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Full Length Article

Systemic Signaling in the Photosynthetic Induction Phase of *Calamagrostis angustifolia* on the Sanjiang Plain Wetland of Northeast China

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Abstract

Deyeuxia angustifolia was grown in the Sanjiang plain wetland. The treatments with different light intensities on the different leaf area at different positions, effects of illumination on the photosynthetic induction process of the leaves without pre-illumination (target leaves) was studied systematically. The possible mechanism and the signal transduction pathway of the systemic regulation were explored. The results showed that illumination of systemic leaves significantly increased the photosynthetic induction rate of target leaves. The time for reaching 50% of the maximum photosynthetic rate in the target leaves was reduced by about 19%, and the time for reaching 90% by about 27%. Either one or multiple systemic leaves were pre-illuminated and the photosynthetic induction rates of target leaves were all significantly accelerated. No significant difference was detected on the extent of the promotion effects of photosynthetic induction rates in target leaves. When the systemic leaves were illuminated with a Photosynthetic Photon Flux Density (PPFD) of 30 μmol m^{-2} s^{-1}, the photosynthetic induction rate of target leaves was not significantly enhanced. When the systemic leaves were illuminated with PPFDs of 100, 600 or 1300 μmol m^{-2} s^{-1}, photosynthetic induction rates of target leaves were significantly increased for all values; however, no significant differences were found on the extents of the enhancement effects on the photosynthetic induction rates of the target leaves when the systemic leaves were treated with more than these three light intensities. An effective systemic signaling could only be produced when the systemic leaves were illuminated with a light intensity above a certain threshold, and as soon the illumination exceeded this threshold, the strength of the systemic signaling did not increase with further increase in the light intensity.

Keywords: Photosynthetic induction; Systemic signaling; Stomatal conductance; PSII photochemical efficiency

Introduction

After dark adaptation, the net photosynthetic rate of an illuminated leaf requires some time to reach the maximum level (Walker 1973). The increasing period of the net photosynthetic rate is called the photosynthetic induction phase. The speed of the photosynthetic induction is the most important factor that indicates whether plants can effectively utilize transient illumination (Pearcy 1994). Due to cover from outer leaves, the leaves of plants below the canopy often remain in a shady condition for an extended period of time. These leaves can only utilize a small amount of light projected through the gaps of the outer leaves and use it for photosynthesis to accumulate organic products (Lichtenthaler *et al.* 1981; Boardman 1997; Lichtenthaler and Babani 2004). The duration of these luminous energies is often short and the light intensity weak; therefore, leaves in an extended shady condition must have a quick photosynthetic induction rate to fully utilize these short and precious light energy resources (Pearcy 1990; Urban *et al.* 2007).

The various organs of higher plants are not isolated from each other. During the long evolutionary process, these organs formed very complex and efficient information exchange mechanisms (Mittler 2002; Mullineaux *et al.* 2006; Mühlenbock *et al.* 2007; Pfannschmidt *et al.* 2009). When part of the plant organs is stimulated, they can release signals to other parts of the plant which have not been stimulated yet, so that the latter can adapt to the environmental stimulation ahead of time.

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This regulatory process is called systemic signaling. As an important regulatory mechanism for plant growth and physiological metabolism, systemic signaling has gained more and more attention and has become one of the hot spots in the field of botany (Lake *et al.* 2001). It has been reported that under the condition in which only a subset of the leaves of the plant are illuminated, the photosynthesis rates of the other leaves can quickly be initiated, and there is a close relationship between the photosynthetic induction and the systemic regulation of the leaves toward the bottom of the canopy (Chazdon 1988, 1991; Bryant and Frigaard 2006). When only some of the plant leaves are illuminated, certain systemic regulation signal can induce a rapid induction of photosynthesis in shaded leaves. Understanding the behavior and the mechanism of this systemic regulation can further enrich the theory of systemic regulation (Hou *et al*. 2014). In previous studies, it was found that systemic regulation exists in the photosynthetic induction phase of hybrid *Rumex* (Hou *et al.* 2014); however, whether there is similar systemic regulation on photosynthetic inductions for different types of plants or different varieties of plants, or if there are any differences of the mechanisms of these regulations still needs to be further studied. Systematic and in-depth investigations on the mechanism and the difference will have vital theoretical and practical significance for the further improvement of solar energy utilization by crops and for enhancing their ability to adapt to the environment.

The Sanjiang plain is located in the Northeast of China and is an alluvial marsh plain formed by the convergence of the Heilongjiang River, the Songhua River, and the Wusuli River. It is the largest and the most concentrated wetland in China and its wetland ecosystem has central importance and international significance (Song *et al.* 2005). The *D. angustifolia* wetland is also an important part of the Sanjiang plain wetland. Its special ecological significance has attracted the attention of many researchers (Ji *et al.* 2006; Hou *et al.* 2011). Although many scholars have studied changes within the community, the greenhouse gas emissions, and the nutrient cycling of the *D. angustifolia* wetland, due to the high density of the *D. angustifolia* population and the often shaded lower leaves, research on the systemic regulation of the photosynthetic induction of the*D. angustifolia* wetland still remains sparse (Sun *et al.* 2008; Sui *et al.* 2015; 2016). In this study, *D. angustifolia* was used as the experimental material to systematically explore the above hypothesis. Furthermore, the theoretical basis for further elucidating coping styles of different *D. angustifolia* varieties to the changing growing environment were provided.

Materials and Methods

Experimental materials

The field of this study was located at the Sanjiang Plain Ecological Positioning Research Station of the Institute of Natural Resources and Ecology of the Heilongjiang Academy of Sciences. The research station is located in the Honghe National Nature Reserve at the northeast of the Sanjiang plain with a latitude of 47^{o} 42' ~ 47^{o} 52' and a longitude of 133^{o} 34' 38" ~ 133^{o} 46' 29". The Honghe Nature Reserve retains the largest swamp area in China (the original marsh landscape of the Sanjiang plain) and is the epitome of the Sanjiang plain. It maintains the integrity of the original marsh ecosystem and is currently the most complete and intact original wetland in China with very rich biodiversity and great importance for conservation. It is recommended as an A-1 class reserve (international significance level) (Fig.1). A typical and representative community of*D. angustifolia* was selected in the Positioning Research Station as the research subject. The *D. angustifolia* is the constructive species with over 80% coverage of the area. The height of the community was 80–110 cm and the density of 600–900 plants/m^2. The experiment was conducted during late April 2016 when the 4^{th} new leaf ofthe *D. angustifolia* seedling was fully expanded. According to the order of unfolding, the leaves were labeled as leaf No. 1, No. 2, No. 3, and No. 4.

Experimental design

There were five different treatment groups in this experiment (Fig. 1–2). By which, the testing materials were divided into four groups. Leaf No. 1 was used as target leaf. The whole plant was covered overnight with opaque black cloth. An approximately 9 am in the next morning, the leaf No. 2 of the second group, No. 2 and No. 3 leaves of the third group, and No. 2, No. 3, and No. 4 leaves of the fourth group were exposed to light with 1200 μmol m^{-2} s^{-1} and treated for 30 min, respectively. The net photosynthetic rate induction process and the PSII actual photochemical efficiency (Φ PSII) induction process were measured for leaf No. 1. The stomatal conductance (*Gs*) and the intercellular CO_2(*Ci*)concentration during the photosynthetic induction were recorded. Group 1 served as the control group and the photosynthetic induction of leaf No. 1 was measured directly after full adaptation to darkness. Six repetitions were conducted per group (Fig.1).

The testing materials were divided into five groups. Leaf No. 1 was used as the target leaf. The whole plant was covered overnight with opaque black cloth. At approximately 9 am the next morning, the No. 4 leaves of groups two to five were subjected to 30, 100, 600 and 1300 μmol m^{-2} s^{-1} PPFD light treatment for 30 min, respectively. The net photosynthetic rate induction process and the Φ PSII induction process of leaf No. 1 were measured. The stomatal conductance (*Gs*), and during the photosynthetic induction were recorded. Group 1 served as the control group and the photosynthetic induction of leaf No. 1 was measured directly after full adaptation to darkness. Six repetitions were conducted per group (Fig. 2).

Methods

Determination of gas exchange parameters: The CIRAS-2 portable photosynthesis system (PP Systems, USA) was used to measure and record the data of the net photosynthetic rate. When the leaves were fully adapted to darkness by overnight coverage with a black opaque cloth and after the light induction on the systemic leaves, the photosynthetic induction process of leaf No. 1 was measured using a 1000 μmol m^{-2} s^{-1} working light. During the measurement process, the temperature was kept at 25°C, relative humidity was 50%, and atmospheric CO_2 concentration (Cr) was 380 μmol/mol. The measured maximum photosynthetic value was set to 100% for standardization. The standardized value of the net photosynthetic rate = (net photosynthetic rate in real time - initial photosynthetic rate) / (maximum net photosynthesis rate - initial net photosynthetic rate) × 100.

Determination of the chlorophyll fluorescence: The modulate fluorometer FMS (Hansatech, UK) was used to measure and record the initiation of ΦPSII on the testing leaves. Steady-state fluorescence (*F*s) was measured during illumination, and a 0.8 s saturating light of 8000 μmol m^{-2} s^{-1} 184 PPFD was imposed to obtain the maximum fluorescence in the light-adapted state (*F*m') every 30 s. The actual photochemical efficiency of photosystem II (ΦPSII) was calculated as follow: ΦPSII = 1 − Fs/Fm' (Genty *et al.* 1989). Previous study showed that the frequent saturation pulses (even for every 10s) do not affect the photosynthetic induction (Yamori *et al.* 2012).

Data analysis

Each experiment was repeated three times. Data represent mean ± SE and statistical analysis was carried out with Excel and SPSS statistical software. One-way ANOVA and LSD were used to analyze all data. Differences were considered significant if $P \leq 0.05$ and very differences were considered significant if $P \leq 0.01$.

Results

Effects of illumination on the photosynthetic rate

Compared to the control, the photosynthetic induction rates of target leave was significantly increased after 1, 2, or 3 pieces of systemic leaves were illuminated with 1200 μmol m^{-2} s^{-1} white light, indicating that the illumination of 1, 2, or 3 pieces of systemic leaves could all generate systemic signaling, thus effectively increasing the photosynthetic induction rates of target leaves. After pre-illumination of the systemic leaves, the net photosynthetic rate of the target leaves reached 80% of the maximum value 10 min after photosynthesis induction, while the leaves of the control group only reached 40% of the maximum value 10 min after

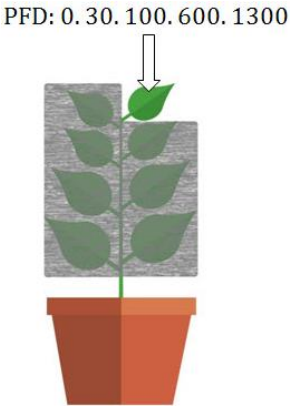

Fig. 1: Sketch map of the material

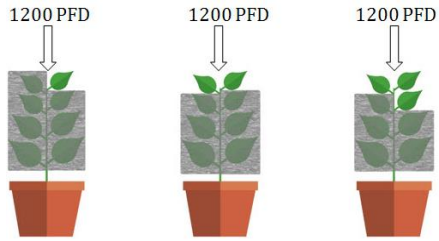

Fig. 2: Sketch map of different PPFD treatment

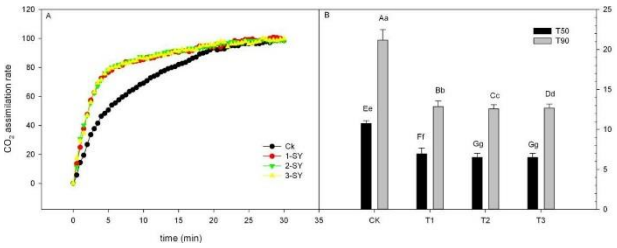

Fig. 3-A: Photosynthetic induction of the target leaf after different number of system leaves was illuminated

Fig. 3-B T_{50} and T_{90} of the photosynthetic induction of the target leaf after different number of system leaves were illuminated, Means ± SE, n=6; Bar graphs depict mean ± SE, values followed by different small letters mean significant difference (p<0.05), values followed by different capital letters mean very significant difference (p<0.01)

CK: Control group; T1: 1 system leaf illuminated; T2: 2 system leaves illuminated; T3: 3 system leaves illuminated; 1-SY: 1 system leaf; 2-SY: 2 system leaves; 3-SY: 3 system leaves

illumination. There were no significant differences in the photosynthetic rates of target leaves after pre-illumination on 1, 2, or 3 pieces systemic leaves, indicating that the regulatory effect produced by 1 piece of systemic leaf had no significant difference compared to the effects produced by 2 or 3 pieces of systemic leaves (Fig. 3A).

The results showed that when different numbers of systemic leaves were illuminated, T_{50} and T_{90} values of target leaves significantly decreased. The T_{50} of target leaves decreased by 25% and the T_{90} decreased by 35% after the systemic leaves were illuminated. However, no significant differences were found between the T_{50} and T_{90} values when 1, 2, or 3 pieces of systemic leaves illuminated (Fig. 3B).

Effects of illumination on the actual photochemical efficiencies of the photosynthesis system II

The ΦPSII induction rate of target leaves was significantly increased after different numbers of systemic leaves were illuminated with 1200 μmol m^{-2} s^{-1} of white light (Fig. 4). After systemic leaves were illuminated, at the 300th second of the ΦPSII induction process, the ΦPSII value of the target leaves had almost reached the maximum level, while the leaves of the control group reached the maximum value at approximately the 1400th second after the initiation of ΦPSII. The induction promoting effect of illuminating 1 piece of systemic leaf showed no significant differences compared to the illumination on 2 or 3 pieces of systemic leaves. This indicates that a relatively small number of systemic leaf illuminations can produce a similar promotional effect as the illumination of large number of systemic leaves.

Effects of illumination on stomata of the target leaves

The stomatal opening rates of target leaves significantly increased during the photosynthetic induction process after different numbers of systemic leaves were illuminated.After the illumination of systemic leaves, the stomatal conductance values of target leaves reached 400 mmol m^{-2} s^{-1} 20 min after the introduction of photosynthesis, while within the same time period, the stomatal conductance of the control leaves only reached 200 mmol m^{-2} s^{-1}. There were no significant differences for the increase of stomatal opening rate whether 1 systemic leaf was illuminated, compared to illuminating 2 or 3 systemic leaves. This indicates that the illumination of a relatively small number of systemic leaves can produce similar promotional effects on the stomatal opening rate as the illumination of a large number of systemic leaves (Fig. 5).

Effects of illumination on the changes of the intercellular CO_2 concentration

The general *C*i value of the target leaves was significantly lower than in the control group during the photosynthetic induction process after different numbers of systemic leaves were illuminated(Fig. 6). However, no significant differences were found for the *C*i values of the target leaves during the photosynthetic induction process among the illuminations on 1, 2, or 3 pieces of systemic leaves, indicating that the illumination of 1 systemic leaf can produce a similar *C*i lowering effect as the illumination of more systemic leaves.

Effects of different light intensity on the photosynthetic rate induction

The response curve of the light-photosynthetic rate of *C. angustifolia* show that the light compensation point of the material ranged between 50 and 100 μmol m^{-2} s^{-1}, while the

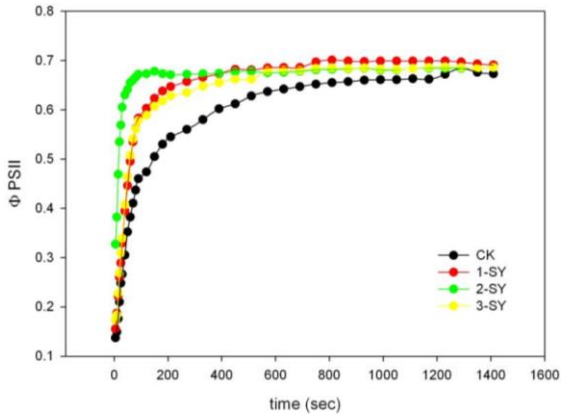

Fig. 4: ΦPSII induction of the target leaf after different number of system leaves were illuminated
1-SY: 1 system leaf; 2-SY: 2 system leaves; 3-SY: 3 system leaves

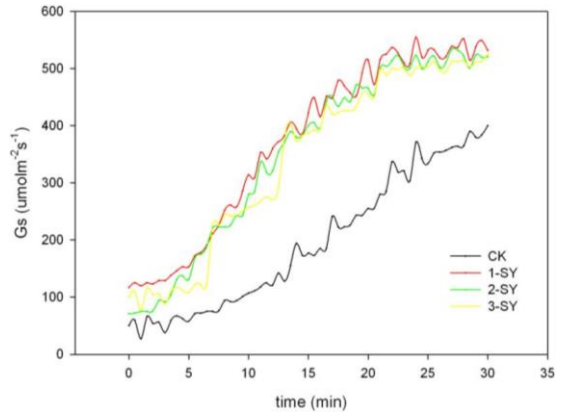

Fig. 5: Stomata opening of the target leaf after different number of system leaves were illuminated
1-SY: 1 system leaf; 2-SY: 2 system leaves; 3-SY: 3 system leaves

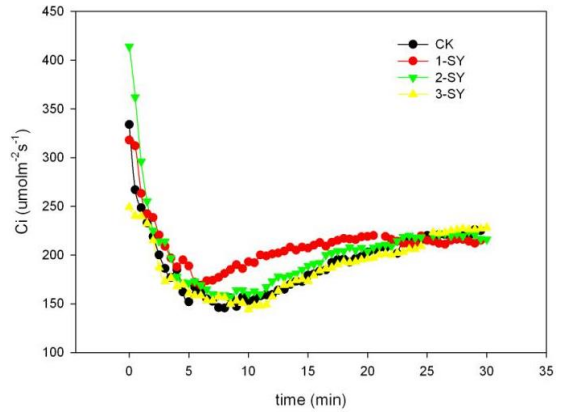

Fig. 6: Ci induction of the target leaf after different number of system leaves were illuminated
1-SY: 1 system leaf; 2-SY: 2 system leaves; 3-SY: 3 system leaves

inflection point of the near saturation intensity was around 1200 μmol m^{-2} s^{-1}; therefore, in this experiment, the four light intensities 30 μmol m^{-2} s^{-1} (slightly below the light

compensation point), 100 μmol m^{-2} s^{-1} (slightly above the light compensation point), 600 μmol $m^{-2}s^{-1}$ (moderate intensity), and 1300 μmol m^{-2} s^{-1} (saturation intensity) were selected to treat the systemic leaves to study the responses of target leaves to different light intensity treatments (Fig. 7).

When the systemic leaves were exposed to light treatment with the different intensities, the photosynthetic induction rates of the target leaves all significantly increased compared to the control group. After light treatment on the systemic leaves with the intensity of 30 μmol m^{-2} s^{-1}, the photosynthetic induction rate of the target leaves showed no significant difference compared to the control group. No significant differences were found for the photosynthetic induction rates among the light treatments of systemic leaves with intensities of 100, 600 or 1300 μmol m^{-2} s^{-1}. The above results suggested that when the utilized light intensity was above a certain threshold, the promotional regulatory effect on the photosynthetic rate of the target leaves was induced. When the utilized light intensity was higher than a certain threshold, the extent of the promotional effect does not increase with the increase of the light intensity; however, when the light intensity is below the threshold, the systemic regulatory effect will not be induced.

After light treatments on the systemic leaves with intensities of 100, 600 or 1300 μmol m^{-2} s^{-1}, the T_{50} and T_{90} of the target leaves significantly decreased. After the systemic leaves were treated with light at an intensity of 30 μmol m^{-2} s^{-1}, the T_{50} and T_{90} of the target leaves showed no significant difference compared to the control group. There were no significant differences of the extent of the promotional effects on the photosynthetic induction rates among target leaves treated with light at intensities of 100, 600 or 1300 μmol m^{-2} s^{-1} (Fig. 8A–B).

Effects of different light intensity treatments on the actual photochemical efficiencies of photosynthesis system II

When systemic leaves were illuminated with light at intensities of 100, 600 and 1300 μmol m^{-2} s^{-1}, respectively, the ΦPSII initiation rates of the target leaves significantly increased compared to the control group, and the time for reaching the maximum value was shortened to 80 sec from about 600 sec (Fig. 9). After systemic leaves were illuminated with light at an intensity of 30 μmol m^{-2} s^{-1}, the ΦPSII initiation of the target leaves showed no significant difference compared to the control. No significant differences were detected for the ΦPSII initiation rates of the target leaves when the systemic leaves were illuminated with light at intensities of 100, 600 or 1300 μmol m^{-2} s^{-1}. The above results suggest that when the incident light intensity reached a certain threshold, the promotional regulatory effect on the ΦPSII initiation can be induced in target leaves; however, if the incident light intensity were above threshold, the extent of the promotional effects on the target leaves would not increase with the increase of the incident light intensity. When the light intensity was below a certain threshold, the systemic signaling was also not induced.

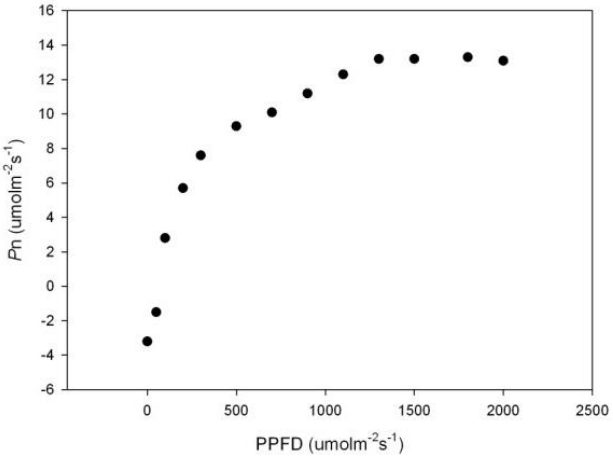

Fig.7: PPFD-Pn response curve of the material used in this experiment

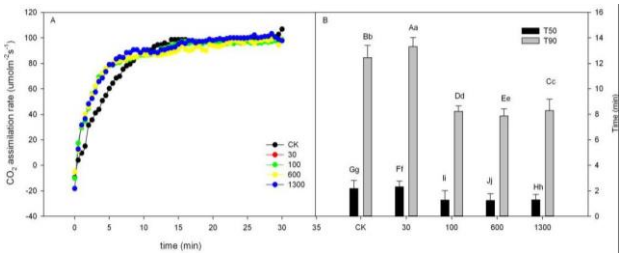

Fig. 8-A: CO_2 assimilation rate of the target leaf after the system leaves were illuminated with light of different intensities

Fig. 8-B T_{50} and T_{90} of the target leaf after system leaves were illuminated with light of different intensities, Means ± SE, n=6

Means ± SE, n=6; Bar graphs depict mean ± SE, values followed by different small letters mean significant difference (P<0.05), values followed by different capital letters mean very significant difference (P<0.01)

CK: Control group; 30: 30 PPFD; 100: 100 PPFD; 600: 600 PPFD; 1300: 1300 PPED

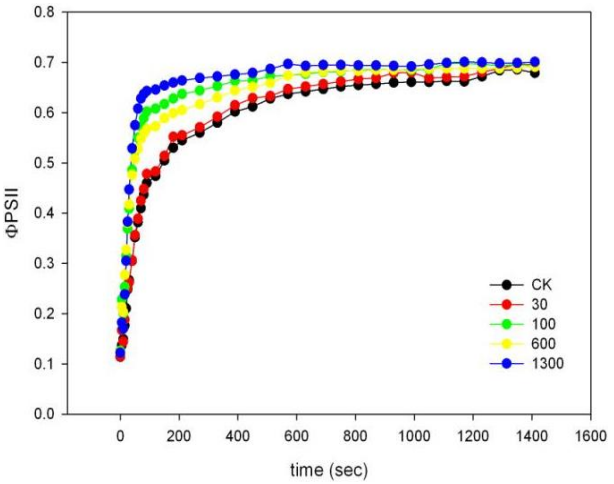

Fig. 9: ΦPSII induction of the target leaf after system leaves were illuminated with light of different intensities

CK: Control group; 30: 30 PPFD; 100: 100 PPFD; 600: 600 PPFD; 1300: 1300 PPED

Effects of different light intensity on stomatal opening of target leaves

When the systemic leaves were illuminated with light at intensities of 100, 600 or 1300 μmol m^{-2} s^{-1}, the stomatal opening rates of the target leaves were all significantly increased during the photosynthetic induction process (Fig. 10). The regulated stomatal conductance reached about 200 mmol m^{-2} s^{-1} in the target leaves on the 15th min of the photosynthetic initiation, while the control leaves showed only about 100 mmol m^{-2} s^{-1}. When the systemic leaves were illuminated with light at an intensity of 30 μmol m^{-2} s^{-1}, the stomatal opening of the target leaves showed no significant difference compared to the control group. When the systemic leaves were illuminated with light at 100 μmol m^{-2} s^{-1}, no significant differences were detected in the stomaltal opening rates compared to the systemic leaves that were illuminated with light at intensities of 600 or 1300 μmol m^{-2} s^{-1}.

Effects of different light intensity on the intercellular CO_2 concentration

In general, when the systemic leaves were illuminated with light at intensities of 100, 600 or 1300 μmol m^{-2} s^{-1}, the *C*i values of target leaves during the photosynthetic induction process were significantly lower than control (Fig. 11). When systemic leaves were illuminated with light at an intensity of 30 μmol m^{-2} s^{-1}, the *C*i value of the target leaves during the photosynthetic induction process showed no significant difference compared to the control. When systemic leaves were illuminated with light at an intensity of 100 μmol m^{-2} s^{-1}, the decreasing degree of *C*i value on the target leaves showed no significant differences compared to those with an illumination of 600 or 1300 μmol m^{-2} s^{-1}.

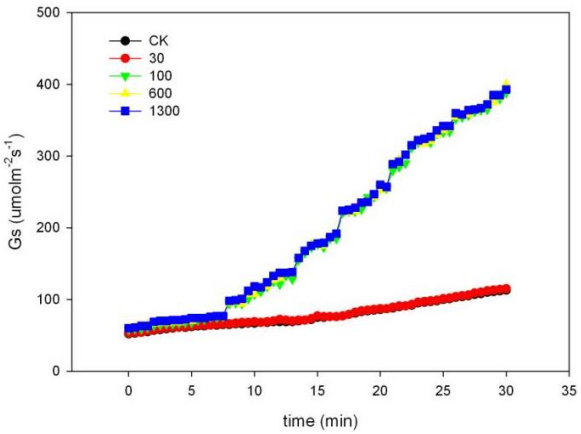

Fig. 10: Stomata opening of the target leaf after the system leaves were illuminated with light of different intensities
CK: Control group; 30: 30 PPFD; 100: 100 PPFD; 600: 600 PPFD; 1300: 1300 PPED

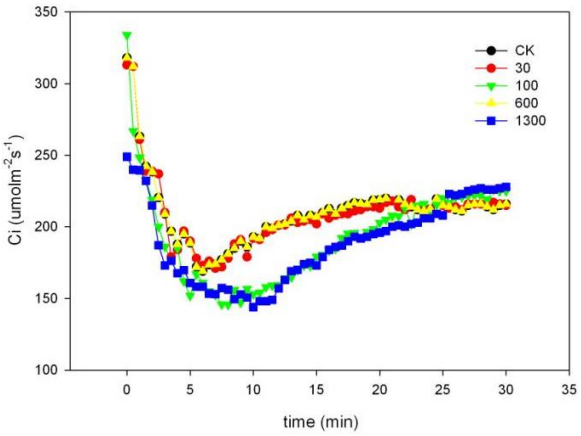

Fig. 11: Ci status of the target leaf after the system leaves were illuminated with light of different intensities
CK: Control group; 30: 30 PPFD; 100: 100 PPFD; 600: 600 PPFD; 1300: 1300 PPED

Discussion

This study found that the photosynthetic induction rate of *C. angustifolia* leaves could be increased *via* systemic signaling. These plants hardly receive sunlight due to the coverage of the upper vegetation. Only when the upper vegetation is blown by wind to form an empty window, or when the sun is at a specific angle, the leaves receive sunlight. Such phases typically commence suddenly, and the duration is short; therefore, these are called light spots (Gross, 1982; Kaitala *et al.* 1982; Olson, 2006). Researchers have reported that 70% of the light received by plant vegetation at the lower part of the forest is in the form of short-timed light spots and the majority of these light spots last less than 10 min (Küppers and Schneider 1993; Yang *et al.* 1994; Ögren and Sundin 1996). Therefore, effectively utilizing these short light spots is extremely important for plant vegetation at the lower part of the forest. To effectively utilize these light spots, understory plants have evolved a variety of adaptive mechanisms, such as broad leaves, taller light-harvesting antenna complexes, and more importantly, a faster photosynthesis induction rate than other plants (Barber *et al.* 1989; Nealson and Conard 1999; Martin *et al.* 2000). In present, it was discovered that when some of the *C. angustifolia* leaves were exposed to light, certain signals produced and transferred to other leaves not exposed to light, allowing these leaves to increase their photosynthetic induction rate when eventually they too were illuminated. This finding revealed the way plant adapted to a dynamic light environment, and also enabled us to deepen the understanding of the ecological adaptation mechanism of plants from the perspective of the whole plant.

The acceleration of photosynthetic initiation induced via systemic signaling is not only important for the survival of understory plants in the forest; this mechanism is also of great significance to agricultural ecosystem. Currently, with increases in crop planting density, available lights for lower leaves are reduced, and most of the available lights are in the form of light spots. When the upper leaves receive lights,

they can produce signals and transmit these to the lower leaves, thus raising the photosynthetic induction rates of the lower leaves, which can greatly increase the utilization efficiency of light spot energy in lower leaves.

Systemic regulation was first proposed by Karpinski *et al.* (1999) and Lake *et al.* (2001). Currently, studies on systemic regulation are mostly concentrated on the sensing ability of mature leaves for environmental changes and are geared at regulating the development of young leaves, which is a slow reaction, as well as the regulation of resistance genes during pathogen infection is a stress response. Whether the systemic signal is involved in the systemic regulation and the nature of the signal transmission pathway remains currently unclear. Although studies have suggested that methyljasmonate, ROS, long-chain fatty acids, as well as specific RNA and NO are likely acting as systemic signals for long-distance transmission (Seo *et al.* 1997; Delledonne *et al.* 1998; Citovsky and Zambryski 2000; Weber, 2002; Apel and Hirt 2004); however, no study confirms the nature of the systemic signal and whether the systemic signal carrier is the same for different systemic regulations.

After the illumination of different numbers of the systemic leaves, the photosynthetic induction rate of the target leaves in *C. angustifolia*, were not directly under the light, which significantly increased, demonstrating that a signal regulatory mechanism exists among *C. angustifolia* leaves, regulating the photosynthetic induction rates of other leaves. Interestingly, illumination of few systemic leaves resulted in the same degree of promotional effect in the target leaves as compared to the illumination of more systemic leaves. This regulatory mechanism is beneficial for other *C. angustifolia* leaves to rapidly and efficiently initiate photosynthesis even though only a small amount of leaves are subjected to a small light spot.

Under natural conditions, light intensities of light spots are often much lower than the direct incident light (Karpinski *et al.* 1999). This experiment used light with different intensities to treat the systemic leaves showed that far below the saturation light intensity. This could still effectively accelerate the photosynthetic induction rate of the target leaves. However, only 30 μmol m^{-2} s^{-1} light resulted in no obvious acceleration effect on the photosynthetic induction of target leaves. This indicated that there is a threshold value for systemic leaves to respond to the light for producing this regulatory effect. Only when the light intensity is higher than the threshold value can systemic regulation be produced, this indicates that once the light intensity of the working light is higher than the threshold, the promotional effect of the photosynthetic induction rates of the target leaves will no longer be affected by the intensity of incident light. There is no quantitative effect on the systemic regulation of photosynthetic induction among *C. angustifolia* leaves. It was also reported (Karpinski *et al.* 1999) that the illumination of a few *A. thaliana* leaves could induce the initiation of the photoprotection mechanism in whole plants, but the authors did not further explore whether illuminating different proportions of the plant could induce the same degree of response. The 30 μmol m^{-2} s^{-1} light intensity used in this study was slightly lower than the light compensation point of the experimental material. Whether the same situation occurred in other plants remains to be further investigated, as well as the optimal level of the threshold, and why there is no promotional effect when the light intensity is below the threshold level. These questions will be addressed by further experiments.

Conclusion

After illumination, *C. angustifolia* leaves produces a signal that significantly accelerated the photosynthetic induction and ΦPSII initiation processes that were not directly illuminated. Few systemic leaves produced the same regulatory effect as many systemic leaves. Under relatively low light intensity, *C. angustifolia* leaves produced an effective promotional signal; however, if the light intensity was below a certain threshold, the regulatory effect could not be produced. When the incident light exceeded this threshold value, the enhancement effect of the systemic signal could no longer increase with the increase of the light intensity.

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