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Kernel number and kernel weight determination in dent and popcorn maize

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ABSTRACT

Yield formation in maize (*Zea mays* L.) dent hybrids has been directly linked to the rate of plant biomass accumulation and partitioning of assimilates to the developing grain. Maize popcorn genotypes have been studied less extensively, but their kernels are known to differ in terms of endosperm structure and typical growth patterns. Our objective was to evaluate how variation in plant growth rate (PGR) at different stages of kernel formation and development affected kernel number per plant (KNP), individual kernel weight (KW) and rate and duration of kernel growth in popcorn genotypes, relative to dent ones. We conducted three experiments (two in Ames, Iowa, and one in Pergamino, Argentina) in which PGRs around flowering and during the linear phase of the grain-filling period of four dent and eight popcorn genotypes were altered by plant density, defoliations and thinning treatments.

Yield per plant, KNP, KW, rate and duration of kernel growth all showed significant kernel type (popcorns vs. dents) effects ($p < 0.01$). KNP was highly correlated with ear biomass accumulated around flowering in dents and popcorns, and popcorns showed a higher efficiency for setting kernels per unit of ear biomass accumulated around flowering ($p < 0.01$). Popcorn inbred R18 in particular showed a significantly higher efficiency, consistent across experiments. Relationships between potential KW at early grain filling or kernel growth rate and the PGR per kernel around flowering were different for dent and popcorn genotypes. Most popcorns established a lower potential KW compared to dent genotypes at similar PGRs per kernel around flowering. Also, popcorn kernels were less prone to decrease KW in response to severe reductions in plant growth during the linear phase of the grain-filling period as promoted by defoliation treatments (significant kernel type × source manipulation treatment interaction, $p < 0.001$). Despite different patterns of KNP and KW determination, yield variation across dent and popcorn genotypes and environments corresponded closely to the potential sink capacity established by the end of the *lag* phase 14 days after anthesis. This result emphasizes the importance of the flowering period to establish KN and KW across different maize germplasm.

1. Introduction

Maize (*Zea mays* L.) grain yield formation is often studied as a function of harvested kernels per unit land area and the average individual kernel weight. Trait dissection of maize kernel number and kernel weight determination has directed research efforts towards understanding their relationship with plant and crop growth at different crop developmental stages (Andrade et al., 1999; Borrás and Gambín, 2010). Studies relating plant growth with reproductive development (i.e., number and size of kernels formed) have focused primarily on dent germplasm. In the present study, we expanded this analysis to include popcorn genotypes, focusing on possible differences in developmental patterns that determine grain yield components across a more diverse germplasm.

It is well established that the number of kernels set per plant varies with plant growth around flowering (Tollenaar et al., 1992; Andrade et al., 1999). The number of kernels per plant that a maize hybrid or inbred will set at a given plant growth rate depends upon the biomass partitioning to the developing ear (Andrade et al., 1999). A slower rate of ear growth, associated with slow plant growth or less partitioning of assimilates to the ear, results in reduced kernel set. Moreover, Echarte and Tollenaar (2006) and D'Andrea et al. (2009) documented genotypic differences in kernel set per unit of ear biomass accumulated around flowering. Information on biomass partitioning to the ear for dent germplasm

Abbreviations: PGR, plant growth rate; KNP, kernel number per plant; KW, kernel weight; WC, water content; MC, moisture concentration; DAA, days after anthesis.

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has increased dramatically in recent years due to its importance in understanding the physiological basis for the anthesis–silking interval and genotype × environment interactions affecting yield formation (Edmeades et al., 1993; Echarte et al., 2004; Borrás et al., 2007). Although there is a general understanding that popcorns are more prolific than dents (Ziegler, 2001), there is also a basic lack of knowledge on how efficient they are for biomass partitioning to the ear around flowering or how partitioning to the ear relates to efficiency of kernel set for popcorns.

Kernel weight at physiological maturity depends on the potential kernel size established early in grain filling, and the plant capacity to provide assimilates needed to fulfill this potential during grain filling (Borrás and Westgate, 2006). Recent studies have revealed that kernel water relations are strongly associated with potential and final kernel weight, and may mediate environmental and genetic effects on this yield component. During the first period of grain filling, called the *lag* phase, the number of starch deposition sites is established (i.e., the number of cells per endosperm and starch granules per cell) (Reddy and Daynard, 1983; Jones et al., 1996). Dry matter accumulation is almost nil during this period, but water accumulation is rapid, driving endosperm expansion and increasing potential sink size. Kernels continue to accumulate water until about mid grain fill, when kernel maximum water content (MWC) is achieved. Borrás et al. (2003) showed that MWC was a fairly reliable predictor of potential kernel weight and was linearly related to the kernel growth rate in dent inbred lines and hybrids grown under favorable conditions. As grain filling advances, kernels progressively desiccate and moisture concentration (MC; on a fresh weight basis) provides an accurate measure of the progress towards physiological maturity. Kernel moisture concentration at physiological maturity appears to be fairly stable among dent germplasm (Gambín et al., 2007). However, popcorn genotypes typically matured at lower MC values than dents (Borrás and Westgate, 2006; Borrás et al. 2009). The origins of these differences in MC at maturity are unknown.

Plants adjust their seed number and potential seed size based on growth conditions around flowering (Sadras, 2007; Gambín and Borrás, 2010). The close relationships between MWC and kernel growth rate with assimilate supply during the *lag* phase strongly implicate source availability early in grain filling as an important determinant in establishing potential kernel sink capacity – and ultimately KW (Borrás and Gambín, 2010). Plant growth rate (PGR) per kernel around flowering has been used as a surrogate of assimilate availability per kernel during the *lag* phase (Gambín et al., 2006, 2008). Kiniry et al. (1990), however, found no KW response in popcorn genotypes when KNP was reduced and plant growth rate per kernel was increased at flowering. Greater resistance to pericarp expansion resulting from greater pericarp thickness (Tracy and Galinat, 1987) or a different content of extensin proteins (Hood et al., 1991) could limit the responsiveness of popcorn kernel expansion to changes in assimilate supply early in grain filling. If so, their relationship with plant growth might differ from that observed in rapidly expanding kernels of dent genotypes.

We evaluated how KNP, KW and kernel growth patterns are affected by changes in plant growth for several contrasting popcorn and dent inbreds and hybrids. We tested whether the allocation of biomass to reproductive structures follows the same pattern in popcorn and dent genotypes through a series of expected responses: (i) the number of kernels set per plant will depend on the biomass allocated to the growing ear around flowering, with minimum differences in the number of kernels set per unit of ear biomass when genotypes are compared, (ii) PGR per kernel at flowering will explain differences in potential KW for all genotypes, and (iii) dent and popcorn genotypes will reduce their KW to a similar proportion (relative reduction) when source strength is reduced to similar levels during the linear phase of the grain-filling period.

2. Materials and methods

Two field experiments (Exps. I and II) were carried out at Iowa State University, Ames, USA, at the Brunner Farm during 2007, and a third study (Exp. III) was conducted at INTA, Pergamino, Argentina, during the 2007/2008 growing season. In Exps. I and II, we used a set of public inbred lines that were selected for diverse KW and kernel growth patterns from a previous screening (Borrás et al., 2009). Based on differences in above ground biomass per plant (small, medium and large plant sizes) and in kernel sizes, selected genotypes were: R18 (small plant type, highly prolific, ~100 mg kernel^{-1}, popcorn), IDS69 (small plant type, ~120 mg kernel^{-1}, popcorn), IDS91 (medium plant type, ~120 mg kernel^{-1}, popcorn), B73 (large plant type, ~270 mg kernel^{-1}, dent), Mo17 (large plant type, ~310 mg kernel^{-1}, dent) and N209 (medium plant type, ~270 mg kernel^{-1}, dent). In Exp. II genotypes consisted of six popcorn (95:2, IDS69, IDS91, R18, R-28-2 and R-53-1) and two dent (B73 and N209) inbred lines. A full description of all these public genotypes can be found at www.ars-grin.gov (verified 1 October, 2009). Genotypes R18, R-28-2 and R-53-1 are classified as popcorn genotypes, as they pop producing flakes when heated, although they were not specifically developed as inbreds for producing commercial popcorn hybrids. In Exp. III, we used three commercial maize hybrids. Two were popcorn genotypes (P625 and P802, Agricultural Alumni Seed Improvement Association Inc.) and one was a dent (AW190, Monsanto Argentina) kernel type. Exps. I and III were conducted for evaluating the effect of altered plant growth on KNP, KW and kernel growth patterns; Exp. II was designed to compare genotypes at a single uniform plant density of 9 pl m^{-2}.

Treatments in Exp. I were a factorial combination of (i) genotypes, (ii) two plant densities (3 and 9 pl m^{-2}), (iii) a defoliation treatment applied at the beginning of grain filling (17 d after 50% anthesis (DAA)), and (iv) control at each plant density. Exp. III was planted at 9 pl m^{-2} and consisted on five treatments designed to alter plant growth rate: (i) a defoliation treatment applied at ca. 15 d before 50% anthesis (DBA), (ii) 50% plant thinning at ca. 15 DBA, (iii) a defoliation at 17 DAA, (iv) 50% plant thinning applied at 17 DAA, and (v) control treatment in which leaf area and plant density were not altered. Defoliation treatments involved removing all leaves starting from the bottom of the plant leaving only the top three or four leaves. Thinning treatments were done by removing every other plant within the row. Both high plant density (Exp. I) and defoliation treatments (Exps. I and III) were intended to reduce PGR. Low plant density (Exp. I) and thinning treatments (Exp. III) were imposed to increase PGR around flowering or during grain filling. Exps. I and II were planted 11 May and 25 May, respectively, in a randomized complete block design with three replicates. Exp. III was planted 5 October in a split-plot design with three replicates, where treatments were the main plots and genotypes the sub-plots. In Exp. I, each plot consisted of 6 (high density) or 8 (low density) rows, 5.5 m long and 0.76 m apart; in Exp. II, plots were 6 rows wide, 5.5 m long and 0.76 m apart. In Exp. III, plots were 5 (control and defoliation treatments) or 7 (thinning treatments) rows wide, 7 m long and 0.70 m apart. In all cases, plots were over planted and thinned at the 3-leaf stage (Ritchie et al., 1993) to the desired plant density. Exps. I and II were rain-fed, but timely rains occurred and plants showed no signs of water stress. Exp. III was irrigated through a sprinkler system. Nitrogen was applied before planting in Exps. I and II with 110 kg N ha^{-1}. Nitrogen was applied at 100 kg N ha^{-1} twice in Exp. III: at the 4-leaf stage (Ritchie et al., 1993) and ca. 20 days before flowering. Pests, weeds and plant diseases were controlled by standard agronomic practice throughout the growth cycle in all experiments.

Individual kernel dry weight and water content were measured throughout kernel development beginning 10 days after 50%