Contribution of the early-established plant hierarchies to maize crop responses to N fertilization

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ABSTRACT

Maize crop production depends on nitrogen (N) availability, N uptake by the crop and the efficiency with which absorbed N is used to produce biomass (NUE_{BIOM}) or grain yield (NUE_{GRAIN}). This framework assumes unique efficiency values for the whole stand, with no distinction among plants in spite of the inherent inter-plant variability of plant growth, especially under crowding stress. In this work we assessed the degree of contribution of different early-established groups of plants to crop responses to N fertilization of two maize hybrids (H) with different tolerance to crowding stress (high for AX820 and low for AX877) cultivated at two stand densities (9 and 12 pl m^{-2}). Groups corresponded to the lower, mid and upper terciles (Ts) of the crop, representing dominated, intermediate and dominant plants, respectively. In most cases, lower and mid Ts had a greater participation in crop biomass and grain yield responses to N fertilization. The response of NUE_{BIOM} and NUE_{GRAIN} to N fertilization was higher for the lower and mid Ts than for the upper T. For each N level, crop NUE_{GRAIN} was negatively related to inter-plant variability in plant NUE_{GRAIN}. When no N was added, the reduction in crop NUE_{GRAIN} of both hybrids was mainly caused by the increased inter-plant variability in plant N uptake (i.e. resource capture). Additionally, the crowding-intolerant AX877 under the most stressful condition (12 pl m^{-2} and no added N) had a reduced crop NUE_{GRAIN} due to the enhanced plant-to-plant variability in grain yield (i.e. resource use). Consequently, the early-established plant-to-plant variability pattern conditioned crop NUE_{GRAIN}; the predominant path was hybrid dependent.

1. Introduction

Maize grain yield responses to N fertilization are mainly associated with the number of kernels per unit land area (Uhart and Andrade, 1995). This grain yield component depends on crop growth rate during a critical 30-day period centered at silking (Andrade et al., 1999), which is affected by N availability (Uhart and Andrade, 1995). From an eco-physiological approach focused on resource supply, crop growth depends on the acquisition of resources (i.e., solar radiation, water and nutrients) and the efficiency with which the acquired resource produces biomass (Galagher and Biscoe, 1978). Focusing on N economy (Moll et al., 1982), crop biomass production depends on N supply, the amount of N uptake by the crop (total N uptake) and N use efficiency for biomass production (NUE_{BIOM}). Similarly, crop grain yield depends on N supply, total N uptake and N use efficiency for grain yield production (NUE_{GRAIN}).

The described framework is generally used to study the performance of maize crops in response to variable N availability. As such, it assumes unique N efficiency values for the whole stand, with no distinction among plants despite the inherent inter-plant variability of plant growth present in most maize crops (Vega and Sadras, 2003; Maddonni and Otegui, 2004). Additionally, plant-to-plant interactions for light

acquisition affect total N uptake (Lemaire et al., 2005; Gastal et al., 2015). Several studies have analyzed the competition for N among individuals within communities of different species and plant morphologies (e.g., pastures, mixed crops, forests) and described it as symmetric (Casper and Jackson, 1997; Berntson and Wayne, 2000); i.e., plant N uptake is proportional to the plant size. Hence, inter-plant variability of N uptake would match that of plant biomass. Inter-plant variability of plant biomass exists even in a community of genetically identical individuals (e.g., F1 hybrids) of similar initial plant size and plant architecture, as documented for maize crops (Maddonni and Otegui, 2004). This pattern became evident early in the cycle, and was exacerbated at high stand densities (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007) and under reduced N availability (Rossini et al., 2011). The early-established inter-plant variability of plant biomass (i.e., a proxy of plant hierarchies) held during the critical period around flowering, and generated variability in kernel number per plant (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007; Rossini et al., 2011; Rossini et al., 2012) that penalized crop grain yield (Glenn and Daynard, 1974; Tollenaar and Wu, 1999). There is no information on associated penalties in crop NUE_{GRAIN}.

Few studies have documented the attenuation of early-established plant hierarchies as a result of enhanced resource availability, e.g., by thinning (Pagano and Maddonni, 2007) or N fertilization (Rossini et al., 2011). In the former study, the early suppressed plants of the stand (i.e., dominated individuals) were the most responsive to thinning, suggesting an asymmetric nature of plant competition for light under crowding (Weiner, 1990; Casper and Jackson, 1997). In the latter study, N fertilization smoothed the initial plant-to-plant variability in plant biomass (i.e., a reduced coefficient of variation was recorded for this trait after N fertilization), but the extent of this benefit was genotype dependent; it was larger in a hybrid tolerant to crowding stress than in an intolerant one. Hence, genotypic differences in the capacity of the early-established plant hierarchies to respond to N fertilization could be expected. Additionally, inter-plant variation in kernel protein concentration was increased under reduced N availability (Mayer et al., 2012), limiting our capacity to infer the nature of N competition (i.e., symmetric or asymmetric) based exclusively on the temporal analysis of plant biomass variability.

To our knowledge, little information exists about the effects of inter-plant variability in N uptake and NUE_{GRAIN} on the performance of maize crops (e.g., Ciampitti et al., 2012), and no attention has been given to differences produced on these variables by plant hierarchies and stand densities. Caviglia and Melchiori (2011) identified the dominated plants as those individuals of the stand with the highest grain yield response to N fertilization, but they classified plants based on their biomass at physiological maturity (Maddonni and Otegui, 2004) rather than at the time of hierarchy establishment early in the cycle (Pagano and Maddonni, 2007). The differential sensitivity to N fertilization among early-established plant hierarchies was not explored, which may be crucial for the correct interpretation of genotypic differences in grain yield stability across environments (Pagano and Maddonni, 2007).

In this work, we studied the N economy at the crop and plant levels, of two maize hybrids classified *a priori* as contrasting in their tolerance to crowding (Rossini et al., 2011). For this purpose and early in the cycle, we used plant biomass to classify plants in three terciles (Ts), representative of dominated (lower T), mid-size (mid T) and dominant (upper T) plants of the stand. We analyzed the contribution of each group of plants to crop responses to N fertilization in terms of total biomass, grain yield, total N uptake and N in grains. We also estimated the response of NUE_{BIOM} and NUE_{GRAIN} of each group of plants to N fertilization. The hypothesis of the present investigation was that the group of dominated plants (lower T) of the crowding-tolerant hybrid would contribute to crop responses to N fertilization in a greater proportion than the group of dominant plants (upper T). Conversely, the different group of plants of the crowding-intolerant hybrid would

contribute more evenly to crop responses to N fertilization. We also hypothesized that the enhanced variability in NUE_{GRAIN} among plants of a stand would penalize crop NUE_{GRAIN}.

2. Materials and methods

2.1. Experiments

Two field experiments were conducted in Argentina during the growing seasons of 2006/2007 (Exp. 1) and 2007/2008 (Exp. 2) in the Experimental Station of the National Institute of Agricultural Technology (INTA) located at Pergamino (34°56′ S 60°34′ W) on a silty-clay loam soil (Typic Argiudoll). Methodologies of Exp. 1 and Exp. 2 were partially published in Rossini et al. (2011). Briefly, two hybrids (H) classified *a priori* as contrasting in their tolerance to crowding stress (Rossini et al., 2011) were used: the tolerant AX820 CL–MG (hereafter AX820) and the intolerant AX877 CL–MG (hereafter AX877). Both single-cross hybrids were produced by the same seed company (Nidera Argentina). Each hybrid was grown at two stand densities (Dn) and two N levels (Nn). Tested stand densities were 9 (D9) and 12 (D12) plants m^{-2}. Nitrogen levels were a control with no added N (N0) and a high N availability treatment fertilized with 200 kg of N ha^{-1} (N200), added as urea at V6 (Ritchie and Hanway, 1982). Fertilization was applied close to the stage when the largest differences in plant biomass among plants of the stand are recorded (Maddonni and Otegui, 2004). Treatments were distributed in a split-plot design with three replicates. N level was randomized in the main plots and all hybrid per stand density combinations (HD) in the sub-plots (herein termed plots). Plots had six rows with an E-W orientation, 0.7 m between rows and 18 m length.

Manual sowing took place on 20-Oct (Exp. 1) or 22-Oct (Exp. 2) at a rate of 3–4 seeds per hill. Plots were thinned to one plant per hill at the end of the heterotrophic phase (ca. V3; Pommel, 1990). All experiments were kept free of weeds by means of chemical (4 L of atrazine 0.5 a.i. ha^{-1} plus 2 L of acetochlor 0.9 a.i. ha^{-1} at sowing) and manual controls. Water stress was prevented by means of sprinkler irrigation, with the uppermost soil profile (1 m) near field capacity throughout the crop cycle.

2.2. Measurements

A total of 10 (Exp. 1) or 12 (Exp. 2) consecutive plants in a row of similar size (visual assessment) and ontogeny were tagged at V3 in each plot. Plant biomass was estimated at V6 (i.e., immediately before N fertilization) by means of allometric models based on nondestructive morphometric measurements. Details of the non-destructive technique and the fitted allometric models were presented in the previous paper (Rossini et al., 2011). All tagged plants were harvested at physiological maturity (R6). Plants were oven dried at 70 °C until constant weight to quantify final plant biomass. Ears were hand shelled, and grains were weighed to compute plant grain yield. Harvest index (HI) was estimated from the ratio between plant grain yield and total plant biomass.

N concentration (%N) in vegetative tissues and grains was assessed for each plant harvested at R6. Micro-Kjeldahl analysis was used for the vegetative fraction, and near infrared transmittance (Infratec, 1227, Tecator, Sweden) for the grain fraction. Calibration of the near-infrared transmittance instrument was performed by Monsanto Argentina with maize hybrids that are highly representative of those grown throughout the world. N content (in g $plant^{-1}$) of each fraction (vegetative and grain) was obtained as the product between N concentration and the corresponding dry weight, and the sum of these contents was used to quantify plant N uptake at R6. N use efficiency (NUE) was computed at the crop and plant levels, as the quotient between total biomass (NUE_{BIOM}) or total grain (NUE_{GRAIN}) yields and N uptake. Nitrogen harvest index (NHI) was also computed at the crop and plant levels, as the ratio between N content in grains and total N uptake.

The N nutrition index (NNI) was calculated to evaluate the N status