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ORIGINAL PAPER

Photosynthetic characterization of Jerusalem artichoke during leaf expansion

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Abstract Gas exchange, chlorophyll a fluorescence and modulated 820 nm reflection were investigated to explore the development of photosynthesis in Jerusalem artichoke (*Helianthus tuberosus* L.) leaves from initiation to full expansion. During leaf expansion, photosynthetic rate (Pn) increased and reached the maximal level when leaves were fully expanded. The same change pattern was also found in the stomatal conductance and chlorophyll content. Lower Pn could not be ascribed to the higher stomatal resistance in developing leaves, as intercellular CO_2 concentration was not significantly lower in these leaves. Lower Pn partly resulted from the lower actual photochemical efficiency of PSII in developing leaves, as more excited energy was dissipated through non-photochemical quenching. The development of primary photochemical reaction and electron transport in the donor side of PSII was completed in the initiating leaves. However, the development of electron transport in the acceptor side of PSII was not accomplished until leaves were fully expanded, indicated by the change in probability that an electron moves further than primary quinone (ψo). PSI activity changed in parallel with ψo suggesting that PSI cooperated well with PSII during leaf expansion. It should be stressed that the development of carbon fixation process was later than primary photochemical reaction but earlier than photosynthetic electron transport during leaf expansion. The later development of photosynthetic electron transport may reduce the production of reactive oxygen species from Mehler reaction, particularly under low carbon fixation.

Keywords Carbon fixation · Leaf expanding · Photosynthetic electron transport · Primary photochemical reaction

Abbreviations

Ci	Intercellular CO_2 concentration
Gs	Stomatal conductance
NPQ	Non-photochemical quenching
Pn	Photosynthetic rate
PI(abs)	PSII performance index on absorption basis
PSI	Photosystem I
PSII	Photosystem II
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
Vj	Relative variable fluorescence at 2 ms
V_k	Relative variable fluorescence at 300 μs
Ψo	Probability that an electron moves further than primary quinone
ψPo	The maximum quantum efficiency for primary photochemistry
φPSII	Actual photochemical efficiency of PSII

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Introduction

Leaf area expansion is a crucial developmental step in plant growth, and has a large effect on plant photosynthesis and crop yield (Hartmut and Alan 1983; Smart 1985). During the leaf development, the morphological and physiological changes almost occur in parallel, which include increase in leaf area and thickness, accumulation of chlorophyll, enlargement in stomatal conductance and synthesis of photosynthetic apparatus and CO_2 assimilation enzymes (Maayan et al. 2008; Gratani and Bonito 2009). Photosynthesis which provides required carbohydrate for the plant growth consists of primary photochemistry reaction, electron transport through photosynthetic apparatus and CO_2 fixation process. In addition, it is also influenced by stomatal conductance and chlorophyll content. Thus, except some "delay greening" species, photosynthetic rate (Pn) gradually increases upon leaf development, and reaches the maximum level when leaves are fully expanded (Gonzalez-Rodriguez and Peters 2010).

To date, variation of photosynthetic performance during leaf growth has been studied extensively in plants (e.g., Roper and Kennedy 1986; Miyazawa and Terashima 2001; Maayan et al. 2008; Gonzalez-Rodriguez and Peters 2010). However, the results are not always consistent, suggesting that various evolutionary strategies exist in different plant species. Noticeably, it is still not clear how plants coordinate the development of primary photochemistry reaction, photosynthetic electron transport and carbon fixation process. Pn has been demonstrated to be closely correlated with Gs during the leaf development (Gonzalez-Rodriguez and Peters 2010). Maayan et al. (2008) have found that ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), a key enzyme in carbon fixation process, was absent in olive leaves at the early developmental stages and only slowly accumulated throughout leaf development, and they have shown that Rubisco level was the dominant factor leading to the increase in Pn during the leaf development. Concomitant with chloroplast maturation and chlorophyll accumulation in leaf growth, function of photosynthetic apparatus is gradually improved. Photosystem II (PSII) is one of the major protein complexes in the photosynthetic apparatus in plants. The maximal quantum yield of PSII (ψPo) reflects the performance of primary photochemistry reaction. It was observed that ψPo increased along with leaf growth (Choinski et al. 2003). However, Jiang et al. (2006c) suggested that primary photochemical reaction of PSII was almost built up at the early beginning of leaf development in grapevine, and they also inferred that oxygen evolving complex might be not perfectly connected to PSII in young leaves. In addition, electron transport in acceptor side of PSII was also proved to be less efficient in young leaves of elm seedlings (Jiang et al. 2006a, b). Photosystem I (PSI) receives electrons from PSII and drives them to the terminal acceptor for producing nicotinamide adenine dinucleotide phosphate. In contrast to PSII, less attention was paid to PSI activity during leaf growth. Only a few functional PSIs were observed to be developed at the initial stages of leaf growth in grapevine, but it matched perfectly with PSII (Jiang et al. 2006c). It should be noticed that young leaves are more susceptible to photodamage, since excited energy captured by light harvesting complexes is less spent on promoting the carbon assimilation. Accordingly, it has been found that photoprotective mechanisms such as xanthophyll cycle and the early light induced protein have been evolved at the early stage of the leaf development for dissipating the excessive excited energy (Jiang et al. 2005; Gonzalez-Rodriguez and Peters 2010).

Jerusalem artichoke (*Helianthus tuberosus* L.) is a C3 warm-season crop species and originates from North America. In the recent years, Jerusalem artichoke has been accepted as a good source of fructose and inuline (Saengthongpinit and Saijaanantakul 2005) that can be used for many purposes like ethanol production, human diet and medical applications (Kaur and Gupta 2002; Szambelan et al. 2004; Takeuchi and Nagashima 2011). It has been reported that Jerusalem artichoke possesses high drought tolerance and can be cultivated at a relatively low cost without irrigation (Monti et al. 2005). In addition, responses of Jerusalem artichoke to salt stress have been extensively investigated, and at present, it has been utilized to exploit abandoned saline land in coastal zone in China (Zhao et al. 2006; Long et al. 2008, 2009; Xue and Liu 2008). However, we still do not have any information about the developmental properties of photosynthesis during leaf expansion in this important crop species.

In this study, gas exchange, chlorophyll *a* fluorescence, modulated 820 nm reflection and chlorophyll content were analyzed in Jerusalem artichoke leaves at the different developmental stages. The main objective was to reveal how it coordinated the development of primary photochemistry reaction, photosynthetic electron transport and carbon fixation.

Materials and methods

Plant materials

Tubers of Jerusalem artichoke (*Helianthus tuberosus* L.) were collected from Laizhou bay, Shandong province, China. They were planted in plastic pots filled with vermiculite (one tuber in each pot) and grown in artificial climatic chambers (Huier, China). The vermiculite was kept wet by watering every day. The photon flux density was approximately 200 μmol m^{-2} s^{-1} (12 h per day from

07:00 to 19:00) in the chambers. Day/night temperature and humidity were controlled at 25/18°C and 65%, respectively, in the chambers. After 1 month, they germinated and were daily watered with Hoagland nutrient solution (pH 5.7). One month later, the seedlings were utilized in our experiment. To avoid the influence of whole plant age on the measurements, we did not follow single leaves during their development. Instead, leaves of different expanding stages, from initiation to full expansion, were chosen. Jerusalem artichoke is an alternate leaf plant. The pair of newly initiating leaves (NIL) were at the top of stem, and expanding leaves (EL) and newly expanded leaves (NEL) were sequentially below NIL. The area of NEL was taken as 100%. The area of expanding leaves (EL) was about 60 ± 5%. The area of newly initiating leaves (NIL) was about 10 ± 5%. In this study, each pot was considered as one replicate, and six pots of seedlings were used.

Gas exchange and modulated chlorophyll fluorescence measurements

Gas exchange and modulated chlorophyll fluorescence were simultaneously detected using an open photosynthetic system (LI-6400XT, Li-Cor, Lincoln, NE, USA) equipped with a fluorescence leaf chamber (6400-40 LCF, Li-Cor). The leaves were dark-adapted for 30 min before the measurements. The minimal fluorescence level in the dark-adapted state (Fo) was measured using a modulated pulse (<0.05 μmol m^{-2} s^{-1} for 1.8 s). Maximal fluorescence (Fm) was measured after applying a saturating actinic light pulse of 8,000 μmol m^{-2} s^{-1} for 0.7 s. Subsequently, actinic light intensity was altered to 800 μmol m^{-2} s^{-1} in leaf cuvette and then maintained for about 30 min. The temperature, CO_2 concentration and relative humidity in the leaf cuvette were depended on ambient conditions. Stomatal conductance (Gs) and intercellular CO_2 concentration (Ci) were recorded simultaneously with Pn. In addition, steady-state fluorescence yield (Fs) was also recorded. A saturating actinic light pulse of 8,000 μmol m^{-2} s^{-1} for 0.7 s was then used to produce maximum fluorescence yield (Fm′) by temporarily inhibiting PSII photochemistry. Using fluorescence parameters determined in both light- and dark-adapted states, the actual photochemical efficiency of PSII (φPSII) and non-photochemical quenching (NPQ) were calculated (Genty et al. 1989).

For the measurement of carboxylation efficiency (CE), photon flux density and temperature were set at 800 μmol m^{-2} s^{-1} and 25°C in the leaf cuvette, respectively. Pn was measured under CO_2 concentrations in a sequence of 700, 500, 400, 300, 200, 150, 100, and 50 μmol mol^{-1}. The leaves were kept under each level of CO_2 concentration for 4 min to let leaves reach steady-state photosynthesis, and the Pn and Ci were then recorded. The correlation curve of Pn related to Ci was established. CE was calculated from the linear portion of the Pn–Ci curve according to Chen et al. (2004).

Measurement of chlorophyll *a* fluorescence transient and modulated 820 nm reflection

The measurements were made using a multifunctional plant efficiency analyzer (M-PEA, Hansatech, UK). This instrument allows the simultaneous measurement of chlorophyll *a* fluorescence transient and modulated 820 nm reflection, as shown in Fig. 1. Oxidation of the reaction center of PSI is known to cause an increase in absorption in the 800–850 nm. Monitoring modulated reflection change near 820 nm is a very convenient way to follow the redox state of PSI. The operating mechanism of this instrument has been elucidated by Strasser et al. (2010) in detail. In this study, leaves were dark adapted for 30 min before they were measured. Dark-adapted leaves were illuminated with 1 s pulse of continuous red light (627 nm, 5,000 μmol photons m^{-2} s^{-1}) and subsequently, with 10 s far-red light (735 nm, 200 μmol photons m^{-2} s^{-1}). The prompt fluorescence transient and modulated 820 nm reflection were recorded

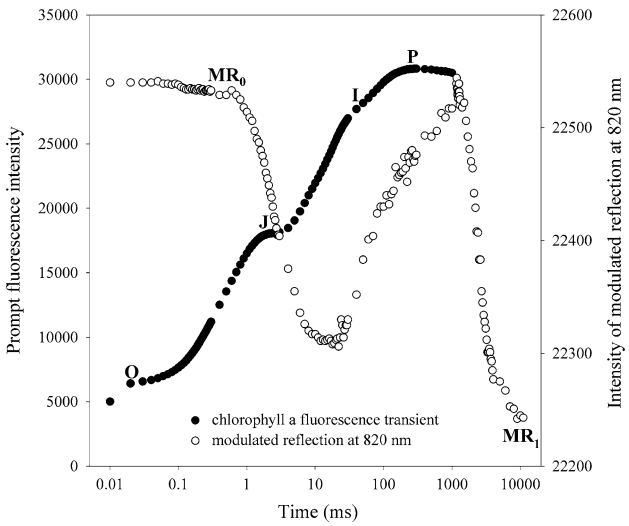

Fig. 1 Kinetics of prompt fluorescence and modulated 820 nm reflection driven by 1 s pulse of strong red actinic light (627 nm, 5,000 μmol photons m^{-2} s^{-1}) and subsequent 10 s pulse of far-red light (735 nm, 200 μmol photons m^{-2} s^{-1}) in a fully expanded leaf of Jerusalem artichoke. MR_0 is the value of modulated 820 nm reflection at the onset of red light illumination (0.7 ms, the first reliable MR measurement). MR_1 is the value of modulated 820 nm reflection after far-red light illumination. O, J, I and P indicate the specific steps in chlorophyll *a* fluorescence transient

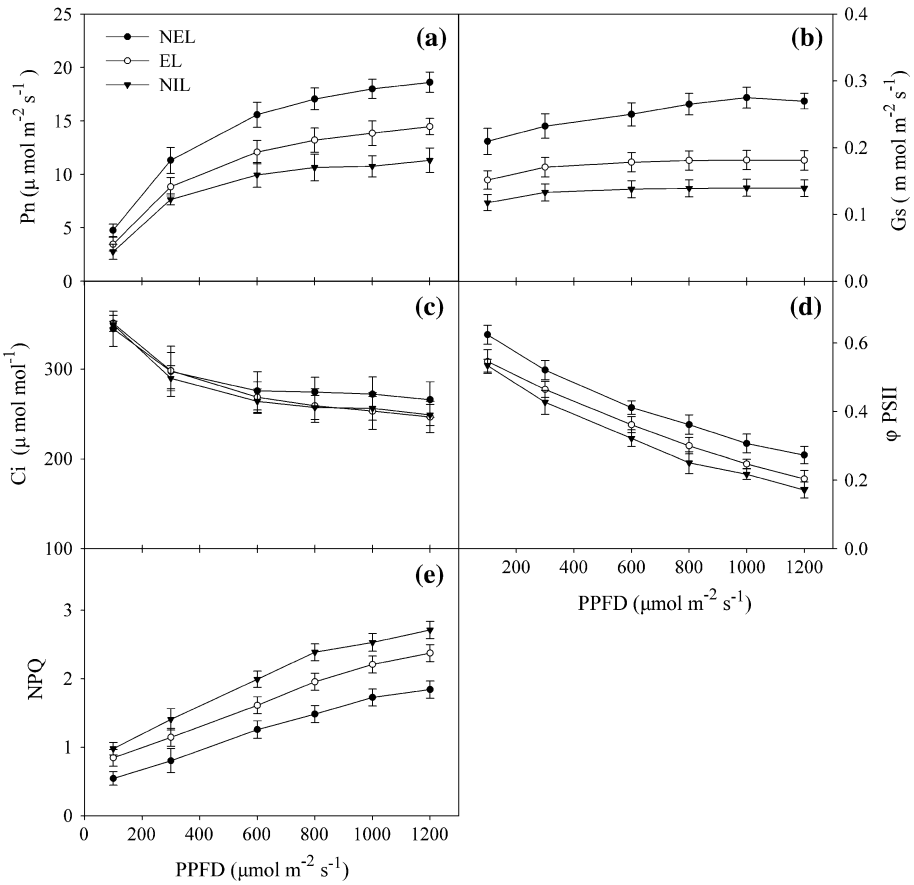

Fig. 2 Photosynthetic rate (Pn, **a**), stomatal conductance (Gs, **b**), intercellular CO_2 concentration (Ci, **c**), actual photochemical efficiency of PSII (φPSII, **d**) and non-photochemical quenching (NPQ, **e**) in Jerusalem artichoke leaves under various photosynthetic photon flux density (PPFD). NEL, newly expanded leaves; EL, expanding leaves; NIL, newly initiating leaves. Each value is the mean (±SD) of six replicates

during the illumination. MR_0 is the value at the onset of the red light illumination when PSI is in reduced form (0.7 ms, the first reliable MR measurement). After the far-red illumination, PSI is completely oxidized, and MR_1 is the value at this time. Thus, PSI redox potential can be calculated as $(MR_0 - MR_1)/MR_0$ (Fig. 1). Chlorophyll *a* fluorescence transients were quantified according to the JIP test by utilizing the following original data: (1) fluorescence intensity at 20 μs (Fo, when all reaction centers of PSII are open); (2) the maximum fluorescence intensity (Fm, when all reaction centers of PSII are closed) and (3) fluorescence intensities at 300 μs (K-step), 2 ms (J-step) and 30 ms (I-step). Using these original data, the following parameters can be calculated for quantifying PSII behavior: PI(abs), Vk, Vj, ψPo and ψo. The calculation for these parameters has been illustrated by Strasser et al. (2004).

Measurement of chlorophyll content

The extraction procedure was similar to Booker and Fiscus (2005) with small modification. Tissue samples (0.25 g) were soaked in 20 ml 95% (v/v) ethanol at 4°C in darkness until the tissues became white. Extracts were used to measure the absorbance at 649 and 665 nm. Chlorophyll content was calculated according to Ma et al. (2011).

Statistical analysis

One-way ANOVA was carried out using SPSS computer package (SPSS Inc. 1999, Chicago, IL, USA) for all sets of data, and significant differences between mean values were determined through LSD test. Differences were considered statistically significant when $P < 0.05$.

Result

Gas exchange parameters, PSII photochemical efficiency and non-photochemical quenching in leaves at different developmental stages

Pn, Gs and φPSII were significantly higher in NEL than those in EL and NIL under different photosynthetic photon flux density, and they are the lowest in NIL (Fig. 2a, b, d). On the contrary, the highest and lowest NPQ were,

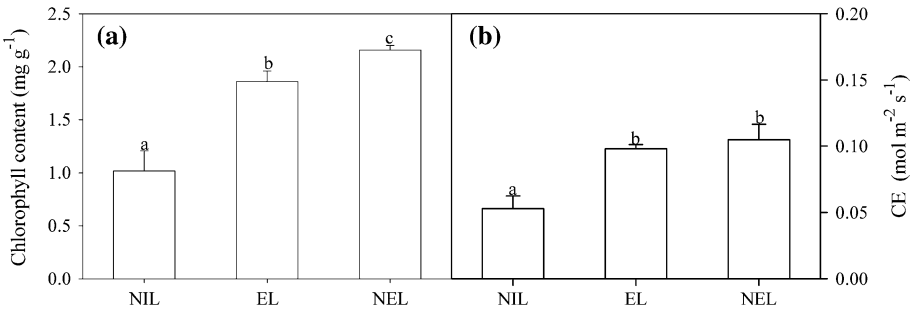

Fig. 3 Chlorophyll content (**a**) and carboxylation efficiency (CE, **b**) in Jerusalem artichoke leaves at different developmental stages. NEL, newly expanded leaves; EL, expanding leaves; NIL, newly initiating leaves. Data in the figure indicate mean of six replicates (±SD). *Different letters* on *error bars* indicate significant difference at $P < 0.05$

respectively, found in NIL and NEL (Fig. 2e). No significant difference was observed in Ci among NEL, EL and NIL (Fig. 2c).

Chlorophyll content and carboxylation efficiency in leaves at different developmental stages

Chlorophyll content was significantly higher in NEL than that in NIL and EL, and it was the lowest in NIL (Fig. 3a). CE was higher in NEL and EL in contrast to NIL, and no significant difference was noted in between NEL and EL (Fig. 3b).

Parameters form chlorophyll *a* fluorescence transient and PSI activity in leaves at different developmental stages

PSI activity was expressed by PSI redox potential in our study (Essemine et al. 2011; Li et al. 2007). PI(abs), PSI activity and ψo were significantly higher in NEL than those in NIL and EL, and no difference was observed in them between NIL and EL (Fig. 4a, b, e). Vj was the lowest in NEL, and the difference in it was not significant between NIL and EL (Fig. 4d). No significant difference was found in V_k and ψPo among NIL, EL and NEL (Fig. 4c, f).

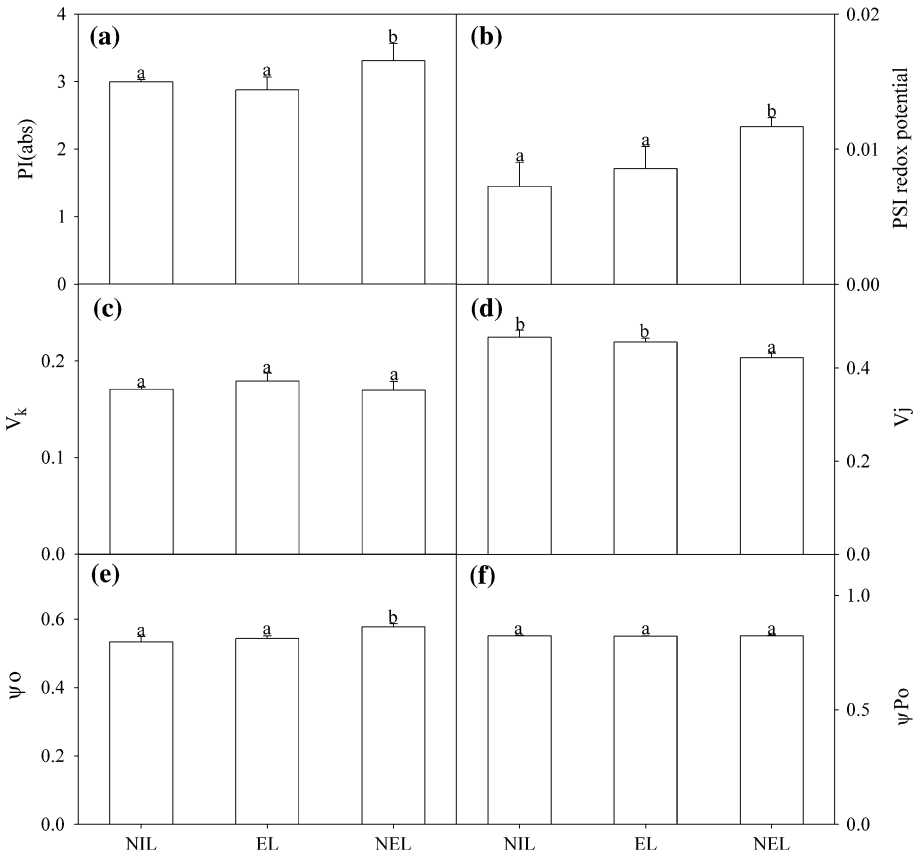

Fig. 4 PSII performance index on absorption basis (PI(abs), **a**), PSI redox potential (**b**), relative variable fluorescence at 300 μs (Vk, **c**) and 2 ms (Vj, **d**), probability that an electron moves further than primary quinone (ψo, **e**) and the maximum quantum efficiency for primary photochemistry (ψPo, **f**) in Jerusalem artichoke leaves at different developmental stages. NEL, newly expanded leaves; EL, expanding leaves; NIL, newly initiating leaves. Data in the figure indicate mean of six replicates (±SD). Different *letters* on *error bars* indicate significant difference at $P < 0.05$

Discussion

Pn increased upon leaf development and reached maximal level when leaves became fully expanded (Fig. 2a). This suggests that photosynthetic metabolism was gradually perfected along with leaf area expanding, and similar result also has been obtained in the studies on other plants (Roper and Kennedy 1986; Choinski et al. 2003; Jiang et al. 2006a, b, c; Maayan et al. 2008). Stomatal conductance determines entry of CO_2 into the leaf and closely associates with Pn, and the close relation between Gs and Pn has been demonstrated in *Ficus carica* during leaf development recently (Gonzalez-Rodriguez and Peters 2010). In addition, it has been proposed that low Pn could be ascribed to high stomatal resistance in young expanding leaves (Schwob et al. 1998). In our study, Gs increased in parallel with Pn during leaf development (Fig. 2a, b). However, according to the theory suggested by Farquhar and Sharkey (1982), lower Gs was not the primary reason leading to lower Pn in the developing leaves, as Ci was not significantly lower in these leaves (Fig. 2c). The change pattern of chlorophyll content was the same with Pn during leaf expansion (Fig. 3a), which has been found in other plants as well (Jiang et al. 2005, 2006a, b; Maayan et al. 2008). The accumulation of chlorophyll surely contributed to the increase of carbon assimilation capacity. Lower φPSII in developing leaves of indicates that the development of photosynthetic electron transport was gradually accomplished during leaf expansion (Fig. 2d). Correspondingly, higher NPQ was observed in the young leaves (Fig. 2e), and it could help to reduce the possibility of photodamage. Therefore, we infer that photoprotective mechanisms have been evolved at the early stage of leaf development. Rubisco, as a key enzyme in the Calvin cycle, catalyzes the first major step of carbon fixation and is accepted as a rate-limiting factor of photosynthesis. The carboxylation efficiency is correlated with Rubisco activity very well (Voncaemmerer and Farquhar 1981). Since CE was significantly lower in NIL in contrast to EL and NEL (Fig. 3b), accomplishment of carbon fixation process played an important role in the development of photosynthesis in Jerusalem artichoke.

PI(abs) is an acute parameter reflecting the entire performance of PSII (Tsimilli-Michael and Strasser 2008). PI(abs) and PSI activity reached the maximal level when leaves were fully expanded (Fig. 4a, b). Thus, we suppose that leaf area expansion process also involved the synthesis and assembly of photosynthetic apparatus in Jerusalem artichoke. So far, it is not definite whether primary photochemical reaction of PSII is the limiting step of photosynthetic capacity during the leaf growth, as contradictory results have been reported in different plants (Lebkuecher et al. 1999; Srivastava et al. 1999; Choinski et al. 2003; Jiang et al. 2005, 2006c). These contradictory results can be attributed to the inconsistent culture protocol or plant species. In this study, no significant difference was observed in ψPo among NIL, EL and NEL (Fig. 4f), indicating that primary photochemical reaction of PSII was almost built up at the early beginning of leaf development in Jerusalem artichoke. K-step occurred in the rise of O–J–I–P transient due to the damage in donor side of PSII, especially the oxygen-evolving complex (OEC), and Vk is the parameter to reflect the change of K-step (Strasser et al. 2004). J-step appears because accumulation of Q_A^- reaches the maximal level, and Vj can be used to reflect the change of J-step (Strasser et al. 2004). Jiang et al. (2006c) detected a higher K-step in young leaves of grapevine, and it was explained that the functional connection between OEC and PSII was not fully built at the beginning of leaf growth. However, Vk was not higher in NIL than that in NEL or EL (Fig. 4c), and we propose that the development of photosynthetic electron transport in the donor side of PSII was completed early in leaf growth. In contrast, the development of electron transport in the acceptor side of PSII was not finished until leaves were fully expanded, since higher Vj and lower ψo were found in NIL and EL than that in NEL (Fig. 4d, e). Therefore, electron transport in the acceptor side of PSII is the limiting factor in PSII development during leaf expansion. PSI activity increased in parallel with ψo, and they both peaked when leaves were fully expanded (Fig. 4b, e). It suggests that PSI cooperated well with PSII during leaf expansion in Jerusalem artichoke.

It should be pointed out that development of primary photochemical reaction was completed at the early stage of leaf growth in Jerusalem artichoke. Subsequently, development of carbon fixation process ended up. At last, electron transport in the acceptor side of PSII was fully developed. This developmental sequential may be an effective adaption to their growth environment. In the young leaves, the trapped energy by PSII reaction centers was largely dissipated as heat due to the inhibition of electron transport in PSII acceptor side. The later development of electron transport may reduce the production of reactive oxygen species from Mehler reaction, particularly when the evolvement of carbon fixation process is not accomplished.

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