



Senescence and yield responses to plant density in stay green and earlier-senescing maize hybrids from Argentina



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ABSTRACT

Increases in maize (*Zea mays* L.) yield over the past few decades have been associated with breeding for tolerance to progressively higher plant densities. Since high plant density exacerbates interplant competition, it has been suggested that improved resource capture through delayed senescence might be advantageous in such situations. The main objectives of this work were to determine (1) the time-course of canopy senescence, (2) post-silking C and N accumulation and (3) yield responses of contemporary maize hybrids with different expression of the stay green (SG) character grown in a range of plant densities from moderate to intense crowding stress. Three experiments consisting of a combination of different plant densities (from 6 to 10 pl m⁻²) and commercial hybrids with different timing of senescence were carried out. High density accelerated leaf senescence at the lower canopy layer. The SG hybrids delayed senescence and retained green leaves at physiological maturity at all tested densities. One of these hybrids (NK880), with a strong SG character, retained green leaves at all canopy layers, even at the lower layer exposed to limiting irradiance. Lower canopy leaves maintained high respiratory rates in NK880, while leaves of the NSG hybrid (DK682) senesced and their respiration became not detectable. At the highest tested density, the NSG DK682 achieved greater grain yields than the SG NK880. Increased density reduced kernel weight (KW), and this decrease was more pronounced for the SG NK880 (6–18% comparing 10 vs. 8 pl m⁻²). In spite of delayed senescence in NK880, no hybrid differences were found for post-silking dry matter accumulation and plant dry matter at physiological maturity. Unexpectedly, plant nitrogen content (Nc) at harvest was similar (Exp. I) or even lower ($P < 0.05$, Exp. II) in the SG NK880. This was the result of lower net N accumulation during the post-silking period (Exp. I) or lower Nc achieved at silking (Exp. II) in the SG NK880. A strong positive relation was found between KW and N concentration in kernels, with %N in kernels being below the critical N concentration to achieve potential KW (around 1.4%) in the SG hybrid. This suggests that yield in NK880 was limited by N. In the SG genotype, N remobilization from vegetative organs did not seem to compensate for the N deficit for optimum grain growth. In summary, at high densities the NK880 hybrid displayed a strong, constitutive SG character, even if it accumulated less N, and senescence delay was not reflected in higher grain yield.

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1. Introduction

In the last decades, maize yield was improved through a tight association between changes in management practices and breeding. Plant density is one of the practices that changed most (Tollenaar and Lee, 2002; Tollenaar et al., 2006). For instance, for the U.S. corn belt, gains in yield of 110 kg ha⁻¹ y⁻¹ in the period 1960–2000 correlated with increases in plant density of 1000 pl ha⁻¹ y⁻¹ (Duvick, 2005). At the same time, during the last eight decades, breeding has mostly improved tolerance to crowding

stress with no increase in potential yield per plant (Duvick, 1997; Tokatlidis and Koutroubas, 2004; Tokatlidis et al., 2005; Tollenaar and Wu, 1999). Nonetheless, there are exceptions to this, such as in Argentina, where breeding has improved not only crop yield at high densities, but also maximum grain yield per plant (at 3 pl m⁻²) for hybrids released between 1960 and 2000 (Luque et al., 2006).

Breeding for tolerance to high plant density raises a number of issues. For example, grain yield per unit area of new hybrids is highly dependent on plant density, with smaller and more variable ranges of optimum densities than older genotypes (Fasoula and Fasoula, 2002; Tokatlidis and Koutroubas, 2004; Tokatlidis et al., 2005). This may result in yield penalties in sites where occasional stress (e.g., drought) makes it difficult to predict optimum density (Duvick, 2005; Tokatlidis et al., 2011). Moreover, at high interplant competition levels stand variability increases because,

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e.g., dominant plants show luxury consumption of nutrients to the detriment of dominated ones (Rossini et al., 2011; Tokatlidis et al., 2005; Tollenaar and Wu, 1999). Whether the trend for higher plant density continues in the future or not, improved understanding of morpho-physiological traits related to crowding stress tolerance could help in breeding efforts to enhance grain yield.

The increase in plant density decreases the amount of resources available per plant (Tollenaar et al., 2006). During the reproductive stage, crowding stress reduces kernel number per plant as kernel number fixation is related to plant growth rate around silking (Andrade et al., 2002). After kernel number is defined, grain filling relies mostly on current assimilate production (Borrás et al., 2004). In maize, remobilization of assimilates stored in vegetative tissues is usually very low (Borrás et al., 2004), and almost none in environments where remobilization is impaired (e.g., in cool climates, Maddonni et al., 1998). Higher plant density accelerates the rate of leaf senescence (Borrás et al., 2003), reducing post-silking net photosynthesis and hence, assimilate availability for kernel growth if leaf area index falls below critical values. When increases in plant density are not enough to compensate for reductions in yield per plant (i.e., at supra-optimal densities), crowding stress results in lower yields per unit area (Echarte et al., 2000; Sarlangue et al., 2007; Tokatlidis et al., 2011; Tokatlidis and Koutroubas, 2004).

An extended post-anthesis period and longer green leaf area (GLA) duration are two of several morpho-physiological traits associated with genetic improvement of maize yield (Duvick, 2005). The stay green trait (SG) is defined as a delay in senescence in comparison with a standard reference genotype (Thomas and Howarth, 2000). Under environmental stress (drought, nitrogen deficiencies), the SG trait has been related to higher yields in maize and sorghum grown in temperate/subtropical regions (Bänziger et al., 1999, 2002; Borrell et al., 2000). Under well-watered conditions, these genotypes might be able to meet nitrogen (N) requirements by the grains with N supplied by root uptake, delaying N remobilization from vegetative parts, and thereby, delaying the onset of senescence (Ciampitti and Vyn, 2011; Rajcan and Tollenaar, 1999b). Many studies of SG genotypes compare older, earlier-senescent vs. modern, SG hybrids (e.g., Ma and Dwyer, 1998; Rajcan and Tollenaar, 1999a,b; Valentinuz and Tollenaar, 2004). Nonetheless, there is little information to address whether in modern maize hybrids the SG trait still represents a yield advantage under crowding stress conditions (i.e., without water limitations but with interplant competition for light and nutrients).

At higher densities plants may face a decrease in the amount of soil resources available per plant, (e.g., water and nutrients, Tollenaar et al., 2006). The SG hybrids have been reported to yield more than NSG hybrids under limiting N fertilization (Ma and Dwyer, 1998; Rajcan and Tollenaar, 1999b), and to have larger post-silking light interception (Richards, 2000). Thus, our original hypotheses were that at high plant densities, and compared to a reference NSG genotype: (1) modern SG hybrids delay canopy senescence even at high plant densities (i.e., the SG trait is a constitutive trait); (2) post-silking C and N accumulation are higher in SG hybrids; and therefore (3) grain yield is higher in SG hybrids. In this paper, our specific objectives were to study (1) the time-course of canopy senescence, (2) post-silking C and N accumulation, and (3) yield responses of maize hybrids with different expression of the SG character grown in a range of plant densities from moderate to intense crowding stress.

2. Materials and methods

2.1. Experimental design and crop management

The experiments were conducted in La Plata (34°54'24" S; 57°55'56" W, Argentina), in the Experimental Field of Facultad de

Ciencias Agrarias y Forestales (Universidad Nacional de La Plata). Treatments consisted of (i) plant densities (6, 8 and 10 pl m⁻² in Exp. I; 7, 8, 9 and 10 pl m⁻² in Exp. II; 8 and 10 pl m⁻² in Exp. III) and (ii) genotypes. The following maize hybrids were chosen because of their different senescence behavior, but similar days to silking and crop cycle length: DK682 and AW190 (standard non stay green, NSG), and AX878 and NK880 (stay green, SG). Previous observations (unpublished) showed that under field conditions in La Plata, chlorophyll and photosynthetic electron transport rate (which is closely related to photosynthesis, Earl and Tollenaar, 1999) of the ear leaf declined more slowly after silking in NK880 and AX878 (SG) than in DK682 and AW190 (NSG).

The field was under fallow before Exp. I, while for Exps. II and III the preceding crop was maize. Treatments (combinations of density × hybrid) were laid out in three (Exp. I) or four (Exp. II) blocks. Treatments were arranged in a split-plot design where plant density was the main plot and genotypes were randomized in each subplot. Subplots consisted of 4 rows (except for Exp. I when five rows were sown) 6.5 m long and 0.7 m apart. Seeds were sown manually on October 27, 2008 (Exp. I, DK682 and NK880); October 29, 2009 (Exp. II, DK682 and NK880); and November 12, 2010 (Exp. III, DK682, AW190, AX878 and NK880). In all experiments, three seeds were placed in each hill, and seedlings were later thinned to one plant per hill at the V2 stage (Ritchie et al., 1996). Seedling emergence took place ca. 7 days after sowing and final plant densities at harvest coincided with the density planned for each treatment.

The soil was a typical argiudol (USDA classification) with a fine texture and an underlying layer (40 cm deep) of expandable clay. Typical total N content in the first 20 cm of soil was 1630 mg kg⁻¹ and total P content was 5.88 mg kg⁻¹. Fertilizers were broadcast at a rate of 18 kg ha⁻¹ of P (triple superphosphate, incorporated into the soil with a disc harrow) prior to sowing and 100 kg ha⁻¹ of N (urea) at V7 in Exp. I; 40 kg ha⁻¹ of N and 100 kg ha⁻¹ of P (diammonium phosphate, DAP) at V3 and 80 kg ha⁻¹ of N (urea) at V7 in Exp. II; and 18 kg ha⁻¹ of N and 46 kg ha⁻¹ of P (DAP) at V3 and 200 kg ha⁻¹ of N (urea) in two doses (at V3 and V7) in Exp. III. These rates of N fertilizer aimed at satisfying N needs for a crop yield of 10000 kg ha⁻¹ (i.e., around the maximum yields expected for this location). Plots were irrigated as needed from emergence to maturity in order to prevent water deficit. Plots were maintained free of weeds by application of herbicides when needed. Silking took place on January 15th in Exp. I, January 10th in Exp. II and January 31st in Exp. III (Fig. 1). In all experiments, differences in silking date between the earliest and latest hybrid were 3 days at most. Thermal time computations started at silking, using mean daily air temperature and a base temperature of 8 °C (Ritchie and NeSmith, 1991). In the three experiments, mean temperatures after silking were always lower than the optimum temperature for maize growth (34 °C, Wilkens and Singh, 2003). For this reason, we used a simple linear model to calculate thermal time, which was expressed as the sum of °C day⁻¹ (°Cd).

2.2. Plant sampling

In Exps. I and II, destructive samplings were made at silking and physiological maturity for chlorophyll and dry matter determinations. In Exp. III, only one final harvest (8 plants per treatment) was made. For each destructive sampling, two adjacent plants from a central row of each subplot (6 or 8 plants per treatment in Exps. I and II respectively) were harvested. Other authors used a similar number of plants sampled per treatment to assess senescence progression, chlorophyll content and for dry mass determinations (Escobar-Gutiérrez and Combe, 2012; Martin et al., 2005; Pommel et al., 2006). The plants sampled were adjacent in the same row, thus reducing the potential biases arising from human plant selection. Moreover, the plants sampled were flanked by visually

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