Influence of variation potential on resistance of the photosynthetic machinery to heating in pea

Vladimir Sukhov*, Lyubov Surova, Oksana Sherstneva and Vladimir Vodeneev

Department of Biophysics, N.I. Lobachevsky State University of Nizhny Novgorod, Nizhny Novgorod 603950, Russia

Correspondence
*Corresponding author, e-mail: vssuh@mail.ru

Received 7 February 2014; revised 27 February 2014
doi:10.1111/ppl.12208

Electrical signals [action potentials (APs) and variation potentials (VPs)] induced by local stimuli are a mechanism that underlies rapid plant response to environmental factors. Such signals induce a number of functional responses, including changes in photosynthesis. Ultimately, these responses are considered to increase plant resistance to stress factors, but this question has been poorly investigated. We studied the influence of VP on photosynthesis and resistance of the photosynthetic machinery to heating in leaves of pea (Pisum sativum). Localized burning induced a VP that decreased photosynthesis parameters [CO2 assimilation rate and quantum yields of photosystem I (PSI) and photosystem II (PSII)]. The photosynthetic response was initiated by a decrease in photosynthesis dark-stage activity, which in turn increased resistance of PSI to heating. Three results supported this hypothesized mechanism: (1) the magnitude of VP-induced decrease in CO2 assimilation and enhanced PSI resistance to heating were highly correlated; (2) the VP influence on PSI resistance to heating was suppressed under a low external CO2 concentration and (3) decreasing external CO2 concentration imitated the VP-induced photosynthetic response and increased PSI resistance to heating.

Introduction

Plant adaptation to changing environmental conditions requires intercellular as well as intracellular signaling. Electrical signals [action potentials (APs) and variation potentials (VPs)] induced by local stimuli are a mechanism underlying rapid plant responses to external factors.

An AP is an electrical signal induced by non-damaging stimuli. Its generation in higher plants is associated with fluxes of Ca2+, K+ and Cl− ions (Felle and Zimmermann 2007) and transient H+-ATPase inactivation (Vodeneev et al. 2006, Sukhov and Vodeneev 2009). An AP is a self-propagated signal that is based on local electrical circuits throughout the plant body (Trebcz et al. 2006, Krol et al. 2010). A VP is an electrical signal induced by damaging stimuli, e.g. burning. It is considered that VP generation is connected with transient H+-ATPase inactivation (Julien et al. 1991, Stahlberg and Cosgrove 1992, 1996); however, fluxes of Ca2+, K+ and Cl− ions may also participate in VP development (Vodeneev et al. 2011, Sukhov et al. 2013a). Two hypotheses for VP propagation have been proposed. According to one hypothesis, a VP is a local electrical response to damage-induced hydraulic wave propagation (Malone and Stankovic 1991, Stahlberg and Cosgrove 1992, Marcus 1999). The second hypothesis proposes that a VP is induced by a wound chemical substance, which propagates from the zone of damage (Ricca 1916). Propagation of this wound substance can be accelerated by damage-induced pressure changes and water flow in the xylem and apoplast (Malone 1994, Rhodes et al. 1999, Vodeneev et al. 2012).

Abbreviations – AP, action potential; PSI, photosystem I; PSII, photosystem II; VP, variation potential; γ(PSI), photosystem I quantum yield; γ(PSII), photosystem II quantum yield.
A variety of functional responses are induced by APs and VPs, such as leaf movement in sensitive plants (Silboaka 1991), pin2 gene expression (Stanković and Davies 1996, Fisahn et al. 2004), inhibition of total protein synthesis (Davies and Stankovic 2006), production of ethylene, abscisic acid and jasmonic acid (Dziubinska et al. 2003, Fisahn et al. 2004, Hlaváčková et al. 2006), reduction in phloem transport (Fromm and Bauer 1994) and an increase in respiration rate (Filek and Kościelniak 1997). Electrical signals also influence photosynthesis (Fromm and Eschrich 1993, Hlaváčková et al. 2006, Krupenina and Bulychev 2007, Krupenina et al. 2008, Grams et al. 2009, Pavlović et al. 2011, Pavlović et al. 2011, Sukhov et al. 2012, 2013b). In particular, VPs and APs can induce rapid (approximately minutes) inactivation of photosynthetic processes that results in decreased quantum yields from photosystem I (PSI) and inactivation of photosynthetic processes that results in VP- and AP-induced photosynthetic response induction. Bulychev and co-workers (Krupenina and Bulychev 2007, Krupenina et al. 2008) showed that the AP influence on photosynthesis in Chara may be associated with Ca\(^{2+}\) flux into the cell. Conversely, higher plants might have a different mechanism of photosynthetic response induction that is connected with H\(^{+}\)-influx (Grams et al. 2009, Sukhov et al. 2012). Two hypothetical mechanisms of fast photosynthetic response induction have been suggested. Bulychev and co-workers (Krupenina and Bulychev 2007, Krupenina et al. 2008), development of the photosynthetic response in Chara is probably associated with photosynthesis dark-stage inactivation, which induces lowering of light-stage activity. Recent studies (Pavlović et al. 2011, Sukhov et al. 2012) provide evidence that supports a key role for dark-stage inactivation in AP- and VP-induced photosynthetic response in higher plants. However, direct influence of electrical signals on PSI (Sukhov et al. 2012) and PSII (Pavlović et al. 2011) is also hypothesized.

The rapid VP-induced inactivation of photosynthesis is not a unique photosynthetic response. Different local stimuli can induce long-term (>20 min after stimulation) inhibition of photosynthesis (Peña-Cortés et al. 1995, Herde et al. 1999), which may be connected with increase in jasmonic acid and abscisic acid contents (Peña-Cortés et al. 1995, Hlaváčková et al. 2006). Changes in the xanthophyll cycle (increase in zeaxanthin and antheraxanthin contents, and decrease in violaxanthin and neoxanthin contents) may play a role in long-term photosynthetic response development (Herde et al. 1999).

Thus, electrical signals induce essentially functional responses, including photosynthetic response. Although supported by little experimental data, Retivin et al. (1997, 1999) assumed that functional responses induced by electrical signals contributed to plant resistance to stressors. We propose that changes in photosynthetic processes induced by electrical signals can modify damage to the photosynthetic machinery induced by stressors and this modification may be a mechanism contributing to the influence of AP and VP on plant resistance. The aim of this study was to investigate the influence of VP on photosynthesis parameters and resistance of PSI and PSII to heating in pea (Pisum sativum).

**Materials and methods**

**Plant material**

Pea (P. sativum) seedlings were cultivated hydroponically in a Binder KBW 240 (Binder GmbH, Tuttlingen, Germany) plant growth chamber at 24°C under a 16/8-h (light/dark) photoperiod. Seedlings used in the experiments were 14–21 days old.

**Electrical measurements**

Electrical signals were induced by burning about 1 cm\(^2\) of the leaf tip (a stimulated leaf) over a flame for 3–4 s, which is a standard damaging stimulus (Sukhov et al. 2012).

Surface electrical potential was measured using Ag/AgCl electrodes (RUE ‘Gomel Measuring Equipment Plant’, Gomel, Belarus). The electrodes were connected to a high-impedance amplifier IPL-113 (Semicco, Novosibirsk, Russia) and a PC. The measurement electrodes contacted unstimulated leaves through ‘Uniage’ conductive gel (Geltek-Medica, Moscow, Russia) as used in our previous studies (Sukhov et al. 2012, Vodeneev et al. 2012).

Electrical activity was monitored with two electrodes (Fig. 1A). One electrode (E\(_3\)) was placed on the stem; the second (E\(_1\)) was connected to the center of an unstimulated leaf. The reference electrode was placed in the standard solution (1 mM KCl, 0.5 mM CaCl\(_2\) and 0.1 mM NaCl) surrounding the roots.

The standard measuring head, which was used for photosynthesis investigation, prevented electrical measurement in the same leaflet from which photosynthesis parameters were recorded. As a result, we placed the E\(_1\) on the conjugate leaflet of the same leaf. The amplitude of the burning-induced VP in conjugate leaflets showed a correlation coefficient of 0.94. Among 16 experiments, a VP did not propagate in both conjugate leaflets in only three experiments. We did not observe variants in...
which the VP propagated in the first conjugate leaflet but was not recorded in the second leaflet. Thus, the VP in the conjugate leaflet could be used for estimation of VP in the leaflet in which photosynthesis parameters were measured.

Photosynthetic parameter measurements

Photosynthetic parameters were measured with a complex comprising a GFS-3000 portable gas exchange measuring system (Heinz Walz GmbH, Effeltrich, Germany), a Dual-PAM-100 measuring system for simultaneous assessment of P700 oxidation and chlorophyll fluorescence (Heinz Walz GmbH) and a Dual-PAM gas-exchange Cuvette 3010-Dual measuring head (Heinz Walz GmbH). The complex was used for simultaneous recording of photosynthetic dark- and light-stage parameters in the lamina (the measured area was 1.3 cm²) of an unstimulated leaf (Fig. 1A).

Initial parameters of PSII fluorescence, dark fluorescence yield (F₀), maximal fluorescence yield (Fₘₘ) and variable fluorescence (Fᵥ = Fₘₘ – F₀), were measured after dark adaptation. Maximal change in the P700 signal (Pₘₘ) reflecting maximal P700 oxidation was measured after preliminary illumination by far red light for 10 s. Steady-state fluorescence yield in the light (F), maximal fluorescence yield in the light (Fₘₘ'), the steady-state P700 signal (P), and the maximal change in the P700 signal in the light (Pₘₘ'' = Pₘₘ' – P) were measured by saturation pulses generated every 10 s. Effective photosystem II quantum yield \( \gamma_{\text{PSII}} \) was calculated with the equation \( \gamma_{\text{PSII}} = (Fₘₘ' - F)/Fₘₘ' \) (Maxwell and Johnson 2000). Photosystem I quantum yield \( \gamma_{\text{PSI}} \) was calculated with the equation \( \gamma_{\text{PSI}} = (Pₘₘ' - P)/Pₘₘ \) (Klughammer and Schreiber 2008).

The CO₂ assimilation rate (A; \( \mu \text{mol CO₂ m}^{-2} \text{s}^{-1} \)) was measured using the GFS-3000 and its associated software. The parameter was calculated in accordance with
von Caemmerer and Farquhar (1981). The relative magnitude of VP-induced decrease in A was calculated as \( \Delta A_{VP}/\Delta A_{hv} \), where \( \Delta A_{VP} \) is the maximum CO₂ assimilation decrease induced by VP and \( \Delta A_{hv} \) is the maximum CO₂ assimilation increase caused by illumination. The error value of VP-induced decrease in CO₂ assimilation was lower in this case. The relative decrease in A was used for calculation of the correlation between CO₂ assimilation decrease and photosystems resistance to heating.

The initial external CO₂ concentration was 360 ppm. Photosynthetically active radiation was 239 \( \mu \)mol m\(^{-2} \) s\(^{-1} \) (blue light, 460 nm). The air humidity was about 20 000 ppm, which corresponded to about 65% relative air humidity at 24°C.

Investigation of leaf heating resistance

Heating of green leaves to a high temperature is often used to estimate thermal stability of the photosynthetic machinery (Lipová et al. 2010). We heated the leaf and recorded photosynthesis parameters for investigation of VP influence on photosynthetic machinery resistance to high temperature (Fig. 1B).

Leaves were locally heated using the complex described in the previous section (GFS-3000, Dual-PAM-100 and Cuvette 3010-Dual) for 1.5 h after placement in the Cuvette 3010 Dual (10 min under dark conditions, 1 h 20 min under actinic light) at an initial leaf-surface temperature (T\(_{leaf}\)) of 23°C. The heating duration was 30 min, after which the temperature returned to the original value in 10 min. T\(_{leaf}\) was increased from 23 to 44–48°C in about 10 min after the start of heating, remained approximately stable from 10 to 30 min, and returned to 23°C in about 10 min after cessation of heating. The rates of temperature changes in the linear part of their dynamics were 3.2 ± 0.1°C min\(^{-1} \) (heating) and 3.4 ± 0.1°C min\(^{-1} \) (return to initial temperature).

Several photosynthesis parameters were monitored for investigation of photosynthetic machinery resistance to heating. \( P_m \) and \( F_v \) reflect the number of photosystems, which can separate charges (Maxwell and Johnson 2000, Klughammer and Schreiber 2008). Therefore, the ratio of final \( P_m \) to initial \( P_m \) (\( P_m^{final}/P_m^{initial} \)) and the ratio of final \( F_v \) to initial \( F_v \) (\( F_v^{final}/F_v^{initial} \)) were calculated to reveal the portions of undamaged PSI and PSII after heating. Initial \( F_v \) and \( P_m \) were recorded after 10 min of dark adaptation before the start of illumination. Finally \( F_v \) and \( P_m \) were recorded after illumination and 10 min of dark adaptation. Final \( \gamma \) (PSI), \( \gamma \) (PSII) and A, which were recorded before cessation of illumination, showed the residual photosystem activities under light conditions.

The duration of dark adaptation (10 min) was selected on the basis of the relaxation kinetics of \( P_m \), \( F_m \), and \( F_v \) after illumination had ended. Neither \( P_m \), \( F_m \) or \( F_v \) were noticeably changed after 10 min of relaxation (Fig. 1C). This result showed that energy-dependent quenching of fluorescence (Müller et al. 2001) was developed in our experiments.

Results

Influence of electrical signals on photosynthesis

Fig. 2A shows typical data for surface potential and photosynthesis parameters in a leaf after localized burning of another leaf. The burning usually induced VP propagation to the stem in unstimulated leaves. The amplitudes of this signal were 44 ± 6 mV in the lamina (n = 11) and 66 ± 3 mV in the stem (n = 14), the duration was roughly tens of minutes, and the shape varied. A few minutes after VP propagation through the lamina, \( \gamma \) (PSI), \( \gamma \) (PSII) and A essentially decreased. Dynamics of the photosynthetic response included an initial decline 5–10 min after VP propagation and a second decrease more than 20 min later. In a few instances (Fig. 2B), VP propagated through the stem, but electrical reactions in the lamina were small (<15 mV) and photosynthetic and transpiration responses were not observed. The latter result supports VP participation in induction of photosynthetic and transpiration responses.

Influence of VP on PSI and PSII damage under heating

Results from preliminary analyses of VP influence on PSI and PSII resistance under heating to different leaves temperatures are shown in Fig. 3. Final \( \gamma \) (PSI) and \( \gamma \) (PSII) did not differ significantly between treated and control leaves at leaf temperatures in the range of 43°C to about 44–45°C; however, final \( \gamma \) (PSI) after VP propagation was significantly higher than in the control after heating of the leaf to about 47°C. Thus, a positive influence of VP on PSI resistance to heating was indicated at leaf temperatures of 45–47°C or higher. We used T\(_{leaf}\) = 46°C in subsequent experiments.

The influence of VP on damage to the photosynthetic machinery under leaf heating (about 46°C) was analyzed (Fig. 4). Final \( \gamma \) (PSI) and \( \gamma \) (PSII) essentially decreased and A was completely suppressed in the control without VP induction. A considerable portion of PSI (0.8) and PSII (0.88) was damaged under heating. The lower damage to PSI than to PSII accorded well with the strong sensitivity of PSII to heating within the range of 40–50°C in pea and the weak suppression of PSI under these temperatures (Oukarroum et al. 2013). The portion of undamaged PSII...
Fig. 2. Typical changes in electrical potential, CO₂ assimilation rate and photosynthesis light-stage parameters (γ(PSI) and γ(PSII)) induced by localized burning (arrow). (A) Variation potential propagated through the leaf (n = 11), (B) variation potential not propagated through the leaf (n = 3). E_s and E_L are changes in electrical potential measured by electrodes on the stem and lamina, respectively.

Fig. 3. Final γ(PSI) and γ(PSII) and leaf temperature under heating recorded 15 min after VP propagation (n = 4). T_leaf under heating was calculated as the average temperature in the period from 10 to 30 min after the start of heating.

(0.12) was similar to that reported for pumpkin after heating to 45°C (Retivin et al. 1999).

Propagation of a VP into the leaf increased final γ(PSI) and the portion of undamaged PSI (from 0.20 to 0.38), but γ(PSII), the portion of undamaged PSII, and CO₂ assimilation rate in treated leaves were not significantly different from those of the control. Correlation coefficients between the relative magnitude of VP-induced decrease in A and photosynthesis parameters after heating were high and significant for final γ(PSI) (r = 0.79) and the portion of undamaged PSI (r = 0.88), and low for γ(PSII) (r = 0.34) and the portion of undamaged PSII (r = 0.13) (Fig. 4D).

A VP was not propagated through the investigated leaf and a photosynthetic response not induced in 1 instance out of 10 leaves. In this case, photosynthesis parameters after heating did not differ significantly from the control (data not shown). The data for this leaf were not included in analyses.

Participation of photosynthesis dark-stage inactivation in VP influence on photosynthetic machinery resistance to heating

Inactivation of the photosynthesis dark stage is considered to be one of the first stages of electrical signal-induced photosynthetic response development in higher plants (Pavlović et al. 2011, Sukhov et al. 2012). The VP-induced photosynthetic response under a low external CO₂ concentration (approximately 15 ppm) was essentially less marked than that under control conditions (Fig. 5A, B). Conversely, the decrease in photosynthesis dark-stage activity at different reduced CO₂ concentrations imitated VP-induced changes in light-stage parameters (Fig. 5C).
Fig. 4. Photosynthesis parameters after 30 min of heating with a leaf surface temperature of 46°C in the control and after VP propagation. (A) Final CO₂ assimilation rate, (B) final γ(PSI) and γ(PSII) and portions of undamaged PSI and PSII, (C) leaf temperature under heating (the average temperature in the period from 10 to 30 min after the start of heating), (D) correlation coefficients between the relative magnitude of VP-induced decrease in A and photosynthesis parameters after heating. The numbers of repetitions were seven (control without VP) and nine (VP induced by localized burning). The VP was induced 15 min before the start of heating. * Significantly different from the control (P < 0.05); # correlation coefficient was significant (P < 0.05).

Fig. 5. Photosynthetic responses induced by VP in control conditions (A), under low external CO₂ concentration (B) and under three decreased external CO₂ concentrations equaling about 200 ppm (C), 100 ppm (D) and 10 ppm (E). The control and initial CO₂ concentrations were 360 ppm. The low external CO₂ concentration (approximately 15 ppm) was estimated 30 min before VP induction. The numbers of repetitions were 11 (control conditions, VP), 7 (low external CO₂ concentration, VP) and 5–13 (three decreased external CO₂ concentrations).
The VP did not increase PSI resistance to heating under a low external CO2 concentration (Fig. 6). Moreover, the VP decreased final γ(PSI) after heating, which indicated that the electrical signal may have negatively influenced PSI resistance under such conditions. It should be noted that photosystems’ resistance in the control under a low external CO2 concentration (Fig. 6) was higher than that in the control under 360 ppm CO2 (Fig. 4).

The influence of external CO2 concentration on photosystems’ resistance to heating was analyzed in more detail. The relationship of PSI and PSII resistance to heating with terminal external CO2 concentration, which decreased 15 min before the start of heating, is shown in Fig. 7. Final γ(PSI) and the portion of undamaged PSI increased as CO2 concentration and its assimilation rate decreased. Final γ(PSII) and the portion of undamaged PSII were weakly affected by CO2 concentration.

**Discussion**

Our results show that localized burning induced VP propagation in pea plants (Fig. 2). In most instances the VP propagated through undamaged leaves without a notable decrease in amplitude and resulted in decreased photosynthesis parameters, including the lowering of CO2 assimilation rate, γ(PSI) and γ(PSII). These responses show good accordance with a number of previous studies of higher plants (Grams et al. 2009, Pavlovič et al. 2011, Sukhov et al. 2012), in which electrical signal-induced decrease in photosynthesis was reported. Proton influx in higher plants (Grams et al. 2009, Sukhov et al. 2013b) and calcium ion influx in *Chara* (Krupenina and Bulychev 2007, Krupenina et al. 2008) are hypothesized to be potential mechanisms of induction of rapid photosynthesis inactivation. Conversely, long-term photosynthesis inactivation (Fig. 2) may be associated with increased jasmonic acid and abscisic acid contents (Peña-Cortés et al. 1995, Hlaváčková et al. 2006).

In the experiments of Pavlovič et al. (2011) and our previous study (Sukhov et al. 2012), decrease in photosynthesis dark-stage activity is among the initial stages of electrical signal-induced photosynthetic responses in Venus flytrap (*Dionaea muscipula*) and geranium (*Pelargonium zonale*). The present results indicate that a similar mechanism may operate in pea, because VP-induced changes in the photosynthesis light stage were essentially suppressed under low dark-stage activity (Fig. 6A, B) and the decline in Calvin cycle activity at
a low external CO₂ concentration decreased γ(PSI) and γ(PSII) similar to the VP-induced response (Fig. 6C).

Retivin et al. (1997) hypothesized that electrical signals may increase plant resistance to stress factors. In particular, Retivin et al. (1999) showed that AP increased PSI resistance to freezing (−8°C) and heating (45°C), but the influence of VP on resistance of the photosynthetic machinery was not investigated. Our present results showed that VP increased PSI resistance to high temperature and did not notably affect PSII resistance under increasing T_{leaf} to 46°C (Fig. 4B). This difference in response may be associated with the different influences of VP and AP on photosynthetic machinery resistance to stress. VP, which is induced by damaging stimuli, is probably a signal for stressors of higher intensity than AP, which is induced by non-damaging stimuli. However, PSI is more resistant than PSII to stresses (Allakhverdiev et al. 2008a, 2008b, Sharkey and Zhang 2010). Thus, VP-induced protection of PSI against high-intensity stressors may be more effective for plant survival than protection of PSII.

Final γ(PSI) and the portion of undamaged PSI were strongly correlated with relative magnitude of VP-induced decrease in A (Figs. 4D). Taking into account this result and the key role of photosynthesis dark-stage inactivation in electrical signal-induced photosynthetic response (Fig. 5; Pavlović et al. 2011, Sukhov et al. 2012), we hypothesize that this inactivation of dark-stage photosynthesis induces an increase in PSI resistance to heating. Suppression of the VP-induced enhanced PSI resistance to heating under a low external CO₂ concentration is strong evidence for the participation of VP-induced photosynthesis dark-stage inactivation in the enhanced PSI resistance. Furthermore, the increased PSI resistance (Fig. 7) induced by lowering the CO₂ concentration 15 min before the start of heating, which inactivated dark-stage photosynthesis and imitated the VP-induced decrease in CO₂ assimilation, additionally supports this hypothesis. However, low CO₂ concentration enhanced PSI resistance to a lesser degree than that induced by VP (Figs 4 and 7), therefore other mechanisms of VP influence on PSI resistance cannot be excluded. Direct influence of electrical signals on PSI (Sukhov et al. 2012) and PSII (Pavlović et al. 2011) supports this possibility. Also, VP influence on PSI resistance can be connected with other physiological processes. In particular, it is known that electrical signals activate respiration (Filek and Kościeniak 1997, Pavlović et al. 2011, Lautner et al. 2014) which can be connected with photosynthetic processes by means of reactive oxygen species (Foyer and Noctor 2009), ATP (Noctor and Foyer 2000), intracellular CO₂ concentration or other intermediates.

The mechanism by which decrease of CO₂ assimilation rate increases PSI resistance to heating is unclear. We speculate that this mechanism is associated with increase in the ATP:ADP ratio in the chloroplast stroma. Increase in this ratio is one of the suggested means by which VP-induced dark-stage inactivation influences light-stage photosynthesis (Pavlović et al. 2011, Sukhov et al. 2012). ATP can increase photosynthetic apparatus resistance to stress factors and reparation (Allakhverdiev et al. 2008a, 2008b). However, data on the influence of electrical signals on ATP are contradictory: some studies (Pyatygin et al. 2008) report AP-induced multiphase changes in ATP concentration in phloem exudates, whereas other studies (Fromm et al. 2013) demonstrate that total ATP content in leaves is not significantly dependent on AP and VP propagation. Thus, the possible participation of changes in ATP:ADP ratio in the influence of VP
on photosynthetic machinery resistance requires further investigation.

Another potential mechanism by which VP-induced change in photosynthesis dark-stage activity influences photosynthetic machinery resistance may involve reactive oxygen species production. Photosynthetic processes in chloroplasts result in production of reactive oxygen species (Asada 1999, Allen 2003, Fischer et al. 2013). Lowering of Calvin cycle activity, induced by artificial decrease in CO₂ concentration, increases H₂O₂ production (Kim and Portis 2004). Furthermore, environmentally induced increase in reactive oxygen species production acts as a signal to induce expression of defense genes (Foyer and Noctor 2009, Fischer et al. 2013). Thus, VP-induced decrease in photosynthesis dark-stage activity may induce changes in gene expression, which contribute to the enhanced photosynthetic machinery resistance to heating.

A third potential mechanism of VP-induced increase in PSI resistance to heating may be associated with cyclic electron flow. If photon flow to PSI approximates to that of PSII (Laisk and Sumberg 1994), we can assume that cyclic electron flow is proportional to γ(PSII), because the electron flow through PSII includes non-cyclic, pseudocyclic and cyclic flows, whereas the electron flow through PSII includes only non-cyclic and pseudocyclic flows (Allen 2003). Figs 2 and 5 show that VP and low external CO₂ concentration increased this difference, which may reflect enhanced cyclic electron flow. This increase may be associated with photosynthesis dark-stage inactivation; however, direct influence of VP on PSI is not excluded (Sukhov et al. 2012). It is known that decrease in non-cyclic electron flow and increase in cyclic electron flow (Bukhov et al. 1999, Zhang and Sharkey 2009, Sharkey and Zhang 2010) are among the typical photosynthetic responses to stressors. Enhanced cyclic electron flow increases the pH gradient in thylakoid membranes (Sharkey and Zhang 2010, Johnson 2011), contributes to regulated energy dissipation in PSII (Gilmore et al. 1998, Müller et al. 2001, Miyake et al. 2004, Johnson 2011) and protects the photosynthetic machinery. We cannot exclude the involvement of this mechanism in VP influence on photosystems’ resistance to heating. However, it must predominantly protect PSI, whereas a positive influence of VP on PSI was not observed in our experiments (Figs 4 and 7). Thus, it is unlikely to be the main mechanism for VP-induced increase in photosynthetic machinery resistance to heating.

Overall, this study shows that localized burning induces VP propagation, which decreases photosynthesis in pea. Photosynthetic response is initiated by photosynthesis dark-stage inactivation. This VP-induced dark-stage inactivation is likely to increase PSI resistance to heating. These changes would increase the probability of plant survival under stressful environmental conditions, but this hypothesis requires further experimental investigation.

Acknowledgements – This work was supported by the Russian Foundation for Basic Research, project no. 14-04-01899 A and project no. 13-04-97152.

References

during the action potential of higher plants with high temporal resolution: requirement of Ca\(^{2+}\) transients for induction of jasmonic acid biosynthesis and PINII gene expression. Plant Cell Physiol 45: 456–459


Edited by A. Krieger-Liszkay