INTRODUCTION

Photosynthesis in plants is based on three light-driven electron flows, namely noncyclic, pseudocyclic, and cyclic flows (Allen, 2003). Cyclic electron flow is connected with photosystem I (PSI) and cytochrome b6f (Joliot and Joliot, 2006; Joliot and Johnson, 2011; Roach and Krieger-Liszczaky, 2014), whereas other flows are also connected with photosystem II (PSII) (Allen, 2003; Roach and Krieger-Liszczaky, 2014). In contrast to noncyclic and pseudocyclic electron flows, cyclic flow only yields ATP synthesis and does not generate NADPH for the Calvin cycle or reactive oxygen species (Allen, 2003).

Cyclic electron flow can be activated by different stressors and might serve as an adaptive mechanism (Bukhov et al., 1999; Rumeau et al., 2007; Zhang and Sharkey, 2009; Zivcak et al., 2013). In particular, under stress conditions, cyclic flow might regulate photosynthetic generation of reactive oxygen species (Zhang and Sharkey, 2009; Roach and Krieger-Liszczaky, 2014), contribute to oxidation of the PSI acceptor side, thereby protecting it from damage (Rumeau et al., 2007; Roach and Krieger-Liszczaky, 2014), and support the transthylakoid proton gradient (Bukhov et al., 1999; Joliot and Joliot, 2006; Zhang and Sharkey, 2009). In turn, support of the pH gradient contributes to ATP synthesis, fluorescence non-photochemical quenching (NPQ), and thylakoid membrane stability (Zhang and Sharkey, 2009; Joliot and Johnson, 2011). Thus, it can be concluded (Roach and Krieger-Liszczaky, 2014) that activation of cyclic electron flow by the direct action of stressors plays an important role in adaptive responses in plants.

Local action by stressors induces electrical signals, namely action potential (AP) induced by non-damaging stimuli and variation potential (VP) caused by damaging stimuli, which propagate through the unstimulated parts of higher plants (Volkov, 2000; Dzubińska, 2003; Brenner et al., 2006; Mancuso and Murgna, 2006; Stahlberg et al., 2006; Trebacz et al., 2006). Self-propagating AP is mainly caused by fluxes of Ca$^{2+}$, K$^+$, and Cl$^-$ ions (Felle and Zimmermann, 2007), while transient H$^+$-ATPase inactivation and proton influx participate in its generation to a lesser degree (Sukhov and Vodeneev, 2009). VP generation is connected with transient plasmalemma H$^+$-ATPase inactivation (Stahlberg et al., 2006); however, fluxes of Ca$^{2+}$, K$^+$, and Cl$^-$ ions might also participate in VP development (Vodeneev et al., 2011; Sukhov et al., 2013b; Katicheva et al., 2014). VP propagation is probably connected with transmission of hydraulic and/or chemical signals (Stahlberg et al., 2006; Trebacz et al., 2006; Vodeneev et al., 2012), which induce an electrical reaction.

Electrical signals can induce numerous functional responses (Dzubińska, 2003; Davies and Stankovic, 2006; Stahlberg et al., 2006; Volkov et al., 2008; Fromm and Lautner, 2012). In particular, they inactivate photosynthesis in unstimulated leaves (Koziolek et al., 2004; Krupenina and Bulychev, 2007; Grams...
et al., 2009; Pavlović et al., 2011; Sukhov et al., 2012, 2013a, 2014a,b; Bulychev and Komarova, 2014). The first stage of photosynthetic response development is possibly ion influx. Investigations of Bulychev and coworkers (Krupenina and Bulychev, 2007) have shown that Ca\(^{2+}\) influx is a potential mechanism for AP influence on photosynthesis in Chara alga. In regard to VP, according to studies by Grams et al. (2009) and our previous investigations (Sukhov et al., 2013a, 2014a), plasmalemma H\(^+\)-ATPase inactivation and subsequent proton influx are main mechanisms for VP influence on photosynthesis in higher plants.

Independent of mechanisms for initial photosynthetic-response induction, subsequent development of this response is mainly connected with inactivation of the photosynthetic dark stage (Krupenina and Bulychev, 2007; Pavlović et al., 2011; Pavlović, 2012; Sukhov et al., 2012, 2014a,b), which decreases quantum yields of photosystem I and II and increases non-photochemical fluorescence quenching. Influence of Ca\(^{2+}\) influx on photosynthetic dark stage can be connected (Krupenina and Bulychev, 2007) with the dependence of Calvin cycle enzymes on calcium concentrations in chloroplast stroma (Wolosiuk et al., 1993). Proton influx into cytoplasm and stroma can influence CO\(_2\) transport, changing carbonic anhydrase (Grams et al., 2009) and/or aquaporin (Gallé et al., 2013) activities and modifying the CO\(_2\)/HCO\(_3^-\) ratio (Bulychev et al., 2001). This influx might also reduce Calvin cycle activity (Wolosiuk et al., 1993). However, the direct influence of AP and VP on the light stage is also possible (Pavlović et al., 2011; Sukhov et al., 2012, 2014a,b). The influence can be related to the rise of fluorescence non-photochemical quenching (Sukhov et al., 2014a) and reduced electron flow through the acceptor side of PSI (Sukhov et al., 2012), which might be caused by acidification of the stroma and lumen (Müller et al., 2001; Alte et al., 2010; Benz et al., 2010).

According to Retivin et al. (1997), rapid and transient increases in plant resistance to stressors (10–25 min after stimulation) are the final result of electrical signal-induced functional responses. The resistance increase in unstimulated parts of plant contributes to plant survival under systemic action of stressor which may follow after electrical signal induction (Retivin et al., 1997). Decrease of photosynthetic machinery damage can be a mechanism contributing to the influence of electrical signals on plant resistance to stressors (Sukhov et al., 2014b). AP (Retivin et al., 1999) and VP (Sukhov et al., 2014b) increase the resistance of photosynthetic machinery to the effects of temperature changes. Our previous results (Sukhov et al., 2014b) have shown that increased resistance of photosynthetic machinery to heat is caused by VP-induced inactivation of the photosynthetic dark stage. Changes in cyclic electron flow can link the VP-induced dark stage inactivation and photosynthetic machinery resistance increase (Sukhov et al., 2014b). However, experimental investigations of electrical signal influence on cyclic electron flow are lacking. Thus, the aim of the present study was to investigate VP influence on cyclic electron flow in pea (Pisum sativum L.).

**MATERIALS AND METHODS**

**PLANT MATERIAL**

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

**STIMULATION AND ELECTRICAL MEASUREMENTS**

VP was induced by heating ~1 cm\(^2\) of a leaf tip (a stimulated leaf) over a flame for 3–4 s, representing a standard damaging stimulus (Koziolek et al., 2004; Vodeneev et al., 2012; Sukhov et al., 2014a,b).

The surface electrical potential was measured using Ag\(^+\)/AgCl electrodes (Gomel Plant of Measuring Equipment, Gomel, Belarus), a high-impedance amplifier IPL-113 (Semic, Novosibirsk, Russia) and a PC. Measurement electrodes contacted an unstimulated leaf via “Uniagel” conductive gel (Geltek-Medica, Moscow, Russia), according to our previous studies (Sukhov et al., 2014a,b). Electrical activity was monitored by two electrodes (Figure 1), with the first (\(E_S\)) placed on a stem and the second (\(E_L\)) connected with a leaflet center of an unstimulated leaf. The distance between the \(E_S\) site and the damaged area was 6–7 cm and the distance between \(E_S\) and \(E_L\) 3–5 cm. It should be noted that, as electrical responses in conjugate leaflets of a leaf were very similar in pea (Sukhov et al., 2014a,b), the electrical reaction, registered by \(E_L\), was used for investigation of VP parameters in conjugate leaflets in which photosynthesis was measured. The \(E_R\) was placed in a standard solution surrounding the root.

**MEASUREMENTS OF PHOTOSYNTHETIC PARAMETERS**

Photosynthetic parameters in intact pea leaves were measured by a system composed of a GFS-3000 portable gas exchange measuring system, a Dual-PAM-100 measuring system for simultaneous assessment of P700 oxidation and chlorophyll fluorescence,
and a measuring head Dual-PAM gas exchange Cuvette 3010-Dual (Heinz Walz GmbH, Effeltrich, Germany). The system was employed for simultaneous recording of photosynthetic dark and light stage parameters in unstimulated leaf lamina (measured area, 1.3 cm²).

The initial parameters of PSI II fluorescence, the dark and maximal fluorescence yields (F₀ and Fₘ, respectively), were measured after dark adaptation for 20 min. The maximal change in the P700 signal (Pₘ) of PSI, reflecting maximal P700 oxidation, was measured after preliminary illumination by far red light for 10 s. The steady-state fluorescence yields in light (F and Fₘ, respectively), and steady-state and maximal signals in light (P and Pₘ, respectively) were measured using saturation pulses generated every 10 s. Quantum yields of PSI (φₚₛᵢ), non-photochemical energy dissipation in PSI because of donor side limitation (φₙₐᵢᴅ), and non-photochemical energy dissipation in PSI connected with acceptor-side limitation (φₐₜₐₜ) were calculated using the equations φₚₛᵢ = (Pₘ − P)/Pₘ, φₙₐᵢ_d = P/Pₘ, and φₐₜₐₜ = (Pₘ − Pₘ)/Pₘ (Klughammer and Schreiber, 2008). The effective quantum yield of PSI (φₚₛᵢ) and fluorescence non-photochemical quenching (NPQ) were calculated using the equations φₚₛᵢ = (Pₘ − P)/Pₘ and NPQ = (Fₘ − Fₘ)/Fₘ (Maxwell and Johnson, 2000). The CO₂ assimilation rate (A, μmol CO₂·m⁻²·s⁻¹) was measured using the GFS-3000 system and its software, and the parameter programmatically calculated according to Von Caemmerer and Farquhar (1981).

The external CO₂ concentration ([CO₂]) was 360 ppm in the control and ∼10–15 ppm under low [CO₂] conditions. In some series of experiments, the CO₂ concentration was decreased from 360 ppm to ∼150 or ∼10–15 ppm. Relative air humidity and leaf temperature were ∼60% and ∼23°C, respectively. Blue actinic light (460 nm) intensity in the control was 239 μmol·m⁻²·s⁻¹. In a separate experimental series, far red light (240 μmol·m⁻²·s⁻¹, 730 nm) was used as actinic light. VP was induced in plants ∼1 h after initiation of actinic light, and photosynthetic responses monitored for 30 min.

**CALCULATIONS OF ELECTRON FLOWS**

Electron flows through PSI [EF(PSI)] and PSII [EF(PSII)] were calculated using Equations (1) and (2) (Miyake et al., 2004, 2005; Huang et al., 2012; Zivcak et al., 2013):

\[ EF(PSI) = \alpha_I \times \phi_{PSI} \times PFD, \]

\[ EF(PSII) = \alpha_{II} \times \phi_{PSII} \times PFD, \]

where PFD was the photosynthetically-active photon flux density of light illuminating a leaf, \( \alpha_I = p \times (1 - dII) \) and \( \alpha_{II} = p \times dII \) the fractions of photon flux distributed to PSI and PSII, dII the fraction of absorbed light distributed to PSII, and \( p \) the fraction of PFD absorbed by leaves.

The electron flow through PSI included noncyclic, pseudocyclic, and cyclic flows, whereas the electron flow through PSII included only noncyclic and pseudocyclic flows (Allen, 2003). Thus, cyclic electron flow [EF(C)] is described as Equation (3) (Miyake et al., 2004, 2005; Huang et al., 2012; Zivcak et al., 2013):

\[ EF(C) = EF(PSI) - EF(PSII). \]

Calculation of EF(C) required values for \( p \) and dII [Equations (1)–(3)]. The value of \( p \) was measured according to Berger et al. (2004), using a standard procedure in IMAGING-PAM M-Series MINI Version (Heinz Walz GmbH) and found to be 0.88 ± 0.01 (\( n = 10 \)).

According to a number of studies (Miyake and Yokota, 2000; Makino et al., 2002; Miyake et al., 2004, 2005), the fraction of absorbed light distributed to PSII was calculated on the basis of the Farquhar, Von Caemmerer and Berry photosynthetic model of Von Caemmerer et al. (2009). According to this model, CO₂ assimilation (A) under electron transport limited conditions is described by the Equation (4):

\[ A = \frac{(C_c - \Gamma^*)}{4(C_c + 2\Gamma^*)} \times EF(PSII) - R_d, \]

where \( \Gamma^* \) is the photosynthetic CO₂ compensation point in the absence of mitochondrial respiration (36.9–39.6 ppm), \( R_d \) the respiration rate in darkness, and \( C_c \) the mole fraction of CO₂ in chloroplasts. Under high [CO₂] (\( C_c \to \infty \)) Equation (4) transforms to Equation (5):

\[ EF(PSII) = 4(A + R_d). \]

Combining Equations (1) and (3) yields:

\[ dII = \frac{4(A + R_d)}{p \times \phi_{PSII} \times PFD}. \]

Equation (6) was in good accordance with the works of Miyake et al. (2004); Miyake et al. (2005). Figure 2A shows dII calculated under different PFDs and an external [CO₂] of 2000 ppm. This condition was electron transport limited because \( A + R_d \) depended on PFD in a linear manner. The value of dII varied from 0.40 to 0.44 and was not significantly dependent on light intensity (\( p > 0.05 \)).

For the purpose of additional dII control, an alternative method for measuring dII was used (Huang et al., 2012) that was simpler than the previous method. It is known that plants have slight cyclic electron flow under low light intensity and that flow magnitude increases with increasing PFD (Miyake et al., 2005; Joliot and Joliot, 2006; Huang et al., 2011; Zivcak et al., 2013). Therefore, EF(PSI) approximately equals EF(PSII) under low light condition (Huang et al., 2012). Taking into account that EF(PSI) = EF(PSII) and using Equations (1) and (2), Equation (7) was deduced:

\[ dII = \frac{1}{\phi_{PSII}/\phi_{PSI} + 1}. \]

Figure 2B shows that dII equaled ∼0.42 under low light conditions (PFD ≤ 65 μmol·m⁻²·s⁻¹). Increases in dII were observed under light intensity equaling 108 μmol·m⁻²·s⁻¹ and greater. This increase probably reflected increased cyclic electron flow, i.e., EF(PSI) ≠ EF(PSII) under moderate and high light conditions. Thus, Equation (7) could also be used for dII calculation under low actinic light (≤ 65 μmol·m⁻²·s⁻¹).
Values for \( d_{II} \) calculated after a 1 h illumination by control actinic light (239 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) were in accordance with the time of VP induction. However, \( d_{II} \) might have depended on the duration of actinic light illumination, which could have influenced results. Values of \( d_{II} \) decreased from about 0.51–0.53 to \( \sim 0.41–0.46 \) with increased light duration \( (t_{1/2} = 20 \text{ min}, \text{ Figure 2C}) \), but it was essentially unchanged from the 60th to 100th min; i.e., \( d_{II} \) was constant in the range of photosynthetic response investigated here.

Initial \( d_{II} \) changes could have been connected with a state-transition and/or PSII damage. State-transition relaxation duration is from minutes to tens of minutes and damage relaxation time in hours (Maxwell and Johnson, 2000; Müller et al., 2001). As a result, state-transition might have been altered under VP rather than with PSII damage. Analysis of \( F_{m}^{\prime} \) relaxation kinetics in darkness after 1 h of actinic light illumination showed that there were insignificant changes in this parameter from the 5th to 40th min (Figure 2D); i.e., there was no essential state-transition under these experimental conditions. In addition, this result supported the observed \( d_{II} \) stability in the time range of VP-induced photosynthetic responses. Thus, taking into account these results, a \( d_{II} \) value of 0.42 was used in the present work.

Far red light, which is absorbed predominantly by PSI, was used as actinic light in an individual series of experiments. In this case, \( EF(PSII) \) was also described by Equation (1); however, far red light absorption by PSII, which is low (Joliot and this case, used as actinic light in an individual series of experiments. In (5 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), but it was essentially unchanged from the 60th to 100th min; i.e., \( d_{II} \) was constant in the range of photosynthetic response investigated here.

\[
EF(PSI) = p \times (1 - d_{II}) \times \phi_{PSI} \times (PFD + FRFD \times \delta),
\]

where \( FRFD \) was the far red light flux density, \( \delta \) the ratio of far red light to actinic light absorption by leaf (730 and 460 nm, respectively), \( PFD = 5 \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \), and \( \delta \) has been calculated from green leaf absorption spectra (Hogewoning et al., 2012) and equaled \( \sim 0.12 \).

Relative \( EF(C) \) was also used in analyses, as the percentage of cyclic electron flow in the total flow. Relative \( EF(C) \) was calculated using Equation (9):

\[
\text{relative } EF(C) = \frac{EF(C)}{EF(C) + EF(PSII)} \times 100%.
\]

RESULTS

PHOTOSYNTHETIC RESPONSES INDUCED BY VARIATION POTENTIAL

Local heating of a leaf induced VP propagation through the stem (Figure 3A). The signal amplitude was 40–90 mV, the duration wide-ranging (from 5 to 60 min), and the profile varied. In the most experiments (\( \sim 80\% \)), VP propagated into leaf lamina with an amplitude of 20–75 mV, with propagation velocities between steam and leaf at 0.02–0.20 cm s\(^{-1}\). In some experiments (\( \sim 20\% \)), only electrical reactions with small amplitude (\( <15 \text{mV} \)) were observed in lamina (Figure 3B).

Figure 4 and Table 1 show that VP reduced CO\(_2\) assimilation rates and electron flows through PSI, increased NPQ and \( \phi_{ND} \), and weakly decreased \( \phi_{NQ} \). The response of \( EF(C) \) comprised two stages: fast inactivation of cyclic flow \( (EF(C)_{\text{min}} - EF(C)_{\text{initial}}) \) and a following slow activation \( (EF(C)_{\text{max}} - EF(C)_{\text{min}}) \). Extremes of \( EF(PSII) \) decrease, \( EF(C) \) fast inactivation, and \( EF(C) \) slow activation were observed at 2.8 ± 0.3,
Table 1 | Photosynthetic parameters and changes induced by VP and [CO2]-lowering.

|                      | VP under [CO2] = 360 ppm | [CO2]-lowering to 10–15 ppm | [CO2]-lowering to 150 ppm | VP under [CO2] = 10–15 ppm |
|----------------------|--------------------------|-----------------------------|---------------------------|---------------------------|
|                      | n                        | A decrease, μmol·m⁻²·s⁻¹    | EF(PSII)                  | EF(C)                      | NPQ                       |
|                      | 17                       | −1.95 ± 0.19*               | 30.1 ± 1.2                | 23.6 ± 1.1*                | −6.5 ± 0.7*               |
|                      | 9                        | −4.08 ± 0.3*               | 33.1 ± 2.2                | 13.5 ± 1.6*                | −19.7 ± 1.3*              |
|                      | 10                       | −1.91 ± 0.20*              | 34.3 ± 1.3                | 25.9 ± 1.1*                | −8.3 ± 0.9*               |
|                      | 11                       | −1.03 ± 0.15*              | 13.7 ± 1.4                | 8.1 ± 1.0*                 | −5.5 ± 0.8*               |
| EF(PSII) initial     | 11.1 ± 1.4               | 11.7 ± 2.3                | 11.3 ± 1.9                | 18.1 ± 1.2                 | 15.0 ± 1.2*               |
| EF(PSII) min         | 8.6 ± 1.2*               | 11.7 ± 2.3                | 11.1 ± 1.8                | 18.6 ± 1.3                 | 15.0 ± 1.2*               |
| EF(C) max            | 14.4 ± 1.1*              | 20.0 ± 1.6*               | 15.3 ± 2.1*               |                          |                          |
| EF(C) peak           | −2.6 ± 0.3*              | 0                         | −0.2 ± 0.1                |                          |                          |
| EF(C) peak − EF(C) initial | 5.8 ± 0.4*       | 8.3 ± 1.1*                | 4.2 ± 0.5*                |                          |                          |
| NPQ initial          | 1.16 ± 0.05              | 1.25 ± 0.14               | 1.29 ± 0.09               | 2.76 ± 0.14               |                          |
| NPQ max              | 1.97 ± 0.08*             | 2.69 ± 0.17*              | 1.86 ± 0.14*              | 3.44 ± 0.16*              |                          |
| NPQ max − NPQ initial | 0.81 ± 0.06*          | 1.34 ± 0.11*              | 0.57 ± 0.08*              | 0.68 ± 0.13*              |                          |
| φND initial          | 0.081 ± 0.009            | 0.071 ± 0.016             | 0.048 ± 0.006             | 0.202 ± 0.005             |                          |
| φND max              | 0.142 ± 0.011*           | 0.182 ± 0.014*            | 0.100 ± 0.012*            | 0.253 ± 0.021*            |                          |
| φND max − φND initial | 0.061 ± 0.008*          | 0.111 ± 0.010*            | 0.033 ± 0.006*            | 0.051 ± 0.009*            |                          |
| φNA initial          | 0.584 ± 0.015            | 0.559 ± 0.027             | 0.563 ± 0.027             | 0.536 ± 0.028             |                          |
| φNA min              | 0.572 ± 0.014*           | 0.531 ± 0.025*            | 0.551 ± 0.028*            | 0.549 ± 0.026             |                          |
| φNA min − φNA initial | −0.012 ± 0.002*       | −0.029 ± 0.007*           | −0.012 ± 0.003*           | 0.013 ± 0.006*            |                          |

*p < 0.05 compared with control, paired Student t-test.

1.0 ± 0.1 and 5.9 ± 0.3 min, respectively, after the start of photosynthetic responses. Fast inactivation and slow activation were probably independent of each other under control conditions because the correlation coefficient (r) between $EF(C)_{\text{min}}$ - $EF(C)_{\text{initial}}$ and $EF(C)_{\text{max}}$ - $EF(C)_{\text{min}}$ was −0.07 (p > 0.05). If only electrical reactions with small amplitudes (<15 mV) were observed in leaf lamina, a photosynthetic response was not developed.

Responses in $EF(C)$ might have been connected with VP-induced changes in dIII. The method for dIII calculation by Huang et al. (2012) could not be used for plants that were stressed after local heating. However, dIII changes must have modified $F_m'$ under dark conditions. VP’s influence on $F_m'$ without actinic light was investigated here. It was shown that VP induced only small decrease of $F_m'$ (3 ± 1%, n = 5), i.e., VP weakly influence dIII.

Inactivation of the photosynthetic dark stage is an initial process of VP-induced photosynthetic responses in pea (Sukhov et al., 2014a,b) and geranium (Sukhov et al., 2012). The present results showed that VP-induced A and $EF(PSII)$ decreases were strongly correlated ($r = 0.78$, p < 0.001). Artificial reduction of dark stage activity through lowering of external [CO2] decreased $EF(PSII)$ and increased $EF(C)$, $\phi_{ND}$ and NPQ (Figure 5), but fast inactivation of cyclic flow was absent. Moreover, VP-induced decreases in A and $EF(PSII)$, increases in $\phi_{ND}$ and NPQ,
Sukhov et al. VP influences cyclic electron flow

FIGURE 5 | [CO2]-lowering-induced changes in photosynthetic light stage parameters and CO2 assimilation (n = 9–10). (A) EF(PSII), EF(C) and NPQ under [CO2]-lowering to 10–15 ppm. (B) φND, φNA, and A under [CO2]-lowering to 10–15 ppm. (C) EF(PSII), EF(C) and NPQ under [CO2]-lowering to 150 ppm. (D) φND, φNA, and A under [CO2]-lowering to 150 ppm. Initial [CO2] was 380 ppm. Arrow, start of [CO2]-lowering.

and slow activation of EF(C) were collectively smaller under low [CO2] conditions (10–15 ppm) than under control conditions (Figure 6, Table 1). In particular, maximum cyclic flow after VP was not distinguishable from the flow before electrical signal propagation under these conditions. However, fast inactivation of cyclic flow induced by VP under low [CO2] was not significantly different from the controls. It should be noted that the correlation coefficient between EF(C)min - EF(C)initial and EF(C)max - EF(C)min was −0.81 (p < 0.01) under low [CO2].

CORRELATION ANALYSIS OF THE MECHANISM OF VP-INDUCED CYCLIC ELECTRON FLOW CHANGES

Changes in EF(PSII) and EF(C) might be different stages of united VP-induced photosynthetic response. This hypothesis was tested by analysis that revealed correlations between photosynthetic parameter changes (Table 2). There were strong connections between VP or [CO2]-lowering-induced reduction of electron flow through PSII and slow activation of cyclic electron flow under control initial conditions. Correlation between decreases in EF(PSII) and fast inactivation of EF(C) was insignificant. Under low [CO2], VP-induced responses of EF(PSII) and EF(C) were weakly connected with each other.

The connection between EF(PSII) decrease and slow EF(C) activation might have been caused by changes in φND. Really, correlation analysis showed that electron flow reductions through PSII induced by VP or [CO2]-lowering was strongly correlated with increases in φND (Table 2). Conversely, φND increases were correlated with slow cyclic electron flow activation under control initial conditions, but the correlation coefficient was insignificant for VP-induced responses under initial low [CO2].

VP-INDUCED CYCLIC ELECTRON FLOW CHANGES UNDER FAR RED LIGHT

Far red light selectively activates PSI and is widely used for cyclic electron flow investigations (Joliot and Johnson, 2011). Here, far red light conditions were used for more detailed investigation of VP’s influence on cyclic electron flow, and Figure 7 and Table 3 show VP-induced photosynthetic responses under far red light. VP decreased A, EF(PSII), and φND and increased φNA and NPQ. VP-induced changes in EF(C) included two stages as described above, inactivation and subsequent activation. Both activation and inactivation were weakly connected with decreased electron flow through PSII. Correlation between EF(PSII) and φND decreases was also insignificant. Conversely, slow EF(C) activation was strongly correlated with decreased φND. Connections
of changes in $\phi_{\text{NA}}$ with decreases in $EF(\text{PSII})$ and increases in $EF(C)$ were insignificant (data not shown). It should be noted that there was a tenuous connection between $EF(C)_{\text{min}} - EF(C)_{\text{initial}}$ and $EF(C)_{\text{max}} - EF(C)_{\text{min}}$ under far red light conditions ($r = -0.65$, $p = 0.06$).

**DISCUSSION**

Electrical signals can inactivate photosynthesis in plants (Koziolek et al., 2004; Krupenina and Bulychev, 2007; Grams et al., 2009; Pavlović et al., 2011; Sukhov et al., 2012, 2013a, 2014a,b). In particular, VP reduces $\phi_{\text{PSII}}$, $\phi_{\text{PSII}}$, and $A$, and increases NPQ in pea (Sukhov et al., 2014a,b). Inactivation of the photosynthetic dark stage appears to be the initiator of photosynthetic responses induced by AP (Pavlović et al., 2011) and VP (Sukhov et al., 2012, 2014a,b). However, direct influence of electrical signals on PSI (Sukhov et al., 2012) and PSII (Pavlović et al., 2011; Sukhov et al., 2014a,b) is also observed.

Our results showed that VP, propagating into a leaf (Figure 3), induced changes in photosynthetic electron flows (Figure 4). VP-induced $EF(\text{PSII})$ decreases were in good accordance with data regarding $\phi_{\text{PSII}}$ decreases caused by electrical signals (see above). However, changes in $EF(C)$, which included fast cyclic electron flow inactivation and its subsequent slow activation, were not previously shown and required detailed analysis.

Here, $d\text{II}$ was shown to be stable in the range of photosynthetic response investigated (Figure 2C), and a state-transition was insignificant under these experimental conditions (Figure 2D). Also, VP weakly influenced $F_m$ without actinic light and, therefore, slightly changed $d\text{II}$. These results revealed that the $EF(C)$ response was not connected with $d\text{II}$ changes.

Slow cyclic electron transport activation induced by VP and $[\text{CO}_2]$-lowering was observed to be connected with decreased $EF(\text{PSII})$ and that this connection was mediated by increased $\phi_{\text{ND}}$ (Table 2). Low activity of the photosynthetic dark stage and noncyclic electron flow are known to be accompanied by high $EF(C)$ (Joliot and Joliot, 2006) as well as $\phi_{\text{ND}}$ value is positively correlated with cyclic flow magnitude (Munekage et al.,

---

**Table 2 | Correlation coefficients between changes in photosynthetic parameters induced by VP and $[\text{CO}_2]$-lowering.**

| Parameters | VP under $[\text{CO}_2] = 360$ ppm | VP under $[\text{CO}_2] = 10–15$ or 150 ppm | VP under $[\text{CO}_2] = 10–15$ ppm |
|------------|-------------------------------|---------------------------------|---------------------------------|
| $n$        | 17                            | 19                              | 11                              |
| $EF(\text{PSII})_{\text{min}} - EF(\text{PSII})_{\text{initial}}$ | 0.11                          | -                               | -0.15                           |
| $EF(C)_{\text{min}} - EF(C)_{\text{initial}}$ | -0.89*                        | -0.85*                          | -0.04                           |
| $EF(\text{PSII})_{\text{max}} - EF(\text{PSII})_{\text{initial}}$ | -0.90*                        | -0.90*                          | -0.73                           |
| $\phi_{\text{ND}}_{\text{max}} - \phi_{\text{ND}}_{\text{initial}}$ | 0.80*                         | 0.77*                           | -0.20                           |
| $EF(C)_{\text{max}} - EF(C)_{\text{min}}$ |                                |                                 |                                 |

*Correlation coefficient is significant ($p < 0.05$), Student t-test.
2002, 2004; Zivcak et al., 2013); however, the mechanisms of these connections remain unclear.

The simplest schema of PSI, based on Klughammer and Schreiber (1994) and Vredenberg and Bulychev (2010) and including $P_{700}$ oxidation and $P_{700}^+$ reduction, was used here for analysis of photosynthetic response mechanisms (Figure 9).

Using this schema, EF(PSII) and EF(C) were described by Equations (10) and (11):
There are two possible mechanisms for the observed connection between increases in $\phi_{ND}$ and $EF(C)$ (Table 2). (i) Increased $k_C$ is the main mechanism for increasing cyclic electron flow induced by VP or [$\text{CO}_2$]-lowering under control conditions. This can be caused by activation of any stage of cyclic electron flow, with the exception of $P_{700}^+$ reduction, and increased concentrations of reduced plastocyanin. In this case, $k_C$ increases contribute to transformation of $P_{700}^+$ into $P_{700}$ and thereby lowers $\phi_{ND}$ (Figure 9). Thus, decreased $\phi_{ND}$, increased photosynthetic cyclic electron flow, and negative correlation between changes in $EF(C)$ and $\phi_{ND}$ must appear that are contrary to the present experimental results (Figures 4, 5, Tables 1, 2). (ii) Decreases in $k_L$ suppress transformation of $P_{700}^+$ into $P_{700}$ and/or increases in $k_{hv}$ activate conversion of $P_{700}$ into $P_{700}^+$ that then increases $\phi_{ND}$ (Figure 9). According to Equation (11), increased $\phi_{ND}$ must activate cyclic electron flow. As a result, $\phi_{ND}$ and $EF(C)$ increase and, in this case, a positive correlation between changes in $EF(C)$ and $\phi_{ND}$ should be observed. The second variant was in perfect accordance with the present experimental results. Thus, the following chain of events is supposed: VP $\rightarrow$ $\phi_{ND}$ increase $\rightarrow$ $EF(C)$ growth.

Similar analysis can be employed for examining connections between increased $\phi_{ND}$ and reduced $EF(PSII)$ (Figures 4, 5, Tables 1, 2). The positive influence of $k_C$ changes was not probable because increased $k_C$ decreases $\phi_{ND}$ (see above) and decreased $k_C$ decreases $EF(C)$ (Equation 11). Increased $k_{hv}$ appeared to increase $\phi_{ND}$ (Figure 9); however, if $\phi_{ND}$ increased and $k_L$ was not changed, then $EF(PSII)$ must increase (Equation 10), which is contrary to experimental results. Moreover, the main reason for $k_{hv}$ changes was modification of $dII$, but $dII$ was probably not affected by VP. Alternatively, decreased $k_{hv}$ suppressed transformation of $P_{700}^+$ into $P_{700}$ and increased $\phi_{ND}$ (Figure 9), while also lowering $EF(PSII)$ (Equation 10). The $k_L$ decrease could have been caused by inactivation of any stage of noncyclic electron transport, which preceded PSI, and which induced decreased concentrations of reduced plastocyanin. This last variant was in a good accordance with the experimental results obtained here (decreased $EF(PSII)$, increased $\phi_{ND}$, and negative correlation between changes in $EF(PSII)$ and $\phi_{ND}$). Decreased $k_L$ reflected decreased electron flow from PSI. Thus, the chain of events was extended to yield: VP $\rightarrow$ $\phi_{ND}$ increase $\rightarrow$ $EF(PSII)$ decrease $\rightarrow$ $\phi_{ND}$ increase $\rightarrow$ $EF(C)$ growth.

The present results indicate that decreased $EF(PSII)$ reflects VP-induced lowering of $\phi_{PSII}$ (Figure 4, Table 1). According to published data (Pavlović et al., 2011; Sukhov et al., 2012, 2014a,b) and the present results, this decrease in $EF(PSII)$ was mainly

---

**FIGURE 8** | Fluorescence non-photochemical quenching (NPQ) was plotted against relative cyclic electron flow (relative $EF(C)$) under different $\text{CO}_2$ concentrations. Relative $EF(C)$ and NPQ were taken from the Tables 1, 4 (unheated plants).

**FIGURE 9** | A simple schema of PSI states, based on Klughammer and Schreiber (1994) and Vredenberg and Bulychev (2010). $P_{700}$ and $P_{700}^+$, oxidized and reduced forms of primary electron donor in PSI, respectively; $A$ and $A^-$, oxidized and reduced forms PSI acceptor, respectively; parameter $k_{ps}$ = $\gamma$ × $PFD$ × $p$ × (1 − $dII$), velocity constant of light-dependent $P_{700}$ oxidation, with $\gamma$, proportionality coefficient; parameters $k_L = k_{PC} × [PC^{-}]$ and $k_C = k_{PC} × [PC^{-}]_C$, velocity constants of electron flow through PS II (mainly noncyclic) and cyclic electron flow, respectively; $k_{pc}$, velocity constant of plastocyanin oxidation by $P_{700}^+$; $[PC^{-}]_L$, concentration of reduced plastocyanin, participating in flow through PS II; $[PC^{-}]_C$, concentration of reduced plastocyanin, participating in cyclic flow; $k_A$, velocity constant of PSI acceptor side oxidation being connected with cyclic, noncyclic and pseudocyclic flows; $\phi_{ND}$, portion of $P_{700}^+A^-$ and $P_{700}^+A$ (Klughammer and Schreiber, 2008); and 1 − $\phi_{ND}$, portion of $P_{700}A^-$ and $P_{700}A$. 

---

www.frontiersin.org
Local heating

VP generation and propagation into leaf

H⁺-ATPase inactivation in plasmalemma of mesophyll cell

Apoplastic pH increase

pH decrease in cytoplasm, chloroplast stroma and lumen

Photosynthetic dark stage inactivation

NADH : NAD⁺ increase

ATP : ADP increase

Inactivation of H⁺-ATP synthase

Decrease in noncyclic electron flow through acceptor side of PSII

Increase in trans-thylakoid ΔpH

Decrease in electron flow through PSII

P⁺ concentration growth (ϕND increase)

Slow cyclic electron flow activation

Fast cyclic electron flow inactivation

Changes in pH gradient on thylakoid membrane, NPQ increase, contribution to ATP synthesis, regulation of reactive oxygen species production, etc

Growth of photosynthetic machinery resistance to stressors

Changes in ferredoxin-NADP⁺ reductase localization

(Continued)
induced by photosynthetic dark stage inactivation. In support of this conclusion, changes in A and EF(PSII) were strongly correlated and reduced CO2 assimilation rate induced by [CO2]-lowering decreased electron flow through PSII was similar to VP’s effect. In addition, VP-induced EF(PSII) changes under low [CO2] conditions were smaller than changes under control conditions. However, VP-induced EF(PSII) decreases were not absent under low [CO2]. Considering that decreased A in these experiments (−1.08 ± 0.21 μmol·m−2·s−1) was indistinguishable from a VP-induced respiration response (−1.10 ± 0.20 μmol·m−2·s−1, Sukhov et al., 2014a), it was concluded that VP could also have suppressed electron flow through PSII without photosynthetic dark stage inactivation. Increased NPQ was a potential mechanism for VP’s influence on PSII because its response is not dependent on electrical signal-induced decrease of CO2 assimilation (Sukhov et al., 2014a). As a result, the following chain of events was proposed here: VP → ... inactivation of photosynthetic dark stage and NPQ increase → EF(PSII) decrease → <sub>ND</sub> increase → EF(C) increase.

VP-connected proton flux from apoplast to cytoplasm, stroma, and lumen is a possible mechanism for initial induction of a photosynthetic response, including decreased <sub>PSII</sub> (Gams et al., 2009; Sukhov et al., 2014a). It is known that VP generation is connected with transient H<sup>+</sup>-ATPase inactivation and proton influx (Stahlberg et al., 2006; Sukhov et al., 2013b), which changes intracellular pH (Gams et al., 2009; Sukhov et al., 2014a). However, decreased intracellular pH can suppress PSII photosynthetic activity and induces NPQ (Gams et al., 2009; Bulychev et al., 2013a,b; Sukhov et al., 2013a, 2014a). Taking into account these facts, it can be proposed that VP → H<sup>+</sup> influx → inactivation of photosynthetic dark stage and NPQ growth → EF(PSII) decrease → <sub>ND</sub> increase → EF(C) growth. Figure 10 shows this possible mechanism of VP influence on cyclic electron flow in more detail.

It should be noted that photosynthetic dark stage inactivation can increase NADH:NADF<sup>+</sup> (Pavlović et al., 2011) that decreases noncyclic electron flow through acceptor side of PSI and may stimulate cyclic electron flow. However, this process (decrease in <sub>ND</sub> in Figure 9) induces increase in P<sub>700</sub>A<sup>-</sup> (<sub>ND</sub>A) that was not observed in experiments with varied CO2 concentrations (Table 1). Thus, change in NADH:NADF<sup>+</sup> in unlikely to be main mechanism of EF(C) growth, but it can play minor role in the process.

VP-induced responses under far red light indicated that another mechanism of cyclic electron flow activation, not connected with noncyclic flow changes, also participated in the photosynthetic response. In this case, EF(C) activation and decreased <sub>ND</sub> were observed and correlation between these parameters was negative (Table 3). Considering Figure 9 and Equation (11), it was concluded that such effects could have been caused by increased <sub>C</sub>. The mechanism of EF(C) activation was not clarified here, but the magnitude of the activation correlated with the magnitude of fast inactivation of cyclic electron flow; i.e., similar mechanisms for both processes were probable. It is known that pH decreases can change ferredoxin-NADP<sup>+</sup> reductase localization (Alte et al., 2010; Benz et al., 2010); in addition, reductase possibly participates in cyclic electron flow (Joliot and Johnson, 2011). Considering this information, it was speculated that stromal pH changes influenced ferredoxin-NADP<sup>+</sup> reductase localization and induced a two-stage EF(C) response, including inactivation and subsequent activation of cyclic flow (Figure 7). VP-induced inactivation of the acceptor side of PSI, which was not connected with decreased photosynthetic dark stage activity (Sukhov et al., 2012) and can caused by changes in ferredoxin-NADP<sup>+</sup> reductase localization (Sukhov et al., 2014a), supported this hypothesis.

Thus, VP increased cyclic electron flow in an absolute (Tables 1, 3) and relative (Table 3) manner. A physiological role for this response could have been connected with increased photosynthetic machinery resistance to environmental stressors. It is known that cyclic electron flow can maintain a high proton gradient on thylakoid membrane and, thereby, contributes to ATP synthesis and NPQ increases (Zhang and Sharkey, 2009; Joliot and Johnson, 2011). Also, cyclic electron flow protects PSI and can regulate reactive oxygen species production by photosynthetic electron transfer chain (Rumeau et al., 2007; Roach and Krieger-Liszkay, 2014). It is known that electrical signals exert influence on the resistance of photosynthetic machinery to stressors in higher plants (Retivin et al., 1999; Sukhov et al., 2014b). In particular, VP increases PSI resistance to heating in pea (Sukhov et al., 2014b), and it was supposed here that VP-induced activation of cyclic electron flow participated in this increased resistance.
Stimulation of NPQ is important mechanism of cyclic electron flow influence on photosynthetic machinery resistance to stressors (Munekage et al., 2002, 2004; Zhang and Sharkey, 2009; Joliot and Johnson, 2011). This stimulation was observed under moderate actinic light (about 200 μmol m−2 s−1) (Munekage et al., 2002, 2004). Miyake et al. (2004, 2005) showed that NPQ was strongly depended on cyclic electron flow when EF(PSI) / EF(PSII) > 1.2–1.3. Table 4 shows that VP activated relative EF(C) from 27 to 38% in pea (EF(PSI) / EF(PSII) increased from 1.37 to 1.61), i.e., activation of cyclic electron flow can influence NPQ. Figure 8 shows that NPQ and relative EF(C) were linearly connected that can be interpreted according to Miyake et al. (2004, 2005) as stimulation of NPQ by cyclic electron flow. Positive correlation between NPQ and relative EF(C) under control conditions also supports this hypothesis. Thus, it may be supposed that VP-induced cyclic electron flow activation stimulates NPQ and, thereby, increases of photosynthetic machinery resistance.

**ACKNOWLEDGMENT**

This work was supported by the Russian Scientific Fund (Project No. 14-26-00098).

**REFERENCES**

Allen, J. F. (2003). Cyclic, pseudocyclic and noncyclic photophosphorylation: new links in the chain. *Trends Plant Sci.* 8, 15–19. doi: 10.1016/S1360-1385(02)00006-7

Alte, F., Stengel, A., Benz, J. P., Petersen, E., Soll, J., Groll, M., et al. (2010). Ferredoxin:NADPH oxidoreductase is recruited to thylakoids by binding to a polyproline type II helix in a pH-dependent manner. *Proc. Natl. Acad. Sci. U.S.A.* 107, 19260–19265. doi: 10.1073/pnas.09124107

Benz, J. P., Stengel, A., Lintala, M., Lee, Y. H., Weber, A., Philippar, K., et al. (2010). Arabidopsis Tic62 and ferredoxin-NAD(P)H oxidoreductase form light-regulated complexes that are integrated into the chloroplast redox poise. *Plant Cell* 21, 3965–3983. doi: 10.1101/pcp.096815

Berger, S., Papadopoulos, M., Schreiber, U., Kaiser, W., and Roitsch, T. (2004). Complex regulation of gene expression, photosynthesis and sugar levels by pathogen infection in tomato. *Physiol. Plant.* 122, 419–428. doi: 10.1111/j.1399-3054.2004.00433.x

Brenner, E. D., Stahlberg, R., Mancuso, S., Vivanco, J., Baluska, F., and Van Volkenburgh, E. (2006). Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci.* 11, 413–419. doi: 10.1016/j.trendsplant.2006.06.009

Bukhov, N. G., Wiese, C., Neimanis, S., and Heber, U. (1999). Heat sensitivity of chloroplasts and leaves: leakage of protons from thylakoids and reversible activation of cyclic electron transport. *Photosyn. Res.* 59, 81–93.

Bulychev, A. A., Cherkashin, A. A., Rubin, A. B., Vredenberg, W. I., Zykov, V. S., and Müller, S. C. (2001). Comparative study on photostatic activity of chloroplasts in acid and alkaline zones of Chara corallina. *Bioelectrochemistry* 53, 225–232. doi: 10.1016/S0300-4588(01)00096-4

Bulychev, A. A., and Komarova, A. V. (2014). Long-distance signal transmission and regulation of photosynthesis in characean cells. *Biochemistry (Moscow)* 79, 273–281. doi: 10.1134/S000627914030134

Bulychev, A. A., Komarova, A. V., and Rubin, A. B. (2013b). Fluorescence transients in chloroplasts of Chara corallina cells during transmission of photoinduced signal with the streaming cytoplasm. * Russ. J. Plant Physiol.* 60, 33–40. doi: 10.1134/S1021443712060039

Davies, E., and Stankovic, B. (2006). “Electrical signals, the cytoskeleton, and gene expression: a hypothesis on the coherence of the cellular responses to environmental insult,” in *Communication in Plants. Neuronal Aspects of Plant Life*, eds F. Baluška, S. Mancuso, and D. Volkmann (Berlin-Heidelberg: Springer-Verlag), 309–320.

Dziubinska, H. (2003). Ways of signal transmission and physiological role of electrical potential in plants. *Acta Soc. Bot. Pol.* 72, 309–318. doi: 10.5586/asp.2003.040

Felle, H. H., and Zimmermann, M. R. (2007). Systemic signaling in barley through action potentials. *Planta* 226, 203–214. doi: 10.1007/s00425-006-0458-y

Fromm, J., and Lautner, S. (2012). “Generation, transmission, and physiological effects of electrical signals in plants,” in *Plant Electrophysiology. Signaling and Responses*, ed A. G. Volkov (Heidelberg-New York-Dordrecht-London: Springer), 207–232. doi: 10.1007/978-3-642-29110-4_8

Galle, A., Lautner, S., Flexas, J., Ribas-Carbo, M., Hansøn, D., Roeggen, J., et al. (2013). Photosynthetic responses of soybean (*Glycine max L.*) to heat-induced electrical signalling are predominantly governed by modifications of mesophyll conductance for CO2. *Plant Cell Environ.* 36, 542–552. doi: 10.1111/j.1365-3042.2012.02594.x

Grams, T. E. E., Lautner, S., Felle, H. H., Matyssek, R., and Fromm, J. (2009). Heat-induced electrical signals affect cytoplasmic and apoplastic pH as well as photosynthesis during propagation through the maize leaf. *Plant Cell Environ.* 32, 319–326. doi: 10.1111/j.1365-3040.2008.01922.x

Hogewoning, S. W., Wientjies, D., Douwstra, P., Trouwborst, G., van Ieperen, W., Croce, R., et al. (2012). Photosynthetic quantum yield dynamics: from photosystems to leaves. *Plant Cell* 24, 1921–1933. doi: 10.1105/tpc.112.097972

Huang, W., Yang, S. J., Zhang, S. B., Zhang, J. L., and Cao, K. F. (2012). Cyclic electron flow plays an important role in photoprotection for the resurrection plant *Piriqueta rufescens* under drought stress. *Plant Cell Environ.* 25, 819–828. doi: 10.1111/j.1365-3040.2011.02543.x

Hwang, W., Zhang, S. B., and Cao, K. F. (2011). Cyclic electron flow plays an important role in photoprotection of tropical trees illuminated at temporal chilling temperature. *Plant Cell Physiol.* 52, 297–305. doi: 10.1093/pcp/pcq166

Joliot, P., and Johnson, G. N. (2011). Regulation of cyclic and linear electron flow in higher plants. *Proc. Natl. Acad. Sci. U.S.A.* 108, 15317–15322. doi: 10.1073/pnas.1110189108

Koziolek, C., Grams, T. E. E., Schreiber, U., and Fromm, J. (2004). Transient knockout of photosynthesis mediated by electrical signals. *New Phytol.* 161, 715–722. doi: 10.1111/j.1469-8137.2004.00985.x

Krupenina, N. A., and Bulychev, A. A. (2007). Action potential in a plant cell of Chara corallina. *Bioelectrochemistry* 72, 309–318. doi: 10.1016/j.bielet.2006.07.004

Maxwell, K., and Johnson, G. N. (2000). Chlorophyll fluorescence – a practical guide. *J. Exp. Bot.* 51, 659–668. doi: 10.1093/jxb/51.345.659

Maxwell, K., and Johnson, G. N. (2000). Chlorophyll fluorescence – a practical guide. *J. Exp. Bot.* 51, 659–668. doi: 10.1093/jxb/51.345.659

Miyake, C., and Yoneyama, A. G. Volkov (Berlin-Heidelberg: Springer-Verlag), 333–349.

Miyake, C., Shinzaki, Y., Miyata, M., and Tomizawa, K. (2004). Enhancement of cyclic electron flow around PSI at high light and its contribution to quenching of Chl fluorescence. *Plant Cell Physiol.* 46, 629–637. doi: 10.1093/pcp/pcp1067

Miyake, C., Shizhinskiy, Y., Miyata, M., and Tomizawa, K. (2004). Enhancement of cyclic electron flow around PSI at high light and its contribution to the induction of non-photochemical quenching of Chl fluorescence in intact leaves of tobacco plants. *Plant Cell Physiol.* 45, 1426–1433. doi: 10.1093/pcp/pch163
Pavlović, A., Slováková, L., Pandolfi, C., and Mancuso, S. (2011). On the mechanism underlying photosynthetic limitation upon trigger hair irritation in the carnivorous plant Venus flytrap (Dionaea muscipula Ellis). J. Exp. Bot. 62, 1991–2000. doi: 10.1039/jxb/er0404

Retivin, V. G., Opritov, V. A., and Fedulina, S. B. (1997). Generation of action potential induces preadaptation of Cucurbita pepo L. stem tissues to freezing injury. Russ. J. Plant Physiol. 44, 432–442.

Retivin, V. G., Opritov, V. A., Lobov, S. A., Tarakanov, S. A., and Khudyakov, V. A. (1999). Changes in the resistance of photosynthesizing cotyledon cells of pumpkin seedlings to cooling and heating, as induced by the stimulation of the root system with KCl solution. Russ. J. Plant Physiol. 46, 689–696.

Roach, T., and Krieger-Lizskay, A. (2014). Regulation of photosynthetic electron transport and photoinduction. Curr. Protein Pept. Sci. 15, 351–362. doi: 10.2174/1389203715666140327105143

Rumeau, D., Peltier, G., and Cournac, L. (2007). Chlororespiration and cyclic electron flow around photosystem I and plant stress response. Plant Cell Environ. 30, 1041–1051. doi: 10.1111/j.1365-3040.2007.01675.x

Schönknecht, G., Neimanns, S., Katona, E., Gerst, U., and Heber, U. (1995). Relationship between photosynthetic electron transport and pH gradient across the thylakoid membrane in intact leaves. Proc. Natl. Acad. Sci. U.S.A. 92, 12185–12189. doi: 10.1073/pnas.92.26.12185

Stahlberg, R., Robert, E., Clandon, R. E., and van Volkenburgh, E. (2006). “Slow wave potentials – a propagating electrical signal unique to higher plants,” in Communication in Plants. Neuronal Aspects of Plant Life, eds F. Baliuski, S. Mancuso, and D. Volkman (Berlin-Heidelberg: Springer-Verlag), 291–309.

Sukhov, V., Akinchits, E., Katicheva, L., and Vodeneev, V. (2013b). Simulation of variation potential in higher plant cells. J. Membr. Biol. 246, 287–296 doi: 10.1007/s00232-013-9528-9

Sukhov, V., Orlova, L., Mysyagin, S., Sinitsina, J., and Vodeneev, V. (2012). Analysis of the photosynthetic response induced by variation potential in geranium. Planta 235, 703–712. doi: 10.1007/s00425-011-1529-2

Sukhov, V., Sherstneva, O., Surova, L., Katicheva, L., and Vodeneev, V. (2014a). Proton cellular influx as a probable mechanism of variation potential influence on photosynthesis in pea. Plant Cell Environ. 37, 2532–2541. doi: 10.1111/pce.12321

Sukhov, V. S., Sherstneva, O. N., Surova, L. M., Rumiantsev, E. A., and Vodeneev, V. A. (2013a). Influence of a variation potential on photosynthesis in pumpkin seedlings (Cucurbita pepo L.). Biochemistry 58, 361–365. doi: 10.1134/S0006350913030184

Sukhov, V., Surova, L., Sherstneva, O., and Vodeneev, V. (2014b). Influence of variation potential on the resistance of the photosynthetic machinery to heating in pea. Physiol. Plant. 152, 773–783. doi: 10.1111/ppl.12208

Sukhov, V., and Vodeneev, V. (2009). A mathematical model of action potential in cells of vascular plants. J. Membr. Biol. 232, 59–67. doi: 10.1007/s00232-009-9218-9

Trebacz, K., Dzubielska, H., and Krol, E. (2006). “Electrical signals in long-distance communication in plants,” in Communication in Plants. Neuronal Aspects of Plant Life, eds F. Baliuski, S. Mancuso, and D. Volkmann (Berlin-Heidelberg: Springer-Verlag), 277–290.

Vodeneev, V., Akinchits, E. K., Orlova, L. A., and Sukhov, V. S. (2011). The role of Ca2+, H+, and Cl– ions in generation of variation potential in pumpkin plants. Russ. J. Plant Physiol. 58, 974–981. doi: 10.1134/S1021443711050256

Vodeneev, V., Orlova, A., Morozova, E., Orlova, L., Akinchits, E., Orlova, O., et al. (2012). The mechanism of propagation of variation potentials in wheat leaves. J. Plant Physiol. 169, 949–954. doi: 10.1016/j.jplph.2012.05.026

Volkov, A. G. (2000). Green plants: electrochemical interfaces. J. Electroanal. Chem. 483, 150–156. doi: 10.1016/S0022-0728(99)00497-0

Volkov, A. G., Adesina, T., Markin, V. S., and Jovanov, E. (2008). Kinetics and mechanism of Dionaea muscipula trap closing. Plant Physiol. 146, 694–702. doi: 10.1104/pp.107.108241

Von Caemmerer, S., Farquhar, G., and Berry, J. (2009). “Biochemical model of C3 photosynthesis, in Photosynthesis In Silico. Understanding Complexity from Molecules to Ecosystems, eds A. Laikis, L. Nedbal, and Govindjee (Dordrecht: Springer), 209–230.

Von Caemmerer, S., and Farquhar, G. D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376–387. doi: 10.1007/BF00384257

Vredenberg, W. J., and Bulychev, A. A. (2010). Photoelectrochemical control of the balance between cyclic- and linear electron transport in photosystem I. Algorithm for P700+ induction kinetics. Biochim. Biophys. Acta 1797, 1521–1532. doi: 10.1016/j.bbmbio.2010.03.019

Werdan, K., Heldt, H. W., and Milovanvce, M. (1975). The role of pH in the regulation of carbon fixation in the chloroplast stroma. Studies on CO2 fixation in the light and dark. Biochim. Biophys. Acta 396, 276–292. doi: 10.1016/0005-2728(75)90041-9

Wolsiuk, R. A., Ballicora, M. A., and Haglelin, K. (1993). The reductive pentose phosphate cycle for photosynthetic CO2 assimilation: enzyme modulation. FASEB J. 7, 622–637.

Zhang, R., and Sharkey, T. D. (2009). Photosynthetic electron transport and proton flux under moderate heat stress. Photosyn. Res. 100, 29–43. doi: 10.1007/s11120-009-9420-8

Zivcak, M., Breštic, M., Balatova, Z., Drevanakova, P., Olsovka, K., Kalaji, H. M., et al. (2013). Photosynthetic electron transport and specific photoprotective responses in wheat leaves under drought stress. Photosyn. Res. 117, 529–546. doi: 10.1007/s11120-013-9885-3

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 23 September 2014; accepted: 11 December 2014; published online: 07 January 2015.

Citation: Sukhov V, Surova L, Sherstneva O, Katicheva L and Vodeneev V (2015) Variation potential influence on photosynthetic cyclic electron flow in pea. Front. Plant Sci. 5:766. doi: 10.3389/fpls.2014.00766

This article was submitted to Plant Biophysics and Modeling, a section of the journal Frontiers in Plant Science.

Copyright © 2015 Sukhov, Surova, Sherstneva, Katicheva and Vodeneev. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.