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Plant biomass and nitrogen partitioning changes between silking and maturity in newer versus older maize hybrids

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ABSTRACT

Characterization of the pre- and post-silking period differences in dry matter (DM) accumulation and nitrogen (N) uptake and partitioning between older and newer maize (*Zea mays* L.) hybrids is useful in the context of providing possible mechanisms of yield and N efficiency gains over the decades of genetic improvement. However, there is substantial uncertainty about the mechanisms by which DM and N partitioning into distinct plant organs at silking (R1) affect their respective post-silking dynamics in modern versus older maize hybrids. Clarity is also lacking about management impacts on how source (leaf and stem) strength and sink (grain) strength drive post-silking DM (PostDM) and post-silking N (PostN) dynamics in genotypes of different eras. In this two-year and two-location study, we compared two newer hybrids (commercialized in 2005) to one older hybrid (commercialized in 1975) in 2012 and to two older hybrids (the same 1975 hybrid, and one commercialized in 1967) in 2013. All hybrids were compared under two N fertilizer rates (55 kg N ha^{-1}, 220 kg N ha^{-1}) and three densities (54,000 pl ha^{-1}, 79,000 pl ha^{-1}, 104,000 pl ha^{-1}). Although both moderate and high plant densities increased leaf N contents at silking and remobilized N from leaves during grain fill, density × hybrid interactions were not significant for these or almost all parameters measured. Older hybrids consistently partitioned more of their total DM at silking to stem than leaf relative to both newer hybrids. Both newer and older hybrids increased PostDM (an average increase from 8.3 to 10.1 Mg ha^{-1}) and PostN (an average increase from 36.3 to 63.6 kg N ha^{-1}) in response to the higher N rate over the 2-year period. Newer hybrids accumulated 2.1–2.3 Mg ha^{-1} more grain DM than the single older hybrid in 2012, and newer hybrids accumulated 1.3 and 3.1 Mg ha^{-1} more grain DM than the 1975 and 1967 hybrids in 2013 when overall PostDM gains were much higher than in 2012. In 2013, more of the Grain N content (GrainN) was derived from post-silking N uptake in newer hybrids versus older hybrids. Plant component DM and N changes between silking and maturity stages in 2013 suggested 33% of final grain N originated from leaves (with no net DM depletion), and 22% of grain N originated from stems (accompanied by a net 20% DM depletion), during grain filling in a rather consistent manner for all four hybrids. However, newer hybrids maintained a higher leaf DM and leaf N content at maturity (despite a lower leaf N concentration and higher grain N harvest index) compared to older hybrids. These results indicated that retaining leaf function by enhancing leaf biomass and N content and, consequently, PostN accumulation during the grain filling, benefited from a higher DM partitioning to leaves at silking in newer hybrids.

1. Introduction

Post-silking N uptake (PostN) and remobilized N (RemN) from other plant organs during grain filling are two primary sources for Grain N content (GrainN) at maturity. The inverse correlation between these two sources is a common theme in the maize literature that has focused on post-silking stage N uptake and allocation (Muchow 1994; Pan et al., 1995; Borrell et al., 2001; Gallais and Coque, 2005; Coque and Gallais, 2007; Ciampitti and Vyn, 2013). Most RemN results from protein turnover, especially rubisco (Triboi and Triboi-Blondel, 2002), a key enzyme for photosynthesis. Because leaf senescence accelerates following the proteolysis of leaf protein, the consequent reduction in new photosynthesis carbon adversely affects PostN (Gallais and Coque, 2005).

Newer maize hybrids normally accumulate more dry matter (DM) at maturity and achieve higher GrainN because of higher PostN (Tollenaar and Lee, 2011; Ciampitti and Vyn, 2012; Ning et al., 2013). Nitrogen fertilizer input increased dramatically from 1960s

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to 1980s, but it remained relatively constant at about 157 kg ha^{-1} from 1980s to 2010 in U.S. (Baker et al., 2011). In contrast, the N accumulation in maize increased from 150 to 250 kg ha^{-1} from 1960s to 2005s (Ciampitti and Vyn, 2014). Although nitrogen harvest index (NHI) as a ratio of grain N content to above ground N content at maturity has not changed by hybrid era, PostN accounted for an average of 56% of final GrainN in newer hybrids (1991–2011) compared to just 50% in older hybrids (prior to 1991) (Ciampitti and Vyn, 2013).

Regulation of the tradeoff between RemN and PostN can be ascertained by determining whole-plant N contents and N partitioning at the beginning and end of the grain fill period. A higher PostN in newer hybrids is also encouraged by formation of a stronger source (N content in leaves and stems) during vegetative growth and a stronger sink (ear N demand) during the grain filling stage (Lee and Tollenaar, 2007). Coque and Gallias (2007) observed that genotypic variation in the proportion of RemN is mainly determined by whole-plant N content at silking and sink strength. Although the equivalent of over 90% of PostN can be transported into grain, the main restriction factor is simply plant post-silking N uptake capability per se (Coque and Gallias, 2007). Whole-plant N content at silking is positively correlated with RemN, and, because newer hybrids tend to have a higher N content at silking, newer hybrids appear to have stronger source strength at the onset of grain filling (Gallais and Coque, 2005; Ciampitti and Vyn, 2013). However, an overly rapid N remobilization early in grain filling stage can result in weak stems and lodging, especially at high plant density (Rajcan and Tollenaar, 1999a). In some modern hybrids, RemN from vegetative organs is more related with ear demand after the mid-grain filling stage (R3) than during the early grain filling (R1–R3) (Ciampitti et al., 2013b). RemN from the stover tends to start around the R2 stage in older hybrids (Below et al., 1981). Karlen et al. (1988), in their study of then-current hybrids observed that N loss from vegetative organ began at silking, but more rapid N translocation to sink started about 200 °C thermal units after silking. A delayed RemN in newer hybrids benefits duration of leaf photosynthesis, which then permits expanded PostN during grain filling (Ciampitti et al., 2013b).

The tradeoff between PostN and RemN is affected by soil N status and plant density management. In N limited conditions, RemN becomes a more important source for GrainN (Tsai et al., 1991; Gallais and Coque, 2005; Abe et al., 2013). In some low-N input conditions both PostN and RemN were equally important to final GrainN (Fonzo et al., 1982; Worku et al., 2007). Typically, high soil-N conditions favor PostN accumulation and the relative fraction of GrainN originating from PostN (Fonzo et al., 1982; Coque and Gallais, 2007; Tsai at al., 1991; Lemaire et al., 2007). Continuous N availability can benefit PostN by prolonging green leaf area retention (Eik and Hanway, 1965) and photosynthesis (Tsai et al., 1991). Higher maize plant density tends to promote RemN more than PostN by increasing above ground N content at silking and accelerating leaf senescence during grain fill (Pan et al., 1995; Ciampitti et al., 2013a). Additionally, the RemN and PostN responses to plant density may also be hybrid dependent. High-yielding hybrids had higher PostN than low-yielding hybrids as N supply increases (Tsai et al., 1991). Newer hybrids had higher post-silking DM accumulation (PostDM) at high density compared to older hybrids with a lower stover DM deduction (Tollenaar, 1991).

Genotypic variation in leaf RemN versus stem RemN has been observed (Tsai et al., 1991; Ta and Weil, 1992; DeBruin et al., 2013). Lemaire et al. (2005) described that leaves – as a metabolic sink – have a higher N concentration than stems – as a structural sink – during vegetative stages. Other studies confirmed that leaf RemN typically far exceeds stem RemN (Below et al., 1981; Tsai et al., 1991; DeBruin et al., 2013). Higher DM partitioning to leaves at silking can stimulate leaf RemN (Beauchamp et al., 1976). On the other hand, Ciampitti and Vyn (2011) showed that hybrids with higher leaf DM at V14 leads to a higher proportion of PostN in GrainN. In addition, hybrids with higher DM partitioning to leaves at silking also tend to have a higher grain yield (Beauchamp et al., 1976; Pan et al., 1995). Plant N deficiency increased DM partitioned to leaf instead of stem at R1 (Ciampitti et al., 2013a). Older era hybrids (about 40 decades ago) tend to accumulate as much N as possible at silking and then translocate a majority of N to grain in reproductive stages. Recent hybrids are focused on enhanced PostN because RemN meets only a fraction of the high demand of GrainN in modern maize production (Ciampitti and Vyn, 2013; Ning et al., 2013). Nevertheless, RemN is still a more stable source compared to PostN under stress conditions, when final grain protein may be more affected by RemN than PostN (Gallias and Coque, 2005).

What is missing from all of the studies described above is a direct and comprehensive evaluation of hybrid era consequences on PostN versus RemN (from both leaf and stem sources) in the management contexts of ranging plant densities and N rates. Typical DM and N conclusions from the past have been based primarily on whole-plant analyses instead of multi-component analyses, and plant densities in previous studies might not represent current plant density in US maize production. The objectives of this study were to: (1) understand DM and N partitioning in leaf and stem at silking of different era hybrids in response to plant densities and N rates; (2) determine the main source of GrainN at maturity—PostN versus RemN (as well as leaf RemN versus stem RemN) with different era hybrids, plant densities and N rates; and (3) evaluate the impacts of DM and N partitioning at silking on post-silking DM and N accumulation.

2. Materials and methods

2.1. Experiment design and management

A 2-year field study was conducted at ACRE (Agronomy Center for Research and Education, 40°28′07″N, 87°00′25″W), West Lafayette, IN and PPAC (Pinney Purdue Agricultural Center, 41°26′41″N, 86°56′41″W), Wanatah, IN. The soil type at ACRE was a Drummer silty-clay loam (fine-silty, mixed, superactive, mesic Typic Endoaquolls) in 2012, and a Chalmers silty-clay loam (fine-silty, mixed, superactive, mesic Typic Endoaquolls) in 2013. The soil type at PPAC was a Sebewa loam (Fine-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Typic Argiaquolls) for both years. Average soil pH, organic matter, exchangeable P, and available K were 6.3, 4.6 g 100 g^{-1}, 22.2 mg kg^{-1}, 94.5 mg kg^{-1} at ACRE in 2012; 6.7, 2.9 g 100 g^{-1}, 34.5 mg kg^{-1}, 106.3 mg kg^{-1} at PPAC in 2012; 6.9, 3.7 g 100 g^{-1}, 22.2 mg kg^{-1}, 105.7 mg kg^{-1} at ACRE in 2013; 6.7, 4.4 g 100 g^{-1}, 17.2 mg kg^{-1}, 91.8 mg kg^{-1} at PPAC in 2013. In both years, the crop rotation was maize after soybean at ACRE, and first-year maize after maize at PPAC. All four experimental fields were chisel plowed in fall and field cultivated in spring.

The experimental design was a split–split plot design, with nitrogen as main plot, plant density as subplot, and hybrids as sub-subplot. Plot size was 3.04 m × 9.15 m with four rows at a row spacing of 0.76 m. Each location had 6 blocks in each year. Three hybrids were evaluated in 2012—DKC61-69 (relative maturity (RM) 111 days), DKC61-72 (RM 111 days), XL72AA (RM 115 days); and the same 3 hybrids plus an additional older-era hybrid (XL45, RM 115 days (Crookston and Hicks, 1978)) were evaluated in 2013. Both DKC61-69 and DKC61-72 were commercially released in 2005. DKC61-69 is designated as VT3 (corn rootworm, European corn borer and glyphosate resistant) while DKC61-72 is designated as Roundup Ready^{TM} (glyphosate resistant only). Hybrids XL72AA and XL45 were popular conventional hybrids in 1975 and