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Inter-plant variability in maize crops grown under contrasting N × stand density combinations: Links between development, growth and kernel set

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ABSTRACT

Genotypic differences in the response of maize kernel number per plant to ear growth rate around silking, caused by contrasting N availability, have been attributed to the effects of this element on reproductive efficiency (i.e. kernel set per unit of ear growth rate). The objective of current research was to assess if reduced reproductive efficiency of some genotypes under N stress is due to the effect of this nutrient on the number of completely developed florets per ear, the number of exposed silks per ear, and/or abortion of pollinated florets. Two field experiments were conducted with two hybrids previously characterized by their contrasting reproductive efficiency (high for AX820 and low for AX877) under N stress, two stand densities (9 and 12 pl m^{-2}) and two levels of added N (0 and 200 kg N ha^{-1}). We established links among plant and ear growth rates, reproductive traits and kernel number per plant. Reduced reproductive efficiency (quantified as kernel number per plant per unit of spikelet growth rate around silking) of both hybrids under N deficiency was mainly due to an enhanced abortion of pollinated florets of the most suppressed plants of the stand (*dominated* individuals). This response did not appear to be the result of low spikelet growth rate around silking, but a direct control of N on sink capacity of fertilized ovaries for assimilates allocation.

1. Introduction

High stand densities used in most current maize production systems of temperate environments enhance intra-specific competition due to the early increase in growth variability among plants (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). This trend has been reported also for maize crops grown under N deficiency (Boomsma et al., 2009), for which fertilization at the start of stem elongation reduced this variation in subsequent stages (Rossini et al., 2011). The response pattern was genotype-dependent, because recovery of crop growth and reduction of inter-plant variability were less pronounced in one hybrid (AX877) than in another one (AX820) (Rossini et al., 2011). Early differences in plant growth within the stand were sustained until the critical period for kernel set around flowering (Maddonni and Otegui, 2004), and affected biomass partitioning to the ear differently among plants (Pagano and Maddonni, 2007; Borrás et al., 2007).

D'Andrea et al. (2008) demonstrated that, under contrasting N supplies, genotypic differences in the response of kernel number per plant to plant growth rate during the critical period were related to the effects of N on biomass partitioning to the ear. This trend was not supported by Rossini et al. (2011), who found a tight relationship between ear growth rate and plant growth rate during the critical period, with no evidence of an N effect on biomass partitioning. There were, however, genotypic effects in the relationship between kernel number per plant and ear growth rate during the critical period. For AX820 this relationship was independent of factors that caused the variation in ear growth rate (e.g. stand density, N), and a single model accommodated the whole data set adequately. For AX877 the relationship was N-dependent, and two models were necessary for the correct fit of its data set. For this hybrid, reduced N availability caused a decrease in reproductive efficiency expressed as kernel number per unit of ear growth rate during the critical period.

Negative effects of stress on biomass partitioning to harvestable reproductive organs during the critical period for kernel set have been reported for different species in a previous research (Vega et al., 2001). This study highlighted that maize plants subjected to reduced irradiance per plant at high stand density experienced a larger decrease in the reproductive/vegetative ratio than sunflower or soybean plants. A clear sign of reduced assimilate allocation to the ear is a longer delay in silking date than in anthesis date with the concomitant increase in the anthesis-silking interval (ASI). This response has been broadly documented at the plant population level (i.e. based on 50% anthesis and 50% silking dates of the stand), particularly for water (Hall et al., 1982; Bolaños and Edmeades,

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1993), N (Jacobs and Pearson, 1991; D'Andrea et al., 2009) and stand density (Edmeades and Daynard, 1979; Sangoi et al., 2002) effects. Therefore, the ASI is generally used as a secondary trait in breeding programs targeting stress-prone environments (Bänziger and Laffite, 1997), particularly because of its simple representation of canopy performance and partitioning to the ear. At the individual plant level, however, the ASI has some limitations for the correct interpretation of the underlying physiological processes responsible of the success or failure for setting a kernel by a fertilized ovary (Uribelarrea et al., 2002). Consequently, other traits at the plant level may give a better explanation to the observed reduction in maize reproductive efficiency in response to N stress, like floret development at silking (i.e. morphogenetic limitations to kernel set), synchrony in silk exposure among florets of the same ear (i.e. pollination timing or pollination failure limitations to kernel set), and/or abortion of fertilized ovaries (i.e. metabolic limitations to kernel set).

Previous studies have shown that the number of completely developed florets per ear is not substantially affected by variations in assimilate provision to this organ caused by stand densities (Otegui, 1997; Cárcova et al., 2000), sowing dates (Cirilo and Andrade, 1994; Otegui and Melón, 1997), nutrient offer (Lemcoff and Loomis, 1986; Uhart and Andrade, 1995b; Monneveux et al., 2005), water availability (Edmeades et al., 1993; Otegui et al., 1995), or above optimum temperatures (Rattalino Edreira et al., 2011). Reports on the pattern of silk exposure from individual ears (Cárcova et al., 2000; Uribelarrea et al., 2002; Lizaso et al., 2003) and the subsequent progress of fertilized ovaries (Otegui et al., 1995; Cárcova et al., 2000; Lizaso et al., 2003; Cárcova and Otegui, 2007) in field conditions are comparatively rare, particularly under stress conditions (Otegui et al., 1995; Rattalino Edreira et al., 2011). Moreover, the studies cited did not analyze the variability of these traits at the plant population level.

In a field study where plants were identified from the onset of the heterotrophic stage onwards (V_3; Ritchie and Hanway, 1982), the number of completely developed florets per ear produced by *dominated* individuals at high stand density did not differ from the number produced by the *dominant* ones (Pagano et al., 2007). Nevertheless, both categories did differ in the rate of progress of floret development within the ear, which was slower in *dominated* than in *dominant* individuals. Consequently, ASI values were larger for the former than for the latter. Additionally, synchrony in silk exposure was reduced in *dominated* plants (i.e. the time lag between early- and late-appearing silks from an ear increased in these plants), due to reduced spikelet growth rate during the critical period. Borrás et al. (2007) determined that the capacity of a plant to reach silking depended upon its capacity to reach a minimum ear biomass during the critical period for kernel set. Individuals with ears below this threshold were barren. Moreover, barrenness was also registered among plants that exposed their silks. In this case, barrenness may be attributed to pollination failure due to lack of pollen at their time of silking (Hall et al., 1981; Bassetti and Westgate, 1993; Uribelarrea et al., 2002). When adequate pollen availability was granted by means of a late-pollinator source, the only explanation for their barrenness was kernel abortion (Westgate and Boyer, 1986; Otegui et al., 1995) caused by growth inhibition of early-pollinated ovaries on the late-pollinated ones (Cárcova and Otegui, 2001, 2007). Therefore, any restriction to plant growth (e.g. by reduced light, water or nutrient availability) around flowering may exert a negative effect on kernel set, partially due to impaired silk exposure (Borrás et al., 2009) but also attributable to reduced pollination synchrony. This lack of synchrony may cause a reduction in the number of ovaries that are fertilized within a critical window of 2–4 days after individual plant silking, which increases kernel abortion (Cárcova and Otegui, 2001, 2007). The inability to reverse abortion caused by N deficiency in fertilized ovaries infused with sucrose, and the partial reduction of abortion when they were infused with N (Below et al., 2000) emphasized the direct role of this nutrient on the ability to use carbon from the grains. This result contrasts with data found by Boyle et al. (1991) and Zinselmeier et al. (1995), who partially reversed reproductive failure induced by water stress by means of sucrose infusion to plants.

Information is available on the general flowering pattern (i.e. anthesis and silking) of *dominant* and *dominated* plants (Borrás et al., 2009). However, there is (i) only one reference linking these traits to early reproductive development and its effects on final kernel number per plant (Pagano et al., 2007), and (ii) no reference linking these traits to growth conditions responsible of the early establishment of contrasting plant categories within the stand; i.e. how the limiting factor type (aerial or soil resource) affects the symmetry among plants for its acquisition (Rossini et al., 2011; Caviglia and Melchiori, 2011). The analysis of population variability in reproductive development may improve our understanding of processes controlling the variation in reproductive efficiency among genotypes, which has been recently document for two maize hybrids grown under contrasting N levels (Rossini et al., 2011). Our objective in current research was to analyze if reduced reproductive efficiency of AX877 under N deficiency is due to N effects on (i) the number of completely developed florets per ear, (ii) the number of silks exposed per ear, and/or (iii) kernel abortion. We hypothesize that the reduced reproductive efficiency of AX877 under N stress is due to an enhanced abortion of pollinated florets, predominantly among the most suppressed plants of the stand (*dominated* individuals).

2. Materials and methods

2.1. Crop husbandry, treatments and experimental design

Field experiments were conducted during 2006–2007 (Exp.1) and 2007–2008 (Exp.2) at the Pergamino station (33°56′S, 60°34′W) of the National Institute for Agricultural Technology (INTA) on a silty clay loam soil (typic Argiudoll). The uppermost soil profile (0–40 cm) had levels of 23 g kg^{-1} for organic matter, 115 mg kg^{-1} for mineral P, and 14 g kg^{-1} for N-NO_3. Treatments included a factorial combination of two single-cross maize hybrids from Nidera Argentina, two stand densities and two N levels. Hybrids were selected for their contrasting reproductive efficiency under N stress by Rossini et al. (2011). These hybrids were the AX820 CL-MG (hereafter AX820) with a high reproductive efficiency, and the AX877 CL-MG (hereafter AX877) with a low reproductive efficiency. Hybrids shared a common female inbred of the Lancaster heterotic group (D. Novoa, Nidera Argentina, personal communication). Hybrid AX820 was released during 2004 and AX877 during 2005. Tested stand densities were 9 (D_9) and 12 (D_{12}) plants m^{-2}. N levels were a control with no added N (N_0), and a fertilized condition with 200 kg of N ha^{-1} (N_{200}) added as urea at V_6, formerly identified as the stage when variability in plant growth among individuals of the stand is stabilized (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). The N_0 treatment was considered a N-stressed condition for modern maize hybrids grown on soils with 23 g kg^{-1} organic matter, as demonstrated in previous work (D'Andrea et al., 2008).

Treatments were distributed in a split-plot design, with N levels in the main plots and all hybrid × stand density combinations in the sub-plots (hereafter termed plots). Plots had six rows, 0.7 m between rows, and 18 m length. Sowing was performed manually on 20-Oct (Exp.1) or 22-Oct (Exp.2), at a rate of 3–4 seeds per hill and thinned to one plant per site at the end of the heterotrophic phase (V_3; Pommel, 1990). All experiments were kept free of weeds by means of chemical controls (4 L ha^{-1} of atrazine