Rehydration of sugar beet plants after water stress: effect of cytokinins

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Abstract

The possibility to improve the recovery of sugar beet plants after water stress by application of synthetic cytokinins N^6-benzyladenine (BA) or N^6-(*m*-hydroxybenzyl)adenosine (HBA) was tested. Relative water content (RWC), net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), chlorophyll (Chl) *a* and Chl *b* contents, and photosystem 2 efficiency characterized by variable to maximal fluorescence ratio (F_v/F_m) were measured in control plants, in water-stressed plants, and after rehydration (4, 8, 24, and 48 h). Water stress markedly decreased parameters of gas exchange, but they started to recover soon after irrigation. Application of BA or HBA to the substrate or sprayed on leaves only slightly stimulated recovery of P_N, E, and g_s in rehydrated plants, especially during the first phases of recovery. Chl contents decreased only under severe water stress and F_v/F_m ratio was not significantly affected by water stress applied. Positive effects of BA or HBA application on Chl content and F_v/F_m ratio were mostly not observed.

Additional key words: benzyladenine, *Beta vulgaris*, chlorophyll, photochemical efficiency of photosystem 2, hydroxybenzyladenosine, net photosynthetic rate, stomatal conductance, transpiration rate, water use efficiency.

Introduction

Cytokinins (CKs) influence a wide range of events during plant growth and development. However, it is still an open question whether CKs also participate in root-to-shoot communication during stress, and/or influence plant response to stress. CKs have opposite effects than water stress on some physiological processes, *e.g.*, they delay plant senescence, increase growth of shoots more than roots, and may induce stomatal opening (for review see Pospíšilová *et al.* 2000). These processes might be important during recovery of plants after water stress. However, the increase in transpiration rate (E) and stomatal aperture, and/or delay in stomatal closure induced by abscisic acid was observed, *e.g.*, in *Anthephora*, *Commelina*, *Kalanchoe*, *Tradescantia*, *Tridax*, *Vicia*, *Vitis*, and *Zea* (Incoll *et al.* 1990, Morsucci *et al.* 1991, Pharmawati *et al.* 1998, Stoll *et al.* 2000), but not in *Beta*, *Commelina*, *Gossypium*, *Linum*, and *Zea* (Radin *et al.* 1982, Blackman and Davies 1983, Radin and Hendrix 1988, Drüge and Schönbeck 1992, Čatský *et al.* 1996). Exogenously applied CK alleviated negative effect of water stress on chlorophyll (Chl) and carotenoid contents, photochemical activities of photosystems 1 and 2, and content and activity of ribulose-1,5-bisphosphate carboxylase or phosphoenolpyruvate carboxylase (Metwally *et al.* 1997, Chernyad'ev and Monakhova 1998, Pandey *et al.* 2000, Singh *et al.* 2001).

From the previous experiments with non-stressed *Phaseolus vulgaris* and *Beta vulgaris* plants we concluded that the stimulation of stomatal opening, E, and net photosynthetic rate (P_N) by exogenously applied CKs (benzyladenine, BA, or hydroxybenzyladenosine, HBA) was rather exceptional than general. The effects strongly depended on plant species and concentration but only weakly on way of application (Pospíšilová *et al.* 2001). Application of 1 µM BA slightly improved recovery of *P. vulgaris* plants during rehydration after

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Abbreviations: ABA - abscisic acid; BA - N^6-benzyladenine; CK - cytokinin; E - transpiration rate, g_s - stomatal conductance; HBA - N^6-(*m*-hydroxybenzyl)adenosine; P_N - net photosynthetic rate, RWC - relative water content; WUE - water use efficiency.
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water stress in terms of increased adaxial and abaxial stomatal conductances (g_s) and P_N, *i.e.*, parameters which were markedly decreased by mild water stress. However, contents of Chl *a*, Chl *b*, and carotenoids, and parameters of Chl *a* fluorescence kinetic were not markedly affected by mild water stress and after rehydration were not stimulated by 1 µM BA. 10 µM BA had mostly negative effects on the parameters measured (Rulcová 2000, Rulcová and Pospíšilová 2001).

The aim of these experiments was to determine the effects of two synthetic CKs (BA and HBA) on different physiological parameters (RWC, E, P_N, g_s, Chl *a* and Chl *b* contents, and photochemical efficiency of photosystem 2) in the course of rehydration of *Beta vulgaris* plants after very mild, mild, and severe water stress.

Materials and methods

Seeds of sugar beet (*Beta vulgaris* L. ssp. *vulgaris* var. *altissima* Döll, cv. Elán) were sown in fine *Perlite* moistened with distilled water. After three weeks individual seedlings were transferred into pots with rough *Perlite* sufficiently moistened with Hewitt nutrient solution and grown in a growth chamber at 16-h photoperiod, irradiance (400 - 700 nm) of 350 µmol m^{-2} s^{-1}, day/night temperature of 25/20 °C, and relative humidity of about 50 %. Air temperature and humidity were measured with the *JUMO Humitherm TDAc-70* (*M.K. Juchheim*, Fulda, Germany). Irradiance was measured with the quantum radiometer/photometer *LI 185B* (*Li-COR*, Lincoln, USA).

In 6 to 9-week-old seedlings (with about 5 to 7 leaves) water stress was induced in half of plants in each experimental set by cessation of watering until visible wilting occurred. Then the stressed plants were re-irrigated and at the same time 1 µM BA or HBA was applied to control (sufficiently water-supplied) plants and to water-stressed plants either into the substrate or sprayed on leaves. The concentration was chosen according to previous experiments (Pospíšilová *et al.* 2001). The following parameters were measured 4, 8, 24, and 48 h after application.

Relative water content (RWC) was measured gravimetrically in leaf discs (0.5 cm^2) saturated in holes of fully moistened polyurethane foam under dark (Čatský 1960). P_N, E, and g_s were measured on attached leaves using commercial gas exchange system *LCA-4* (*ADC BioScientific*, Hoddesdon, UK) with leaf chamber *LC4/PLC4BT-1/E* at a temperature of 25 °C, irradiance of 700 µmol(photon) m^{-2} s^{-1}, relative air humidity of 50 %, and CO_2 concentration of 370 µmol mol^{-1}. Water use efficiency (WUE) was calculated as P_N/E ratio. Mature leaves characterized in the control with P_N, E, and g_s at or near maximum were usually used. Chl *a* fluorescence characteristics of the adaxial surface of attached leaves were measured after a 15-min dark period with a *PAM Chlorophyll Fluorometer* (*Walz*, Effeltrich, Germany) at room temperature and ambient CO_2 concentration. F_0 was determined at a modulation frequency of 1.6 kHz. Actinic radiation (650 nm; 100 µmol m^{-2} s^{-1}) was provided by *102L LED* lamp. Saturating pulses of "white light" (duration 700 ms, 2 500 µmol m^{-2} s^{-1}) were applied in 100 s intervals. Data sampling, control, and calculation were served by the *DA 100 Data Acquisition System* (*Walz*, Effeltrich, Germany). The nomenclature of Van Kooten and Snel (1990) was used. Chl *a* and *b* contents were determined after extraction of leaves by dimethylformamide for 24 h with the spectrophotometer *Hitachi U-3300* (Tokyo, Japan) using the method of Porra *et al.* (1989).

Experiments were repeated 6 times with BA or HBA applied to substrate and 3 times with BA and HBA sprayed on leaves. Treated plants were always compared with control plants treated with distilled water. For each parameter a mean and standard error of mean were calculated.

Results and discussion

In control plants, RWC was higher than 90 %. During water stress induced by cessation of watering for 4 to 7 d RWC decreased. Plants were divided into three groups according to lowest RWC reached: plants with very mild stress (RWC higher than 80 %), mild water stress (RWC from 65 to 80 %), and severe water stress (RWC lower than 65 %). While g_s, E, and P_N markedly decreased in all water stressed plant groups, Chl *a* and Chl *b* contents per leaf area unit decreased only under severe water stress. Therefore under mild water stress stomatal limitation to photosynthesis markedly prevailed to non-stomatal limitation. Much more important stomatal than non-stomatal limitation to photosynthesis under mild water stress was observed in many plant species (*e.g.*, Berkowitz 1998, Escalona *et al.* 1999, Montagu and Woo 1999, Rulcová and Pospíšilová 2001). Chl *a* fluorescence kinetic parameters were not significantly affected by water stress. Therefore no signals of photoinhibition appeared in these plants.

After irrigation RWC gradually increased to prestress level, and the parameters of gas exchange recovered in all three stressed plant groups. P_N (Fig. 1), E (Fig. 2), and g_s

(Fig. 3) started to recover already 4 h after irrigation. When the plants were rehydrated after very mild water stress, P_N, E, and g_s reached values of control plants 8 h after irrigation. This proved that the stress was really mild. When the plants were rehydrated after mild or severe water stress, P_N, E, and g_s reached values of control plants 24 h after irrigation. Therefore also this water stress did not induce permanent damage of plants. WUE was highest during recovery from severe water stress and lowest during recovery from very mild water stress (Fig. 4). Chl *a* and Chl *b* contents, which decreased only under severe water stress, did not reach the control values 48 h after irrigation (Table 2). Photochemical efficiency of photosystem 2 measured as variable to maximum fluorescence ratio was not significantly affected by water stress and did not change during recovery (Table 3). P_N of *Solanum tuberosum* was recovered from mild water stress 24 h after irrigation (Basu *et al.* 1998). Parameters of gas exchange in *Phaseolus vulgaris* recovered completely after mild water stress (Rulcová 2000, Rulcová and Pospíšilová 2001), however, in the same plant species P_N and g_s were not completely recovered 48 h after severe water stress (Cruz de Carvalho *et al.* 1998). Recovery of P_N and g_s of *Prunus armeniaca* after severe water stress lasted four days (Torrecillas *et al.* 1999).

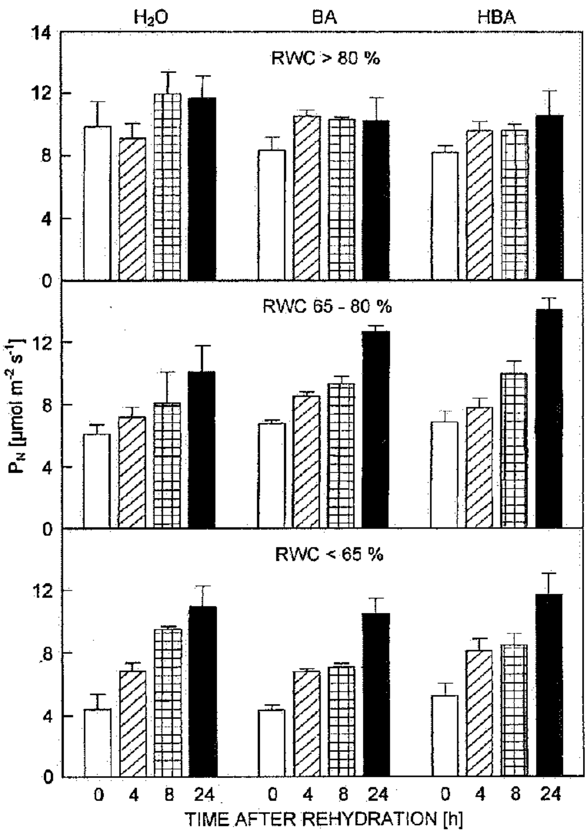

Fig. 1. Net photosynthetic rate (P_N) during rehydration of sugar beet leaves from very mild, mild and severe water stress as affected by 1 μM BA or HBA application into substrate. Means ± SE, $n = 6$.

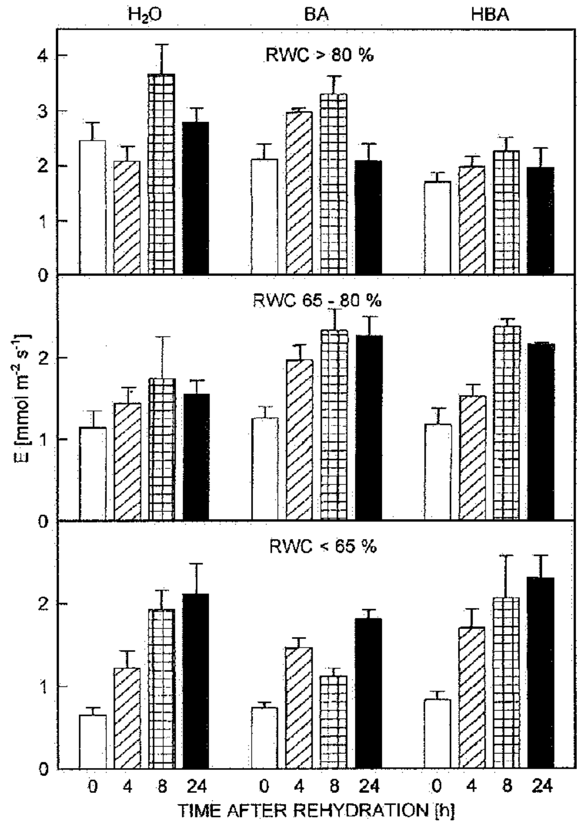

Fig. 2. Transpiration rate (E) during rehydration of sugar beet leaves from very mild, mild and severe water stress as affected by 1 μM BA or HBA application into substrate. Means ± SE, $n = 6$.

Similarly as in previous experiments (Pospíšilová *et al.* 2001) BA and HBA, either added to the substrate or sprayed on the leaves, had no consistent positive effects of gas exchange parameters in control (unstressed) plants. Also Chl *a* and Chl *b* contents were not increased after BA or HBA application in control plants (data not shown). No positive effect of HBA application during vegetative growth of *B. vulgaris* in the field on g_s, E, P_N, and Chl *a* and Chl *b* contents was found. However, HBA application before harvest or both applications increased P_N, and Chl *a* and Chl *b* contents probably due to delay of leaf senescence (Čatský *et al.* 1996). Increased P_N after BA treatment was found in *B. vulgaris*, *Pisum sativum*, *Festuca pratensis*, and *F. arundinacea* by Chernyad'ev (1997). Badenoch-Jones *et al.* (1996) found positive effect of BA on E in *Avena sativa* but not in *Triticum aestivum* under the same conditions. Therefore, the effects of CKs on photosynthetic parameters strongly depend on plant species and age.

The recovery of water-stressed plants after rehydration was not markedly and consistently improved by BA or HBA application. In plants rehydrated after very mild water stress (RWC > 80 %) P_N, E, and g_s was slightly higher in treated than in control plants only 4 h after BA application to the substrate (Figs. 1, 2, 3) or BA and HBA sprayed on leaves (data not shown). In plants rehydrated after mild water stress (80 % > RWC > 65 %) slight positive effect of BA and HBA application to the

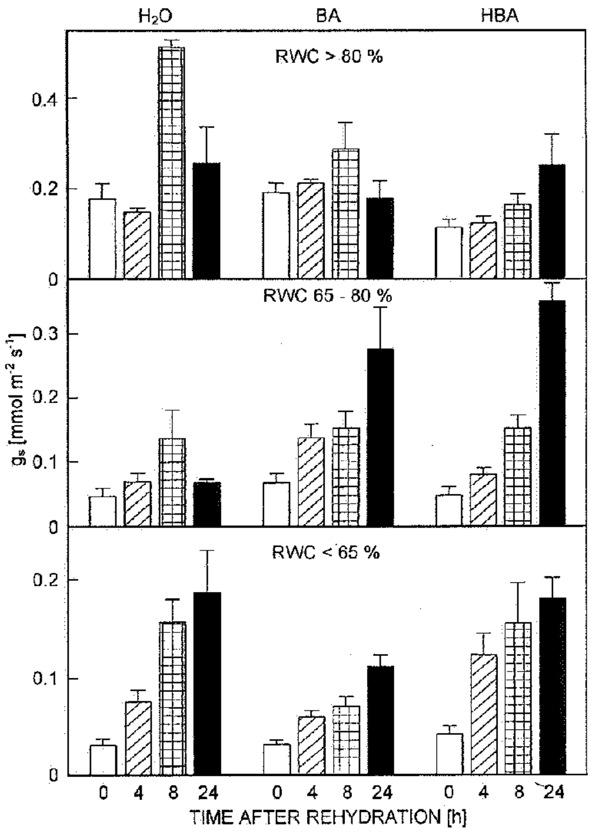

Fig. 3. Stomatal conductance (g_s) during rehydration of sugar beet leaves from very mild, mild and severe water stress as affected by 1 μM BA or HBA application into substrate. Means ± SE, n = 6.

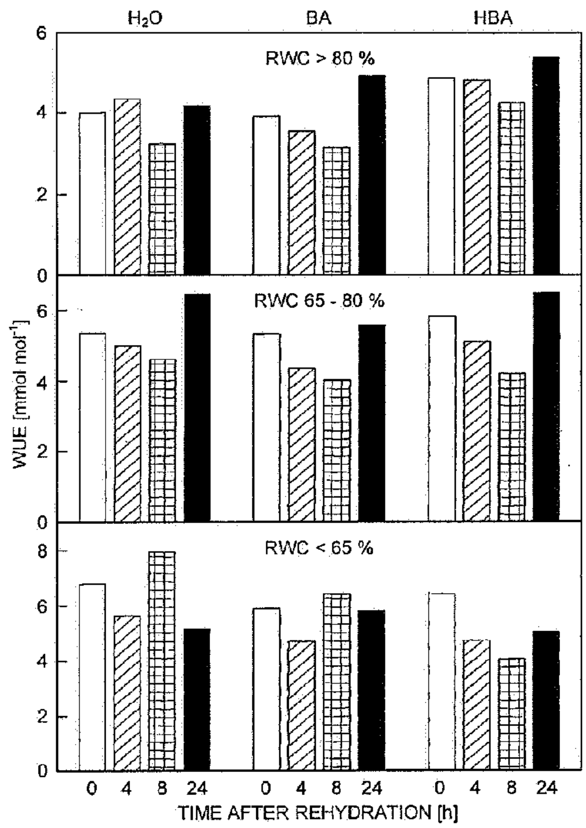

Fig. 4. Water use efficiency (WUE) during rehydration of sugar beet leaves from very mild, mild and severe water stress as affected by 1 μM BA or HBA application into substrate. Means ± SE, n = 6.

Table 1. P_N, E, g_s, and WUE during rehydration of sugar beet leaves from mild water stress (80 % > RWC > 65 %) as affected by 1 μM BA or HBA sprayed on leaves. Means ± SE, n = 5.

Treatment	Rehydration [h]	P_N [μmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	g_s [mmol m^{-2} s^{-1}]	WUE [mmol mol^{-1}]
H_2O	0	6.97 ± 2.55	1.47 ± 0.65	0.05 ± 0.02	4.74
	4	8.30 ± 0.33	1.46 ± 0.04	0.08 ± 0.01	5.68
	24	10.99 ± 2.16	2.88 ± 0.59	0.19 ± 0.05	3.82
	48	13.99 ± 0.67	3.85 ± 0.41	0.29 ± 0.05	3.83
BA	0	7.62 ± 1.47	1.61 ± 0.69	0.08 ± 0.05	4.73
	4	8.29 ± 1.54	1.31 ± 0.05	0.06 ± 0.01	6.32
	24	11.11 ± 1.08	2.06 ± 0.17	0.10 ± 0.02	5.39
	48	13.90 ± 1.47	3.96 ± 0.27	0.34 ± 0.10	3.51
HBA	0	8.96 ± 2.44	1.96 ± 0.70	0.09 ± 0.05	4.57
	4	9.27 ± 1.00	1.87 ± 0.32	0.09 ± 0.02	4.95
	24	9.50 ± 1.98	2.10 ± 0.10	0.10 ± 0.01	4.52
	48	14.09 ± 1.15	3.50 ± 0.57	0.22 ± 0.05	4.02

Table 2. Effects of 1 μM BA or HBA applied to the substrate or sprayed on the leaves on Chl *a* and Chl *b* contents after rehydration of sugar beet leaves. Contents were measured in water-stressed plants and 48 h after irrigation and application of cytokinins. Mean Chl *a* and Chl *b* contents before water stress were 256.2 and 86.3 mg m^{-2}. Means ± SE, $n = 6$.

Treatments	Application	Rehydration [h]	RWC [%]	Chl *a* [mg m^{-2}]	Chl *b* [mg m^{-2}]
H_2O	leaves	0	64	188.8 ± 31.5	65.1 ± 9.1
		48	91	193.9 ± 12.2	58.8 ± 7.1
	substrate	0	58	163.6 ± 8.0	53.0 ± 3.4
		48	89	141.1 ± 5.7	44.6 ± 2.0
BA	leaves	0	62	152.0 ± 5.6	59.9 ± 11.4
		48	92	168.4 ± 9.8	58.7 ± 2.5
	substrate	0	58	162.8 ± 5.5	52.8 ± 2.3
		48	89	137.7 ± 4.4	41.9 ± 1.2
HBA	leaves	0	66	187.7 ± 9.4	60.9 ± 5.9
		48	90	209.8 ± 18.2	72.1 ± 8.2
	substrate	0	58	155.9 ± 26.1	50.2 ± 7.0
		48	89	109.4 ± 14.7	34.6 ± 2.6

substrate on P_N, E, and g_s was observed in all phases of recovery (Figs. 1, 2, 3), while in the case of CKs sprayed on leaves the gas exchange parameters were slightly stimulated only 4 h after HBA application (Table 1). In plants rehydrated after severe water stress (RWC < 65 %) positive effect of HBA on P_N was found 4 h after application (Fig. 1) and positive effect of HBA on E and g_s was found in all phases of recovery (Figs. 2, 3).

Table 3. Effects of 1 μM BA or HBA applied to the substrate or sprayed on the leaves on photochemical efficiency of photosystem 2 measured as variable to maximal fluorescence ratio (F_v/F_m) in water-stressed plants and 24 h after irrigation and application of cytokinins. Mean F_v/F_m before water stress was 0.82; $n = 4$.

Treatments	Application	Rehydr. [h]	RWC [%]	F_v/F_m
H_2O	leaves	0	63	0.81
		48	88	0.76
	substrate	0	71	0.76
		48	87	0.76
BA	leaves	0	66	0.80
		48	91	0.76
	substrate	0	69	0.79
		48	86	0.79
HBA	leaves	0	69	0.80
		48	90	0.77
	substrate	0	66	0.76
		48	89	0.78

However, positive effect of BA on E was observed only 4 h after application. When CKs were sprayed on leaves, slight positive effects of BA or HBA application were observed only on P_N 48 h after application (data not shown). The smaller and less consistent effect of CKs sprayed on leaves in comparison with CKs added to the substrate was probably due to restricted CKs uptake in the former case due to low permeability of cuticle and closed stomata in water-stressed plants. The effect of BA and HBA on WUE was not consistent (Fig. 4, Table 1).

The results agree with previous results with *P. vulgaris* plants where also only slight positive effects of 1 μM BA application to the substrate or sprayed on leaves on P_N, E, and g_s were observed 72 h after application (Rulcová 2000, Rulcová and Pospíšilová 2001). In mature sugar beet plants grown in pots in open air and rehydrated from water stress, positive effect of BA or HBA application on P_N and E was observed 15 to 21 d after application (Pulkrábek and Jozefyová 2001). Increased E in rehydrated plants treated by cytokinins before water stress was observed by Todorov *et al.* (1998).

Positive effect of CK application during rehydration on chlorophyll content and on photochemical efficiency of photosystem 2 measured as variable to maximal fluorescence ratio (F_v/F_m) was mostly not found (Tables 2, 3). The exceptions were slightly increased Chl *a* and Chl *b* contents after HBA sprayed on the leaves. Application of BA alleviated negative effect of NaCl on chlorophyll content in detached wheat leaves, but not in intact seedlings (Mumtaz *et al.* 1997).

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