

PHOTOSYNTHETIC ADAPTABILITY IN MATURE AND YOUNG LEAVES OF *MEDICAGO SATIVA L.* SEEDLINGS UNDER TRANSPLANTED CONDITION FROM GREENHOUSE TO SUNLIGHT

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Abstract

The effect of transplanting alfalfa (*Medicago sativa*) seedlings from artificial, low-intensity light into bright sunlight was investigated. The variance of photosynthetic function in young and mature leaves was investigated in plants grown in a low-light greenhouse environment (controls) and then the plants were subjected to high-intensity light for 12 hrs (treatment). The results showed that the photosynthetic capacity of young leaf blades was significantly lower than that of mature blades, and, the ability to capture and use light was low for young leaves. In control plants, the parameters of chlorophyll-dependent photochemical efficiency (Φ_{PSII}), electron transfer rate (ETR), photochemical quenching coefficient (qP) and non-photochemical quenching coefficient (qN) were all significantly lower in younger than mature leaves. There was no significant difference in the photochemical efficiency (F_v/F_m) or light energy distribution parameters between young and mature leaves of control plants. After light treatment, the photosynthetic carbon assimilation capacity and photochemical activity of the PS II reaction center decreased significantly, and both net photosynthetic ratio and chlorophyll b fluorescence parameters changed significantly more than in young leaves than in mature leaves under different PFD. This was particularly evident for F_v/F_m of the young leaves, whose decrease proved that the adaptability of young leaves to convert light was significantly lower than that of mature leaves. Obvious differences in the degree and mechanism of protection against light damage exist between young and mature leaves. Mature leaves dissipated excess excitation energy. In contrast, young leaves dissipated excess excitation by inactivation of the photosynthetic reaction center.

Introduction

The seeds of alfalfa (*Medicago sativa*) are relatively small, which limits their germination under stress conditions. For this reason, indoor seeding is frequently employed to enhance the seeds' capability to germinate. In a greenhouse the light intensity is typically lower than outside, so seedlings developing indoors have to adapt to the sudden change in light intensity when they are transplanted into the field (Zhang *et al.* 2011). Plant leaves grown under low light intensity have typical characteristics similar to plants grown in the shade, such as thin blades with a relatively low chlorophyll content (Lichtenthaler *et al.* 1981), low resistance to photo-destruction (Guo *et al.* 2009), and a lower ability to use light especially intense light (Zhao *et al.* 2010, Zeng *et al.* 2014). Therefore, when plants grown indoors are suddenly exposed to intense sunlight, their photosynthesis is inhibited, and photo-destruction or photo-bleaching can occur (Guo *et al.* 2015). For instance, Yang *et al.* (2001) observed significant photo inhibition when cotton plants (*Gossypium* spp.) were exposed to intense light, and Zhou *et al.* (2015) showed that natural light significantly decreased the photosynthetic performance and photochemical efficiency of two varieties of wheat (*Triticum aestivum*) that had germinated under low-intensity light conditions. It

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was further reported that the fluorescence parameters F_v/F_m and PI_{ABS} of Chinese cherry (*Cerasus pseudocerasus*) significantly decreased after indoors grown seedlings were transplanted into natural sunlight (Wei *et al.* 2014). Likewise, the photosynthetic capability, electron transfer ability, and photosynthetic heat dissipation of white mulberry (*Morus alba*) seedlings grown under low light intensity were significantly lower than for plants grown under natural sunlight. Although *Morus alba* seedlings can accumulate appreciable amounts of RuBP under low light conditions, the photosynthetic rates of the leaves did not significantly increase after exposure to natural sunlight (Hu *et al.* 2010).

The leaf blades are the main plant parts responsible for photosynthesis, and >90% of the dry matter generated during plant growth is derived from photosynthates, sugars directly originating from photosynthesis (Peng *et al.* 2012). The photosynthates of higher plants are mainly produced in fully developed leaves (Jiang *et al.* 2005, Tian *et al.* 2014), while the photosynthetic capability for young leaves is lower than that of mature leaves, because the chloroplast structure and the resistance to photo-destruction are not then fully developed. In particular, the activity of the light-captivating system (Zhang *et al.* 2014) and carbon assimilation ability are weaker in young blades than in mature leaf blades (Olson *et al.* 2006).

Proteomic analysis performed by Wang *et al.* (2012) identified that the content of rubisco in young blades of the rubber tree (*Hevea brasiliensis*) was significantly lower than that of mature leaf blades. The xanthophyll lutein content in young leaves of soybean (*Glycine max*) is relatively high, but even more components can be accumulated after decyclization under light, which can decrease potential photoinhibition following exposure intense light (Jiang *et al.* 2005). The young leaf blades of cotton plants can effectively dissipate excessive light energy by the quenching of singlet oxygen by carotenoids, by increasing light respiration and by heat dissipation, thus avoiding photoinhibition under field conditions (Li *et al.* 2012). However, a few studies are available on the photosynthetic functioning of young and mature leaf blades of *Medicago sativa* seedlings after they are transplanted from low light to natural sunlight. The mechanisms employed by leaf blades at different unfolding stages to adapt to light intensity changes need to be investigated. In the present study, the photosynthetic functions of young and mature leaf blades of *Medicago sativa* seedlings grown under low-intensity light and transplanted into sunlight were investigated. The study provided fundamental insights that may guide a more rational transplantation of *Medicago sativa* seedlings, reducing photo-induced damage to the young plants.

Materials and Methods

Experiments were conducted in the Laboratory of Plant Physiology, Northeast Forestry University, Harbin, China, during March of 2017. A variety of *Medicago sativa* called “Zhaodong Alfalfa” was provided by the Crop Research Division, Academy of Agricultural Reclamation, Heilongjiang, China. Seed was sown on a float tray (50 × 25 × 8 cm) with 50 seedling holes. The seedling medium used was turf soil mixed 2 : 1 with vermiculite. The cultures were kept at a cyclic temperature of 25°C during 12 hrs light exposure followed by 12 hrs dark periods at 23°C. Light was applied at an intensity of 200 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ until treatment was initiated. Five seeds were sown in each seedling hole. Thinning was performed after germination to keep 3 seedlings per seedling hole. Per experiment, 5 random seedlings were selected to record their mature and young leaf blades performance by photosynthetic gas exchange and chlorophyll fluorescence as described below. Prior to the actual experiments, light intensity was increased to 2000 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ generated by LED red and blue mixed light for treatment (TR) readings, while control (CK) plants were only exposed to the 200 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ light. After exposure at these respective conditions for 12 hrs, the actual experiments were started and measurements of the photosynthetic and chlorophyll fluorescence parameters of the young and mature leaf blades were recorded.

A Li-6400 photosynthetic measurement system was used to determine the net photosynthetic rate (P_n) of young and mature blades. P_n values were measured under variable light intensities (PFD) of 1500, 1200, 1000, 800, 500, 200, 100, 50, and 0 $\mu\text{mol}/(\text{m}^2/\text{s})$. The same leaf blades were first used for control experiments and then, following exposure to high-intensity light, for treatment measurements, to limit biological variation. Photosynthesis Work Bench software was used to calculate the regression coefficients R^2 , apparent quantum efficiency (AQY), light compensation point (LCP), light saturation point (LSP), and net photosynthetic rate when light was saturated (P_{\max}).

The same young and mature leaf blades of the alfalfa plants described above were adapted to 30 min in the dark adaption prior to determination of the maximum fluorescence (F_m) and initial fluorescence (F_0). These were measured using the portable modulated luminoscope (FMS-2, Hansatech, England) with different light intensities (100, 200, 400, 600, 800, 1000, 1200 $\mu\text{mol}/(\text{m}^2/\text{s})$). Fluorescence parameters were measured at 3 min after light exposure, which included minimum fluorescence (F_o'), maximum fluorescence (F_m'), and steady-state fluorescence (F_s). The photochemical efficiency (Φ_{PSII}), electron transfer rate (ETR), photochemical quenching coefficient (qP), and non-photochemical quenching coefficient (qN) were calculated using equations 1-4 (Zhang *et al.* 2013):

$$\Phi_{\text{PSII}} = (F_m/F_s)/F_m' \quad (1)$$

$$ETR = 0.5 \times 0.85 \times \Phi_{\text{PSD}} \times PFD \quad (2)$$

$$qP = (F_m' - F_s)/(F_m' - F_o') \quad (3)$$

$$qN = (F_m - F_m')/F_v \quad (4)$$

In addition, the PS II maximum photochemical efficiency (F_v/F_m), energy distribution parameter under the intensity at 800 $\mu\text{mol}/(\text{m}^2/\text{s})$, quantum yield used for photochemical reactions (Y_{PSII}), quantum yield depending on proton gradient and lutein circulation (Y_{NPQ}), fluorescence quantum yield and heat dissipation quantum yield ($Y_{\text{f,D}}$), and heat dissipation quantum yield (Y_{NF}) were calculated based on equations 5 - 8:

$$Y_{\text{PSII}} = [1 - (F_s/F_m')] \cdot [(F_v/F_m)/(F_v/F_{mM})] \quad (5)$$

$$Y_{\text{NPQ}} = [(F_s/F_m') - (F_s/F_m)] \cdot [(F_v/F_m)/(F_v/F_{mM})] \quad (6)$$

$$Y_{\text{f,D}} = (F_s/F_m) \cdot [(F_v/F_m)/(F_v/F_{mM})] \quad (7)$$

$$Y_{\text{NF}} = 1 - [(F_v/F_m)/(F_v/F_{mM})] \quad (8)$$

where F_v/F_{mM} is the maximum F_v/F_m value for all measurements; that means F_v/F_m is the maximum PSD photochemical efficiency observed without photoinhibition (Hendrickson *et al.* 2004).

Excel and SPSS software were used for analyzing the data obtained. All data are presented as average values of three replicates. One-way ANOVA and LSD methods were used for comparing the statistical significance of differences between data in different groups.

Results and Discussion

After culture of alfalfa seedlings under low-light conditions as described in the methods, treatment (TR) plants but not control (CK) plants were exposed to high-intensity light for 12 hrs. The plants were then exposed to light of variable intensities (PFD 250 - 1500 $\mu\text{mol}/(\text{m}^2/\text{s})$) while their photosynthetic rate P_n was determined for young and mature blades by means of their photosynthetic carbon assimilation capacity. As shown in Fig. 1, photosynthesis was higher in mature blades (open symbols) than in young leaf blades (black symbols), and higher in control plants not previously exposed to high-intensity light (CK, circles) than in plants pre-exposed to 2000 $\mu\text{mol}/(\text{m}^2/\text{s})$ light (TR, triangles). The figure further showed that the photosynthetic rate

increased with increasing PFD, reaching a maximum at approximately $750 \text{ } \mu\text{mol}/(\text{m}^2/\text{s})$. The maximum P_n values remained lower in young blades than in mature blades at all light intensities tested under the same light regime, though young control blades performed better than mature treated blades.

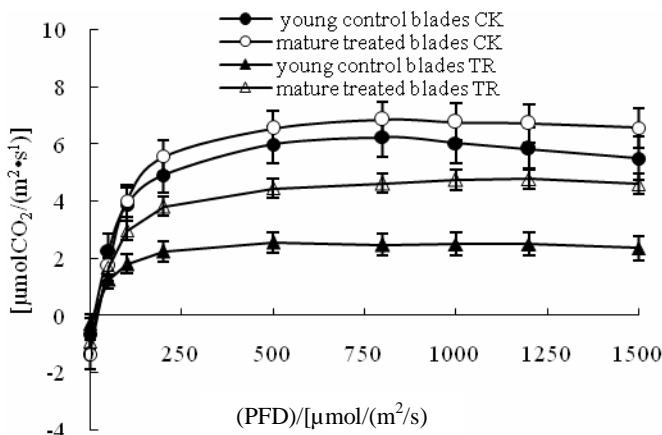


Fig. 1. The effect of increasing light intensity on net photosynthetic rates P_n of young (black symbols) and mature (open symbols) blades of *Medicago sativa*. Control plants (CK, circles) were only exposed to low-intensity light prior to the experiment, while treatment plants (TR, triangles) had been exposed to 12 hrs high-intensity light ($2000 \text{ } \mu\text{mol}/(\text{m}^2/\text{s})$) prior to the experiment.

Table 1. Photosynthetic parameters for young and mature alfalfa blades of control and treated plants.

Parameter	Apparent quantum yield AQY	Dark respiration rate R_d [$\mu\text{mol}/(\text{m}^2/\text{s})$]	Light compensation point LCP [$\mu\text{mol}/(\text{m}^2/\text{s})$]	Light saturation point LSP [$\mu\text{mol}/(\text{m}^2/\text{s})$]	Maximum net photosynthetic rate P_{\max} [$\mu\text{mol}/(\text{m}^2/\text{s})$]
Young blades CK	0.09	0.65	7.74	681.31	6.12
Young blades TR	0.06	0.29	5.39	657.01	2.53
Difference	-33.33%	-55.38%	-30.36%	-3.56%	-58.66%
Mature blades CK	0.11	1.44	15.45	798.79	6.87
Mature blades TR	0.10	0.94	11.56	833.52	4.70
Difference	-9.99%	-34.72%	-25.18%	+4.35%	-31.59%

The data were used to fit into a P_n -PFD curve and the values of the apparent quantum yield AQY , dark respiration rate R_d , light compensation point LCP , light saturation point LSP , and maximum net photosynthetic rate P_{\max} were calculated. The values are summarized in Table 1. All values were lower for young blades than for mature blades, though the differences varied between the parameters. Every calculated parameter decreased following treatment (pre-exposure to

high-intensity light) compared to controls, with the exception of LSP for mature blades. For example, the decrease of AQY of young blades following treatment was 33.33% (from 0.09 - 0.06) while the decrease in R_d and P_{max} values was more than 50% (Table 1). For mature blades these parameters decreased less strongly. Following treatment, the LSP value of young blades decreased by 24 $\mu\text{mol}/(\text{m}^2/\text{s})$ (3.56% decrease), but for mature blades it increased with 35 $\mu\text{mol}/(\text{m}^2/\text{s})$ (4.35% increase relative to CK treatment, Table 1).

The photochemical efficiency Φ_{PSII} decreased as light intensity increased, both for young and mature blades, as shown in Fig. 2a. The decrease was stronger for plants that had received treatment (triangles) compared to controls (circles). For the latter, the Φ_{PSII} values for young and mature blades did not significantly change when PFD remained below 400 $\mu\text{mol}/(\text{m}^2/\text{s})$, while Φ_{PSII} values were marginally lower for young blades (black circles) than for mature blades. At higher PFD the values of Φ_{PSII} started to decrease and the difference between young and mature blades became more pronounced, up to a 10.62% difference at 1200 $\mu\text{mol}/(\text{m}^2/\text{s})$. However, treated blades resulted in both a stronger decrease with PFD increase, and a larger difference between young and mature blades (Fig. 2a).

Electron transfer rates increased gradually with increasing light intensity (Fig. 2b), with only a slight difference for young and mature blades in control plants. The blades of treated plants followed the same trends as long as PFD remained at or below 200 $\mu\text{mol}/(\text{m}^2/\text{s})$, but at higher light intensities the ETR of TR plants plateaued at a level below that of CK plants, and there was a noted difference between young and blades.

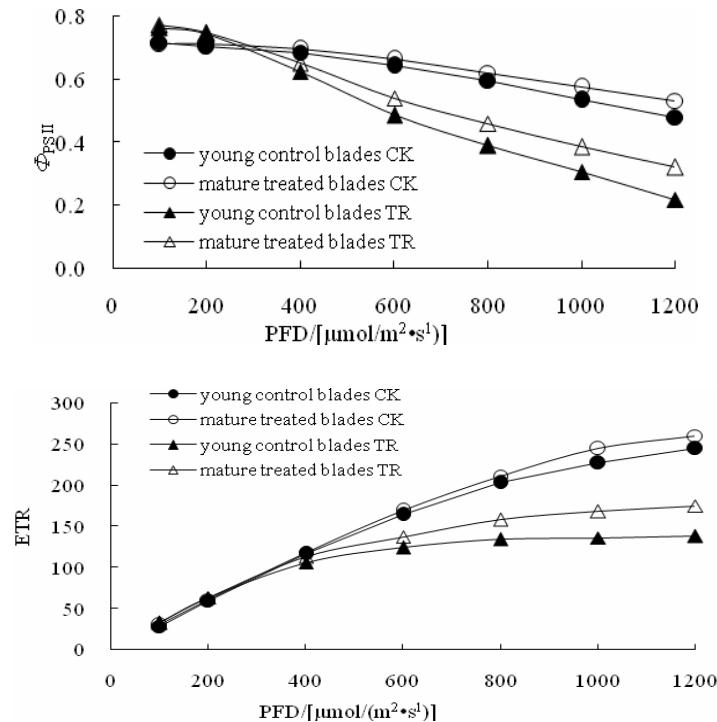


Fig. 2. Photoresponse curves of photochemical efficiency Φ_{PSII} (top) and electron transfer rate ETR (bottom) for young (black symbols) and mature (open symbols) alfalfa blades. Results are shown for control (CK, circles) and treated (TR, triangles) plants.

The values of the photochemical and non-photochemical quenching coefficients qP and qN changed more strongly in response to light intensity for treated than for control blades (Fig. 3). For control plants, under low light intensity the values of qP were slightly lower for young blades than for mature blades, and both decreased slightly as the light intensity increased, though the difference between young and mature blades was not significant. In contrast, treated plants resulted in significantly lower qP values when light intensity increased, and the difference between young and mature leaves increased as well (Fig. 3a). The difference between treated and control plants increased with PFD.

The qN values of treated leaves were lower than those of control leaves at light intensities below $300 \mu\text{mol}/(\text{m}^2/\text{s})$ (Fig. 3b), but their values increased more steeply with increasing PFD than in controls reaching a plateau eventually. The maximum difference between TR and CK was observed with PFD between 600 and $1000 \mu\text{mol}/(\text{m}^2/\text{s})$.

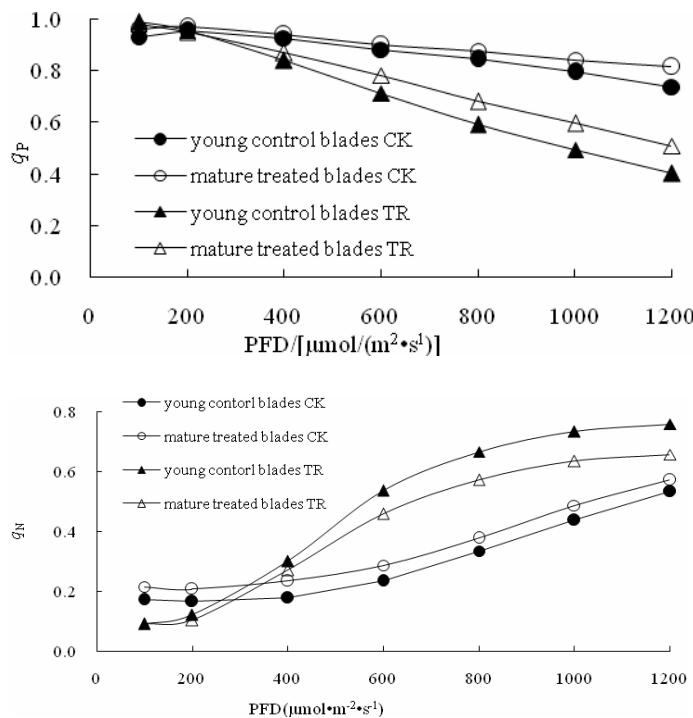


Fig. 3. Photoresponse curves of photochemical quenching coefficient qP (top) and non-photochemical quenching coefficient qN (bottom).

In control plants, the PS II maximum photochemical efficiency (F_v/F_m) was slightly 2.14% lower in young blades than mature blades but the difference was not significant ($p > 0.05$) (Fig. 4). The high-intensity light treatment resulted in a 4.99% decrease of F_v/F_m values for young blades relative to controls ($p < 0.05$).

The following energy distribution parameters were determined: quantum yield used for photochemical reactions (Φ_{PSII}), quantum yield depending on proton gradient and lutein circulation (Φ_{NPQ}), fluorescence quantum yield and heat dissipation quantum yield ($\Phi_{\text{f,D}}$), and heat dissipation quantum yield (Φ_{NF}). Their distribution was relatively similar for young and mature blades of

control plants (Fig. 5). However, following light treatment these parameters changed significantly for young and mature blades, with a decrease of photochemical efficiency Φ_{PSII} by 5.66% and an increase of 7.15% for Φ_{NPQ} values for young blade relative to controls; those values changed less dramatically for mature blades (2.63% decrease and 2.57% increase, respectively). That means that transplanting young seedlings to high-intensity light has a higher impact on the quantum yield used for photochemical reactions and on the heat dissipation quantum yield of young blades than of mature blades. Such transfer further decreases Φ_{NPQ} and slightly lowers Φ_{NPQ} in young leaves compared to mature blades.

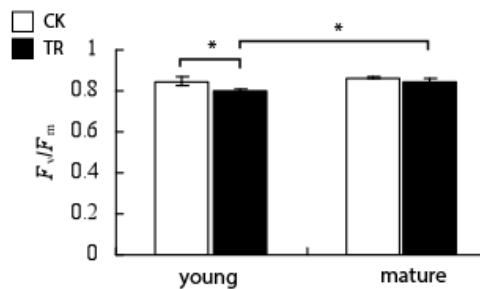


Fig. 4. The effect of light treatment on F_v/F_m values of young and mature blades.

■ Φ_{NF} □ Φ_{PSII} ▨ Φ_{NPQ} ▩ Φ_{FD}

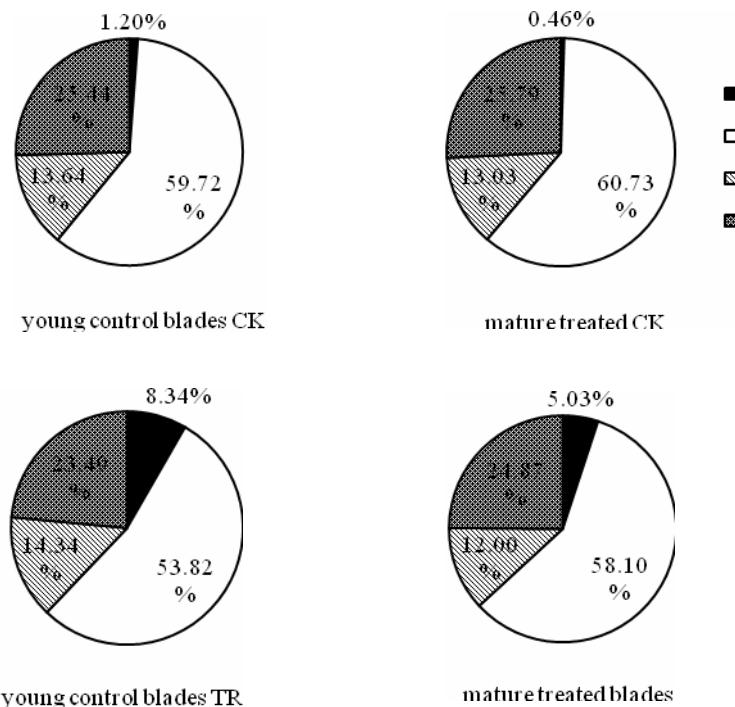


Fig. 5. Relative distribution of energy parameters for young and mature blades of treated and control plants.

Photosynthesis is the major energy source for plant growth, but its efficiency is decreased under unfavorable conditions (Zhang *et al.* 2017). Photoresponse curves describe how photosynthesis depends on PFD, and can assist in describing how photosynthetic parameters vary as a result of changes in light intensity (Zhang *et al.* 2016). In this study, the photosynthetic capability of young and adult alfalfa blades was compared with and without transfer of plants from low to high-intensity light. The light treatment significantly lowered photosynthetic activity, with a stronger effect in young compared to mature blades. This was mainly reflected by relatively lower values of AQY , R_d , LCP , and P_{max} values, with a minor effect on LSP . The reason for these observations is that young blades have a lower capability to capture and use light energy. A previous study involving tobacco plants found that after exposure to natural sunlight, the net photosynthetic rate and PS II photochemical activity decreased (Liu *et al.* 2007, Su *et al.* 2010), similar to the present observations with alfalfa. The amplitudes of changes of AQY , R_d and P_{max} for young blades were significantly lower than those for mature blades. LCP and LSP are important indices that reflect the adaptability of plants to light (Sun *et al.* 2009). In this study, LSP values for young blades decreased when they were transplanted to intense light, while those for mature blades increased, indicating that mature blades were better equipped to adapt to light intensity changes.

The Φ_{PSII} values of young and mature blades decreased with increasing PFD, while ETR increased. However, following transplantation to intense light, the ETR increase plateaued at a lower level, characteristic of light saturation, which was also indicated by their lower photosynthetic rate P_n . Again, this saturation effect was stronger for young blades, whereby the effect on ETR was larger than that on P_n . This may be because ETR can only reflect the linear transfer of electrons, while alternative electron transfer pathways also exist, which was identical to the observations from a previous study (An *et al.* 2015). Under low light intensity, different PFD (100~1200 $\mu\text{mol}/(\text{m}^2/\text{s})$) resulted in lower Φ_{PSII} and ETR values for young than in mature blades (Flexas *et al.* 2000). The difference became more significant when PFD was further increased, indicating that the light energy utilization rate for young blades was significantly lower than mature blades.

When PFD increased, the plant blades downregulated the PS II reaction center or activated heat dissipation to avoid photo-destruction caused by excessive light energy. This was reflected by lower qP and larger qN values (Ort *et al.* 2002, Li *et al.* 2016). The effects on qP and qN values were again significantly stronger on young blades than mature blades. At higher PFD, the activity of the PS II reaction center of young blades was significantly lower than that of mature blades, which was in accordance with Φ_{PSII} results. However, under different PFD, the qN for young blades was lower than that of mature blades as well, indicating that young blades generally have a lower capability for heat dissipation. When low-intensity light changed to high intensity, the decrease of qP was significantly stronger than that for mature leaves, indicating that the light energy utilization rate and adaptive capability of light for young blades were intrinsically lower. Under unfavorable conditions, excessive excitation energy may exist in the photosynthetic system, for which the plant leaves can activate other electron transfer pathways to alleviate any possible harm (e.g., light respiration and water-water circulation) (Noctor *et al.* 2002). Wei *et al.* (2014) reported that cherry seedlings can consume excessive excitation energy by heat transfer. When light intensity was suddenly increased, mimicking in-house grown seedlings being transplanted into the field, a PFD increase led to higher qN for young blades than for mature blades, which was different from control plants not undergoing such transfer. Obviously, mature blades were relatively well able to utilize and redirect excessive excitation energy from the photosynthetic system, limiting photo-induced damage.

The changes in light intensity will naturally affect the light energy utilization mechanism. Yang *et al.* (2010) found that after transplanting corn seedlings to natural light, the plants could avoid

photo-destruction by activating the non-radioactive energy mechanism that depends on lutein cycling. Li *et al.* (2005) reported similar results. Plant blades of different ages have different defense mechanisms for light. The young blades for *Torreya grandis* (a conifer species) can utilize excessive energy by increasing the pH value, change Φ_{NPQ} values mediated by lutein concentrations, and decrease Chlorophyll b content to avoid light capture. However, mature blades can increase fluorescence and $Y_{(NO)}$ to dissipate excessive energy (Chen *et al.* 2015). In present study, F_v/F_m values for young and mature blades of control alfalfa plants did not significantly differ, indicating that photoinhibition of PS II reaction center did not occur. In addition, the energy distribution parameters for young and mature blades were basically similar, which was probably due to the large difference in energy adsorbed between young and mature blades. However, when seedlings were transferred from low to high-intensity light, a decrease of Φ_{PSII} and an increase of Φ_{NF} was observed that was stronger for young blades than that for mature blades. This is in accordance with the observed F_v/F_m changes and indicates that the light intensity change had resulted in a strong decrease of PS II reaction center activity in young blades. The larger proportion of Φ_{NPQ} was relevant to the lutein circulation ratio of the proton gradient of the thylakoid membrane that was used to prevent excessive energy from destructing PS II function. After light intensity changes, Φ_{NPQ} was significantly lower and $\Phi_{f,D}$ was higher for young blades than for mature blades, indicating that the protection system for lutein circulation was inhibited, and that the main heat dissipation pathway was based on the dissipation of thermal energy. In addition, light energy Φ_{NF} consumed by the deactivated reaction center would significantly increase, which indicated that under light exchange, the deactivated reaction center was the main heat dissipation site. However, after light intensity changes, mature blades can still activate the lutein circulation to consume excessive energy, and effectively protect their photosynthesis reaction center from being destructed by excessive energy. This capacity is much weaker in young leaves.

Under low light intensity, the photosynthetic capability of young alfalfa blades was significantly lower than that of mature blades, while the F_v/F_m values of blades of both developmental stages did not significantly differ. However, when seedlings were transplanted to high-intensity light, the defense capability of young blades to protect against photo destruction, by enhanced photosynthetic performance and heat dissipation, was significantly weaker than that of mature blades, leading to larger PS II photoinhibition. Therefore, to alleviate the photoinhibition during transplant and to increase the potential survival rate of seedlings grown indoors during transplanting into the field, young leaves need to be protected, to preventing photoinhibition or photo-destruction.

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