

Regulation of photosynthetic function in maize plants under spatially heterogeneous light environment at reproductive stage

Han-Yu Wu

Institute of Botany Chinese Academy of Sciences

Mei-Yu Qiao

Institute of Botany

Wang-Feng Zhang

Shihezi University

Ke-Ru Wang

Institute of Crop Sciences

Shao-Kun Li

Institute of Crop Sciences

Chuang-Dao Jiang (✉ jcdao@ibcas.ac.cn)

Research article

Keywords: Light environment, Photosynthesis, Gas exchange, Chlorophyll a fluorescence transient, Reproductive growth

Posted Date: July 26th, 2019

DOI: <https://doi.org/10.21203/rs.2.12013/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Background: To cope with spatially heterogeneous light environment, photosynthesis of plants can be regulated systemically. Till present, most of these studies were carried out with various plants in the vegetative growth period. Yet the regulation of photosynthesis at reproductive stage has remained elusive under spatially heterogeneous light environment in the field. **Methods:** Therefore, the changes of light intensity within canopy, chlorophyll content, gas exchange and chlorophyll a fluorescence transient were carefully investigated at heading and grain-filling stages of maize under various planting densities. **Results:** In this study, high planting density of maize induced significantly spatial heterogeneity of light environment within canopy. Chlorophyll content, photosynthetic capacity and photosystem II performance in the ear leaf and the fourth leaf below the ear were reduced apparently with the increase of plant density. Moreover, these differences between the both leaves were enlarged with increasing plant density. After the tassel and top leaves of the maize plants were removed (RTL), the spatial heterogeneity of the light environment decreased. The photosynthetic capacity and photosystem II performance in the ear leaf decreased slightly after RTL, while these parameters in the fourth leaf below the ear were improved considerably. Obviously, the removal of the tassel and top leaves reduced the spatial heterogeneity of photosynthetic function of maize plants. **Conclusions:** Taken together, these results demonstrate that maize plants could enhance the spatial heterogeneity of their photosynthetic function to adapt heterogeneous light environment at the reproductive stage; the systemic regulation of photosynthesis under spatially heterogeneous light environment could be weakened by reproductive growth.

Background

Light is the basic driving force of photosynthesis, and also an important environmental factor affecting photosynthetic regulation. Generally, plants adapt to their light environment by regulating leaf structure, components and photosynthetic function. Under high light, leaf area diminishes and leaves become thicker. At the same time, there are clear reductions in chlorophyll content and the ratio of photosystem II to photosystem I (PSII/PSI), while chlorophyll a/b, electron carrier levels and Rubisco content increase [1,2]. Hence, the photosynthetic capacity of leaves growing under high light is relatively high, as is the ability to dissipate excess excitation energy [1,3–4]. Under weak light, the opposite photosynthetic adaptations occur [3,5–8]. Most of these studies have been carried out in homogeneous or hypothetically homogeneous light environments, but these cannot reflect the way photosynthesis is regulated in the field's spatially heterogeneous light environments.

Actually, in the field, the upper canopy leaves of the canopy are mostly exposed to strong light, while the lower leaves are exposed to weak light. It is reported that the light environment of mature leaves influences the stomatal development, morphological characteristics and photosynthetic function of new leaves [9–11]. Our previous studies also demonstrated that shading mature leaves of sorghum not only induces an obviously lowered photosynthetic capacity and strengthened high light sensitivity of their own, but also new developed leaves [10,12]. Therefore, the development of photosynthetic performance in

new leaves depends on the light environment and photosynthetic function of the plant's mature leaves to some extent. Accordingly, photosynthetic performance of upper canopy leaves can be systemically regulated by lower canopy leaves in plants [13–15]. This allows individual plant to adapt to spatially heterogeneous light environment by keeping relative uniformity photosynthetic performance in leaves within canopy. Till present, most of these studies have been carried out in the vegetative growth period. As we know, during the reproductive growth period, reproductive organs are a massive sink which may also affect the regulation of photosynthesis [16–18]. However, it is unclear how photosynthesis of plants would be regulated at reproductive stage under spatially heterogeneous light environments in the field.

In practice, high planting density is one of the most effective strategies for maximizing maize yield [19]. However, high planting density of maize drastically reduces the light intensities at the middle and lower canopy [20–22], and thus results in a spatially heterogeneous light environments within canopy. To explore the regulation of photosynthesis under spatially heterogeneous light environment, the changes of light intensity within canopy, chlorophyll content, gas exchange and chlorophyll *a* fluorescence transient (OJIP) were carefully studied in the reproductive period of maize (Zhengdan 958) under three planting densities in the field. This study may provide experimental support for the high yield of maize in China.

Results

Effects of planting density on light environment within canopy

As shown in Fig. 1, higher light intensity of the ear leaf compared with the fourth leaf below the ear was observed under all planting densities at both heading stage and grain-filling stage. Compared with the ear leaf, the light intensity of the fourth leaf below the ear decreased by about 30% at low planting density and by 80% at high planting density. As planting density increased, the decrease of light intensity became more pronounced in the fourth leaf below the ear compared to the ear leaf, so that at high planting density, the light intensity of the fourth leaf below the ear was 70% lower than at the low planting density (Fig. 1). In contrast, the ear leaf light intensity changed very slightly as density increased. These data indicate that close planting enhanced spatial heterogeneity of light environment.

Here Insert Figure 1

The removal of the tassel and 1–3 top leaves close the tassel (RTL) is generally believed that this method could improve light intensity penetrating the canopy. In this study, RTL increased the light intensity reaching the ear leaf by a small amount, but it significantly increased the light intensity at the fourth leaf below the ear (Fig. 2). This confirms that RTL can improve the light environment, especially at the lower canopy.

Here Insert Figure 2

Effects of planting density on chlorophyll content

The total chlorophyll content in the ear leaves from heading stage (July) to the grain-filling stage (August) was maintained at a relatively high level. The chlorophyll content decreased with increasing planting density, but the extent of the decrease was not significant (Fig. 3). The chlorophyll content was lower at the fourth leaf below the ear than at the ear leaf. As the planting density increased, the chlorophyll content of the fourth leaf below the ear was markedly reduced. It was about 35% lower at high planting density than at low planting density for the fourth leaf below the ear.

Here Insert Figure 3

RTL reduced the chlorophyll content in both the ear leaf and the fourth leaf below the ear, and more so with increasing planting density (Fig. 4). However, chlorophyll content decreased less in the fourth leaf below the ear compared to the ear leaf. This suggests that RTL has different effects on chlorophyll content at the ear leaf compared to the fourth leaf below the ear.

Here Insert Figure 4

Effects of planting density on gas exchange

Under low planting density, the photosynthetic rate and stomatal conductance of the ear leaf maintained a higher state at the heading (July) and grain-filling stage (August), and decreased slightly as density increased (Fig. 5). The fourth leaf below the ear had a lower photosynthetic rate and stomatal conductance than the ear leaf under all planting densities. The photosynthetic rate and stomatal conductance of the fourth leaf below the ear decreased gradually with increasing planting density.

Here Insert Figure 5

The photosynthetic rate and stomatal conductance (Fig. 6) of the ear leaf decreased after RTL, but there was no obvious change in photosynthetic rate with increased planting density. In contrast, the photosynthetic rate of the fourth leaf below the ear significantly increased after RTL. Compared with CK, the photosynthetic rate of the fourth leaf below the ear increased by 18.1%, 22.1% and 36.6% at low, medium and high planting densities, respectively. These results confirm that RTL can decrease the photosynthetic rate of the ear leaf, while increasing the photosynthetic rate of the fourth leaf below the ear.

Here Insert Figure 6

Effects of planting density on chlorophyll a fluorescence transient

The chlorophyll *a* fluorescence transient (OJIP curve) contains abundant information about the primary photochemical reaction of PSII and is widely used in the study of PSII function. At the heading stage, the chlorophyll *a* fluorescence transient of the ear leaf was slightly affected by the planting density, but at the grain-filling stage the relative fluorescence yield of J and I phases of OJIP increased significantly as density increased (Fig. 7A and Fig. 7B). For the fourth leaf below the ear, at heading stage, the relative fluorescence yield of J and I phases of OJIP increased with increasing planting density, and it did so significantly at the grain-filling stage.

Here Insert Figure 7

Fig. 8 shows how OJIP changed after RTL. The relative fluorescence yields of J and I phases in both the ear leaf and the fourth leaf below the ear decreased, indicating that RTL resulted in an increase in the quantum yield of electron transport. As planting density increased, this decrease was much larger in the fourth leaf below the ear compared with the ear leaf.

Here Insert Figure 8

$PI_{(CSO)}$ refers to the photosynthetic performance index on cross section basis, and reflects the function of PSII. At both the heading stage (July) and grain-filling stage (August), the $PI_{(CSO)}$ was higher in the ear leaf than the fourth leaf below the ear. Compared with the ear leaf, $PI_{(CSO)}$ in the fourth leaf below the ear reduced 10% and 25% under the high planting density condition at heading stage and grain filling stage, respectively (Fig. 9A, B). As the density increased, the $PI_{(CSO)}$ of both the ear leaf and the fourth leaf below the ear went down. Relative to low planting density, the $PI_{(CSO)}$ of the ear leaf under high planting density decreased by about 20%, while the $PI_{(CSO)}$ of the fourth leaf below the ear dropped 30% at least.

We also calculated Ψ_{E0} , which represents the quantum yield of electron transport beyond Q_A . In all cases, these measurements displayed similar patterns to $PI_{(CSO)}$ (Fig. 9C, D). After RTL, the $PI_{(CSO)}$ and Ψ_{E0} of the ear leaf and the fourth leaf below the ear increased. The enhancement of $PI_{(CSO)}$ and Ψ_{E0} in the ear leaf was relatively small, but the increase in the fourth leaf below the ear was significant (Fig. 10). These results suggest that although high planting density reduces the photosynthetic performance and electron transport efficiency of PSII, RTL improves these parameters.

Here Insert Figure 9

Here Insert Figure 10

Discussion

Regulation of leaf photosynthetic function under weak light resulting from close planting

In this study, close planting resulted in weak light within crop canopy. With increasing plant density, the light-saturated photosynthetic rate of the ear leaf decreased slightly at heading stages. Moreover, in the 3 planting densities, there was little difference in the chlorophyll *a* fluorescence transient of the ear leaf at this stage. Thus, on certain extent, ear leaf could acclimate to the weak light environment resulting from high planting density at heading time. However, at the grain-filling stage, the slight decline in the quantum yield of electron transport of PSII was observed in parallel with the light-saturated photosynthetic rate. As we know, leaves could increase or maintain the quantum yield of electron transport of PSII, thus adapt to weak growth light. So, the decline in chlorophyll content, the quantum yield of electron transport of PSII and the light-saturated photosynthetic rate of the ear leaf may not reflect its acclimation to weak light. It has been demonstrated that weak light can also induce leaf senescence. During leaf senescence, not only the chlorophyll content and photosynthetic capacity, but also the quantum yield of electron transport decrease gradually. Therefore, we thought that ear leaf began to senesce at this time.

In addition to the ear leaf, our data also showed that the light intensity, chlorophyll content and photosynthetic rate in the fourth leaf below the ear decreased obviously with increasing plant density. However, the quantum yield of electron transport of the fourth leaf below the ear decreased apparently with increasing plant density. Moreover, the decrease in the quantum yield of electron transport at high planting density were noticeably at heading stage, and were greater at grain filling stage. Accordingly, the decreased chlorophyll content, quantum yield of electron transport and light-saturated photosynthetic rate of the fourth leaf below the ear is indicative of senescence at high planting density, and the senescence began at heading stage.

Overall, the weak light environment within maize canopy resulting from high planting density could accelerate leaf senescence in the field. Actually, the fourth leaf below the ear was elder than the ear leaf. Furthermore, its' light intensity was weaker than the ear leaf. So, the two causes may result in the differences in photosynthetic regulation between the ear leaf and the fourth leaf below the ear with the increasing of planting density.

Optimization of photosynthetic function in maize plants under spatially heterogeneous light environment

In this study, low planting density led to higher light intensity at the ear leaf and the fourth leaf below the ear. When the cultivation density was increased, light intensity at the fourth leaf below the ear markedly declined compared with that of the ear leaf (Fig. 1). The difference in light intensity between the two leaves increased rapidly with increased planting density (Fig. 11). Therefore, close planting significantly enhanced the spatial heterogeneity of light environment within maize canopy. The chlorophyll content, photosynthetic capacity and performance index of PSII of the fourth leaf below the ear decreased sharply

at high planting density; while these parameters were reduced in ear leaves only slightly. Therefore, maize plants growing at high planting density could enhance the spatial heterogeneity of their photosynthetic function at the reproductive stage, and thus adapt to their heterogeneous light environment.

However, with the increasing of plant density, RTL increased the light intensity of the ear leaf by 9.2%, 20.9% and 32.1%, respectively; and it increased the light intensity of the fourth leaf below the ear by 23.4%, 132.1% and 221.1%, respectively (Fig. 2). Clearly, RTL clearly reduced the spatial heterogeneity of the light environment within maize canopy when planting density is high (Fig. 11). Moreover, the uniformity of leaf chlorophyll content, performance index of PSII and photosynthetic capacity within plants were clearly enhanced in RTL treatment with increasing plant density, as reflected by the ratio of the parameters of the ear leaf to the fourth leaf below the ear (Fig. 11). Therefore, RTL in field conditions could improve spatially heterogeneous light environment and photosynthesis in the lower leaves within canopy, thus optimizing photosynthetic function of maize plants and increasing yield.

Here Insert Figure 11

Regulation of photosynthetic function in maize plants under spatially heterogeneous light environment

Our previous study with sorghum showed that artificial shading a plant's lower leaves negatively and markedly affects the photosynthetic capacity of the upper leaves [10]. However, in the present study, the photosynthetic capacity of the ear leaf was maintained at a very high level during the heading and grain filling stages. Even under the high-density planting condition, the saturated photosynthetic rate of the ear leaf was only about 10% lower than that of low planting density, while the saturated photosynthetic rate in the fourth leaf below the ear declined by 35% at the high planting density relative to the low planting density. These results indicated systematic regulation of photosynthesis appears to be weakened at reproductive stage at high planting density.

On one hand, the close proximity of the ear leaf to the tassel and ear may enhance its photosynthetic capacity by considerable sink strength[23]. Furthermore, we noticed that RTL improved the light environment of the maize canopy, and more so in the fourth leaf below the ear than at the ear leaf (Fig. 2). Compared to control plants, RTL resulted in a significant increase in the photosynthetic rate of the fourth leaf below the ear with increasing plant density (Fig. 5 and Fig. 7). With systemic regulation of photosynthesis, the photosynthetic rate of the ear leaf should also have increased, and yet we measured a slight decrease. These data demonstrated again that at reproductive stage the systematic regulation of photosynthesis may be modified by sink strength of reproductive organ in maize.

Additionally, at close planting, the senescence in fourth leaf below the ear was exacerbated significantly under spatially heterogeneous light environment, which might also influence the systemic regulation of photosynthesis on certain extent.

Conclusions

Accordingly, we thought that maize plants could enhance the spatial heterogeneity of their photosynthetic function to adapt heterogeneous light environment at the reproductive stage; the systemic regulation of photosynthesis under spatially heterogeneous light environment might be weakened by reproductive growth.

Methods

Plant material and experimental design

The experiment was carried out in Qitai county (E 89° 46' 01", N 43° 50' 41"), Xinjiang Province of China in 2017. Meteorological data for the 2016 maize growing seasons was obtained from meteorological stations located near the experimental sites which the mean daily temperature during maize growing season was 20.08 °C, the diurnal temperature variation was 14.12 °C, the accumulated solar radiation was 1571MJ m⁻². Zhengdan 958 (ZD958) was utilized as plant material, which is a hybrid of Zheng58 as the female parent and Chang7-2 as the male parent. The seeds of ZD958 were provided by the Crop Institute of Academy of Agricultural Sciences, Henan Province, China. In this study, 3 planting densities: low density (15 000 plants hm⁻²), medium density (75 000 plants hm⁻²) and high density (135 000 plants hm⁻²) were set up. Maize seeded in alternating wide-narrow row patterns (alternating row spaces of 70 and 40 cm, respectively). Base fertilizer was applied at rates of 75,150 kg ha⁻¹ N as urea, 188,225 kg ha⁻¹ P₂O₅ (super phosphate), and 5375 kg ha⁻¹ K₂O (potassium sulfate) prior to sowing. In addition, normal water and fertilizer management was carried out throughout by drip irrigation under film, to avoid potential nutrients and drought stresses.

To improve the light environment within canopy of maize, the removal of the tassel and 1–3 top leaves close the tassel (RTL) is one of the important measures. Therefore, maize seedlings in 3 planting densities are divided into 2 treatments: control (CK) and removing the tassel and top 3 leaves close the tassel (RTL). After full pollination of maize at the heading stage (July 25th), the top 3 leaves were cut off, along with the tassel in three planting density. The light intensity, total chlorophyll content, gas exchange and chlorophyll *a* fluorescence transient (OJIP) of the ear leaf and the fourth leaf below the ear were measured at the heading stage and grain-filling stage.

Light intensity measurement

Between 10:00–14:00, the light intensity was measured on a clear day by canopy analyzer (SUNSCAN, Delta, UK) with a 1 m line quantum sensor. In the experiments, all leaves were kept in their natural position and measurements were made on leaf surface. At least five measurements of PAR (photosynthetically active radiation) were made at each plot at the heading and grain-filling stages.

Chlorophyll content measurement

At heading and grain-filling stages, five leaf disks (1 cm in diameter) were drilled with a perforator. These leaf disks were placed in test tubes, and a 10 mL solution of 80% acetone was added. Each treatment was repeated at least 5 times using 5 plants. Control tubes contained 10 mL of 80% acetone. Test tubes were placed in the dark for 48 h, oscillated every 12 hours, and then mixed evenly after the green of the leaf disc completely faded. The absorbance at 663 nm, 645 nm and 440 nm was determined by spectrophotometer (UV-1800, China), and the pigment content was calculated according to the method of Arnon [24].

Gas exchange measurement

Net photosynthetic rate (P_n) and stomatal conductance (G_s) were measured using a portable photosynthesis system (Ciras-2, PP Systems, USA) between 10:00 am and 14:00 pm. For each treatment, at least five leaves were measured. The light intensity was $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, the concentration of carbon dioxide was controlled at $380 \pm 20 \mu\text{mol mol}^{-1}$, the humidity was $75\% \pm 5$, and the temperature of leaf chamber was ambient temperature.

Chlorophyll a fluorescence transient measurement

The chlorophyll *a* fluorescence was measured with a handy plant efficiency analyzer (Hansatech, UK). Fully dark-adapted leaves (>30 min) were used to determine the chlorophyll *a* fluorescence transient at 22:00. Chlorophyll *a* fluorescence transient were recorded during 1-s pulse of red radiation ($3000 \mu\text{mol m}^{-2} \text{s}^{-1}$) provided by an array of six light-emitting diodes. The fluorescence signals were recorded within a time scan from $10 \mu\text{s}$ to 1 s with a data acquisition rate of 100 readings/ms for the first 2 ms, and 1 readings/ms after 2 ms. The following original data were retained: the maximum chlorophyll fluorescence yield (F_m), the fluorescence intensity at $50 \mu\text{s}$ considered as minimum intensity (F_o), the fluorescence intensity at 2 s (J step). The quantum yield of electron transport beyond $Q_A(\Psi_{E0})$ and performance index on cross section basis ($PI_{(CS0)}$) were calculated[25]: $\Psi_{E0} = [1 - (F_o/F_m)] * \Psi_o$; $PI_{(CS0)} = [(RC)/(CS_x)] * [(\Psi_{P0}/(1-\Psi_{P0})) * (\Psi_o/(1-\Psi_o))]$. Twenty repetitions were measured for each treatment.

Statistical analysis

Data were analyzed by SPSS (version 11.5) and the graphics software SigmaPlot (version 12.5) was used to create artwork.

Abbreviations

G_s : Stomatal conductance

P_n : Net photosynthetic rate

$PI_{(CS_0)}$: Performance index on cross section basis

Ψ_{E_0} : Quantum yield of electron transport

Declarations

Ethic approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Not applicable

Competing interests

The authors declare that they have no conflict of interest.

Funding

This study was supported by the National Natural Science Foundation of China (31571576). The funders have no role in the study design, data analysis and interpretation, and manuscript writing, but just provide the financial support.

Authors' contributions

H-YW, C-DJ and M-YQ performed the experiments; C-DJ, S-KL, W-FZ and K-RW designed the experiments; H-YW, C-DJ, S-KL and W-FZ analyzed the data; H-YW and C-DJ were the major contributors in writing the manuscript. All authors read and approved the final manuscript.

Acknowledgments

Not applicable

References

1. Mathur S, Jain L, Jajoo A (2018) Photosynthetic efficiency in sun and shade plants. *Photosynthetica* 56:354–365
2. Su YY (2018) The effect of different light regimes on pigments in *Coscinodiscus granii*. *Photosynth Res*. Springer. <https://doi.org/10.1007/s11120-018-0608-7>
3. Brouwer B, Ziolkowska A, Bagard M, Keech O, Gardestrom P (2012) The impact of light intensity on shade-induced leaf senescence. *Plant Cell Environ* 35:1084–1098
4. Zhang TJ, Zheng J, Yua ZC, Gua XQ, Tian XS, Peng CL, Chow WS (2018) Variations in photoprotective potential along gradients of leaf development and plant succession in subtropical forests under contrasting irradiances. *Environ Exp Bot* 154:23–32
5. Brouwer B, Gardeström P, Keech O (2014) In response to partial plant shading, the lack of phytochrome A does not directly induce leaf senescence but alters the fine-tuning of chlorophyll biosynthesis. *J Exp Bot*, pp 4037–4049
6. Whitney H (2016) Plant Science: How some plants adapt to shade. *Nature* 431
7. Bi HG, Liu PP, Jiang ZG, Ai XZ (2017) Overexpression of the rubisco activase gene improves growth and low temperature and weak light tolerance in *Cucumis sativus*. *Plant Physiol* 161:224–234
8. Pignon CP, Jaiswal D, Mcgrath JM, Long SP (2017) Loss of photosynthetic efficiency in the shade. An Achilles heel for the dense modern stands of our most productive C4 crops. *J Exp Bot* 68:335–345
9. Lake JA, Quick WP, Beerling DJ, Woodward FI (2001) Plant development: signals from mature to new leaves. *Nature* 411:154
10. Jiang CD, Wang X, Gao HY, Shi L, Chow WS (2011) Systemic regulation of leaf anatomical structure, photosynthetic performance, and high-light tolerance in *Sorghum*. *Plant Physiol* 155:1416–1424
11. Murakami K, Matsuda R, Fujiwara K (2014) Light-induced systemic regulation of photosynthesis in primary and trifoliolate leaves of *Phaseolus vulgaris*: effects of photosynthetic photon flux density (PPFD) versus spectrum. *Plant Biol* 16:16–21
12. Li T, Liu YJ, Shi L, Jiang CD (2015) Systemic regulation of photosynthetic function in field-grown sorghum. *Plant Physiol Bioch* 94:86–94.
13. Coupe SA, Palmer BG, Lake JA, Overy SA, Oxborough K, Woodward FI, Gray JE, Quick WP (2006) Systemic signalling of environmental cues in *Arabidopsis* leaves. *J Exp Bot* 57:329–341
14. Slesak I, Libik M, Karpinska B, Karpinski S, Miszalski Z (2007) The role of hydrogen peroxide in regulation of plant metabolism and cellular signalling in response to environmental stresses. *Acta Biochim Pol* 54:39–50
15. Guo ZX, Wang F, Xiang X, Ahammed GJ, Wang M, Onac E, Zhou J, Xia XJ, Shi K, Yin XR, Chen K, Yu JQ, Foyer CH, Zhou YH (2016) Systemic induction of photosynthesis via illumination of the shoot apex is mediated sequentially by phytochrome B, auxin and hydrogen peroxide in tomato. *Plant Physiol* 172:1259–1272

16. Iglesias DJ, Lliso I, Tadeo FR, Talon M (2002) Regulation of photosynthesis through source: sink imbalance in citrus is mediated by carbohydrate content in leaves. *Physiol Plant* 116:563–572
17. Kasai M (2008) Regulation of leaf photosynthetic rate correlating with leaf carbohydrate status and activation state of Rubisco under a variety of photosynthetic source/sink balances. *Physiol Plant* 134:216–226
18. Brown AV, Hudson KA (2017) Transcriptional profiling of mechanically and genetically sink-limited soybeans. *Plant Cell Environ* 40:2307–2318
19. Ittersum MK, Cassman KG (2013) Yield gap analysis rationale, methods and applications- introduction to the special issue. *Field Crops Res* 143:1–3
20. Larbi A, Vazquez S, Jendoubi H, Msallem M, Abadia A, Morales F (2015) Canopy light heterogeneity drives leaf anatomical, eco-physiological, and photosynthetic changes in olive trees grown in a high-density plantation. *Photosynth Res* 123:141–155
21. Xue J, Gou L, Shi ZG, Zhao YS, Zhang WF (2017) Effect of leaf removal on photosynthetically active radiation distribution in maize canopy and stalk strength. *J Integr Agr* 16:85–96
22. Wu HY, Zhang YJ, Zhang WF, Wang KR, Li SK, Jiang CD (2019) Photosynthetic characteristics of senescent leaf induced by high planting density of maize at heading stage in the field. *Acta Agronomica Sinica* 45(2): 246–253
23. Zhou BW, Serret MD, Elazab A, Pie JB, Araus JL, Aranjuelo I, and Alvaro (2016) Wheat ear carbon assimilation and nitrogen remobilization contribute significantly to grain yield. *J Integr Plant Biol* 58: 914–926
24. Arnon DI (1949) Copper enzymes in isolated chloroplasts: polyphenoloxidase in *Beta vulgaris*. *Plant Physiol* 24:1–5
25. Strasser RJ, Tsimill-Michael M, Srivastava A (2004) Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou G, Govindjee (eds). *Chlorophyll a Fluorescence: A Signature of Photosynthesis*, pp 321–362

Figures

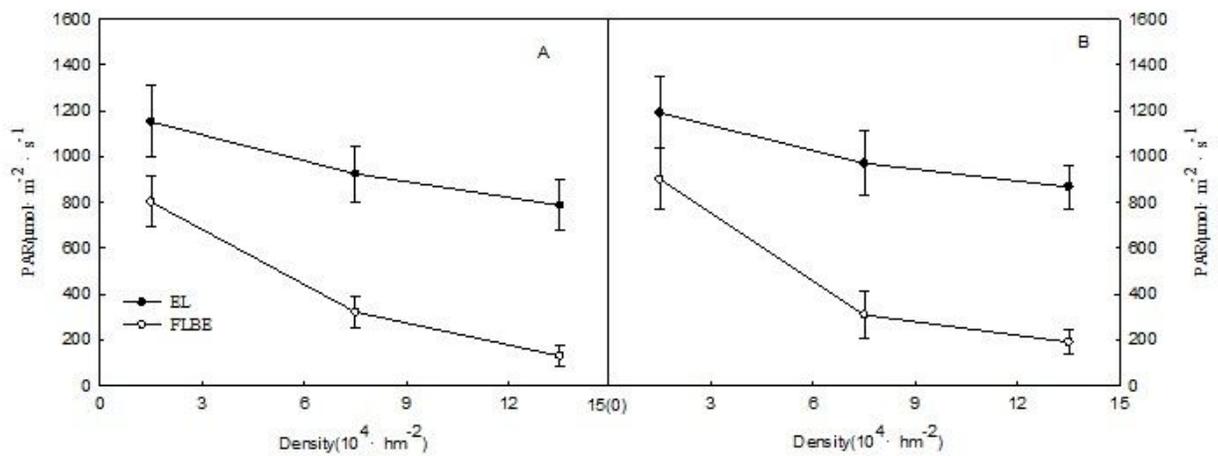


Figure 1

Effects of planting density on PAR (Photosynthetically Active Radiation) of the ear leaf and the fourth leaf below ear in maize plants at heading and grain filling stages. A represents heading stage; B represents grain filling stage; EL represents ear leaf; FLBE represents the fourth leaf below ear.

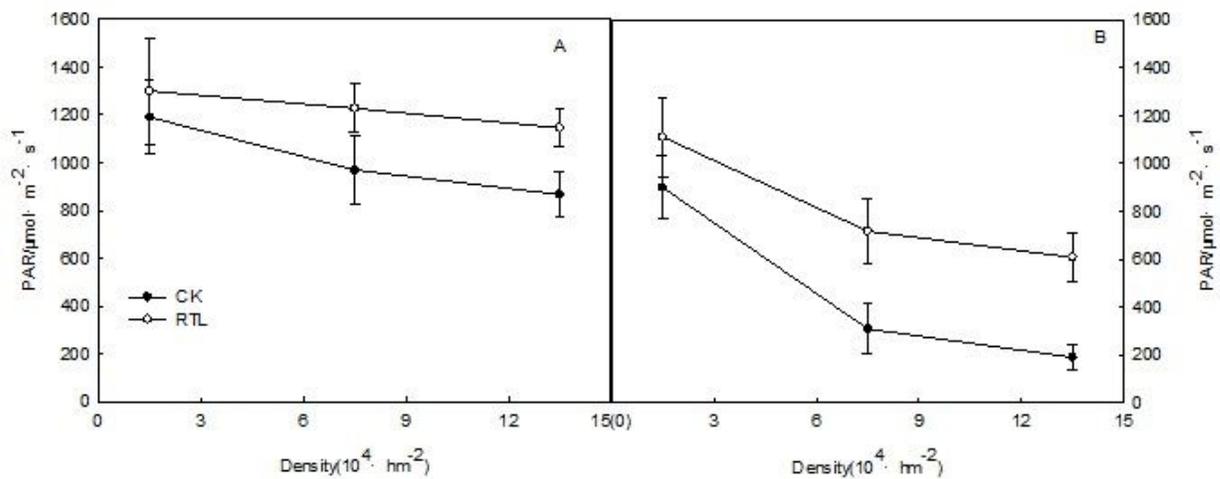


Figure 2

Effects of RTL on PAR (Photosynthetically Active Radiation) of ear leaf and the fourth leaf below ear of maize plants at grain filling stage under various planting densities. CK represents plants with tassel and top leaves; RTL represents removing tassel and top leaves.

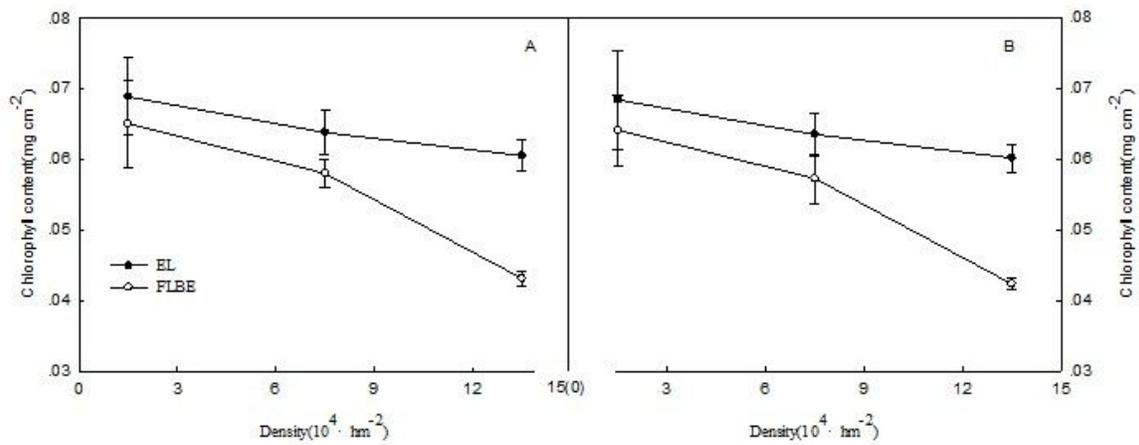


Figure 3

Effects of planting density on total chlorophyll content of the ear leaf and the fourth leaf below ear in maize plants at heading and grain filling stages. A represents heading stage; B represents grain filling stage; EL represents ear leaf; FLBE represents the fourth leaf below ear.

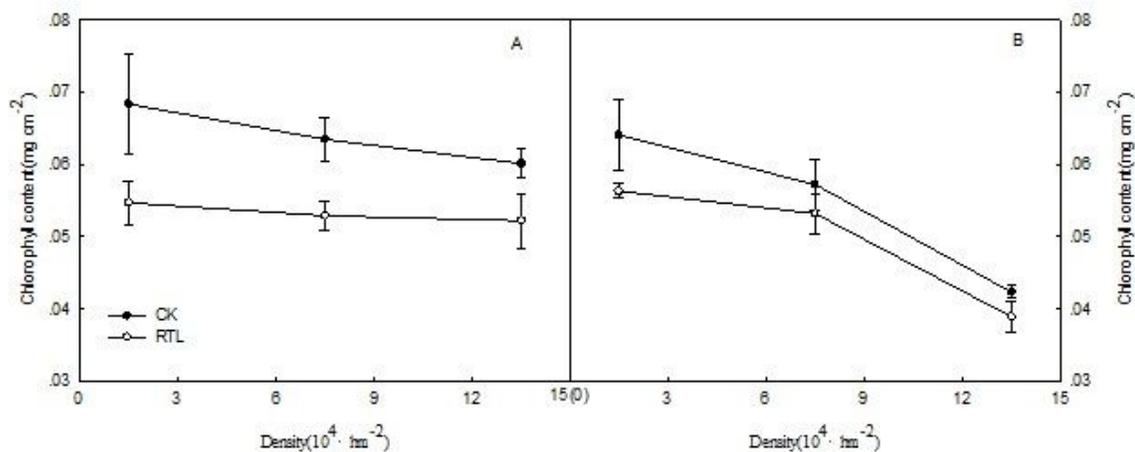


Figure 4

Effects of RTL on chlorophyll content of the ear leaf and the fourth leaf below ear of maize plants at heading stage and grain filling stage under various planting densities. CK represents plants with tassel and top leaves; RTL represents removing tassel and top leaves.

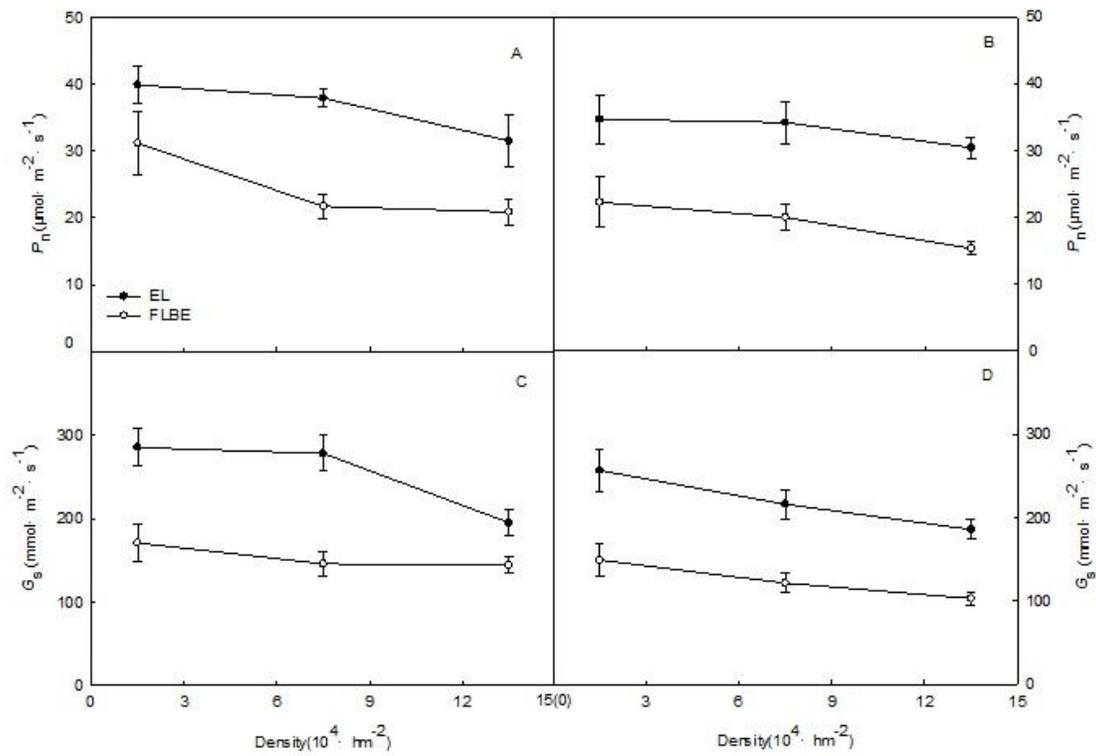


Figure 5

Effects of planting density on net photosynthetic rate and stomatal conductance of the ear leaf and the fourth leaf below ear in maize plants at heading and grain filling stages. A and C represent heading stage; B and D represent grain filling stage; EL represents ear leaf; FLBE represent the fourth leaf below ear.

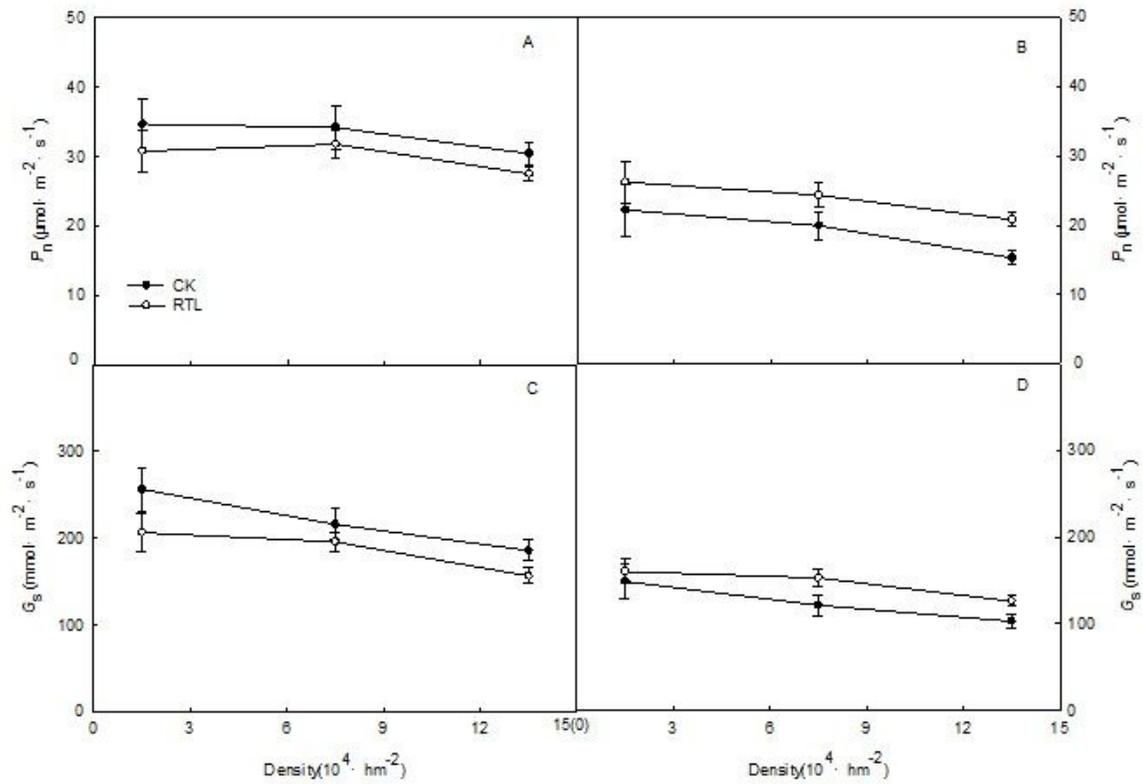


Figure 6

Effects of planting density on chlorophyll a fluorescence transient (OJIP) of the ear leaf and the fourth leaf below ear in maize plants at heading and grain filling stages. A and C represent heading stage; B and D represent grain filling stage.

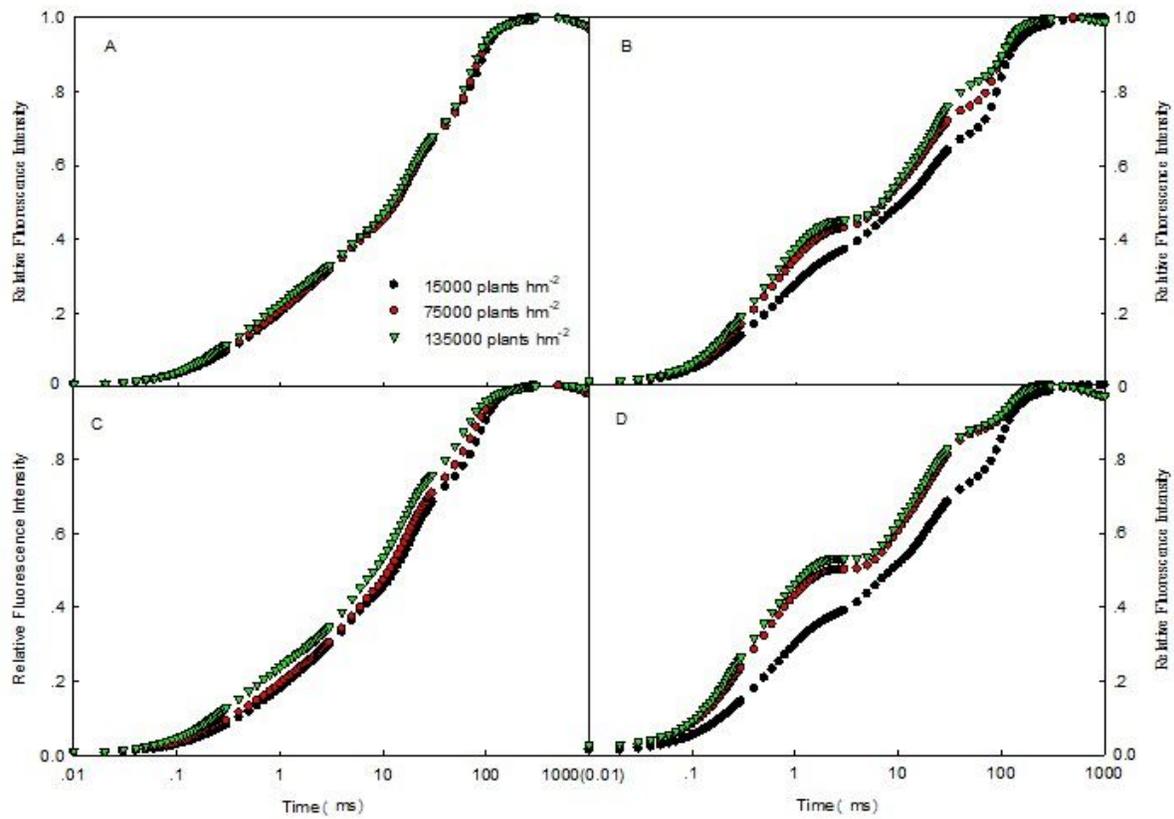


Figure 7

Effects of RTL on net photosynthetic rate and stomatal conductance of the ear leaf and the fourth leaf below ear of maize at grain filling stage under various planting densities. CK represent plants with tassel and top leaves; RTL represent removing tassel and top leaves.

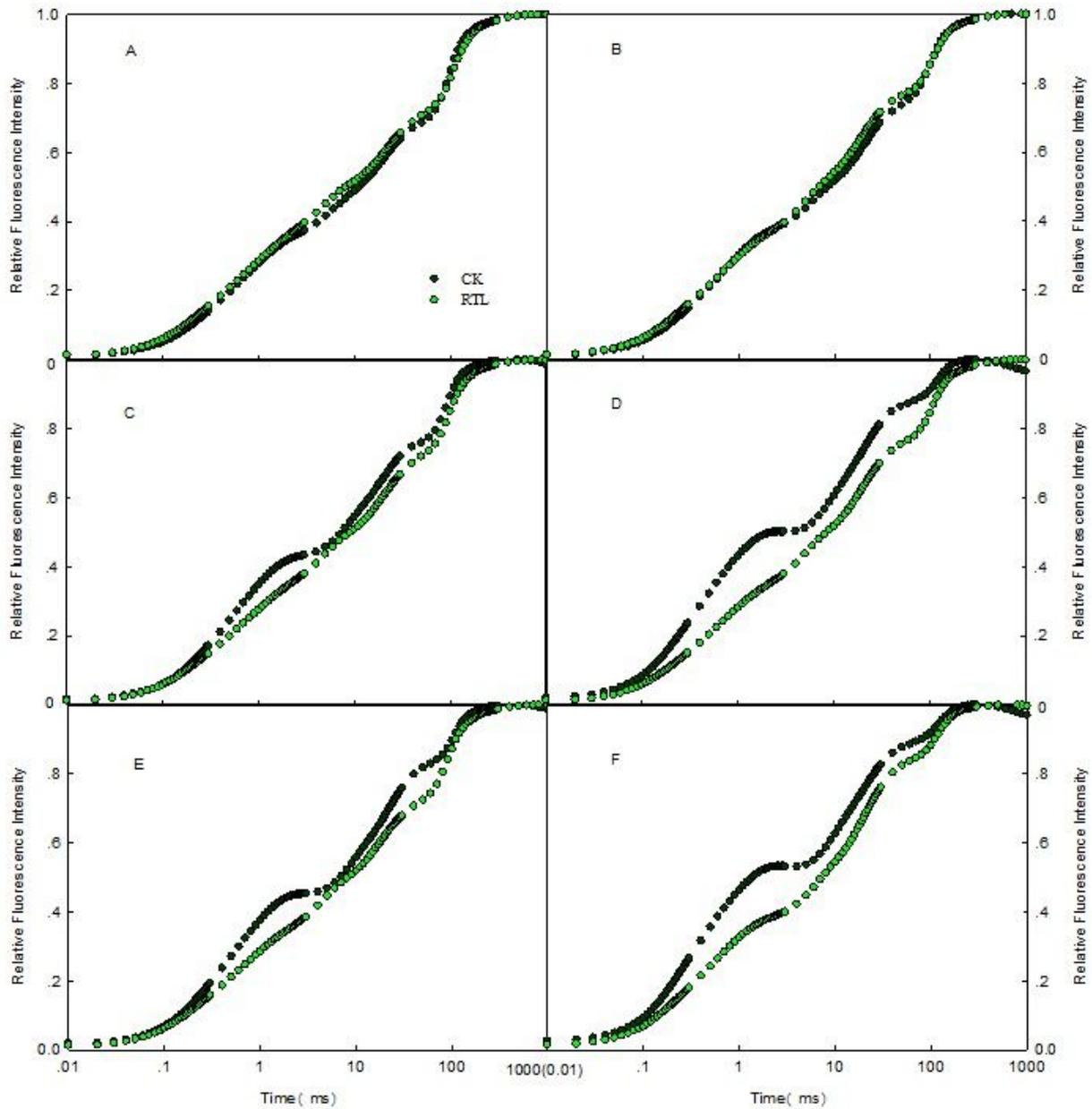


Figure 8

Effects of RTL on chlorophyll a fluorescence transient (OJIP) of the ear leaf and the fourth leaf below ear of maize plants at grain filling stage under various planting densities. CK represent plants with tassel and top leaves; RTL represents removing tassel and top leaves.

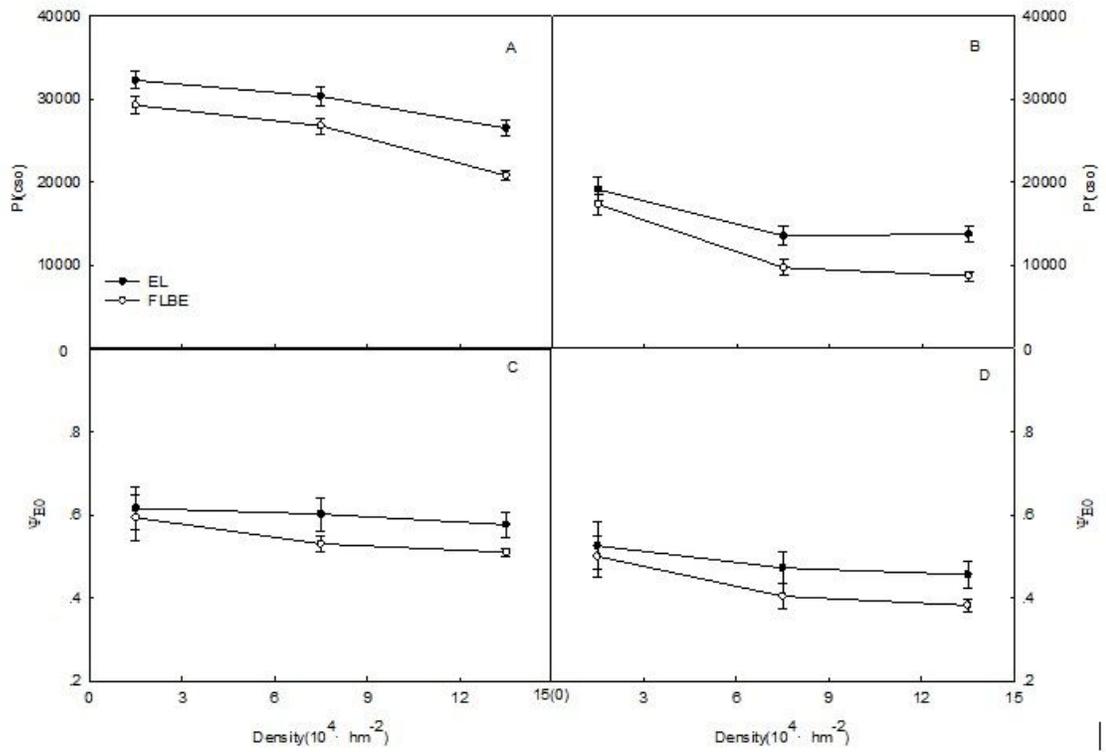


Figure 9

Effects of planting density on the performance index on cross section basis and the quantum yield of electron transport beyond QA of the ear leaf and the fourth leaf below ear in maize plants at heading and grain filling stages. A represents heading stage; B represents grain filling stage; EL represents ear leaf; FLBE represents the fourth leaf below ear.

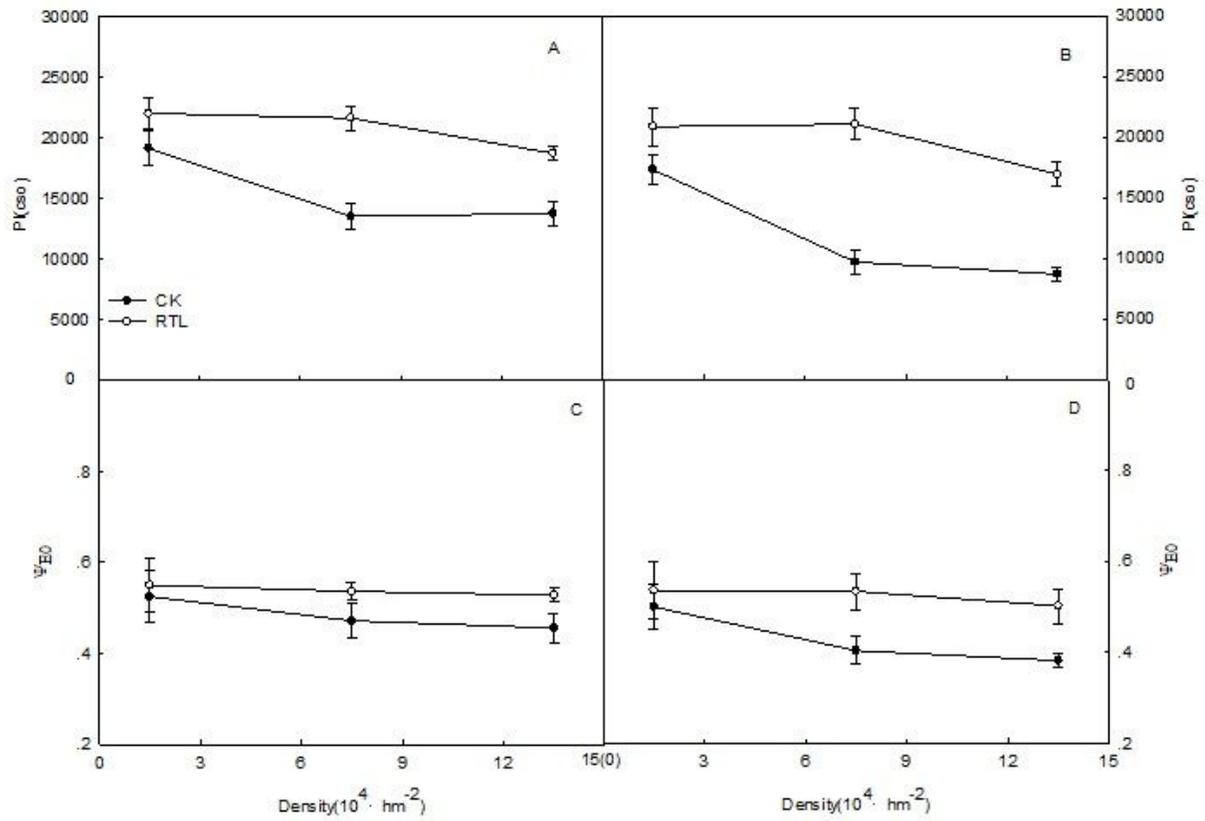


Figure 10

Effects of RTL on the performance index on cross section basis and the quantum yield of electron transport beyond QA of the ear leaf and the fourth leaf below ear of maize plants at grain filling stage under various planting densities. CK represents plants with tassel and top leaves; RTL represent removing tassel and top leaves.

