bi-plots, one including yield per plant and its numerical components (KNP and KW), a second including KNP and the three physiological mechanism studied behind KNP differences (partitioning coefficient, kernel set efficiency and plant growth rate), and a third one with KW and the two possible mechanism behind KW differences (assimilates available per kernel around flowering and assimilates available per kernel during grain-filling). This allowed identifying differences between flint and dent kernel types. Because analyzed traits have different units standardization was needed (Yan and Rajcan, 2002).

3. Results

3.1. Yield and phenology differences between kernel types

Yield results showed environment, kernel type and genotype within kernel type significant effects, and the interactions environment × kernel type and environment × genotype within kernel type were also significant ($p < 0.001$; Table 1). This indicated that there were significant differences between flints and dents, and that genotypes within each kernel type had different yields. It also indicated that the different yield between flints and dents was not constant across the environments tested. On average flints yielded 80% of dents, across environments yielding 11.1–15.7 Mg ha^{-1} (Table 1). The highest yield difference between flints and dents was observed at Franck, with flints yielding 70% of dents, and the lowest yield difference at Zavalla during 2012/2013, where flints yielded 87% of dents.

There was no trend showing yield difference to be higher at environments with lower or higher yields. The significant interaction between environment and kernel type did not represent an important fraction of the total variability (i.e., 3%). At the same time, the interaction environment × genotype within kernel type explained 25% of total variability, showing that genotypes within each kernel type did show significant yield variability across environments.

There was a significant kernel type effect on time from planting to flowering and time from flowering to physiological maturity ($p < 0.001$, Table 2), but the time from planting to physiological maturity was similar ($p > 0.05$, data not shown). Flint kernel type showed a slightly shorter time from planting to flowering, and a slightly longer time from flowering to physiological maturity when compared to dents. It is relevant to emphasize that although phenology differences between kernel types were statistically significant they were biologically not relevant.

However these kernel type phenology small differences it is important to emphasize that clear genotype differences in phenology within each kernel type were evident ($p < 0.001$).

3.2. Yield components: kernel number and kernel weight

Yield components were analyzed at Zavalla during two growing seasons (2011/2012 and 2012/2013). Kernel number per plant was significantly different between kernel types ($p < 0.001$, Table 2), where dent genotypes produced more kernels per plant than flints. There were also significant genotype differences within each kernel type ($p < 0.001$).

Kernel weight was significantly higher in dents when compared to flints, and significant variation existed among genotypes within each kernel type ($p < 0.001$, Table 2). Differences between environments was also significant for this trait ($p < 0.01$). The interactions environment × kernel type and environment × genotype within kernel type were significant at $p < 0.05$ and $p < 0.01$, respectively. These results indicated that KW differences between flints and dents were not always similar, and that genotypes within each kernel type varied their KW differently across growth environments.

3.3. Plant growth rate around flowering, biomass partitioning and kernel set efficiency around flowering

In order to understand the mechanisms why flint genotypes showed lower kernels per plant when compared to dents we studied specific traits related to plant growth. We were specifically interested in understanding if kernel types showed differences in plant growth rate around the flowering period, in biomass partitioning to the ear during this same period, and in the efficiency in kernel set per unit of accumulated ear biomass at around flowering.

Flint genotypes showed a reduced plant growth rate around flowering when compared to dents, and there were significant genotypic differences within each kernel type (Table 2).

The partitioning of plant biomass to the ear around the flowering period was also significantly different when kernel types are compared ($p < 0.001$). Biomass partitioning was lower in flint

Table 1
Average yield of 24 dent and 7 flint genotypes grown at five environments. Yield (Mg ha^{-1}) is reported with 14.5% grain moisture. For specific individual genotype data see Supplemental Table 1.

	Zavalla 2011/2012	Zavalla 2012/2013	Franck	Venado Tuerto	Laguna Grande
Average environment	11.6	11.1	11.2	15.7	13.2
Average dent	12.1	11.5	12.0	16.5	13.7
Average flint	9.9	10.0	8.4	12.7	11.3
Flint–dent ratio	82%	87%	70%	77%	83%
Environment (E)			***		
Kernel type			***		
Genotype (kernel type)			***		
E x kernel type			***		
E x genotype (kernel type)			*** (2.2)[a]		

*** $p < 0.001$.
[a] L.S.D. is the least significant difference at $p < 0.05$.

Table 2
Grain yield per plant, average kernel number per plant, individual kernel weight, time to flowering, grain-filling duration, individual plant growth rate around flowering, partitioning coefficient of biomass at flowering, kernel set efficiency per unit of accumulated ear biomass around flowering, assimilate availability per kernel during flowering and assimilate availability per kernel during grain filling for 24 dent and 7 flint genotypes tested at two environments (Zavalla 2011/2012 and Zavalla 2012/2013). For specific individual genotype data see Supplemental Table 2.

Kernel type	Grain yield per Plant	Kernel number per Plant	Kernel weight	Time to flowering	Grain filling duration	Plant growth rate	Partitioning coeficient	Kernel set efficiency	Assimilates per Kernel during flowering	Assimilates per Kernel during grain filling
	($g\ pl^{-1}$)	($kernel\ pl^{-1}$)	($mg\ kernel^{-1}$)	(°Cd)	(°Cd)	($mg\ °Cd^{-1}\ pl^{-1}$)	($g\ g^{-1}$)	($kernels\ g^{-1}$)	($mg\ °Cd^{-1}\ kernel^{-1}$)	($mg\ °Cd^{-1}\ kernel^{-1}$)
Average dents	126	473	265	992	983	229	0.13	27	0.485	0.261
Average flint	100	438	230	973	1020	188	0.12	33	0.432	0.255
Environment (E)	***(5)	***	**	***	***	***	***	ns	***	***
Kernel type	***(4)	***	***	***	**	***	***(0.01)	***(2)	***	ns
Genotype (kernel type)	ns	***(43)[a]	***	***	***	**	***	***	***	***
E × kernel type	ns	***(15)	*(6)[a]	***(7)	***(17)	***(12)	ns	*(2)	***(0.019)	ns
E × genotype (kernel type)	ns	ns	**(22)	**(26)	***(65)	*(46)	***(0.01)	***(9)	***(0.076)	***(0.084)

ns: not significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
[a] L.S.D. is the least significant difference at $p < 0.05$.

genotypes when compared to dents. Values for flint genotypes varied from 0.08 to 0.14 $g\ g^{-1}$, and dents showed a range from 0.10 to 0.18 $g\ g^{-1}$. There was no kernel type interaction with the environment ($p > 0.05$), but only genotypes within each kernel type showed to significantly interact with the growing season ($p < 0.001$).

As a consequence of lower plant biomass accumulation rate during flowering and a lower partitioning of this biomass to the developing ear flint genotypes showed lower ear biomass accumulation 15 days after anthesis when compared to dents. Averaged across environments and genotypes within each kernel type, accumulated ear biomass at the end of the flowering period in flints genotypes was ca. 20% less than dents (16.4 $g\ pl^{-1}$ in flints and 20.3 $g\ pl^{-1}$ in dents).

Kernel set efficiency per unit of accumulated ear biomass was higher in flints than dents (33 kernel g^{-1} vs. 27 kernel g^{-1}, for flints and dents, respectively, $p < 0.001$). Large significant genotype differences in kernel set efficiency within each kernel type were evident, for example the flint genotypes ACA929 and MILL522 presented average values across environments of 24 and 53 kernel g^{-1}, respectively.

3.4. Assimilates available per kernel around flowering and grain-filling

As differences in yield between kernel types were not only related to differences in KNP but also to KW differences, we further studied traits related with KW determination. We analyzed the relationship between final KW and availability of assimilates per kernel around flowering and grain-filling periods. Differences in assimilate availability per kernel during the flowering period are known to impact in the potential KW established during the early stages of grain filling, while differences in assimilate availability per kernel during the effective grain-filling period are known to affect the capacity of the plant to full-fill the potential KW established earlier.

Assimilate availability per kernel around flowering showed significant differences between environments, kernel type and genotypes within kernel type ($p < 0.001$; Table 2). The interactions environment × kernel type and environment × genotype within kernel type were significant ($p < 0.001$).

Assimilates available per kernel during the grain-filling period was not different when kernel types are compared, only for genotypes within each kernel type ($p < 0.001$). The interaction environment × kernel type was not significant, but only the environment × genotype within kernel type was ($p < 0.001$).

The relationship between genotype specific KW and its assimilate availability per kernel around flowering was significant ($p < 0.01$, $r^2 = 0.30$). However, no significant correlation was found between genotype specific KW and assimilate availability per kernel during the grain-filling period. These results help understand that the lower KW of flint genotypes when compared to dents was mostly related to a lower assimilate availability per kernel during the period when potential KW is being established (around flowering). It was not related to a reduced assimilate availability per kernel during the effective grain-filling period. The same was true for understanding differences among genotypes within each kernel type.

3.5. Physiological strategies for each kernel type

We did an ordination analysis for genotypes and traits (GT biplot) to further understand and describe kernel type differences in yield, KNP and KW differences (Fig. 1).

Fig. 1 describes the ordination analysis depicting genotype yield per plant and how it correlated with its two numerical components KNP and KW. With this analysis it became evident that genotypes

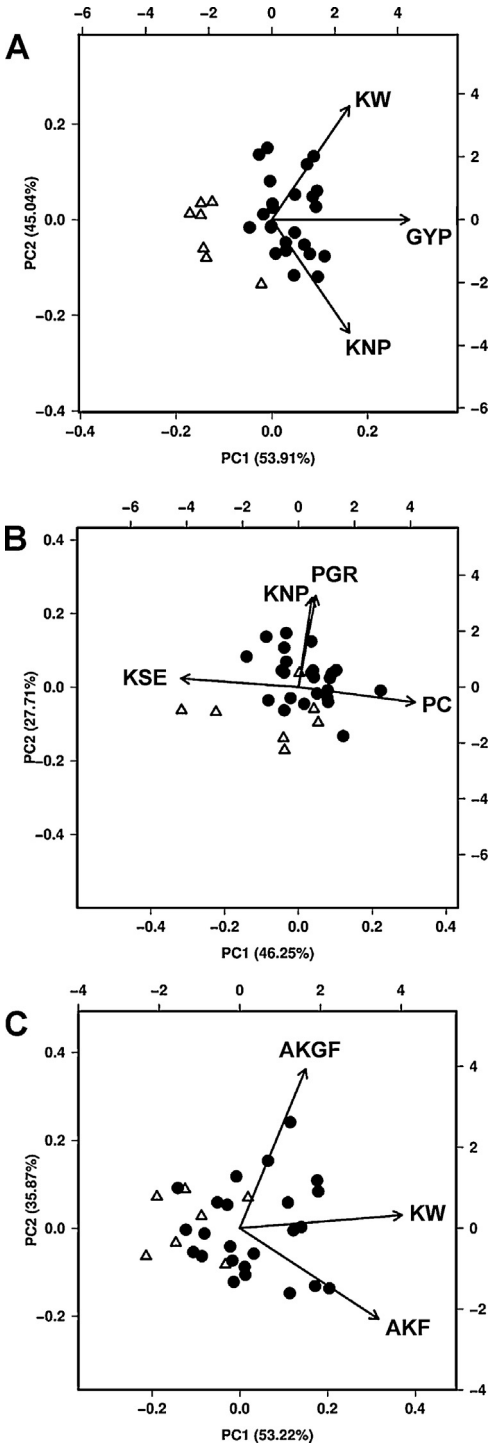

Fig. 1. Bi-plot of first and second principal components for flint and dent genotypes. Dent genotypes are represented as full circles and flint genotypes as empty triangles. Traits are represented as black arrows. (A) represents grain yield per plant (GYP) and its two numerical components (KNP, kernel number per plant, and KW, kernel weight); (B) represents kernel number per plant and its relation with the three physiological mechanisms studied (PGR, plant growth rate during the flowering period, PC, partitioning coefficient of plant biomass during flowering to the ear, and KSE, kernel set efficiency per unit of accumulated ear biomass). (C) represents kernel weight and its relation to the two physiological mechanisms studied (AKF, assimilate availability per kernel during flowering, and AKGF, assimilate availability per kernel during the grain filling period).

with the highest yields had different combinations of KNP and KW. Most important, dents and flints could be clearly grouped due to their contrasting yield. Flint genotypes were grouped as the lowest yielding ones due to poor combinations of both numerical components, KNP or KW.

Genotype KNP was analyzed in relation to its physiological components (plant growth rate, biomass partitioning and kernel set efficiency, Fig. 1B). Plant growth rate was highly correlated with KNP, both vectors mostly overlapping, while biomass partitioning and kernel set efficiency showed poor association with these two traits. Biomass partitioning and kernel set efficiency were negatively correlated. When analyzing how flints and dents grouped, it was evident that flint genotypes had reduced KNP when compared to dents mostly due to lower plant growth rates during the flowering period. Specific flint genotypes showed higher than average kernel set efficiency or biomass partitioning, but these traits were predominantly not correlated to KNP.

When analyzing KW and the two analyzed traits, assimilate availability per kernel around flowering and around the grain-filling period, genotype KW was positively associated with assimilate availability per kernel during flowering. Flint genotypes had lower assimilates available per kernel during the flowering period, while mostly similar to dents during the grain-filling period.

4. Discussion

Flint kernel type showed lower yields compared to regular dent germplasm (flints yielded on average ca. 80% of dents), and results showed the trend was mostly consistent across environments. Yield selection in flint germplasm is conditioned by a minimum grain quality level demanded to reach a specific quality norm (MAGyP, 2015) and the expectations of mills and final consumers (Gwirtz and Garcia-Casal, 2014). This restriction implies an extra breeding effort. Historically yield improvement in crops has carried a negative trade-off with grain quality (Duvick and Cassman, 1999; Weih, 2003). Many cases have been reported in crops other than maize where selection of cultivars for high grain yield implied grain quality reductions. Anderson et al. (1997) found reductions in grain quality for high yielding cultivars in wheat. In soybean, negative correlations between yield and protein concentration have been described in many studies (Wilcox and Guodong, 1997; Wilcox and Shibles, 2001; Rotundo et al., 2009). It is evident that breeding for yield and maintaining (or increasing) grain quality at the same time is feasible, but could limit genetic yield gains.

Flint genotypes have shown that their lower yields are due to reduced KNP and KW (Fig. 1A). The most important mechanism behind flint genotypes setting lower KNP was a reduced plant biomass accumulation rate around flowering. There were some differences between kernel types in terms of plant biomass partitioning around flowering and in kernel set efficiency per unit of accumulated biomass, but it is evident from Fig. 1B that the main driver for KNP differences between flints and dents was plant growth rate differences. Previous studies described differences in plant biomass partitioning around flowering between commercial dent genotypes to describe genotypic differences in yield determination and genotype × environment interactions (Echarte et al., 2004; Echarte and Tollenaar, 2006; Borrás et al., 2009). And new evidences show that genotype differences in plant growth rate around flowering are common (Hernández et al., 2014; Amelong et al., 2015). Our study has shown that the genotypes with the highest yields were the ones with the highest plant growth rate irrespective of kernel type (Fig. 1B). These results highlight the relevance of high plant biomass accumulation at around flowering for achieving high kernel numbers.

The present study re-enforces the issue that maize genotypic differences in KW are usually related to changes in assimilate availability per kernel at the same time kernel number is being determined, and not during the period when kernels are being filled (Sadras, 2007; Gambín and Borrás, 2010). This was the case for a smaller set of maize commercial genotypes (Gambín et al., 2006), and was also true when popcorns and dents were compared (Severini et al., 2011). Kernel sink capacity is established during the early stages of kernel development, and maize final KW is highly dependent upon this (Borrás and Gambín, 2010). Cirilo et al. (2011) have shown that plant growth per kernel during the grain-filling period was critical for the size and hardness of maize kernels, but the study was more related to changes in crop management for a reduced set of genotypes rather than understanding mechanisms behind genotypic differences.

It is important to emphasize that the present article describes plant physiological mechanisms for genotypes that are currently commercialized in Argentina. And we focused on these plant attributes because we understand they could be independently manipulated from kernel quality. Our working hypothesis is that the plant traits that are different between kernel types (flint and dents) do not have any direct impact on kernel quality. We hypothesize they are independent, and that there is room for improving yield through many of the identified mechanisms without negatively impacting grain quality. It is known, however, that plant growth and biomass partitioning to developing kernels do affect grain composition (Borrás et al., 2002; Cirilo et al., 2011). But we also consider that kernel hardness is mediated by small genetic changes, and known correlations between protein concentration and kernel hardness might be spurious correlations driven by only some specific minor proteins. There is a need to determine which specific kernel attributes contribute to kernel hardness, like specific zein profiles within the kernel endosperm (Lending and Larkins, 1989; Robutti et al., 1997; Holding and Larkins, 2006).

5. Conclusions

Dent genotypes showed higher yields when compared to flints across all environments tested. However, there were large genotype differences in yield within each kernel type, both in flints and dents.

Lower yields in flint genotypes when compared to dents were related to lower KNP and KW. These differences were mostly related to flint kernel type having a lower plant biomass accumulation rate around the flowering period, and a lower plant growth per established kernel also during the flowering period. There were no differences in plant growth per kernel during the grain-filling period when kernel types are compared, showing that flint and dent kernels do have the same amount of assimilates to fulfill their potential KW established early during grain filling. Flints also showed lower plant biomass partitioning to the growing ear during flowering and a higher kernel set efficiency when compared to dents, however these differences were more marginal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.eja.2015.04.001.

References

Abendroth, L.J., Roger, W.E., Matthew, J.B., Marlay, S.K., 2011. Corn Growth and Development. Iowa State University Extension, Ames, Iowa.
Amelong, A., Gambín, B.L., Severini, A.D., Borrás, L., 2015. Predicting maize kernel number using QTL information. Field Crops Res. 172, 119–131.
Anderson, W.K., Shackley, B.J., Sawkins, D., 1997. Grain yield and quality: does there have to be a trade-off? In: Wheat: Prospects for Global Improvement. Springer, pp. 249–254.
Andrade, F.H., Vega, C., Uhart, S., Cirilo, A., Cantarero, M., Valentinuz, O., 1999. Kernel number determination in maize. Crop Sci. 39, 453–459.
Borrás, L., Gambín, B.L., 2010. Trait dissection of maize kernel weight: towards integrating hierarchical scales using a plant growth approach. Field Crops Res. 118, 1–12.
Borrás, L., Curá, J.A., Otegui, M.E., 2002. Maize kernel composition and post-flowering source–sink ratio. Crop Sci. 42, 781–790.
Borrás, L., Astini, J.P., Westgate, M.E., Severini, A.D., 2009. Modeling anthesis to silking in maize using a plant biomass framework. Crop Sci. 49, 937–948.
Brun, E.L., Dudley, J.W., 1989. Breeding potential in the USA and Argentina of corn populations containing different proportions of flint and dent germplasm. Crop Sci. 29, 570–577.
Chapman, S.C., Edmeades, G.O., 1999. Selection improves drought tolerance in tropical maize populations: II. Direct and correlated responses among secondary traits. Crop Sci. 39, 1315–1324.
Cirilo, A.G., Actis, M., Andrade, F.H., Valentinuz, O.R., 2011. Crop management affects dry-milling quality of flint maize kernels. Field Crops Res. 122, 140–150.
Commission Regulation, 1997. Commission Regulation (EC) N°641/97 of 14 April 1997 amending Commission Regulation (EC) N°1249/96 of 28 June 1996 on rules of application (cereals sector import duties) for Council Regulation (EEC) N°/92. Off. J. Eur. Communities L98, 2–4.
Duvick, D.N., Cassman, K.G., 1999. Post-green revolution trends in yield potential of temperate maize in the North-Central United States. Crop Sci. 39, 1622–1630.
Echarte, L., Tollenaar, M., 2006. Kernel set in maize hybrids and their inbred lines exposed to stress. Crop Sci. 46, 870–878.
Echarte, L., Andrade, F.H., Vega, C.R.C., Tollenaar, M., 2004. Kernel number determination in Argentinean maize hybrids released between 1965 and 1993. Crop Sci. 44, 1654–1661.
Gambín, B.L., Borrás, L., 2010. Resource distribution and the trade-off between seed number and seed weight: a comparison across crop species. Ann. Appl. Biol. 156, 91–102.
Gambín, B.L., Borrás, L., Otegui, M.E., 2006. Source–sink relations and kernel weight differences in maize temperate hybrids. Field Crops Res. 95, 316–326.
Gwirtz, J.A., Garcia-Casal, M.N., 2014. Processing maize flour and corn meal food products. Ann. N.Y. Acad. Sci. 1312, 66–75.
Hernández, F., Amelong, A., Borrás, L., 2014. Genotypic differences among Argentinean maize hybrids in yield response to stand density. Agron. J. 106, 2316–2324.
Holding, D.R., Larkins, B.A., 2006. The development and importance of zein protein bodies in maize endosperm. Maydica 51, 243.
Hunter, J.L., TeKrony, D.M., Miles, D.F., Egli, D.B., 1991. Corn seed maturity indicators and their relationship to uptake of carbon-14 assimilate. Crop Sci. 31, 1309–1313.
Lending, C.R., Larkins, B.A., 1989. Changes in the zein composition of protein bodies during maize endosperm development. Plant Cell 1, 1011–1023.
MAGyP, 2015. Ministerio de Agricultura, Ganadería y Pesca de la República Argentina. Norma XXIX from Resolución Número 757. Boletín Oficial, October 17th 1997, p. 17. http://www.infoleg.gov.ar (verified 1/30/15.).
Muchow, R.C., 1990. Effect of high temperature on grain-growth in field-grown maize. Field Crops Res. 23, 145–158.
Otegui, M.E., 1995. Prolificacy and grain yield components in modern Argentinian maize hybrids. Maydica 40, 371–376.
Paulsen, M.R., Hill, L.D., 1985. Corn quality factors affecting dry milling performance. J. Agric. Eng. Res. 31, 255–263.
R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org/
Robutti, J.L., Borras, F.S., Eyherabide, G.H., 1997. Zein compositions of mechanically separated coarse and fine portions of maize kernels 1. Cereal Chem. 74, 75–78.
Rooney, L.W., Serna-Saldivar, S.O., 2003. Food use of whole corn and dry-milled fractions. In: White, P.J., Johnson, L.A. (Eds.), Corn: Chemistry and Technology. American Association of Cereal Chemists, Saint Paul, pp. 495–535.
Rotundo, J.L., Borrás, L., Westgate, M.E., Orf, J.H., 2009. Relationship between assimilate supply per seed during seed filling and soybean seed composition. Field Crops Res. 112, 90–96.
SAS Institute, 1999. The SAS Online Doc v. 8. SAS Institute Cary, NC.
SENASA, 2012. Servicio Nacional de Sanidad y Calidad Agroalimentaria. Coordinación de Productos Granarios. Estadística: Exportaciones de maíz flint a la UE por destino y en Tm (200-2012). http://www.senasa.gov.ar

Sadras, V.O., 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Res. 100, 125–138.
Severini, A.D., Borrás, L., Westgate, M.E., Cirilo, A.G., 2011. Kernel number and kernel weight determination in dent and popcorn maize. Field Crops Res. 120, 360–369.
Vega, C.R.C., Sadras, V.O., Andrade, F.H., Uhart, S.A., 2000. Reproductive allometry in soybean, maize and sunflower. Ann. Bot. 85, 461–468.
Weih, M., 2003. Trade-offs in plants and the prospects for breeding using modern biotechnology. New Phytol. 158, 7–9.
Wilcox, J.R., Guodong, Z., 1997. Relationships between seed yield and seed protein in determin()ate and indeterminate soybean populations. Crop Sci. 37, 361–364.
Wilcox, J.R., Shibles, R.M., 2001. Interrelationships among seed quality attributes in soybean. Crop Sci. 41, 11–14.
Yan, W., Rajcan, I., 2002. Biplot analysis of test sites and trait relations of soybean in Ontario. Crop Sci. 42, 11–20.