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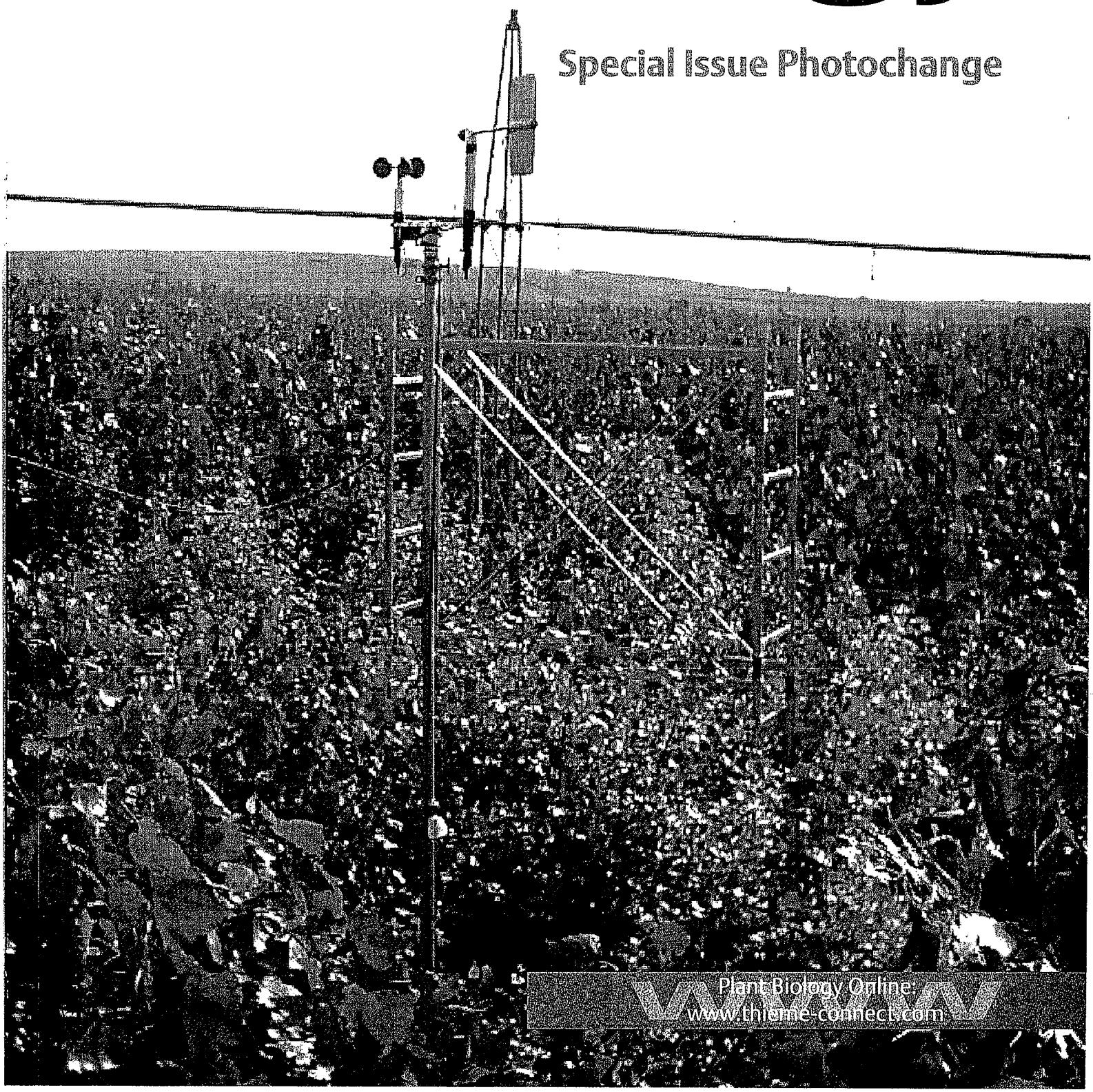

# Thermoluminescence Study of Photosystem II Activity in *Haberlea rhodopensis* and Spinach Leaves During Desiccation

V. Peeva and L. Maslenkova

Acad. M. Popov Institute of Plant Physiology, Bulgarian Academy of Sciences, Sofia, Bulgaria

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***Abstract:*** Thermoluminescence glow curve parameters were used to access the functional features of PS II in the Balkan endemic *Haberlea rhodopensis*. This representative of the higher desiccation-tolerant plants is unique for the European flora. An unusual high temperature of TL emission from *Haberlea* leaves after excitation by one flash at 5 °C was observed. The position of the main TL B band ($S_2Q_B^-$) was at 45–47 °C, while this temperature was 30–32 °C in drought-sensitive mesophytic spinach. Consistent with the up-shift in TL emission, the lifetime of the $S_2$ state was also increased, showing a stabilization of charge storage in PS II complex in this resurrection plant. In addition, a part of PS II centres was less susceptible to DCMU. We consider the observed unusual TL characteristics of *Haberlea rhodopensis* reflect some structural modifications in PS II (especially in D1 protein), which could be related to the desiccation tolerance of this plant. This suggestion was supported by the different manner in which dehydration affected the TL properties in desiccation-tolerant *Haberlea* and desiccation-sensitive spinach plants.

***Key words:*** Desiccation tolerance, thermoluminescence, PS II, resurrection plants, *Haberlea rhodopensis*.

***Abbreviations:***

| | |
|---|---|
| DCMU: | 3-(3,4-dichlorophenyl)-1,1-dimethylurea |
| PS II: | photosystem II |
| OEC: | PS II oxygen-evolving complex |
| RH: | relative humidity |
| RWC: | relative water content |
| TL: | thermoluminescence |
| $Q_A$: | first quinone electron acceptor of PS II |
| $Q_B$: | second quinone electron acceptor of PS II |
| $S_2$ and $S_3$: | charge storage states of water-oxidizing complex |

## Introduction

Drought is one of the major factors characterizing global environmental change. Water deficiency adversely impacts plant photosynthetic performance (Hsiao, 1973). The inhibition of photosynthetic process could be ascribed to both stomatal and non-stomatal limitations in dependence on the strength and duration of the water deficit and on the sensitivity of the plant species (Boyer, 1976; Bradford and Hsiao, 1982; Bjorkman and Powles, 1984; Kaiser, 1987).

Under conditions of severe or prolonged water deficit, most plants are homoiohydric, i.e., desiccation-intolerant. Their chloroplast structure and composition and the photochemical reactions, particularly PS II activity, have been shown to be directly affected. The harmful effects of severe dehydration were manifested in considerable changes of electron transport capacity and in reduction of $O_2$ evolution (Govindjee et al., 1981; Havaux et al., 1986; Chen and Hsu, 1995; He et al., 1995), but the primary target of PS II drought inhibition is still controversial. Damage to electron donation from the water oxidizing system (Canaani et al., 1986), considerable depletion of the PS II core and structural reorganisation of the remaining centres (Giardi et al., 1996), changes in PS II membrane protein metabolism (He et al., 1995), and inhibition of both the oxygen-evolving complex and the acceptor side of PS II (Skotnica et al., 2000) have been considered as some possible reasons for PS II impairment in water-stressed plants.

Besides bryophytes and lichens, few vascular plants possess a unique capability to survive extended periods of severe water deficit in a physiological state called "anabiosis" (Gaff and Hallam, 1974; Bewley, 1979). In such a desiccated state the physiological functions, including the photosynthetic activity, of these poikilohydric or "resurrection" plants completely cease. Nevertheless, during rehydration, this actvity can be fully restored, with different rates in homoiochlorophyllous and in poikilochlorophyllous plants (Gaff, 1989; Tuba et al., 1996). Many different aspects of the desiccation tolerance in vascular plants have received considerable attention (Ingram and Bartels, 1996; Yordanov et al., 2000), but the exact mechanism(s) of this phenomenon is still not well understood. The complete reconstitution of chloroplast structure and functional activity in resurrection plants suggests some peculiarities of thylakoid membrane or chloroplasts stroma composition (Schwab and Heber, 1984; Schwab et al., 1989), which make these plants a very suitable model system for investigation of the mechanisms related to the PS II perturbation and the adaptive plasticity during water stress.

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As the object of this investigation, we chose a unique species of the European flora – the Balkan endemic *Haberlea rhodopensis* Friv. (Gesneriaceae), belonging to a very small group of desiccation-tolerant vascular flowering plants. This plant is a tertiary paleophylic relic with limited and remotely partitioned habitats. It prefers the shady, mostly northward slopes of limestone ridges in creek gorges and mountain zones with higher humidity. Attached to the smallest cracks in rocks, numerous plants group in abundant chains and stringcourses, thus retaining a substantial amount of humus soil to promote their development.

In the present study, the flash-induced thermoluminescence curve parameters have been used to investigate the functional features of PS II in the resurrection plant *Haberlea rhodopensis*, in comparison to a mesophitic desiccation-sensitive higher plant *Spinacia oleracea*. We try to characterise more precisely the effects of desiccation on the redox functioning of both donor and acceptor side of PS II in the investigated species.

## Materials and Methods

### *Plant material*

Well hydrated *Haberlea rhodopensis* Friv. (Gesneriaceae) plants were collected from their natural habitat (the vicinity of Asenovgrag, Bulgaria) during the period of flowering in May–June. Detached leaves were used in our dehydration and rehydration experiments. Comparative experiments were done with intact, photosynthetically active leaves from the desiccation-sensitive mesophytic plant *Spinacia oleracea* L. (Chenopodiaceae) purchased from the local market. Young, fully expanded leaves from the middle of rosettes, with similar size and appearance were used in order to obtain reproducible results. During dehydration of *Haberlea* and spinach leaves under our experimental conditions, leaf pigment composition does not show significant changes.

### *Desiccation and rehydration*

Freshly detached leaves from well hydrated plants were placed between plastic nets and subjected to dehydration in air of about 60% RH, in the dark at room temperature (23 ± 1 °C). Control samples of detached leaves were placed into Petri dishes on moist filter paper and kept under the same conditions. Rehydration experiments on desiccated leaves were carried out by wrapping the leaves in wet paper towels for 24 h at room temperature in the dark. Three separate experiments of desiccation and rehydration led to essentially similar results.

### *Determination of relative water content (RWC)*

The RWC of both *Haberlea* and spinach leaves were determined gravimetrically by weighing them before and after oven drying at 80 °C to a constant mass, and expressed as a percentage of water content in water-saturated tissues, as described in Turner (1981), using the equation:

$$\mathrm{RWC}\ (\%) = \frac{\mathrm{m(fresh)} - \mathrm{m(dry)}}{\mathrm{m(saturated)} - \mathrm{m(dry)}} \cdot 100$$

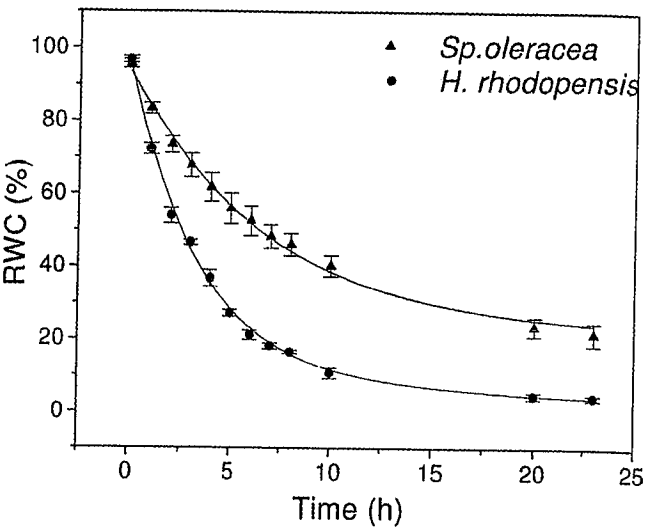


**Fig. 1** Changes in RWC in detached *Haberlea* (●) and spinach (▲) leaves during dehydration in the dark at room temperature and 60% RH.

### *Thermoluminescence*

Thermoluminescence (TL) measurements were carried out in a room with a green safe light, using a computerized setup described elsewhere (Zeinalov and Maslenkova, 1996). Leaf segments were placed on a sample holder and covered with a thin plastic plate. TL was excited by single turnover flashes (10 µs half-band width, 1 Hz frequency), given at 5 °C or in the presence of DCMU, at – 10 °C and quickly cooled in liquid nitrogen before being warmed to 50 °C with 0.6 °C/s heating rate.

Vacuum infiltration of the leaves with the PS II electron transport inhibitor DCMU was accomplished according to Rutherford et al. (1984).

For the thermoluminescence measurements of the life time of $S_2Q_B^-$ state, dark-adapted samples were illuminated with one flash at room temperature, kept at about 25 °C for different dark intervals (0–3 min), and cooled to 77 K for subsequent TL measurements (Rutherford et al., 1984).

### *Statistics*

Means and standard deviations for RWC, $S_2$ deactivation and thermoluminescence B peak parameters (amplitudes and temperature positions) were calculated from five replicates of each dehydration and rehydration treatment in three separate experiments.

## Results and Discussion

### *Kinetics of RWC in detached leaves*

The decrease in relative water content of *Haberlea* and spinach leaves during dehydration under our experimental conditions is shown in Fig. 1. Freshly detached leaves from well watered *Haberlea* and spinach plants showed similar starting RWC values of about 95%, but the kinetics of water loss in the two species were quite different. The leaves from spinach plant lost their water gradually, like other mesophytic plants (Schwab

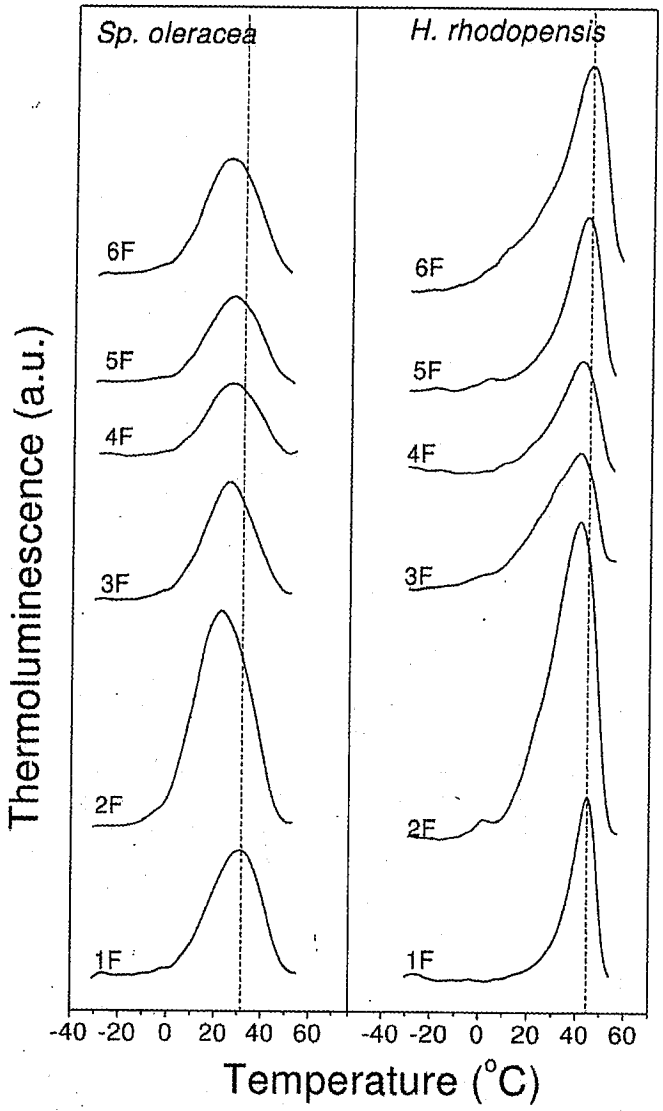


**Fig. 2** TL B band ($S_2Q_B^-$) emission of fully hydrated (control) *Haberlea rhodopensis* and spinach leaves as a function of the number of flashes (F), from 0 to 6, given at 5 °C. The leaves were dark-adapted for 30 min at room temperature.

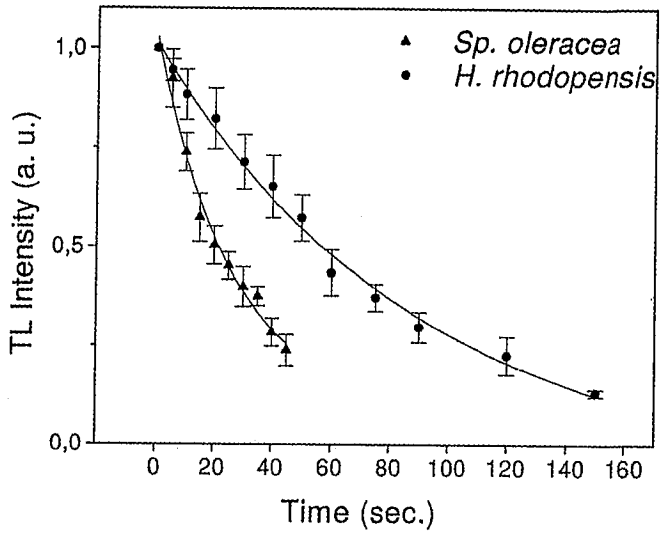


**Fig. 3** The decay of the B band ($S_2Q_B^-$) as a function of time. Dark-adapted leaf segments were excited with a single saturating flash at about 25 °C and stored in the dark for different intervals before being frozen. *Haberlea rhodopensis* (●); *Spinacia oleracea* (▲).

et al., 1989; Matouskova et al., 1999), and after 20 h of dehydration RWC reached values of about 30%. Spinach leaves typically desiccated to 10% RWC within 35–40 h. Conversely, detached leaves from the resurrection plant desiccated faster, especially in the first hours of the desiccation period and needed less than 5 h to reach 30% RWC. Their RWC dropped below 10% in about 20 h. Fully hydrated leaves and leaves dehydrated to about 60%, 40%, 25%, and below 10% RWC (desiccated) from both investigated species were used in the desiccation experiments.

### *Flash-induced thermoluminescence from control* Haberlea *and spinach leaves*

In order to characterize more precisely the features of PS II in the resurrection plants, we compared the thermoluminescence emission in well hydrated intact (detached) leaves of *Haberlea* and of a desiccation-sensitive (spinach) mesophytic plant (Fig. **2**). Thermoluminescence proved to be a very sensitive and reliable biophysical method for investigation of the functioning of PS II donor and acceptor side components (for reviews see Sane and Rutherford, 1986; Vass and Inoue, 1992; Vass and Govindjee, 1996). TL signals resulted from the thermal activated recombination of the trapped electrons and stabilized positive "holes" on the reduced quinone acceptors ($Q_A$ or $Q_B$) and on the $S_2$ (or $S_3$) oxidation state of the water splitting complex, respectively. Illumination of dark-adapted spinach leaves with a single flash (1F), generating an $S_2Q_B^-$ charge pair, induced a TL light emission, the so-called B band, at around 32 °C (Fig. **2**), which is usually observed in higher plants (Rutherford et al., 1982). The most striking feature of the TL emission observed in the *Haberlea* leaves was the shift of the B peak emission temperature to 45–47 °C. Similarly, different emission temperatures were registered when more than one flash was given (Fig. **2**). Alterations in the TL band temperatures show changes in the stability, redox potential, or activation energy of the reactivating charge pairs (Rutherford et al., 1984). The B peak position at higher temperature is indicative of more stable stored $S_{2(3)}Q_B^-$ charge pairs in the resurrection plant. With intact photosynthetically active cells, such a high TL B peak emission temperature had been reported for another type of stress-tolerant organism, namely a thermophylic cyanobacterium or desiccation-tolerant ferns and lichens (Govindjee et al., 1985; Maslenkova and Homann, 2000; Sass et al., 1996). Krieger et al. (1998) reported a 46 °C B band originating from PS II centres in a facultative CAM plant *Mesembryanthemum crystallinum* and assumed its induction to be connected with the metabolic state of the leaves under CAM conditions.

Consistent with the increased emission temperature of the B band of *Haberlea* leaves, the lifetime of the $S_2$ state, as reflected by the disappearance of the TL B band after a single flash, was also increased. Our data showed (Fig. **3**) a longer lifetime ($t_{1/2}$ = 53 s) in comparison to $t_{1/2}$ = 20 s in spinach leaves.

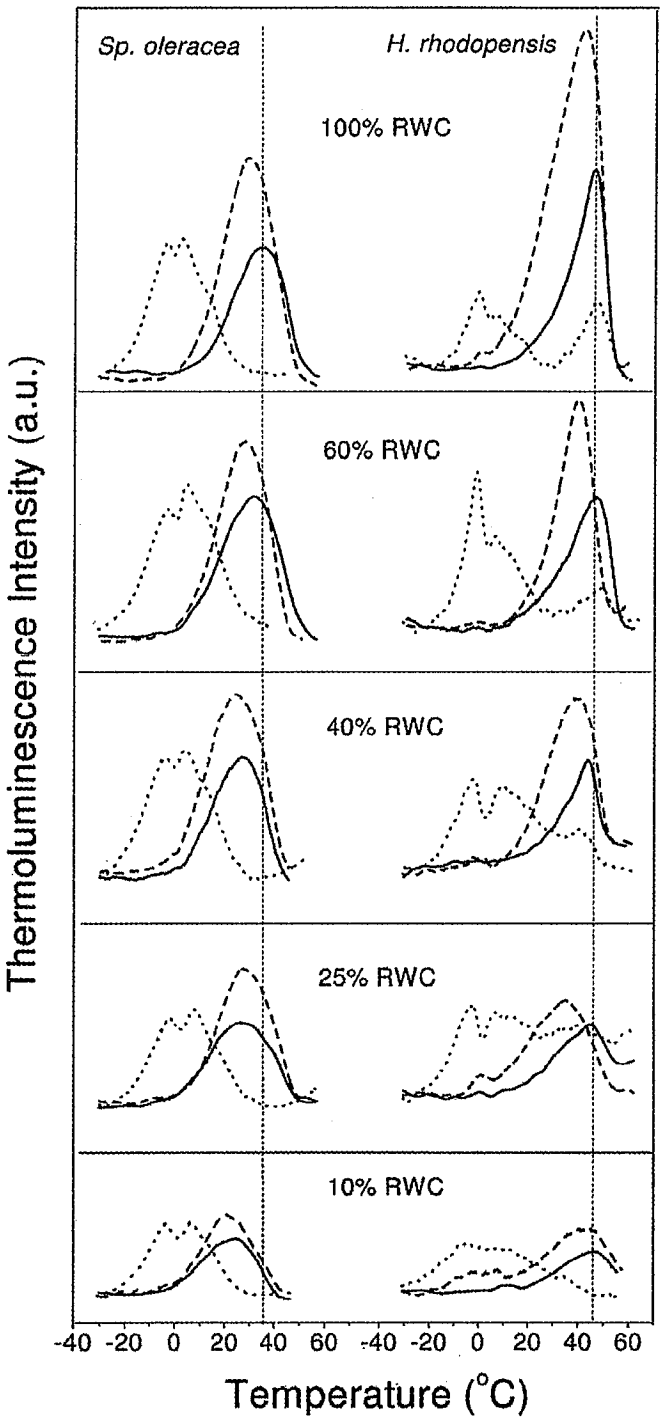


**Fig. 4** Effect of dehydration on the thermoluminescence of the B band after 1F ($S_2Q_B^-$) – solid line; 2F ($S_3Q_B^-$) – dashed line, and Q band ($S_2Q_A^-$) – dotted line in *Haberlea rhodopensis* and spinach studied in fully hydrated leaves, leaves dehydrated to about: 60% RWC, 40% RWC, 25% RWC and desiccated leaves (RWC below 10%).

The intensity of the TL B band exhibited a typical period four-oscillation pattern, with the maximum on the second flash when control leaves of both investigated species were illuminated by a flash series (Fig. **2**). TL oscillations are related to dark distribution of the S states of OEC and the $Q_B/Q_B^-$ ratio (Rutherford et al., 1984), thus suggesting no differences in these parameters between species.

The high emission temperature of the TL B band from *Haberlea* leaves could be attributed to some changes in the properties of redox partners on the donor or on the acceptor side of PS II, or to both. One way to test the contribution of $Q_B^-$ is to monitor TL after infiltration of the leaves with DCMU, which specifically inhibits electron transport between the primary ($Q_A$) and the secondary ($Q_B$) quinone acceptors. Recordings in Fig. **4** (upper row) show that DCMU treatment of spinach leaves leads to a significant down-shift in B peak position, concomitantly with a decrease in its amplitude and the appearance of a new, so-called Q band peaking at around 0 °C, which is thought to originate from $S_2Q_A^-$ charge recombination (Rutherford et al., 1982). In 20 µM DCMU-treated *Haberlea* leaves, the Q band also appeared at approximately the same temperature. Since the S states are the common pole for positive charges of the B and Q band, the distinct differences of B peak temperature position in *Haberlea* and spinach leaves suggest major alterations in the redox property of $Q_B^-$ in the resurrection plant. Surprisingly, a part of B band in *Haberlea* leaves was still clearly expressed, even at higher inhibitor concentrations. These results show that some PS II reaction centres in *Haberlea* leaves with more stable stored $S_2Q_B^-$ charge pairs are less susceptible to DCMU. Ohad et al. (1990) reported a similar residual B peak in a *Chlamydomonas* cell suspension exposed to high light in the presence of DCMU, and consider this proof for conformational changes in PS II reaction centres. Hideg et al. (1993) observed incomplete suppression of the B band by DCMU after UV-B irradiation and assume this to reflect same acceptor-side modifications. The observed differences in TL parameters of *Haberlea* in comparison with spinach leaves suggest some peculiarities in the structure and charge storage in PS II of this resurrection plant that could be related to its survival during desiccation–rehydration cycles.

### *Changes in thermoluminescence characteristics during desiccation*

The effect of desiccation on the functioning of PS II oxygen-evolving centres was monitored by changes in TL curves parameters in comparative experiments in the dark with dehydrated spinach and *Haberlea* leaves. The traces in Figs. **4** and **5** reveal that dehydration to different RWC affects the TL properties of *Haberlea* and spinach leaves in quite different ways. While the B peak emission temperature was clearly down-shifted in spinach with the decrease in the leaf RWC (with 10 °C at 10% RWC), it was unchanged in desiccating *Haberlea* leaves. On the other hand, the decrease in TL intensity of the B band during dehydration was significantly more expressed in the resurrection plant. The B band amplitude in *Haberlea* leaves desiccated to 10% RWC was only 20% of the B peak amplitude of fully hydrated leaves. According to TL theory, the amplitude of the B band is proportional to the number of centres having $S_2(S_3)Q_B^-$ charge pairs after flashes, while the maximal emission temperature of this band is a measure for redox span between the separate charges. Thus, the obtained results show that severe dehydration of resurrection plants *Haberlea* mainly affects the number of PS II reaction centres, without destabilising the remaining operative centres. After rehydration of desiccated *Haberlea* leaves (Fig. **5**), the number of operating PS II centres was nearly completely restored, judging from restoration of B peak amplitude. This process was very rapid (rehydration for only 2 h restored more than 80% of B band). Severe dehydration of the leaves from mesophytic spinach

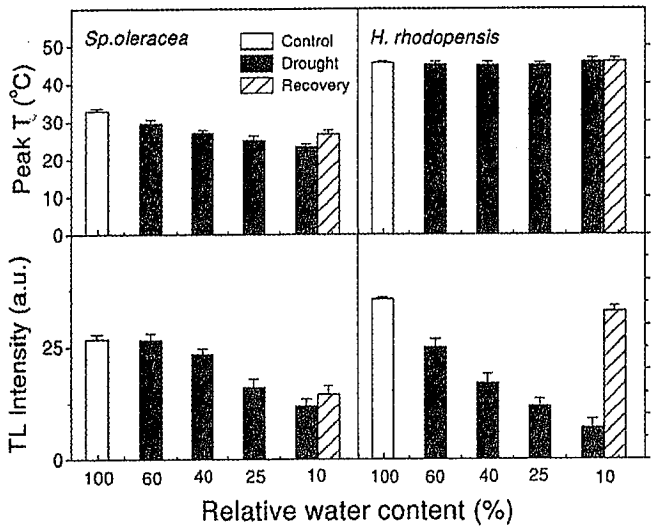


**Fig. 5** Dependence of peak temperatures and relative TL intensities of the B band ($S_2Q_B^-$) in *Haberlea* and spinach leaves on RWC.

plants also inhibits the number of operating centres, but leads predominantly to a well-expressed downshift of B peak position close to the Q band position. These observations are in accordance with the previous TL investigation of Skotnica et al. (2000) with desiccating barley leaves. It may be concluded that in spinach leaves subjected to severe dehydration the electron transport between primary ($Q_A$) and secondary ($Q_B$) quinone acceptors is inhibited, and damaged OEC occur. Such PS II centres do not restore their photochemical activity during rehydration. However, dehydration of *Haberlea* leaves significantly decreases the total number of PS II RC, while the remaining operative centres do not show any changes in their energetic state.

## Conclusions

The uniquely high temperature of thermoluminescence B peak emission from leaves of *Haberlea rhodopensis*, and the different TL pattern observed in *Haberlea* compared to that in desiccation-sensitive spinach during dehydration indicate some modifications of the redox properties of $Q_B$ (especially in D1 protein), most likely related to the desiccation tolerance of this resurrection plant. Specific lipid and sterol composition of *Haberlea* leaves (Stefanov et al., 1992), as well as the presence of different protective compounds, may contribute to these modifications. A set of comparative experiments on TL and oxygen flash patterns of isolated *Haberlea* and spinach thylakoid membranes are in progress to clarify this possibility.

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V. Peeva

Acad. M. Popov Institute of Plant Physiology
Bulgarian Academy of Sciences
Acad G. Bonchev Str., Bl. 21
Sofia 1113
Bulgaria

E-mail: vili@obzor.bio21.bas.bg

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