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The effect of additional red irradiation on the photosynthetic apparatus of *Pisum sativum*

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Abstract

Pisum sativum (L.) plants were grown under "white" luminescent lamps, W [45 μmol(quantum) $m^{-2} s^{-1}$] or under the same irradiation supplemented with narrow spectrum red light-emitting diodes (LEDs), RE [λ_{max} = 660 nm, $\Delta\lambda$ = 20 nm, 40 μmol(quantum) $m^{-2} s^{-1}$]. Significant differences in the chlorophyll (Chl) *a* fluorescence parameters, degree of State 1–State 2 transition, and the pigment-protein contents were found in plants grown under differing spectral composition. Addition of red LEDs to the "white light" resulted in higher effective quantum yield of photosystem 2 (PS2), *i.e.* F'_v/F'_m, linear electron transport (ϕ_{PS2}), photochemical quenching (q_P), and lower non-photochemical quenching (q_N as well as NPQ). The RE plants were characterised by higher degree State 1–State 2 transition, *i.e.* they were more effective in radiant energy utilisation. Judging from the data of "green" electrophoresis of Chl containing pigment-protein complexes of plants grown under various irradiation qualities, the percentage of Chl in photosystem 2 (PS2) reaction centre complexes in RE plants was higher and there was no difference in the total Chl bound with Chl-proteins of light-harvesting complexes (LHC2). Because the ratio between oligomeric and monomeric LHC2 forms was higher in RE plants, we suggest higher LHC2 stability in these ones.

Additional key words: chlorophyll; light-emitting diodes; light-harvesting complex; non-photochemical quenching; photosystem 2; *Pisum sativum*; photochemical quenching; spectral composition of radiation.

Introduction

In many plant species, the composition of photosynthetic apparatus is modified in response to different radiation quality and irradiance (Leong *et al.* 1984, Walters *et al.* 1994). Major changes in the organisation and composition of the photosynthetic apparatus in response to varying irradiance are well described: high-irradiance-grown plants exhibit a higher irradiance-saturated rate of photosynthesis which correlates with increased contents of ATP synthase, electron transport components, and enzymes of the Calvin cycle; low-irradiance-grown plants show much higher contents of the light-harvesting complexes (LHC1, LHC2) of photosystems (PS) 1 and 2, which correlates with an increase in the proportion of thylakoid membranes found in the appressed state (Lichtenthaler *et al.* 1982, Anderson and Osmond 1987). In contrast, less information exists about plant responses to differences in spectral composition of radiation. Plants grown under radiation absorbed preferentially by PS1 or PS2 show differences in the stoichiometry of the two photosynthetic reaction centres (PS1 and PS2) and pigment contents (Chow *et al.* 1990, Walters *et al.* 1994). Although the phytochrome family of proteins is involved in sensing of red and far-red radiation in plants (Franklin *et al.* 2003) there are no comprehensive evidences for the participation of phytochrome in the composition of the photosynthetic apparatus (Lopez-Juez *et al.* 1990, Smith *et al.* 1993).

At the same time the effect of changed radiation quality on functional state of the photosynthetic apparatus requires thorough analysis in view of optimisation of plant growing and increasing their productivity in greenhouses. Spectral composition of the luminescent lamps used for growing plants in greenhouses includes all regions of visible radiation. However, spectrum of most of them has lower percent of radiation in red region (650–700 nm) than Sun radiation (Protasova *et al.* 1990).

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Abbreviations: Chl, chlorophyll; F_0, ground value of fluorescence; F_v, F_m, variable and maximum fluorescence in the dark-adapted state, respectively; F_v/F_m, maximum quantum efficiency of PS2 photochemistry; F'_v/F'_m, maximum quantum efficiency of PS2 under given irradiance; LEDs, light-emitting diodes; LHC2, light-harvesting complexes of PS2; PS, photosystem; Q_A, primary quinone of PS2; q_P, q_N, photochemical and non-photochemical quenching of chlorophyll fluorescence, respectively; RE, red-enriched "white growth light"; W, "white growth light"; ϕ_{PS2}, quantum efficiency of linear electron transport through PS2.

Addition of appropriate lamps or light filters to the "white light" (W) of luminescent lamps can improve the quality of artificial sources and increase the amount of radiation in red region. The addition of red lamps to W leads to changes in the morphological and biochemical characteristics of plants (Astaphurova *et al*. 2001). Lamps and filters are not enough effective as they cover wide spectral regions. LEDs nowadays represent innovative artificial radiation sources. They can be used for providing a concentrated effect in certain PAR regions due to the huge radiation ability in narrow spectral ranges. Moreover, LEDs are potential radiation sources for growing plants in spaceflight systems because of their safety and rugged design, small mass and volume, narrow spectral output, wavelength specificity, and longevity. Appropriate combinations of red and blue LEDs have great potential for use as radiation source to drive photosynthesis due to the ability to harvest irradiance output near the peak absorption regions of chlorophyll, Chl (Goins *et al*. 1997). Since changes in the functional state of the photosynthetic apparatus occurring by the addition of red LEDs to the fluorescent "white" lamps have not been adequately studied, our research directly addresses this important issue. The aim of this work was to study functional changes of photosynthetic apparatus of pea plants grown under "white" luminescent lamps with or without red addition, in particular pigment-protein content of isolated chloroplasts, Chl fluorescence induction (FI) parameters, and the degree of State 1–State 2 transition in pea leaves.

Materials and methods

Pea plants (*Pisum sativum* L.) were grown in Knop medium for 14 d (14/10 h light/dark photoperiod) under W of luminescent lamps *LB-40* (*GRL Factory*, Poltava, Ukraine) at 45 μmol(quantum) m^{-2} s^{-1} of photon flux density (PFD) and under W supplemented with red LEDs [*L-53SRC-F*, λ_{max} = 660 nm, $\Delta\lambda$ = 20 nm, 40 μmol(quantum) m^{-2} s^{-1}; *Kingbright*, Germany]. All plants were grown at 20–22 °C. Spectral radiation energy distribution of the luminescent lamp *LB-40* (*line*) and "'red"' LEDs *L-53SRC-F* (*dotted line*) is presented on Fig. 1. PFD was measured by using a quantum sensor *US-SQS*, *LI-250* (*LI-COR*, USA).

Chl fluorescence was measured using a *XE-PAM* fluorometer (*Walz*, Germany). Minimal fluorescence (F_0) of dark-adapted leaves was determined at low PFD [near 0.2 μmol(quantum) m^{-2} s^{-1}]. Maximal fluorescence (F_m) of dark-adapted and light-adapted (F'_m) leaves was detected at saturating irradiance (1 s) of halogen lamps [5 000 μmol(quantum) m^{-2} s^{-1}]. "Actinic lights" used were 500 and 1 500 μmol(quantum) m^{-2} s^{-1} PFD. FI parameters q_P, q_N, NPQ, ϕ_{PS2}, F_v/F_m, and F'_v/F'_m were calculated as described in Schreiber *et al.* (1986), Bilger and Björkman (1990), Genty *et al.* (1989), and Maxwell *et al.* (2000).

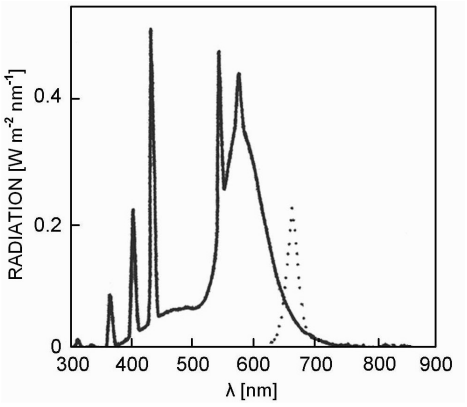

Fig. 1. Spectral radiation energy distribution of the luminescent lamp *LB-40* (*line*) and "red" LEDs *L-53SRC-F* (*dotted line*).

State 1–State 2 transitions were estimated by fluorescence changes of leaves according to Hodges and Barber (1983) with some modifications. The leaves were preirradiated for 10 min with non-modulated far-red radiation (radiation 1) (>700 nm, 10 μmol m^{-2} s^{-1}) in order to oxidise the plastoquinone (PQ) pool. Fluorescence measurements were initiated by turning on a modulated blue-green radiation (radiation 2) and turning off the non-modulated radiation 1. Radiation 2 was transmitted by an interference filter (480 nm, 3.5 μmol m^{-2} s^{-1}). The efficiency of radiation utilisation (vF) was estimated as a ratio (State 1 level – State 2 level)/State 2 level as in Lichtenthaler *et al*. (1981). A half-time ($t_{½}$) parameter which evaluates the degree of State transitions was calculated according to Hodges (1983). Results were calculated using *Excel Origin* and *UT60E Interface Program V2.02*.

Chl-protein complexes were analysed by SDS-PAGE under non-denaturing conditions as described in Anderson (1980). Chl content was measured in 80 % acetone according to Arnon (1949). After electrophoresis the gels were analysed using *TotalLab V1.10* program.

Results are the averages from three independent experiments, each of them was analysed four times, standard errors of mean were always less than 5 %.

Results

Chl fluorescence parameters are presented in Table 1. Parameter F_v/F_m, known as a potential maximum quantum yield of PS2 photochemistry, was almost equal in W and RE plants. F_v/F_m is used to estimate the PS2 efficiency in dark-adapted leaves when the PQ pool is fully oxidised and F'_v/F'_m, effective quantum yield of PS2,

Table 1. Chlorophyll fluorescence induction parameters of pea plants grown under white (W) or red-enriched (RE) radiation. Means of 3 biological and 5 analytical repeats ± SEM.

	"Actinic light" [μmol(quantum) m^{-2} s^{-1}]			
	500		1 500	
	W	RE	W	RE
F_v/F_m	0.744±0.001	0.755±0.001	0.749±0.001	0.766±0.010
q_P	0.823±0.009	0.859±0.008	0.412±0.041	0.571±0.002
NPQ	1.080±0.113	0.744±0.190	1.660±0.107	1.440±0.082
q_N	0.679±0.030	0.551±0.094	0.832±0.022	0.791±0.028
F'_v/F'_m	0.489±0.018	0.563±0.057	0.331±0.031	0.386±0.045
ϕ_{PS2}	0.404±0.019	0.484±0.054	0.143±0.030	0.227±0.019
F_s/F_m	0.042±0.004	0.036±0.003	0.081±0.004	0.054±0.002

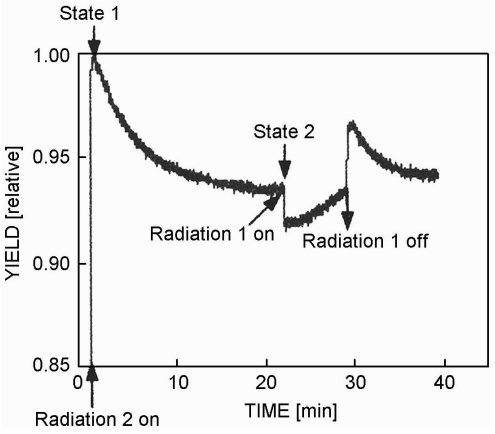

Fig. 2. Relative changes in the yield of modulated fluorescence during State transitions.

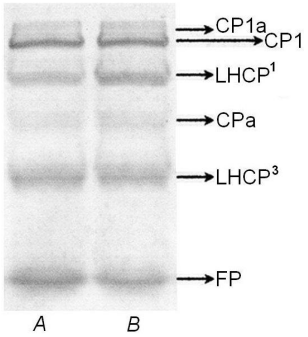

Fig. 3. The SDS-PAGE of chlorophyll-protein complexes of "white" (*A*) and red-enriched (*B*) plants. CP1a – PS1 reaction centre complex, partly containing its light-harvesting complex 1 (LHC1); CP1 – PS1 reaction centre complex without LHC1; CPa – PS2 reaction centre complex; $LHCP^1$ – oligomeric form of LHC2; $LHCP^3$ – monomeric form of LHC2; FP – free pigment.

is used to evaluate the maximum efficiency of PS2 photochemistry at a given irradiance when the PQ pool is partly reduced. F'_v/F'_m was higher in RE plants under both "actinic light" irradiances [500 and 1 500 μmol(quantum) m^{-2} s^{-1}] (Table 1). Photochemical quenching (q_P) related to a proportion of open PS2 centres at certain conditions was higher in pea plants grown under RE. However, non-photochemical quenching (q_N as well as NPQ) associated with thermal energy dissipation in the antenna system was lower in RE plants. Increase in PFD of "actinic light" from 500 to 1 500 μmol(quantum) m^{-2} s^{-1} resulted in larger decrease of q_P and increase of q_N.

To determine the real quantum yield of linear electron transport through PS2 the parameter ϕ_{PS2} was used (Genty *et al.* 1989). We found that plants grown under red LEDs had high ϕ_{PS2} at both actinic irradiances. However, higher ϕ_{PS2} was observed at 500 μmol(quantum) m^{-2} s^{-1}. The F_s/F_m ratio is regarded as a rough measure for the PQ redox state (Pfannschmidt *et al.* 2001); our data indicate that it was more reduced in W than RE plants. Increase in F_s/F_m was observed under higher actinic irradiance.

Another process that might be affected by changes in the thylakoid composition is the so-called "State transition", which, as believed, serves to optimise radiant energy utilisation, particularly under irradiance limiting conditions (Allen 1995). Relative changes in the yield of modulated fluorescence during state transitions are shown in Fig. 2. Table 2 demonstrates that changes in the degree of State 1–State 2 transitions in pea plants as a result of alterations in the yield of modulated fluorescence depend on the radiation spectrum. The $t_{½}$ value indicating the half-time for State 1–State 2 transition and estimated from the maximum and minimum fluorescence levels in radiation 2 was lower in RE plants (1.860±0.190) than in W ones (2.440±0.057). Increase in the vF parameter (0.148±0.003) found in RE plants shows their higher efficiency of energy utilisation compared to the Wl ones (0.107±0.008).

Table 2. Comparative characteristics of State 1–State 2 transition parameters in pea leaves. Means of 3 biological and 5 analytical repeats ± SEM.

	W	RE	Difference [%]
$t_{½}$	2.440±0.057	1.860±0.190	–24
vF	0.107±0.008	0.148±0.003	38

Table 3. Distribution of chlorophyll (Chl) in the Chl-protein complexes of thylakoids. Means of 3 biological and 5 analytical repeats ± SEM.

	Total Chl content on the gel		
	W	RE	Difference [%]
CP1a + CP1	23.10±0.04	23.50±0.02	101.7
$LHCP^1$	17.86±0.26	22.92±0.32	128.3
CPa	7.75±0.51	8.62±0.20	111.2
$LHCP^3$	22.90±0.04	19.39±0.21	84.7
FP	28.37±0.46	25.85±0.66	91.1
$LHCP^3/LHCP^1$	1.28±0.02	0.85±0.02	66.4
$LHCP^1 + LHCP^3$	40.76±0.24	42.30±0.14	103.8

Five Chl-protein bands corresponding to pigment-protein complexes of PS1, PS2, and LHC2 were resolved by non-denaturating green SDS-electrophoresis and named according to the nomenclature of Anderson (1980) (Fig. 3). The distribution of Chl content in pigment-protein complexes of W and RE plants is given in Table 3. Total relative amount of the main Chl-*a/b*-protein complex LHC2 (sum of its oligomeric and monomeric forms, $LHCP^1$+$LHCP^3$) was similar in W and RE plants (40.76 and 42.30 %) (Table 3). However, their ratio ($LHCP^3/LHCP^1$) significantly differed: 1.28 for W plants and 0.85 for the RE ones. This shows a redistribution of LHC2 forms (monomeric and oligomeric) in favour of oligomers in RE plants. Table 3 demonstrates that the relative amount of oligomeric forms in RE plants increased by 28 %, whereas the amount of monomeric ones conversely decreased by 16 %. There was also slight increase in the percentage of Chl in CPa complex in RE plants (11 %). On the other hand, the relative content of PS1 reaction centre Chl *a*-protein complexes, namely CPla and CP1, did not significantly differ in both variants.

Discussion

Acclimation to the spectral radiation quality of *P. sativum* demonstrated a wide range of responses including both functional changes of the photosynthetic apparatus and its pigment-protein composition. PS2 plays major role in transformation of radiant energy in chloroplasts, therefore, parameters reflecting the efficiency of PS2 are wildly used for monitoring the activity of the photosynthetic apparatus. Both W and RE plants showed no significant changes in the potential quantum yield of photochemistry of PS2 after acclimation to the respective radiation sources. However, the effective quantum yield at a given irradiance, F'_v/F'_m, was higher in RE plants and accompanied with decrease in the level of quenching in antenna (NPQ). As F'_0 did not change, the increase in F'_v/F'_m was related to higher F'_m value.

Photochemical quenching, q_P, depends on both the inflow of electrons to Q_A and their outflow to PQ pool. Increase in the actinic irradiance resulted in decrease of q_P (oxidised level of Q_A) due to more intense electron inflow to Q_A. Higher q_P observed in RE plants, particularly at 1 500 μmol(quantum) m^{-2} s^{-1}, could be related to faster PQ pool oxidation as a result of increase in the outflow electron rate to PS1. These data were confirmed by the F_s/F_m ratio that estimated the redox state of PQ and indicated its more oxidised level in RE plants (Table 1). On the other hand, a significantly higher electron inflow to Q_A manifested by low q_N (less dissipation in LHC2) was observed in RE plants. In addition, the real quantum yield efficiency of linear electron transport through PS2, ϕ_{PS2}, was higher in RE plants (Table 1). The comparison of ϕ_{PS2} in two groups of plants under different actinic radiation allows propose that higher q_P in RE than W plants is determined mainly by ϕ_{PS2}.

The process of non-photochemical quenching (thermal dissipation of energy) is a main mechanism of regulation of functional size of PS2 antenna and protection of the photosynthetic apparatus against photo-oxidative damage (Štroch *et al.* 2004). Plants grown under red LEDs showed decrease in q_N value at both actinic irradiances. Taken together these data indicate a decrease in the electron transport capacity and increase in dissipation of absorbed photon energy in W plants compared to the RE ones.

The decrease of q_P below 0.6 and increase in q_N are indicators of irradiation stress (Horton *et al.* 1996, Lichtenthaler and Burkard 1999). We found that RE plants characterised by higher q_P and F'_v/F'_m at 1 500 μmol(quantum) m^{-2} s^{-1} were more resistant to high irradiance than the W ones (Table 1).

PS1 and PS2 operate largely in series, and therefore their excitation must be balanced to optimise photosynthetic performance. State transition is a dynamic mechanism that redistributes energy between photosystems and enables plants to react rapidly to changes in radiation quality and irradiance (Iordanov *et al.* 1987, Allen 1995). This mechanism resulting from protein phosphorylation/dephosphorylation of the light-harvesting Chl-*a/b*-complex and its migration from grana thylakoids to the stroma ones plays a decisive role in both short-term regulation of energy harvesting and protection of PS2 against photodamage (Carlberg and Andersson 1993). Changes in State transitions could be controlled by various factors such as redox state of the PQ pool and cytochrome *b/f* complex, fluidity of the membrane, PS2/PS1 ratio, and kinase-phosphatase activities (Hodges and Barber 1983).

We found that contribution of State 1–State 2 transition in energy redistribution between photosystems was more pronounced in RE plants than in the W plants (Table 2). This might be related to higher rate of PQ pool

reduction and provide better protection from over-excitation of PS2 of RE plants. We found also that the parameter vF, which gives a measure of the relative change between State 1 to State 2 transition and reflects the efficiency of radiant energy utilisation (Lichtenthaler *et al.* 1981), is higher in RE plants than in the W ones (Table 2). Along with our other results (decrease in $t_{½}$ of State 1–State 2 transition) (Table 2) and higher content of pigments (Topchiy *et al.* 2004) the fact indicates that the functional reaction of photosynthetic apparatus to RE is similar to corresponding characteristics of shade plants (Hodges and Barber 1983). However, in contrast to the "shade" and "sun" plants the Chl *a/b* ratios for RE and W plants were very close. According to Walters and Horton (1995) the Chl *a/b* ratio does not change when plants are grown under different spectral quality.

According to our results the differences in spectral radiation quality influence the composition of the pigment-proteins (Fig. 3, Table 3), which is an important characteristics for the functional state of the photosynthetic apparatus. Photosynthetic membrane includes three pigment-protein complexes: PS1, PS2, and LHC2 participate in radiant energy transformation. LHC2 comprises 4 different complexes referred to as LHC2a, LHC2b, LHC2c, and LHC2d (also known as CP29, LHC2, CP26, and CP24) (Bassi and Dainese 1987, Peter and Thornber 1991). LHC2b is the main light-harvesting complex organised into trimers in fully green plants. The trimers are mixtures of three polypeptides of approximate molecular masses of 28, 27, and 25 kDa coded for by *Lhcb1*, *Lhcb2*, and *Lhcb3*, respectively (Horton and Ruban 1996). The other three (CP29, CP26, and CP24) complexes are 'minor' ones.

The main effect of RE on pigment-protein composition of chloroplasts is redistribution of LHC2 forms: relative content of oligomeric LHC2 forms increases and contents of monomeric forms and free Chl decrease as compared with W plants. These effects may be explained with the assumption that monomers and pigments in LHC2 isolated from RE plants are more tightly bound than in W plants. This supposition is supported by fluorescence data (Table 1) showing that in RE plants q_P is higher and q_N is lower than in W plants. Such changes of fluorescence characteristics of the photosynthetic apparatus indicate higher radiant energy utilisation and transfer to reaction centre, that could take place in more integral, compact LHC2 complex with shorter distances between components. The dependence of quenching on organisation of LHC2 polypeptides was shown by Wentworth *et al*. (2001) and Garab *et al*. (2002), according to whom monomeric form or the minor complexes (CP29 and CP26) quench fluorescence more rapidly and to a higher extent than the trimeric form of LHC2, which is more compactly organised.

The other effect of RE on pigment-protein composition of chloroplasts was an increase in the amount of pigment-proteins complexes of PS2 reaction centre. As the amount of Chl loaded on the gel was the same in both variants, increase in the level of one pigment-protein complex should be accompanied by the decrease in content of the other one. However, we did not observe differences in the amount of pigment-proteins of PS1 and LHC1 in W and RE plants and registered changes in the amount of pigment-proteins complexes of PS2 and free Chl only. Thus we propose that the pigment-protein complex of PS2 reaction centre is more stable in RE plants than in the W ones.

Hence, addition of red radiation of LEDs to the "white light" of luminescent lamps leads to functional transformations of the photosynthetic apparatus of pea plants: higher efficiency of PS2, faster redistribution of energy between photosystems, and changes in the content of Chl-proteins. Correction of spectral composition of light sources in red spectral band by LEDs might be prospective for plant growing in greenhouses due to a concentrated effect in essential PAR regions.

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