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Photosynthesis and chlorophyll fluorescence response to low sink demand of tubers and roots in *Dahlia pinnata* source leaves

S.T. YAN[1,2,5], X.D. LI[1], W.D. LI[3], P.G. FAN[1], W. DUAN[1] and S.H. LI[4]*

Institute of Botany, Chinese Academy of Sciences, 100093 Beijing, P.R. China[1]
Graduate School, Chinese Academy of Sciences, 100093 Beijing, P.R. China[2]
School of Chinese Pharmacy, Beijing University of Chinese Medicine, 100029 Beijing, P.R. China[3]
Wuhan Botanical Garden, Chinese Academy of Sciences, 430074 Wuhan, P.R China[4]
Citrus Institute of Chinese Academy of Agricultural Sciences,400712 Chongqing, P.R. China[5]

Abstract

Photosynthetic rate (P_N) and chlorophyll (Chl) fluorescence induction of source leaves in response to a low sink demand created by girdling the branch (GB) between the root-tuber-system and the leaves were studied in *Dahlia pinnata* L. cv. Rigolet during the stage of rapid tuber growth in the greenhouse. GB resulted in significantly lower values of P_N, stomatal conductance (g_s), and transpiration rate (E), but in higher leaf temperature (T_l) compared with those of controls. With exception of maximum quantum yield of photosystem 2 (PS 2) photochemistry (F_v/F_m) and maximum ratio of quantum yields of photochemical and concurrent non-photochemical processes in PS 2 (F_v/F_0), no significant differences were observed in Chl fluorescence parameters between girdled and control leaves on days 1 and 2 after GB, indicating no apparent damage in the photosynthetic apparatus. However, longer girdling duration resulted in higher non-photochemical Chl fluorescence quenching (NPQ), but lower F_v/F_0, actual efficiency of energy conversion in PS 2 under steady-state conditions (Φ_{PS2}), and photochemical quenching coefficient (qP) in comparison with controls from 10:00 to 16:00 or 15:00 on days 4 and 5, respectively, indicating reversible injury in the photosynthetic apparatus.

Additional key words: intercellular CO_2 concentration, net photosynthetic rate, stomatal conductance, transpiration rate.

Introduction

Carbon assimilation in higher plants depends largely on their sink-source activities. Decreased sink demand, such as by removal of fruits (Wibbe and Blanke 1995, Marcelis *et al.* 2004) or tubers (Basu *et al.* 1999), generally reduces net photosynthetic rate (P_N) of leaves. In contrast, reduction in the number of source leaves by partial defoliation (Chanishvili *et al.* 2005, Macedo *et al.* 2006, McCormick *et al.* 2009) or increasing crop load (Quilot *et al.* 2004) results in higher P_N.

Many studies have tried to elucidate the regulation mechanism of the above phenomenon. The end-product feedback inhibition hypothesis, first put forward by Bousingalt in 1868 (cited in Neales and Incoll 1968), which stated that the accumulation of assimilates may be responsible for a reduced P_N. It was the first theory explaining the decline of photosynthetic capacity after weakened sink demand (Herold 1980, Layne and Flore 1995, Quereix *et al.* 2001). However, this hypothesis still remains to be conclusively proven (Nautiyal *et al.* 1999, Li *et al.* 2001, Li *et al.* 2005). For example, low sink demand after fruit removal decreased P_N without influencing accumulation of sugars in leaves (Rom and Ferree 1986, Marcelis 1991), and accumulation of sugars in leaves did not result in decreasing P_N under low sink demand (Roper

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Abbreviations: Chl - chlorophyll; c_i - intercellular CO_2 concentration; E - transpiration rate; F_m, F_m' - maximum Chl fluorescence yield in dark-adapted and light-adapted leaves, respectively; F_0, F_0' - minimum Chl fluorescence yield in dark- and light-adapted leaves; F_s - the steady-state Chl fluorescence; F_v, F_v' - variable Chl fluorescence in dark- and light-adapted leaves; F_v/F_m - maximum quantum yield of PS 2 photochemistry; F_v/F_0 - maximum ratio of quantum yields of photochemical and concurrent non-photochemical processes in PS 2; GB - girdling the branches; g_s - stomatal conductance; NPQ - non-photochemical Chl fluorescence quenching; T_l - leaf temperature; TCA - trichloroacetic acid; PS 2 - photosystem 2; PFD - photosynthetically active radiation; P_N - net photosynthetic rate; qP - photochemical quenching coefficient; Φ_{PS2} - actual efficiency of photochemical energy conversion in PS 2 under steady-state.

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* Corresponding author; fax: (+86) 27 87510599, e-mail: shhli@wbgcas.ac.cn

et al. 1988, Nautiyal *et al.* 1999). Thus, several other hypotheses have been suggested during the last 30 years to explain the regulation of photosynthesis under modified source-sink relationships including mechanical damage to chloroplasts by large starch grains (Grub and Machler 1990), inorganic phosphate limitation (Herold 1980) and imbalance of carbon-to-nitrogen ratio (Urban *et al.* 2004a,b).

Recently, we showed that low sink demand after fruit removal in peach trees resulted in a significant accumulation of sorbitol and starch without decreasing activities of related enzymes of carbon metabolism in the source leaves (Li *et al.* 2007). Decreased CO_2 assimilation resulting from a low sink strength may therefore be regulated by some mechanism other than the end product inhibition of the activities of related biosynthetic enzymes. Two factors, decreased stomatal aperture and increased leaf temperature (T_l), play an important role in regulating P_N under a lower sink-source ratio, indicating that the low stomatal conductance (g_s) should be a trigger or promoter of reduced P_N and the high T_l a regulator of P_N under a lower sink demand (Li *et al.* 2001, 2005). Thus, decreased P_N under lower sink demand might be caused by both non-stomatal and stomatal limitations (Wu *et al.* 2008).

Most studies were carried out on perennial fruit trees (Rom and Ferree 1986, Li *et al.* 2001, Urban *et al.* 2004a,b, Urban and Lechaudel 2005, Wu *et al.* 2008, Duan *et al.* 2008) or annual crops such as wheat (Yin *et al.* 1998, Ahamadi *et al.* 2009), tomato (Heuvelink and Buiskool 1995, Van Quy *et al.* 2001), and soybean (Egli and Bruening 2003), all of which have fruits as the most important sink. However, there is no study on ornamental species. Dahlia is one of them with important value for its beautiful flowers and useful tubers in the world. Its root system (including the tuber) is the most important sink during rapid tuber growth. Thus dahlia should be an ideal plant for a source-sink relationship study to understand the effect of the root system on P_N. The present work was focused on stomatal and non-stomatal limitations of P_N under lower sink demand.

Materials and methods

Uniformly-sized, single-sprouted seed tubers of dahlia (*Dahlia pinnata* L.) cv. Rigolet were planted in ceramic pots (15 cm in diameter, 20 cm in height) containing loamy soil and sand (3:1, v/v) mixed with granular fertilizer (150 mg nitrogen in ammonium, 100 mg phosphorus and 100 mg potassium per kg soil, pH 5.5 - 6) and grown in a greenhouse at the Institute of Botany, Chinese Academy of Sciences, in the western suburb of Beijing. The plants were cultivated as one stem with two branches and irrigated every 2 d. Uniform 2-month-old plants were chosen for source-sink manipulation. The experiment was carried out under greenhouse conditions during 16 - 21 September 2006; the days of the study were sunny except for the third day, and the tubers were rapidly grown during the experimental period just before appearance of floral buds. Mechanical and chemical girdling treatments were applied to the base of one branch with a horizontal score using a razor blade and 10 % trichloroacetic acid (TCA), which blocked assimilate transport from source leaves to the sink of the tubers and roots, while a vertical score of the same length was applied to the other branch of the same plant as a control in order to remove the possible impact of mechanical injury. Five replicates for the girdling and control were established.

Diurnal gas exchange parameters, leaf temperature (T_l) and photosynthetically active radiation (PAR) were measured using a portable photosynthesis system (*LI-6400, Li-Cor,* Lincoln, NE, USA) on the terminal leaflet of the third mature leaf from the top of the five replicate plants for each treatment, from 08:00 to 17:00 at intervals of about 1 h on days 1, 2, 4 and 5 after GB.

Chl fluorescence parameters were also measured on the same terminal leaflet of the third mature leaf from the top in the five replicate plants for each treatment. The estimations were performed at the same time as the gas exchange measurements by using a plant efficiency analyzer (*PEA*, *Hansatech*, Norfolk, UK) and a fluorescence monitoring system (*FMS-2*, *Hansatech*). Minimum (F_0), maximum (F_m) and variable ($F_v = F_m - F_0$) Chl fluorescence were measured or calculated after a dark adaptation period of 30 min within a clip holder. After reading F_0, a saturating 1.0 s light pulse (irradiance 3 000 μmol m^{-2} s^{-1}) was applied to induce a maximum fluorescence. Light-induced changes in Chl fluorescence were measured with the *FMS-2*. Steady state Chl fluorescence (F_s) was recorded after adapting plants to ambient irradiance. A saturating actinic light pulse (> 6 000 μmol m^{-2} s^{-1}) for 0.7 s was used to produce the maximum Chl fluorescence yield in a light adapted state (F_m'). After switching off the actinic light the leaves were illuminated with far-red radiation to re-oxidize the plastoquinone pool to determine the minimum Chl fluorescence yield in the light-adapted state (F_0'). By using Chl fluorescence measured in both dark-adapted and light-adapted leaves, the following fluorescence parameters were calculated: the maximum efficiency of PS 2 photochemistry, F_v/F_m (Kitajima and Butler 1975), the maximum ratio of quantum yields of photochemical and concurrent non-photochemical processes in PS 2 (F_v/F_0) (Roháček 2002), the photochemical quenching coefficient, $qP = (F_m' - F_s)/(F_m' - F_o')$ (Van Kooten and Snel 1990), the non-photochemical Chl fluorescence quenching, $NPQ = (F_m/F_m') - 1$ (Bilger and Björkman 1990) and the actual efficiency of photochemical energy conversion in PS 2, $\Phi_{PS2} = (F_m' - F_s)/F_m'$ (Genty *et al.* 1989).

The experiment was in a completely randomized design, and statistical analyses were performed using the *SPSS* (Chicago, IL, USA) ver. *13.0* statistical package. Means comparisons between the girdling treatment and control were made by the independent *t*-test at $P < 0.05$.

Results

The diurnal variation in P_N and other gas exchange parameters in response to girdling on day 1 after GB were similar to that found on days 2, 4, and 5 after GB. Thus, only the results obtained on days 2 and 4 after GB are

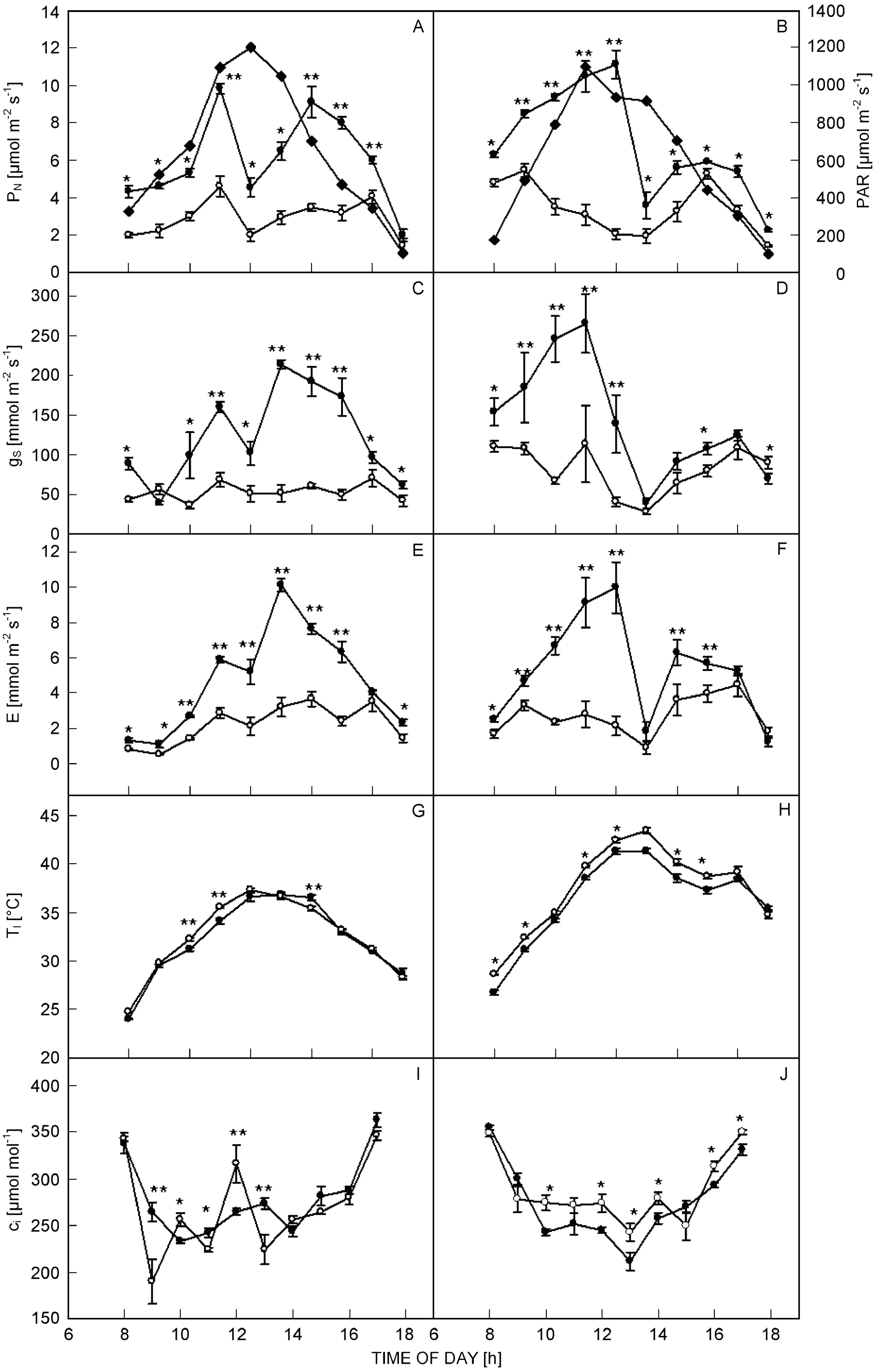

Fig. 1. Diurnal variations in net photosynthesis rate (P_N), stomatal conductance (g_s), transpiration rate (E), leaf temperature (T_l) and intercellular CO_2 concentration (c_i) in source leaves under low sink demand ('girdling' treatment, *open circles*) on day 2 (*A*, *C*, *E*, *G*, *I*) and 4 (*B*, *D*, *F*, *H*, *J*) after the treatment, compared with the control ('no girdling', *closed circles*). Daily variations in photosynthetically active radiation (PAR, *rhombs*) are also given in the plots *A* and *B*. Values are the means ± SE (*n* = 5). ** and * indicate significant difference at the $P < 0.01$ and $P < 0.05$ between the treated and control plants, respectively.

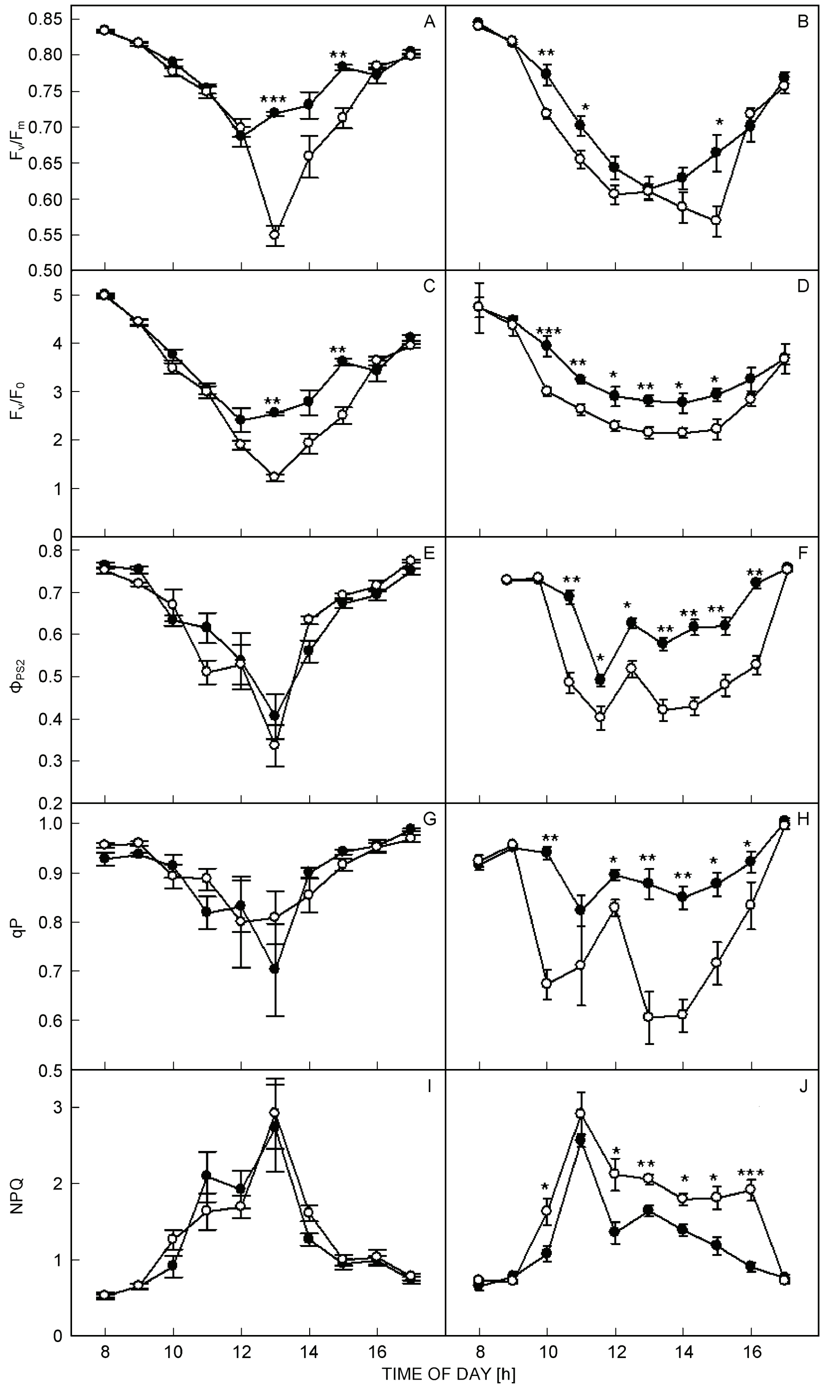

Fig. 2. Diurnal variations in the maximum efficiency of PS 2 photochemistry (F_v/F_m), the maximum ratio of quantum yields of photochemical and concurrent non-photochemical processes in PS 2 (F_v/F_o), actual efficiency of photochemical energy conversion in PS 2 under steady-state conditions (Φ_{PS2}), photochemical quenching coefficient (qP) and non-photochemical Chl fluorescence quenching (NPQ) in source leaves under low sink demand ('girdling' treatment, *open circles*) on days 2 (*A*, *C*, *E*, *G*, *I*) and 4 (*B*, *D*, *F*, *H*, *J*) after the treatment, compared with the control ('no girdling', *closed circles*). Means ± SE ($n = 5$). ** and * indicate significant difference at the $P < 0.01$ and $P < 0.05$ between the treated and control plants, respectively.

presented (Fig. 1). P_N for control plants exhibited a diurnal variation with double maxima (Fig. 1*A,B*). It quickly increased with PAR in the morning and reached the first maximum value at 11:00 on day 2 (Fig. 1*A*) or 12:00 on day 4 (Fig. 1*B*) when PAR was peaking, then decreased to a much lower value at 12:00 (day 2) or 13:00 (day 4). P_N then rose to another peak at 14:00 (Fig. 1*A*) or 15:00 (Fig. 1*B*). Girdling significantly reduced the magnitude of the two P_N maxima as well as led to significantly lower P_N throughout most of days 2 and 4 (Fig. 1*A,B*).

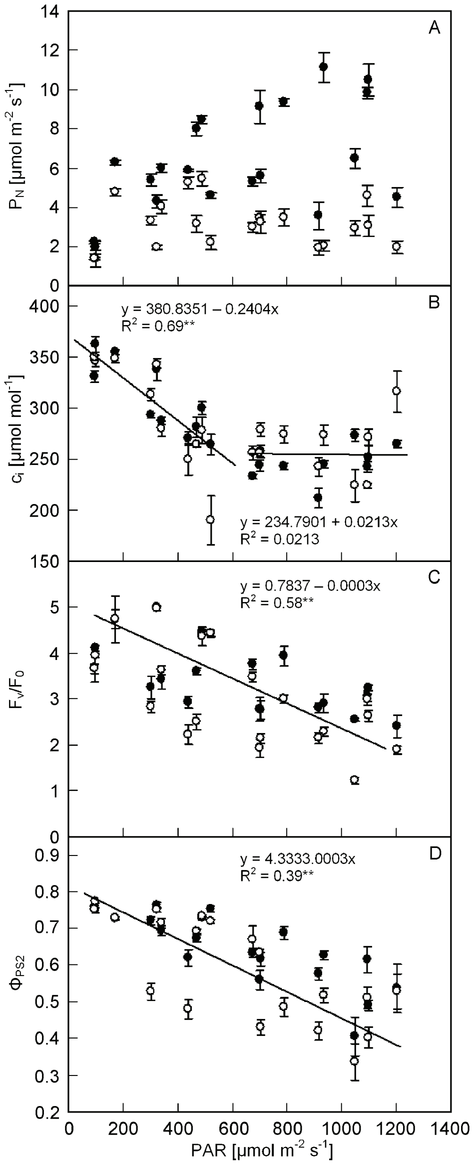

Fig. 3. Responses of net photosynthetic rate, P_N (*A*), intercellular CO_2 concentration, c_i (*B*), the maximum ratio of quantum yields of photochemical and concurrent non-photochemical processes in PS 2, F_v/F_o (*C*), and actual efficiency of photochemical energy conversion in PS 2 under steady-state conditions (Φ_{PS2}) (*D*) to the photosynthetic active radiation (PAR). The *open* and *closed circles* represent the data from 'girdling' treatment and the control 'no girdling'. Means ± SE ($n = 5$).

The g_s values for control plants also exhibited a similar diurnal pattern with double peaks, not overly pronounced in the case of GB plants (Figs. 1*C,D*). Girdling significantly reduced g_s to 24 - 43 % of control values. Significant differences were observed in g_s between the girdling treatment and the control except for the afternoon on day 4 (Figs. 1*D*).

The E values for control plants exhibited one peak on day 2 (Fig. 1*E*) and double peaks on day 4 (Fig. 1*F*). Girdling suppressed the peaks and showed little variation throughout the day. The E values for treated plants were significantly lower than those of controls except in late afternoon on day 4 (Fig. 1*F*).

Leaf temperature (T_l) increased in the morning in accordance with PAR and reached a maximum value after 12:00, thereafter decreasing for both control and GB plants (Fig. 1*G,H)*. Significantly higher T_l values were found in GB plants in comparison with controls at most hours on day 4 (Fig. 1*H*), and only at 10:00, 11:00 and 15:00 on day 2 (Fig. 1*G*).

The c_i in control plants decreased from the early morning to noon and then increased in the afternoon (Fig. 1*I,J*). Girdling did not markedly change the general pattern of diurnal c_i variation. The c_i values in GB plants were higher at 10:00 and 12:00 and lower at 09:00, 11:00, and 13:00 on day 2 (Fig.1*I*), but significantly higher from 10:00 to 17:00 except at 15:00 on day 4 (Fig. 1*J*) in comparison with those of control plants.

The GB plants showed similar diurnal variation in Chl fluorescence to controls. The diurnal patterns of F_v/F_m, F_v/F_o, Φ_{PS2}, and qP decreased during the morning, reached minimum around 12:00, then rose gradually in the afternoon (Fig. 2*A-H*). NPQ showed an opposite pattern, increasing in the morning and decreasing in the afternoon (Fig. 2*I,J*). No significant differences in Φ_{PS2}, qP and NPQ were found between GB and control plants on day 2 (Fig. 2*E,G,I*). Significantly lower F_v/F_m and F_v/F_o values resulted from the girdling at 13:00 and 15:00 (Fig. 2*A,C*). However, the responses on day 4 differed from those on day 2. The differences between the girdling and control treatments on day 4 were generally observed at noon and in the afternoon. Girdling resulted in significantly higher NPQ (Fig. 2*J*) and lower F_v/F_o, Φ_{PS2}, and qP values from 10:00 to 15:00 or 16:00 in comparison with controls (Fig. 2*D,F,H*).

P_N of GB plants responded to PAR differently from controls (Figs. *1A,B*, 3*A*). Control P_N increased in parallel with PAR when PAR was less than about 900 μmol m^{-2} s^{-1}, and then decreased with PAR above 900 μmol m^{-2} s^{-1}. However, P_N in the girdling treatment did not respond to PAR variation. Compared with the control on day 4, c_i in GB plants was higher than c_i in the control when PAR was above 600 μmol m^{-2} s^{-1} (Fig. 3*B*). F_v/F_o and Φ_{PS2} of control and GB plants were negatively correlated to PAR (Fig. 3*C,D*) on day 4 and the values in GB plants were mostly lower than those of control plants.

Discussion

Our results showed that reducing sink demand of the root system and tuber by girdling a branch to block the transport of assimilates out of source leaves *via* the phloem resulted in a significant reduction of P_N in dahlia plants

(Fig. 1*A,B*). Moreover, the lower P_N observed after girdling was accompanied by markedly decreased g_s (Fig. 1*C,D*) and E values (Figs. 1*E,F*), but increased T_l (Fig. 1*G,H*). These results are in agreement with our previous studies on peach trees (Li *et al*. 2001, 2005, 2007), indicating that reducing sink demand, here by girdling the branch between the source leaves and the root system including tubers, could inhibit P_N of source leaves in a manner similar to that after removing fruits in peach trees. The lower g_s and increased T_l occurred around noon when PAR was high (Fig. 1*C,D,G,H*). Thus, the P_N response in dahlia after removing sink demand of the root system and tubers should be similar to that in peach trees.

Reduced P_N in higher plants can result from stomatal or non-stomatal limitations. Reduced P_N accompanied by increased or unchanged c_i is attributable to non-stomatal limitation, but that followed by decreased c_i results from stomatal limitations (Farquhar and Sharkey 1982, Yu *et al.* 2009). The stomatal or non-stomatal limitations in P_N depend on PAR in peach trees (Wu *et al.* 2008). In this study, c_i varied with PAR (Fig. 3*B*). The c_i values of the GB plants depended on the time after treatment. Girdling resulted in lower c_i at 09:00, 11:00 and 13:00 on day 2 after GB (Fig. 1*I*) compared with controls, suggesting stomatal limitation. However, lower P_N after girdling was accompanied by higher c_i compared to controls on day 4 after GB, indicating the occurrence of non-stomatal limitation (Fig. 1*J*).

Further evidence for the non-stomatal limitations is provided by the response of Chl fluorescence parameters. Very similar values of the Chl fluorescence parameters in GB and control plants on day 2 (Fig. 2) indicated no damage of the photosynthetic apparatus due to girdling. However, girdling affected the values of Chl fluorescence parameters on day 4 (Fig. 2). Lower F_v/F_m and F_v/F_o value in GB than in control plants indicated enhancement of the photoinhibition (Krause and Weis 1991, Krause *et al.* 1982, Qiu and Lu 2003). Furthermore, these differences between GB and control plants occurred primarily under high PAR (Fig. 3*C,D*).

The higher T_l resulting from stomatal closure in GB plants probably contributed to the inhibition of the PS 2 reaction-center complex. T_l above optimum can reduce the rates of RuBP regeneration, cause disruption of electron transport activity and specific inactivation of the oxygen-evolving enzymes of PS 2 (Salvucci and Crafts-Brandner 2004). Leaves under high temperature use a much smaller fraction of the absorbed light for photosynthesis than those under the optimum temperature, and consequently excess excitation energy is dissipated as heat. This was reflected in increase in NPQ (Ivanov and Edwards 2000, Roy Chowdhury *et al*. 2009, Zhang *et al.* 2009), explaining partly the inhibitory effects of low sink demand on P_N on the day 4 after GB. Leaves on girdled branches had a much lower photosynthetic capacity (Fig. 2*F*); they used a smaller fraction of the absorbed light for electron transport processes than those in the control. Thus, there was a need to dissipate more excitation energy as heat in girdled branch leaves. In fact, higher NPQ values of girdled branch leaves, which occurred on day 4, resulted in removing excess excitation energy (Fig. 2*J*).

In summary, the reduction of P_N in dahlia plants under lower sink demand may be due to both stomatal and non-stomatal limitations shortly after treatment. Non-stomatal limitation may play a more important role in the later stages.

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