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Research article

The mechanisms of low nitrogen induced weakened photosynthesis in summer maize (*Zea mays* L.) under field conditions

Shanshan Wei [1], Xiangyu Wang [1], Deyang Shi, Yanhong Li, Jiwang Zhang, Peng Liu,
Bin Zhao, Shuting Dong*

State Key Laboratory of Crop Biology, Agronomy College, Shandong Agricultural University, Tai'an 271018, Shandong Province, PR China

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ABSTRACT

Soil nitrogen (N) shortage is a problem which affects many developing nations. Crops grown with low soil N levels show a marked decrease in the rate of photosynthesis and this deficiency reduces crop yield significantly. Therefore, developing a better understanding of the mechanisms by which low N levels cause decreased photosynthesis is crucial for maize agriculture. To better understand this process, we assessed the responses of photosynthesis traits and enzymatic activities in the summer maize cultivar Denghai 618 under field conditions with and without the use of N fertilisers. We measured photosynthesis parameters, and compared proteome compositions to identify the mechanisms of physiological and biochemical adaptations to N deficiency in maize. We observed that parameters that indicated the rate of photosynthesis decreased significantly under N deficiency, and this response was associated with leaf senescence. Moreover, we identified 37 proteins involved in leaf photosynthesis, and found that N deficiency significantly affected light-dependent and light-independent reactions in maize leaf photosynthesis. Although further analysis is required to fully elucidate the roles of these proteins in the response to N deficiency, our study identified candidate proteins which may be involved in the regulatory mechanisms involved in reduced photosynthesis under low N conditions in maize.

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1. Introduction

The increase in global maize production over the past half-century has been made possible by extensive use of nitrogen (N) fertilisers. Despite such use, soil N deficiency remains a major constraint on crop productivity in many developing countries. Therefore, increasing plant tolerance to low-N conditions would improve maize production, especially in regions with low soil N levels.

Leaf area and leaf photosynthetic rate are directly linked to plant dry matter production. Maize grain yield is strongly influenced by the extent of photosynthesis as the kernel undergoes grain filling (Muchow, 1988). Maize leaf size is responsive to N levels, and an association is evident between N concentration and photosynthetic capacity (Vos et al., 2005). The extent of photosynthesis during grain filling can be affected by many factors, including maize variety, climatic condition, CO_2 level, and temperature. Another major factor affecting photosynthesis is the available N level of the soil (Jaaffar and Gardner, 1988).

Given the diverse roles that nitrogen plays in plant physiology and development, N deficiency has a crippling effect on plants. N deficiency significantly reduces a plant's capacity for photosynthesis (Boussadia et al., 2010) by reducing the rates of leaf photosynthesis and new leaf area expansion. Moreover, N deficiency

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Abbreviations: CAP, canopy apparent photosynthesis; LAI, leaf area index; Pn, net photosynthetic rate; SLN, total N concentration of ear leaf; CAB, chlorophyll *a-b* binding protein; ATPase, ATP synthase; AST, aspartate aminotransferase; FBA, fructose-bisphosphate aldolase; FBP, fructose-1,6-bisphosphatase; GAPDH, glyceraldehyde-3-phosphate dehydrogenase; MDH, malate dehydrogenase; PEPC, phosphoenolpyruvate carboxylase; PGK, phosphoglycerate kinase; PPDK, pyruvate, phosphate dikinase; PRK, phosphoribulokinase; RPI, ribose-5-phosphate isomerase; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase; SBP, sedoheptulose-1,7-bisphosphatase; TKT, transketolase; TPI, triosephosphate isomerase; ASP, aspartic acid; ATP, adenosine triphosphate; DHAP, dihydroxyacetone phosphate; E-4-P, erythrose 4-phosphate; F-1,6-BP, fructose-1,6-bisphosphate; F-6-P, fructose-6-phosphate; GAP, glyceraldehyde-3-phosphate; OAA, oxaloacetic acid; PEP, phosphoenolpyruvic acid; 1,3-PGA, 1,3-phosphoglycerate; 3-PGA, 3-phosphoglycerate; R-5-P, ribose-5-phosphate; Ru-1,5-BP, ribulose-1,5-bisphophate; Ru-5-P, ribulose-5-phosphate; S-1,7-BP, sedoheptulose-1,7-bisphosphate; S-7-P, sedoheptulose-7-phosphate.

* Corresponding author.
E-mail address: stdong@sdau.edu.cn (S. Dong).

[1] Both authors contributed equally to the article.

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induces and accelerates leaf senescence (Massignam et al., 2012), which is accompanied by transcriptional activation of many genes that are involved directly or indirectly in senescence-related biochemical and cellular changes. Many senescence-associated genes have been identified in *Arabidopsis thaliana* (Buchanan-Wollaston et al., 2005), of which many encode senescence-related transcription factors (Ay et al., 2013). Furthermore, N deficiency leads to the degradation of photosynthetic pigments and proteins, and reduced enzyme synthesis in plants (Polesskaya et al., 2004).

N also plays a central role in the production of plant proteins. Therefore, N deficiency leads to changes in the expression levels of proteins, as well as the activity levels of enzymes, which invariably leads to changes in plant metabolism (Wei et al., 2015). For example, N levels affect the post-translational modification of phosphoenolpyruvate carboxylase (PEPCase) (Prinsi et al., 2009). Earlier studies in several other crops have also indicated that N deficiency reduces ribulose bisphosphate carboxylase/oxygenase (Rubisco) activity (Heitholt et al., 1991), as well as reducing the actual amount of Rubisco produced by the plant. In addition, N deficiency impacts overall plant metabolism through wide reprogramming of primary and secondary metabolic pathways (Scheible et al., 2004).

Gaining a more complete mechanistic picture of how plants adapt and respond to low N conditions is important since N plays important roles in growth and physiology. This is especially critical for crops like maize, which serves as a staple food source worldwide. In addition, a better understanding of the proteins and genes that influence responses to low N can improve the utilisation efficiency of N fertilisers and assist in developing better methods to evaluate plant responses to possible deficiencies. In this study, we aimed to evaluate the response of summer maize to N deficiency stress, and to identify the regulatory mechanisms that result in lower photosynthesis rates. We first demonstrated that the summer maize cultivar Deinghai 618 exhibits reduced photosynthesis rates when grown under low N conditions. Next, we identified proteins that are expressed differentially under low N conditions in maize, most of which are involved in photosynthesis and metabolism. Our data confirmed the effect of N deficiency on the photosynthesis rate in maize and provides a list of proteins that are candidates for involvement in this process.

2. Materials and methods

2.1. Trial site and conditions

Field evaluations were conducted during the 2013 cropping season (from mid-June to late September) at the Shandong Agricultural University Experimental Farm in Shandong, China (117°09′E, 36°10′N). This area has a semi-humid, warm temperate, monsoonal continental climate. The soil at the site is neutral sandy loam, and the nutrient status of the top 30 cm prior to seeding was 18.6 g kg^{-1} organic matter, 0.89 g kg^{-1} available N, 43.05 mg kg^{-1} available phosphate, and 78.91 mg kg^{-1} available potassium.

2.2. Experimental design

Denghai 618 was the maize variety tested. Maize was hand-planted on 15 June 2013. Two rates of N application were used: 0 (N0) and 360 (N1) kg N ha^{-1}; the planting density was 90,000 pl ha^{-1}. The experimental treatments were randomised using a complete block design with three replicates. Each plot was 12 m long × 3 m wide, and consisted of five rows spaced at 0.6 m. The three middle rows of all plots were used for data collection. The final plant densities at harvest were the planned densities. Phosphorus (P_2O_5)- and potassium (K_2O)-containing fertilisers were applied before sowing, at 90 $kg \cdot ha^{-1}$ and 120 kg ha^{-1} per plot, respectively. The N fertiliser was urea applied as a top dressing in two equal portions: one half at the jointing stage, and the other half at the large-bell stage. Irrigation, weeds, diseases, and insect pests were adequately controlled; no factor other than the N level limited growth.

2.3. Physiological measurements

All measurements were performed at the plot centres during the tasselling stage (VT), and at 20 and 40 days after VT (20 and 40 DAT); the central regions of five ear leaf blades (without midribs) were sampled for chemical analyses. Samples were immediately immersed in liquid N_2 and stored at −80 °C prior to analysis of chlorophyll (Chl) content, enzyme activities, and protein levels.

2.3.1. Net photosynthetic rate (Pn)

The net photosynthetic rate (Pn) of ear leaves from three uniformly healthy plants in each plot was measured using a portable system (CIRAS-II, UK) under artificial light of 1600 μmol m^{-2} s^{-1}. The CO_2 concentration in the leaf chamber was maintained at 360 μmol mol^{-1} using a CO_2 injector fitted with a high-pressure liquid CO_2 cartridge. All measurements were conducted between 9:00 and 11:00 a.m. after tasselling on clear days, using an open system.

2.3.2. Leaf area index (LAI)

Five representative plants were selected to determine the leaf area index (LAI). The length (L) and maximum width (W) of each lamina were recorded, and the LAI calculated as $0.75 \times L \times W \times N/S$, where was N is the number of plants in a unit area of land and S is the unit area.

2.3.3. Canopy-apparent photosynthesis (CAP)

Canopy-apparent photosynthesis (CAP) levels were measured using a modified closed gas exchange system fitted with an infrared gas analyser (GXH-305, Beijing, China; Liu et al., 2015). The aluminium-framed chamber consisted of a 1 × 1.33 × 3-m body with a removable door. The lid height depended on the plant height (maximum: 2.94 m). The chamber was covered with 0.6-mm-thick Mylar; the light transmission rate could attain 95%. Two blast blowers (power level 250 w h^{-1}) were used to stir the air inside the chamber. CO_2 concentration decreased linearly, and was usually measured within 1 min after closing the lid of the chamber. Three replicate measurements for each treatment were made daily between 10:00 a.m. and 12:00 noon local time. CO_2 exchange rates were expressed on a soil-area basis. Each canopy photosynthetic rate was calculated as described by Liu et al. (2015).

2.3.4. Chlorophyll fluorescence parameters

Chlorophyll fluorescence parameters were determined using the same leaves employed for Pn measurements with the aid of a portable pulse-modulated fluorometer (FMS-2, UK). The minimal and maximal fluorescence (F_0 and F_m) were determined after full-dark adaptation for 15 min. The steady-state fluorescence (Fs) and the maximum fluorescence in the light-adapted state (Fm′) were determined under actinic light of 1200 μmol m^{-2} s^{-1} for 10 min, and after delivery of a 1-s pulse of saturating radiation at 4000 μmol m^{-2} s^{-1}, respectively. The maximum quantum efficiency (Fv/Fm) and the effective quantum yield of photosystem II (Φ_{PSII}) were calculated as indicated by Baerr et al. (2005).

2.3.5. Chlorophyll content

Ear leaf samples (0.1 g) were sliced and placed in 25 mL of an extraction solution composed of equal volumes of acetone and

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