



# Effects of pollination-prevention on leaf senescence and post-silking nitrogen accumulation and remobilization in maize hybrids released in the past four decades in China

Lan Yang<sup>a</sup>, Song Guo<sup>a,b</sup>, Fanjun Chen<sup>a</sup>, Lixing Yuan<sup>a</sup>, Guohua Mi<sup>a,\*</sup>

<sup>a</sup> Key Laboratory of Plant-Soil Interactions, MOE, College of Resources and Environmental Science, China Agricultural University, Beijing 100193, PR China

<sup>b</sup> Soil and Fertilizer Research Institute Sichuan Academy of Agricultural Science, Chengdu 610066, PR China

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## ABSTRACT

In order to understand the regulation of source-sink relationship on leaf senescence in maize, we investigated the effect of pollination prevention on leaf senescence, post-silking dry matter and nitrogen accumulation and remobilization in different vegetative organs in one landrace and ten representative maize hybrids released between 1973 and 2000 in China. When pollination was prevented by covering silk with paper bags at silking stage, leaf senescence of Nongda 60, Yedan 13, Shendan 7 and Zhengdan 958 was delayed as shown by the remaining green leaf area per plant at maturity. However, pollination-prevention did not have obvious effect on the leaf senescence of Baimaya, Danyu 6, Yedan 2 and Xianyu 335. By contrast, pollination-prevention accelerated the leaf senescence of maize hybrids Zhongdan 2, Danyu13 and Yedan 4. It was found that leaf senescence of the late-released (since 1985) Chinese hybrids tended to be delayed by pollination-prevention, except XY335. From silking to physiological maturity, nitrogen content increased in the stem (plus the sheath, cob, husk, and tassel) and root of the non-pollinated plants. However, there was still a net reduction in leaf nitrogen content. We also found that pollination-prevention reduced leaf nitrogen remobilization efficiency, with genotypic difference and variation between the two years of testing. The results suggested that the response of leaf senescence to pollination-prevention is at least partially due to the change of leaf nitrogen remobilization efficiency. Leaf senescence tended to be delayed if leaf nitrogen remobilization efficiency is highly reduced by pollination-prevention.

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## 1. Introduction

In maize, it is believed that longer leaf duration (“stay-green”) is one of the key traits in modern breeding for high grain yield (Mueller and Vyn, 2016; Lee and Tollenaar, 2006). Correspondingly, post-silking nitrogen (N) uptake has been increased significantly (Pommel et al., 2006; Rajcan and Tollenaar, 1999; Bender et al., 2013). However, the stay-green trait was found to have negative effect on vegetative N remobilization and grain N concentration (Martin et al., 2005; Gallais et al., 2007; Coque et al., 2008; Thomas and Ougham, 2014). Grain N concentration has been greatly decreased in modern maize hybrids compared with the old ones (Duvick and Cassman, 1999; Chen et al., 2013). Because leaf N is a major contributor to grain N, there has been growing

interest in adjusting leaf senescence and improving N remobilization efficiency in maize to increase N use efficiency and grain N concentration (Schippers et al., 2015). For example, the activity of glutamine synthetase 1 (GS1) was found to play a role in efficient N remobilization. In GS1 mutants Gln1.3 and Gln1.4, less N is re-translocated from the leaf to the grains (Martin et al., 2006). Asparagine synthases (ZmAS3 and ZmAS4) are also likely to play an important role in N remobilization (Cañas et al., 2010). These studies have been mostly focused on the process of protein turnover, N metabolism within the leaf and N export from the leaf.

Nitrogen remobilization from the leaves is related to the formation of reproductive organs. As the major sink for N deposition during grain filling phase, the size and existence of the grain sink in maize may have great feedback effect on the remobilization of N from the vegetative organs. In soybean, it was found that the leaves of the de-podded plants remained green and did not exhibit the normal senescing pattern (Mondal et al., 1978). Similarly, some researches indicated that the leaves in the earless (no grain and cob)

\* Corresponding author.

E-mail address: [miguohua@cau.edu.cn](mailto:miguohua@cau.edu.cn) (G. Mi).

maize plants remained green for a longer time (Jerome and Moss, 1962; Christensen et al., 1981; Pan et al., 1986). Nevertheless, in other studies, prevention of pollination or removal of the ears after flowering caused premature senescence of the leaves above the ear (Allison and Weinmann, 1970; Below et al., 1981; Christensen et al., 1981; Crafts-Brandner et al., 1984a,b). Christensen et al. (1981) found that the remobilization of N from the leaf does not depend on the presences of an ear. Crafts-Brandner et al., (1984a,b) suggest that ear per se does not dictate the rate or completion of the senescence.

The different responses of leaf senescence to sink-removal treatments can be genotype dependent (Crafts-Brandner et al., 1984a). Modern breeding activities during the past four decades have greatly changed the characteristics of N uptake and remobilization (Chen et al., 2013; Ciampitti and Vyn, 2013; Chen et al., 2014). It would be interesting to see if modern breeding has any effect on the response of leaf senescence to grain sink removal. In the present study, one landrace and 10 maize hybrids released from 1973 to 2000 in China have been used to evaluate the regulatory role of grain sink removal on leaf senescence and N remobilization from different vegetative organs. The aims are (1) to determine if the response of leaf senescence to grain sink removal is related to breeding process during the past decades; (2) to understand if the differential response of leaf senescence to grain sink removal among different hybrids is related to their difference in stay-green ability, N partitioning characters and/or leaf N remobilization potential during grain filling phase.

## 2. Materials and methods

### 2.1. Soil and plant materials

The experiments were conducted in 2013 and 2014 at Shangzhuang Experimental Station of China Agricultural University in Beijing. The soil type is a typical Ustochrept soil with silty loam texture. The chemical properties of the soil in 2013 (0–30 cm) and 2014 (0–40 cm) were as follows: extracted mineral N ( $N_{\min}$ ) 3.1 and 3.2 mg kg<sup>-1</sup>, pH 7.3 and 7.2, Olsen-P 29.8 and 17.1 mg kg<sup>-1</sup>, NH<sub>4</sub>OAc extracted K 82.7 and 65.7 mg kg<sup>-1</sup>, organic matter 8.5 and 9.5 g kg<sup>-1</sup>, respectively. The field was irrigated with a sprinkler ten days before sowing and was plowed just before sowing.

A land race (Baimaya, BMY) and ten major maize hybrids released in the past four decades in China were used for the experiment (Table 1). The hybrids were Danyu 6 (DY6), Zhongdan 2 (ZD2), Yedan 2 (YD2), Danyu 13 (DY13), Shendan 7 (SD7), Nongda 60 (ND60), Yedan 4 (YD4), Yedan 13 (YD13), Zhengdan 958 (ZD958) and Xianyu 335 (XY335). Xianyu 335 is bred by Pioneer USA and its parents have no relationship with the other Chinese hybrids. These hybrids were the dominant hybrids grown in Northeast China at the time of their release, and had been ever accumulatively used more than 2.8 million ha in popularly cultivated period in China. ZD958 and XY335 are still the most popular commercial hybrids across North and Northeast of China (Zhao et al., 2011; Chen et al., 2013; Ma et al., 2014).

Seeds were sown on May 4, 2013 and April 29, 2014, respectively. Before sowing, plots were fertilized with 72 kg N ha<sup>-1</sup> (urea), 90 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> (super phosphate), and 100 kg K<sub>2</sub>O ha<sup>-1</sup> (potassium chloride). Then 168 kg N ha<sup>-1</sup> were banded as top dressing at V6 stage (33 days after sowing in 2013, and 37 days after sowing in 2014). Weed growth in plots was controlled by herbicides before seedling emergence and hand cultivation during the growth season. Plots were kept free of insects and diseases by using fungicide and pesticide when necessary.

In 2013, the dates of silking for the hybrids are: July 6 for BMY; July 10 for XY335 and YD4; July 11 for ZD958 and YD2; July 13 for

DY6, ND60, and SD7; July 15 for DY13, YD13, and ZD2. In 2014, the dates of silking for the hybrids are: July 1 for BMY; July 6 for YD2, YD4, XY335, and ZD958; July 8 for DY6, ZD2, ND60, and SD7; July 15 for DY13 and YD13. The plants were harvested at physiological maturity when the black layer formed in the base of the kernels. The dates in 2013 are: August 26 for BMY, DY6, YD2, and XY335; August 29 for DY13, YD4, and YD13; August 31 for ND60, SD7, and ZD2; September 6 for ZD958. The dates in 2014 are: August 20 for BMY and DY6; August 21 for YD2 and XY335; August 26 for DY13, YD4, and YD13; August 29 for ND60, SD7, and ZD2; September 4 for ZD958. During maize growth period, the sunshine hours in 2013 were 9.7% lower than in 2014 (Fig. S1). The precipitation in 2013 (470 mm) was 58.6% higher than in 2014 (296 mm). No irrigation was conducted in 2013. At silking stage in 2014, the plots were irrigated to relieve drought stress.

### 2.2. Experimental design

The experiments were a randomized block design with four replicates. Each plot was 4 m long and 4.8 m wide. The distance between rows and plants was 60 cm and 28 cm, separately. The planting density was 60,000 plants per hectare. At silking stage when the silks were shown in 50% of the plants, two treatments were conducted: (1) Pollination: pollen was collected and applied to the silks when at silking stage; (2) Non-pollination: the silks were covered upon appearing with paper bags to prevent any pollination. As a result, no grains were formed on the cob. Sixty plants were treated in each plot and these plants were marked for sampling.

### 2.3. Plant sampling

At silking and physiological maturity stage, three healthy and uniform plants from each plot were cut at the soil surface and separated into the leaves, the stem (plus the sheath, cob, husk, and tassel) and the grains (only at physiological maturity). Roots were excavated within a soil volume of 60 cm (length) × 28 cm (width) × 40 cm (depth) for each plant. Roots were gently washed free of soil using a banister brush, dried at 70 °C to a constant weight (Ning et al., 2012). At maturity two rows from each plot were harvested for yield measurement. The non-pollinated plants were harvested at the same time as the control plants.

At both sampling dates, green leaf area (GLA) was determined using the formula  $GLA = \text{leaf length} \times \text{maximum leaf width} \times 0.75$  (Chen et al., 2014). Leaf chlorophyll index was estimated between 09:00 A.M. and 12:00 A.M. using a SPAD-502 Plus chlorophyll meter (Tokyo, Japan). The mean of eight readings taken along the ear blade (four on each side of the lamina) was recorded. A linear relationship between leaf chlorophyll content and SPAD meter readings has been previously determined (Dwyer et al., 1991). All samples were heated at 105 °C for 30 min, dried at 70 °C to constant weight. After weighed to obtain dry matter (DM) weight, the samples were ground into fine powder for N measurement. Nitrogen concentration was measured using a standard Kjeldahl procedure (Chen et al., 2015). Harvest index (HI), N harvest index (NHI), N remobilization, N remobilization efficiency% (NRE) in vegetative organs, as well as post-silking N uptake were calculated based on single plant as described below (Chen et al., 2015):

$$HI = \text{Grain yield} / \text{Total plant DM at maturity}$$

$$NHI = \text{Grain N} / \text{Total plant N at maturity}$$

$$\text{N remobilization amount} = \text{vegetative N content at silking} - \text{vegetative N at maturity}$$

$$\text{N remobilization efficiency} \% = \text{N remobilization amount} / \text{vegetative N content at silking}$$

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