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Photochemistry and gas exchange in cold conditions in Zn-deficient red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants

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ABSTRACT

The responses of red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants to a low Zn supply and cold conditions (10°/7°C day/night temperature) were investigated in a hydroponic growing medium. A low Zn supply caused a significant reduction of shoot and root dry weight – up to 55% and 45% for the control and 62% and 52% for cold-treated plants, respectively. The total soluble carbohydrates and starch declined in Zn-deficient plants. Exposure to low temperatures, however, led to a decline in starch but an increase in soluble sugars. In Zn-sufficient plants, low temperatures increased the excitation capture efficiency of open photosystem II (PS II) reaction centres (RCs) (F'_v/F'_m), the quantum yield of PS II (Φ_{PSII}), the electron transport rate (ETR) and the proportion of active chlorophyll associated with the RCs of PS II (F_v/F_0). Low temperatures did not affect net CO_2 uptake in Zn-sufficient plants, though a reduction of stomatal conductance occurred. The results demonstrated that although cold-treated plants were slightly more susceptible to Zn deficiency, cold treatment caused greater shoot biomass (up to 32%) in plants supplied with adequate Zn. The adaptation of red cabbage plants to cold conditions is attributable to improved photochemical events in the leaves, a maintenance of the net CO_2 assimilation rate, lower water loss and the accumulation of anthocyanins as antioxidants.

Key words: chlorophyll fluorescence, cold temperature, Zn deficiency

Abbreviations:

Chl - chlorophyll, Φ_{PSII} - effective quantum yield of PS II, ETR - electron transport rate, F'_v/F'_m - excitation capture of open PS II, F_0 - initial fluorescence of dark adapted leaves, F_m - maximum fluorescence of dark adapted leaves, F_v/F_m - maximum quantum yield of PS II, A - net assimilation rate, E - net transpiration rate, qN - non-photochemical quenching, qP - photochemical quenching, PAR - photosynthetically active radiation, RCs - reaction centres, ROS - reactive oxygen species, g_s - stomatal conductance, F_v - variable fluorescence of dark adapted leaves, F_v/F_0 - proportion of active chlorophyll associated with the RCs of PS II

INTRODUCTION

Zinc deficiency is a widespread micronutrient disorder in plants and causes severe reductions in crop production. Some of the metabolic changes brought about by Zn deficiency can be explained by the function of Zn as a structural component of a special enzyme or its involvement in specific steps; in particular, metabolic pathways (Marschner

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1995). However, there are changes in the synthesis and metabolic processes that could not be explained directly by the presence of Zn in the metabolic pathway or enzyme structure. Such responses are regarded to be rather indirect effects of Zn deficiency.

The light energy absorbed by chlorophyll (Chl) can be utilised photochemically to drive photosynthetic electron transport, be dissipated non-photochemically as heat or be re-emitted as fluorescence. These events are competing processes and therefore changes in Chl fluorescence reflect changes in photosynthetic function. Abiotic stresses can directly or indirectly affect the photosynthetic characteristics of the leaves and alter their Chl fluorescence properties (Gray et al. 2003). Photosynthetic efficiency can be assayed in a non-destructive way by measuring Chl fluorescence (Maxwell and Johnson 2000).The effects of Zn deficiency on photochemical processes as well as on CO_2 net assimilation rates have been reported for some plant species (Wang and Jin 2005, Hajiboland and Beiramzadeh 2008). These effects are likely mediated by changes in the ultrastructure of thylakoid membranes (Chen et al. 2007), changes in stomatal conductance (Sharma et al. 1995) and carbohydrate metabolism (Marschner 1995).

Environmental stresses that limit the CO_2 fixation rate and restrict carbon metabolism may lead to an over-energisation of the photosystem reaction centres resulting from an inadequate supply of $NADP^+$ (Elstner and Osswald 1994). Molecular oxygen may then become reduced instead of $NADP^+$, which results in the production of reactive oxygen species (ROS). Allowed to accumulate, ROS can cause damage to cellular components and severely disrupt metabolic functions. Under normal conditions, plants possess scavenging systems that keep active oxygen species below damaging levels (Apel and Hirt 2004). However, under conditions such as Zn deficiency, the balance between ROS production and scavenging is severely disturbed because Zn is a structural constituent of superoxide dismutase and has an inhibitory effect on superoxide-producing NADH oxidase (Marschner 1995).

The nutritional status of plants has a significant influence on the tolerance of plants to environmental stresses such as drought, cold, salinity and high light intensity (Marschner 1995). Because of the wide spectrum of Zn deficiency effects, particularly on photochemistry and CO_2 fixation as described above, we expected that Zn deficiency would affect the stress tolerance of plants, and the extent of growth impairment by environmental stresses would be influenced greatly by their Zn nutritional status.

Chilling stress occurs commonly in the production of vegetables during the early growth season or during winter cultivations. Cabbage is commonly injured by low temperatures (Sasaki et al. 1996). Cruciferous vegetables act as good sources of natural antioxidants due to their high levels of carotenoids, tocopherols and ascorbic acid. Red cabbage is particularly rich in anthocyanins, with potent antioxidant and health promoting properties (Kaur and Kapoor 2001). There are no published works on the effects of Zn deficiency in plants subjected to chilling stress. The objective of this research was to study the effect of Zn nutritional status on the photochemistry and CO_2 fixation and leaf pigments of red cabbage plants subjected to cold conditions.

MATERIAL AND METHODS

Seeds of red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants purchased from a commercial source were surface-sterilised using sodium-hypochlorite at 5% and were then germinated in the dark on filter paper soaked with a saturated $CaSO_4$ solution. Eight-day-old young seedlings were pre-cultured for two weeks in 50% conventional modified Hoagland nutrient solution (Johnson et al. 1957) without Zn addition, then were transferred to full strength chelator-buffered treatment solutions containing either a low (2.0 µM $ZnSO_4$, 32 pM free Zn^{2+} activity) or adequate (25 µM $ZnSO_4$, 725 pM free Zn^{2+} activity) Zn supply (Hajiboland and Amirazad 2010). Plants were grown under control (25°/18°C day/night temperature in a growth chamber) and cold (10°/7°C, in a germinator) temperature regimes under 70/80% day/night humidity and photosynthetically active radiation (PAR) of 400 µmol m^{-2} s^{-1}.

Plants were harvested 60 days after sowing. The plants were divided into leaves and roots, washed with double-distilled water and after blotting, the dry, fresh weight was determined. After drying at 70°C for two days, the dry weight of the plants was determined. Before harvest, chlorophyll fluorescence and gas exchange parameters were determined.

Chlorophyll fluorescence parameters were recorded using a portable fluorometer (OSF1, ADC Bioscientific Ltd., UK). Definitions and calculations were described elsewhere (Hajiboland and Amirazad 2010). CO_2 assimilation and transpiration rates were measured in parallel with

Chl fluorescence measurements in the same leaf with a calibrated portable gas exchange system (LCA-4, ADC Bioscientific Ltd., UK) between 10:00 am and 1:00 pm at harvest. Gas exchange measurements were conducted with a PAR of 400 μmol m^{-2} s^{-1} at the leaf surface measured by a quantum sensor attached to the leaf chamber of the gas exchange unit. Measurements for chlorophyll fluorescence and gas exchange parameters were carried out on the second youngest, fully expanded and attached leaf. An average of four records from different parts of each individual leaf was considered for each replicate.

Leaf chlorophyll *a*, *b*, anthocyanins and carbohydrates were extracted and determined according to the optimised methods described elsewhere (Hajiboland and Amirazad 2010).

The experiments were undertaken in a complete randomised block design with four replications (pots) per treatment and one plant per pot. Statistical analyses were carried out using sigma stat (3.02) with the Tukey test ($p < 0.05$).

RESULTS

A low Zn supply caused a significant reduction in shoot and root dry weight under both temperature treatments (Fig. 1). The reduction of dry matter production of shoots and roots due to Zn deficiency reached up to 55% and 45%, respectively, for the control plants. For the cold treated plants, the reduction of shoot and root growth due to low Zn supply was 62% and 52%, which was slightly higher than in the plants grown under control temperature conditions. Low temperatures did not affect root dry weight, but rather caused an increase in dry shoot weight of Zn sufficient plants up to 32% (Fig. 1). Cold treated leaves were apparently slightly distorted as a result of increased leaf lamina thickness, greater number of leaf veins and an increased thickness of the lateral veins and midrib. Leaf surface area was not affected significantly,

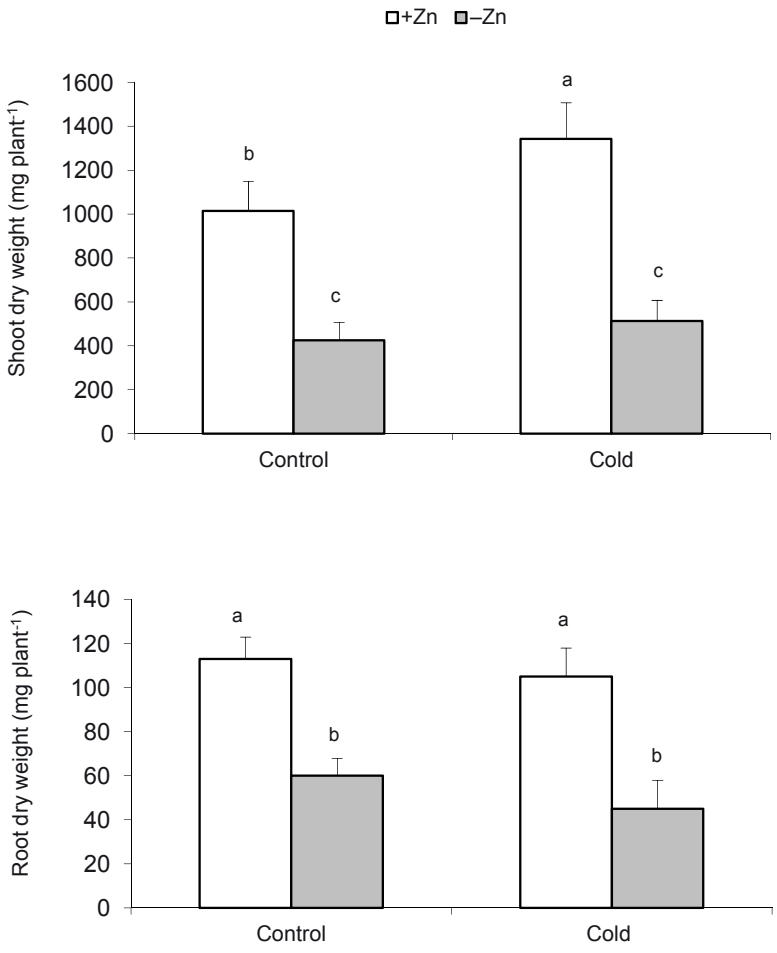

Figure 1. Shoot and root dry weight (mg $plant^{-1}$) of red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants grown for two months in a nutrient solution with adequate (+Zn) and low (–Zn) Zn supply under control (25/18ºC) and cold (10/7ºC) conditions. Bars indicated by the same letter are not significantly different ($p < 0.05$)

but leaves were darker red in colouration than the control plants (data not shown).

Leaf chlorophyll (Chl) *a* content decreased significantly due to the low Zn supply in both temperature treatments (Tab. 1). The reduction of Chl *a* due to the low Zn supply was as high as 24% and 15% for plants grown under control and cold conditions, respectively. Chlorophyll *b* concentration was reduced by about 13% and 30% under control and cold conditions due to the low Zn supply. Cold treatment affected the Chl *a*/*b* ratio differentially depending on Zn nutritional status; an increase of Chl *a*/*b* was observed in Zn deficient plants,whereas there was a significant reduction in Zn sufficient plants. Low Zn supply and particularly cold treatment caused a significant increase of leaf anthocyanins. Zinc deficiency resulted in 32% and 30% increases in the control group and cold treated plants, and low temperature enhanced anthocyanins by as much as 58% and 56% in Zn deficient and Zn sufficient plants, respectively (Tab. 1).

Table 1. Concentration of chlorophyll a, b (mg g^{-1} FW), the ratio of chlorophyll a/b and concentration of anthocyanins (mg cyanidin-3-glucosid g^{-1} FW), in leaves and total soluble sugars and starch (mg g^{-1} FW) in leaves and roots of red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants grown for two months in a nutrient solution with adequate (+Zn) and low (–Zn) Zn supply under control (25/18ºC) and cold (10/7ºC) conditions

Treatments		Chl *a*	Chl *b*	Chl *a*/*b*	Anthocyanins
Control	+Zn	1.60±0.01* [a]	0.87±0.02 [a]	1.84±0.03 [b]	1.9±0.1 [d]
	–Zn	1.22±0.05 [b]	0.76±0.01 [b]	1.60±0.07 [c]	2.5±0.1 [c]
Cold	+Zn	1.49±0.05 [a]	0.90±0.02 [a]	1.66±0.05 [c]	3.0±0.1 [b]
	–Zn	1.27±0.00 [b]	0.64±0.01 [c]	1.98±0.05 [a]	3.9±0.1 [a]
		Soluble sugars		Starch	
		Shoot	Root	Shoot	Root
Control	+Zn	5.9±0.2 [b]	4.5±0.1 [b]	10.02±0.10 [a]	1.69±0.07 [a]
	–Zn	4.4±0.1 [c]	3.8±0.1 [c]	9.73±0.07 [a]	1.20±0.06 [b]
Cold	+Zn	8.5±0.1 [a]	6.4±0.1 [a]	5.09±0.07 [b]	0.85±0.07 [c]
	–Zn	5.7±0.1 [b]	4.7±0.1 [b]	4.04±0.03 [c]	0.33±0.04 [d]

*Data in each column followed by the same letter are not significantly different ($p < 0.05$)

Table 2. Chlorophyll fluorescence parameters, including F_0 (initial fluorescence), F_m (maximum fluorescence), F_v/F_m (photochemical efficiency of PS II), F_v/F_0 (ratio of variable to initial fluorescence), F'_v/F'_m (excitation capture of open PS II), *qP* (photochemical quenching), *qN* (non-photochemical quenching), Φ_{PSII} (quantum yield of PS II) and ETR (electron transport rate) in leaves of red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra*) plants grown for two months with an adequate (+Zn) and low (–Zn) Zn supply under control (25/18ºC) and cold (10/7ºC) conditions

Treatments		F_0	F_m	F_v/F_m
Control	+Zn	523±59* [a]	2541±503 [a]	0.790±0.039 [a]
	–Zn	421±40 [b]	1941±229[ab]	0.779±0.050 [a]
Cold	+Zn	446±14[ab]	2350±119[ab]	0.839±0.003 [a]
	–Zn	370±19 [b]	1970±97 [b]	0.812±0.003 [a]
		F_v/F_0	F'_v/F'_m	*qP*
Control	+Zn	3.59±0.24 [b]	0.703±0.038 [b]	0.998±0.044 [a]
	–Zn	3.60±0.07 [b]	0.773±0.031 [a]	0.995±0.032 [a]
Cold	+Zn	4.44±0.08 [a]	0.777±0.009 [a]	0.990±0.095 [a]
	–Zn	4.30±0.10 [a]	0.808±0.003 [a]	0.959±0.024 [a]
		qN	Φ_{PSII}	ETR
Control	+Zn	0.425±0.155 [a]	0.709±0.024 [c]	119±4.1 [c]
	–Zn	0.108±0.037 [b]	0.769±0.017 [b]	129±2.8 [b]
Cold	+Zn	0.242±0.051 [b]	0.809±0.015 [a]	136±2.5 [a]
	–Zn	0.161±0.024 [b]	0.774±0.016[ab]	130±2.6[ab]

*Data of each parameter followed by the same letter are not significantly different ($p < 0.05$)

Zinc deficient leaves had significantly lower soluble sugars under the control and cold treatments compared with Zn sufficient ones (Tab. 1). However, cold treatments caused a significant increase in soluble sugars – up to 44% and 42% for the shoots and roots of Zn-sufficient plants and 30% and 24% for Zn-deficient plants, respectively. The starch content of roots, but not leaves, declined by as much as 29% due to a low Zn supply in plants grown under control temperatures. In the cold-treated plants, a significant reduction of starch content due to low Zn supply was observed – about 21% and 29% in shoots and roots, respectively. In contrast to soluble sugars, cold-treated plants had significantly lower starch contents than the control. This reduction was 49% and 50% for Zn-sufficient and 58% and 73% for Zn-deficient leaves and roots, respectively (Tab. 1).

A low Zn supply and cold treatment caused only a slight reduction of initial fluorescence (F_0) and maximum fluorescence (F_m) in the plants (Tab. 2). A significant effect of low Zn supply on F_0 was observed only in plants grown under control but not under cold conditions. The optimal photochemical efficiency of PS II in dark-adapted leaves (F_v/F_m) slightly increased in cold temperatures, but the effect of low Zn was negligible. The ratio of F_v/F_0 was not affected by Zn nutrition but was significantly influenced by cold treatment. An increase of up to 24% due to low temperatures was observed in the ratio of F_v/F_0 in Zn-deficient and 19% in Zn-sufficient plants. A consistent increase was observed in the F'_v/F'_m ratio due to both low Zn supply and cold treatment. However, the effect of a low Zn supply was significant in the control but not in the cold-treated plants.

The amount of oxidized PS II reaction centres ready for reduction, i.e. photochemical quenching (*qP*), that reflects the capacity to utilise absorbed energy through metabolism and growth decreased slightly in Zn-deficient leaves under cold conditions (Tab. 2). The non-photochemical quenching (*qN*) that reflects the capacity to dissipate excess absorbed energy as heat was also depressed by a low Zn supply, which was significant in the control plants. Cold temperatures lowered *qP* only slightly in Zn-deficient, but not in Zn-sufficient, plants. In contrast, the low temperature lowered *qN*in Zn-sufficient, but not Zn-deficient, plants significantly. ΦPS II and ETR increased due to a low Zn supply only in the control plants and in turn, cold treatments caused a significant increase (up to 14%) in ΦPS II and ETR only in the Zn-sufficient plants (Tab. 2).

Low Zn plants had a significantly lower net assimilation rate (*A*), transpiration (*E*) and stomatal conductance (g_s) (Fig. 2). Cold treatment influenced these parameters only in a few cases. The net assimilation rate decreased by about 29% due to low Zn supply in the control group of plants, while this effect was as high as 51% on cold-treated plants. Cold treatment caused a reduction of *A* only in Zn-deficient, but not Zn-sufficient, plants. In contrast to *A*, the effect of low temperatures on the reduction of *E* was significant in both Zn-sufficient (48%) and Zn-deficient (43%) plants. Similarly to *A*, a low supply of Zn caused a significant reduction of the transpiration rate under both temperature

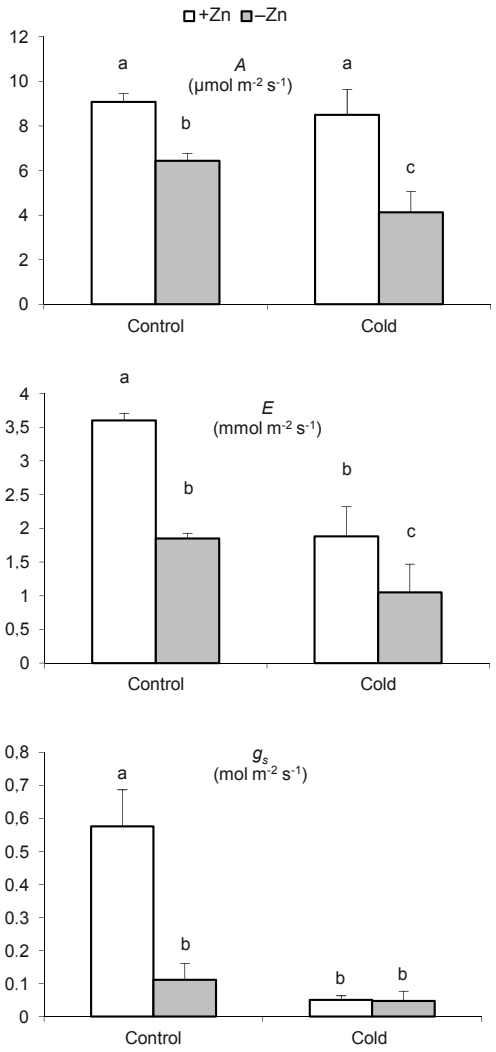

Figure 2. Gas exchange parameters, including net photosynthetic rate (*A*), transpiration rate (*E*) and stomatal conductance (g_s) in red cabbage (*Brassica oleracea* L. var. *capitata* f. *rubra)* plants grown for two months with an adequate (+Zn) and low (–Zn) Zn supply under control (25/18ºC) and cold (10/7ºC) conditions. Bars indicated by the same letter are not significantly different ($p < 0.05$)

treatments. In parallel with net assimilation and the transpiration rate, the stomatal opening was influenced by both Zn nutrition and temperature treatments slightly or significantly. Zinc-deficient plants grown under the control temperature had up to 81% lower stomatal conductance compared with Zn-sufficient plants. Low temperature treatment strongly decreased g_s values; however, it was not further affected by a low Zn supply in cold-treated plants (Fig. 2).

DISCUSSION

A low Zn supply significantly impaired the plants' dry matter production. The growth of plants suffering from Zn deficiency was stunted because of the shortening of petioles, and a drastic decrease in leaf surface area and number of leaves. The strong reduction of leaf size and number indicates a critical role for Zn in both cell expansion and division (Marschner 1995).

Cold treatment did not influence plant growth with low Zn supplies either in the shoots or roots, but Zn-sufficient plants subjected to low temperatures showed a significant increase in leaf biomass. Possible mechanisms for growth stimulation under cold conditions will be discussed below. The altered leaf morphology was likely the result of cell wall thickening, increased lignin formation and altered tissue patterning in leaves. Similar changes were reported for some species under chilling stress (Weiseret al. 1990). Detailed studies are needed on the anatomical and morphological alterations in the leaves of red cabbage under cold conditions.

A comparison of the content of Chl *a* with Chl *b* reveals a preferential damage of Chl *a* under Zn deficiency conditions; therefore, the relative abundance of this pigment decreased in Zn-deficient plants. In contrast, a preferential reduction of Chl *b* was observed under cold conditions. Therefore, a low Zn supply caused a reduction of the Chl *a*/*b* ratio in the control group of plants but resulted in an increasein cold-treated ones. An increase in the F_v/F_0 ratio, the proportion of active Chl associated with the RCs of PS II, could be partly attributed to more protection of Chl *a* under low temperatures, particularly in Zn-deficient plants.

Zinc-deficient red cabbage leaves accumulated more anthocyanins than the control ones. Although the effect of anthocyanins as strong antioxidants has been evidenced in experiments with rats or animal cell cultures, a growing body of experimental evidence does indeed indicate that anthocyanins contribute to the control of levels of ROS in plant cells (Anderson and Jordheim 2006). Anthocyanins are synthesised in the cytoplasm as colourless tautomers, and both the cytosolic and vacuolar red forms of anthocyanins have strong antioxidant potential in plant cells (Anderson and Jordheim 2006). Under Zn deficiency conditions, which caused an imbalance between production and scavenging ROS, the accumulation of anthocyanins could be important in the alleviation of oxidative stress. The accumulation of H_2O_2 and malondialdehyde, an end product of lipid peroxidation, was observed in Zn-deprived red cabbage plants (Hajiboland and Amirazad 2010).

The total soluble and insoluble carbohydrates declined in Zn-deficient plants. This reduction could be the result of impaired leaf photosynthesis (see below), and/or modified sugar metabolism. Zinc deficiency greatly depresses the activity of aldolase and starch synthetase (Marschner 1995). In addition, a clear reduction of both soluble and non-soluble carbohydrates in leaves and roots suggested that the lower supply of photo-assimilates strongly limited plant growth under Zn-deficiency conditions. However, this finding is the opposite of several other reports, which showed an accumulation of carbohydrates due to impaired growth and decreased demand (Marschner 1995). This indicates that the low Zn supply in our study affected leaf photosynthesis and carbohydrate metabolism much more than dry matter production.

Cold conditions caused a reduction in starch simultaneously with increased soluble sugars. Sugar contents are raised by exposure to non-freezing low temperatures, which results in freezing tolerance (cold acclimation) in several species (Alberdi and Corcuera 1991). The types of sugar accumulated under cold conditions vary amongst plant species; in rye, for example, sucrose and fructose (Antikainen and Pihakaski 1994), while in spinach sucrose, fructose and glucose are accumulated under cold conditions (Guy et al. 1992). In addition to the colligative effects, i.e. the lowering of osmotic potential, sugars have been shown to function as protectants of plasma membranes and proteins from the effects of freezing and dehydration (Steponkus 1984). In cabbage (*Brassica oleracea* L. 'Banchurisou'), sucrose, fructose and glucose increased on exposure to low temperature. However, what extent the freezing tolerance of plants depends on the types of sugar accumulated at low temperatures is not clear (Sasaki et al. 1996). In contrast to our results, starch accumulated during cold acclimation in cabbage plants, but without any

relationship with freezing tolerance (Sasaki et al. 1996). Regarding the effect of sugar accumulation on freezing tolerance, it seems likely that Zn deficiency increases susceptibility to freezing injury because of the significantly lower carbohydrate synthesis and accumulation. Further investigation is needed to confirm this hypothesis.

Zinc deficiency (Wang and Jin 2005) and low temperatures (Lin et al. 2007) both influence Chl fluorescence parameters in leaves. In this study, the initial Chl fluorescence yield (F_0),which reflects the minimal fluorescence yield when all primary electron acceptor quinone molecules (Q_A) are in an oxidized state, decreased in Zn-deficient leaves. In addition, Zn-deficient leaves had a slightly or significantly smaller maximal fluorescence yield (F_m) value compared to the control, which likely indicates a diminished pool of plasto-quinone (Ouzounidou et al. 2003). However, the preservation of F_v/F_m and F_v/F_0 and an increase in F'_v/F'_m indicated that the photosynthesis processes conserved their normal activities in Zn-deprived leaves. A slight reduction of photochemical quenching (*qP*) in cold-treated plants in response to the low Zn supply may suggest a tendency in Zn-starved leaves to be photo-inhibited when treated with low temperatures. Photo-inhibition of photosynthesis has been reported for chilling-susceptible plants under high irradiance as well as for plants exposed to moderate irradiance at chilling temperatures (Somersalo and Krause 1989). The slight change in *qP* observed in this study indicates that red cabbage is a plant with a tolerance to low temperatures even under the effects of other stresses that provoke oxidative damage, e.g. Zn deficiency.

Cold treatment caused the F_v/F_0 ratio to significantly increase under both Zn supply levels. This may indicate that more Chl is associated with reaction centres (RCs) under cold conditions likely for the compensation of lower efficiency for PS II operation. In accordance with this suggestion, the Chl *a*/*b* ratio was increased by cold treatment. Cold treatment did not influence *qP* in Zn-sufficient plants, indicating that the utilisation of energy for metabolism was not affected by chilling stress. In addition, the excitation capture efficiency of open PS II RCs (F'_v/F'_m) increased under the cold treatment, which was significant in Zn-sufficient plants. In contrast to *qP*, *qN* was influenced not only by low Zn supply, but also by cold treatment. Non-photochemical fluorescence quenching is one of the mechanisms that prevent or alleviate damage to the photosynthetic apparatus. In this mechanism, excess radiation energy is dissipated as heat in the light-harvesting antenna of PS II (Müller et al. 2001). A reduction of leaf carotenoid content due to low Zn supply (Hajiboland and Amirazad 2010) could be the cause of the reduction of qN in low Zn plants. Depressed leaf qN was reported for other species exposed to low temperatures (Lin et al. 2007).

It has been reported that, in response to a sudden shift from warm to cold temperatures, annual cold-tolerant plants show a decrease in light-saturated rates of CO_2 uptake with minimal changes in quantum yield for CO_2 uptake. However, once leaves are acclimated, a strong recovery of photosynthesis under cold temperatures is observed (Ensminger et al. 2006). In our study, red cabbage as a cold-tolerant cruciferous plant was likely acclimated to low temperature during the long-term growth period. Although cold conditions strongly lowered stomatal conductance, CO_2 assimilation was not influenced in Zn-sufficient plants. This means that electron transport and the utilisation of electrons for further biochemical processes were not affected by cold temperatures and sufficient oxidised electron acceptors were present in the reaction chain. In contrast, low Chl content (Pätsikkä et al. 2002) and lowered metabolism due to low temperatures likely caused an excess of reducing power ($NADP + H^+$) in Zn-deficient plants, therefore photo-inhibition is expected to occur.

CONCLUSION

Cold stimulated leaf growth in Zn-sufficient plants is partly attributable to the improved photochemical properties of leaves. A slight increase in F_v/F_m, a significant increase in F_v/F_0, F'_v/F'_m, Φ_{PSII} and ETR implies that cold-treated leaves have a higher photochemical efficiency compared with the control ones. The maintenance of net CO_2 assimilation though lower stomatal conductance, lower water loss and a considerable increase in the anthocyanin content of leaves, which causes more protection against ROS, are possible causes for the leaf growth stimulation by cold treatment observed for Zn-sufficient plants.

REFERENCES

Alberdi M., Corcuera L.J., 1991. Cold acclimation in plants. Phytochem. 30: 3177-3184.

Anderson O.M., Jordheim M., 2006. The Anthocyanins. In: Flavonoids: chemistry, biochemistry and applications. O.M. Anderson and K.R. Markham (eds), CRC Press, Boca Raton: 471-553.

Antikainen M., Pihakaski S., 1994. Early developments in RNA, protein, and sugar levels during cold stress in winter rye (*Secale cereale*) leaves. Ann. Bot. 74: 335-341.

Apel K., Hirt H., 2004. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Ann. Rev. Plant Biol. 55: 373-399.

Chen W., Yang X., He Z., Feng Y., Hu F., 2007. Differential changes in photosynthetic capacity, 77K chlorophyll fluorescence and chloroplast ultrastructure between Zn-efficienct and Zn-inefficient rice genotypes (*Oryza sativa* L.) under low Zn stress. Physiol. Plant. 132: 89-101.

Elstner E.F., Oswald W., 1994. Mechanisms of oxygen activation during plant stress. Proc. Royal. Soc. Edinburgh, 102B: 131-154.

Ensminger I., Busch F., Huner N.P.A., 2006. Photostasis and cold acclimation: sensing low temperature through photosynthesis. Physiol. Plant. 126: 28-44.

Gray G.R., Hope B.J., Qin X., Taylor B.G., Whitehead C.L., 2003. The characterization of photoinhibition and recovery during cold acclimation in *Arabidopsis thaliana* using chlorophyll fluorescence imaging. Physiol. Plant. 119: 365-375.

Guy C.L., Huber J.L.A., Huber S.C., 1992. Sucrose phosphate synthase and sucrose accumulation at low temperature. Plant Physiol. 100: 502-508.

Hajiboland R., Amirazad F., 2010. Growth, photosynthesis and antioxidant defence system in Zn-deficient red cabbage plants. Plant Soil Environ. 56: 209-217.

Hajiboland R., Beiramzadeh N., 2008. Growth, gas exchange and function of antioxidant defense system in two contrasting rice genotypes under Zn and Fe deficiency and hypoxia. Acta Biol. Szeged.52: 283-294.

Johnson C.M., Stout P.R., Broyer T.C., Carlton A.B., 1957. Comparative chloride requirements of different plant species. Plant Soil 8: 337-353.

Kaur C., Kapoor H.C., 2001. Antioxidants in fruits and vegetables-the millenium's health. Int. J. Food Sci. Tech. 36: 703-725.

Lin K.H., Hwang W.C., Lo H.F., 2007. Chilling stress and chilling tolerance of sweet potato as sensed by chlorophyll fluorescence. Photosynthetica 45: 628-632.

Marschner H., 1995. Mineral Nutrition of Higher Plants. Academic Press Inc., London, United Kingdom.

Maxwell K., Johnson G.N., 2000. Chlorophyll fluorescence: a practical guide. J. Exp. Bot. 51: 659-668.

Müller P., Li X-P., Niyogi K.K., 2001. Non-photochemicalquenching. A response to excess light energy. Plant Physiol. 125: 1558-1566.

Ouzounidou G., Ilias I., Kabataidid M., Chatzimichail A., 2003. Comparative study of nutrient deficiencies on growth and photochemistry of tobacco. J. Plant Nutr. 26: 1605-1616.

Pätsikkä E., Kairavuo M., Šeršen F., Aro E-M., Tyystjärvi E., 2002. Excess copper predisposes photosystem II to photoinhibition in vivo by outcompeting iron and causing decrease in leaf chlorophyll. Plant Physiol. 129: 1359-1367.

Sasaki H., Ichimura K., Oda M., 1996. Changes in sugar content during cold acclimation and deacclimation of cabbage seedlings. Ann. Bot. 78: 365-369.

Sharma P.N., Tripathi A., Bisht S.S., 1995. Zinc requirement for stomatal opening in cauliflower. Plant Physiol. 107: 751-756.

Somersalo S., Kruse G.H., 1989. Photoinhibition at chilling temperature. Fluorescence characteristics of unhardened and cold acclimated spinach leaves. Planta 177: 409-416.

Steponkus P.L., 1984. Role of the plasma membrane in freezing injury and cold acclimation. Ann. Rev. Plant Physiol. 35: 543-584.

Wang H., Jin J.Y., 2005. Photosynthetic rate, chlorophyll fluorescence parameters, and lipid peroxidation of maize leaves as affected by zinc deficiency. Photosynthetica 43: 591-596.

Weiser R.L., Wallner S.J., Waddell J.W., 1990. Cell wall and extension mRNA changes during cold acclimation of pea seedlings. Plant Physiol. 93: 1021-1026.

PRZEMIANY FOTOCHEMICZNE I WYMIANA GAZOWA U KAPUSTY CZERWONEJ (*BRASSICA OLERACEA* L. VAR. *CAPITATA* F. *RUBRA*) PRZY NIEDOBORZE CYNKU W WARUNKACH CHŁODOWYCH

Streszczenie: W uprawie hydroponicznej badano reakcję kapusty czerwonej (*Brassica oleracea* L. var. *capitata* f. *rubra*) w warunkach niskiego zaopatrzenia w Zn i w temperaturach chłodowych (10°/7°C dzień/noc). Niskie zaopatrzenie w cynk spowodowało znaczącą redukcję suchej masy zarówno pędów jak i korzeni, wynoszącą odpowiednio 55% i 45% w kombinacji kontrolnej i 62% i 52% dla roślin z warunków chłodowych. Również całkowita zawartość cukrów rozpuszczalnych i skrobi malała w warunkach deficytu Zn. Jednakże działanie w takich warunkach temperatur chłodowych prowadziło do spadku zawartości skrobi z równoczesnym wzrostem zawartości cukrów rozpuszczalnych. U roślin nawożonych Zn, temperatury chłodowe powodowały wzrost wydajności otwartych centrów reakcji PS II (RCs) (*F'v*/*F'm*), wydajności kwantowej PS II (Φ_{PSII}), tempa transportu elektronów (ETR) i udziału aktywnego chlorofilu związanego z centrum reakcji PS II (Fv/F_0). U takich roślin nie obserwowano negatywnego wpływu temperatur chłodowych na tempo fotosyntezy netto, chociaż obserwowano redukcję przewodnictwa szparkowego. Uzyskane

wyniki wskazują, że chociaż rośliny traktowane chłodem były nieco bardziej podatne na niedobór cynku, to u roślin zaopatrzonych wystarczającą dawką cynku temperatury chłodowe spowodowały wytworzenie większej biomasy pędu (do 32%). Przystosowanie czerwonej kapusty do temperatur chłodowych jest powiązane z poprawą zjawisk fotochemicznych w liściach, utrzymaniem tempa fotosyntezy netto, niższym tempem transpiracji (utraty wody) oraz akumulacją antocyjanów, jako substancji antyoksydacyjnych.

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