

# Enhanced photoprotection at the early stages of leaf expansion in field-grown soybean plants

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## Abstract

Gas exchange, chlorophyll a fluorescence kinetics, chloroplast pigments and antioxidant enzymes were investigated to explore the development of photoprotective mechanisms in soybean leaves from emergence to full expansion under field conditions. During leaf development, photosynthesis ( $P_n$ ) gradually increased. Although the maximum quantum yield of PSII photochemistry ( $F_v/F_m$ ) was quite high at the initial stages of leaf development, it was appreciably lower than that in fully expanded leaves. During daily courses, reversible decrease in  $F_v/F_m$  was noted at various stages, implying that no photodamage occurred. When exposed to irradiance, a substantial elevation in the actual PSII efficiency ( $\Phi_{PSII}$ ) together with a remarkable decrease in non-photochemical quenching (NPQ) was observed with the process of leaf development. In this study, we observed that newly initiating leaves possessed relative larger xanthophyll pool size  $(V + A + Z)/Chl$ , but it began to decrease with leaf expanding until fully expanded. Further experiments revealed that the decline of relative xanthophyll cycle pool size during leaf expanding was owing to the fact that the chlorophyll contents per area increased faster than that of the xanthophyll cycle pigments. In addition, activities of the antioxidative enzymes, such as SOD, APX, CAT, POD and GR, were also enhanced at the early stages of leaf expansion. We suggested that photoprotective mechanisms, including xanthophyll cycle and antioxidant enzymic system, have developed firstly as soon as leaf emerged. It was the timely development of the mechanisms in young leaves that dissipate excess excitation energy protecting leaves against photodamage at the early stages of leaf development. The relative leaf water content increased with the process of leaf development and exhibited significant negative linear correlation with NPQ, xanthophyll cycle pigments and antioxidant enzyme activities in soybean leaves. We proposed that the changes in leaf turgor might be involved in triggering the activation of photoprotective mechanisms together with high irradiance at the initiating stages of leaf expanding.

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**Keywords:** Photosynthesis; Chlorophyll fluorescence; Xanthophyll cycle; Antioxidant enzyme

## 1. Introduction

At the beginning of leaf ontogenesis, the capacity of carbon assimilation is low until the leaf fully expanded [1–4]. Thus, when young leaves exposed to high irradiance, only a fraction of absorbed irradiance can be utilized in photochemical reaction via carbon assimilation, which means that much more excessive excited energy is produced. The remaining excited energy captured by light harvesting complexes must be dissipated harmlessly, or too much excessive excited energy could largely lead to production of damaging reactive oxygen species as byproducts of photosynthesis, which can damage the photosynthetic

**Abbreviations:** A, antheraxanthin; APX, ascorbate peroxidase; CAT, catalase; Chl, chlorophyll;  $F_o$ , minimal fluorescence in dark-adapted state;  $F_m$ , maximum fluorescence in dark-adapted state;  $F_v$ , maximum variable fluorescence in dark-adapted state ( $=F_m - F_o$ );  $F_v/F_m$ , maximum quantum yield of photosystem II;  $F_s$ , steady fluorescence under irradiance;  $F'_m$ , maximum fluorescence in light-adapted state;  $F'_v$ , maximum variable fluorescence in light-adapted state ( $=F'_m - F'_o$ ); GR, glutathione reductase; NPQ, non-photochemical quenching; PFD, photon flux density;  $P_n$ , net photosynthetic rate; PSII, photosystem II;  $\Phi_{PSII}$ , the actual PSII efficiency under irradiance; POD, peroxidase; SOD, superoxide dismutase; V, violaxanthin; Z, zeaxanthin

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apparatus [5,6]. A number of researchers have demonstrated that plants have developed several mechanisms to deal with excessive irradiance in order to avoid photodamage.

Among many of the photoprotective mechanisms, one of the most important mechanisms is the release of excessive excitation energy as heat [6]. This kind of energy dissipation in photosystem II (PSII) is dependent on the presence of zeaxanthin (Z) and antheraxanthin (A), the de-epoxidized components of xanthophyll cycle [6,7–9]. The role of xanthophyll cycle under conditions of cold-temperature stress [10], water stress [11], and nutrition deficiency [12,13], has been widely investigated. Recently, characteristics of xanthophyll cycle pigments and excited energy dissipation in senescence leaves have been extensively explored [14–16]. However, only a few papers have focused on the changes of xanthophyll cycle pigments in young leaves [17–19], especially, at the early stages of leaf expansion.

Although main excessive excited energy can be dissipated by thermal dissipation relying on xanthophyll cycle, the production of reactive oxygen species is still unavoidable during photosynthesis, especially under high irradiance [5,20]. Biehler and Fock [21] reported that in water-stressed wheat leaves, about 30% of the photosynthetic electrons are consumed in Mehler-peroxidase reaction leading to the production of  $O_2^{\bullet-}$ . To counteract the toxicity of reactive oxygen species, plants have developed a highly efficient antioxidant enzymic defense system, mainly including superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD) and glutathione reductase (GR), increasing tolerance to different stress factors, which has become an interesting research subject in recent years [22,23]. For this regard, we wondered whether the antioxidant enzymic defense system could be fully developed at the beginning of leaf expansion.

Because newly expanded leaves commonly initiate at the top of canopy or branch, they have to endure stronger irradiance than most of the fully expanded leaves that locate at lower position in the canopy. Therefore, we wondered how young leaves cope with excessive irradiance in the field. Whether can photoprotective mechanisms be duly established at the early stages of leaf expansion? Can these photoprotective mechanisms effectively protect leaves from photodestruction during leaf development? For these purposes, the changes in the gas exchange parameters, chlorophyll a fluorescence parameters and xanthophyll cycle pigments as well as the antioxidant enzymes have been investigated during leaf expansion in field-grown soybean plants.

## 2. Materials and methods

### 2.1. Plant materials

Soybean (*Glycine max* L.) plants (cv. Ludou 13) were grown in field situated at Tai'an Shandong province, where a

clay soil was used. The density of the plants was 13 plants/ $m^2$ . Nutrition and water were supplied sufficiently throughout, thus potential nutrients and drought stresses were avoided. Measurements were performed in June at the beginning of flowering stage of soybean. To avoid the influence of whole plant age on the measurements and to assure all measurements were performed at the same field condition, we did not follow single leaves during their development, instead we chose leaves of different development stages, from emergence to full expansion, at top of the main stem at the beginning of flowering stage of soybean. Areas of different development leaves were determined by a leaf area meter (LI-3000A, Licor, USA). The area of fully expanded leaf was taken as 100%, the relative area of those unexpanded leaves were expressed as percentage of fully expanded leaves (leaf area of those unexpanded leaf/area of fully-expanded leaf)  $\times$  100%. Measurements were performed with several single leaves of different development stages simultaneously. All leaves used in this experiment were at the top of the plants and were not shaded by other leaves during their development. During the experiment period, the weather showed the typical early days of summer in Eastern China. The PPFD, air temperature and relative humidity were determined by a portable photosynthesis system (CIRAS-1, PP Systems, UK) and depicted in Table 1.

### 2.2. Determination of leaf water status

Leaf water potential ( $\Psi_w$ ) was measured with a HR-33-T-R Dew Point Microvoltmeter (Wescor, USA) after leaf discs were equilibrated in the chamber for 2 h. Relative water content (RWC) was determined gravimetrically. After measurement of fresh weight, leaves were kept in room (PPFD  $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) floating on distilled water in Petri dishes. After attaining constant turgid weight (4 h), leaves were dried. Relative water content (%) was calculated from

Table 1  
Environmental factors in field where the different leaves were sampled in the study

Time	Relative leaf area (%)	PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Air temperature ( $^{\circ}\text{C}$ )	Relative air humidity (%)
9:00 a.m.	100	$795 \pm 39$	$26.8 \pm 0.34$	$70.2 \pm 1.72$
	84	$753 \pm 43$	$27.1 \pm 0.26$	$71.3 \pm 1.35$
	43	$734 \pm 53$	$27.0 \pm 0.35$	$69.5 \pm 1.53$
	20	$784 \pm 49$	$27.3 \pm 0.57$	$67.1 \pm 1.13$
	11	$768 \pm 54$	$27.5 \pm 0.55$	$68.5 \pm 0.95$
	Average	$767 \pm 56$	$27.1 \pm 0.62$	$69.32 \pm 1.83$
2:00 p.m.	100	$1379 \pm 13$	$34.5 \pm 0.19$	$49.59 \pm 0.56$
	84	$1352 \pm 21$	$34.8 \pm 0.24$	$49.89 \pm 0.67$
	43	$1360 \pm 29$	$34.2 \pm 0.22$	$49.53 \pm 0.67$
	20	$1349 \pm 31$	$34.7 \pm 0.31$	$49.13 \pm 0.23$
	11	$1381 \pm 33$	$34.6 \pm 0.28$	$49.43 \pm 0.63$
	Average	$1364 \pm 35$	$34.6 \pm 0.32$	$49.51 \pm 0.89$

All the data were measured with a portable photosynthetic system (CIRAS-1, PP systems, UK).

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