THE EFFECT OF THE D1 PROTEIN MUTATION ONTO THE ENERGY UTILIZATION IN PHOTOSYSTEM II OF PLANTS WITH DIFFERENT WATER BALANCE

Ph.D. Thesis

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INTRODUCTION

In nature, plants are usually exposed to a wide range of fluctuating light intensities and often absorb more light energy than they are able to utilize for photochemistry. This excess excitation can lead to the formation of singlet oxygen or other reactive oxygen species, which can irreversibly damage the photosynthetic apparatus. To prevent this scenario photoprotective mechanisms to safely drive away the excess excitation had to be evolved, along with the processes for photochemical utilization. One of these photoprotective processes is the non-radiative energy dissipation (thermal dissipation), which is defined as the light-dependent, non-photochemical quenching (NPQ) of chlorophyll (Chl) *a* fluorescence. The largest part of NPQ is a fast relaxing, reversible, energy- and ΔpH-dependent component, the qE. Although the exact molecular mechanism of NPQ is not yet fully understood several of its preconditions are well known, such as acidification of the thylakoid lumen, de-epoxidation of the xanthophyll-cycle pigments and/or protonation of PsbS and other light-harvesting complex proteins (LHCs).

It was shown in all of the atrazine-resistant plants (*Chenopodium album*, *Epilobium adenocaulon*, *Erigeron canadensis*, *Senecio vulgaris*, *Solanum nigrum*), hitherto investigated, that the capacity of NPQ, and its qE component, in particular, were lessened (Váradi *et al*., 2003). There is a general consensus that NPQ is controlled by factors that are encoded in the nucleus, although the *psbA* gene, which encodes the photosystem II (PSII) reaction centre D1 protein and carries the mutation in the atrazine-resistant plants, is localized in the chloroplast genome. Therefore, it is not entirely clear in what way the D1 protein can contribute to the formation of efficient non-photochemical dissipative processes in the antenna.

In order to find a correlation between the mutation on the D1 protein and the allocation of the absorbed light energy in the antenna system of PSII, we applied the technique of reciprocal cross breeding to produce hybrids (F1, F2 down to F6) of atrazine-sensitive (AS) and atrazine-resistant (AR) biotypes of *Solanum nigrum*, and followed the inheritance of the qE component and the energy allocation pattern.

The different susceptibility of the atrazine-resistant plants to the ambient temperature and their ability to adapt to different environmental conditions are well documented (Ducruet & Lemoine, 1985) as well as their increased susceptibility to high light (Hart & Stemler, 1990). Nowadays, the drought stress is one of the most important environmental factors, which limits the growth and/or productivity of the plants. In their natural environment the lack of water often goes hand in hand with high ambient temperature and/or elevated light intensity (photoinhibition). To the best of our knowledge, the effects of water deficit (drought stress) on the process of photosynthesis have not yet been investigated on D1 protein mutant plants, therefore the second part of the Thesis is dedicated to this subject.

SCOPE OF THE THESIS

The present study was undertaken in order to investigate the utilization of the absorbed energy in the antenna system of PSII. In this subject our aims were:

- To find a correlation, if there is any, between the mutation on the D1 protein and the energy allocation pattern of the absorbed light energy in the antenna system of PSII: the relationship between photochemical energy utilization and thermal dissipation.
- To understand the reasons behind the lower NPQ capacity, or that of its qE component, in the D1 protein mutant plants through scrutinising the photoprotective mechanisms with the aid of chlorophyll *a* fluorescence analysis.
- To establish a suitable model system, by using the technique of reciprocal cross breeding, on which these properties can be investigated and the role of the nuclear and cytoplasmic factors on the regulation of qE can be examined.

Our investigation concerning the subject matter of drought stress was focussed on the following goal:

- To explore the effects of progressive water detention on the water balance and gas exchange properties of intact plant leaves, as well as on their photosynthetic efficiency, in AS and AR biotypes of *S. nigrum*.

MATERIALS AND METHODS

The plant material

In this study we have used a weed species *Solanum nigrum* L. (black nightshade) for our investigation. These plants underwent natural selection in their habitat. Two biotypes were used, the atrazine-sensitive wild type and an atrazine-resistant line carrying a mutation on their PSII reaction centre D1 protein. The mutation responsible for the atrazine resistant trait is the exchange of an amino acid at the 264th codon of the *psbA* gene, which encodes the D1 protein: $Ser_{264} \rightarrow Gly$ (Hirschberg & McIntosh, 1983; Gawronski *et al*., 1992).

We have also used two mutant lines of *Arabidopsis thaliana* L. with reduced NPQ capacity: the antisense *lhcb2* and the *psbS* deletion *npq4-1* lines (Andersson *et al*., 2003; Ruban *et al*., 2003; Li *et al*., 2000; 2002). The ecotype Columbia-0 (Col-0) was used as the wild-type control plant.

Growth conditions, water detention

The plants were grown under controlled conditions in pots containing commercial soil mixture in growth chambers. The maximum level of the photosynthetically active radiation was kept at 350 μmol photons m^{-2} s^{-1} (16 h light periods, 25/20°C day/night temperature and about 50-60% relative humidity) and the plants were watered every other day. The 35- to 40-day-old plants were regarded as having a good water balance and used as controls. 40-42 days after the seeding we stopped watering some of the plants and performed gas exchange measurements on them at every 3-4 days to follow the effects of water detention. Based on the gas exchange parameters and their water content the plants were grouped into three distinct categories: mildly drought (5-7 days without watering), moderately drought (after 13-15 days) and severely drought (lacking water for 18-19 days). These categories were termed as dehydration state 1, 2 and 3, (DH1, DH2 and DH3) respectively. During the different dehydration states some of the plants were given water again and we re-examined them 24 h later. These plants were termed as RH1, RH2 and RH3, referring to re-hydration from state 1, 2 and 3, respectively. Always the youngest, fully developed leaves at similar positions were used for the experiments.

The different species of *Arabidopsis thaliana* were grown under controlled conditions in pots containing commercial soil mixture in growth chambers. The maximum level of the photosynthetically active radiation was kept at 350 μmol photons m^{-2} s^{-1} (16 h light periods, 25/20°C day/night temperature and about 50-60% relative humidity). The youngest, fully developed leaves of the plants of about 6-week-old were used for the experiments.

Reciprocal cross breeding and genetic analysis

The F1 hybrids of *S. nigrum* were produced by reciprocal cross breeding of the AS and AR parent populations. Pollens of the AS (♂) plants were manually transferred to the stigmata of the AR (♀) counterparts and *vice versa* pollens of the AR (♂) plants were passed along onto the stigmata of the wild-type AS (♀) weeds. These products of the first reciprocal breeding process were termed as ARF1 and ASF1, respectively. The F2 generation was produced via self-pollination of the F1 heterozygote hybrids (the *S. nigrum* is autogamous) and these were termed as ARF2 and ASF2, respectively. The F2 plants were used in the investigation of the inheritance of leaf margins, in order to prove whether the segregation of this Mendelian trait has taken place. In the parent population there are three different types of leaf margin, which exhibit Hardy-Weinberg equilibrium; we used this distribution to estimate the expected occurrence of the different leaf margins in the subsequent generation. The cross breedings were continued down to the F6 generation and the plants were labelled as ARF6 and ASF6, respectively. With all *S. nigrum* lines the seedlings were sprayed with 8 kg active ingredient/hectare atrazine.

Water balance

Relative water content of leaves

In order to monitor their state of dehydration the relative water content (RWC) of the leaves was determined according to the following expression: $(FW–DW)/FW_S$, where FW and DW are the fresh weight and dry weight of the leaves, respectively, and FW_S is their weight after soaking them for 24 h in a water bath. The dry weight was measured after putting the leaves in a 85°C stove for 24 h. All weights are measured in grams [g].

Water potential of leaf tissues

The average water potential of the leaf tissues was determined by using a pressure chamber (Model 600, PMS Instruments Company, USA).

Stomatal conductance

The conductance of the gas exchange pores was measured in the growth chambers on the abaxial surface of the leaves using an AP4 type diffusion porometer (DELTA T, UK).

Gas exchange measurements

The rate of CO_2 assimilation (A) as a response to the actinic light was recorded by a LCA-3 infrared gas analyser (IRGA) (ADC, UK). The rate of assimilation was calculated by the software of the instrument, according to the expressions introduced by von Caemmerer and Farquhar (1981). The rate of CO_2 assimilation as a function of the intercellular CO_2 concentration (C_i) was determined with a LCpro+ IRGA instrument at different levels of ambient CO_2 concentration, in an atmosphere of 0 to 1500 μmol CO_2 mol^{-1}, and 21% O_2 content. The irradiance at the leaf surface was kept at 800 μmol photons m^{-2} s^{1}. The data were plotted against the intercellular CO_2 concentration, as calculated by the software (Farquhar *et al*., 1990).

Chlorophyll fluorescence measurements

The fast chlorophyll *a* fluorescence transients (OJIP traces) were recorded by a HandyPEA plant efficiency analyser (Hansatech Instruments, UK). The leaves were dark-adapted for 30 min and then irradiated for 1 s with a continuous light, which had a wavelength of 650 nm, and 3000 μmol photons m^{-2} s^{-1} photon flux. The OJIP transient traces were analysed according to the JIP-test (Strasser *et al*., 2000; Tsimilli-Michael & Strasser, 2008) with the aid of the Biolyzer 4HP software.

The steady-state levels of the Chl*a* fluorescence parameters were determined by using a dual channel modulated fluorometer (FMS2, Hansatech Instruments, UK) on leaves after a 60 min dark adaptation period. The response curves of the modulated Chl*a* fluorescence parameters, as a function of the actinic light or the time of irradiation, were recorded by a PAM 200 (Teaching PAM, Walz, Germany) pulsed amplitude modulation fluorometer, on previously dark-adapted leaves. Throughout the Thesis we have followed the nomenclature of van Kooten and Snel (1990). The different fluorescence parameters (F_o, F_m, F'_o, F'_m and F), were then used to determine the fate of the absorbed excitation energy in the antenna system of PSII, according to the models of Demmig-Adams *et al*. (1996) and Hendrickson *et al*. (2004). This excitation energy can either be utilised during photochemistry or dissipated to the environment as a result of photoprotective mechanisms.

Photosynthetic pigment analysis

The amounts of the different photosynthetic pigments were determined by HPLC and spectrophotometric methods. For this purpose small discs were cut out of the leaves, found at similar positions on the plants, and they were kept in liquid nitrogen until the measurements. The Chl and total carotenoid contents were determined by using 80% acetone extracts of the plant material, according to the spectrophotometric

method of Lichtenthaler (1987). The HPLC pigment analysis was performed following the descriptions in Váradi *et al*. (2003). The interconversion of the xanthophyll cycle pigments (violaxanthin (Vio), antheraxanthin (Ant) and Zeaxanthin (Zea)) was quantified by introducing the de-epoxidation index (DEi), according to the formula: DEi = [½ × Ant + Zea]/[Vio + Ant + Zea]. The size of the xanthophyll cycle pool was expressed as the sum of these pigments: Vio + Ant + Zea, normalised to unit area [μmol m^{-2}].

DNA sequencing

Total genomic DNA was extracted from four-week-old leaves of *S. nigrum* lines following the instructions of the manufacturer (Zenon Biotechnology Ltd., Hungary). Using *psbS* specific primers we propagated three overlapping fragments of about 600 bp, 1360 bp and 159 bp from the plant material of the two parent line of *S. nigrum*. The 386 bp fraction of the *psbA* gene, containing the A → G nucleotide exchange (S264G mutation) was amplified by using the SniD1 primer in the D1 mutant (AR, ARF2, ARF6) and in the wild-type (AS, ASF2 and ASF6) lines. The results of the amplification were separated on 2% agarose gel and the fragments were isolated and cloned into the pGEM-T Easy vector. The products were then analysed by an automated microcapillary DNA sequencer.

Immunoblot analysis

PsbA (D1) and PsbS protein contents of the leaves were determined by Western blot analysis. Leaf discs, cut out of the AS and AR lines of *S. nigrum*, were quickly frozen in liquid nitrogen, then grinded down to fine powder and homogenised by the addition of Laemmli buffer. After incubation the proteins were separated by using SDS-polyacrylamide gel electrophoresis (Laemmli, 1970).

The proteins were transferred to a nitrocellulose membrane in a blotting buffer containing methanol. Blocking of non-specific binding was achieved by putting the membranes, for two hours, in TBS-T buffer, containing 5% milk powder, then primary antibodies, specific to the PsbA and PsbS proteins (Agrisera), were added and the membranes were left to incubate for another two hours. After the unbound antibodies were removed during a three times 5 min washing cycle in TBS-T buffer, the membranes were exposed to goat anti-rabit IgG secondary antibody, which was conjugated to a horseradish peroxidise (HRP) enzyme (Millipore), and incubated for two hours in TBS-T buffer containing 5% milk powder. This was followed by a three times 5 min washing cycle in TBS-T buffer and then the membranes were further incubated with ECL plus HRP substrate for five minutes. The chemiluminescence was detected on Hyperfilm ECL photographic film, which was then developed and digitalized before its analysis with the 1D Scan software package.

RESULTS

- The turn out of the reciprocal crossing of the AS and AR biotypes of *S. nigrum* were analysed by following the inheritance of a Mendelian trait of the plants, the leaf margin, which proved the hybrid status of the nuclei in the F2 plant material.

- The result of the reciprocal crossings proved that the differences in NPQ capacity is not influenced by the regulatory factors in the nuclei of the hybrids down to the F6 generation. This finding is in accordance with the DNA analysis of the AS and AR biotypes of *S. nigrum*, which showed no alteration in the amino acid sequence of the PsbS protein and there were no differences in the expression of the PsbS and D1 proteins, either.

- Using *in vivo* Chl*a* fluorescence techniques a slowdown in the PSII linear electron transport rate (J_{ETR}) was observed in the AR parent and hybrid lines, as well as a decrease in the photochemical quenching coefficient, and a drop off in the NPQ and its fast relaxing qE component, in particular.

- All AR lines exhibited a roughly 20% decrease in their activity for de-epoxidation, however, there was no significant difference in the size of the xanthophyll-cycle pool in the two biotypes and in their hybrids. The reduced capacity of the xanthophyll-cycle in the AR biotypes can partially explain the impaired NPQ (or qE) found in these plants.

- Based on the models used to determine the energy allocation pattern in PSII we conclude that a smaller fraction of the absorbed light was converted to chemically stored energy (Φ_{PSII}) in the AR lines, which can be related to the 50% lower photosynthetic performance index (PI_{abs}). Despite the lower light induced photoprotective NPQ (or qE) capacity of the AR lines the efficiency of the regulated thermal dissipation of the excitation energy (Φ_{NPQ} or Φ_{DL}) was not affected by the mutation on the D1 protein. As a compensatory mechanism to counteract the lower PSII efficiency in the mutant lines a significant increase in the non-regulated energy losses (Φ_{NO} or Φ_{E}) was observed, which represents dissipation processes of non-photoprotective nature hence possibly contributing to the lower fitness of the AR plants.

- The analysis of the fast Chl*a* fluorescence transients (OJIP) of the dark-adapted leaves of the AR biotypes also revealed a decline in PSII performance on the acceptor side. The JIP-test parameters, characterizing the reduction of the final electron acceptors of PSI, were found to be within statistical significance in both biotypes and in their hybrids except the δ_{Ro} parameter, representing the probability to transfer an electron from the intersystem electron carriers to reduce the final electron acceptors on the acceptor side of PSI, which has increased significantly in the AR lines. This, presumably, can compensate the lower rate of electron flow on the acceptor side of PSII as well as the decreased PI_{abs}, resulting similar PI_{total} values in the different biotypes of *S. nigrum*.

- These results show, that the D1 protein has an influence on the Chl*a* fluorescence properties in the AS and AR biotypes of *S. nigrum*. We believe that the highly conserved D1 protein plays an essential role in the formation of thermal dissipation processes to de-activate the excess excitation energy, as it was demonstrated by the co-

inheritance of the S264G mutation on the D1 protein, which is encoded in the chloroplast genome, and the low levels of NPQ (or qE) capacity.

- Based on the water balance parameters (stomata conductance, water potential) and the CO_2 assimilation rate it seems that the AR biotype was more tolerant towards the detention of water. Both the water balance parameters and the CO_2 assimilation rate started decreasing somewhat later in the AR biotype than in its AS counterpart. This was also substantiated by a weaker photorespiration, a higher rate of maximal assimilation (A_{max}), increased carboxylation efficiency (ε) and a higher regeneration rate of RuBP (J_{max}). The difference between the two biotypes gradually diminished with the progression of water detention and it practically disappeared during the intermediate phase of dehydration. The results of the investigations with the F2 generation of the reciprocal cross breeding show that the higher drought tolerance of the parent population of the AR biotype cannot be linked to the D1 mutation as the traits present in the parent population become blurred in the F2 generation. We conclude that the lower fitness of the AR lines cannot be explained by their weakened tolerance towards water detention.

- In both biotypes and in their hybrids, which suffered severe dehydration, the magnitude of PSII efficiency (Φ_{PSII}) and that of the linear electron transport rate drops back to similar levels. The NPQ has increased dramatically in all AR lines, whereas the increase was much less pronounced in their AS counterparts. Surprisingly, this seemed to correlate with the observations related to Φ_{NPQ} as well, unlike in the case of their well watered controls. The levels of a complementary process, Φ_{NO}, were found to be somewhat decreased in the AR lines, while an increase was observed in the wild-type plants as compared to their well watered control pairs. Based on the fluorescence parameters it seems reasonable to conclude that the photoprotection mechanisms induced by severe water stress are more efficient in the AR lines than in their AS counterparts. This can be, up to a certain extent, substantiated by the enhancement of the cyclic electron transport around the PSI, which can contribute to maintaining the NPQ by building up a transmembrane ΔpH and lessening the excitation pressure on PSII. We can assume that the drought-induced structural rearrangement of chloroplasts can also contribute to the development of a more efficient heat dissipating mechanism in the AR plants, however, in order to gain a better understanding of this phenomenon further investigations are required.

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