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Photosynthesis of a yellow-green mutant line in maize

X.M. ZHONG#, S.F. SUN#, F.H. LI, J. WANG, and Z.S. SHI+

Special Corn Institute of Shenyang Agricultural University, Shenyang -110866, China

Abstract

This study compared the relationship between chlorophyll (Chl) content, gas exchange, Chl fluorescence characteristics, and leaf color, using paired near-isogenic lines (NILs) of a medium-green leaf inbred line SN12 and a yellow-green leaf mutant SN62 to explore the photosynthesis of the yellow-green mutant. The SN62 was found in a female parent, Xianyu 335, which grew normally, although there were small yellow spots on the leaves at the seedling stage and yellow-green leaves appeared from the seedling to the maturation stage. The results indicated that Chl *a* (*b*), quantum efficiency of PSII, and maximal quantum yield of PSII photochemistry of SN62 were significantly lower than those of SN12, but there were almost no differences in the net photosynthetic rate (P_N). There was no significant correlation between Chl *a* (*b*) and P_N of inbred lines with different leaf colors. In the reproductive stage, photochemical quenching, effective quantum yield of PSII photochemistry, and the electron transport rate of SN62 increased obviously, and all parameter values exceeded the values of SN12. It explained that increasing the openness of the PSII reaction center was able to compensate for the lower Chl content, which was beneficial for harvesting more light energy for photochemical reactions. It also ensured that P_N was not reduced.

Additional key words: gene mutation; photochemical reaction; potential productivity, photosynthesis.

Introduction

The leaf color is green since Chl predominates in normal leaves (Pan 1995). Leaf color variation with a higher mutation frequency is easily identified as a characteristic in higher plants and was first reported in the 1930's (Suzuki *et al*. 1997). To date, leaf color mutants have been found in almost all higher plants, such as rice (Hu *et al*. 1981), soybean (Ghirardi and Melis 1988), maize (Greene *et al*. 1998), barley (Król *et al*. 1995), wheat (Falbel 1996), tomato (Falbel and Staehelin 1996), rape (Zhao *et al*. 2001), and *Arabidopsis* (Carol *et al*. 1999). In the gene database of maize, there are 165 mutant genes of leaf color, with the great majority of them being recessive mutations in the same locus. Obvious phenotype characteristics of these mutant genes include abnormal leaf colors, which is mostly expressed at the seedling stage. It generally shows olivine (63 genes), whitening (18 genes), spot (26 genes), and stripe (58 genes), to name a few. Olivine and whitening leaf mutants have been found and reported often. Hoisington and Neuffer (1983) identified *nec4,* the olivine mutant gene, in chromosome 2 of maize. Buckner and Robertson (1993) found *yl* on the chromosome 6 using the same cytogenetical method. Chen *et al.* (2008) identified an etiolation gene *al* between *bnlg1064* and *umc1026* in the short arm of the maize chromosome 2, at 2.2 Mb of physical distance. Currently, there are a few articles on the cloning leaf color mutant genes in maize. Sawers (2006) cloned *ZmCHLI,* a Mg-chelatase gene, at the same locus with *OY1* gene. The mutant of *ZmCHLI* is semidominant and shows an olivine leaf phenotype.

In recent years, some leaf mutations have been used as trait markers in hybrid breeding and production (Zhao *et al.* 2000, Zhao *et al.* 2004). Recently, with increasing attention on its use value, leaf color mutants have been widely used in fundamental research concerning mecha-

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+Corresponding author; tel.: +86 024 88487135, fax: +86 024 88487139; e-mail: xuemei.zhong@163.com

Abbreviations: BS – bell–bottom stage; Car – carotenoids; Chl – chlorophyll; ETR – electron transport rate; F_0 – minimal fluorescence; F_m – maximum fluorescence; F_m' – maximum fluorescence; F_s – steady-state fluorescence; FS – filling stage; F_v/F_0 – quantum efficiency of PSII; F_v/F_m – maximal quantum yield of PSII photochemistry; MS – maturation stage; NILs – near-isogenic lines; NPQ – nonphotochemical quenching of PSII; SS – seedling stage; P_N – net photosynthetic rate; PS – powder stage; q_P – photochemical quenching coefficient; Φ_{PSII} – effective quantum yield of PSII photochemistry.

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nisms of plant photosynthesis, the Chl biosynthesis pathway, the structure and function of chloroplast, regulatory mechanisms of heredity and development, crop trait markers, *etc*., (Dong *et al.* 1995, Larkin *et al.* 2003) along with development of production applications.

Leaf color mutant research has not proved that the photosynthetic efficiency of light green leaves is absolutely lower than that of normal leaves (Dai *et al.* 2000, Kurata *et al.* 2005). Xu *et al.* (2004) found a weak ability to absorb light in mutants with low Chl, but a high efficiency was found in their electron transport. Our study used a yellow-green leaf mutant found in the female parent, Xianyu 335, which grew normally, although it shows yellow-green leaves from the seedling to mature stage and some small yellow spots occured on every leaf during the seedling stage.

Research on heredity and gene mutation of leaf color mutants has been done in maize. However, few articles have addressed phenotype selection in maize breeding with respect to the relationship between leaf color and photosynthesis in maize. This study compared the relationship between chlorophyll content, gas exchange, chlorophyll fluorescence characteristics, and leaf color, using paired NILs of a medium-green leaf inbred line SN12 and a yellow-green leaf mutant SN62 to explore the photosynthesis of the yellow-green mutant.

Materials and methods

Experimental design: The experiment was carried out on the south farm of the Shenyang Agricultural University (41°49'N, 123°34'E), which is classified as a north temperate climate, with a semihumid continental climate often affected by monsoons. The annual average temperature is 8ºC, with an annual average rainfall of 628 mm, the average light intensity of 793 μmol(photon) m^{-2} s^{-1} from May to September, and a frost-free period of about 150–170 days. The experiment applied a randomized block design, three times repeated. The row length of a plot was 4.0 m, and row width of 0.6 m. There were six rows in each plot and 14.4 m^2 for each plot. The basic physical and chemical properties of the experimental soil was 27.20 g(organic matter) kg^{-1}, 2.35 g(total nitrogen) kg^{-1}, 118.35 mg(alkaline hydrolysed nitrogen) kg^{-1}, 11.19 mg (available phosphorus) kg^{-1}, and 107.32 mg(available potassium) kg^{-1}. SN62 and SN12 were a pair of NILs, and they were found in the female parent Xianyu 335. SN12 was a normal inbred line with medium-green leaf color. SN62 was a yellow-green mutant and its leaves and bud sheaths were yellow-green and pink, respectively. There were irregular small yellow patches on the leaves during the seedling stage in SN62. With the growth of SN62, patches became shallow gradually or even disappeared completely; yellow-green leaves appeared from the seedling to mature stage. Seedlings emerged on May 4, 2013.

Photosynthetic pigment content: Leaf samples (100 mg), with the midrib removed, were soaked in 80% acetone: ethanol:water (4.5:4.5:1) at 4ºC and placed in dark conditions for 24 h. Supernatant was collected and absorbance measured by *UV-2000* spectrophotometer (*Unico, Instrument, Ltd., Co.*, Shanghai, China) at 663 and 647 nm for Chl *a* and Chl *b*, respectively. The concentration of Chl was calculated according to the equations of Lichtenthaler and Buschmann (2001):

$$\text{Chl } a = 12.25\, A_{663} - 2.79\, A_{647}$$
$$\text{Chl } b = 21.50\, A_{647} - 5.10\, A_{663}$$
$$\text{Car} = (1{,}000\, A_{470} - 3.27\, \text{Chl } a - 104\, \text{Chl } b)/229$$

Photosynthetic rate (P_N): P_N was measured on sunny mornings from 09:00 to 10:00 h using a *Li-6400* portable photosynthesis system (*LI-COR Biosciences Inc*., Lincoln, NE, USA) equipped with an artificial irradiance source (*6400-02B RedBlue*). The light intensities for the measurement were adjusted to 1,400 μmol(photon) m^{-2} s^{-1}. The CO_2 flux was adjusted to maintain a concentration of 380 μmol mol^{-1} inside the chamber and the leaf chamber temperature was maintained at 25°C. The data were recorded at the middle of the fully expanded leaf during the seeding stage (SS) and the bell–bottom stage (BS) and at the middle of the ear leaf during the pollination stage (PS) and filling stage (FS).

P_N-PPFD response: P_N was determined at thirteen levels of PAR (0, 20, 50, 100, 200, 400, 600, 800; 1,000; 1,200; 1,400; 1,600; and 1,800 μmol m^{-2} s^{-1}) at 380 μmol(CO_2) m^{-2} s^{-1}, at a temperature of 25°C in the chamber. PAR was decreased gradually from 1,800 to 0 μmol m^{-2} s^{-1}. Measurements were recorded automatically at 180-s intervals for each PAR per leaf, and three plants per variety (a fully expanded and non-self-shaded ear leaf per plant) were measured during the FS stage.

Chl fluorescence parameters were measured using a photosynthesis yield analyzer (*Mini-Pam, Walz*, Effeltrich, Germany). The minimal fluorescence (F_0) was measured in 30 min dark-adapted leaves using weak modulated irradiance (< 0.1 μmol m^{-2} s^{-1}). A 600-ms saturating flash was applied to determine the maximum fluorescence (F_m) and photochemical efficiency of PSII (F_v/F_m). Then the leaves were continuously irradiated with white actinic light (800 μmol m^{-2} s^{-1}) in order to measure the steady-state fluorescence yield (F_s) and maximum fluorescence yield (F_m') of irradiated leaves. The following Chl fluorescence parameters were calculated: F_v/F_m calculated according to van Kooten and Snel (1990), $\Phi_{PSII} = (F_m' - F_s)/F_m'$, ETR = $\Phi_{PSII} \times \text{PAR} \times 0.5 \times 0.84$. PAR is the photosynthetically active radiation generated by the internal halogen lamp of the instrument, 0.84 is the instrument default absorption coefficient, and 0.5 assumes that the photons absorbed are equally partitioned between two photosystems according to Genty *et al.* (1989). Effective quantum yield of PSII photochemistry (Φ_{PSII}), electron transport rate (ETR), photochemical quenching (q_P), and nonphotochemical quenching (NPQ) are calculated by the following formulas: $(F_m' - F_s)/F_m'$, $\Phi_{PSII} \times PAR \times 0.5 \times 0.84$, $(F_m' - F_s)/(F_m' - F_0')$, and $F_m/F_m' - 1$, respectively.

Statistics: *Microsoft Excel* software was used for data processing, and *Origin 8.0* for mapping. Analysis of variance (*ANOVA)* was done by version *12.0* of the *SPSS* software (*SPSS Inc.*, Chicago, IL, USA). When we found significant differences, we used the least significant difference (LSD) test to compare specific pairs of values. *P* values lesser than 0.05 and 0.01 were considered as statistically significant and extremely significant, respectively.

Results

Photosynthetic pigments: Chl content was the lowest in SN12 at the seedling stage; then after a sharp increase, it reached a maximum in the PS stage, while it decreased significantly during the FS stage (Fig. 1). The Car content was the highest at the BS stage and then decreased at the FS. Light was the most important outside factor affecting the formation of Chl. Meteorological records showed that the rainy season coincided with the period when maize undergoes pollination, and light intensity was only 200–400 μmol(photon) m^{-2} s^{-1}, which resulted in the lower Chl content than that of an average year. Chl *a*, Chl *b*, total Chl, and Car contents of SN62 were lower than those in SN12, except at the SS stage. Chl content was the lowest in the SS stage. At this stage, Chl *a* and total Chl of SN62 were significantly 56.3% and 55.6% lower, respectively, than those in SN12. Chl *a* and total Chl content of SN62 began to decline in the BS stage. The lower Chl and Car contents were the main reason for the yellow-green color of leaves.

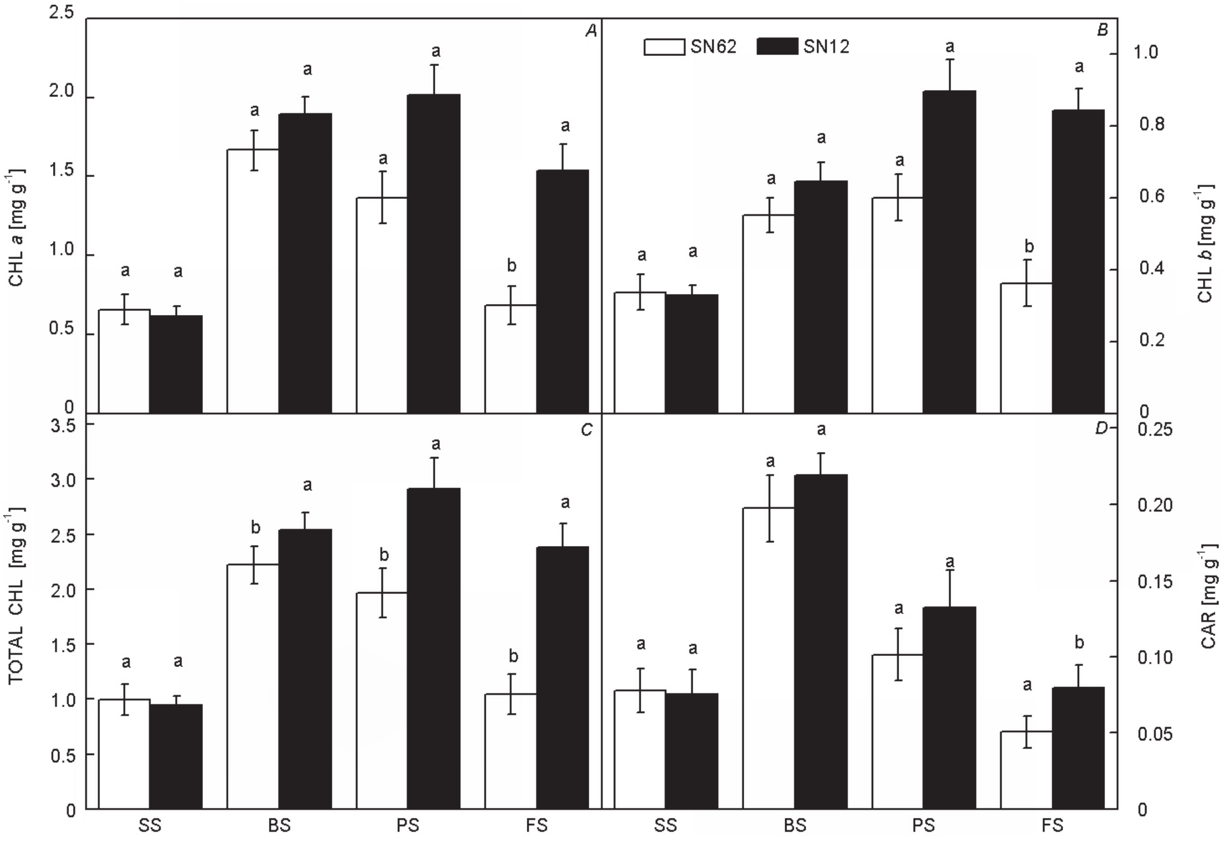

Fig. 1. Comparison of contents of photosynthetic pigments. Chl – chlorophyll; Car – carotenoids. *Vertical bars* denote SE (*n* = 5). *Small and capital letters* indicate differences in different inbred lines at $P<0.05$ and $P<0.01$, respectively, according to least significant difference (LSD) tests. SS – seedling stage, BS – bellmouth stage; PS – powder stage; FS – filling stage.

Comparison of P_N: P_N of two inbred lines showed the same dynamic changes at different growth stages (Fig. 2). It reached a maximum in the BS and then began to decline. P_N of SN62 was always lower than that of SN12 from the SS to the FS stage, but the difference was not significant except at the SS stage. The Chl content of the yellow-green mutant SN62 was significantly lower than that of SN12 at the FS, but there was no significant difference in the P_N. This also confirmed that there was no significant correlation between P_N and the Chl content in maize of varying leaf colors.

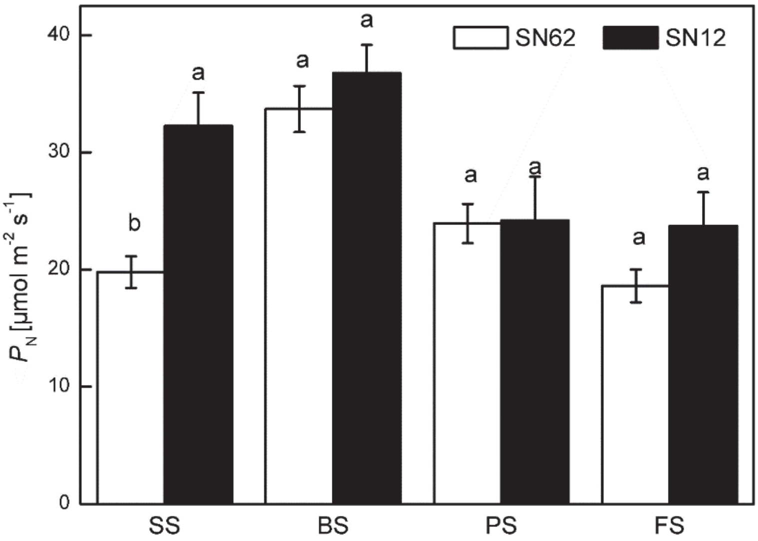

Fig. 2. Comparison of net photosynthetic rates (P_N). *Vertical bars* denote the SE ($n = 5$). *Small and capital letters* indicate differences in different inbred lines at $P<0.05$ and $P<0.01$, respectively, according to the least significant difference (LSD) test. SS – seedling stage, BS – bellmouth stage; PS – powder stage; FS – filling stage.

Comparison of Chl fluorescence parameters in inbred lines and in different leaves: F_v/F_m and F_v/F_0 are used to measure the conversion efficiency of primary light energy and the PSII potential activity of plant leaves, respectively, and are important photochemical reaction parameters. F_v/F_m is an important indicator for measuring the photoinhibition degree (Krause and Weis 1991). Comparing the changes of F_v/F_0 and F_v/F_m at different growth stages of two inbred lines (Fig. 4), the values of yellow-green leaf mutant SN62 were significantly lower than the medium-green leaf inbred line SN12, which were consistent with the differences in the Chl content. SN12 was always the highest at different growth stages. Although the values were relatively low, the F_v/F_m and F_v/F_0 of the yellow-green leaf mutant SN62 showed no obvious difference at different growth stages, which indicated that conversion efficiency of primary light energy and potential activity of PSII were relatively stable.

P_N-PPFD response in different inbred lines: A higher light saturation point could be more effective in avoiding light damage and for maintaining the normal activity of photosynthetic organs. At the FS stage, the P_N of SN12 and SN62 showed an increasing trend with higher light intensity (Fig. 3). The P_N of SN12 and SN62 rose slowly from 1,000 to 1,200 μmol(photon) m^{-2} s^{-1}, and it reached a maximum at 1,600 μmol(photon) m^{-2} s^{-1}. The light saturation point of SN12 and SN62 were both at 1,600 μmol m^{-2} s^{-1}.

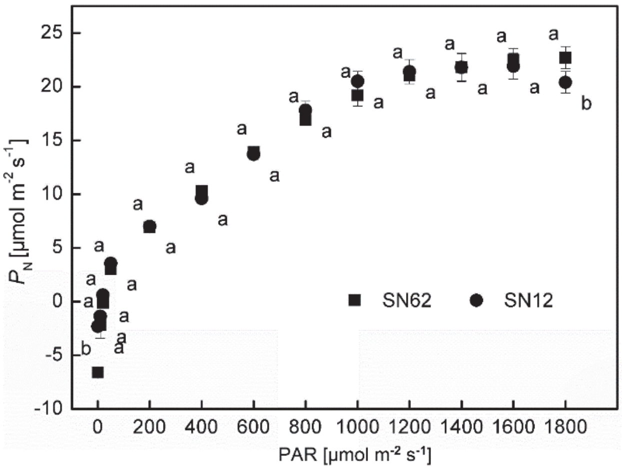

Fig. 3. P_N-PPFD response in different inbred lines. PAR – photosynthetically active radiation, P_N – photosynthetic rate. *Vertical bars* denote SE ($n = 3$). *Small letters* indicate differences in different inbred lines at $P<0.05$, according to the least significant difference (LSD) test.

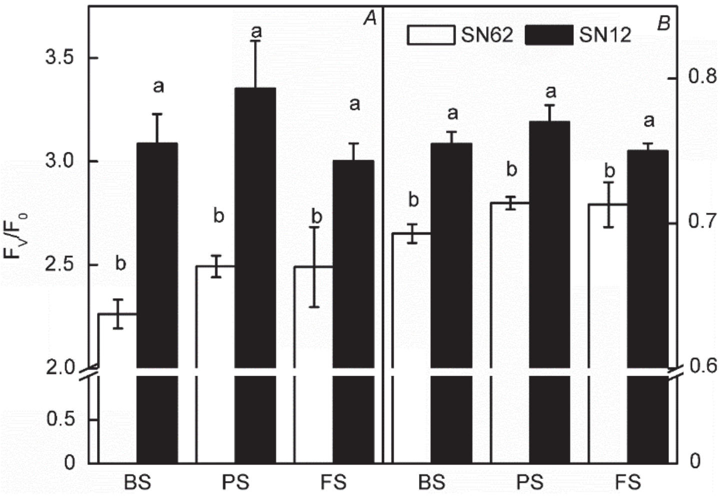

Fig. 4. Variation in characteristics of quantum efficiency (F_V/F_0) and maximal quantum yield of PSII photochemistry (F_V/F_m) in maize inbred lines with different leaf colors. *Vertical bars* denote SE (*n* = 5). *Small* and *capital letters* indicate differences in different inbred lines at $P<0.05$ and $P<0.01$, respectively, according to the least significant difference (LSD) test. SS – seedling stage, BS – bellmouth stage; PS – powder stage; FS – filling stage.

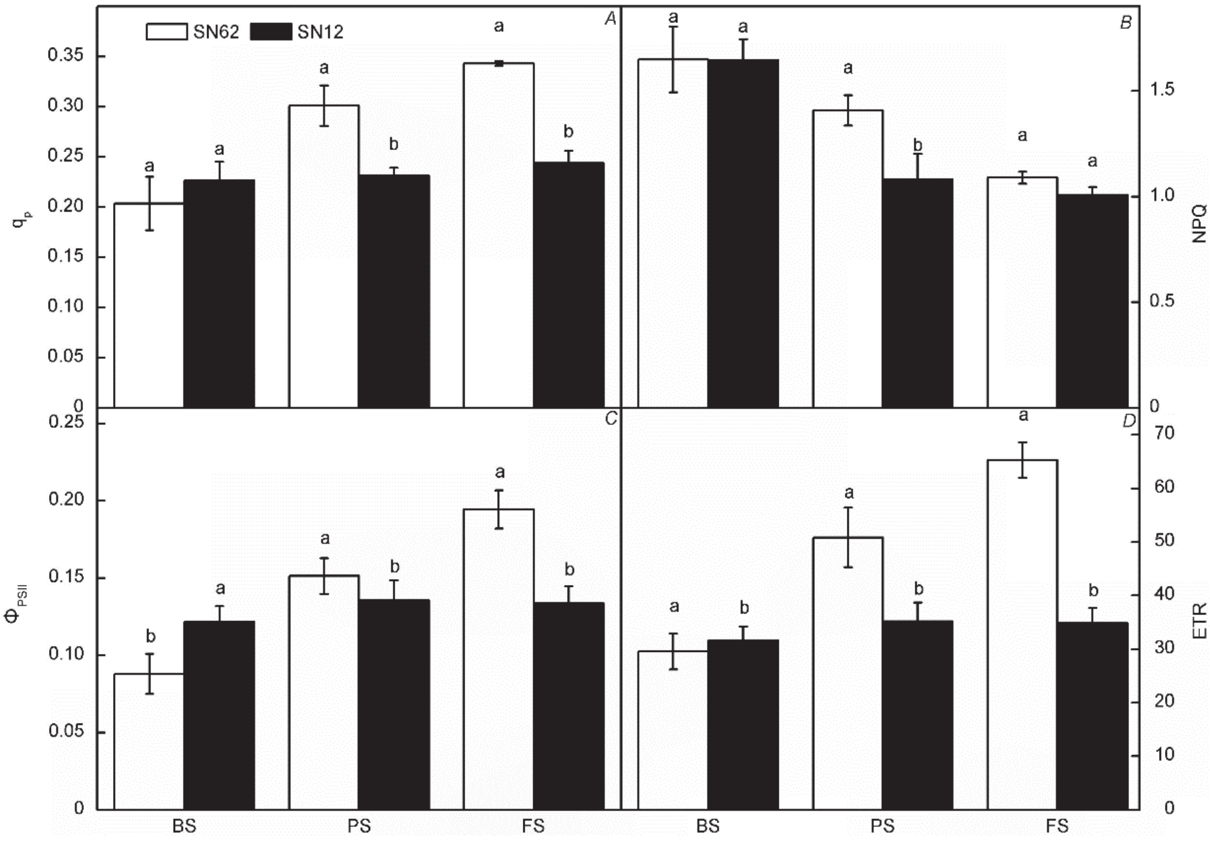

Fig. 5. Variations in characteristics of NPQ, q_P, Φ_{PSII}, and ETR in the inbred lines with different leaf colors. *Vertical bars* denote SE (*n* = 5). *Small and capital letters* indicate differences in different inbred lines at $P<0.05$ and $P<0.01$, respectively, according to the least significant difference (LSD) test. SS – seedling stage, BS – bellmouth stage; PS – powder stage; FS – filling stage.

NPQ, q_P, Φ_{PSII}, and ETR in inbred lines with different leaf colors: The changing trends of NPQ were the same from the BS to the FS in both inbred lines. NPQ reached its maximum at the BS and decreased sharply at the PS and FS (Fig. 5). There were significant differences in SN12 and SN62 at the PS and FS. NPQ of the yellow-green leaf mutant SN62 was always higher than that of SN12. The maximum difference among the inbred lines appeared at the PS; NPQ of SN62 was 30.1% higher than that of SN12. Compared to NPQ, Φ_{PSII}, q_P, and ETR were different and even showed an opposite trend. At the BS, there was small difference in NPQ between the inbred lines. The q_P of SN62 was slightly lower than that of SN12. Φ_{PSII} and ETR of SN62 were significantly lower than that of SN12 with normal leaf colors, which indicated that the yellow-green leaf was mainly due to the low Chl content during the vegetative growth stage. The lower Chl content caused the decrease in the conversion efficiency of primary light energy in PSII, and affected the actual photochemical efficiency and electron transfer efficiency of leaves. In the PS, q_P, Φ_{PSII}, and ETR of the yellow-green mutant SN62 increased, and all three parameters of SN62 exceeded those in SN12. During the FS, all three parameters of SN62 continued to rise. The gap between SN62 and SN12 further expanded. The q_P, Φ_{PSII}, and ETR of SN12 were 40.6%, 44.8%, and 45.5% lower than that of SN62, which showed that the yellow-green mutant was able to enhance the openness of the PSII reaction center to capture more light energy for the photochemical reaction during the key stage of reproductive growth, thus improving the efficiency of photosynthesis. This was a self-regulation mechanism of the yellow-green leaf mutant under adverse conditions.

Discussion

High photosynthetic efficiency breeding in maize attempts to improve photosynthetic production capacity, reduce respiration, and improve production by investigating morphological and physiological characteristics. Much work has been carried out in recent years, but the selection of high photosynthetic efficiency varieties according to their leaf colors is still controversial. For a long time, Chl content has been used as an index for solar absorption and to indicate the utilization ability of leaf (Lin *et al.* 2009). Ramesh *et al.* (2002) reported that there was a positive correlation between the Chl content and yield. However, it has been also found that not all plants with the higher Chl content show a higher photosynthetic capacity and grain yield (Lin *et al.* 2003, Zhang *et al.* 2012).

Compared to the medium-green inbred line SN12, the Chl content of the yellow-green leaf mutant SN62 was lower, while its P_N was not significantly lower than the SN12 except in the SS. SN62 was able to absorb and use light energy during the late growth stages and to maintain the higher activity and photosynthetic electron transport efficiency in the PSII reaction center, which ensured that its P_N was not reduced. This result also supported the conclusion that the leaf colors of maize had no significant correlation with the P_N. It was found that the Chl content of SN62 was the lowest and fell earlier at different developmental stages. F_v/F_m and F_v/F_0 of SN62 were significantly lower than those of SN12. This was consistent with the results for the Chl content, which indicated that there were defects in the Chl synthesis and original conversion efficiency of PSII of SN62. The P_N of SN62 was not significantly lower than that of SN12, indicating that the Chl content of the inbred lines with different leaf colors had no significant correlation with their photosynthetic rate. At the reproductive stage, q_P, Φ_{PSII}, and ETR in SN62 rose obviously, and all three parameters were higher than those of the medium-green leaf of the inbred line SN12. This explained that the yellow-green mutant SN62 was able to compensate for the lower Chl content and original light energy conversion efficiency by expanding the openness of the PSII reaction center and harvesting more light energy for photochemical reactions. Therefore, the higher PSII reaction activity, photochemical efficiency, and apparent electron transfer efficiency were primary reasons for maintaining a relatively high P_N of the yellow-green leaf mutant with the lower Chl content.

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