



Review

Physiological perspectives of changes over time in maize yield dependency on nitrogen uptake and associated nitrogen efficiencies: A review

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ABSTRACT

Over the past 3 decades, the study of various mechanisms involved in maize grain yield (GY) formation and its relationship with nitrogen (N) uptake dynamics has been increasingly acknowledged in the scientific literature. However, few studies have combined investigations of GY response to N fertilizer with detailed physiologically based analyses of plant N dynamics such as N uptake quantities, timing, and (or) partitioning – and the complex interactions of those with specific genotypes (G), management practices (M), and (or) production environments (E). Limited reporting of both N and yield dynamics at plant-component, individual-plant, and community levels has contributed to a considerable knowledge gap as to whether the physiological mechanisms that govern maize plant N dynamics and their relationship with GY formation have changed with time. We therefore undertook a comprehensive review to discern trends in physiological aspects of maize response to changing plant densities and fertilizer N rates (M components) under the umbrella of evolving $G \times E$ interactions. We reviewed 100 published and unpublished papers based on field experiments which consistently reported total plant N uptake at maturity and maize GY (frequently among other physiological variables). Our analyses were limited nearly exclusively to experiments involving hybrid (as distinct from inbred) response to M input levels where plant density data was available. Dissection of the complex interactions among years, plant densities and N rates began with division of treatment mean data (close to ~3000 individual points) into two time periods defined by year(s) of the original research: (i) studies from 1940 to 1990 – “Old Era” and, (ii) studies from 1991 to 2011 – “New Era”. For the Old Era, maize GY averaged 7.2 Mg ha^{-1} at a mean plant density of 5.6 pl m^{-2} with a total plant N uptake of 152 kg N ha^{-1} , a grain harvest index (HI) of 48% and N harvest index (NHI) of 63%. For the New Era, maize GY averaged 9.0 Mg ha^{-1} at a mean plant density of 7.1 pl m^{-2} , total plant N uptake of 170 kg N ha^{-1} , a grain HI of 50% and a NHI of 64%. The most striking findings in terms of overall GY and plant N uptake were: (1) on a per-unit-area basis, both potential GY and NIE (GY/N uptake) increased from Old to New Era at comparable N uptake levels, and (2) on a per-plant basis, total plant N uptake at maturity had not changed between Eras despite increased plant density in the New Era genotypes. Other important findings in terms of plant growth and component partitioning responses to N were (i) a consistently strong dependency between dry matter and N allocation to the ear organ in both Eras; (ii) higher total plant biomass (BM) accumulation and N uptake, on an absolute basis, during the post-silking period with New Era genotypes accompanied by relatively smaller changes in HI and NHI; (iii) a strong correlation between plant N uptake at silking time and per-plant GY and its components in both Eras; (iv) New Era ($56.0 \text{ kg GY grain kg}^{-1} \text{ N}$) was primarily associated with reduced grain %N, and to a minor degree with NHI gains; and (v) New Era genotypes showed higher tolerance to N deficiency stress (higher GY when no N fertilizer was applied), and larger GY response per unit of N applied, relative to Old Era hybrids. This improved understanding of the physiological factors underlying progress in maize yield response to N over time, within the context of changing $G \times E \times M$ factors, serves to help guide maize programs focused on achieving further improvements in N use efficiency.

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1. Introduction

Maize (*Zea mays* L.) grain yields (GY) have steadily risen over the last century due to both genetic (from double-X to single-X hybrids, recurrent pedigree breeding systems, marker-assisted breeding, transgenic technologies, etc.) and management (irrigation, fertilizers, tillage practices, planting date, plant density, integrated pest management, etc.) changes. Furthermore, the progressive improvement in maize yields during the last 4–6 decades was not country-specific (Tollenaar and Lee, 2011). Over the last 50 years, the productivity in the United States and China (the current #1 and #2 producers of maize in the world) increased approximately 4 Mg ha^{-1} (CAST, 2006; Cassman and Liska, 2007; FAO, 2011). In France, maize productivity increased $\sim 7 \text{ Mg ha}^{-1}$ over the last 60 years (Derieux et al., 1987; Agreste, 2009). Additionally, in Argentina and Canada, maize yields increased ~ 5.5 and $\sim 4 \text{ Mg ha}^{-1}$, respectively, during the last 40 years (SAGPYA, 2011; OMAFRA, 2009). However, there is ample scope for maize yield improvement in some developing countries, such as India, which achieved an accumulated gain of just 1 Mg ha^{-1} during the last 50-year period (FAO, 2011).

Maize yield potential is defined as the maximum yield obtained by a genotype (G) developed in an adapted environment (E), with non-limiting water and nutrients resources, under no pressure of pests and diseases, using the best management (M) practices (e.g. planting time, plant density, N fertilizer rate, tillage practices, crop rotation, etc.) for the specific hybrid, weather and soil conditions (Evans, 1993). The latter definition highlights the most critical constraint in maize improvement, namely, the complexity of the $G \times E \times M$ interactions. Unfortunately, despite earlier and persuasive concerns articulated by Duvick and Cassman (1999), there is still considerable uncertainty about whether maize yield potential has truly increased since the late 1970s, as well as much under-informed speculation about the most important physiological determinants of maize yield in production systems at peak yield-potential levels. On-farm reports suggested that very high yields (i.e. above 20 Mg ha^{-1}) were already attained decades ago (~ 21 – 23 Mg ha^{-1} in the North of USA; Robertson et al., 1978; Nelson and Reetz, 1986). Other maize yield records followed the same trend, and they can be reviewed at Tollenaar and Lee (2002). If it is possible to accept the validity of these sources of information, one hypothesis that then arises is “potential maize yields did not change during the last 40 years”. Surpassing the stated maize yield barrier of perhaps 24 Mg ha^{-1} will require more balanced research

investments in plant physiology and management systems to complement genetic improvement efforts.

Suggested pathways to higher yield potential in maize frequently focus on achieving greater total plant biomass (BM). For instance, in their recent review, Tollenaar and Lee (2011) proposed focusing efforts in a “resource-effective” fashion by improving plant BM accumulation (“source”) and (or) grain biomass (“sink”). Yet maize yield is dependent on more than just total BM and its partitioning to grain (i.e. assimilate). Plant nutrient uptake, assimilation and allocation are equally important. For example, a previous report documented the direct influence of an N shortage on C flux allocated to the ear during the critical period (± 15 days) around silking, which consequently impacted final kernel number (Kn) of maize (Uhart and Andrade, 1995). Other studies have also documented the negative impacts of N reductions on Kn (Jacobs and Pearson, 1991; Lemcoff and Loomis, 1994). In addition, D’Andrea et al. (2008) showed a very strong association between ear N content and both ear growth rate (EGR) and relative Kn of the apical ear. Similarly, Ciampitti et al. (unpublished) demonstrated that the whole-plant N status prior to silking has a very strong influence on the achievable per-unit-area maize GY at physiological maturity, primarily via plant N uptake impacts on the per-plant Kn and, secondarily, on the kernel weight (Kw). Furthermore, during the post-silking period an adequate ear N supply was observed to be essential for high maize GY formation (“homeostatic effect”), while low plasticity in the ear N content trait was observed relative to the proportion of BM allocated to the ear during the grain filling period (Ciampitti and Vyn, 2011). The previous reports clearly demonstrated the major effect that N nutrition status during the entire growing season exerts over the maize GY formation.

From a physiological viewpoint, a balanced increase in both source and sink strength components from late vegetative stages ($\sim V12$) until at least mid-grain filling period ($\sim R3$ – $R4$) will be most likely to achieve GY gains in maize. Nitrogen is associated with the source component primarily via the impact of ribulose biphosphate carboxylase/oxygenase in leaf tissue on the photosynthesis process (Sinclair and de Wit, 1975). Also of relevance is the essential role of N to the “functional stay green” capability of leaves as they age. Functional stay green is not only linked to delayed leaf senescence, but is also related to retention of the plant’s photosynthetic rate (“functional longevity”), specifically during the post-silking period (Lee and Tollenaar, 2007).

It is important to acknowledge that total plant N uptake at physiological maturity can be dissected in two components, (i) N uptake

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