



Carbon assimilation, leaf area dynamics, and grain yield in contemporary earlier- and later-senescing maize hybrids



Horacio A. Acciaresi^{a,d}, Eduardo A. Tambussi^{b,e}, Mariana Antonietta^{b,e}, María S. Zuluaga^a, Fernando H. Andrade^{c,e}, Juan J. Guiamet^{b,d,*}

^a Cátedra de Cerealicultura, Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, cc 31, 1900 La Plata, Argentina

^b Instituto de Fisiología Vegetal (CONICET-UNLP), cc 327, 1900 La Plata, Argentina

^c Unidad Integrada INTA Balcarce-Universidad Nacional de Mar del Plata, cc 276, 7620 Balcarce, Argentina

^d CICBA, Argentina

^e CONICET, Argentina

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ABSTRACT

Maize breeding during the past 50 years has been associated with a delay of leaf senescence, but it is not clear whether this trait is likewise associated with higher grain yield in modern hybrids. Post-silking growth, leaf area dynamics, photosynthetic parameters and yield were compared in modern maize hybrids differing in canopy senescence rate. In the first two experiments, four hybrids were grown in the field at Balcarce, Argentina (37°45' S, 58°18' W). In spite of differences in chlorophyll retention and photosynthesis of the ear leaf, post-silking growth and grain yield were very similar in all four hybrids while kernel N concentration was lower in the later-senescing hybrids. In a third experiment, a later-senescing (NK870) and an earlier-senescing (DK682) hybrid were grown to analyze the potential photosynthetic contribution of delayed leaf senescence. Leaf area and chlorophyll content were larger in NK870, especially at the lower canopy level (0.75 m above the ground). However, hybrids did not differ for canopy light interception. Because photosynthetic photon flux density below 1 m above the ground was less than 10% of incident radiation and photosynthesis quantum yield did not change during senescence, the potential photosynthetic output of lower leaves below 1 m was very low. Lower leaves of NK870 had N concentrations higher than those needed to sustain photosynthesis at the light conditions below 1 m. Therefore, we show that delayed senescence does not necessarily improve post-silking C accumulation because: (i) canopy light interception is not reduced by senescence except at very late stages of grain filling; (ii) contrasting hybrids show more pronounced senescence differences at canopy levels receiving less than 10% of incident radiation; (iii) delayed senescing hybrids present lower kernel N concentrations while extra N is retained in leaves exposed to a light limiting micro-environment. Delayed senescence at lower canopy levels may be unproductive, at least under non-stressing conditions.

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1. Introduction

Maize grain yield increased significantly over the past 50 years. For example, the rate of yield increase in Ontario (Canada) approximated 1.5% yr⁻¹ between 1940 and 1990 (Tollenaar and Wu, 1999), whereas average maize yields doubled between 1969 and 2007 in Argentina (www.minagri.gob.ar). In part, this increase has been due to the release of improved hybrids. Genetic gains for yield equalled 13.2 g m⁻² yr⁻¹ between 1965 and 1997 in Argentina (Luque et al.,

2006). Genetic improvement of maize yield can be related to increased tolerance to various types of stress (e.g., low soil water and/or N availability, increased population density, competition from weeds) and also to increased post-silking dry matter accumulation (Tollenaar and Wu, 1999). To some extent, this has been associated with an improvement in resource capture (light, water, and nutrients). Prolonged canopy functioning through delayed leaf senescence is one of several traits that have contributed to the increased yield potential of the new hybrids (Tollenaar and Wu, 1999; Valentinuz and Tollenaar, 2004).

In Argentina, maize canopy senescence proceeds at a relatively slow rate (1.4 cm² per plant °C d⁻¹) until silking – 400 °C d after silking, when rates of green leaf area loss climb to 5.5 cm² per plant °C d⁻¹ (Borrás et al., 2003). The second, faster phase of senescence coincides with the reproductive stage (Borrás et al.,

* Corresponding author at: Instituto de Fisiología Vegetal (CONICET-UNLP), cc 327, 1900, La Plata, Argentina. Tel.: +54 221 4236618; fax: +54 221 4233698.

E-mail addresses: jguiamet@fcnym.unlp.edu.ar, jguiamet@gmail.com (J.J. Guiamet).

2003). The onset and/or the rate of senescence varies depending on environmental conditions, year, population density, and source–sink relations. Increased population density and decreased source–sink ratios frequently accelerate senescence (Rajcan and Tollenaar, 1999b; Borrás et al., 2003; Valentinuz and Tollenaar, 2004; Antonietta et al., 2014). Compared to older genotypes, senescence occurs later or at slower rates in modern hybrids (e.g., Valentinuz and Tollenaar, 2004; Duvick, 2005), i.e., chlorophyll and photosynthetic activity persist longer after silking in modern hybrids (Ding et al., 2005). In maize and sorghum, delayed senescence is associated with increased C and N assimilation during the grain filling period (Ma and Dwyer, 1998; Rajcan and Tollenaar, 1999a,b; Borrell et al., 2000a,b). Later-senescing hybrids of maize exhibit increased source–sink ratios during grain filling, as implied from their smaller decrease of stover mass compared to older, earlier-senescing hybrids (Rajcan and Tollenaar, 1999a). This has led to the proposal that an increased source–sink ratio during grain filling results in increased supply of assimilates to the roots in these genotypes. Persistence of root activity might extend assimilation of N up to physiological maturity. In fact, several studies have shown that the percentage of grain N supplied by current N assimilation during grain filling is larger in delayed senescence than in normally senescing hybrids (Ma and Dwyer, 1998; Rajcan and Tollenaar, 1999b; He et al., 2004).

In most hybrids, loss of green leaf area starts at the base of the plant, and progresses upwards during reproductive growth (e.g., Sadras et al., 2000). A large part of the difference in chlorophyll retention between earlier and later-senescing hybrids is expressed in the lower, shaded leaves of the canopy (He et al., 2005; Antonietta et al., 2014), where retention of chlorophyll and photosynthetic capacity might not be utilized fully because of relatively low irradiance. For example, transgenic stay-green lines of tobacco did not show a higher C gain (compared to wild type) because of the respiratory costs associated with delayed senescence of unproductive leaves in shaded parts of the canopy (Boonman et al., 2006).

In Argentina, genetic gains for grain yield between 1965 and 1997 were related to an increase in kernel number, and this was accompanied by increased post-silking accumulation of dry mass and light interception extended up to physiological maturity (Luque et al., 2006). Increased light interception up to physiological maturity suggests that genetic improvement of maize in Argentina also involved a delay of leaf senescence, as reported by Valentinuz and Tollenaar (2004) for North America and Ding et al. (2005) for China. However, recent evidence shows that, in spite of these gains in light interception, grain filling may still be source-limited in modern, high-yielding Argentinean hybrids (Cerrudo et al., 2013), which suggests that it might be advantageous to further delay senescence. Although it seems clear from comparisons of older vs. newer hybrids that genetic improvement over the past decades delayed senescence in maize, growth and yield of contemporary hybrids differing in their senescence behaviour has been studied much less. To test the impact of delayed senescence on grain yield of modern, contemporary hybrids of maize, we compared the dynamics of leaf photosynthetic activity, post-silking growth, and grain yield in four modern hybrids differing in their rates of senescence. Additionally, we estimated the potential photosynthetic contribution of delayed senescence of lower leaves in hybrids with longer persistence of functional leaves.

2. Materials and methods

2.1. Growth conditions

Field experiments were carried out at Estación Experimental Agropecuaria INTA Balcarce, Argentina (37°45' S, 58°18 W)

during the 2004–05 (Exp. I), 2005–06 (Exp. II) and 2006–07 (Exp. III) growing seasons. In Exps. I and II, four maize hybrids (DK682, DK696, AX890 and NK870) were sown in a randomized block design with three replicate plots per hybrid. Previous visual observations showed that canopy senescence occurred earlier in DK682 and DK696 (earlier-senescing) than in AX890 or NK870 (later-senescing), while, at the same time, these four hybrids had similar days to silking and to relative maturity. Therefore, these contemporary, modern hybrids seemed appropriate to compare the impact of delayed senescence on yield and post-silking growth of maize. To estimate the potential photosynthetic gains possibly due to delayed senescence, two hybrids (DK682 and NK870) were chosen for Exp. III because they have similar kernel numbers but contrasting senescence behaviour, based on the results of Exps. I and II. Each plot consisted of four rows, 10 m long and 0.70 m apart. At sowing (October 18, 2004, October 24, 2005 and October 18, 2006), three seeds were placed manually in each hill (0.2 m apart in each row). After emergence, seedlings were thinned to 7 plants m⁻². Plots were fertilized with 30 kg P ha⁻¹ at sowing and 160 kg N ha⁻¹ at the V6 stage (Ritchie and Hanway, 1982) and watered by sprinkler irrigation as needed to prevent water deficits. Atrazine plus acetochlor were applied at pre-emergence to control weeds.

2.2. Leaf area, dry mass and yield determination

Two plants per plot, adjacent in the same row, were harvested at regular intervals for dry mass and leaf area determinations. Plants were separated into stem plus sheaths, leaf laminae, and ears. The green area of each individual leaf blade was measured with a LiCor LI 3100 Area Meter, and all organs were dried at 60 °C for at least 4 days until constant weight was achieved.

At physiological maturity, all ears of plants in an area of 4.2 m² in each plot were harvested, threshed and dried at 60 °C to constant weight. Yield data were expressed as grain dry weight (g) per m⁻². Mean individual kernel weight (KW) was determined by weighing 1000 kernels per replicate for each hybrid. Kernel number per plant (KNP) was estimated on the basis of KW and grain yield, essentially as in Echarte et al. (2000).

2.3. Ear and leaf N concentration

In Exps. I and II, mature kernels were harvested at physiological maturity, dried, milled to a fine powder and N concentration (% on a dry mass basis) was measured after Kjeldahl digestion. In Exp. III, leaves used for N determination were dried and weighed separately, milled to a fine powder and their N concentration was measured as indicated above.

2.4. Chlorophyll and photosynthesis measurements

To estimate leaf chlorophyll (chl) content, four to five measurements evenly distributed along the length of the leaves from two plants per plot were made with a SPAD 502 Chlorophyll Meter (Minolta, Japan) and averaged. Photosynthesis was estimated from chlorophyll fluorescence measurements (Exps. I, II and III) and through gas exchange analysis with a portable photosynthesis system in Exp. III. A pulse-amplitude modulated FMS2 (Hansatech, UK) chlorophyll fluorometer was used to measure the effective PSII quantum yield of maize leaves in the field, at midday. Care was taken to make measurements on fully illuminated spots of the leaves to estimate photosynthetic capacity at full irradiance. Photosynthetic electron transport rate (ETR) was calculated as in Rosenqvist and van Kooten (2003), except that, to account for the changes in absorbance due to chl loss during senescence, leaf absorbance was estimated from the relationship between absorbance (measured with an integrating sphere; basically as in Long

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