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Source/sink ratio and the relationship between maximum water content, maximum volume, and final dry weight of maize kernels

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Abstract

Final kernel weight (KW) is closely related to maximum kernel volume (KV) and maximum kernel water content (KWC). It is not clear, however, how changes in the reproductive sink capacity, assimilate availability during grain filling and physical restriction to kernel expansion affect the relationship between KW and KWC or between KW and KV. Three experiments were conducted at Balcarce, Argentina and Ames, USA. Defoliation, thinning, plant density, restricted pollination and volume restriction treatments were imposed to manipulate KV, sink and source capacity. KW varied from 111 to 436 mg across all hybrid–treatments combinations and was related to the source/sink ratio during grain filling ($r^2 = 0.85$). Treatment variation in KW was related primarily to changes in kernel growth rate, except for the complete defoliated treatment, which also shortened the duration of grain filling. KW was correlated with maximum KWC ($r^2 = 0.77$, $p < 0.001$) and with maximum KV ($r^2 = 0.91$, $p < 0.001$). The developmental patterns for KW, KWC and KV during grain filling were not affected by the source/sink manipulations, except for severe defoliation. In the latter case, maximum KWC was not a good estimate of final KW. KV, however, was sensitive to reductions in carbohydrate supply during grain filling and was closely correlated to KW. Physical restriction to kernel expansion reduced kernel weight 13% relative to its control ($p < 0.01$). But restricting kernel expansion did not alter the general relationships between KW and KWC or between KW and KV, because kernel density was not affected.

Keywords: Source/sink ratio; Kernel weight; Kernel water content; Kernel volume; Maize

1. Introduction

Biomass accumulation in maize kernels begins shortly after fertilization and progresses in a sigmoid pattern in which three phases can be distinguished (Bewley and Black, 1985). The first phase corresponds to the *lag phase*, which is a formative period during which sink capacity is set (Jones et al., 1996; Reddy and Daynard, 1983). It is characterized by a rapid increase in kernel water content with little dry matter deposition (Saini and Westgate, 2000). The second phase of seed growth, known as the effective grain filling period, involves active biomass accumulation and is generally more important than the *lag phase* in actual grain size determination (Westgate et al., 2004). During this phase, kernel water content reaches its maximum value and begins to decline closely coordinated with dry matter deposition. In the third phase, kernels achieve their maximum dry weight (commonly referred to as physiological maturity) and enter a quiescent state (Saini and Westgate, 2000).

Variation in final grain weight reflects the interaction between source capacity and sink strength (i.e. the source/sink ratio) during the effective grain filling period (Borrás and Otegui, 2001; Westgate et al., 2004; Andrade et al., 2005). Source capacity is determined by the photosynthetic activity of the crop and by the availability of carbohydrate reserves (Uhart and Andrade, 1991; Rajcan and Tollenaar, 1999; Westgate et al., 2004). Sink capacity is the product of sink number and sink activity (Yang et al., 2004). In general, kernel number is the main determinant of sink capacity (Westgate et al., 2004). As shown by Borrás et al. (2004), a decrease in the post-flowering source/sink ratio can reduce final kernel weight dramatically; while a many-fold increase in assimilate availability per kernel only increases kernel weight slightly.

Abbreviations: KW, kernel weight; KWC, water content; KV, kernel volume; GDD, growing degree days; PWGK, plant weight gain per kernel

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Final kernel weight is closely correlated with maximum kernel volume in wheat (*Triticum aestium* L.; Millet and Pinthus, 1984), rice (*Oriza sativa* L.; Murata and Matsushima, 1975), soybeans (*Glycine max* L.; Egli et al., 1987), sorghum (*Sorghum bicolor* (L.) Moench; Gambín and Borrás, 2005) and maize (Kiniry et al., 1990; Saini and Westgate, 2000; Gambín et al., 2005), since final kernel density is essentially constant (Millet and Pinthus, 1984; Gambín and Borrás, 2005). Seed water content has been used as an estimate of seed volume (Saini and Westgate, 2000; Borrás et al., 2003; Borrás and Westgate, 2006), but direct measurements of kernel volume have been rarely made in maize. As suggested by Westgate and Boyer (1986), once maximum water content is achieved maximum kernel volume is largely determined. In a recent study on sorghum, however, Gambín and Borrás (2005) found that kernel volume continues to increase after maximum water content has been attained, apparently due to dry matter deposition. If this also were the case for maize, lack of assimilates could prevent kernels from reaching their maximum volume. In these situations, the relationship between maximum water content and kernel volume might not hold, and therefore the former variable would not be a reliable estimator of final kernel weight (Borrás and Westgate, 2006).

The capacity to increase in volume also is critical for dry matter accumulation in soybean (Egli et al., 1987). Physical restriction of pod expansion severely limits cotyledon weight gain, while 'releasing' cotyledons from this restriction *in culture* greatly increases their capacity for growth (Egli et al., 1987). To our knowledge, there are no records in the literature indicating how maize kernel growth would response to an imposed physical restriction.

The objective of this study was to determine how the relationships between maximum water content, maximum kernel volume and final kernel weight are affected by changes in the reproductive sink capacity, assimilates availability during grain filling and physical restriction to kernel expansion. Understanding these relationships is essential for predicting kernel weight responses when favorable and/or unfavorable growth conditions occur during reproductive growth.

2. Materials and methods

Data presented in this work were obtained from three experiments carried out without any discernible nutrient or water limitations. Experiments 1 and 2 were conducted during the 2002/2003 and 2003/2004 growing seasons, respectively, at the INTA Research Station near Balcarce, Buenos Aires, Argentina (37°45′S, 58°18′W). Hybrid Dekalb 615 (Hybrid A) was sown on 15 October both years, following a randomized complete block design with three replications. Each plot consisted of four rows 0.7 m apart and 12 m long. Final population density was 8 plants m^{-2} in both years. Two defoliation treatments, which decreased leaf area relative to controls by 50% (M) and 85% (S), were applied 20 days after silking to reduce the source/sink ratio during grain filling (Table 1). Silking was taken as the time when 50% of the plants in a row presented visible silks.

Table 1
Description of treatments applied to hybrid Dekalb 615 in Balcarce, Argentina (Experiments 1 and 2) and hybrids Dekalb 5878, Fontanelle 4402 and Fontanelle 4741 in Ames, USA (Experiment 3)

Experiment	Treatment		
	Designation	Plant density (plants m^{-2})	Description
1–2	S	8	Severe defoliation (85% leaf removal)
1–2	M	8	Medium defoliation (50% leaf removal)
1–2	C	8	Control (no leaf removal)
3	2F	2	Free pollination
3	2R	2	Restricted pollination (ears covered 1 day after silking)
3	2V[a]	2	Free pollination, volume restriction 20 days after silking
3	4F	4	Free pollination
3	4R	4	Restricted pollination (ears covered 1 day after silking)
3	8F	8	Free pollination
3	8R	8	Restricted pollination (ears covered 1 day after silking)
3	8T	8	Free pollination, thinned to 2 plants m^{-2} at silking
3	8D	8	Free pollination, all leaves removed 20 days after silking

[a] Applied only to hybrid Dekalb 5878.

Experiment 3 was conducted during the 2004 growing season at the Bruner Research Farm of Iowa State University near Ames, IA, USA (42°2′N, 93°37′W). Commercial hybrids Dekalb 5878, Fontanelle 4402 and Fontanelle 4741 (Hybrid B, Hybrid C and Hybrid D, respectively) were sown on 11 May 2004 at approximately 8 plants m^{-2}, and thinned to 1 of 3 plant densities: 2, 4 and 8 plants m^{-2} by the 4th leaf stage. Each hybrid by population density combination was sown in strip plots of eight rows 0.76 m apart and 36 m long. Within each plot, individual plants were tagged and their silking dates were recorded. The sub-apical ears of these plants were removed when present. Various treatments were imposed on each hybrid-plant density combination to alter the source/sink relationship during grain filling (Table 1). Treatments were applied on at least 30 tagged plants of each plot. In the freely pollinated 8 plants m^{-2} density, a complete defoliation (D) was applied in half of the plot to all three hybrids 20 days after silking. For restricted pollination (−R), ears were covered with glassine bags 1 day after silking. For volume restriction (−V), a non-elastic but flexible plastic mesh was tightly wrapped around the intact ear 20 days after silking. The mesh was designed to restrict expansion but allow air exchange through the husks. The volume restriction treatment was applied only to freely pollinated hybrid B grown at 2 plant m^{-2}.

In all three experiments, grain samples were collected at 4 to 7-day intervals starting 10 days after silking until physiological maturity. At each sampling, ears were harvested from three randomly selected plants and transported to the laboratory in a humidified container, where 10 kernels were removed from the lower third of each ear. Kernel fresh weight was recorded, and then kernels were dried to constant weight in a forced-air oven