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# EFFECT OF PS II ANTENNAE SIZE ON THE INDUCTION KINETICS OF PROMPT AND DELAYED CHLOROPHYLL FLUORESCENCE*

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**Summary**. The role of pigment antennae size in some functional characteristics of PS II was studied. Wild type and *chlorina f2* mutant of barley grown at normal (50 μE.m$^{-2}$.s$^{-1}$) and low (2.5 μE.m$^{-2}$.s$^{-1}$) light intensity were investigated. The photosynthetic activity was estimated by analysis of induction kinetics of simultaneously recorded prompt and delayed chlorophyll fluorescence. Increasing of PS I size relative to PS II in a sequence: wild type "shade", wild type "light", *chlorina-f2* "shade", *chlorina-f2* "light" led to pronounced modification of induction kinetics of both prompt and delayed fluorescence, especially in their initial part. DF induction maximum $I_2$ appeared after illumination of ca.100–200 ms and correlated with D-P transition of variable fluorescence was found to be most sensitive for changes in both antennae size and measuring temperature. Increased PS I activity compared to PS II led to delay in processes occurring during the first second of the induction period (i.e. the PQ pool reduction) and to earlier activation of slower processes (PS I activation and light induced formation of proton gradient). The decrease of PS II antennae size was combined with the decrease of temperature resistance of plants and with a slow down of the dark reactions of photosynthesis.

***Key words***: barley, *chlorina f2*, delayed fluorescence, electron transport, high and low temperature, photosystem II antennae size, variable chlorophyll fluorescence

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***Abbreviations***: Chl – chlorophyll, IK – induction kinetics, LHC – light-harvesting complex, PF and DF – prompt and delayed chlorophyll fluorescence, PS – photosystem, $Q_A$ – primary quinone electron acceptor of PSII, $Q_B$ – secondary quinone electron acceptor of PSII, PQ – plastoquinone, RC – reaction centre, TM – thylakoid membrane, $F_{PSI}$ and $F_{PSII}$ – quantum efficiencies of PSI and PSII, $F_o$, $F_i$, $F_p$, $F_m$, M and $F_v$ – parameters of the chlorophyll fluorescence induction kinetics, $I_{1–5}$ and $D_{1,2}$ – parameters of the delayed fluorescence induction kinetics.

## Introduction

Under natural light conditions the photosynthetic apparatus normally operates at unsaturated light intensity, when the quantum efficiencies of both PSII ($F_{PSII}$) and PSI ($F_{PSI}$) are high (Genty and Harbinson, 1996). At this condition leaves are capable of balancing the distribution of excitation energy between PSI and PSII. The relatively greater loss of $F_{PSII}$ as compared to $F_{PSI}$ at low irradiances, implies that an overexcitation of PSII (Harbinson et al., 1989; Genty et al., 1990b) due to the larger PSII antennae size takes place. The opposite effect was observed after photoinhibition (Genty et al., 1990a) or during irradiation with far-red enriched light (Andrews et al., 1993). A greater loss of $F_{PSI}$ compared to $F_{PSII}$ was characteristic for chlorophyll *b* deficient mutants (Andrews et al., 1995), such as *chlorina* mutants of barley.

The *chlorina-f2* mutant of barley had a high photosynthetic rate (Highkin and Frenkel, 1962) and chloroplast activity in the Hill reaction (Boardman and Highkin, 1966). The light-harvesting complex was greatly reduced in *chlorina-f2* and some of the polypeptides of PSI were also reduced but in lesser degree (Bellemare et al., 1982). Bossmann et al. (1997) have shown that *chlorina-f2* and some other *chlorina* mutants of barley lack Lhca4, Lhcb1 and Lhcb6, whereas the amounts of Lhcb2, Lhcb3 and Lhcb4 are reduced. Lhca1, 2 and 3, as well as Lhcb5 and PsbS seem to be unaffected compared to the wild type.

Prompt and delayed chlorophyll fluorescence (denoted PF and DF) are commonly used as a criteria for integrity of photosynthetic apparatus, a general indicator of the plants' ability to store and utilize photosynthetic energy and as an indication of the thylakoid membrane energization state (Kramer and Crofts, 1996). DF and PF are emitted from PSII antennae complexes. The course of induction kinetics (IK) of both luminescence types depends on electron transfer rates in donor and acceptor sides of PSII, PSI activity and TM energization (Krause and Weis, 1991; Golstev and Yordanov, 1997). The intensity of both PF and DF depends on the redox state of electron carriers especially in the acceptor side of PSII. Dynamics of the redox states is determined by adsorbed energy flow to PSI and PSII, as well as particular electron transport rates, that are temperature dependent.

In this study the induction kinetics of prompt and delayed chlorophyll fluorescence were used to investigate the effect of different pigment antennae size of PS I and PS II on the kinetics of light utilization processes in plants of wild type and *chlorina-f2* mutant of barley, grown at different light conditions.

## Materials and Methods

Barley (*Hordeum vulgare* L.) wild type and *chlorina-f2* mutant were grown for 10 days in a climatic chamber at controlled conditions of temperature (25 °C/20 °C, day/night) and light (50 or 2.5 μmol photons.$m^{-2}$.$s^{-1}$, 16 h.$d^{-1}$). The plants grown at 50 and 2.5 μmol photons.$m^{-2}$.$s^{-1}$ were designated as "light" and "shade" plants, respectively. Pigments were extracted from leaf discs in 80% acetone. After centrifugation the chlorophyll concentration was determined using the method of Lichtenthaler (1987).

Prompt and delayed chlorophyll fluorescence (PF and DF) induction kinetics were recorded simultaneously as in Goltsev and Yordanov (1997) using fluorometer Fl-2006 (manufactured by "Test", Russia). The maximal intensity of modulated light on the level of object was 1200 μmol.$m^{-2}$.$s^{-1}$. PF values were registered every 11 ms as an integral emission during 5.5 ms illumination period. DF signal was read by ADC every 50 μs during registration period. DF values of the induction curve situated via time interval of 11 ms represent a sum of two fast kinetic components ($\tau_1 \sim 200 \div 800$ μs and $\tau_2 \sim 1.5 \div 3.5$ ms) and a "tail" of slow components ($\tau > 20$ ms). Before measurements plants were kept in darkness for 1 h and then the detached leaf segments were transferred to a measuring chamber. The sample holder had a working surface 20 $mm^2$. The samples were placed in a thermostabilized holder for 3 min at required temperature and the chlorophyll fluorescence induction kinetics were recorded at the same temperature. The temperature ranges of $5 \div 45$ °C were explored with step of 5 °C.

## Results

### Chlorophyll concentration in wild type and chlorina-f2 leaves

It is known that *chlorina-f2* mutant of barley lacks Chl *b* and its Chl *a* content per leave area is reduced (Thornber and Highkin, 1974; Andrews et al., 1995). When wild type of barley plants are grown at low light intensity a tendency to a Chl *a* content increase is observed (Table 1), although no significant difference between the Chl *a* content in "light" and "shade" wild type leaves is found. C*hlorina-f2* plants grown at low light intensity, however, have about 15% more Chl *a* per leaf area than those grown at normal light. Total chlorophyll content of the "shade" as compared to the "light" plants increases with ca. 7 and 14% in wild type and *chlorina-f2*, respectively. On the other hand, the Chl *a*/*b* ratio in the wild type tends to decrease with the lowering

**Table 1.** Effects of growth irradiance on the chlorophyll (Chl) content, Chl *a*/*b*, $F_o$ and $F_p$ in leaves of wild type and *chlorina-f2* mutant of barley. Plants were grown for 10 days under different light conditions. Leaf segments were dark adapted for 1 h before measuring of induction kinetics. The chlorophyll fluorescence induction kinetics were measured at 20 °C. Data are means ± SD of three independent experiments.

| Genotype/Growth condition | Chl *a* | Total Chl | Chl *a*/*b* | $F_o$ | $F_p$ |
|---|---|---|---|---|---|
| | μg cm$^{-2}$ | | | rel.u. | |
| wild type – "shade" | 12.9 ± 0.1 | 18.9 ± 0.1 | 2.13 ± 0.02 | 21.9 ± 0.9 | 53.1 ± 2.4 |
| wild type – "light" | 12.3 ± 0.8 | 17.6 ± 0.7 | 2.36 ± 0.20 | 13.9 ± 0.9 | 38.7 ± 3.1 |
| *chlorina f2* – "shade" | 7.8 ± 0.6 | 9.1 ± 0.9 | 5.84 ± 0.78 | 9.5 ± 0.6 | 21.9 ± 2.0 |
| *chlorina f2* – "light" | 6.7 ± 0.5 | 8.0 ± 0.5 | 5.66 ± 0.85 | 8.0 ± 0.5 | 23.5 ± 1.8 |

of growth irradiance, while at the same growth conditions the Chl *a*/*b* ratio increases in *chlorina-f2*. The data show that the increase in the total Chl content observed for the wild type might be due to the rise of Chl *b* content, while that of the mutant is probably caused by an increase of Chl *a* concentration. The lower values obtained for Chl *a*/*b* ratio as compared to the published data (Boardman and Highkin, 1966; Bolton et al., 1978) might be a consequence of inaccuracy of the spectrophotometric method used for determining Chl *a*/*b* ratios above 6 (Boardman and Thorne, 1971).

## Induction kinetics of prompt and delayed chlorophyll fluorescence

Changes in the chlorophyll content have an effect on variable chlorophyll fluorescence. The initial fluorescence intensity $F_o$, which reflects the fluorescence yield from light-harvesting pigment/protein complex (LHC) of PS II in the open reaction centre (RC) state, is significantly affected. In "shade" plants from both wild type and *chlorina-f2* $F_o$ increases with the antennae size increase (Table 1). In wild type leaves the maximal fluorescence yield ($F_p$) rises similarly to $F_o$, which reflects reduction of the PQ pool and closing of the PS II reaction centres. In *chlorina-f2* leaves $F_p$ slightly decreases in "shade" plants in spite of the higher chlorophyll content. These results show that in the mutant plants PS I antennae size increases more significantly than in PS II. The total number of PS II reaction centres on a total chlorophyll basis, generally increases with growth irradiance increase, whereas the RC density of PS I is slightly dependent on growth irradiance (Leong and Anderson, 1984; Anderson, 1986; Evans, 1987).

Fig. 1 shows the simultaneously recorded PF and DF induction kinetics presented in semi-logarithmic scale for wild type and *chlorina-f2* mutant grown at different light intensities. The maximums in DF intensity registered during the first second of the induction period are thought to be due to the dynamics of the redox reactions of the PS II acceptor side (Goltsev and Yordanov, 1997). The time necessary to reach the DF maximum $I_1$ is the same as that needed to reach the inflection point of the $F_o$-$F_i$ rise of PF curve. The amplitude of $I_1$ is proportional to the luminescence of the dark adapted (open) RCs. Maximum $I_2$ is observed at the moment of maximal rate of $F_i$-$F_p$

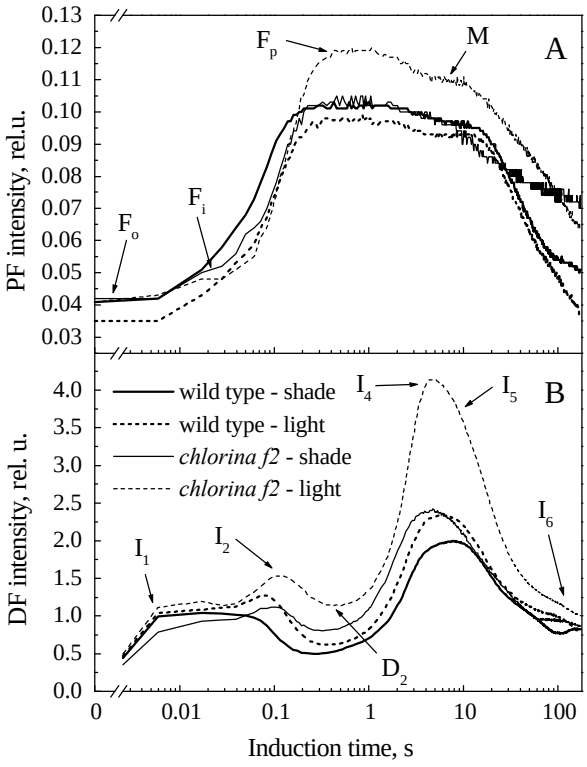


**Fig. 1.** Induction kinetics of prompt (A) and delayed (B) chlorophyll fluorescence of wild type and *chlorina-f2* mutant of barley grown for 10 days under different light conditions. Data are normalized to the Chl *a* content of each sample. The leaf segments were dark adapted for 1 h before measuring of the induction kinetic. The chlorophyll fluorescence induction kinetics were measured at 20 °C. Values are mean of a minimum 5 replicates. PF induction kinetics parameters are denoted: $F_o$ – initial fluorescence level; $F_i$, $F_p$ and M – fluorescence intensities at I, P and M levels (O-I-D-P-S-M-T) nomenclature. DF induction kinetics parameters are denoted: $I_1$-$I_6$ – DF intensities at local maximums; $D_2$ – DF intensity at local minimum after second maximum $I_2$.

increase in PF and its amplitude reflects the maximal rate of PQ pool reduction. The maximal PQ reduction (and closing of PS II reaction centres) corresponds to a minimum in DF, noted as $D_2$. The time of $D_2$ corresponds to the time of PF maximum $F_p$. Appearance of the DF induction maximums, denoted as $I_4$ and $I_5$, is related to the creation of photoinduced proton gradient which increases the radiative rate constant in RC of PS II (Wraight and Crofts, 1971; Gaevskii and Morgun, 1993). It is supposed that maximum $I_4$ is related to the dynamics of photoinduced proton gradient and the

maximum $I_5$ to the secondary ion transport. An intensive increase of the proton gradient is possible only after activation of the PS I and the noncyclic electron transport. That is why the $D_2$-$I_4$ transition can be related to PS I activity. The decrease in the DF intensity observed after the maximum $I_5$ seems to reflect a number (series) of dark photosynthetic processes, like NADP.$H_2$ accumulation, activation of dark reactions in the Calvin cycle, ATP synthesis and is usually used as a criterion for the activity of the dark photosynthetic stage (Veselovskii and Vesselova, 1990).

Table 2 shows the DF parameters for "shade" and "light" type of wild type and *chlorina-f2* barley. The amplitudes of $I_1$ maximum of *chlorina-f2* are about twice lower than those of wild type leaves, although there is no significant difference between

**Table 2.** Effect of growth irradiance on the amplitudes of DF induction maximums ($I_1$, $I_2$ and $I_4$) and on the induction minimum $D_2$ in leaves of wild type and *chlorina-f2* mutant of barley. The conditions of plant growth and of induction kinetics measurement were as in Table 1. Data are means ± SD of three independent experiments. DF parameters are presented in rel.u.

| Genotype/Growth condition | $I_1$ | $I_2$ | $D_2$ | $I_4$ |
|---|---|---|---|---|
| wild type - "shade" | 482 ± 35 | 427 ± 19 | 273 ± 24 | 738 ± 51 |
| wild type - "light" | 452 ± 42 | 519 ± 34 | 269 ± 21 | 810 ± 65 |
| *chlorina f2* - "shade" | 247 ± 41 | 258 ± 24 | 204 ± 23 | 540 ± 72 |
| *chlorina f2* - "light" | 266 ± 31 | 393 ± 21 | 233 ± 15 | 652 ± 51 |

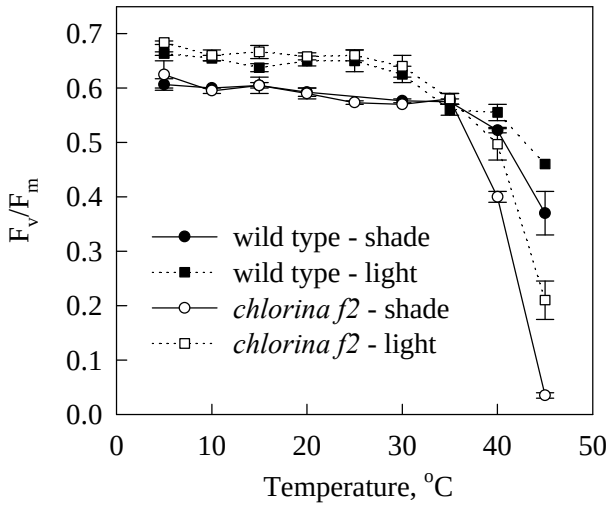


**Fig. 2.** Dependence of the fluorescence ratio $F_v/F_p$ on the temperature for wild type and *chlorina-f2* mutant of barley grown for 10 days under different light conditions. The samples were dark adapted for 1 h at room temperature and for 3 min at corresponding temperature, and induction kinetics were recorded at the same temperature. Data are means of a minimum 5 replicates.

the "light" and "shade" plants of the same genotype. Evidently, this parameter is not sensitive enough to small differences in the chlorophyll content.

In contrast to $I_1$, the maximum $I_2$ decreases in plants grown at low light intensity. In parallel the $D_2$ amplitude increases and that of $I_4$ decreases (Table 2). The rate of the slow $D_2$-$I_4$ phase also decreases with the increase of PS II antennae size (Fig. 1B). The amplitude of $I_4$ increases in the following order: wild type – "shade", wild type – "light", *chlorina-f2* – "shade", *chlorina-f2* – "light", which might be related to higher density of PS II reaction centres in *chlorina-f2* compared to that of the wild type due to reduced PS II antennae size in the mutant (Fig. 1).

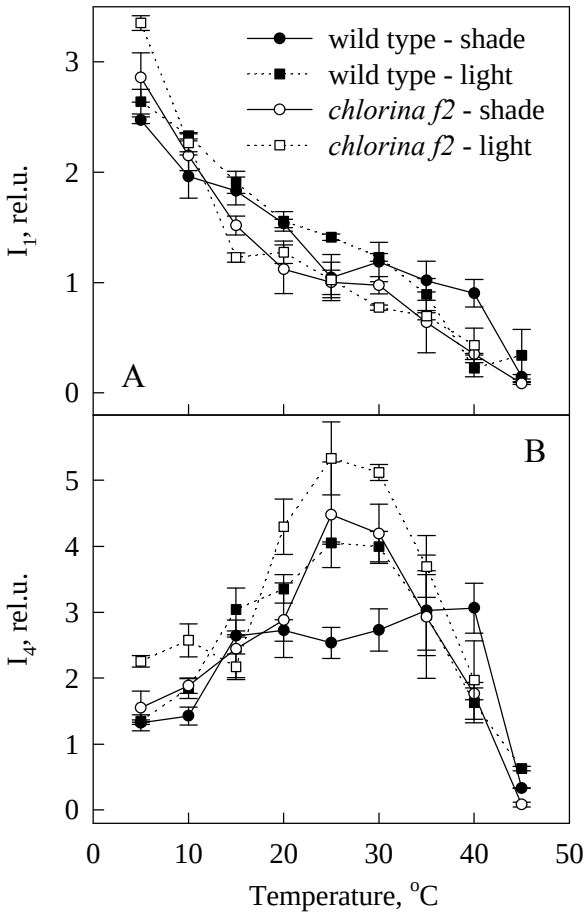


**Fig. 3.** Amplitudes of DF maximums $I_1$ (A) and $I_4$ (B) in leaves of wild type and *chlorina-f2* mutant of barley as a function of measuring temperature. The conditions of plant growth and of induction kinetics measurement were as in Fig. 2. Values are normalized to the Chl *a* content of each sample. Data are means ±SD of three separate experiments.

The greater decrease in PF intensity from $M_1$ to stationary level (Fig. 1A) in "light" plants indicates that the dark photosynthetic processes are more intensive in plants grown at higher light.

From values of the $F_v/F_m$ ratio (Fig. 2) one can conclude that the quantum efficiency of the primary photosynthetic reaction is practically the same in wild type and *chlorina-f2* leaves and that it is independent of the temperature within the range 5–35 °C. Similar values for the $F_v/F_m$ ratio for the wild type and *chlorina-f2* mutant of barley were obtained by Havaux and Tardy (1997). The $F_v/F_m$ ratio is lower in plants from both genotypes grown at lower light intensity, i. e. the additionally synthesized chlorophyll/protein complexes are not strongly functionally bound to the RC of PS I and PS II, and the excitation energy transfer is less effective for temperatures above 35 °C. Some changes in the photosynthetic apparatus leading to decrease in the quantum efficiency of photosynthesis occur. These changes are more pronounced in the plants with small PS II antennae size, i. e. in *chlorina-f2* mutants.

Fig. 3 shows the temperature dependencies of DF parameters. The $I_1$ amplitude (Fig. 3A) was similar for the plants analyzed in the temperature range 5–45 °C. Using a mathematical model for the kinetics of the early processes in the donor and acceptor side of PS II during the dark-adapted to the stationary "light" state transition Goltsev and Yordanov (1997) have shown that the appearance of $I_1$ (respectively the $F_o$-$F_i$ rise) can be a result not only of subpopulation of $Q_B$-nonreducing PS II, but of

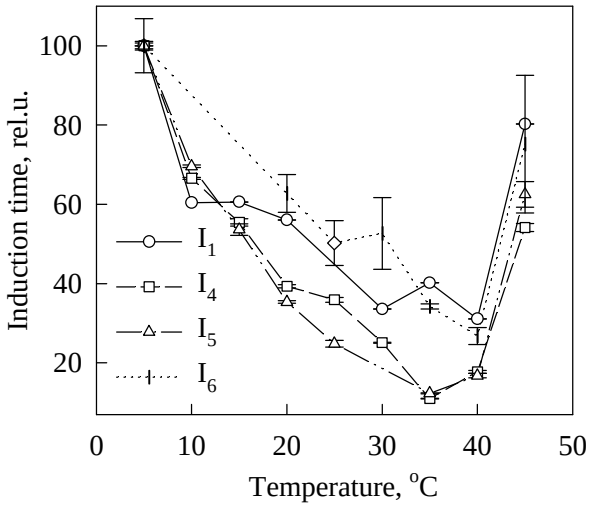


**Fig. 4.** The time of appearance of DF maximums $I_1$ $I_2$, $I_4$ and $I_6$ in leaves of wild type barley, grown for 10 days at low light irradiances *vs*. the temperature of the measurements. The conditions of plant growth and of induction kinetics measurement were as in Fig. 2. Data are presented as a percent of the values obtained at 5 °C. Data are means ± SD of three separate experiments.

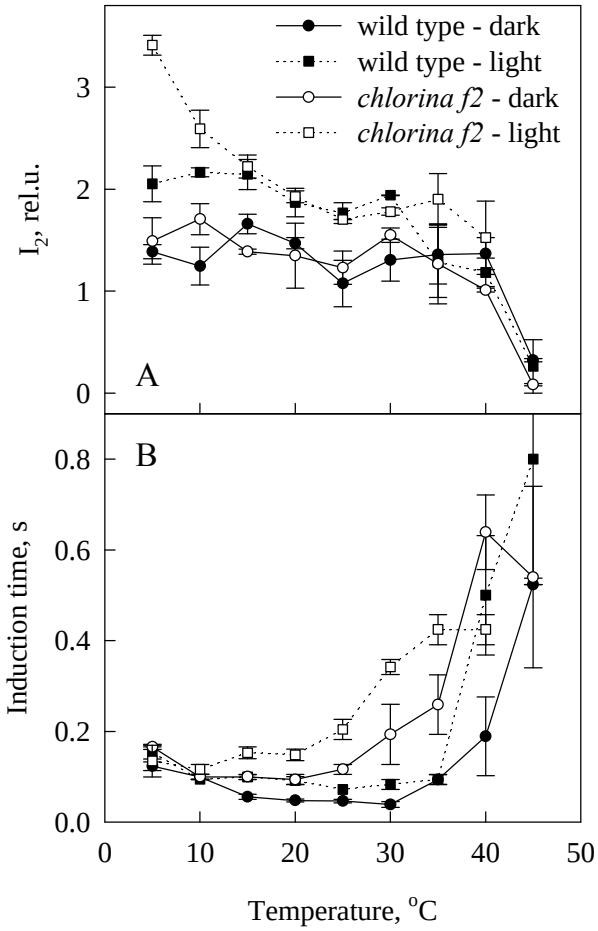


**Fig. 5.** Amplitude (A) and time (B) of DF induction maximum $I_2$ in leaves of wild type and *chlorina-f2* mutant of barley as a function of temperature of measurement. The conditions of plant growth and of induction kinetics measurement were as in Fig. 2. Values in (A) are normalized to the Chl *a* content of each sample. Data are means ± SD of three separate experiments.

a transient quasistationary concentration of "open" PS II reaction centres during the induction period. This concentration will be proportional to the rate constant of electron transfer to $Q_B$ and PQ pool, and will decrease with the temperature increase at a given intensity of the exciting light. This assumption may explain the drop in $I_1$ amplitude with the increase of the measuring temperature.

Temperature dependence of the amplitude of $I_4$ (Fig. 3B), however, has a noticeable optimum in a different temperature range for the "shade" and "light" plants investigated. It might be related either to PS I activation at optimal temperature (Armond

et al., 1977; Ivanov and Velitchkova, 1990) or to the oxygen-evolving system inactivation at elevated temperatures (Krause and Weis, 1984).

Temperature variation leads to a shift of DF induction maximums. The time necessary to reach $I_1$, $I_4$, $I_5$ and $I_6$ maximums of DF for the investigated plant types have similar temperature dependences (data not shown). In Fig. 4 the times for reaching these maximums in leaves from barley wild type, grown at low light irradiance, are presented. The shift of DF induction maximums shows that at higher temperature the transition of the photosynthetic apparatus from dark-adapted to stationary "light" adapted state is accelerated, i. e. the constants of the rate limiting reactions leading to the appearance of each of DF maximums are higher. The strong delay of the induction maximum at 45 °C is probably induced by inactivation of the photosynthetic apparatus at this temperature (Yordanov et al., 1995).

The clearest difference between the investigated plants is observed for the maximum $I_2$ of DF (Fig. 5). The temperature inactivation of the wild type takes place at 45 °C while that of *chlorina-f2* at about 35–40 °C (Fig. 5A). In contrast to the other DF maximums, the time for reaching the $I_2$ maximum in the wild type decreases slightly with elevating the temperature and for *chlorina-f2* even increases (Fig. 5B). The slow down of this peak observed at temperature higher than 40°C could be explained by weaker affinity of the PQ to the $Q_B$-binding site of D1-protein. This effect, observed for the mutant at temperatures above 10 °C, is an indication for earlier PS I activation and faster electron transfer from the PQ pool compared to the wild type.

## Discussion

It is known that there is no absolute correlation between growth irradiance and photosynthetic pigment content in leaves of higher plants (Björkman, 1981). It may be expected that in most leaves the concentration of pigments is high enough so that leaf absorbance is only weakly dependent on pigment (Genty and Harbison, 1996). In contrast to the wild type, the chlorophyll concentration in *chlorina-f2* is greatly reduced. Lowering the growth irradiance leads to more pronounced increase of total chlorophyll content in the mutant (Table 1). It is usually reported that low growth irradiance leads to a decrease of Chl *a*/*b* ratio. This is considered to be a result of an increase in the absorbance cross-section of PS II relative to PS I (Boardman, 1977; Anderson, 1986; Montane et al., 1998). In the experiments presented here a decrease of Chl *a*/*b* ratio was observed for leaves from wild type but not from the mutant. The strongly reduced PS II antennae size in the mutant (Bossmann et al., 1997) do not allow the compensatory increase of the total chlorophyll content to be a result of increased LHC II. It is evident from the $F_o$ and $F_p$ values (Table 1) that the PS I antennae size of the mutant is bigger than that of the wild type. The $F_p$ increase in *chlorina-f2* accompanied by a decrease in both $F_o$ and chlorophyll concentration (i. e. increase

of $F_v$) for "light" plants suggests stronger functional relationship between the antennae chlorophyll/protein complexes and the reaction centre and more effective energy transfer in the mutant than in the wild type. This follows from the similarity between the primary photochemical reaction efficiency observed for the wild type and the mutant grown at same light conditions (Fig. 2). This similarity is observed in a wide temperature range. An increase of the quantum efficiency of the primary photochemical reaction of wild type barley with the increase of the growth irradiance, despite of reduced PS II antennae size, has been shown by Montane and co-workers (1998).

The increased $I_2$ and $D_2$ values measured for "light" plants from wild type and *chlorina-f2* (Table 2, Fig. 5A) indicate that the size of PQ pool is bigger in these plants. An increase of PQ pool as a result of an increased irradiance has been previously shown (Björkman, 1981; Anderson, 1986) and is consistent with the key role of PQ in the limitation and regulation of the photosynthetic electron transport. The bigger PQ pool in the "light" plants will be slowly reduced upon illumination during the measurements and more PS II reaction centres will stay in an "open" state. This will lead to an increase of $I_2$ amplitude and will shift it toward the later times of the induction kinetics (Fig. 5B). This correlates with the slowing down of the PF transition from $F_o$ to $F_p$ level and with the increase of time to reach the DF minimum $D_2$ (Fig. 1). At the same time the DF induction maximum is reached faster in "light" plants.

The increase of PS I size compared to PS II in a sequence: wild type "shade", wild type "light", *chlorina-f2* "shade", *chlorina-f2* "light" leads to earlier PS I activation during the transition of photosynthetic apparatus from dark adapted to stationary "light" state. This also contributes to the earlier formation of $I_4$. The rise of DF intensity to $I_4$ starts before the complete reduction of the PQ pool. Since at this moment the DF minimum $D_2$ is still not reached, the $D_2$ values obtained for plants grown at higher light intensity are bigger (Table 2, Fig. 1B). Earlier activation of PS I would result in a delay of $I_2$. This effect is more significant and starts at lower temperatures for plants with smaller PS II antennae size when the balance between the two photosystems is smaller (Fig. 5B).

The time for reaching $I_5$ maximum of DF is the same as the time of the $M_1$ maximum in PF curve. We may assume that the DF changes in this period are due to the dynamics of PS I activity and subsequent opening of PS II reaction centres (Goltsev and Yordanov, 1997). The higher activity of the dark photosynthetic reactions observed in "light" plants (Fig 1A) is consistent with the greater rates of $CO_2$ fixation (Björkman, 1981) and increased ATP-ase concentrations in those plants (Leong and Anderson, 1984; Evans, 1987; Chow and Hope, 1987).

Temperature dependencies of PF and DF parameters suggest the key role of PS II antennae size for the resistance of higher plants to high temperature. The stronger decrease of the $F_v/F_m$ values in the mutants than in the wild type plants with the temperature increase above 35 °C shows that the reduced antennae size decreases the termostability of the investigated plants (Fig. 2). Lower inactivation temperature in the

mutant was observed for $I_2$ amplitude (Fig. 5A). The lowered temperature resistance in *chlorina-f2* has been observed by Havaux and Tardy (1997).

Temperature dependence of $I_4$ amplitude shows that the temperature optimum is within a wide temperature range 15–40 °C only for wild type grown at low light intensity while for plants with smaller antennae size it is in a range as narrow as 25±30 °C. One can suppose that the antennae size of "shade" wild type plants is kept in evolution and therefore the adaptation ability in this plant is most stronger. Development of plants at conditions of higher light pressure because of higher growth light intensities (for wild type "light") or of a genetically reduced PS II antennae size (for *chlorina-f2*) results in the synthesis of photosynthetic apparatus with a good functional activity only in a narrow temperature range.

In conclusion, this study shows that the change in the excitation energy balance between the two photosystems by varying the size of the antennae complexes modifies the induction kinetics of PF and more significantly the DF. The enhanced PS I activity as compared to PS II leads to delay of the processes during the first second of the induction period (PQ pool reduction) and to earlier activation of slower processes (PS I activation and development of photoinduced proton gradient). The decrease of PS II antennae size is coupled with the decrease of the temperature resistance of plants and with a slow down of the dark reactions of photosynthesis.

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