DOI: 10.1007/s11099-011-0020-4 PHOTOSYNTHETICA 49 (1): 119-126, 2011

Changes in chloroplast morphology of different parenchyma cells in leaves of *Haberlea rhodopensis* Friv. during desiccation and following rehydration

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Abstract

The size, shape, and number of chloroplasts in the palisade and spongy parenchyma layers of *Haberlea rhodopensis* leaves changed significantly during desiccation and following rehydration. The chloroplasts became smaller and more rounded during desiccation, and aggregated in the middle of the cell. The size and number of chloroplasts in the palisade parenchyma cells were higher than in spongy parenchyma. The good correlation observed between the size or number of chloroplasts and the cross-sectional area of mesophyll cells, the cross-sectional width of the leaf and its water content suggested that the palisade cells were more responsive to water availability than the spongy cells. Changes in chloroplast number during desiccation and rehydration process are characteristic features for desiccation-tolerant plants (especially in homoiochlorophyllous strategy).

Additional key words: chloroplast; desiccation tolerance; homoiochlorophyllous; mesophyll; palisade parenchyma; spongy parenchyma.

Introduction

Desiccation-tolerant (DT) plants which may be subdivided into poikilochlorophyllous (PDT) and homoiochlorophyllous (HDT) types, can survive the loss of 80–95% of their cell water content (Tuba *et al*. 1998). PDT species are adapted to sites where drought periods are extended over weeks or months, whereas HDT species, involving *Haberlea rhodopensis*, easily manage in sites with frequent oscillations between dry and wet stages in shorter periods of time (Kappen and Valladares 2007).

In hydrated state the mesophyll cells of DT plants have a large central vacuole, cytoplasm and cell organs are situated at the cell periphery (Farrant *et al*. 2009). Similarly, in fully hydrated leaves of normal vascular plants (*e.g.* some Poaceae taxa), cell organelles are also located in the cell periphery (Black and Mollenhauer 1971). During desiccation, folding of the cell wall and some plasma membrane withdrawal can be observed. Complexity of the cytoplasm is reduced and vacuoles are fragmented into numerous smaller vesicles which become filled with a lipophilic substance, generating a back-pressure for the desiccating cell (Farrant *et al*. 2003). In mesophyte species cellular water deficit can result in a concentration of solutes, changes in cell volume and membrane shape (Bray 1997).

Number, size, and shape of the chloroplasts can vary with leaf size, light intensity, water availability, and quantity of minerals (Wang and Zhang 2004, Papadakis *et al*. 2007, Königer *et al*. 2008). Location of the chloroplasts in the cells was also influenced by light and moisture conditions of their environment (McCain 1995, Bartoskova *et al*. 1999, Williams *et al*. 2003). Under low light illuminations (20–250 μmol m^{-2} s^{-1}) chloroplasts localize along the periclinal walls (Eckardt 2003). Nevertheless, in leaves exposed to higher light intensities (above 1,000 μmol m^{-2} s^{-1}), chloroplasts move to the edges of the mesophyll cells (Wada *et al*. 2003). Shape of the chloroplasts can also change during desiccation; they become less rounded and have ellipsoidal shape

Received 5 November 2010, *accepted* 25 January 2011.
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Abbreviations: Ac – cross-sectional area of chloroplasts; Am – cross-sectional area of mesophyll cells; DT – desiccation tolerant; HDT – homoiochlorophyllous DT; Lc – length of chloroplasts; Nc – chloroplast number per cell; PCE – piece; PDT – poikilochlorophyllous DT; PP – palisade parenchyma; SP – spongy parenchyma; W – cross-sectional width of the leaf; Wc - width of chloroplasts; WC – water content.

(Abdelkader *et al*. 2007, Barhoumi *et al*. 2007). Quantity distribution of chloroplasts between mesophyll layers is different in mesophyte species; palisade mesophyll cells usually contain twice as much chloroplast than spongy cells (Igboanugo 1989, Radwan *et al*. 2008).

Structural changes during desiccation are usually small in the homoiochlorophyllous species, the structure of thylakoid membranes with associated chlorophyll complexes apparently seem to be unchanged (Gaff 1989). In contrast to HDT strategy, in the dry leaves of the PDT species a breakdown process of photosynthetic proteins can be observed during dismantling of the photosynthetic apparatus and thylakoid membranes become vesiculated (Farrant *et al*. 2003, Ingle *et al*. 2007). In desiccated condition, these plants lose their chlorophyll and starch contents and chloroplasts are stored in a stable form (Sherwin and Farrant 1996). In HDT species inner membranes of chloroplast and levels of the photosynthetic proteins were largely maintained during dehydration. Moreover, chloroplasts have well-defined thylakoid membranes and starch structures, however, most thylakoids were crushed to form large stacks, they can be blistered and membranes were separated under desiccated state (Ingle *et al*. 2007, Farrant *et al*. 2009, Wang *et al*. 2009). Subcellular organization was fully recovered following 16-h wetting period in *Selaginella lepidophylla* (HDT pteridophyte species) while it was observed after 48-h rehydration in the leaves of *Craterostigma wilmsii* and *Myrothamnus flabellifolia* (HDT plants) just as *Xerophyta humilis* (PDT plant) (Brighigna *et al*. 2002, Farrant *et al*. 2003).

To the best of our knowledge, there are no investigations so far on the changes of numerical data and correlations of chloroplasts during dehydration-rehydration cycle not only in *H. rhodopensis* but even in HDT plants. The aim of the present study was to follow the changes in the chloroplast shape, size and number during 72 h of dehydration of *Haberlea* plants to severe desiccated state (30% WC) and following 96 h of rehydration. Moreover, we would like to find if there were any differences between mesophyll tissues considering quantitative changes of their chloroplast content during a whole desiccation-rehydration cycle.

Materials and methods

Plant material: *Haberlea rhodopensis* Friv. (Gesneriaceae) is a perennial herbaceous, shade-adapted plant species of the Balkan region. Plants were collected from their natural habitat in fully hydrated state (control) and stored in a chamber at room temperature (22–25ºC) and low light intensity (about 100 μmol m^{-2} s^{-1}). All measurements were performed from 5–10 leaves of 5 plants per experiment.

Desiccation and rehydration procedure: Whole *Haberlea* plants were desiccated slowly and gently over 3 days in a special dehydration box. This box is a 45 × 25 cm closed system assuring continuously air steaming by an air pump inside the box through the silica gel which bonds the air humidity coming from the plants. Following desiccation the plants were rehydrated for 96 h in a reconstructed exsiccator providing permanent humidity by a water pump and direct spraying on the plant surface. Both dehydration and rehydration of plants was performed at room temperature (22–25ºC) and light intensity of about 100 μmol m^{-2} s^{-1}. Illumination was supplied by a cold light (*FLQ 150, Hund Wetzlar*, Germany) source. All measurements were carried out on fully hydrated (control) plants, after 24, 48, and 72 h of dehydration as well as following 24, 48, 72, 78, and 96 h of rehydration.

The water content (WC) of leaves was determined gravimetrically using the fresh (FM) and dry (DM) mass of the samples drying at 80ºC to a constant mass and referred to a percentage of water content (Tuba 1987), using the equation:

$$WC\ [\%] = [(FM–DM)/FM] \times 100.$$

Light microscopy: After cutting the leaves from whole plants, samples were dehydrated in an ascending acetone series and xylol, then they were embedded in paraplast. 8–10 μm thick cross sections were cut with sliding microtome (*Reichert GmbH Vienna*, Austria) from the medial region of the leaf blade. After staining with 2% (v/w) aqueous toluidine blue, samples were fixed in Canada balsam (Sárkány and Szalai 1957). Sections were photographed at magnification of × 100 with *G9 Power Shot* camera (*Canon Inc*., Japan, Tokyo) adapted to a *DM 2500* light microscope (*Leica Microsystems Inc.,* Wetzlar, Germany). Ocular micrometer (*Reichert GmbH,* Vienna, Austria) was used for calibration of the microscope. Leaf thickness (W), length (Lc), width (Wc), area (Ac) of chloroplasts, chloroplast number per cell (Nc), and cell size of spongy and palisade mesophyll cells (Am) were determined with the software *Image Tool 3.0* which was developed by the Department of Dental Diagnostic Science, The University of Texas Health Science Center (UTHSCSA), San Antonio, Texas.

Statistical analysis: All statistical analyses of variance (*ANOVA*) were performed using *Statistica 5.1* software. Effects of dehydration or rehydration time, mesophyll type, and their interactions were analyzed using a two-way *ANOVA* ($p \leq 0.05$). If significant differences were determined by *ANOVA*, *Tukey*'s test was used to test for significant differences in variability between sampling time points. Pearson correlation analysis was used to compare the water content of leaves, leaf thickness, and area of mesophyll cells with the size, shape, and number of chloroplasts in palisade or spongy parenchyma cells.

Results

The water content of leaves (WC) decreased by 60% compared to the control after 72 h of dehydration (Table 1). However, following 96 h of rehydration it was back to the control level. As a result of desiccation to WC of 30% the chloroplasts became smaller (Fig. 1*A–C*) than control ones and they were aggregated in the middle of the cell both in palisade and spongy parenchyma (Fig. 2). The chloroplast length (Lc), width (Wc) and cross-section area (Ac) decreased approximately by 30% during desiccation period in both parenchyma tissues. At the end of rehydration (96 h), their size was reconstructed and they spread in the cytoplasm similarly to the control (Figs. 1,2). The statistical analysis also confirmed that the size of chloroplasts underwent significant changes during desiccation and following rehydration. Samples differed from each other notably in the consecutive sampling time points. Chloroplast size of spongy and palisade cells were also dissimilar (Table 2). In spongy tissue Lc and Wc showed significant correlation with some measured histological characters (leaf thickness and area of mesophyll cells), while in palisade layer they correlated rather with WC (Table 3).

Table 1. Changes of water content (WC) of *Haberlea rhodopensis* leaves during desiccation and following rehydration. The values are shown as mean ± standard deviation (SD) (n = 5).

Treatment	Time [h]	WC [%]
Control	-	77.83 ± 1.43
Desiccation	24	73.80 ± 0.84
	48	78.80 ± 1.22
	72	30.55 ± 6.30
Rehydration	24	65.12 ± 2.82
	48	76.47 ± 2.63
	72	80.78 ± 1.54
	96	79.88 ± 2.93

The area of palisade mesophyll cells was usually larger about spongy cell's area with 100–150 μm^2 during dehydration and with 250–300 μm^2 during rehydration (Fig. 3*A*). The cell size (Am) increased by 73% in the palisade layer and 37% in the spongy tissue after 96 h of rehydration of fully desiccated (72 h) plants. The cross-sectional width of the leaf (W) also increased by 71% during rehydration (Fig. 3*B*).

The Lc/Wc index was used to determine the shape of chloroplasts. Its values changed between 1.2–1.4, indicating that the chloroplasts's shape was slightly ovoid in any sampling time and in both parenchyma types during the whole dehydration-rehydration cycle (Fig. 1*D*). The significant variation in the shape of chloroplasts during dehydration-rehydration process with parenchyma type and time was also confirmed by the statistical analysis (*ANOVA*) (Table 2). It was established that in control samples the spongy cells had more longish chloroplasts than chloroplasts of palisade cells which were rounded (Fig. 1*D*). The chloroplast shape of spongy cells was connected with the size of chloroplasts. Namely, their chloroplasts became almost round and significantly smaller during desiccation. However, in palisade parenchyma negative correlation was observed between Lc/Wc and number of chloroplasts (Nc). Accordingly, more desiccated cells contained less and more rounded chloroplasts than rehydrated cells (Table 3, Fig. 1*D*).

In comparison to parenchyma tissues, palisade cells usually contained with 0.2–0.3 μm longer and wider chloroplasts than spongy parenchyma cells and the area of their chloroplasts was larger with 0.5–1.0 μm^2 during the whole study period (Fig. 1*A–C*).

In any leaf samples collected during both desiccation and rehydration, the chloroplast number was higher in the palisade cells than in the spongy ones. In spongy parenchyma Nc changed between 10–16 per cell. Nc of palisade cells varied between 16–22 during dehydration-rehydration period (Fig. 4). In both type of parenchyma tissues, Nc increased during desiccation and after rehydration compared to the control. Changes of Nc of the spongy and palisade parenchyma cells were higher during rehydration (30% and 37%, respectively) than during desiccation (17% and 14% respectively).

Above results were confirmed by the analysis of variance (Table 2). Regardless of reduction in the size of both mesophyll cell types during 72 h of dehydration, Nc slightly increased. It can be due to the water-stress-induced high portion of chloroplast inside the cell. The number of chloroplasts could not show any significant correlation with WC (r_{NcPP} = 0.2713; r_{NcSP} = 0.3565; n = 8; p<0.05) in case of either the spongy or palisade cells. This was supported by HDT strategy because these DT plants don't lose their chlorophylls during desiccation.

Discussion

The results clearly showed that the size, shape and number of chloroplasts vary significantly during dehydration-rehydration process with time and parenchyma type (Table 2). During desiccation the smaller Ac may be explained by the blistering of the thylakoid membranes, while aggregation of the cell organs could be due to the reduction of the complexity of the cytoplasm and the withdrawal of the plasmalemma (Sherwin and Farrant 1996, Wang *et al*. 2009). The correlation of Ac with WC in palisade layer indicated that its cells were more susceptible to variation of water conditions (Table 3). The area of the palisade mesophyll

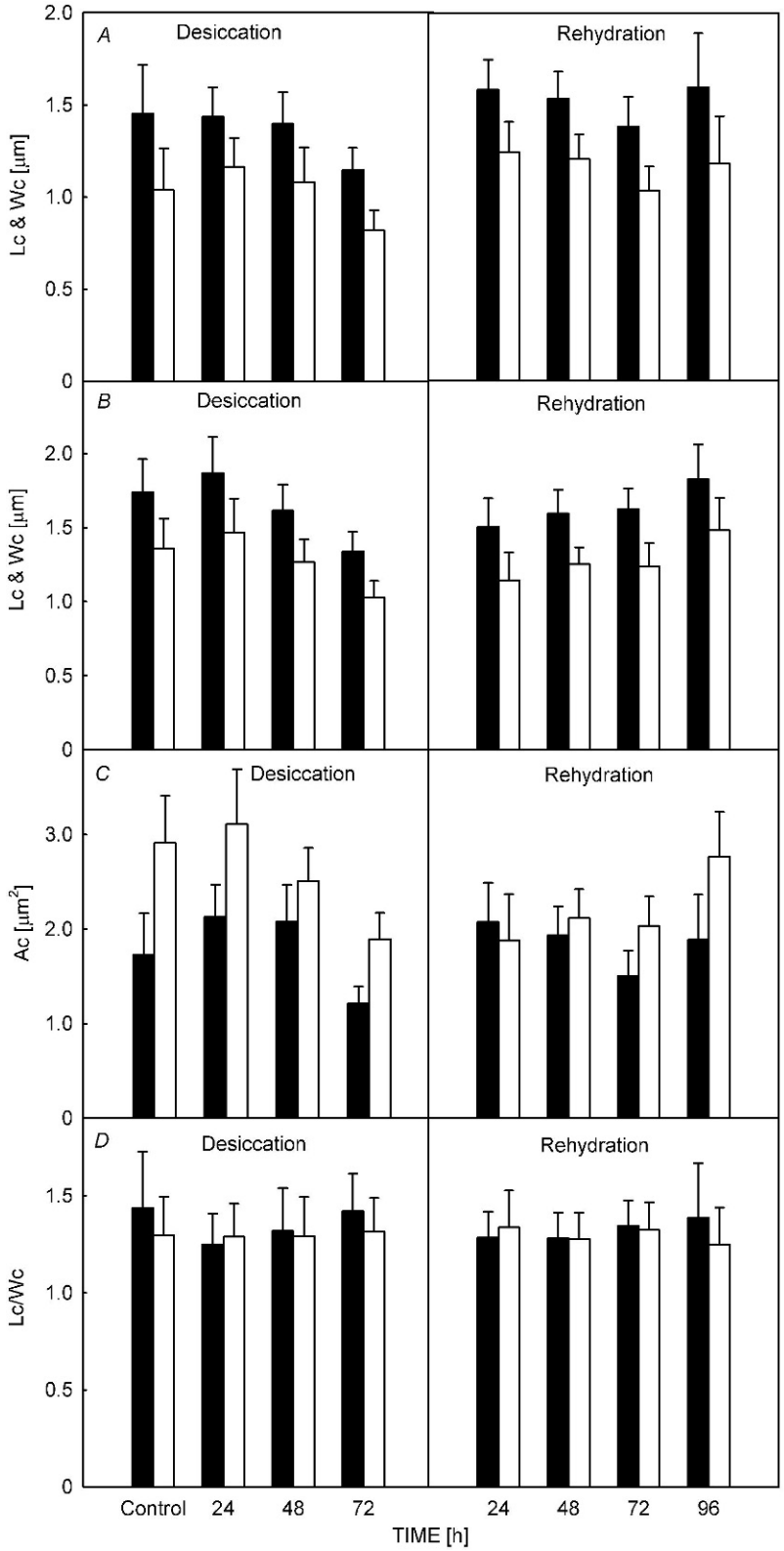

Fig. 1. Changes of histological parameters of chloroplasts during desiccation and following rehydration. *A*: cross-sectional length (*black bar*s) and width (*white bar*s) of chloroplasts in spongy layer, *B*: cross-sectional length (*black bar*s) and width (*white bar*s) of chloroplasts in palisade layer, *C*: cross-sectional area of chloroplasts (Ac) in spongy (*black bar*s) and palisade layer (*white bar*s), *D*: cross-sectional length and width ratio of chloroplasts (Lc/Wc) in spongy (*black bar*s) and palisade layer (*white bar*s). The values are shown as mean ± standard deviation (SD) (n = 50).

cells changed more (73%) during dehydration-rehydration cycle than spongy cells (37%), confirming that palisade cells were more sensitive to variation of water conditions (Fig. 3*A*).

Jeong *et al*. (2002) reported strong correlation between mesophyll cell size and chloroplast number in normal vascular plants, which could explain the differences in chloroplast number between larger palisade cells and smaller spongy cells. During desiccation the slight increase of Nc could be due to some leaf shrinkage

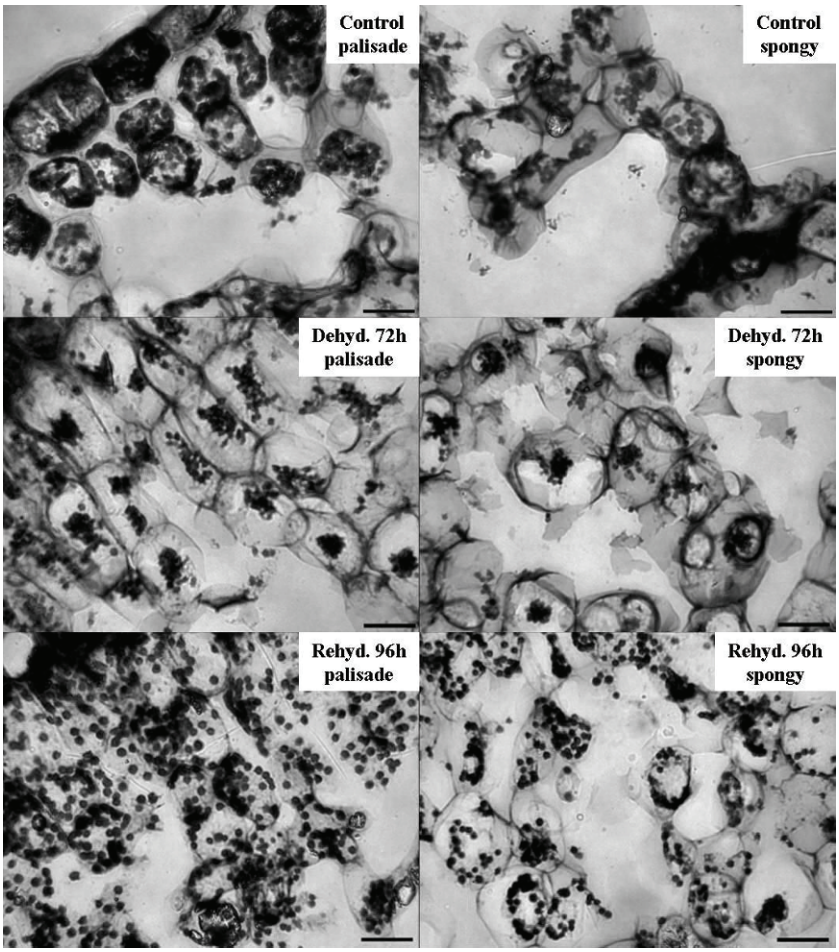

Fig. 2. Distribution of the chloroplasts in the palisade and spongy parenchyma layers of *Haberlea rhodopensis* leaves at different states of desiccation-rehydration cycle: full hydrated (control) palisade parenchyma, full hydrated (control) spongy parenchyma, dehydrated (72 h) palisade parenchyma, dehydrated (72 h) spongy parenchyma, rehydrated (96 h) palisade parenchyma, rehydrated (96 h) spongy parenchyma. All sections were stained with toluidine blue. *Bar* = 10 μm.

Table 2. Differences among chloroplast parameters by two-way *ANOVA* test. Two independent variables are: rehydration time and mesophyll type. Df − degree of freedom; SS − sum of squares; MS − mean squares; F − value of *Fisher* test; all data are significant at $p < 0.001$. Nc – chloroplast number per cell; Lc – cross-sectional length of chloroplasts; Wc – cross-sectional width of chloroplasts; Ac – cross-sectional area of chloroplasts.

Factors and effects		df	SS	MS	F	*p*
Nc [PCE]	time	7	1,382.82	197.55	24.74	1.38E-30
	parenchyma type	1	7,417.62	7,417.62	929.09	3.29E-135
	time × parenchyma type	7	483.06	69.01	8.64	3.05E-10
Lc [μm]	time	7	1.38E-07	1.97E-08	53.28	3.14E-62
	parenchyma type	1	7.63E-08	7.63E-08	206.15	1.13E-41
	time × parenchyma type	7	3.80E-08	5.43E-09	14.67	4.86E-18
Wc [μm]	time	7	1.13E-07	1.62E-08	51.55	1.85E-60
	parenchyma type	1	6.62E-08	6.62E-08	210.82	1.76E-42
	time × parenchyma type	7	3.60E-08	5.14E-09	16.37	3.38E-20
Lc/Wc	time	7	0.92	0.13	3.62	7.49E-04
	parenchyma type	1	0.36	0.36	10.03	1.60E-03
	time × parenchyma type	7	1.02	0.15	4.01	2.56E-04
Ac [μm^2]	time	7	8.62E-23	1.23E-23	78.99	1.42E-86
	parenchyma type	1	6.65E-23	6.65E-23	426.44	5.48E-76
	time × parenchyma type	7	3.44E-23	4.91E-24	31.51	1.35E-38

which is an adaptive feature of *Haberlea* plants to avoid light-induced damages and started when water content declined by 50% (Fig. 4). *H. rhodopensis* is well adapted to short-time dehydration periods when the plants try to maintain their optimal photosynthetic activity despite of water loss. The photosynthesis was one of the latest

Table 3. Correlation coefficients (*r*) and their statistical significances between histological and physiological characters of *Haberlea rhodopensis* leaves and some investigated chloroplast parameters (** $p<0.010$, * $p<0.050$, unmarked − no significant). Ac – cross-sectional area of chloroplasts; Am – cross-sectional area of mesophyll cells; Lc – cross-sectional length of chloroplasts; Nc – chloroplast number per cell; PP – palisade parenchyma; WC – water content; SP - spongy parenchyma; W – width of the leaf cross-section; Wc - cross-sectional width of chloroplasts. Critical *r* for df = 6 ($p<0.05$) = 0.6215.

	Lc [μm]		Wc [μm]		Lc/Wc	
	SP	PP	SP	PP	SP	PP
Ac [μm^2]	0.7372*	0.8843**	0.8642**	0.8898**	–0.7114*	–0.6171
Nc [PCE]	0.0559	0.2408	0.0701	0.3362	–0.1426	–0.7339*
W [μm]	0.8951**	0.4730	0.4834	0.7720*	–0.1987	–0.3635
Am [μm^2]	0.6298*	0.0664	0.0696	0.3930	0.2478	–0.0506
WC [%]	0.5527	0.7272*	0.7213*	0.4597	–0.0859	–0.4996

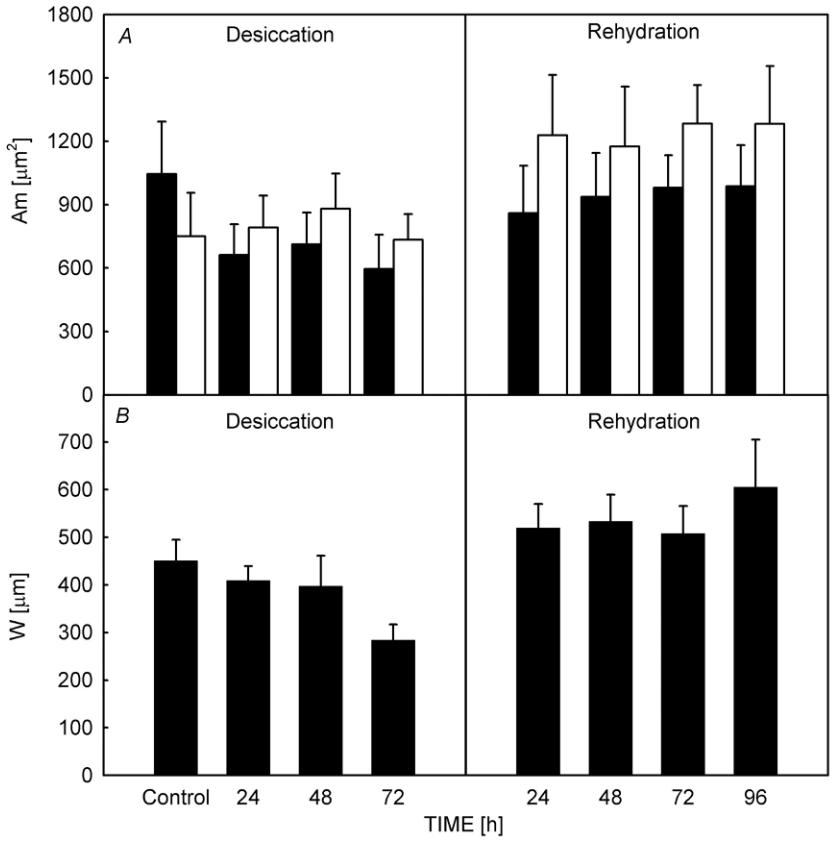

Fig. 3. Changes of histological parameters of *Haberlea rhodopensis* leaves during desiccation and rehydration. *A*: cross-sectional area (Am) of spongy (*black bar*s) and palisade mesophyll cells (*white bar*s), *B*: cross-sectional width of the leaf (W). The values are shown as mean ± standard deviation (SD) ($n = 50$).

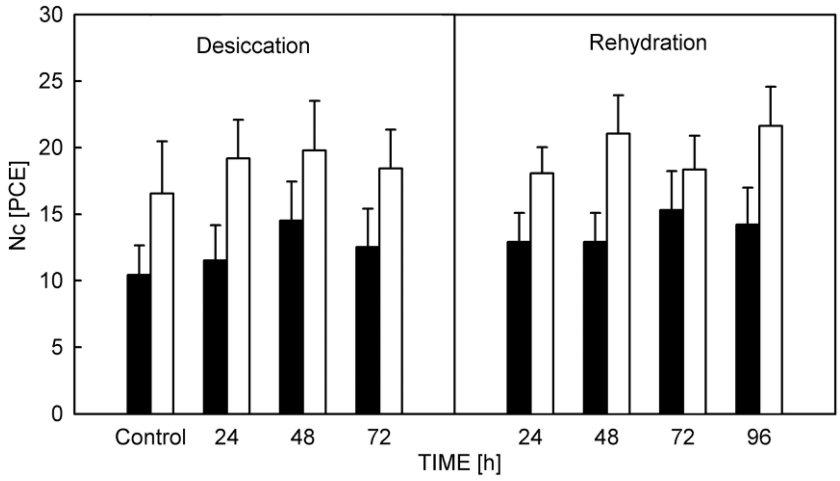

Fig. 4. Changes of the chloroplast number per cell (Nc) of spongy (*black bar*s) and palisade parenchyma cells (*white bar*s) in *Haberlea rhodopensis* leaves during desiccation and following rehydration. The values are shown as mean ± standard deviation (SD) ($n = 50$).

physiological processes switched off by plant organization during dehydration, thus the chloroplast should be active and provide the energy the plant needed for protection under stress condition. Our previous investigations showed that similarly to chlorophyll content, the photochemical activity of PSII significantly decreased when leaf water content was reduced more than 70% (Georgieva *et al*. 2005, 2007). Moreover, the integrity of thylakoids was preserved and the amount of chlorophyll-protein complexes hardly changed during desiccation (Georgieva *et al.* 2007, 2009). It was also found that dehydration induced accumulation of stress proteins (Georgieva *et al.* 2010) which protect membranes against desiccation (Vicré *et al.* 2004). Damages during desiccation were limited to a repairable level and maintaining the physiological and morphological integrity in the dry state enabling full recovery after rehydration. The larger amount of chloroplasts, which increased continuously during rehydration in the parenchyma cells, may refer to the high level regeneration ability of photosynthetic apparatus of HDT plant species just as the fast and intensive recovery of chloroplast structure (Georgieva *et al*. 2005, 2007). Not decreasing but rising Nc during both desiccation and rehydration could be related to HDT strategy – namely, these DT plants don't lose their chlorophylls during desiccation and they are well adapted to short-term dehydration periods.

In conclusion, our result demonstrated some chloroplast structural changes during dehydration and rehydration which can typify only HDT plants. Consequently, Ac and Nc in palisade parenchyma cells was higher than in spongy parenchyma, and numerical changes of these parameters were more expressed in palisade tissue under stress conditions. Furthermore, significant relationships observed between the size, shape or number of chloroplasts and other investigated parameters (W and Am) also suggested that the palisade cells were more responsive to water availability. These results may be also important in the investigations of photosynthetic process of DT (especially HDT) plants.

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