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Genetic improvement in density and nitrogen stress tolerance traits over 38 years of commercial maize hybrid release

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ABSTRACT

Research attention to improving source and sink strength in maize production is requisite for enhancing yield. Improvement in source strength has been achieved with higher post-silking dry matter accumulation, whereas historical improvement in sink strength has been mostly attributed to increasing kernel number (KN) per unit area, in part because KN is known to be more vulnerable to abiotic stresses compared to kernel weight (KW). However, KW can also vary widely as it is dependent on both genotype and dry matter accumulation during the post-silking period. In order to illustrate the consequences of breeding efforts over a 4-decade period for enhancing source and sink strength at varying nitrogen rates and plant densities, a 2-year and 2-location study was conducted in 2013 and 2014. Eight commercial hybrids from DeKalb released from 1967 to 2005 were compared at 2 nitrogen rates (55 and 220 kg N ha^{-1}) and 3 plant densities (54,000 (D1), 79,000 (D2) and 104,000 (D3) plants ha^{-1}). Breeding progress increased grain yield per hectare (GY) by an average of 66 kg ha^{-1} $year^{-1}$, and grain yield per plant (GYP) by 0.91 g $plant^{-1}$ $year^{-1}$ across all treatments and environments. This yield increase with hybrid improvement was attributed more to an increase in KW (1.29 mg $kernel^{-1}$ $year^{-1}$ across all treatments and both locations), than to any increase in KN. The overall source-sink ratio (SSR – ratio of post-silking dry matter accumulation to kernel number per plant) also increased by an average of 1.25 mg $kernel^{-1}$ $year^{-1}$ across all treatment and locations. The hybrid improvement in SSR was more pronounced at the high N rate or low plant density. Post-silking dry matter accumulation (PostDM) increased by an average of 54 kg ha^{-1} $year^{-1}$ across all treatments and locations. KW was highly correlated with ear growth rate (EGR) during grain fill. New hybrids had much higher KW gain per unit of EGR. Newer hybrids also had a longer active grain filling period, but the correlation of post-silking dry matter accumulation to the duration of active grain filling period was weak. This study showed that the breeding progress for yield gain in these DeKalb hybrids was achieved by (i) longer duration of the grain filling period plus longer leaf stay green that accompanied a higher PostDM of newer hybrids, (ii) enhanced source to sink strength during grain filling by a higher SSR in newer hybrids, (iii) improved efficiency for transferring source from cob and husk to grain by increasing KW gain per unit of EGR, and (iv) enhanced stress tolerance in newer hybrids to maintain grain yield even under high density.

Introduction

Maize grain yield improvements over the decades have been attributed in rather equal proportions to management and genetic advances (Duvick, 2005). Duvick (2005) observed that there were some traits that breeders intended to change and, on the other hand, there were other traits that improved simultaneously when breeders were narrowly focused on enhancing grain yield. One trait that is of consistent focus is the enhancement in source and sink strength, as well as improving the efficiency of nutrient partitioning from source to sink (Tollenaar and Lee, 2011). Source strength can be quantified using post-silking dry matter accumulation (PostDM). However, PostDM is affected by both pre- and post-silking canopy attributes such as leaf area index (LAI), radiation use efficiency, and specific leaf nitrogen (SLN) (Cirilo et al., 2009). The consequences of breeding improvements on LAI are inconsistent. In one com-

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parison, a 1988 widely used hybrid achieved a higher LAI than a 1959 widely used hybrid in Ontario (Tollenaar and Aguilera, 1992; Tollenaar et al., 1997). Duvick (1984) reported that LAI differences were minimal among hybrids from 1930 to 1980 when a series of 48 Pioneer hybrids were tested in Iowa across 3 densities. Specific leaf nitrogen, representing leaf N per leaf area, was associated with higher N-use efficiency in newer hybrids even at low N supply (McCullough et al., 1994). DeBruin et al. (2013) used SLN at silking for estimating grain yield, KW and KN at maturity; the threshold of SLN for maximum grain yield, KW and KN were 1.5, 1.6 and 1.3 g m^{-2}, respectively.

Kernel number per area (KN), kernel number per plant (KNP) and potential kernel weight are direct variables that contribute to sink strength. Kernel number per area have increased in response to targeted genetic and management (e.g. higher plant density) improvements. Kernel number per plant is well known to be affected by plant growth rate (PGR) during the critical period surrounding silking (Tollenaar et al., 1992; Uhart and Andrade, 1995; Echarte et al., 2004). The association between KNP and PGR was shown to be curvilinear before KNP reaches its maximum and then this association reaches a plateau (Otegui and Andrade, 2000). Andrade et al. (1999, 2002) showed that the incremental rate for KNP of the apical ear decreased to 0 when PGR reached 4 g $plant^{-1}$ d^{-1}. Breeding efforts to increase KNP have been successful when a lower threshold of ear growth rate (EGR) was needed to achieve maximal KNP during the critical period for newer hybrids compared to older hybrids (D'Andrea et al., 2008). Ear growth rate (EGR) during the critical period was proved to be a good estimator of KNP, and KNP reached a maximum when EGR during critical period was over 1.6 g $plant^{-1}$ d^{-1} (D'Andrea et al., 2008). Echarte et al. (2006) indicated that ear demand included KNP and kernel growth rate. Given this, EGR can be treated as a component of ear demand and overall sink strength.

Potential kernel weight is determined about 12–15 days after onset of grain filling period at end of lag phase (Borrás and Gambín, 2010). Whether kernel weight (KW) at maturity achieves its potential kernel weight depends on conditions during grain filling period such as persistence of green leaf area and redistribution of assimilated biomass during grain filling period (Hammer et al., 2010). One lesser-known change in ear traits that potentially coincides with grain yield gain is the increased KW achieved by newer hybrids under well-watered conditions, that trait change was noted in a series of ERA hybrids from 1953 to 2001 tested in Chile (Barker et al., 2005).

It is well known that KW is determined during the grain filling stage, including the lag phase (when KW increases very little) and the active grain filling stage (when KW increases linearly with thermal time) (Maddonni et al., 1998; Echarte and Andrade, 2003). Maddonni et al. (1998) showed that hybrids with a larger potential KW (>300 mg $kernel^{-1}$) had a longer lag phase and a higher kernel growth rate with a longer active grain filling period compared to hybrids with smaller potential KW (≤300 mg $kernel^{-1}$). However, Borrás and Otegui (2001) showed that KW was not correlated with the length of active grain filling period; instead, KW was correlated with the kernel growth rate during grain filling period for both large and small kernel hybrids.

The comparison between source strength and sink strength during grain filling period can be quantified using the source-sink ratio (SSR), which is often known as the ratio of post-silking dry matter accumulation divided by kernel number per plant (Rajcan and Tollenaar, 1999b; Borrás et al., 2003; Borrás and Otegui, 2001; Sala et al., 2007). Modern hybrids exhibited a higher SSR during the post-silking period and these changes were associated with increasing leaf longevity during grain filling period (Rajcan and Tollenaar, 1999b). KW is also affected by the source capacity variation (such as post-silking dry matter accumulation and duration of grain filling period) when ear demand increased due to higher yield potential, especially in newer hybrids compared to older hybrids (Echarte et al., 2006). Breeding efforts to prolong the active grain filling period has been well documented (Ma and Dwyer, 1998; Mi et al., 2003).

Because grain yield gain over time in maize also benefited from steadily increasing plant density, there can be indirect consequences of density on canopy and grain component traits. Cardwell's study on yield gain in Minnesota from 1930 to 1980 demonstrated that increased plant density (30,740–49,780 plants ha^{-1}) over these 50 years had contributed to 21% of the total grain yield gain (Cardwell, 1982). Duvick (2005) also showed newer hybrids perform better under 79,000 plants ha^{-1} than older hybrids for a series of Pioneer hybrids. However, the highest density in that study is now a rather common density in commercial U.S. maize production. Higher density can increase light interception by increasing leaf area index (Tollenaar and Lee, 2002), but higher densities may also increase abiotic stresses that can lead to a reduction in KNP (Poneleit and Egli, 1979; Echarte et al., 2000). Andrade et al. (1999) indicated that the number of kernels set per unit of PGR decreased at high densities and that higher densities therefore contributed to a lower final KNP. High density can also reduce KW due to a reduction in leaf area per plant (Borrás et al., 2003). The performance uncertainty of KNP and KW in newer hybrids both near and well above current plant densities should be investigated.

Maize hybrid evaluations are commonly made under high N conditions due to a large yield loss under N deficient conditions (D'Andrea et al., 2008). However, N deficiency has a large influence on canopy variables, such as green leaf number during the grain filling period, LAI and SLN, which will cause reduction in radiation use efficiency and light interception and eventually lower KN and KW. A series of DeKalb hybrids from 1930s to 1980s showed similar yield increase rates per year under both low fertility and high fertility conditions (Castleberry et al., 1984). However, other previous studies including more recent hybrids (i.e. released after year 2000) showed higher grain yield increases per year under non-stressed conditions. For instance, Barker et al. (2005) observed that a series of Pioneer ERA hybrids (1950–2001) had higher grain yield gain per year under well-watered than in drought stress conditions. Hence, because of the uncertain consequences of abiotic stress factors like N deficiency on hybrids of different eras, the consequence of different N levels on grain yield gain per year warrants further investigation.

Given the risks of yield reduction under both N deficiency and high density stress factors, as well as the opportunities for increasing knowledge to help guide future genetic selection, it is necessary to clarify the traits that have changed over more than three decades of breeding programs under multiple N rates and densities. Therefore, the objectives of this study were to: 1) determine the effects of N rate, plant density and hybrid era on canopy traits, grain yield and its components; 2) evaluate the existence of hybrid interactions with N rate and plant density on these vegetative and reproductive traits; and 3) study whether the correlations between KW and ear growth rate during grain filling period changed with almost 40 years of Dekalb hybrid development.

2. Materials and methods

2.1. Experiment design and management

A field study was conducted at ACRE (Agronomy Center for Research and Education, 40∘28′07"N, 87∘00′25"W), West Lafayette, IN, USA and PPAC (Pinney Purdue Agricultural Center, 41∘26′41"N, 86∘56′41"W), Wanatah, IN, USA in 2013 and 2014. The soil type