Photoinhibition of photosynthesis in Antarctic lichen *Usnea antarctica*. I. Light intensity- and light duration-dependent changes in functioning of photosystem II

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Abstract

The paper deals with the differences in sensitivity of Antarctic lichen to photoinhibition. Thalli of *Usnea antarctica* were collected at the James Ross Island, Antarctica (57°52´57´´W, 63°48´02´´S) and transferred in dry state to the Czech Republic. After rewetting in a laboratory, they were exposed to 2 high light treatments: short-term (30 min), and long-term (6 h). In short-term treatment, the sample were exposed to 1000 and 2000 μmol m^{-2} s^{-1} of photosynthetically active radiation (PAR). In long-term experiment, PAR of 300, 600, and 1000 μmol m^{-2} s^{-1} were used. Photosynthetic efficiency of *U. antarctica* thalli was monitored by chlorophyll fluorescence parameters, potential (F_V/F_M) and actual (Φ_{PSII}) quantum yield of photochemical processes in photosystem II in particular. In short-term treatments, the F_0, F_V and F_M signals, as well as the values of F_V/F_M, and Φ_{PSII} showed light-induced decrease, however substantial recovery after consequent 30 min. in dark. Longer exposition (60 min) to high light led to more pronounced decrease in chlorophyll fluorescence than after 30 min treatment, however dark recovery was faster in the thalli treated before for longer time (60 min). Long-term treatment by high light caused gradual decrease in F_V/F_M and Φ_{PSII} with the time of exposition. The extent of the decrease was found light dose-dependent. The time course was biphasic for F_V/F_M but not for Φ_{PSII}. The study showed that wet thalli of *Usnea antarctica* had high capacity of photoprotective mechanisms to cope well either with short- or long-term high light stress. This might be of particular importance in the field at the James Ross Island, particularly at the begining of growing season when melting water is available and, simultaneously, high light stress may happen on fully sunny days.

Key words: chlorophyll fluorescence, high light, potential quantum yield, effective quantum yield

Abbreviations: ROS - reactive oxygen species, PSII - photosystem II, D1 - D1 protein, LHCs - light harvesting complexes, F_0 - basic fluorescence, F_V - variable fluorescence, F_V/F_M - potential photosynthetic quantum yield of photosystem II, Φ_{PSII} - effective photosynthetic quantum yield of photosystem II

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Introduction

Lichens are poikilohydric organisms that respond to high light and consequent increase in thallus temperature by gradual drying and dehydration-dependent loss of photosynthetic activity. In moist and/or cold habitats, including polar and mountainous ecosystems, many lichen species are exposed to high light in fully hydrated state. Such exposure to high light in the hydrated state produces photoinhibition in chlorolichens and cyanolichens The effect is much more pronounced in cyanolichens, which do not reverse photosynthetic depression after a recovery period as chlorolichens do (see *e.g.* Gasulla et al. 2012).

Physiological effects of high light to photosynthetic apparatus of lichens are similar to those of desiccation (Jensen et Feige 1991). Both stresses lead to production of reactive oxygen species (ROS) in core of photosystem II (PS II) and neighbouring pigment-protein complexes of light harvesting complexes (LHCs). High light-induced ROS act as strong oxidative agens that cause negative changes in thylakoidal photosynthetic apparatus. Oxidation on donor side of PS II, excessive reduction on the acceptor side of PSII, and consequently, destruction of D1 protein are major damages to PS II (Anderson et Barber 1996). Therefore, under both high light stress and dehydration, reactive oxygen species are considered major cause of damage in photosynthetic organisms (Demmig-Adams et Adams III, 2000). During photoinhibition, however, several mechanism are activated that minimize such damages to photosynthetic apparatus. Such protective mechanism comprise mainly thermal dissipation of absorbed light energy. The mechanisms are present in higher plants (Adams III et al. 2006) as well as in lichens.

Both in chlorolichens and cyanolichens, photoinhibition could be diminished by several photoprotective mechanisms (Demmig-Adams et al. 1990a). Among them, formation of zeaxanthin during the initial phases of photoinhibition is well known (Demmig-Adams et al. (1990b) and documented for number of chlorolichens from polar regions, *e.g. Usnea antarctica* (Barták et al. 2003), *Umbilicaria antarctica* (Barták et al. 2004). This effect, however, was not observed in cyanolichens. Short-term changes in gluthatione pool (Vráblíková et al. 2005), as well as its redox state is another antioxidative mechanism activated by high light in chlorolichens (Štěpigová et al. 2007). Content of carotenoids (Valladares et al. 1995) and phenolic compounds (Buffoni Hall et al. 2002) is also reported to protect lichens form light-induced ROS, especially the environments rich in high UV-B. Appart from the above-mentioned biochemical photoprotective mechanisms activated in the photosynthetic apparatus of lichen photobionts, there are several other mechanisms helping the lichens to minimize negative effects of high light. The mechanisms comprise dehydration-dependent movements of thalli parts that provides self-shading effect (Barták et al. 2006), and production of light-screening compounds by mycobiont hyphae forming the upper cortex (Gauslaa et Solhaug 2004). The ability of lichens to exploit such mechanisms depends strongly on the physical characteristics of particular habitat, prevailing light environment in particular (Gauslaa et Solhaug 1996, 2000).

Majority of studies of photoinhibition in the lichens and mosses from polar regions are made under controlled laboratory conditions. Several field experiments, however, have been made to study photoinhibition in Antarctica using both gas exchange and chlorophyll fluorescence approach in the field (*e.g.* Kappen et al. 1998). Among them, the study made on

Antarctic mosses (Lovelock et al. 1995) pointed out reversible photoinhibition in an Antarctic moss measured at wet state. Field studies made on Antarctic lichens could hardly distiguish between limitation of photosynthetic processes related to thallus dehydration and progressive photoinhibition because the processes co-occur simultaneously. That was why the photoinhibition of Antarctic lichens is studied under constant thallus hydration in laboratory-based facilities. Last studies showed large capacity of lichens to cope with short-term high light stress. For *Usnea antarctica*, Barták et al. (2003) reported substantial decrease of chlorophyll fluorescence parameters found immediatelly after photoinhibitory treatment, as well as their fast recovery. In the study, fast phase of recovery (lasting typically 30 min) was attributed to structural changes in PSII and LHC and the effects of antioxidative mechanisms. Slow phase of recovery (lasting from tens to hundreds of minuts) was attributed to resynthetic processes that repair damaged components of PSII an LHCs. Long-term photoinhibition exploiting the exposition of wet lichen thalli to high light for the periods longer than 1 h, has been applied in Central European (Barták et al. 2008) but not Antarctic lichens. To fill the gap, we decided to compare the negative effects of short- and long-term exposition of *Usnea antarctica* to high light using a chlorophyll fluorescence approach. In this paper, we bring the results of photoinhition of PSII and analyze time- and light dose-dependent changes of F_V/F_M and Φ_{PSII}. Forthcoming paper (MS in prep.) will focus activation of quenching mechanism during short- and longh-term photoinhibition in *Usnea antarctica*.

Material and Methods

Lichen collection and handling

Thalli of fruticose lichen *Usnea antarctica* were collected at the James Ross Islands, Halozetes Valley, during summer field campains (Jan. - Feb. 2012). They were transferred in dry state to the laboratory in Brno, Czech Republic, where stored in a fridge at 5°C, for three months. For experiments, the thalli were re-wetted 48 or 72 hours before the begining of the experiments (*see* below). The thalli were placed into Petri dishes on Pehazell® cellulose wadding and hydrated by regular spraying with demineralized water. Optimum hydration was checked fluorometrically. When F_V/F_M reached maximum values, the sample was considered optimally hydrated. During hydration period, the thalli were stored at 5°C at low irradiance of 10 μmol m^{-2} s^{-1} or 100 μmol m^{-2} s^{-1} of photosynthetically active radiation (checked by a *Li-1600* radiometer Li-Cor, USA). The two iradiances during hydration period were used because of two different experimental designs. The thalli treated by 10 μmol m^{-2} s^{-1} were used in the experimental set-up mimicking long-term but low-light photoinhibition. The other pretreatment (100 μmol m^{-2} s^{-1}) was used for the experiment mimicking short-term photoinhibion (*see* High light treatments).

High light treatments

In our experiments, short-term high light stress was achieved by the exposition of the *U. antarctica* thalli to two irradiances: 1000 and 2000 μmol m^{-2} s^{-1}, duration of which was 30 and 60 min at each irradiance. During the exposition, the

Petri dishes with thalli were kept on a thermostated metal block (Peltier cooling unit, Con Brio, Czech Republic) surrounded by melting ice to reach constant low temperature of thallus (5°C, checked by a infrared thermometer) througout experiment. Light was provided by a source consisting of several white superbright LEDs. During the expositions, individual *U. antarctica* thalli were placed horizontally on the metal block, *i.e.* contrastingly to natural arrangement in the field, they were irradiated from side not from top. In long-term light treatments, thalli of *U. antarctica* were exposed to light (300, 600, and 1000 μmol m^{-2} s^{-1}, respectively) for 240 min under the same physical conditions as described above. Both in short-term and long-term treatments, the extent of treatment-induced photoinhition was evaluated as the change in chlorophyll fluorescence parameters.

Fig. 1. Wet thalli of *Usnea antarctica* used for the experiments studying photoinhibition.

Chlorophyll fluorescence measurements

Light treatment-induced changes in photosynthetic apparatus of *U. antarctica* were evaluated by several chlorophyll fluorescence parameters. In short-term experiment, the values of chlorophyll fluorescence parameters (i) before photoinhibitory treatment, (ii) immediately after, and (iii) after 60 min of dark recovery were recorded. In long-term experiment, the parameters were measured (i) before light treatment, and (ii) during light treatment (each 30 min) so that time course of chlorophyll fluorescence change could be determined.

For chlorophyll fluorescence measurements, a FluorCam (HFC-010, Photon Systems Instuments, Czech Republic – short-term treatment) and PAM-2000 (Heinz Walz, Germany – long-term tratment) were used. The chlorophyll fluorescence parameters were evaluated on dark-adapted thalli (10 min) using the measurement of slow Kautsky kinetics supplemented with quenching analysis. The method consisted of determination of basic fluorescence (F_0), maximum fluorescence (F_M) in dark adapted state, steady-state fluorescence recorded on the

sample exposed to actinic light for 5 min (F_S), maximum fluorescence measured on actinic light-adapted sample (F_M') and maximum chlorophyll fluorescence (F_M'') measured after 1 min of dark relaxation. For each treatment, at least three replicates were measured.

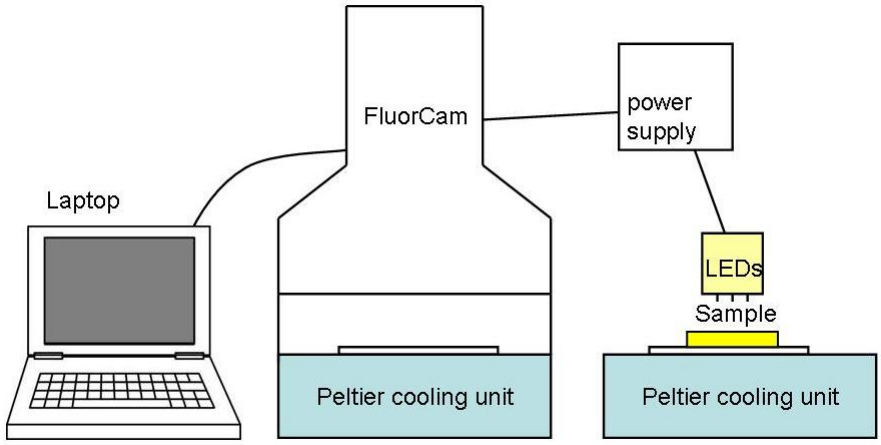

Fig. 2. Simplified scheme of exposition and measuring set up. Source of laptop clipart: http://www.clker.com/clipart-14661.html.

Results

Short-term exposition of *U. antarctica* thalli was aimed to show the changes in the shape of kinetics of chlorophyll fluorescence (*see* Fig. 3) as well as absolute signals recorded after saturation pulses (F_M, F_M') and the parameters (F_V/F_M, Φ_{PSII}) derived from them. From the kinetics follows that all these characteristics are affected by short-term high-light treatment. In general, chlorophyll fluorescence kinetics recorded immediately after the short-term exposition to high light were typical by a decrease in basic chlorophyll fluorescence (F_0), chlorophyll fluorescence during actinic light period (F_V), as well as steady-state chlorophyll fluorescence (F_S). The decrease in the three above-specified parameters was more pronounced in the thalli treated by 2000 μmol m^{-2} s^{-1} than in those treated by 1000 μmol m^{-2} s^{-1}. The expectation, that the decrease would be more pronounced in those thalli exposed to photoinhibitory light for 60 min (compared to those treated for 30 min) was not proven. The thalli showed oposite response. With prolonged duration of photoinhibitory treatment at particular light intensities (1000, 2000 μmol m^{-2} s^{-1}), rather smaller extent of decrease in particular chlorophyll fluorescence levels (F_0, F_V, F_S) was found immediately after the treatment.

The shapes of chlorophyll fluorescence kinetics were affected by high light treatment. Compared to pre-photoinhibition shape, the kinetics were strongly flattened in those recorded immediately after high-light treatment, especially in the range delimited by peak chlorophyll fluorescence (F_P) and steady-state chlorophyll fluorescence F_S. Moreover, the chlorophyll fluorescence (F_V) values found at the dip following F_P were smaller than

F_0 at the same curves. Such response, *i.e.* the decrease of F_V below F_0 value is indicative of strong quencher present either in PS II or its closest neighbourhood.

Recovery from photoinhibition was apparently high light dose- and duration-dependent. As regards the shape of the chlorophyll fluorescence kinetics and the values of their particular signals recorded between the time of F_0 and F_S, it is clear that they were almost fully recovered in the 60 minutes treatments, while only partial recovery was apparent in 30 minutes treatments. When calculated from the kinetic presented in Fig. 3, the typical chlorophyll fluorescence parameters (Table 1) showed different, *i.e.* light dose- and light duration-dependent sensitivity to photoinhibiton and recovery.

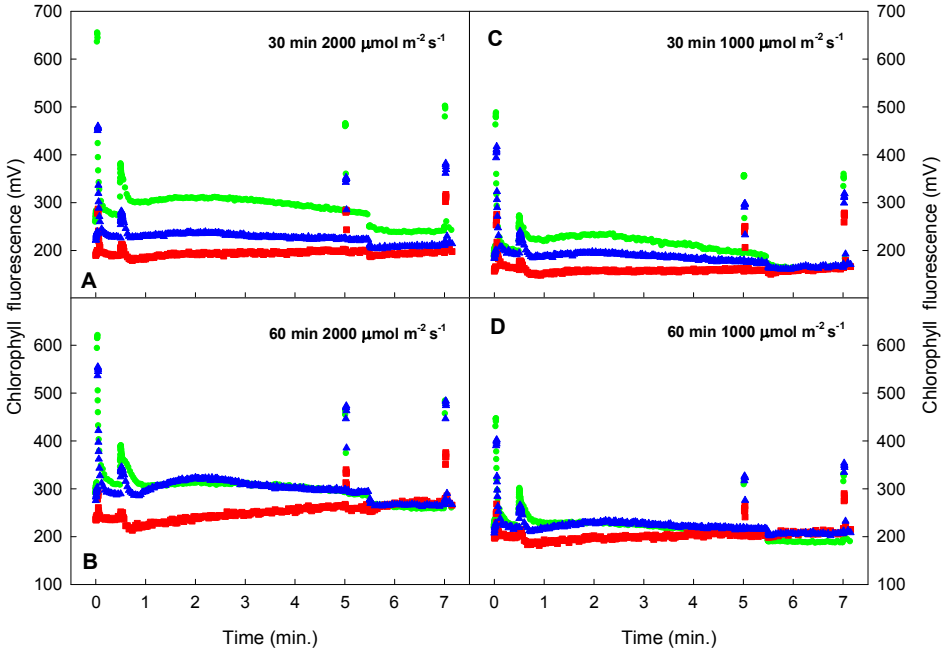

Fig. 3. Kinetics of chlorophyll fluorescence recorded before (green line), after (red line) photoinhibitory treatment and after 60 min dark recovery (blue line).

Long-term exposition to high light led to gradual photoinhibition of photosynthetic processes in PS II indicating cummulative stress to PS II. Decline of potential yield of photosynthetic processes in photosystem II (F_V/F_M) was fastest and most pronounced when the highest dose of photosynthetically active radiation, *i.e.* 1000 µmol m^{-2} s^{-1} was used (Fig. 4). Light-induced decrease in F_V/F_M caused by 300 and 600 µmol m^{-2} s^{-1} showed similar trend but reached higher value at the end of light exposition period (0.34 and 0.27) than under those recorded when the highest light dose was used. In all PAR treatments, biphasic F_V/F_M decrease was apparent. The most significant fall of about 25-40% of maximum value was found during initial phase of light treatment, *i.e.* within the first 50 min of exposition to particular light. Then, slow phase of F_V/F_M decline was recorded between 50 and 360 min of light exposition period. Within the slow phase, following decrease of about similar or smaller extent than during the first phase was found.

1000 μmol m^{-2} s^{-1}								
Exposition	***30 min***				***60 min***			
	F_0/F_M	F_V/F_M	F_P-F_0/F_P	Φ_{PSII}	F_0/F_M	F_V/F_M	F_P-F_0/F_P	Φ_{PSII}
Before HL	0.416	0.584	0.246	0.448	0.519	0.481	0.224	0.346
After HL	0.580	0.420	0.096	0.363	0.772	0.228	0.038	0.239
Recovery	0.465	0.535	0.184	0.238	0.550	0.450	0.167	0.327

2000 μmol m^{-2} s^{-1}								
Exposition	***30 min***				***60 min***			
	F_0/F_M	F_V/F_M	F_P-F_0/F_P	Φ_{PSII}	F_0/F_M	F_V/F_M	F_P-F_0/F_P	Φ_{PSII}
Before HL	0.423	0.577	0.272	0.392	0.491	0.509	0.218	0.370
After HL	0.689	0.322	0.063	0.295	0.819	0.180	0.034	0.151
Recovery	0.508	0.492	0,173	0.363	0.531	0.469	0.155	0.372

Table 1. Chlorophyll fluorescence parameters derived from kinetics supplemented with saturation pulses. For particular photoinhibitory treatments, the values (means of 3 replicates) were measured before, and after exposition to high light (HL). Consequently, the values were recorded after 60 min dark recovery.

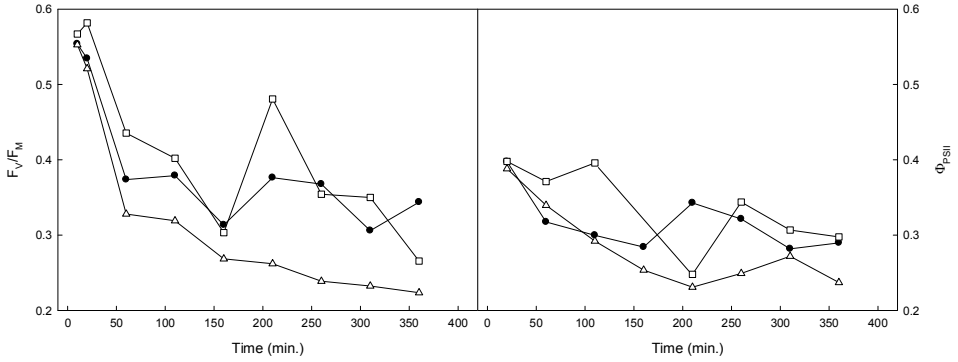

Fig. 4. Time courses of potential (F_V/F_M - left) and effective (Φ_{PSII} - right) quantum yield of photosystem II recorded during long-term exposition of *Usnea antarctica* to 300 (●), 600 (□) and 1000 (△) μmol m^{-2} s^{-1} of PAR.

Light-induced decrease in effective quantum yield of PS II (Φ_{PSII}) showed somewhat ambiguous trend. General trend, *i.e.* decrease of Φ_{PSII} with time of exposition to light was found for all PAR treatments (Fig. 4). However, fast and slow phase of Φ_{PSII} decrease could not be distinguished. For smallest (300) and highest (1000 μmol m^{-2} s^{-1}) light doses, more or less regular Φ_{PSII} fall with duration of light was apparent. For 600 μmol m^{-2} s^{-1}, irregularly fluctuating values were recorded in between 60 and 270 min of light duration. At the end of exposition period, Φ_{PSII} declined at regular rate. Overall decline from maximum value (about 0.4) to the minimum found at the end of exposition period was PAR-dependent. Φ_{PSII} reached the minimum of about 0.3 for 300 and 600 μmol m^{-2} s^{-1} treatment. It was found lower (Φ_{PSII} = 0.23) when 1000 μmol m^{-2} s^{-1} was used.

Discussion

Short-term experiment showed decrease in F_V/F_M and Φ_{PSII} as well as fast recovery. The results are comparable to the earlier study made on *U. antarctica* (Barták et al. 2003) in which 70 and 60% recovery was found for F_V/F_M and Φ_{PSII} after 240 min of dark recovery. In our study, background chlorophyll fluorescence F_0 decreased immediately after short-term high-light stress. Therefore, all the chlorophyll fluorescence parameters derived from F_0 were affected (*see* Table 1). Some studies, however, reported an increase in F_0 caused by photoinhibitory treatment (Manrique et al. 1993). Such difference could be explained as a consequence of different set up of both experiments. In our measurements, higher light values and much shorter exposition time were used. Therefore, F_0 decrease might be considered as a short-term response of lichen photosynthetic apparatus to high light stress. When exposed for long period, such as *e.g.* 3 days (Manrique et al. 1993), photosynthetic apparatus tends to acclimate to higher light doses that could lead to the increase in F_0. Our data presented in Fig. 3 suggest that acclimatory changes in structure and function of photosystem II may happen even after 1 h of exposition to high light. It is because the shape of chlorophyll fluorescence kinetics gets back to control faster in lichen thalli treated for 1 h than those treated only for 30 min. This supports the idea that acclimatory changes to high light in PS II may start soon after the photoinhibitory light began. They may comprise structural arrangement of PSII and LHC, redox state of plastoquinone as well as the balance between photochemical and biochemical processes of photosynthesis.

In long-term experiment, gradual decrease in F_V/F_M was found, similarly to the evidence from *Lasallia pustulata* exposed to high light for several hours (Barták et al. 2008). Our data could be interpreted that wet thalli of *U. antarctica* exhibited decrease in F_V/F_M reaching more or less constant value after 6 h treatment by 1000 μmol m^{-2} s^{-1}. Smaller decrease in F_V/F_M recorded for lower light doses throughout the exposition period indicates that *U. antarctica* may thrive well under such light, exhibiting less damage to PSII. The same conclusion might be made for effective quantum yield. Photochemical processes of *U. antarctica* photosynthesis tend to decrease gradually, the extent of their inhibition is light dose-dependent. This again demonstrates the ability of long-term treated *U. antarctica* to maintain substantial photosynthesis at the irradiances below 600 μmol m^{-2} s^{-1}.

Lichen responses to high light and dehydration may involve similar mechanisms, such as light- or dehydration-dependent xanthophyll cycle pigments conversion, and state 1-2 transition. Both mechanism quench excess light energy captured by PSII and convert to thermal dissipation of energy. Last studies (*e.g.* Heber et al. 2000, 2006, 2007), however, indicated that there is another effective quencher in photosynthetic apparatus of PS II of desiccating lichens. It is not related to zeaxanthin formation and independent on light. According to Heber et al. (2006), it may involve conformational changes in pigment-protein complexes in PS II. Thus, highly-effective dissipation centers are formed in which excitation energy is trapped (Heber et al. 2010). In such centers, the first excited state of chlorophyll molecule is thermally taken back to ground state before charge separation takes place (Heber et Lüttge 2011). In such way, overenergization of PSII and ROS formation is avoided. Moreover, presence of strong quencher in core of PSII and/or PSII antennae is reported by Veerman et al. (2007) for *Parmelia sulcata* desiccating on light. Chemical structure of the quencher, how-

ever, is not know. Our study showed that wet thalli of *Usnea antarctica* had high capacity of photoprotective mechanisms to cope well either with short- or long-term high light stress. This might be of particular importance in the field at the begining of growing season when air and surface temperatures are above zero. Within this period, melting water from snowfields and glaciers is available and supply lichen thalli for long periods. Under such circumstances, photoinhibition may occur on fully sunny days, because high quantities of light reaches wet lichen thalli. In our experiment exploiting short-term high-light stress, however, fast recovery of chlorophyll fluorescence parameters towards prephotoinhibition values indicated that *U. antarctica* has low susceptibility to photoinhibition.

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